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A TREATISE

ON

HUMAN PHYSIOLOGY;

DESIGNED FOR THE USE OF

STUDENTS AND PRACTITIONERS OF MEDICINE.

BY

JOHN C. DALTON, M.D.,

PROFESSOR OF PHYSIOLOGY AND HYGIENE IN THE COLLEGE OF PHYSICIANS AND SURGEONS, NEW YORK; MEMBER OF THE NEW YORK ACADEMY OF MEDICINE; OF THE NEW YORK PATHOLOGICAL SOCIETY; OF THE AMERICAN ACADEMY OF ARTS AND SCIENCES, BOSTON, MASS.; OF THE BIOLOGICAL DEPARTMENT OF THE ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA; AND OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA.

Fifth Edition, Revised and Enlarged.

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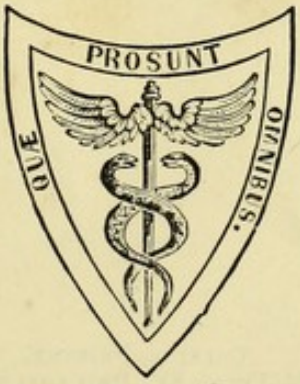
TWO HUNDRED AND EIGHTY-FOUR ILLUSTRATIONS.



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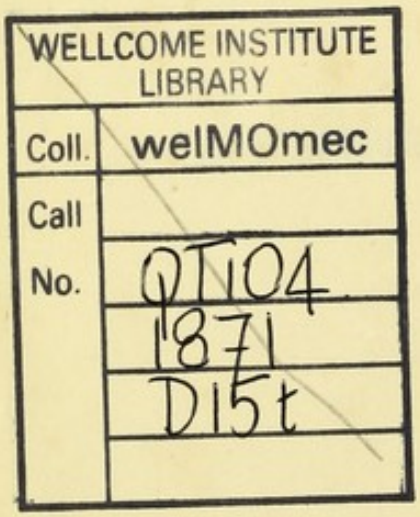
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TO MY FATHER,

JOHN C. DALTON, M.D.,

IN

HOMAGE OF HIS LONG AND SUCCESSFUL DEVOTION

TO THE

SCIENCE AND ART OF MEDICINE,

AND IN

GRATEFUL RECOLLECTION OF HIS PROFESSIONAL PRECEPTS AND EXAMPLE,

This Volume

IS RESPECTFULLY AND AFFECTIONATELY

INSCRIBED.

Preface to the Fifth Edition.

IN preparing the present edition of this work, the general plan and arrangement of the previous editions have been retained, so far as they have been found useful and adapted to the purposes of a text-book for students of medicine. The incessant advance of all the natural and physical sciences, never more active than within the last few years, has furnished many valuable aids to the special investigations of the physiologist; and the progress of physiological research, during the same period, has required a careful revision of the entire work, and the modification or re-arrangement of many of its parts. At this day, nothing is regarded as of any value in natural science which is not based upon direct and intelligible observation or experiment; and accordingly the discussion of doubtful or theoretical questions has been avoided, as a general rule, in the present volume, while new facts, from whatever source, if fully established, have been added and incorporated with the results of previous investigation. A number of new illustrations have been introduced, and a few of the older ones, which seemed to be no longer useful, have been omitted. In all the changes and additions thus made, it has been the aim of the writer to make the book, in its present form, a faithful exponent of the actual condition of physiological science.

New York, October, 1871.

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HUMAN PHYSIOLOGY.

INTRODUCTION.

I. PHYSIOLOGY is the study of the phenomena presented by organized bodies, animal and vegetable.

These phenomena are different from those presented by inorganic substances. They require, for their production, the existence of peculiarly formed animal and vegetable organisms, as well as the presence of various external conditions, such as warmth, light, air, moisture, &c.

They are accordingly more complicated than the phenomena of the inorganic world, and require for their study, not only a previous acquaintance with the laws of chemistry and physics, but, in addition, a careful examination of other characters which are peculiar to them.

These peculiar phenomena, by which we so readily distinguish living organisms from inanimate substances, are called *Vital phenomena*, or the *phenomena of Life*. Physiology consequently includes the study of all these phenomena, in whatever order or species of organized body they may originate.

We find, however, upon examination, that there are certain general characters by which the vital phenomena of vegetables resemble each other, and by which they are distinguished from the vital phenomena of animals. Thus, vegetables absorb carbonic acid, and exhale oxygen; animals absorb oxygen, and exhale carbonic acid. Vegetables nourish themselves by the absorption of unorganized liquids and gases, as water, ammonia, saline solutions, &c.; animals require for their support animal or vegetable substances as food, such as meat, fruits, milk, &c. Physiology, then,

is naturally divided into two parts, viz., Vegetable Physiology, and Animal Physiology.

Again, the different groups and species of animals, while they resemble each other in their general characters, are distinguished by certain minor differences, both of structure and function, which require a special study. Thus, the physiology of fishes is not exactly the same with that of reptiles, nor the physiology of birds with that of quadrupeds. Among the warm-blooded quadrupeds, the carnivora absorb more oxygen, in proportion to the carbonic acid exhaled, than the herbivora. Among the herbivorous quadrupeds, the process of digestion is comparatively simple in the horse, while it is complicated in the ox, and other ruminating animals. There is, therefore, a special physiology for every distinct species of animal.

Human Physiology treats of the vital phenomena of the human species. It is more practically important than the physiology of the lower animals, owing to its connection with human pathology and therapeutics. But it cannot be made the exclusive subject of our study; for the special physiology of the human body cannot be properly understood without a previous acquaintance with the vital phenomena common to all animals, and to all vegetables; beside which, there are many physiological questions that require for their solution experiments and observations, which can only be made upon the lower animals.

While the following treatise, therefore, has for its principal subject the study of Human Physiology, this will be illustrated, whenever it may be required, by what we know in regard to the vital phenomena of vegetables and of the lower animals.

II. Since Physiology is the study of the active phenomena of living bodies, it requires a previous acquaintance with their structure, and with the substances of which they are composed; that is, with their anatomy.

Anatomy, again, requires a previous acquaintance with inorganic substances; since some of these inorganic substances enter into the composition of the body. Chloride of sodium, for example, water, and phosphate of lime, are component parts of the animal frame, and therefore require to be studied as such by the anatomist. Now these inorganic substances, when placed under the requisite external conditions, present certain active phenomena, which are characteristic of them, and by which they may be recognized.

Thus lime, dissolved in water, if brought into contact with carbonic acid, alters its condition, and takes part in the formation of an insoluble substance, carbonate of lime, which is thrown down as a deposit. A knowledge of such chemical reactions as these is necessary to the anatomist, since it is by them that he is enabled to recognize the inorganic substances, forming a part of the animal body.

It is important to observe, however, that a knowledge of these reactions is necessary to the anatomist only in order to enable him to judge of the presence or absence of the inorganic substances to which they belong. It is the object of the anatomist to make himself acquainted with every constituent part of the body. Those parts, therefore, which cannot be recognized by their form and texture, he distinguishes by their chemical reactions. But afterward, he has no occasion to decompose them further, or to make them enter into new combinations; for he only wishes to know these substances *as they exist in the body*, and not as they may exist under other conditions.

The unorganized substances which exist in the body as component parts of its structure, such as chloride of sodium, water, phosphate of lime, &c., are called the *proximate principles* of the body. Mingled together in certain proportions, they make up the animal fluids, and associated also in a solid form, they constitute the tissues and organs, and in this way make up the entire frame.

Anatomy makes us acquainted with all these component parts of the body, both solid and fluid. It teaches us the structure of the body in a state of rest; that is, just as it would be after life had suddenly ceased, and before putrefaction had begun. On the other hand, Physiology is a description of the body in a state of activity. It shows us its movements, its growth, its reproduction, and the chemical changes which go on in its interior; and in order to comprehend these, we must know, beforehand, its entire mechanical, textural, and chemical structure.

It is evident, therefore, that the description of the *proximate principles*, or the chemical substances entering into the constitution of the body, is, strictly speaking, a part of Anatomy. But there are many reasons why this study is more conveniently pursued in connection with Physiology; for some of the proximate principles are derived directly, as we shall hereafter show, from the external world, and some are formed from the elements of the food in the process of digestion; while most of them undergo certain changes in the

interior of the body, which result in the formation of new substances; all these active phenomena belonging necessarily to the domain of Physiology.

The description of the proximate principles of animals and vegetables will therefore be introduced into the following pages.

The description of the minute structures of the body, or *Microscopic Anatomy*, is also so closely connected with some parts of Physiology as to make it convenient to speak of them together; and this will accordingly be done, whenever the nature of the subject may make it desirable.

III. The study of Physiology, like that of all the other natural sciences, is a study of *phenomena*, and of phenomena alone. The essential nature of the vital processes, and their ultimate causes, are questions which are beyond the reach of the physiologist, and cannot be determined by the means of investigation which are at his disposal.

Consequently, all efforts to solve them will only serve to mislead the investigator, and to distract his attention from the real subject of examination. Much time has been lost, for example, in discussing the probable *reason* why menstruation returns, in the human female, at the end of every four weeks. But the observation of nature, which is our only means of scientific investigation, cannot throw any light on this point, but only shows us the fact that menstruation *does* really occur at the above periods, together with the phenomena which accompany it, and the conditions under which it is hastened or retarded, and increased or diminished, in intensity, duration, &c. If we employ ourselves, consequently, in the discussion of the *reason* above mentioned, we shall only become involved in a network of hypothetical surmises, which can never lead to any definite result. Our time, therefore, will be much more profitably devoted to the study of the above phenomena, which can be learned from nature, and which constitute afterward, a permanent acquisition.

The physiologist, accordingly, confines himself strictly to the study of the vital phenomena, their characters, their frequency, their regularity or irregularity, and the conditions under which they originate.

When he has discovered that a certain phenomenon always takes place in the presence of certain conditions, he has established what is called a general principle, or a LAW of Physiology.

As, for example, when he has ascertained that sensation and motion occupy distinct situations in every part of the nervous system.

This "Law," however, it must be remembered, is not a discovery by itself, nor does it give him any new information, but is simply the expression, in convenient and comprehensive language, of the facts with which he is already acquainted. It is very dangerous, therefore, to make these laws or general principles the subjects of our study instead of the vital phenomena, or to suppose that they have any value, except as the expression of previously ascertained facts. Such a misconception would lead to bad practical results. For if we were to observe a phenomenon in discordance with a "law" or "principle," we might be led to neglect or misinterpret the phenomenon, in order to preserve the law. But this would be manifestly incorrect. For the law is not superior to the phenomenon, but, on the contrary, depends upon it, and derives its whole authority from it. Such mistakes, however, have been repeatedly made in Physiology, and have frequently retarded its advance.

IV. There is only one means by which Physiology can be studied: that is, the observation of nature. Its phenomena cannot be reasoned out by themselves, nor inferred, by logical sequence, from any original principles, nor from any other set of phenomena whatever.

In Mathematics and Philosophy, on the other hand, certain truths are taken for granted, or perceived by intuition, and the remainder afterward derived from them by a process of reasoning. But in Physiology, as in all the other natural sciences, there is no such starting point, and it is impossible to judge of the character of a phenomenon until after it has been observed. Thus, the only way to learn what action is exerted by nitric acid upon carbonate of soda is to put the two substances together, and observe the changes which take place; and all our knowledge of the properties of these two bodies is derived from this and similar experiments.

Neither can we infer the truths of Physiology from those of Anatomy, nor the truths of one part of Physiology from those of another part; but all must be ascertained directly and separately by observation.

For, although one department of natural science is almost always a necessary preliminary to the study of another, yet the facts of

the latter *can never be in the least degree inferred from those of the former, but must be studied by themselves.*

Thus Chemistry is essential to Anatomy, because certain substances, as we have already shown, belonging to Chemistry, such as chloride of sodium, occur as constituents of the animal body. Chemistry teaches us the composition, reactions, mode of crystallization, solubility, &c., of chloride of sodium; and if we did not know these, we could not extract it, or recognize it when extracted from the body. But, however well we might know the chemistry of this substance, we could never, on that account, *infer* its presence in the body or otherwise, nor in what quantities nor in what situations it would present itself. These facts must be ascertained for themselves, by direct investigation, as a part of anatomy proper.

So, again, the structure of the body in a state of rest, or its anatomy, is to be first understood; but its active phenomena or its physiology must then be ascertained by direct observation and experiment. The most intimate knowledge of the minute structure of the muscular and nervous fibres could not teach us anything of their physiology. It is only by experiment that we ascertain one of them to be contractile, the other sensitive.

Many of the phenomena of life are chemical in their character, and it is requisite, therefore, that the physiologist know the ordinary chemical properties of the substances composing the animal frame. But no amount of previous chemical knowledge will enable him to foretell the reactions of any chemical substance in the interior of the body; because the peculiar conditions under which it is there placed modify these reactions, as an elevation or depression of temperature, or other external circumstance, might modify them outside the body.

We must not, therefore, attempt to deduce the chemical phenomena of physiology from any previously established facts, since these are no safe guide; but must study them by themselves, and depend for our knowledge of them upon direct observation alone.

V. By the term *Vital phenomena,* we mean those phenomena which are manifested in the living body, and which are characteristic of its functions.

Some of these phenomena are physical or mechanical in their character; as, for example, the play of the articulating surfaces upon each other, the balancing of the spinal column with its appendages, the action of the elastic ligaments. Nevertheless, these

phenomena, though strictly physical in character, are often entirely peculiar and different from those seen elsewhere, because the mechanism of their production is peculiar in its details. Thus the human voice and its modulations are produced in the larynx, in accordance with the general physical laws of sound; but the arrangement of the elastic and movable vocal chords, and their relations with the columns of air above and below, the moist and flexible mucous membrane, and the contractile muscles outside, are of such a special character that the entire apparatus, as well as the sounds produced by it, is peculiar; and its action cannot be properly compared with that of any other known musical instrument.

In the same manner, the movements of the heart are so complicated and remarkable that they cannot be comprehended, even by one who is acquainted with the anatomy of the organ, without a direct examination. This is not because there is anything essentially obscure or mysterious in their nature, for they are purely mechanical in character; but because their conditions are so peculiar, owing to the tortuous course of the muscular fibres, their arrangement in interlacing layers, their attachments and relations, that their combined action produces an effect altogether peculiar, and one which is not similar to anything outside the living body.

A very large and important class of the vital phenomena are those of a chemical character. It is one of the characteristics of living bodies that a succession of chemical actions, combinations and decompositions, is constantly going on in their interior. It is one of the necessary conditions of the existence of every animal and every vegetable, that it should constantly absorb various substances from without, which undergo different chemical alterations in its interior, and are finally discharged from it under other forms. If these changes be prevented from taking place, life is immediately extinguished. Thus animals constantly absorb, on the one hand, water, oxygen, salts, albumen, oil, sugar, &c., and give up, on the other hand, to the surrounding media, carbonic acid, water, ammonia, urea, and the like; while between these two extreme points, of absorption and exhalation, there take place a multitude of different transformations which are essential to the continuance of life.

Some of these chemical actions are the same with those which are seen outside the body; but most of them are entirely peculiar, and do not take place, and cannot be made to take place, anywhere else. This, again, is not because there is anything particularly mysterious or extraordinary in their *nature*, but because the con-

ditions necessary for their accomplishment exist in the body, and do not exist elsewhere. All chemical phenomena are liable to be modified by surrounding conditions. Many reactions, for example, which will take place at a high temperature, will not take place at a low temperature, and *vice versâ*. Some will take place in the light, but not in the dark; others will take place in the dark, but not in the light. Because a chemical reaction, therefore, takes place under one set of conditions, we cannot be at all sure that it will take place under others, which are different.

The chemical conditions of the living body are exceedingly complicated. In the animal solids and fluids there are many substances mingled together in varying quantities, which modify or interfere with each other's reactions. New substances are constantly entering by absorption, and old ones leaving by exhalation; while the circulating fluids are constantly passing from one part of the body to another, and coming in contact with different organs of different texture and composition. All these conditions are peculiar, and so modify the chemical actions taking place in the body, that they are unlike those met with anywhere else.

If starch and iodine be mingled together in a watery solution, they unite with each other, and strike a deep opaque blue color; but if they be mingled in the blood, no such reaction takes place, because it is prevented by the presence of certain organic substances which interfere with it.

If dead animal matter be exposed to warmth, air, and moisture, it putrefies; but if introduced into the living stomach, this process is prevented, because the fluids of the stomach cause the animal substance to undergo a peculiar transformation (digestion), after which the bloodvessels immediately remove it by absorption. There are also certain substances which make their appearance in the living body, of animals or vegetables, and which cannot be formed elsewhere; such as fibrin, albumen, casein, pneumic acid, the biliary salts, morphine, &c. These substances cannot be manufactured artificially, simply because the necessary conditions cannot be imitated. They require for their production the presence of a living organism.

The chemical phenomena of the living body are, therefore, not different in their nature from any other chemical phenomena; but they are different in their conditions and in their results, and are consequently peculiar and characteristic.

Another set of vital phenomena are those which are manifested

in the processes of reproduction and development. They are again entirely distinct from any phenomena which are exhibited by matter not endowed with life. An inorganic substance, even when it has a definite form, as, for example, a crystal of fluor spar, has no particular relation to any similar form which has preceded, or any other which is to follow it. On the other hand, every animal and every vegetable owes its origin to preceding animals or vegetables of the same kind; and the manner in which this production takes place, and the different forms through which the new body successively passes in the course of its development, constitute the phenomena of reproduction. These phenomena are mostly dependent on the chemical processes of nutrition and growth, which take place in a particular direction and in a particular manner; but their results, viz., the production of a connected series of different forms, constitute a separate class of phenomena, which cannot be explained in any manner by the preceding, and require, therefore, to be studied by themselves.

Another set of vital phenomena are those which belong to the nervous system. These, like the processes of reproduction and development, depend on the chemical changes of nutrition and growth. That is to say, if the nutritive processes did not go on in a healthy manner, and maintain the nervous system in a healthy condition, the peculiar phenomena which are characteristic of it could not take place. The nutritive processes are necessary conditions of the nervous phenomena. But there is no other connection between them; and the nervous phenomena themselves are distinct from all others, both in their nature and in the mode in which they are to be studied.

A troublesome confusion might arise if we were to neglect the distinction which really exists between these different sets of phenomena, and confound them together under the expectation of thereby simplifying our studies. Since this can only be done by overlooking real points of difference, its effect will merely be to introduce erroneous ideas and suggest unfounded similarities, and will therefore inevitably retard our progress instead of advancing it.

It has been sometimes maintained, for example, that all the vital phenomena, those of the nervous system included, are to be reduced to the chemical changes of nutrition, and that these again are to be regarded as not different in any respect from the ordinary chemical changes taking place outside the body. This, however, is not only erroneous in theory, but conduces also to a vicious mode of study

For it draws away our attention from the phenomena themselves and their real characteristics, and leads us to deduce one set of phenomena from what we know of another; a method which we have already shown to be unsafe and pernicious.

It has also been asserted that the phenomena of the nervous system are identical with those of electricity; for no other reason than that there exist between them certain general resemblances. But when we examine the phenomena in detail, we find that, beside these general resemblances, there are many essential points of dissimilarity, which must be suppressed and kept out of sight in order to sustain the idea of the assumed identity. This assumption is consequently a forced and unnatural one, and the simplicity which it was intended to introduce into our physiological theories is imaginary and deceptive, and is attained only by sacrificing a part of those scientific truths, which are alone the real object of our study. We should avoid, therefore, making any such unfounded comparisons; for the theoretical simplicity which results from them does not compensate for the loss of essential scientific details.

VI. The study of Physiology is naturally divided into three distinct Sections:—

The first of these includes everything which relates to the NUTRITION of the body in its widest sense. It comprises the history of the proximate principles, their source, the manner of their production, the proportions in which they exist in different kinds of food and drink, the processes of digestion and absorption, and the constitution of the circulating fluids; then the physical phenomena of the circulation and the forces by which it is accomplished; the changes which the blood undergoes in different parts of the body; all the phenomena, both physical and chemical, of respiration; those of secretion and excretion, and the character and destination of the secreted and excreted fluids. All these processes have reference to a common object, viz., the preservation of the internal structure and healthy organization of the individual. With certain modifications, they take place in vegetables as well as in animals, and are consequently known by the name of the *vegetative functions*.

The Second Section, in the natural order of study, is devoted to the phenomena of the NERVOUS SYSTEM. These phenomena are not exhibited by vegetables, but belong exclusively to animal organizations. They bring the animal body into relation with the external world, and preserve it from external dangers, by means of

sensation, movement, consciousness, and volition. They are more particularly distinguished by the name of the *animal functions*.

Lastly comes the study of the entire process of REPRODUCTION. Its phenomena, again, with certain modifications, are met with in both animals and vegetables; and might, therefore, with some propriety, be included under the head of vegetative functions. But their distinguishing peculiarity is, that they have for their object the production of new organisms, which take the place of the old and remain after they have disappeared. These phenomena do not, therefore, relate to the preservation of the individual, but to that of the species; and any study which concerns the species comes properly after we have finished everything relating to the individual.

SECTION I.

NUTRITION.

CHAPTER I.

PROXIMATE PRINCIPLES IN GENERAL.

THE study of NUTRITION begins naturally with that of the *proximate principles*, or the substances entering into the composition of the different parts of the body, and the different kinds of food. In examining the body, the anatomist finds that it is composed, first, of various parts, which are easily recognized by the eye, and which occupy distinct situations. In the case of the human body, for example, a division is easily made of the entire frame into the head, neck, trunk, and extremities. Each of these regions, again, is found, on examination, to contain several distinct parts, or "organs," which require to be separated from each other by dissection, and which are distinguished by their form, color, texture, and consistency. In a single limb, for example, every bone and every muscle constitutes a distinct organ. In the trunk, we have the heart, the lungs, the liver, spleen, kidneys, spinal cord, &c., each of which is also a distinct organ. When a number of organs, differing in size and form, but similar in texture, are found scattered throughout the entire frame, or a large portion of it, they form a connected set or order of parts, which is called a "system." Thus, all the muscles taken together constitute the muscular system; all the bones, the osseous system; all the arteries, the arterial system. Several entirely different organs may also be connected with each other, so that their associated actions tend to accomplish a single object, and they then form an "apparatus." Thus the heart, arteries, capillaries, and veins, together, form the circulatory apparatus; the stomach, liver, pancreas, intestine, &c., the digestive apparatus. Every organ, again, on microscopic examination, is seen to be made

up of minute bodies, of definite size and figure, which are so small as to be invisible to the naked eye, and which, after separation from each other, cannot be further subdivided without destroying their organization. They are, therefore, called "anatomical elements." Thus, in the liver, there are hepatic cells, capillary blood-vessels, the fibres of Glisson's capsule, and the ultimate filaments of the hepatic nerves. Lastly, two or more kinds of anatomical elements, interwoven with each other in a particular manner, form a "tissue." Adipose vesicles, with capillaries and nerve tubes, form adipose tissue. White fibres and elastic fibres, with capillaries and nerve tubes, form areolar tissue. Thus the solid parts of the entire body are made up of anatomical elements, tissues, organs, systems, and apparatuses. Every organized frame, and even every apparatus, every organ, and every tissue, is made up of different parts, variously interwoven and connected with each other, and it is this character which constitutes its *organization.*

But beside the above solid forms, there are also certain fluids, which are constantly present in various parts of the body, and which, from their peculiar constitution, are termed "animal fluids." These fluids are just as much an essential part of the body as the solids. The blood and the lymph, for example, the pericardial and synovial fluids, the saliva, which always exists more or less abundantly in the ducts of the parotid gland, the bile in the biliary ducts and the gall-bladder: all these go to make up the entire body, and are quite as necessary to its structure as the muscles or the nerves. Now, if these fluids be examined, they are found to be made up of many different substances, which are mingled together in certain proportions; these proportions being constantly maintained at or about the same standard by the natural processes of nutrition. Such a fluid is termed an *organized fluid.* It is organized by virtue of the numerous ingredients which enter into its composition, and the regular proportions in which these ingredients are maintained. Thus in the plasma of the blood, we have albumen, fibrin, water, chlorides, carbonates, phosphates, &c. In the urine, we find water, urea, urate of soda, creatine, creatinine, coloring matter, salts, &c. These substances, which are mingled together so as to make up, in each instance, by their intimate union, a homogeneous liquid, are called the PROXIMATE PRINCIPLES of the animal fluid.

In the solids, furthermore, even in those parts which are apparently homogeneous, there is the same mixture of different ingredients. In the hard substance of bone, for example, there is, first

water, which may be expelled by evaporation; second, phosphate and carbonate of lime, which may be extracted by the proper solvents; third, a peculiar animal matter, with which these calcareous salts are in union; and fourth, various other saline substances, in special proportions. In the muscular tissue, there is chloride of potassium, lactic acid, water, salts, albumen, and an animal matter termed musculine. The difference in consistency between the solids and fluids does not, therefore, indicate any radical difference in their constitution. Both are equally made up of proximate principles, mingled together in various proportions.

It is important to understand, however, exactly what are proximate principles, and what are not such; for since these principles are extracted from the animal solids and fluids, and separated from each other by the help of certain chemical manipulations, such as evaporation, solution, crystallization, and the like, it might be supposed that every substance which could be extracted from an organized solid or fluid, by chemical means, should be considered as a proximate principle. That, however, is not the case. A proximate principle is properly defined to be *any substance, whether simple or compound, chemically speaking, which exists, under its own form, in the animal solid or fluid,* and which can be extracted by means which do not alter or destroy its chemical properties. Phosphate of lime, for example, is a proximate principle of bone, but phosphoric acid is not so, since it does not exist as such in the bony tissue, but is produced only by the decomposition of the calcareous salt; still less phosphorus, which is obtained only by the decomposition of the phosphoric acid.

Proximate principles may, in fact, be said to exist in all solids or fluids of mixed composition, and may be extracted from them by the same means as in the case of the animal tissues or secretions. Thus, in a watery solution of sugar, we have two proximate principles, viz: first, the water, and second, the sugar. The water may be separated by evaporation and condensation, after which the sugar remains behind, in a crystalline form. These two substances have, therefore, been simply separated from each other by the process of evaporation. They have not been decomposed, nor their chemical properties altered. On the other hand, the oxygen and hydrogen of the water were not proximate principles of the original solution, and did not exist in it under their own forms, but only in a state of combination; forming, in this condition, a fluid substance (water), endowed with sensible properties entirely different from

theirs. If we wish to ascertain, accordingly, the nature and properties of a saccharine solution, it will afford us but little satisfaction to extract its ultimate chemical elements; for its nature and properties depend not so much on the presence in it of the ultimate elements, oxygen, hydrogen, and carbon, as on the particular forms of combination, viz., water and sugar, under which they are present.

It is very essential, therefore, that in extracting the proximate principles from the animal body, only such means should be adopted as will isolate the substances already existing in the tissues and fluids, without decomposing them, or altering their nature. A neglect of this rule has been productive of much injury in the pursuit of organic chemistry; for chemists, in subjecting the animal tissues to the action of acids and alkalies, of prolonged boiling, or of too intense heat, have often obtained, at the end of the analysis, many substances which were erroneously described as proximate principles, while they were only the remains of an altered and disorganized material. Thus, the fibrous tissues, if boiled steadily for thirty-six hours, dissolve, for the most part, at the end of that time, in the boiling water; and on cooling the whole solution solidifies into a homogeneous, jelly-like substance, which has received the name of *gelatine*. But this gelatine does not really exist in the body as a proximate principle, since the fibrous tissue which produces it is not at first soluble, even in boiling water, and its ingredients become altered and converted into a gelatinous matter only by prolonged ebullition. So, again, an animal substance containing acetates or lactates of soda or lime will, upon incineration in the air, yield carbonates of the same bases, the organic acid having been destroyed, and replaced by carbonic acid; or sulphur and phosphorus, in the animal tissue, may be converted by the same means into sulphuric and phosphoric acids, which, decomposing the alkaline carbonates, become sulphates and phosphates. In either case, the analysis of the tissues, so conducted, will be a deceptive one, and useless for all anatomical and physiological purposes, because its real ingredients have been decomposed, and replaced by others, in the process of manipulation.

It is in this way that different chemists, operating upon the same animal solid or fluid, by following different plans of analysis, have obtained different results; enumerating as ingredients of the body many artificially formed substances, which are not, in reality, proximate principles, thereby introducing much confusion into physiological chemistry.

It is to be kept constantly in view, in the examination of an animal tissue or fluid, that the object of the operation is simply *the separation of its ingredients from each other*, and not their decomposition or ultimate analysis. Only the simplest forms of chemical manipulation should, therefore, be employed. The substance to be examined should first be subjected to evaporation, in order to extract and estimate its water. This evaporation must be conducted at a heat not above 212° F., since a higher temperature would destroy or alter some of the animal ingredients. Then, from the dried residue, chloride of sodium, alkaline sulphates, carbonates, and phosphates may be extracted with water. Coloring matters may be separated by alcohol. Oils may be dissolved out by ether, &c. &c. When a chemical decomposition is unavoidable, it must be kept in sight and afterward corrected. Thus the glyko-cholate of soda of the bile is separated from certain other ingredients by precipitating it with acetate of lead, forming glyko-cholate of lead; but this is afterward decomposed, in its turn, by carbonate of soda, reproducing the original glyko-cholate of soda. Sometimes it is impossible to extract a proximate principle in an entirely unaltered form. Thus the fibrin of the blood can be separated only by allowing it to coagulate; and once coagulated, it is permanently altered, and can no longer present all its original characters of fluidity, &c., as it existed beforehand in the blood. In such instances as this, we can only make allowance for an unavoidable difficulty, and be careful that the substance suffers no further alteration. By bearing in mind the above considerations, we may form a tolerably correct estimate of the nature and quantity of all of the proximate principles existing in the substance under examination.

The manner in which the proximate principles are associated together, so as to form the animal tissues, is deserving of notice. In every animal solid and fluid, there is a considerable number of proximate principles, which are present in certain proportions, and which are so united with each other that the mixture presents a homogeneous appearance. But this union is of a complicated character; and the presence of each ingredient depends, to a certain extent, upon that of the others. Some of them, such as the alkaline carbonates and phosphates, are in solution directly in the water. Some, which are insoluble in water, are held in solution by the presence of other soluble substances. Thus, phosphate of lime is held in solution in the urine by the bi-phosphate of soda. In the blood, it is dissolved by the albumen, which is itself fluid by union

with the water. The same substance may be fluid in one part of the body, and solid in another part. Thus in the blood and secretions the water is fluid, and holds in solution other substances, both animal and mineral, while in the bones and cartilages it is solid — not crystallized, as in ice, but amorphous and solid, by the fact of its intimate union with the animal and saline ingredients, which are abundant in quantity, and which are themselves present in the solid form. Again, the phosphate of lime in the blood is fluid by solution in the albumen; but in the bones it forms a solid substance with the animal matter of the osseous tissue; and yet the union of the two is as intimate and homogeneous in the bones as in the blood. A proximate principle, therefore, never exists alone in any part of the body, but is always intimately associated with a number of others, by a kind of homogeneous mixture or solution.

Every animal tissue and fluid contains a number of proximate principles which are present, as we have already mentioned, in certain characteristic proportions. Thus, water is present in very large quantity in the perspiration and the saliva, but in very small quantity in the bones and teeth. Chloride of sodium is comparatively abundant in the blood and deficient in the muscles. On the other hand, chloride of potassium is more abundant in the muscles, less so in the blood. But these proportions, it is important to observe, are nowhere absolute or invariable. There is a great difference, in this respect, between the chemical composition of an inorganic substance and the anatomical constitution of an animal fluid. The former is always constant and definite; the latter is always subject to certain variations. Thus, water is always composed of exactly the same relative quantities of oxygen and hydrogen; and if these proportions be altered in the least, it thereby ceases to be water, and is converted into some other substance. But in the urine, the proportions of water, urea, urate of soda, phosphates, &c., vary within certain limits in different individuals, and even in the same individual, from one hour to another. This variation, which is almost constantly taking place, within the limits of health, is characteristic of all the animal solids and fluids; for they are composed of different ingredients which are supplied by absorption or formed in the interior, and which are constantly given up again, under the same or different forms, to the surrounding media by the unceasing activity of the vital processes. Every variation, then,

in the general condition of the body, as a whole, is accompanied by a corresponding variation, more or less pronounced, in the constitution of its different parts. This constitution is consequently of a very different character from the chemical constitution of an oxide or a salt. Whenever, therefore, we meet with the analysis of an animal fluid, in which the relative quantity of its different ingredients is expressed in numbers, we must understand that such an analysis is always approximative, and not absolute.

The proximate principles are naturally divided into three different classes.

The first of these classes comprises all the proximate principles which are purely INORGANIC in their nature. These principles are derived mostly from the exterior. They are found everywhere, in unorganized as well as in organized bodies; and they present themselves under the same forms and with the same properties in the interior of the animal frame as elsewhere. They are crystallizable, and have a definite chemical composition. They comprise such substances as water, chloride of sodium, carbonate and phosphate of lime, &c.

The second class of proximate principles is known as CRYSTALLIZABLE SUBSTANCES OF ORGANIC ORIGIN. This is the name given to them by Robin and Verdeil,[1] whose classification of the proximate principles is the best which has yet been offered. They are crystallizable, as their name indicates, and have a definite chemical composition. They are said to be of "organic origin," because they first make their appearance in the interior of organized bodies, and are not found in external nature as the ingredients of inorganic substances. Such are the different kinds of sugar, starch, and oil.

The third class comprises a very extensive and important order of proximate principles, which go by the name of the ORGANIC SUBSTANCES proper. They are sometimes known as "albuminoid" substances or "protein compounds." The name organic substances is given to them in consequence of the striking difference which exists between them and all the other ingredients of the body. The substances of the second class differ from those of the first by their

[1] Chimie Anatomique et Physiologique. Paris, 1853.

exclusively organic origin, but they resemble the latter in their crystallizability and their definite chemical composition; in consequence of which their chemical investigation may be pursued in nearly the same manner, and their chemical changes expressed in nearly the same terms. But the proximate principles of the third class are in every respect peculiar. They have an exclusively organic origin; not being found except as ingredients of living or recently dead animals or vegetables. They have not a definite chemical composition, and are not crystallizable; and the forms which they present, and the chemical changes which they undergo in the body, are such as cannot be expressed by ordinary chemical phraseology. This class includes such substances as albumen, fibrin, casein, &c.

CHAPTER II.

PROXIMATE PRINCIPLES OF THE FIRST CLASS.

THE proximate principles of the first class, or those of an *inorganic* nature, are very numerous. Their most prominent characters have already been stated. They are all crystallizable, and have a definite chemical composition. They are met with extensively in the inorganic world, and form a large part of the crust of the earth. They occur abundantly in the different kinds of food and drink; and are necessary ingredients of the food, since they are necessary ingredients of the animal frame. Some of them are found universally in all parts of the body, others are met with only in particular regions; but there are hardly any which are not present at the same time in more than one animal solid or fluid. The following are the most prominent of them, arranged in the order of their respective importance.

1. WATER.—Water is universally present in all the tissues and fluids of the body. It is abundant in the blood and secretions, where its presence is indispensable in order to give them the fluidity which is necessary to the performance of their functions; for it is by the blood and secretions that new substances are introduced into the body, and old ingredients discharged. And it is a necessary condition both of the introduction and discharge of substances naturally solid, that they assume, for the time being, a fluid form; water is therefore an essential ingredient of the fluids, for it holds their solid materials in solution, and enables them to pass and repass through the animal frame.

But water is an ingredient also of the solids. For if we take a muscle or a cartilage, and expose it to a gentle heat in dry air, it loses water by evaporation, diminishes in size and weight, and becomes dense and stiff. Even the bones and teeth lose water by evaporation in this way, though in smaller quantity. In all these solid and semi-solid tissues, the water which they contain is useful

by giving them the special consistency which is characteristic of them, and which would be lost without it. Thus a tendon, in its natural condition, is white, glistening, and opaque; and though very strong, perfectly flexible. If its water be expelled by evaporation it becomes yellowish in color, shrivelled, semi-transparent, inflexible, and totally unfit for performing its mechanical functions. The same thing is true of the skin, muscles, cartilages, &c.

The following is a list, compiled by Robin and Verdeil from various observers, showing the proportion of water per thousand parts, in different solids and fluids:—

	Quantity of Water in 1,000 parts in		
Teeth	100	Bile	880
Bones	130	Milk	887
Cartilage	550	Pancreatic juice	900
Muscles	750	Urine	936
Ligaments	768	Lymph	960
Brain	789	Gastric juice	975
Blood	795	Perspiration	986
Synovial fluid	805	Saliva	995

According to the best calculations, water constitutes, in the human subject, between two-thirds and three-quarters of the entire weight of the body.

The water which thus forms a part of the animal frame is derived from without. It is taken in the different kinds of drink, and also forms an abundant ingredient in the various articles of food. For no articles of food are taken in an absolutely dry state, but all contain a larger or smaller quantity of water, which may readily be expelled by evaporation. The quantity of water, therefore, which is daily taken into the system, cannot be ascertained in any case by simply measuring the quantity of drink, but its proportion in the solid food, taken at the same time, must also be determined by experiment, and this ascertained quantity added to that which is taken in with the fluids. By measuring the quantity of fluid taken with the drink, and calculating in addition the proportion existing in the solid food, we have found that, for a healthy adult man, the ordinary quantity of water introduced per day, is a little over 4½ pounds.

After forming part of the animal solids and fluids, and taking part in the various physical and chemical processes of the body, the water is again discharged; for its presence in the body, like that of all the other proximate principles, is not permanent, but only

temporary. After being taken in with the food and drink, it is associated with other principles in the fluids and solids, passing from the intestine to the blood, and from the blood to the tissues and secretions. It afterward makes its exit from the body, from which it is discharged by four different passages, viz., in a liquid form with the urine and the feces, and in a gaseous form with the breath and the perspiration. Of all the water which is expelled in this way, about 48 per cent. is discharged with the urine and feces,[1] and about 52 per cent. by the lungs and skin. The researches of Lavoisier and Seguin, Valentin, and others, show that from a pound and a half to two pounds is discharged daily by the skin, a little over one pound by exhalation from the lungs, and a little over two pounds by the urine. Both the absolute and relative amount discharged, both in a liquid and gaseous form, varies according to circumstances. There is particularly a compensating action in this respect between the kidneys and the skin, so that when the cutaneous perspiration is very abundant the urine is less so, and *vice versâ*. The quantity of water exhaled from the lungs varies also with the state of the pulmonary circulation, and with the temperature and dryness of the atmosphere. The water is not discharged at any time in a state of purity, but is mingled in the urine and feces with saline substances which it holds in solution, and in the cutaneous and pulmonary exhalations with animal vapors and odoriferous substances of various kinds. In the perspiration it is also mingled with saline substances, which it leaves behind on evaporation.

2. Chloride of Sodium.—This substance is found, like water, throughout the different tissues and fluids of the body. The only exception to this is perhaps the enamel of the teeth, where it has not yet been discovered. Its presence is important in the body, as regulating the phenomena of endosmosis and exosmosis in different parts of the frame. For we know that a solution of common salt passes through animal membranes much less readily than pure water; and tissues which have been desiccated will absorb pure water more abundantly than a saline solution. It must not be supposed, however, that the presence or absence of chloride of sodium, or its varying quantity in the animal fluids, is the only condition which regulates their transudation through the animal membranes. The manner in which endosmosis and exosmosis take place in the

[1] Op. cit., vol. ii. pp. 143 and 145.

animal frame depends upon the relative quantity of all the ingredients of the fluids, as well as on the constitution of the solids themselves; and the chloride of sodium, as one ingredient among many, influences these phenomena to a great extent, though it does not regulate them exclusively.

It exerts also an important influence on the solution of various other ingredients, with which it is associated. Thus, in the blood it increases the solubility of the albumen, and perhaps also of the earthy phosphates. The blood-globules, again, which become disintegrated and dissolved in a solution of pure albumen, are maintained in a state of integrity by the presence of a small quantity of chloride of sodium.

It exists in the following proportions in several of the solids and fluids:[1]—

Quantity of Chloride of Sodium in 1,000 parts in the

Muscles	2.0	Perspiration	2.2
Bones	2.5	Urine	3.0
Cartilage	2.8	Bile	3.5
Milk	1.0	Blood	4.5
Saliva	1.5	Mucus	6.0

In the blood it is rather more abundant than all the other saline ingredients taken together.

Since chloride of sodium is so universally present in all parts of the body, it is an important ingredient also of the food. It occurs, of course, in all animal food, in the quantities in which it naturally exists in the corresponding tissues; and in vegetable food also, though in smaller amount. Its proportion in muscular flesh, however, is much less than in the blood and other fluids. Consequently, it is not supplied in sufficient quantity as an ingredient of animal and vegetable food, but is taken also by itself as a condiment. There is no other substance so universally used by all races and conditions of men, as an addition to the food, as chloride of sodium. This custom does not simply depend on a fancy for gratifying the palate, but is based upon an instinctive desire for a substance which is necessary to the proper constitution of the tissues and fluids. Even the herbivorous animals are greedy of it, and if freely supplied with it, are kept in a much better condition than when deprived of its use.

The importance of chloride of sodium in this respect has been well demonstrated by Boussingault, in his experiments on the

[1] Robin and Verdeil.

fattening of animals. These observations were made upon six bullocks, selected, as nearly as possible, of the same age and vigor, and subjected to comparative experiment. They were all supplied with an abundance of nutritious food; but three of them (lot No. 1) received also a little over 500 grains of salt each per day. The remaining three (lot No. 2) received no salt, but in other respects were treated like the first. The result of these experiments is given by Boussingault as follows:—[1]

"Though salt administered with the food has but little effect in increasing the size of the animal, it appears to exert a favorable influence upon his qualities and general aspect. Until the end of March (the experiment began in October) the two lots experimented on did not present any marked difference in their appearance; but in the course of the following April, this difference became quite manifest, even to an unpractised eye. The lot No. 2 had then been without salt for six months. In the animals of both lots the skin had a fine and substantial texture, easily stretched and separated from the ribs; but the hair, which was tarnished and disordered in the bullocks of the second lot, was smooth and glistening in those of the first. As the experiment went on, these characters became more marked; and at the beginning of October the animals of lot No. 2, after going without salt for an entire year, presented a rough and tangled hide, with patches here and there where the skin was entirely uncovered. The bullocks of lot No. 1 retained, on the contrary, the ordinary aspect of stall-fed animals. Their vivacity and their frequent attempts at mounting contrasted strongly with the dull and unexcitable aspect presented by the others. No doubt, the first lot would have commanded a higher price in the market than the second."

Chloride of sodium acts also in a favorable manner by exciting the digestive fluids, and assisting in this way the solution of the food. For food which is tasteless, however nutritious it may be in other respects, is taken with reluctance and digested with difficulty; while the attractive flavor which is developed by cooking, and by the addition of salt and other condiments in proper proportion, excites the secretion of the saliva and gastric juice, and facilitates consequently the whole process of digestion. The chloride of sodium is then taken up by absorption from the intestine, and is deposited in various quantities in different parts of the body.

[1] Chimie Agricole, Paris, 1854, p. 271.

It is discharged with the urine, mucus, cutaneous perspiration, &c., in solution in the water of these fluids. According to the estimates of M. Barral,[1] a small quantity of chloride of sodium disappears in the body; since he finds by accurate comparison that all the salt introduced with the food is not to be found in the excreted fluids, but that about one-fifth of it remains unaccounted for. This portion is supposed to undergo a double decomposition in the blood with phosphate of potassa, forming chloride of potassium and phosphate of soda. By far the greater part of the chloride of sodium, however, escapes under its own form with the secretions.

3. Chloride of Potassium.—This substance is found in the muscles, the blood, the milk, the urine, and various other fluids and tissues of the body. It is not so universally present as chloride of sodium, and not so important as a proximate principle. In some parts of the body it is more abundant than the latter salt, in others less so. Thus, in the blood there is more chloride of sodium than chloride of potasssium, but in the muscles there is more chloride of potassium than chloride of sodium. This substance is always in a fluid form, by its ready solubility in water, and is easily separated by lixiviation. It is introduced mostly with the food, but is probably formed partly in the interior of the body from chloride of sodium by double decomposition, as already mentioned. It is discharged with the mucus, the saliva, and the urine.

4. Phosphate of Lime.—This is perhaps the most important of the mineral ingredients of the body next to chloride of sodium. It is met with universally, in every tissue and every fluid. Its quantity, however, varies very much in different parts, as will be seen by the following list:—

Quantity of Phosphate of Lime in 1,000 parts in the

Enamel of the teeth	885	Muscles	2.5
Dentine	643	Blood	0.3
Bones	550	Gastric juice	0.4
Cartilages	40		

It occurs also under different physical conditions. In the bones, teeth, and cartilages it is solid, and gives to these tissues the resistance and solidity which are characteristic of them. The calcareous salt is not, however, in these instances, simply deposited mechanically in the substance of the bone or cartilage as a granular powder,

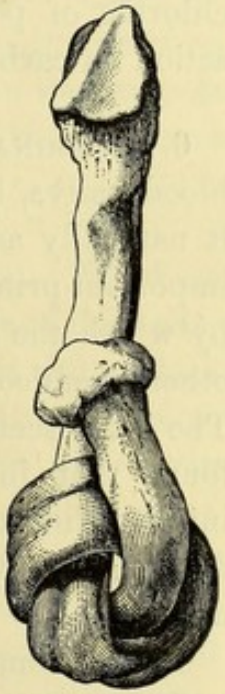
[1] In Robin and Verdeil, op. cit., vol. ii. 193.

but is intimately united with the animal matter of the tissues, like a coloring matter in colored glass, so as to present a more or less homogeneous appearance. It can, however, be readily dissolved out by maceration in dilute muriatic acid, leaving behind the animal substance, which still retains the original form of the bone or cartilage. It is not, therefore, united with the animal matter so as to lose its identity and form a new chemical substance, as where an acid combines with an alkali to form a salt, but in the same manner as salt unites with water in a saline solution, both substances retaining their original character and composition, but so intimately associated that they cannot be separated by mechanical means.

In the blood, phosphate of lime is in a liquid form, notwithstanding its insolubility in water and in alkaline fluids, being held in solution by the albuminous matters of the circulating fluid. In the urine, it is retained in solution by the bi-phosphate of soda.

In all the solid tissues it is useful by giving to them their proper consistence and solidity. For example, in the enamel of the teeth, the hardest tissue of the body, it predominates very much over the animal matter, and is present in greater abundance there than in any other part of the frame. In the dentine, a softer tissue, it is in somewhat smaller quantity, and in the bones smaller still; though in the bones it continues to form more than one-half the entire mass of the osseous substance. The importance of phosphate of lime, in communicating to bones their natural stiffness and consistency, may be readily shown by the alteration which they suffer from its removal. If a long bone be macerated in dilute muriatic acid, the earthy salt, as already mentioned, is entirely dissolved out, after which the bone loses its rigidity, and may be bent or twisted in any direction without breaking. (Fig. 1.)

Fig. 1.



FIBULA TIED IN A KNOT, after maceration in a dilute acid. (From a specimen in the museum of the Coll. of Physicians and Surgeons.)

Whenever the nutrition of the bone during life is interfered with from any pathological cause, so that its phosphate of lime becomes deficient in amount, a softening of the osseous tissue is the consequence, by which the bones yield to external pressure, and become more or less distorted. (Osteo-malakia.)

The phosphate of lime in the body, like most of the inorganic

proximate principles, is derived directly from the food; as it exists, in various proportions, not only in all kinds of animal food, but also in all the cereal grains, the nutritive roots and tuberous plants, and even in nearly all the fruits.

After forming, for a time, a part of the tissues and fluids, it is discharged from the body by the urine, the perspiration, mucus, &c. Much the larger portion is discharged by the urine. A small quantity also occurs in the feces, but this is probably only the superfluous residue of what is taken in with the food.

5. Carbonate of Lime.—Carbonate of lime is to be found in the bones, and sometimes in the urine. The concretions of the internal ear are almost entirely formed of it. It very probably occurs also in the blood, teeth, cartilages, and sebaceous matter; but its presence here is not quite certain, since it may have been produced from the lactate, or other organic combination, by the process of incineration. In the bones, it is in much smaller quantity than the phosphate. Its solubility in the blood and the urine is accounted for by the presence of free carbonic acid, and also of chloride of potassium, both of which substances exert a solvent action on carbonate of lime.

6. Carbonate of Soda.—This substance exists in the bones, blood, saliva, lymph, and urine. As it is readily soluble in water, it naturally assumes the liquid form in the animal fluids. It is important principally as giving to the blood its alkalescent reaction, by which the solution of the albumen is facilitated, and various other chemico-physiological processes in the blood accomplished. The alkalescence of the blood is, in fact, necessary to life; for it is found that, in the living animal, if a mineral acid be gradually injected into the blood, so dilute as not to coagulate the albumen, death takes place before its alkaline reaction has been completely neutralized.[1]

The carbonate of soda of the blood is partly introduced as such with the food; but the greater part of it is formed within the body by the decomposition of other salts, introduced with certain fruits and vegetables. These fruits and vegetables, such as apples, cherries, grapes, potatoes, &c., contain malates, tartrates, and citrates of soda and potassa. Now, it has been often noticed that, after

[1] Cl. Bernard. Lectures on the Blood; reported by W. F. Atlee, M. D. Philadelphia, 1854, p. 31.

the use of acescent fruits and vegetables containing the above salts, the urine becomes alkaline in reaction from the presence of the alkaline carbonates. Lehmann[1] found, by experiments upon his own person, that, within thirteen minutes after taking half an ounce of lactate of soda, the urine had an alkaline reaction. He also observed that, if a solution of lactate of soda were injected into the jugular vein of a dog, the urine became alkaline at the end of five, or, at the latest, of twelve minutes. The conversion of these salts into carbonates takes place, therefore, not in the intestine but in the blood. The same observer[2] found that, in many persons living on a mixed diet, the urine became alkaline in two or three hours after swallowing ten grains of acetate of soda. These salts, therefore, on being introduced into the animal body, are decomposed. Their organic acid is destroyed and replaced by carbonic acid; and they are then discharged under the form of carbonates of soda and potassa.

7. Carbonate of Potassa.—This substance occurs in very nearly the same situations as the last. In the blood, however, it is in smaller quantity. It is mostly produced, as above stated, by the decomposition of the malate, tartrate, and citrate, in the same manner as the carbonate of soda. Its function is also the same as that of the soda salt, and it is discharged in the same manner from the body.

8. Phosphates of Magnesia, Soda, and Potassa.—All these substances exist universally in all the solids and fluids of the body, but in very small quantity. The phosphates of soda and potassa are easily dissolved in the animal fluids, owing to their ready solubility in water. The phosphate of magnesia is held in solution in the blood by the alkaline chlorides and phosphates; in the urine, by the acid phosphate of soda.

A peculiar relation exists between the alkaline phosphates and carbonates in different classes of animals. For while the fluids of carnivorous animals contain a preponderance of the phosphates, those of the herbivora contain a preponderance of the carbonates: a peculiarity readily understood when we recollect that muscular flesh and the animal tissues generally are comparatively abundant in phosphates; while vegetable substances abound in salts of the

[1] Physiological Chemistry. Philadelphia ed., vol. i., p. 97.

[2] Physiological Chemistry, vol. ii., p. 130.

organic acids, which give rise, as already described, by their decomposition in the blood, to the alkaline carbonates.

The proximate principles included in the above list resemble each other not only in their inorganic origin, their crystallizability, and their definite chemical composition, but also in the part which they take in the constitution of the animal frame. They are distinguished in this respect, first by being derived entirely from without. There are a few exceptions to this rule; as, for example, in the case of the alkaline carbonates, which partly originate in the body from the decomposition of malates, tartrates, &c. These, however, are only exceptions; and in general, the proximate principles belonging to the first class are introduced with the food, and taken up by the animal tissues in precisely the same form under which they occur in external nature. The carbonate of lime in the bones, the chloride of sodium in the blood and tissues, are the same substances which are met with in the calcareous rocks, and in solution in sea water. They do not suffer any chemical alteration in becoming constituent parts of the animal frame.

They are equally exempt, as a general rule, from any alteration while they remain in the body, and during their passage through it. The exceptions to this rule are very few; as, for example, where a small part of the chloride of sodium suffers double decomposition with phosphate of potassa, giving rise to chloride of potassium and phosphate of soda; or where the phosphate of soda itself gives up a part of its base to an organic acid (uric), and is converted in this way into a bi-phosphate of soda.

Nearly the whole of these substances, finally, are taken up unchanged from the tissues, and discharged unchanged with the excretions. Thus we find the phosphate of lime and the chloride of sodium, which were taken in with the food, discharged again under the same form in the urine. They do not, therefore, for the most part, participate directly in the chemical changes going on in the body; but only serve by their presence to enable those changes to be accomplished in the other ingredients of the animal frame, which are necessary to the process of nutrition.

CHAPTER III.

PROXIMATE PRINCIPLES OF THE SECOND CLASS.

THE proximate principles belonging to the second class are divided into three principal groups, viz: starch, sugar, and oil. They are distinguished, in the first place, by their organic origin. Unlike the principles of the first class, they do not exist in external nature, but are only found as ingredients of organized bodies. They exist both in animals and in vegetables, though in somewhat different proportions. All the substances belonging to this class have a definite chemical composition; and are further distinguished by the fact that they are composed of oxygen, hydrogen, and carbon alone, without nitrogen, whence they are sometimes called the "non-nitrogenous" substances.

1. STARCH ($C_{12}H_{10}O_{10}$).—The first of these substances seems to form an exception to the general rule in a very important particular, viz., that it is not crystallizable. Still, since it so closely resembles the rest in all its general properties, and since it is easily convertible into sugar, which is itself crystallizable, it is naturally included in the second class of proximate principles. Though not crystallizable, furthermore, it still assumes a distinct form, by which it differs from substances that are altogether amorphous.

Starch occurs in some part or other of almost all the flowering plants. It is very abundant in corn, wheat, rye, oats, and rice, in the parenchyma of the potato, in peas and beans, and in most vegetable substances used as food. It constitutes almost entirely the different preparations known as sago, tapioca, arrowroot, &c., which are nothing more than varieties of starch, extracted from different species of plants.

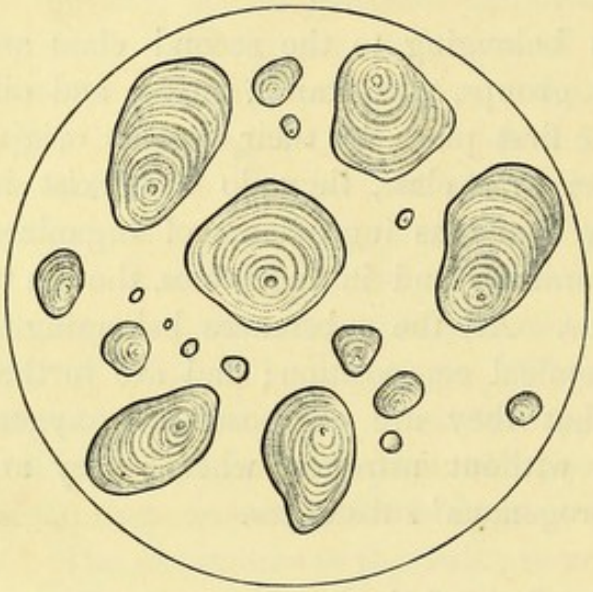
The following is a list showing the percentage of starch occurring in different kinds of food:—[1]

[1] Pereira on Food and Diet, New York, 1843, p. 59.

Quantity of Starch in 100 parts in			
Rice	85.07	Wheat flour	72.00
Maize	80.92	Iceland moss	44.60
Barley meal	67.18	Kidney bean	35.94
Rye meal	61.07	Peas	32.45
Oat meal	59.00	Potato	15.70

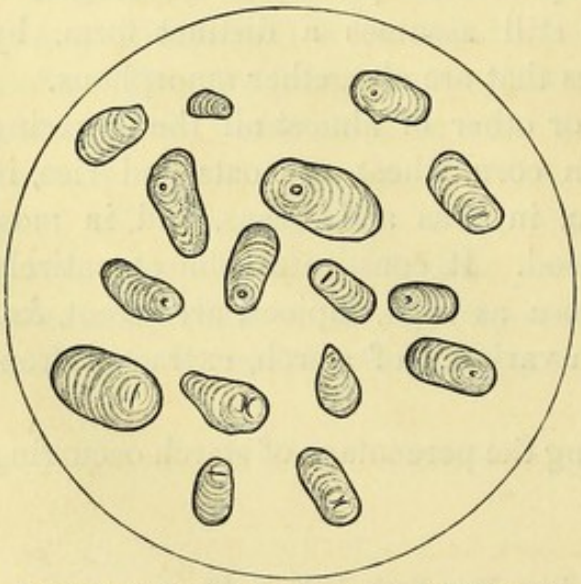
When purified from foreign substances, starch is a white, light powder, which gives rise to a peculiar crackling sensation when rubbed between the fingers. When examined by the microscope, it is seen to be composed of solid granules, which, while they have a general resemblance to each other, differ somewhat in various particulars. The starch grains of the potato (Fig. 2) vary considerably in size. The smallest have a diameter of $\frac{1}{1000}$, the largest $\frac{1}{400}$ of an inch. They are irregularly pear-shaped in form, and are marked by concentric laminæ, as if the matter of which they are composed had been deposited in successive layers. At one point on the surface of every starch grain, there is a minute pore or depression, called the *hilum*, around which the circular markings are arranged in a concentric form.

Fig. 2.



Grains of Potato Starch.

Fig. 3.



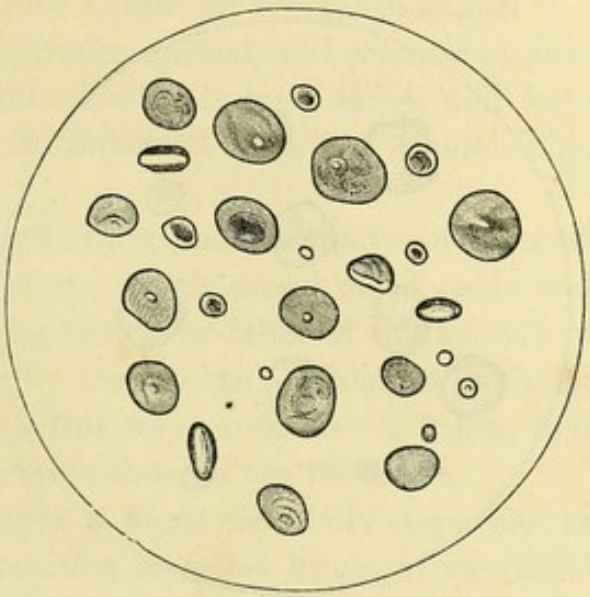
Starch Grains of Bermuda Arrowroot.

The starch granules of arrowroot (Fig. 3) are generally smaller and more uniform in size, than those of the potato. They vary from $\frac{1}{2000}$ to $\frac{1}{300}$ of an inch in diameter. They are elongated and cylindrical in form, and the concentric markings are less distinct than in the preceding variety. The hilum

has here sometimes the form of a circular pore, and sometimes that of a transverse fissure or slit.

The grains of wheat starch (Fig. 4) are still smaller than those of arrowroot. They vary from $\frac{1}{10000}$ to $\frac{1}{700}$ of an inch in diameter. They are nearly circular in form, with a round or transverse hilum, but without any distinct appearance of lamination. Many of them are flattened or compressed laterally, so that they present a broad surface in one position, and a narrow edge when viewed in the opposite direction.

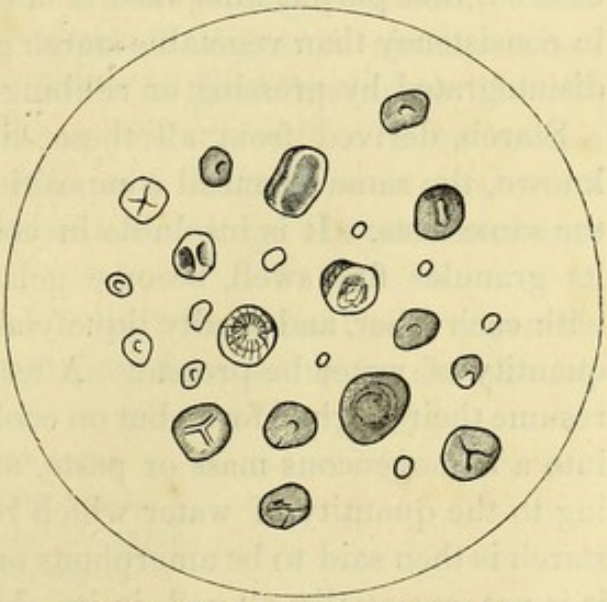
Fig. 4.



Starch Grains of Wheat Flour.

The starch grains of Indian corn (Fig. 5) are of nearly the same size with those of wheat flour. They are somewhat more irregular and angular in shape; and are often marked with crossed or radiating lines, as if from partial fracture.

Fig. 5.



Starch Grains of Indian Corn.

Starch is also an ingredient of the animal body. It was first observed by Purkinje, and afterward by Kölliker,[1] that certain bodies are to be found in the interior of the brain, about the lateral ventricles, in the fornix, septum lucidum and other parts, which present a certain resemblance to starch grains, and which have therefore been called "corpora amylacea." Subsequently Virchow[2] corroborated the above observations, and ascertained the corpora amylacea to be

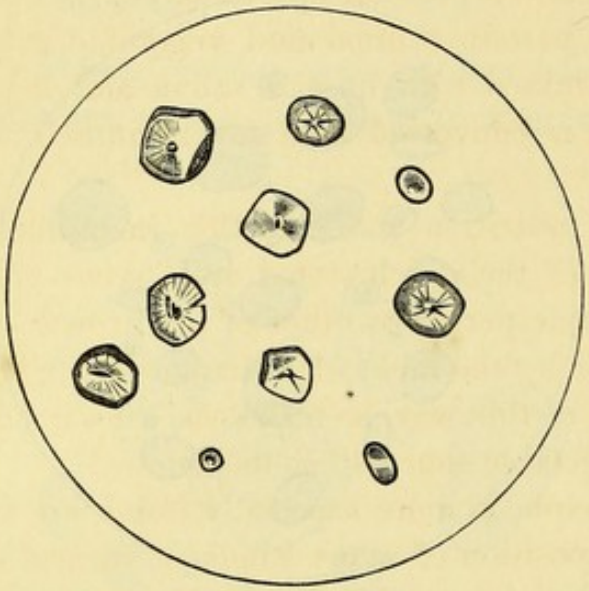
[1] Handbuch der Gewebelehre, Leipzig, 1852, p. 311.

[2] In American Journal Med. Sci., April, 1854, p. 466.

really substances of a starchy nature; since they exhibit the usual chemical reactions of vegetable starch.

The starch granules of the human brain (Fig. 6) are transparent and colorless, like those from plants. They refract the light strongly, and vary in size from $\frac{1}{4700}$ to $\frac{1}{1100}$ of an inch. Their average is $\frac{1}{1800}$ of an inch. They are sometimes rounded or oval, and sometimes angular in shape. They resemble considerably in appearance the starch granules of Indian corn. The largest of them present a very faint concentric lamination, but the greater number are destitute of any such appearance. They have nearly always a distinct hilum, which is sometimes circular and sometimes slit-shaped. They are also often marked with delicate radiating lines and shadows. On the addition of iodine, they become colored, first purple, afterward of a deep blue. They are less firm in consistency than vegetable starch grains, and can be more readily disintegrated by pressing or rubbing them upon the glass.

Fig. 6.



Starch Grains from Wall of Lateral Ventricles; from a woman aged 35.

Starch, derived from all these different sources, has, so far as known, the same chemical composition, and may be recognized by the same tests. It is insoluble in cold water, but in boiling water its granules first swell, become gelatinous and opaline, then fuse with each other, and finally liquefy altogether, provided a sufficient quantity of water be present. After that, they cannot be made to resume their original form, but on cooling and drying merely solidify into a homogeneous mass or paste, more or less consistent, according to the quantity of water which remains in union with it. The starch is then said to be amorphous or "hydrated." By this process it is not essentially altered in its chemical properties, but only in its physical condition. Whether in granules, or in solution, or in an amorphous and hydrated state, it strikes a deep blue color on the addition of free iodine.

Starch may be converted into sugar by three different methods. First, by boiling with a dilute acid. If starch be boiled with dilute

nitric, sulphuric, or muriatic acid during thirty-six hours, it first changes its opalescent appearance, and becomes colorless and transparent; losing at the same time its power of striking a blue color with iodine. After a time, it begins to acquire a sweet taste, and is finally altogether converted into a peculiar species of sugar.

Secondly, by contact with certain animal and vegetable substances. Thus, boiled starch mixed with human saliva and kept at the temperature of 100° F., is converted in a few minutes into sugar.

Thirdly, by the processes of nutrition and digestion in animals and vegetables. A large part of the starch stored up in seeds and other vegetable tissues is, at some period or other of the growth of the plant, converted into sugar by the molecular changes going on in the vegetable fabric. It is in this way, so far as we know, that all the sugar derived from vegetable sources has its origin.

Starch, as a proximate principle, is more especially important as entering largely into the composition of many kinds of vegetable food. With these it is introduced into the alimentary canal, and there, during the process of digestion, is converted into sugar. Consequently, it does not appear in the blood, nor in any of the secreted fluids.

2. SUGAR.—This group of proximate principles includes a considerable number of substances, which differ in certain minor details, while they resemble each other in the following particulars: They are readily soluble in water, and crystallize more or less perfectly on evaporation; they have a distinct sweet taste; and finally, by the process of fermentation, they are converted into alcohol and carbonic acid.

These substances are derived from both animal and vegetable sources. The varieties of sugar most familiar to us are the following:—

Cane sugar,
Grape sugar,
Sugar of starch,
Milk sugar,
Liver sugar.

The cane and grape sugars are held in solution in the juices of the plants from which they derive their name. Sugar of starch, or *glucose*, may be produced by boiling starch for a long time with a dilute

acid, and is also formed, in certain plants, by the transformation of their starchy ingredients. Liver sugar and sugar of milk are produced in the tissues of the liver and the mammary gland, by a process of secretion. Honey contains a mixture of several varieties of sugar, including cane sugar and glucose, collected from the sweet juices of flowering plants and mingled with certain animal ingredients.

These varieties of sugar differ but little in their ultimate chemical composition. The following formulæ have been established for three of them.

Cane sugar	$= C_{12}H_{11}O_{11}$
Milk sugar	$= C_{12}H_{12}O_{12}$
Glucose	$= C_{12}H_{14}O_{14}$

Cane sugar is sweeter than most of the other varieties, and more soluble in water. Some sugars, such as liver sugar and sugar of honey, crystallize only with great difficulty; but this is probably owing to their being mingled with other substances, from which it is difficult to separate them completely. If they could be obtained in a state of purity, they would doubtless crystallize as perfectly as cane sugar. The different sugars vary also in the readiness with which they undergo fermentation. Some of them, as grape sugar and liver sugar, enter into fermentation very promptly; others, such as milk and cane sugar, with considerable difficulty.

The above are not to be regarded as the only varieties of sugar existing in nature. On the contrary, it is probable that nearly every different species of animal and vegetable produces a distinct kind of sugar, differing slightly from the rest in its degree of sweetness, its solubility, its crystallization, its aptitude for fermentation, and perhaps in its elementary composition. Nevertheless, there is so close a resemblance between them that they are all properly regarded as belonging to a single group.

The test most commonly employed for detecting the presence of sugar is that known as *Trommer's test.* It depends upon the fact that the saccharine substances have the power of reducing the persalts of copper when heated with them in an alkaline solution. The test is applied in the following manner: A very small quantity of sulphate of copper in solution should be added to the suspected liquid, and the mixture then rendered distinctly alkaline by the addition of caustic potassa. The whole solution then takes a deep

blue color. On boiling the mixture, if sugar be present, the insoluble suboxide of copper is thrown down as an opaque red, yellow, or orange-colored deposit; otherwise no change of color takes place.

This test requires some precautions in its application. In the first place, it is not applicable to all varieties of sugar. Cane sugar, for example, when pure, has no power of reducing the salts of copper, even when present in large quantity. Maple sugar, also, which resembles cane sugar in some other respects, reduces the copper, in Trommer's test, but slowly and imperfectly. Beet-root sugar, according to Bernard, presents the same peculiarity. If these sugars, however, be boiled for two or three minutes with a trace of sulphuric acid, they become converted into glucose, and acquire the power of reducing the salts of copper. Milk sugar, liver sugar, and sugar of honey, as well as grape sugar and glucose, all act promptly and perfectly with Trommer's test in their natural condition.

Secondly, care must be taken to add to the suspected liquid only a small quantity of sulphate of copper, just sufficient to give to the whole a distinct blue tinge, after the addition of the alkali. If a larger quantity of the copper salt be used, the sugar in solution may not be sufficient to reduce the whole of it; and that which remains as a blue sulphate will mask the yellow color of the suboxide thrown down as a deposit. By a little care, however, in managing the test, this source of error may be readily avoided.

Thirdly, there are some albuminous substances which have the power of interfering with Trommer's test, and prevent the reduction of the copper even when sugar is present. Certain animal matters, to be more particularly described hereafter, which are liable to be held in solution in the gastric juice, have this effect. This source of error may be avoided, and the substances in question eliminated when present, by treating the suspected fluid with animal charcoal, or by evaporating and extracting it with alcohol before the application of the test.

A more delicate form of the copper test for glucose, is that known as *Fehling's liquor*, which is an alkaline solution of a double tartrate of copper and potash. It is made as follows:—

Pure crystallized Sulphate of Copper, 500 grains.

Neutral Tartrate of Potassa, 2000 grains.

A solution of Caustic Soda (of the specific gravity 1.12), 8750 grains.

The neutral tartrate of potassa, dissolved in a little water, is first mixed with the solution of caustic soda. Then the sulphate of copper, dissolved in about $4\frac{1}{2}$ fluid ounces of water, is gradually added to the alkaline liquor, which assumes a clear deep-blue color. The whole is finally diluted with water to the volume of $31\frac{5}{8}$ fluid ounces. The advantage of Fehling's test liquor is that the quantity of copper salt contained in a given volume is accurately known, and consequently not only the presence, but also the amount of sugar in any liquid may be determined by the quantity of test-liquid which it decomposes at a boiling temperature. One cubic centimetre (about $\frac{1}{4}$ of a fluid drachm) of Fehling's liquor is exactly decolorized by .077 of a grain of glucose. The test is also a very delicate one. One drop of Fehling's liquor will detect $\frac{1}{1000}$ of a grain of glucose, dissolved in one cubic centimetre of water, if the test be carefully applied.

One precaution however must be taken in the use of this test. As Fehling's liquor is apt to become changed after being exposed for some time to the air, so that it will partially precipitate on boiling even without the presence of sugar, it is essential in every case where a suspected liquid is examined for sugar, that a small portion of the test liquid employed should be previously boiled in order to be sure that it will not precipitate spontaneously.

A less convenient but still valuable test for sugar is that of *fermentation.* The saccharine fluid is mixed with a little yeast, and kept at a temperature of 70° to 100° F. until the fermenting process is completed. By this process, as already mentioned, the sugar is converted into alcohol and carbonic acid. The gas, which is given off in minute bubbles during fermentation, should be collected and examined. The remaining fluid is purified by distillation and also subjected to examination. If the gas be found to be carbonic acid, and the remaining fluid contain alcohol, there can be no doubt that sugar was present at the commencement of the operation.

The following list shows the percentage of sugar in various articles of food.[1]

[1] Pereira, op. cit., p. 55.

Quantity of Sugar in 100 parts in			
Figs	62.50	Wheat flour	5.40
Cherries	18.12	Rye meal	3.28
Peaches	16.48	Indian meal	1.45
Tamarinds	12.50	Peas	2.00
Pears	11.52	Cow's milk	4.77
Beets	9.00	Ass's milk	6.08
Sweet almonds	6.00	Human milk	6.50
Barley meal	5.21		

Beside the sugar, therefore, which is taken into the alimentary canal in a pure form, a large quantity is also introduced as an ingredient of the sweet-flavored fruits and vegetables. All the starchy substances of the food are also converted into sugar in the process of digestion. Two of the varieties of sugar, at least, originate in the interior of the body, viz., sugar of milk and liver sugar. The former exists in a solid form in the substance of the mammary gland, from which it passes in solution into the milk. The liver sugar is found in the substance of the liver, and also in the blood of the hepatic veins. The sugar which is introduced with the food, as well as that which is formed in the liver, disappears by decomposition in the animal fluids, and does not appear in any of the excretions.

3. Fats.—These substances, like the sugars, are derived from both animal and vegetable sources. There are three principal varieties of them, which may be considered as representing the class, viz:—

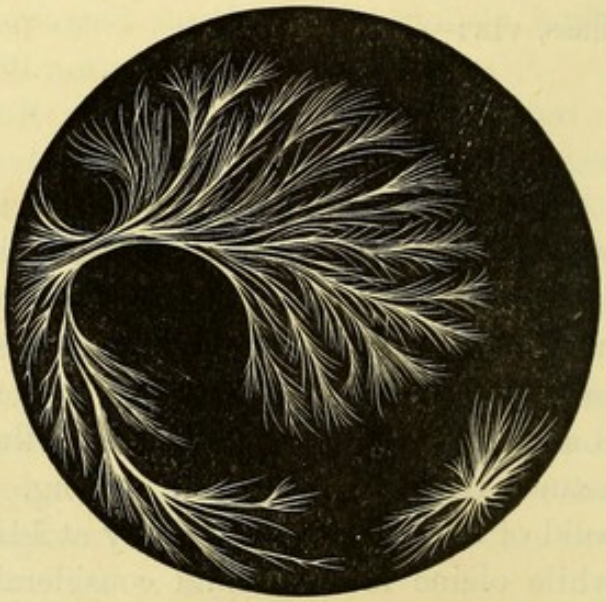
Oleine	$= C_{91} H_{87} O_{15}$
Margarine	$= C_{76} H_{75} O_{12}$
Stearine	$= C_{142} H_{141} O_{17}$

The principal difference between the oleaginous and saccharine substances, so far as regards their ultimate chemical composition, is that in the sugars the oxygen and hydrogen always exist together in the proportion to form water; while in the fats the proportions of carbon and hydrogen are nearly the same, but that of oxygen is considerably less. The fats are all fluid at a high temperature, but assume the solid form on cooling. Stearine, which is the most solid of the three, liquefies only at 143° F.; margarine at 118° F.; while oleine remains fluid considerably below 100° F., and even very near the freezing point of water. The fats are all insoluble in water, but readily soluble in ether. By prolonged boiling in water with a caustic alkali, they are decomposed, and as the result of the decomposition there are formed two new bodies; first, glycerine,

which is a neutral fluid substance, and secondly, a fatty acid, viz: oleic, margaric, or stearic acid, corresponding to the kind of fat which has been used in the experiment. The glycerine remains in a free state, while the fatty acid unites with the alkali employed, forming an oleate, margarate, or stearate. This combination is termed a *soap*, and the process by which it is formed is called *saponification*. This process, however, is not a simple decomposition of the fatty body, since it can only take place in the presence of water; several equivalents of which unite with the elements of the fatty body, and enter into the composition of the glycerine, &c., so that the fatty acid and the glycerine together weigh more than the original fatty substance which was decomposed. It is not proper, therefore, to regard an oleaginous body as formed by the union of a fatty acid with glycerine. It is formed, on the contrary, in all probability, by the direct combination of its ultimate chemical elements.

The different kinds of oil, fat, lard, suet, &c., contain the three oleaginous matters mentioned above, mingled together in different proportions. The more solid fats contain a larger quantity of stearine and margarine; the less consistent varieties, a larger proportion of oleine. Neither of the oleaginous matters, stearine, margarine, or oleine, ever occur separately; but in every fatty substance they are mingled together, so that the more fluid of them hold in solution the more solid. Generally speaking, in the living body, these mixtures are fluid, or nearly so; for though both stearine and margarine are solid, when pure, at the ordinary temperature of the body, they are held in solution, during life, by the oleine with which they are associated. After death, however, as the body cools, the stearine and margarine sometimes separate from the mixture in a crystalline form, since the oleine can no longer hold in solution so large a quantity of them as it had dissolved at a higher temperature.

Fig. 7.



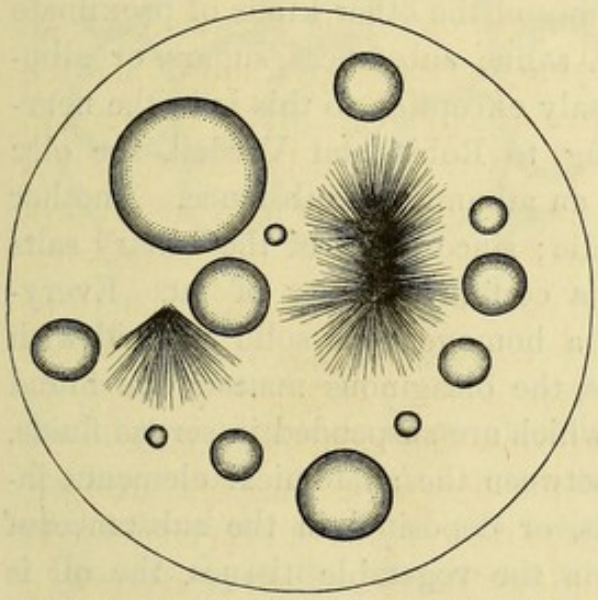
STEARINE crystallized from a Warm Solution in Oleine.

These substances crystallize in very slender needles, which are sometimes straight, but more often somewhat curved or wavy in their outline. (Fig. 7.)

They are always deposited in a more or less radiated form; and have sometimes a very elegant, branched, or arborescent arrangement.

When in a fluid state, the fatty substances present themselves under the form of drops or globules, which vary indefinitely in size, but which may be readily recognized by their optical properties. They are circular in shape, and have a faint amber color, distinct in the larger globules, less so in the smaller. They have a sharp, well defined outline (Fig. 8); and as they refract the light strongly, and act therefore as double convex lenses, they present a brilliant centre, surrounded by a dark border. These marks will generally be sufficient to distinguish them under the microscope.

Fig. 8.



Oleaginous Principles of Human Fat. Stearine and Margarine crystallized; Oleine fluid.

The following list shows the percentage of oily matter present in various kinds of animal and vegetable food.[1]

Quantity of Fat in 100 parts in

Filberts	60.00	Ordinary meat	14.30
Walnuts	50.00	Liver of the ox	3.89
Cocoa-nuts	47.00	Cow's milk	3.13
Olives	32.00	Human milk	3.55
Linseed	22.00	Asses' milk	0.11
Indian Corn	9.00	Goats' milk	3.32
Yolk of eggs	28.00		

The oleaginous matters present a striking peculiarity as to the form under which they exist in the animal body; a peculiarity which distinguishes them from all the other proximate principles. The rest of the proximate principles are all intimately associated together by molecular union, so as to form either clear solutions or

[1] Pereira, op. cit., p. 81.

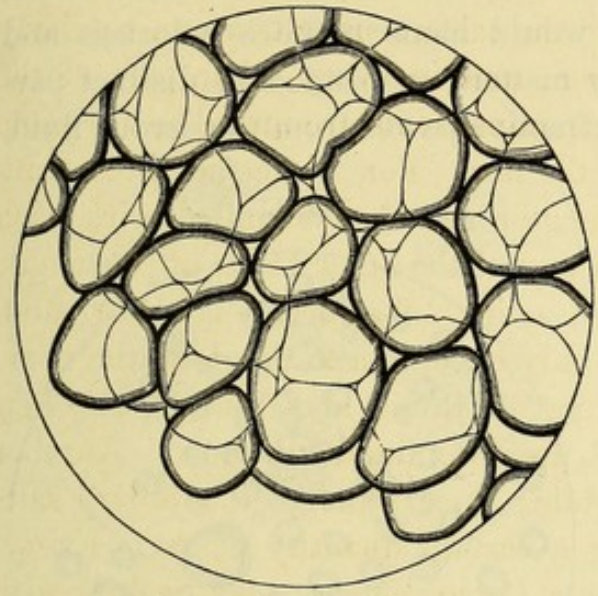
homogeneous solids. Thus, the sugars of the blood are in solution in water, in company with the albumen, the phosphate of lime, chloride of sodium, and the like; all of them equally distributed throughout the entire mass of the fluid. In the bones and cartilages, the animal matters and the calcareous salts are in similarly intimate union with each other; and in every other part of the body the animal and inorganic ingredients are united in the same way. But it is different with the fats. For, while the three principal varieties of oleaginous matter are always united with each other, they are not united with any of the other kinds of proximate principles; that is, with water, saline substances, sugars, or albuminous matters. Almost the only exception to this is in the nervous tissue; in which, according to Robin and Verdeil, the oily matters seem to be united with an albuminoid substance. Another exception is, perhaps, in the bile; since some of the biliary salts have the power of dissolving a certain quantity of fat. Everywhere else, instead of forming a homogeneous solid or fluid with the other proximate principles, the oleaginous matters are found in distinct masses or globules, which are suspended in serous fluids, interposed in the interstices between the anatomical elements, included in the interior of cells, or deposited in the substance of fibres or membranes. Even in the vegetable tissues, the oil is always deposited in this manner in distinct drops or granules.

Owing to this fact, the oils can be easily extracted from the organized tissues by the employment of simply mechanical processes. The tissues, animal or vegetable, are merely cut into small pieces and subjected to pressure, by which the oil is forced out from the parts in which it was entangled, and separated, without any further manipulation, in a state of purity. A moderately elevated temperature facilitates the operation by increasing the fluidity of the oleaginous matter; but no other chemical agency is required for its separation. Under the microscope, also, the oil-drops and granules can be readily perceived and distinguished from the remaining parts of the tissue, and can, moreover, be easily recognized by the dissolving action of ether, which acts upon them, as a general rule, without attacking the other proximate principles.

Oils are found, in the animal body, most abundantly in the adipose tissue. Here they are contained in the interior of the adipose vesicles, the cavities of which they entirely fill, in a state

of health. These vesicles are transparent, and have a somewhat angular form, owing to their mutual compression. (Fig. 9.) They vary in diameter, in the human subject, from $\frac{1}{300}$ to $\frac{1}{200}$ of an inch, and are composed of a thin, structureless animal membrane, forming a closed sac, in the interior of which the oily matter is contained. There is here, accordingly, no union whatever of the oil with the other proximate principles, but only a mechanical inclusion of it in the interior of the vesicles. Sometimes, when emaciation is going on, the oil partially disappears from the cavity of the adipose vesicle, and its place is taken by a watery serum; but the serous and oily fluids always remain distinct, and occupy different parts of the cavity of the vesicle.

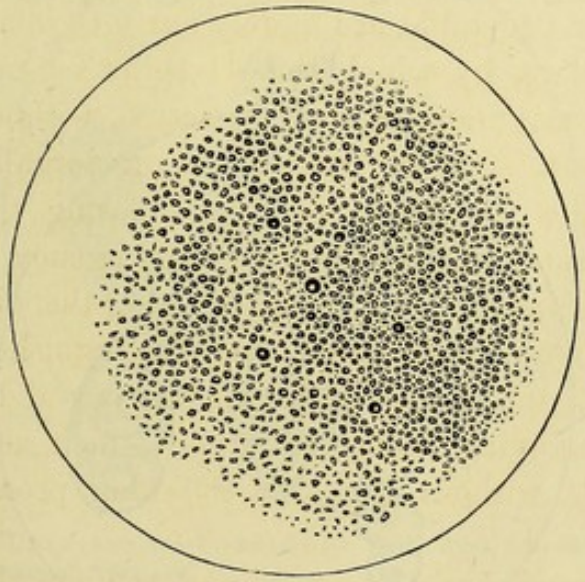
Fig. 9.



Human Adipose Tissue.

In the chyle, the oleaginous matter is in a state of *emulsion* or suspension in the form of minute particles in a serous fluid. Its subdivision is here more complete, and its molecules more minute, than anywhere else in the body. It presents the appearance of a fine granular dust, which has been known by the name of the "molecular base of the chyle." A few of these granules are to be seen which measure $\frac{1}{1000}$ of an inch in diameter; but they are generally much less than this, and the greater part are so small that they cannot be accurately measured. (Fig. 10.) For the same reason they do not present the brilliant centre and dark border of the larger oil-globules; but appear

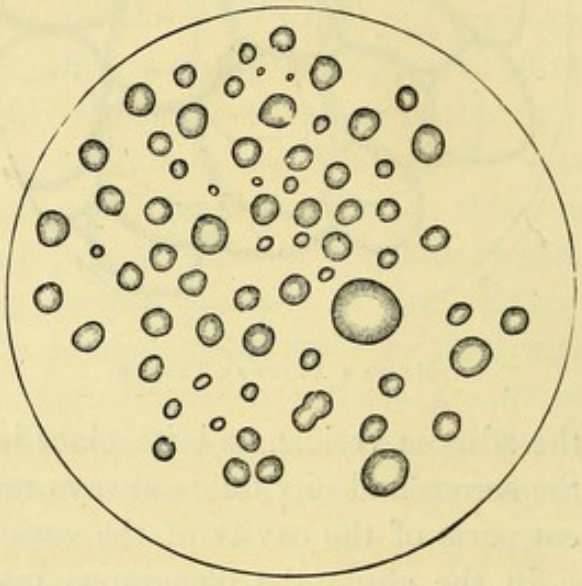
Fig. 10.



Chyle, from commencement of Thoracic Duct, from the Dog.

by transmitted light only as minute dark granules. The white color and opacity of the chyle, as of all other fatty emulsions, depend upon this molecular condition of the oily ingredients. The albumen, salts, &c., which are in intimate union with each other, and in solution in the water, would alone make a colorless and transparent fluid; but the oily matters, suspended in distinct particles, which have a different refractive power from the serous fluid, interfere with its transparency and give it the white color and opaque appearance which are characteristic of emulsions. The oleaginous nature of these particles is readily shown by their solubility in ether.

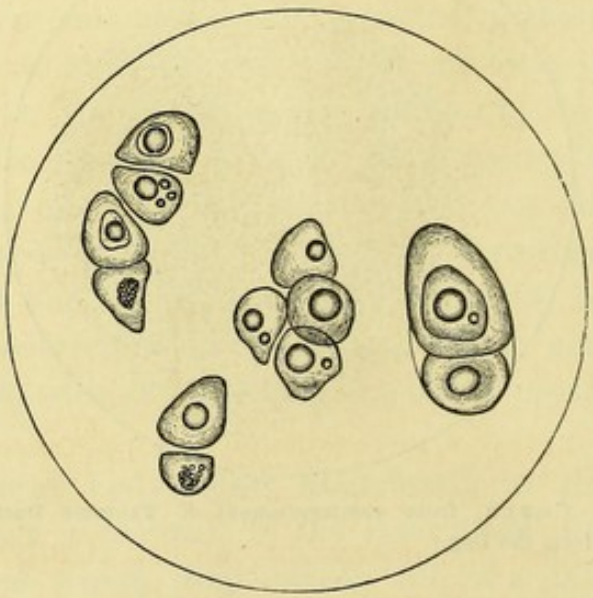
Fig. 11.



Globules of Cow's Milk.

In the milk, the oily matter occurs in larger masses than in the chyle. In cow's milk (Fig. 11), these oil-drops, or "milk-globules," are not quite fluid, but have a pasty consistency, owing to the large quantity of margarine which they contain, in proportion to the oleine. When forcibly amalgamated with each other and collected into a mass by prolonged beating or churning, they constitute butter. In cow's milk, the globules vary somewhat in size, but their average diameter is $\frac{1}{4000}$ of an inch. They are simply suspended in the serous fluid of the milk, and are not covered with any albuminous membrane.

Fig. 12.

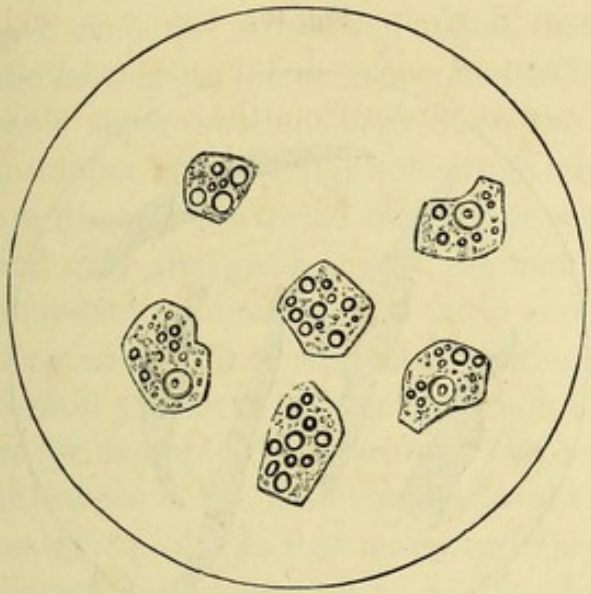


Cells of Costal Cartilages, containing Oil-Globules. Human.

In the cells of the laryngeal, tracheal, and costal cartilages (Fig. 12), there is always more or less fat deposited in the form of rounded globules, somewhat similar to those of the milk.

In the glandular cells of the liver, oil occurs constantly, in a state of health. It is here deposited in the substance of the cell (Fig.13), generally in smaller globules than the preceding. In some cases of disease, it accumulates in excessive quantity, and produces the state known as fatty degeneration of the liver. This is consequently only an exaggerated condition of that which normally exists in health.

Fig. 13.

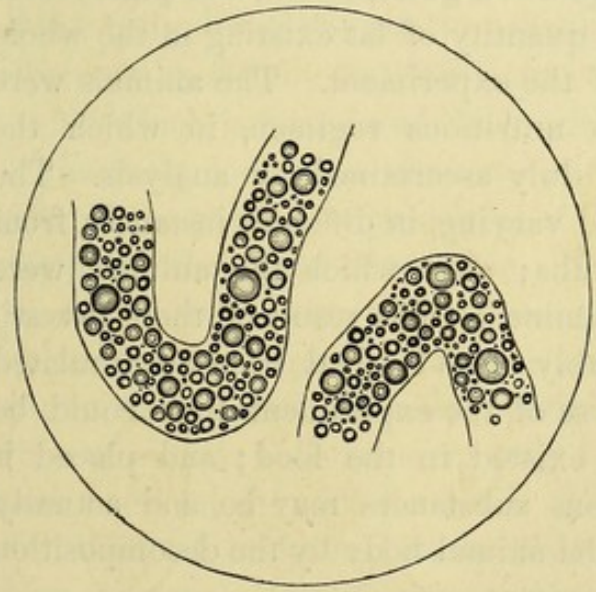


Hepatic Cells. Human.

In the carnivorous animals oil exists in considerable quantity in the convoluted portion of the uriniferous tubules. (Fig. 14.) It is here in the form of granules and rounded drops, which sometimes appear to fill nearly the whole calibre of the tubules.

It is found also in the secreting cells of the sebaceous and other glandules, deposited in the same manner as in those of the liver, but in smaller quantity. It exists, beside, in large proportion, in a granular form, in the secretion of the sebaceous glandules.

Fig. 14.



Uriniferous Tubules of Dog, from Cortical Portion of Kidney.

It occurs abundantly in the marrow of the bones, both under the form of free oil-globules and inclosed in the vesicles of adipose tissue.

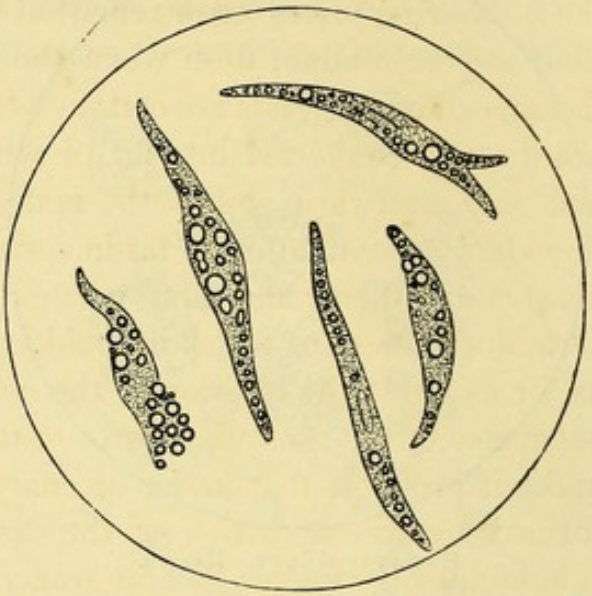
It is found in considerable quantity in the substance of the yellow wall of the corpus luteum, and is the immediate cause of the peculiar color of this body.

It occurs also in the form of granules and oil-drops in the muscular fibres of the uterus (Fig. 15), in which it begins to be

deposited soon after delivery, and where it continues to be present during the whole period of the resorption or involution of this organ.

In all these instances, the oleaginous matters remain distinct in form and situation from the other ingredients of the animal frame, and are only mechanically entangled among its fibres and cells, or imbedded separately in their interior.

Fig. 15.



Muscular Fibres of Human Uterus, three weeks after parturition.

A large part of the fat which is found in the body may be accounted for by that which is taken in with the food, since oily matter occurs in both animal and vegetable substances. Fat is, however, formed in the body, independently of what is introduced with the food. This important fact has been definitely ascertained by the experiments of MM. Dumas and Milne-Edwards on bees,[1] M. Persoz on geese,[2] and finally by those of M. Boussingault on geese, ducks, and pigs.[3] The observers first ascertained the quantity of fat existing in the whole body at the commencement of the experiment. The animals were then subjected to a definite nutritious regimen, in which the quantity of fatty matter was duly ascertained by analysis. The experiments lasted for a period varying, in different instances, from thirty-one days to eight months; after which the animals were killed and all their tissues examined. The result of these investigations showed that considerably more fat had been accumulated by the animal during the course of the experiment than could be accounted for by that which existed in the food; and placed it beyond a doubt that oleaginous substances may be, and actually are, formed in the interior of the animal body by the decomposition or metamorphosis of other proximate principles.

It is not known from what proximate principles the fat is produced, when it originates in this way in the interior of the body. Particular kinds of food certainly favor its production and accu-

[1] Annales de Chim. et de Phys., 3d series, vol. xiv. p. 400. [2] Ibid., p. 408.
[3] Chimie Agricole, Paris, 1854.

mulation to a considerable degree. It is well known, for instance, that in sugar-growing countries, as in Louisiana and the West Indies, during the few weeks occupied in gathering the cane and extracting the sugar, all the negroes employed on the plantations, and even the horses and cattle, that are allowed to feed freely on the saccharine juices, grow remarkably fat; and that they again lose their superabundant flesh when the season is past. Even in these instances, however, it is not certain whether the saccharine substances are directly converted into fat, or whether they are first assimilated and only afterward supply the materials for its production. The abundant accumulation of fat in certain regions of the body, and its absence in others; and more particularly its constant occurrence in certain situations to which it could not be transported by the blood, as for example the interior of the cells of the costal cartilages, the substance of the muscular fibres of the uterus after parturition, &c., make it probable that under ordinary conditions the oily matter is formed by decomposition of the tissues upon the very spot where it subsequently makes its appearance.

In the female during lactation a large part of the oily matter introduced with the food, or formed in the body, is discharged with the milk, and goes to the support of the infant. But in the female in the intervals of lactation, and in the male at all times, the oily matters almost entirely disappear by decomposition in the interior of the body; since the small quantity which is discharged with the sebaceous matter by the skin bears only an insignificant proportion to that which is introduced daily with the food.

The most important characteristic, in a physiological point of view, of the proximate principles of the second class, relates to their origin and their final destination. Not only are they all of a purely organic origin, making their appearance first in the interior of vegetables; but the sugars and the oils are formed also, to a certain extent, in the bodies of animals; continuing to make their appearance when no similar substances, or only an insufficient quantity of them, have been taken with the food. Furthermore, when introduced with the food, or formed in the body and deposited in the tissues, these substances do not reappear in the secretions. They, therefore, for the most part disappear by decomposition in the interior of the body. They pass through a series of changes by which their essential characters are destroyed; and they are finally replaced in the circulation by other substances, which are discharged with the excreted fluids.

CHAPTER IV.

PROXIMATE PRINCIPLES OF THE THIRD CLASS.

THE substances belonging to this class are very important, and form by far the greater part of the entire mass of the body. They are derived both from animal and vegetable sources. They have been known by the name of the "protein compounds" and the "albuminoid substances." The name *organic substances* was given to them by Robin and Verdeil, by whom their distinguishing properties were first accurately described. They have not only an organic origin, in common with the proximate principles of the second class, but their chemical constitution, their physical structure and characters, and the changes which they undergo, are all so different from those met with in any other class, that the term "organic substances" proper appears particularly appropriate to them.

Their first peculiarity is that they are not crystallizable. They always, when pure, assume an amorphous condition, which is sometimes solid (organic substance of the bones), sometimes fluid (albumen of the blood), and sometimes semi-solid in consistency, midway between the solid and fluid condition (organic substance of the muscular fibre).

Their chemical constitution differs from that of bodies of the second class, first in the fact that they all contain the four chemical elements, oxygen, hydrogen, carbon, and nitrogen; while the starches, sugars, and oils are destitute of the last named ingredient. The organic matters have therefore been sometimes known by the name of the "nitrogenous substances," while the sugars, starch, and oils have been called "non-nitrogenous." Some of the organic matters, viz., albumen, fibrin, and casein, contain sulphur also, as an ingredient; and others, viz., the coloring matters, contain iron. The remainder consist of oxygen, hydrogen, carbon, and nitrogen alone.

The most important peculiarity, however, of the organic substances, relating to their chemical composition, is that it is not definite. That is to say, they do not always contain precisely the same proportions of oxygen, hydrogen, carbon, and nitrogen; but

the relative quantities of these elements vary within certain limits, in different individuals and at different times, without modifying, in any essential degree, the peculiar properties of the animal matters which they constitute. This fact is altogether a special one, and characteristic of organic substances. No substance having a definite chemical composition, like phosphate of lime, starch, or olein, can suffer the slightest change in its ultimate constitution without being, by that fact alone, totally altered in its essential properties. If phosphate of lime, for example, were to lose one or two equivalents of oxygen, an entire destruction of the salt would necessarily result, and it would cease to be phosphate of lime. For its properties as a salt depend entirely upon its ultimate chemical constitution; and if the latter be changed in any way, the former are necessarily lost.

But the properties which distinguish the organic substances, and which make them important as ingredients of the body, do not depend immediately upon their ultimate chemical constitution, and are of a peculiar character; being such as are only manifested in the interior of the living organism. Albumen, therefore, though it may contain a few equivalents more or less of oxygen or nitrogen, does not on that account cease to be albumen, so long as it retains its fluidity and its aptitude for undergoing the processes of absorption and transformation, which characterize it as an ingredient of the living body.

It is for this reason that considerable discrepancy has existed at various times among chemists as to the real ultimate composition of these substances, different experimenters often obtaining different analytical results. This is not owing to any inaccuracy in the analyses, but to the fact that the organic substance itself really has a different ultimate constitution at different times. The most approved formulæ are those which have been established by Liebig for the following substances:—

Fibrin	$= C_{298}H_{228}N_{40}O_{92}S_2$
Albumen	$= C_{216}H_{169}N_{27}O_{68}S_2$
Casein	$= C_{288}H_{228}N_{36}O_{90}S_2$

Owing to the above mentioned variations, however, the same degree of importance does not attach to the quantitative ultimate analysis of an organic matter, as to that of other substances.

This absence of a definite chemical constitution in the organic substances is undoubtedly connected with their incapacity for crystallization. It is also connected with another almost equally peculiar fact, viz., that although the organic substances unite with acids and

with alkalies, they do not play the part of an acid towards the base, or of a base towards the acid; for the acid or alkaline reaction of the substance employed is not neutralized, but remains as strong after the combination as before. Futhermore, the union does not take place, so far as can be ascertained, in any definite proportions. The organic substances have, in fact, no combining equivalent; and their molecular reactions and the changes which they undergo in the body cannot therefore be expressed by the ordinary chemical phrases which are adapted to inorganic substances. Their true characters, as proximate principles, are accordingly to be sought for in other properties than those which depend upon their exact ultimate composition.

One of these characters is that they are *hygroscopic*. As met with in different parts of the body, they present different degrees of consistency; some being nearly solid, others more or less fluid. But on being subjected to evaporation they all lose water, and are reduced to a perfectly solid form. If after this desiccation they be exposed to the contact of moisture, they again absorb water, swell, and regain their original mass and consistency. This phenomenon is quite different from that of capillary attraction, by which some inorganic substances become moistened when exposed to the contact of water; for in the latter case the water is simply entangled mechanically in the meshes and pores of the inorganic body, while that which is absorbed by the organic matter is actually united with its substance, and diffused equally throughout its entire mass. Every organic matter is naturally united in this way with a certain quantity of water, some more and some less. Thus the albumen of the blood is in union with so much water that it has the fluid form, while the organic substance of cartilage contains less and is of a firmer consistency. The quantity of water contained in each organic substance may be diminished by artificial desiccation, or by a deficient supply; but neither of them can be made to take up more than a certain amount. Thus if the albumen of the blood and the organic substance of cartilage be both reduced by evaporation to a similar degree of dryness and then placed in water, the albumen will absorb so much as again to become fluid, but the cartilaginous substance only so much as to regain its usual nearly solid consistency. Even where the organic substance, therefore, as in the case of albumen, becomes fluid under these circumstances, it is not exactly a solution of it in water, but only a reabsorption by it of that quantity of fluid with which it is naturally associated.

Another peculiar phenomenon characteristic of organic substances is their *coagulation*. Those which are naturally fluid suddenly assume, under certain conditions, a solid or semi-solid consistency. They are then said to be coagulated; and after coagulation they cannot be made to resume their original condition. Thus fibrin coagulates on being withdrawn from the bloodvessels, albumen on being subjected to the temperature of boiling water, casein on being placed in contact with an acid. When an organic substance thus coagulates, the change which takes place is a peculiar one, and has no resemblance to the precipitation of a solid substance from a watery solution. On the contrary, the organic substance merely assumes a special condition; and in passing into the solid form it retains all the water with which it was previously united. Albumen, for example, after coagulation, retains the same quantity of water in union with it, which it held before. After coagulation, accordingly, this water may be driven off by evaporation, in the same manner as previously; and on being again exposed to moisture, the organic matter will again absorb the same quantity, though it will not resume the fluid form.

By coagulation, an organic substance is permanently altered; and though it may be afterwards dissolved by certain chemical re-agents, as, for example, the caustic alkalies, it is not thereby restored to its original condition, but only suffers a still further alteration.

In many instances we are obliged to resort to coagulation in order to separate an organic substance from the other proximate principles with which it is associated. This is the case, for example, with the fibrin of the blood, which is obtained in the form of flocculi, by beating freshly-drawn blood with a bundle of rods. But when separated in this way, it is already in an unnatural condition, and no longer represents exactly the original fluid fibrin, as it existed in the circulating blood. Nevertheless, this is the only mode in which it can be examined, as there are no means of bringing it back to its previous condition.

Another important property of the organic substances is that they readily excite, in other proximate principles and in each other, those peculiar indirect chemical changes which are termed *catalyses* or *catalytic transformations*. That is to say, they produce the changes referred to, not directly, by combining with the substance which suffers alteration, or with any of its ingredients; but simply by their presence which induces the chemical change in an indirect manner. Thus, the organic substances of the intestinal fluids induce a cata-

lytic action by which starch is converted into sugar. The albumen of the blood, by contact with the organic substance of the muscular fibre, is transformed into a substance similar to it. The entire process of nutrition, so far as the organic matters are concerned, consists of such catalytic transformations. Many crystallizable substances, which when pure remain unaltered in the air, become changed if mingled with organic substances, even in small quantity. Thus the casein of milk, after being exposed for a short time to a warm atmosphere, becomes a catalytic body, and converts the sugar of the milk into lactic acid. In this change there is no loss nor addition of any chemical element, since lactic acid has precisely the same ultimate composition with sugar of milk. It is simply a transformation induced by the presence of the casein. Oily matters, which are entirely unalterable when pure, readily become rancid at warm temperatures, if mingled with an organic impurity.

Fourthly, The organic substances, when beginning to undergo decay, induce in certain other substances the phenomena of *fermentation.* Thus, the mucus of the urinary bladder, after a short exposure to the atmosphere, causes the urea of the urine to be converted into carbonate of ammonia, with the development of gaseous bubbles. The organic matters of grape juice, under similar circumstances, give rise to fermentation of the sugar, by which it is converted into alcohol and carbonic acid.

Fifthly, The organic substances are the only ones capable of undergoing the process of *putrefaction.* This process is a complicated one, and is characterized by a gradual liquefaction of the animal substance, by many mutual decompositions of the saline matters which are associated with it, and by the development of peculiarly fetid and unwholesome gases, among which are carbonic acid, nitrogen, sulphuretted, phosphoretted, and carburetted hydrogen, and ammoniacal vapors. Putrefaction takes place constantly after death, if the organic tissue be exposed to a moist atmosphere at a moderately warm temperature. It is much hastened by the presence of other organic substances, in which decomposition has already commenced.

The organic substances are readily distinguished, by the above general characters, from all other kinds of proximate principles. They are quite numerous; nearly every animal fluid and tissue containing at least one which is peculiar to itself. They have not as yet been all accurately described. The following list, however, comprises the most important of them, and those with which we are

at present most thoroughly acquainted. The first seven are fluid, or nearly so, and either colorless or of a faint yellowish tinge.

1. FIBRIN.—Fibrin is found in the blood; where it exists, in the human subject, in the proportion of two to three parts per thousand. It is fluid, and mingled intimately with the other ingredients of the blood. It occurs also, but in much smaller quantity, in the lymph. It is distinguished by what is called its "spontaneous" coagulation; that is, it coagulates on being withdrawn from the vessels, or on the occurrence of any stoppage to the circulation. It is rather more abundant in the blood of some of the lower animals than in that of th human subject. In general, it is found in larger quantity in the blood of the herbivora than in that of the carnivora.

2. ALBUMEN.—Albumen occurs in the blood, the lymph, the fluid of the pericardium, and in that of the serous cavities generally. It is also present in the fluid which may be extracted by pressure from the muscular tissue. In the blood it occurs in the proportion of about seventy-five parts per thousand. The white of egg, which usually goes by the same name, is not identical with the albumen of the blood, though it resembles it in some respects; it is properly a secretion from the mucous membrane of the fowl's oviduct, and should be considered as a distinct organic substance. Albumen coagulates on being raised to the temperature of 160° F.; and the coagulum, like that of all the other proximate principles, is soluble in caustic potassa. It coagulates also by contact with alcohol, the mineral acids, ferrocyanide of potassium in an acidulated solution, tannin, and the metallic salts. The alcoholic coagulum, if separated from the alcohol by washing, does not redissolve in water. A very small quantity of albumen has been sometimes found in the saliva.

3. CASEIN.—This substance exists in milk, in the proportion of about forty parts per thousand. It coagulates by contact with all the acids, mineral and organic; but is not affected by a boiling temperature. It is coagulated also by the juices of the stomach. It is important as an article of food, being the principal organic ingredient in all the preparations of milk. In a coagulated form, it constitutes the different varieties of cheese, which are more or less highly flavored with various oily matters remaining entangled in the coagulated casein.

What is called vegetable casein or "legumine," is different from the casein of milk, and constitutes the organic substance present in various kinds of peas and beans.

4. GLOBULINE.—This is the organic substance forming the principal mass of the red globules of the blood. It is nearly fluid in its natural condition, and readily dissolves in water. It does not dissolve, however, in the serum of the blood; and the globules, therefore, retain their natural form and consistency, unless the serum be diluted with an excess of water. Globuline resembles albumen in coagulating by the action of heat. It differs from it, however, in the degree of temperature necessary to coagulation. For while a tolerably abundant solution of albumen is solidified at 160° F., a solution of globuline only becomes turbid at 180°, and requires for its complete coagulation a temperature of 200°.

5. PEPSINE.—This substance occurs as an ingredient in the gastric juice. It is not the same substance which Schwann extracted by maceration from the mucous membrane of the stomach, and which is regarded by Robin, Bernard, &c., as only an artificial product of the alteration of the gastric tissues. There seems no good reason, furthermore, why we should not designate by this name the organic substance which really exists in the gastric juice. It occurs in this fluid in very small quantity, not over fifteen parts per thousand. It is coagulable by heat, and also by contact with alcohol. But if the alcoholic coagulum be well washed, it is again soluble in a watery acidulated fluid.

6. PANCREATINE.—This is the organic substance of the pancreatic juice, where it occurs in great abundance. It coagulates by heat, and by contact with sulphate of magnesia in excess. In its natural condition it is fluid, but varies somewhat in its degree of fluidity.

7. MUSCOSINE is the organic substance which is found in the different varieties of mucus, and which imparts to them their consistency and other physical characters. The distinguishing character of mucosine is its viscidity, by which it is at the same time glutinous and lubricating to the touch. It has the power of absorbing water to some extent, and becomes thinner and more fluid in proportion to the quantity of water which unites with it. It does not solidify by heat, but is coagulated by acetic acid and by the contact of alcohol.

Some of the mucous secretions are so mixed with other fluids that their consistency is more or less diminished; others, which remain pure, like that of the mucous follicles of the cervix uteri, are nearly semi-solid. No doubt there are different varieties of mucosine produced by the mucous membranes of different regions of the body; but little is known with regard to their specific characters.

The next three organic substances are solid or semi-solid in consistency.

8. OSTEINE is the organic substance of the bones, in which it is associated with a large proportion of phosphate of lime. It exists, in those bones which have been examined, in the proportion of about two hundred parts per thousand. It is this substance which by long boiling of the bones is transformed into gelatine or glue. In its natural condition, however, it is insoluble in water, even at the boiling temperature, and becomes soluble only after it has been permanently altered by ebullition.

9. CARTILAGINE.—This forms the organic ingredient of cartilage. Like that of the bones, it is altered by long boiling, and is converted into a peculiar kind of gelatine termed "chondrine." Chondrine differs from the gelatine of bones principally in being precipitated by acids and certain metallic salts which have no effect on the latter. Cartilagine, in its natural condition, is very solid, and is closely united with the calcareous salts.

10. MUSCULINE.—This substance forms the principal mass of the muscular fibre. It is semi-solid, and insoluble in water, but soluble in dilute muriatic acid, from which it may be again precipitated by neutralizing with an alkali. It closely resembles albumen in its chemical composition, and like it, contains, according to Scherer, two equivalents of sulphur.

The four remaining organic substances form a somewhat peculiar group. They are the *coloring matters* of the body. They exist always in small quantity, compared with the other ingredients, but communicate to the tissues and fluids a very distinct coloration. They all contain iron as one of their ultimate elements.

11. HEMATINE is the coloring matter of the red globules of the

blood. It is nearly fluid like the globuline, and is united with it in a kind of mutual solution. It is much less abundant than the globuline, and exists in the proportion of about one part of hæmatine to seventeen parts of globuline. The following is the formula for its composition which is adopted by Lehmann:—

Hematine . . . . . $= C_{44}H_{22}N_3O_6Fe$.

When the blood-globules from any cause become disintegrated, the hæmatine is readily imbibed after death by the walls of the blood-vessels and the neighboring parts, staining them of a deep red color. This coloration has sometimes been mistaken for an evidence of arteritis; but is really a simple effect of post-mortem imbibition, as above stated.

12. Melanine.—This is the blackish-brown coloring matter which is found in the choroid coat of the eye, the iris, the hair, and more or less abundantly in the epidermis. So far as can be ascertained, the coloring matter is the same in all these situations. It is very abundant in the black and brown races, less so in the yellow and white, but is present to a certain extent in all. Even where the tinges produced are entirely different, as, for example, in brown and blue eyes, the coloring matter appears to be the same in character, and to vary only in its quantity and the mode of its arrangement; for the tinge of an animal tissue does not depend on its local pigment only, but also on the muscular fibres, fibres of areolar tissue, capillary bloodvessels, &c. All these ingredients of the tissue are partially transparent, and by their mutual interlacement and superposition modify more or less the effect of the pigment which is deposited below or among them.

Melanine is insoluble in water and the dilute acids, but dissolves slowly in caustic potassa. Its ultimate composition resembles that of hæmatine, but the proportion of iron is smaller.

13. Biliverdine is the coloring matter of the bile. It is yellow by transmitted light, greenish by reflected light. On exposure to the air in its natural fluid condition, it absorbs oxygen and assumes a bright grass-green color. The same effect is produced by treating it with nitric acid or other oxidizing substances. It occurs in very small quantity in the bile, from which it may be extracted by precipitating it with milk of lime (Robin), from which it is afterward separated by dissolving out the lime with muriatic acid. Obtained in this form, however, it is insoluble in water, having been coagulated by contact with the calcareous matter; and is not, therefore, precisely in its original condition.

14. UROSACINE is the yellow coloring matter of the urine. It consists of the same ultimate elements as the other coloring matters, but occurs in the urine in such minute quantity, that the relative proportion of its elements has never been determined. According to Dr. Thudichum,[1] it is easily soluble in water, less so in ether, and still less in alcohol; — and by some simple change in its composition, probably by oxidation, its yellow color passes into a red. It readily adheres to insoluble matters when they are precipitated from the urine, and is consequently found almost always, to a greater or less extent, as an ingredient in urinary calculi formed of the urates or of uric acid. When the urates are thrown down also in the form of a powder, as a urinary deposit, they are usually colored more or less deeply, owing to the red or yellowish red urosacine which is precipitated with them.

The organic substances which exist in the body require for their production an abundant supply of similar substances in the food. All highly nutritious articles of diet, therefore, contain more or less of these substances. Still, though nitrogenous matters must be abundantly supplied, under some form, from without, yet the particular kinds of organic substances, characteristic of the tissues, are formed in the body by a transformation of those which are introduced with the food. The organic matters derived from vegetables, though similar in their general characters to those existing in the animal body, are yet specifically different. The gluten of wheat, the legumine of peas and beans, are not the same with animal albumen and fibrin. The only organic substances taken with animal food, as a general rule, are the albumen of eggs, the casein of milk, and the musculine of flesh; and even these, in the food of the human species, are so altered and coagulated by the process of cooking, as to lose their specific characters before being introduced into the alimentary canal. They are still further changed by the process of digestion, and are absorbed under another form into the blood. But from their subsequent metamorphoses there are formed, in the different parts of the body, osteine, cartilagine, hæmatine, globuline, and all the other varieties of organic matter that characterize the different tissues. These varieties, therefore, originate as such in the animal economy by the catalytic changes which the ingredients of the blood undergo in nutrition.

[1] British Medical Journal, Nov. 5th, 1864.

Only a very small quantity of organic matter is discharged with the excretions. The coloring matters of the bile and urine, and the mucus of the urinary bladder, are almost the only ones that find an exit from the body in this way. There is a minute quantity of organic matter exhaled in a volatile form with the breath, and a little also, in all probability, from the cutaneous surface. But the entire quantity so discharged bears but a very small proportion to that which is daily introduced with the food. The organic substances, therefore, are decomposed in the interior of the body. They are transformed by the process of destructive assimilation, and their elements are finally eliminated and discharged under other forms of combination.

CHAPTER V.

OF FOOD.

UNDER the term "food" are included all those substances, solid and liquid, which are necessary to sustain the process of nutrition. The first act of this process is the absorption from without of all those materials which enter into the composition of the living frame, or of others which may be converted into them in the interior of the body.

The proximate principles of the first class, or the "inorganic substances," require to be supplied in sufficient quantity to keep up the natural proportion in which they exist in the various solids and fluids. As we have found it to be characteristic of these substances, except in a few instances, that they suffer no alteration in the interior of the body, but, on the contrary, are absorbed, deposited in its tissue, and pass out of it afterward unchanged, nearly every one of them requires to be present under its own proper form, and in sufficient quantity in the food. The alkaline carbonates, which are formed, as we have seen, by a decomposition of the malates, citrates and tartrates, constitute almost the only exception to this rule.

Since water enters so largely into the composition of nearly every part of the body, it is equally important as an ingredient of the food. In the case of the human subject, it is probably the *most* important substance to be supplied with constancy and regularity, and the system suffers more rapidly when entirely deprived of fluids, than when the supply of solid food only is withdrawn. A man may pass eight or ten hours, for example, without solid food, and suffer little or no inconvenience; but if deprived of water for the same length of time, he becomes rapidly exhausted, and feels the deficiency in a very marked degree. Magendie found, in his experiments on dogs subjected to inanition,[1] that if the animals

[1] Comptes Rendus, vol. xiii. p. 256.

were supplied with water alone they lived six, eight, and even ten days longer than if they were deprived at the same time of both solid and liquid food. Chloride of sodium, also, is usually added to the food in considerable quantity, and requires to be supplied with tolerable regularity; but the remaining inorganic materials, such as calcareous salts, the alkaline phosphates, &c., occur naturally in sufficient quantity in most of the articles which are used as food.

The proximate principles of the second class, so far as they constitute ingredients of the food, are naturally divided into two groups: 1st, the sugar, and 2d, the oily matters. Since starch is always converted into sugar in the process of digestion, it may be included, as an alimentary substance, in the same group with the sugars. There is a natural desire in the human species for both saccharine and oleaginous food. In the purely carnivorous animals, however, though no starch or sugar be taken, yet the body is maintained in a healthy condition. It has been supposed, therefore, that saccharine matters could not be absolutely necessary as food; the more so since it has been found, by the experiments of Cl. Bernard, that, in carnivorous animals kept exclusively on a diet of flesh, sugar is still formed in the liver, as well as in the mammary gland. The above conclusion, however, which has been drawn from these facts, does not apply practically to the human species. The carnivorous animals have no desire for vegetable food, while in the human species there is a natural craving for it, which is almost universal. It may be dispensed with for a few days, but not with impunity for any great length of time. The experiment has often enough been tried, in the treatment of diabetes, of confining the patient to a strictly animal diet. It has been invariably found that, if this regimen be continued for some weeks, the desire for vegetable food on the part of the patient becomes so imperative that the plan of treatment is unavoidably abandoned.

A similar question has also arisen with regard to the oleaginous matters. Are these substances indispensable as ingredients of the food, or may they be replaced by other proximate principles, such as starch or sugar? It has already been seen, from the experiments of Boussingault and others, that a certain amount of fat is produced in the body over and above that which is taken with the food; and it appears also that a regimen abounding in saccharine substances is favorable to the production of fat. It is altogether probable, therefore, that the materials for the production of fat may be

derived, under these circumstances, either directly or indirectly from saccharine matters. But saccharine matters alone are not entirely sufficient. M. Huber[1] thought he had demonstrated that bees fed on pure sugar would produce enough wax to show that the sugar could supply all that was necessary to the formation of the fatty matter of the wax. Dumas and Milne-Edwards, however, in repeating Huber's experiments,[2] found that this was not the case. Bees, fed on pure sugar, soon cease to work, and sometimes perish in considerable numbers; but if fed with honey, which contains some waxy and other matters beside the sugar, they thrive upon it; and produce, in a given time, a much larger quantity of fat than was contained in the whole supply of food.

The same thing was established by Boussingault with regard to starchy matters. He found that in fattening pigs, though the quantity of fat accumulated by the animal considerably exceeded that contained in the food, yet fat must enter to some extent into the composition of the food in order to maintain the animals in a good condition; for pigs, fed on boiled potatoes alone (an article abounding in starch but nearly destitute of oily matter), fattened slowly and with great difficulty; while those fed on potatoes mixed with a greasy fluid fattened readily, and accumulated, as mentioned above, much more fat than was contained in the food.

The apparent discrepancy between these facts may be easily explained, when we recollect that, in order that the animal may become fattened, it is necessary that he be supplied not only with the materials of the fat itself, but also with everything else which is necessary to maintain the body in a healthy condition. Oleaginous matter is one of these necessary substances. The fats which are taken in with the food are not destined to be simply transported into the body and deposited there unchanged. On the contrary, they are altered and used up in the processes of digestion and nutrition; while the fats which appear in the body as constituents of the tissues are, in great part, of new formation, and are produced from materials derived, perhaps, from a variety of sources.

It is certain, then, that either one or the other of these two groups of substances, saccharine or oleaginous, must enter into the composition of the food; and furthermore, that, though the oily matters may sometimes be produced in the body from the sugars,

[1] Natural History of Bees, Edinburgh, 1821, p. 330.

[2] Annales de Chim. et de Phys., 3d series, vol. xiv. p. 400.

it is also necessary for the perfect nutrition of the body that fat be supplied, under its own form, with the food. For the human species, also, it is natural to have them both associated in the alimentary materials. They occur together in most vegetable substances, and there is a natural desire for them both, as elements of the food.

They are not, however, when alone, or even associated with each other, sufficient for the nutrition of the animal body. Magendie found that dogs, fed exclusively on starch or sugar, perished after a short time with symptoms of profound disturbance of the nutritive functions. An exclusive diet of butter or lard had a similar effect. The animal became exceedingly debilitated, though without much emaciation; and after death, all the internal organs and tissues were found infiltrated with oil. Boussingault[1] performed a similar experiment, with a like result, upon a duck, which was kept upon an exclusive regimen of butter. "The duck received 1350 to 1500 grains of butter every day. At the end of three weeks it died of *inanition*. The butter oozed from every part of its body. The feathers looked as though they had been steeped in melted butter, and the body exhaled an unwholesome odor like that of butyric acid."

Lehmann was also led to the same result by some experiments which he performed upon himself for the purpose of ascertaining the effect produced on the urine by different kinds of food.[2] This observer confined himself first to a purely animal diet for three weeks, and afterwards to a purely vegetable one for sixteen days, without suffering any marked inconvenience. He then put himself upon a regimen consisting entirely of non-nitrogenous substances, starch, sugar, gum, and oil, but was only able to continue this diet for two, or at most for three days, owing to the marked disturbance of the general health which rapidly supervened. The unpleasant symptoms, however, immediately disappeared on his return to an ordinary mixed diet. The same fact has been established more recently by Prof. Wm. A. Hammond,[3] in a series of experiments which he performed upon himself. He was enabled to live for ten days on a diet composed exclusively of boiled starch and water. After the third day, however, the general health began

[1] Chimie Agricole, p. 166.

[2] Journal für praktische Chemie, vol. xxvii. p. 257.

[3] Experimental Researches, &c., being the Prize Essay of the American Medical Association for 1857.

to deteriorate, and became very much disturbed before the termination of the experiment. The prominent symptoms were debility, headache, pyrosis, and palpitation of the heart. After the starchy diet was abandoned, it required some days to restore the health to its usual condition.

The proximate principles of the third class, or the organic substances proper, enter so largely into the constitution of the animal tissues and fluids, that their importance, as elements of the food, is easily understood. No food can be long nutritious, unless a certain proportion of these substances be present in it. Since they are so abundant as ingredients of the body, their loss or absence from the food is felt more speedily and promptly than that of any other substance except water. They have, therefore, sometimes received the name of "nutritious substances," in contradistinction to those of the second class, which contain no nitrogen, and which have been found by the experiments of Magendie and others to be insufficient for the support of life. The organic substances, however, when taken alone, are no more capable of supporting life indefinitely than the others. It was found in the experiments of the French "Gelatine Commission"[1] that animals fed on pure fibrin and albumen, as well as those fed on gelatine, become, after a short time, much enfeebled, refuse the food which is offered to them, or take it with reluctance, and finally die of inanition. This result has been explained by supposing that these substances, when taken alone, excite after a time such disgust in the animal that they are either no longer taken, or if taken are not digested. But this disgust itself is simply an indication that the substances used are insufficient and finally useless as articles of food, and that the system demands instinctively other materials for its nourishment.

The instinctive desire of animals for certain substances is the surest indication that they are in reality required for the nutritive process; and on the other hand, the indifference or repugnance manifested for injurious or useless substances, is an equal evidence of their unfitness as articles of food. This repugnance is well described by Magendie, in the report of the commission above alluded to, while detailing the result of his investigations on the nutritive qualities of gelatine. "The result," he says, "of these first trials was that pure gelatine was not to the taste of the dogs experimented on. Some of them suffered the pangs of hunger with the gelatine

[1] Comptes Rendus, 1841, vol. xiii. p. 2°7.

within their reach, and would not touch it; others tasted of it, but would not eat; others still devoured a certain quantity of it once or twice, and then obstinately refused to make any further use of it."

In one instance, however, Magendie succeeded in inducing a dog to take a considerable quantity of pure fibrin daily throughout the whole course of the experiment; but notwithstanding this, the animal became emaciated like the others, and died at last with the same symptoms of inanition.

The alimentary substances of the second class, however, viz., the sugars and the oils, have been sometimes thought less important than the albuminous matters, because they do not enter so largely or so permanently into the composition of the solid tissues. The saccharine matters, when taken as food, cannot be traced farther than the blood. They undergo already, in the circulating fluid, some change by which their essential character is lost, and they cannot be any longer recognized. The appearance of sugar in the mammary gland and the milk is only exceptional, and does not occur at all in the male subject. The fats are, it is true, very generally distributed throughout the body, but it is only in the brain and nervous matter that they exist intimately united with the remaining ingredients of the tissues. Elsewhere, as already mentioned, they are deposited in distinct drops and granules, and so long as they remain in this condition must of course be inactive, so far as regards any chemical nutritive process. In this condition they seem to be held in reserve, ready to be absorbed by the blood, whenever they may be required for the purposes of nutrition. On being reabsorbed, however, as soon as they again enter the blood or unite intimately with the substance of the tissues, they at once change their condition and lose their former chemical constitution and properties.

It is for these reasons that the albuminoid matters have been sometimes considered as the only "nutritious" substances, because they alone constitute under their own form a great part of the ingredients of the tissues, while the sugars and the oils rapidly disappear by decomposition. It has even been assumed that the process by which the sugar and the oils disappear is one of direct combustion or oxidation, and that they are destined solely to be consumed in this way, not to enter at all into the composition of the tissues but only to maintain the heat of the body by an incessant process of combustion in the blood. They have been therefore termed the "combustible" or "heat-producing" elements, while the

albuminoid substances were known as the nutritious or "plastic" elements.

This distinction, however, has no real foundation. In the first place, it is not at all certain that the sugars and the oils which disappear in the body are destroyed by combustion. This is merely an inference which has been made without any direct proof. All we know positively in regard to the matter is that these substances soon become so altered in the blood that they can no longer be recognized by their ordinary chemical properties; but we are still ignorant of the exact nature of the transformations which they undergo. Furthermore, the difference between the sugars and the oils on the one hand, and the albuminoid substances on the other, so far as regards their decomposition and disappearance in the body, is only a difference in time. The albuminoid substances become transformed more slowly, the sugars and the oils more rapidly. Even if it should be ascertained hereafter that the sugars and the oils really do not unite at all with the solid tissues, but are entirely decomposed in the blood, this would not make them any less important as alimentary substances, since the blood is as essential a part of the body as the solid tissues, and its nutrition must be provided for equally with theirs.

It is evident, therefore, that no single proximate principle, nor even any one class of them alone, can be sufficient for the nutrition of the body; but that the food, to be nourishing, must contain substances belonging to *all* the different groups of proximate principles. The albuminoid substances are first in importance because they constitute the largest part of the entire mass of the body; and exhaustion therefore follows more rapidly when they are withheld than when the animal is deprived of other kinds of alimentary matter. But starchy and oleaginous substances are also requisite; and the body feels the want of them sooner or later, though it may be plentifully supplied with albumen and fibrin. Finally, the inorganic saline matters, though in smaller quantity, are also necessary to the continuous maintenance of life. In order that the animal tissues and fluids remain in a healthy condition and take their proper part in the functions of life, they must be supplied with all the ingredients necessary to their constitution; and a man may be starved to death at last by depriving him of chloride of sodium or phosphate of lime just as surely, though not so rapidly, as if he were deprived of albumen or oil.

In the different kinds of food, accordingly, which have been

adopted by the universal and instinctive choice of man, the three different classes of proximate principles are all more or less abundantly represented. In all of them there exists naturally a certain proportion of saline substances; and water and chloride of sodium are generally taken with them in addition. In milk, the first food supplied to the infant, we have casein which is an albuminoid substance, butter which represents the oily matters, and sugar of milk belonging to the saccharine group, together with water and saline matters, in the following proportions:—[1]

Composition of Cow's Milk.

Water		87.02
Casein		4.48
Butter		3.13
Sugar of milk		4.77
Soda	0.60	
Chlorides of potassium and sodium		
Phosphates of soda and potassa		
Phosphate of lime		
" magnesia		
Alkaline carbonates		
Iron, &c.		
		100.00

The cereal grains contain albuminoid matters, starch, gum, fat, and salts. The mineral ingredients comprise, according to Payen[2] and others, the phosphates of lime and magnesia, sulphate of potassa, traces of the chlorides of sodium and potassium, together with sulphur and silica.

In wheat flour, gluten is the albuminoid matter, sugar and starch the non-nitrogenous principles.

Composition of Wheat Flour.

Gluten	7.30	Gum	3.30
Starch	72.00	Water	12.00
Sugar	5.40		
			100.00

The other cereal grains mostly contain oil in addition to the above.

[1] The accompanying analyses of various kinds of food are taken from Pereira on Food and Diet, New York, 1843.

[2] Précis des substances alimentaires. Paris, 1865, p. 265.

Composition of Dried Oatmeal.

Starch	59.00
Bitter matter and sugar	8.25
Gray albuminous matter	4.30
Fatty oil	2.00
Gum	2.50
Husk, mixture, and loss	23.95
	100.00

Eggs contain albumen and salts in the white, with the addition of oily matter in the yolk.

Composition of Eggs.

	White of Egg.	Yolk of Egg.
Water	80.00	53.78
Albumen and mucus	15.28	12.75
Yellow oil	...	28.75
Salts	4.72	4.72
	100.00	100.00

In ordinary flesh or butcher's meat, we have the albuminoid matter of the muscular fibre and the fat of the adipose tissue.

Composition of Ordinary Butcher's Meat.

Meat devoid of fat	85.70	Water	63.42
		Solid matter	22.28
Fat, cellular tissue, &c.			14.30
			100.00

From what has been said above, it will easily be seen that the nutritious character of any substance, or its value as an article of food, does not depend simply upon its containing either one of the alimentary substances mentioned above in large quantity; but upon its containing them mingled together in such proportion as is requisite for the healthy nutrition of the body. What these proportions are cannot be determined from simple chemical analysis, nor from any other data than those derived from direct observation and experiment.

The total quantity of food required by man has been variously estimated. It will necessarily vary, indeed, not only with the constitution and habits of the individual, but also with the quality of the food employed; since some articles, such as corn and meat, contain very much more alimentary material in the same bulk than fresh fruits or vegetables. Any estimate, therefore, of the total quantity should state also the kind of food used; otherwise it will

be altogether without value. From experiments performed while living on an exclusive diet of bread, fresh meat, and butter, with coffee and water for drink, we have found that the entire quantity of food required during twenty-four hours by a man in full health, and taking free exercise in the open air, is as follows:—

Meat	16 ounces	or 1.00 lb.	Avoirdupois.
Bread	19 "	" 1.19 "	"
Butter or fat	3½ "	" 0.22 "	"
Water	52 fluid oz.	" 3.38 "	"

That is to say, rather less than two and a half pounds of solid food, and rather over three pints of liquid food.

Another necessary consideration, in estimating the value of any substance as an article of food, is its digestibility. A vegetable or animal tissue may contain an abundance of albuminoid or starchy matter, but may be at the same time of such an unyielding consistency as to be insoluble in the digestive fluids, and therefore useless as an article of food. Bones and cartilages, and the fibres of yellow elastic tissue, are indigestible, and therefore not nutritious. The same remark may be made with regard to the substances contained in woody fibre, and the hard coverings and kernels of various fruits. Everything, accordingly, which softens or disintegrates a hard alimentary substance renders it more digestible, and so far increases its value as an article of food.

The preparation of food by cooking has a twofold object: first, to soften or disintegrate it, and second, to give it an attractive flavor. Many vegetable substances are so hard as to be entirely indigestible in a raw state. Ripe peas and beans, the different kinds of grain, and many roots and fruits, require to be softened by boiling, or some other culinary process, before they are ready for use. With them, the principal change produced by cooking is an alteration in consistency. With most kinds of animal food, however, the effect is somewhat different. In the case of muscular flesh, for example, the muscular fibres themselves are almost always more or less hardened by boiling or roasting; but, at the same time, the fibrous tissue by which they are held together is gelatinized and softened, so that the muscular fibres are more easily separated from each other, and more readily attacked by the digestive fluids. But beside this, the organic substances contained in meat, which are all of them very insipid in the raw state, acquire by the action of heat in cooking, a peculiar and agreeable flavor. This flavor excites

the appetite and stimulates the flow of the digestive fluids, and renders, in this way, the entire process of digestion more easy and expeditious.

The changes which the food undergoes in the interior of the body may be included under three different heads: first, *digestion*, or the preparation of the food in the alimentary canal; second, *assimilation*, by which the elements of the food are converted into the animal tissues; and third, *excretion*, by which they are again decomposed, and finally discharged from the body.

CHAPTER VI.

DIGESTION.

DIGESTION is that process by which the food is reduced to a form in which it can be absorbed from the intestinal canal, and taken up by the bloodvessels. This process does not occur in vegetables. For vegetables are dependent for their nutrition, mostly, if not entirely, upon a supply of inorganic substances, as water, saline matters, carbonic acid, and ammonia. These materials constitute the food upon which plants subsist, and are converted in their interior into other substances, by the nutritive process. These materials, furthermore, are constantly supplied to the vegetable under such a form as to be readily absorbed. Carbonic acid and ammonia exist in a gaseous form in the atmosphere, and are also to be found in solution, together with the requisite saline matters, in the water with which the soil is penetrated. All these substances, therefore, are at once ready for absorption, and do not require any preliminary modification. But with animals and man the case is different. They cannot subsist upon these inorganic substances alone, but require for their support materials which have already been organized, and which have previously constituted a part of animal or vegetable bodies. Their food is almost invariably solid or semi-solid at the time when it is taken, and insoluble in water. Meat, bread, fruits, vegetables, &c., are all taken into the stomach in a solid and insoluble condition; and even those substances which are naturally fluid, such as milk, albumen, white of egg, are almost always, in the human species, coagulated and solidified by the process of cooking, before being taken into the stomach.

In animals, accordingly, the food requires to undergo a process of digestion, or liquefaction, before it can be absorbed. In all cases, the general characters of this process are the same. It consists essentially in the food being received into a canal, running through the body from mouth to anus, called the "alimentary canal," in which it comes in contact with certain digestive fluids, which act

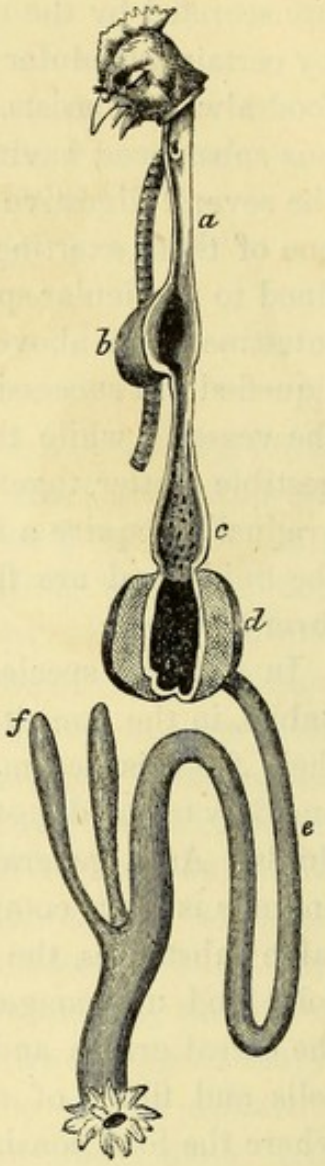
upon it in such a way as to liquefy and dissolve it. These fluids are secreted by the mucous membrane of the alimentary canal, and by certain glandular organs situated in its neighborhood. Since the food always consists, as we have already seen, of a mixture of various substances, having different physical and chemical properties, the several digestive fluids are also different from each other; each one of them exerting a peculiar action, which is more or less confined to particular species of food. As the food passes through the intestine from above downward, those parts of it which become liquefied are successively removed by absorption, and taken up by the vessels; while the remaining portions, consisting of the indigestible matter, together with the refuse of the intestinal secretions, gradually acquire a firmer consistency owing to the absorption of the fluids, and are finally discharged from the intestine under the form of feces.

In different species of animals, however, the difference in their habits, in the constitution of their tissues, and in the character of their food, is accompanied with a corresponding variation in the anatomy of the digestive apparatus, and the character of the secreted fluids. As a general rule, the digestive apparatus of herbivorous animals is more complex than that of the carnivora; since, in vegetable substances, the nutritious matters are often present in a very solid and unmanageable form, as, for example, in raw starch and the cereal grains, and are nearly always entangled among vegetable cells and fibres of an indigestible character. In those instances where the food consists mostly of herbage, as grass, leaves, &c., the digestible matters bear only a small proportion to the entire quantity; and a large mass of food must therefore be taken, in order that the requisite amount of nutritious material may be extracted from it. In such cases, accordingly, the alimentary canal is large and long; and is divided into many compartments, in which different processes of disintegration, transformation, and solution are carried on.

In the common fowl, for instance (Fig. 16), the food, which consists mostly of grains, and frequently of insects with hard, coriaceous integument, first passes down the œsophagus (*a*) into a diverticulum or pouch (*b*) termed the crop. Here it remains for a time mingled with a watery secretion in which the grains are macerated and softened. The food is then carried farther down until it reaches a second dilatation (*c*), the proventriculus, or secreting stomach. The mucous membrane here is thick and

glandular, and is provided with numerous secreting follicles or crypts. From them an acid fluid is poured out, by which the food is subjected to further changes. It next passes into the gizzard (*d*), or triturating stomach, a cavity inclosed by thick muscular walls, and lined with a remarkably tough and horny epithelium. Here it is subjected to the crushing and grinding action of the muscular parietes, assisted by grains of sand and gravel, which the animal instinctively swallows with the food, by which it is so triturated and disintegrated, that it is reduced to a uniform pulp, upon which the digestive fluids can effectually operate. The mass then passes into the intestine (*e*), where it meets with the intestinal juices, which complete the process of solution; and from the intestinal cavity it is finally absorbed in a liquid form, by the vessels of the mucous membrane.

Fig. 16.

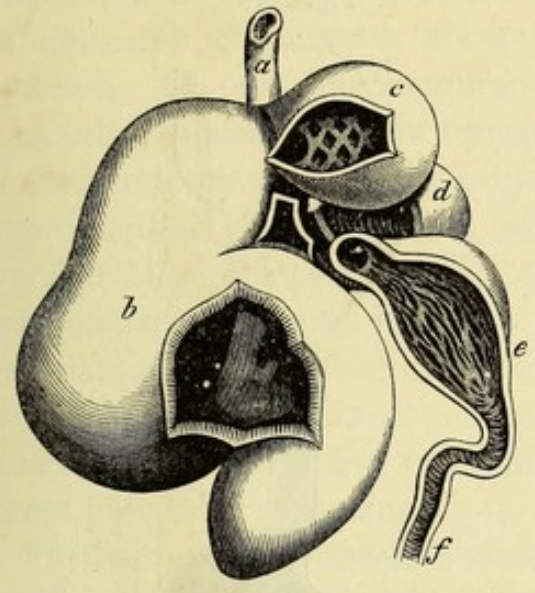


Alimentary Canal of Fowl. — *a*. Œsophagus. *b*. Crop. *c*. Proventriculus, or secreting stomach. *d*. Gizzard, or triturating stomach. *e*. Intestine. *f*. Two long cæcal tubes which open into the intestine a short distance above its termination.

In the ox, again, the sheep, the camel, the deer, and all ruminating animals, there are four distinct stomachs through which the food passes in succession; each lined with mucous membrane of a different structure, and adapted to perform a different part in the digestive process. (Fig. 17.) When first swallowed, the food is received into the *rumen*, or paunch (*b*), a large sac, itself partially divided by incomplete partitions, and lined by a mucous membrane thickly set with long prominences or villi. Here it accumulates while the animal is feeding, and is retained and macerated in its own fluids. When the animal has finished browsing, and the process of rumination commences, the food is regurgitated into the mouth by an inverted action of the muscular walls of the paunch and œsophagus, and slowly masticated. It then descends again along the œsophagus; but instead of entering the first stomach, as before, it is turned off by a muscular valve into the second stomach, or *reticulum* (*c*), which is distinguished by the intersecting folds of its mucous membrane, which give it

a honey-combed or reticulated appearance. Here the food, already triturated in the mouth, and mixed with the saliva, is further macerated in the fluids swallowed by the animal, which always accumulate in considerable quantity in the reticulum. The next cavity is the *omasus*, or "psalterium" (*d*), in which the mucous membrane is arranged in longitudinal folds, alternately broad and narrow, lying parallel with each other like the leaves of a book, so that the extent of mucous surface, brought in contact with the food, is very much increased. The exit from this cavity leads directly into the *abomasus*, or "rennet" (*e*), which is the true digestive stomach, in which the mucous membrane is softer, thicker, and more glandular than elsewhere, and in which an acid and highly solvent fluid is secreted. Then follows the intestinal canal with its various divisions and variations.

Fig. 17.



Compound Stomach of Ox.—*a*. Œsophagus. *b*. Rumen, or first stomach. *c*. Reticulum, or second. *d*. Omasus, or third. *e*. Abomasus, or fourth. *f*. Duodenum. (From Rymer Jones.)

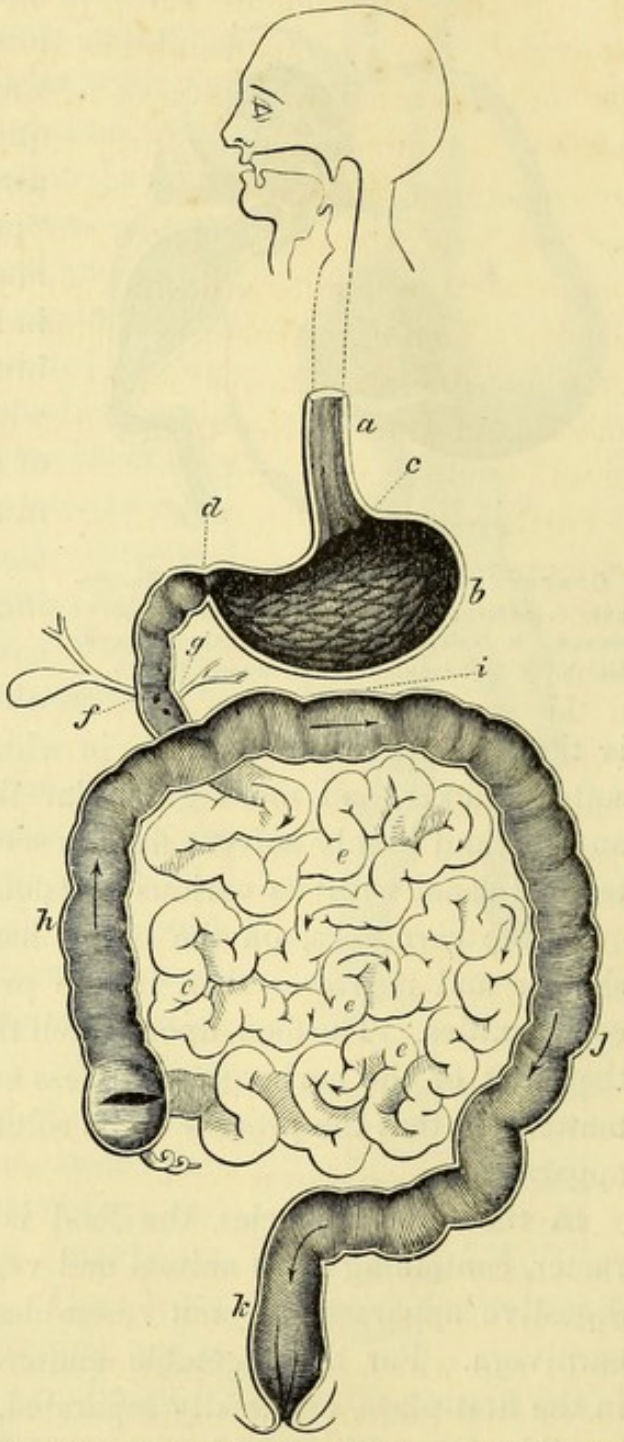
In the carnivora, on the other hand, the alimentary canal is shorter and narrower than in the preceding, and presents fewer complexities. The food, upon which these animals subsist, is softer than that of the herbivora, and less encumbered with indigestible matter; so that the process of its solution requires a less extensive apparatus.

In the human species, the food is naturally of a mixed character, containing both animal and vegetable substances. But the digestive apparatus in man resembles almost exactly that of the carnivora. For the vegetable matters which we take as food are, in the first place, artificially separated, to a great extent, from indigestible impurities; and secondly, they are so softened by the process of cooking as to become nearly or quite as digestible as animal substances.

In the human species, however, the process of digestion, though simpler than in the herbivora, is still complicated. The alimentary canal is here, also, divided into different compartments or cavities, which communicate with each other by narrow orifices. At its

commencement (Fig. 18), we find the cavity of the *mouth*, which is guarded at its posterior extremity by the muscular valve of the isthmus of the fauces. Through the pharynx and œsophagus (*a*), it communicates with the second compartment, or the *stomach* (*b*), a flask-shaped dilatation, which is guarded at the cardiac and pyloric orifices by circular bands of muscular fibres. Then comes the *small intestine* (*e*), different parts of which, owing to the varying structure of their mucous membranes, have received the different names of duodenum, jejunum, and ileum. In the duodenum we have the orifices of the *biliary* and *pancreatic* ducts (*f*, *g*). Finally, we have the *large intestine* (*h*, *i*, *j*, *k*), separated from the smaller by the ileo-cæcal valve, and terminating, at its lower extremity, by the anus, at which is situated a double sphincter, for the purpose of guarding its orifice. Everywhere the alimentary canal is composed of a mucous membrane and a muscular coat, with a layer of submucous areolar tissue between the two. The muscular coat is everywhere composed of a double layer of longitudinal and transverse fibres, by the alternate contraction and relaxation of which the food is carried through the canal from above downward. The mucous

Fig. 18.



HUMAN ALIMENTARY CANAL. — *a*. Œsophagus. *b*. Stomach. *c*. Cardiac orifice. *d*. Pylorus. *e*. Small intestine. *f*. Biliary duct. *g*. Pancreatic duct. *h*. Ascending colon. *i*. Transverse colon. *j*. Descending colon. *k*. Rectum.

membrane presents, also, a different structure, and has different properties in different parts. In the mouth and œsophagus, it is smooth, with a hard, whitish, and tessellated epithelium. This kind of epithelium terminates abruptly at the cardiac orifice of the stomach. The mucous membrane of the gastric cavity is soft and glandular, covered with a transparent, columnar epithelium, and thrown into minute folds or projections on its free surface, which are sometimes reticulated with each other. In the small intestine, we find large transverse folds of mucous membrane, the *valvulæ conniventes*, the minute villosities which cover its surface, and the peculiar glandular structures which it contains. Finally, in the large intestine, the mucous membrane is again different. It is here smooth and shining, free from villosities, and provided with a different glandular apparatus.

Furthermore, the digestive secretions, also, vary in these different regions. In its passage from above downward, the food meets with no less than five different digestive fluids. First it meets with the *saliva* in the cavity of the mouth; second, with the *gastric juice*, in the stomach; third, with the *bile;* fourth, with the *pancreatic fluid;* and fifth, with the *intestinal juice.* It is the most important characteristic of the process of digestion, as established by modern researches, that the *various elements of the food are affected in different ways by these different digestive fluids;* and as the result of their combined action, the ingredients of the alimentary mass are successively reduced to a fluid condition, and are then taken up by the vessels of the intestinal mucous membrane.

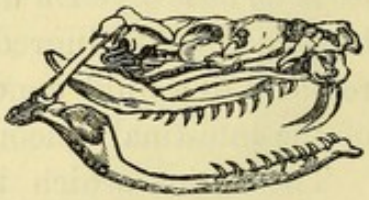
The action which is exerted upon the food by the digestive fluids is not that of a simple chemical solution. It is a transformation, by which the ingredients of the food are altered in character at the same time that they undergo the process of liquefaction. The active agent in producing this change is in every instance an organic matter, which enters as an ingredient into the digestive fluid; and which, by coming in contact with the food, exerts upon it a catalytic action, and transforms its ingredients into other substances. It is these newly formed substances which are finally absorbed by the vessels, and mingled with the general current of the circulation.

In our study of the process of digestion, the different digestive fluids will be examined separately, and their action on the alimentary substances in the different regions of the digestive apparatus successively investigated.

Mastication.—In the first division of the alimentary canal, viz., the mouth, the food undergoes simultaneously two different operations, viz., mastication and insalivation. Mastication consists in the cutting and trituration of the food by the teeth, by the action of which it is reduced to a state of minute subdivision. This process is entirely a mechanical one. It is necessary, in order to prepare the food for the subsequent action of the digestive fluids. As this action is chemical in its nature, it will be exerted more promptly and efficiently if the food be finely divided than if it be brought in contact with the digestive fluids in a solid mass. This is always the case when a solid body is subjected to the action of a solvent fluid; since, by being broken up into minute particles, it offers a larger surface to the contact of the fluid, and is more readily attacked and dissolved by it.

In the structure of the teeth, and their physiological action, there are certain marked differences, corresponding with the habits of the animal, and the kind of food upon which it subsists. In fish and serpents, in which the food is swallowed entire, and in which the process of digestion, accordingly, is comparatively slow, the teeth are simply organs of prehension. They have generally the form of sharp, curved spines, with their points set backward (Fig. 19), and arranged in a double or triple row about the edges of the jaws, and sometimes covering the mucous surfaces of the mouth, tongue, and palate. They serve merely to retain the prey, and prevent its escape, after it has been seized by the animal. In the carnivorous quadrupeds, as those of the dog and cat kind, and other similar families, there are three different kinds of teeth adapted to different mechanical purposes. (Fig. 20.) First, the incisors, twelve in number, situated at the anterior part of the jaw, six in the superior, and six in the inferior maxilla, of flattened form, and placed with their thin edges running from side to side. The incisors, as their name indicates, are adapted for dividing the food by a cutting motion, like that of a pair of shears. Behind them come the canine teeth, or tusks, one on each side of the upper and under jaw. These are long, curved, conical, and pointed; and are used as weapons of offence, and for laying hold of and retaining the prey. Lastly, the molars, eight or more in number on each side, are larger and broader than the incisors, and provided with serrated

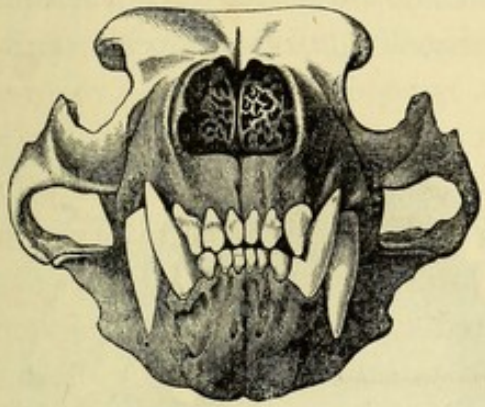
Fig. 19.



Skull of Rattlesnake. (After Achille-Richard.)

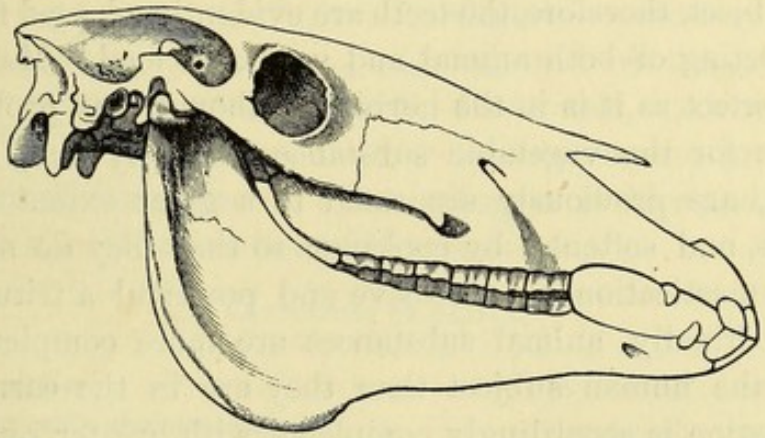
edges, each presenting several sharp points, arranged generally in a direction parallel with the line of the jaw. In these animals, mastication is very imperfect, since the food is not ground up, but only pierced and mangled by the action of the teeth before being swallowed into the stomach. In the herbivora, on the other hand, the incisors are present only in the lower jaw in the ruminating animals, though in the horse they are found in both the upper and lower maxilla. (Fig. 21.) They are used merely for cutting off the grass or herbage, on which the animal feeds. The canines are either absent or slightly developed, and the real process of mastication is

Fig. 20.



SKULL OF POLAR BEAR. Anterior view; showing incisors and canines.

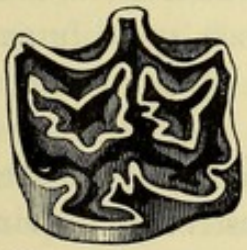
Fig. 21.



SKULL OF THE HORSE.

performed altogether by the molars. These are large and thick (Fig. 22), and present a broad, flat surface, diversified by variously folded and projecting ridges of enamel, with shallow grooves between them. By the lateral rubbing motion of the roughened surfaces against each other, the food is effectually comminuted and reduced to a pulpy mass.

Fig. 22.

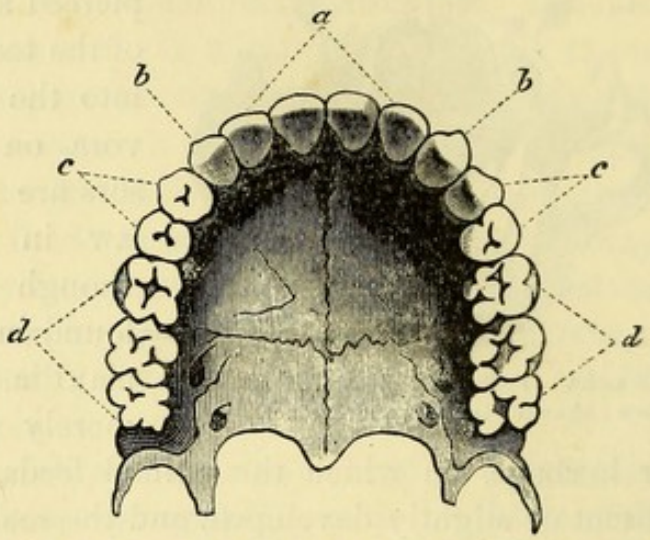


MOLAR TOOTH OF THE HORSE. Grinding surface.

In the human subject, the teeth combine the characters of those of the carnivora and the herbivora. (Fig. 23.) The incisors (*a*), four in number in each jaw, have, as in other instances, a cutting

edge running from side to side. The canines (*b*), which are situated immediately behind the former, are much less prominent and pointed than in the carnivora, and differ less in form from the incisors on the one hand, and the first molars on the other. The molars, again (*c*, *d*), are thick and strong, and have comparatively flat surfaces, like those of the herbivora; but instead of presenting curvilinear ridges, are covered with more or less conical eminences, like those of the carnivora. In the human subject, therefore, the teeth are evidently adapted for a mixed diet, consisting of both animal and vegetable food. Mastication is here as perfect as it is in the herbivora, though less prolonged and laborious; for the vegetable substances used by man, as already remarked, are previously separated to a great extent from their impurities, and softened by cooking; so that they do not require, for their mastication, so extensive and powerful a triturating apparatus. Finally, animal substances are more completely masticated in the human subject than they are in the carnivora, and their digestion is accordingly completed with greater rapidity.

Fig. 23.



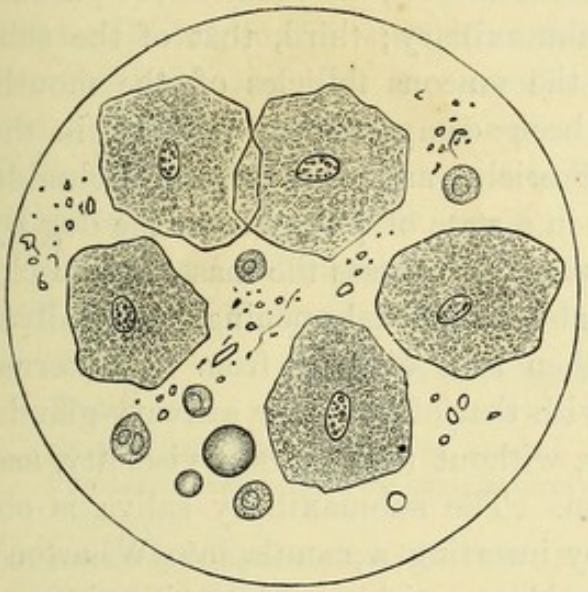
Human Teeth—Upper Jaw.—*a*. Incisors. *b*. Canines *c*. Anterior molars. *d*. Posterior molars.

We can easily estimate, from the facts above stated, the importance, to the digestive process, of a thorough preliminary mastication. If the food be hastily swallowed in undivided masses, it must remain a long time undissolved in the stomach, where it will become a source of irritation and disturbance; but if reduced beforehand, by mastication, to a state of minute subdivision, it is readily attacked by the digestive fluids, and becomes speedily and completely liquefied.

Saliva.—At the same time that the food is masticated, it is mixed in the cavity of the mouth with the first of the digestive fluids, viz., the saliva. Human saliva, as it is obtained directly from the buccal cavity, is a colorless, slightly viscid and alkaline fluid, with a

specific gravity of 1005. When first discharged, it is frothy and opaline, holding in suspension minute, whitish flocculi. On being allowed to stand for some hours in a cylindrical glass vessel, an opaque, whitish deposit collects at the bottom, while the supernatant fluid becomes clear. The deposit, when examined by the microscope (Fig. 24), is seen to consist of abundant epithelium scales from the internal surface of the mouth, detached by mechanical irritation, minute, roundish, granular, nucleated cells, apparently epithelium from the mucous follicles, a certain amount of granular matter, and a few oil-globules. The supernatant fluid has a faint bluish tinge, and becomes slightly opalescent by boiling, and by the addition of nitric acid. Alcohol in excess causes the precipitation of abundant whitish flocculi. According to Bidder and Schmidt,[1] the composition of saliva is as follows:—

Fig. 24.



Buccal and Glandular Epithelium, with Granular Matter and Oil-globules; deposited as sediment from human saliva.

Composition of Saliva.

Water	995.16
Organic matter	1.34
Sulpho-cyanide of potassium	0.06
Phosphates of soda, lime, and magnesia	.98
Chlorides of sodium and potassium	.84
Mixture of epithelium	1.62
	1000.00

The organic substance present in the saliva is of two kinds. The first, which is known by the name of *ptyaline*, is derived from the secretions of the submaxillary and sublingual glands. It is this substance which gives the saliva its viscidity. It is coagulable by alcohol, but not by a boiling temperature. The other organic matter present in the saliva, which is derived from the secretion of the parotid gland, is not viscid, but coagulates by heat. The whole saliva therefore becomes slightly turbid on being raised to a boiling temperature. The sulpho-cyanogen may be detected by a solution

[1] Verdauungssæfte und Stoffwechsel. Leipzig, 1852.

of chloride of iron, which produces the characteristic red color of sulpho-cyanide of iron. The alkaline reaction of the saliva varies in intensity during the day, but is nearly always sufficiently distinct.

The saliva is not a simple secretion, but a mixture of four distinct fluids, which differ from each other in the source from which they are derived, and in their physical and chemical properties. These secretions are, in the human subject, first, that of the parotid gland; second, that of the submaxillary; third, that of the sublingual; and fourth, that of the mucous follicles of the mouth. These different fluids have been comparatively studied, in the lower animals, by Bernard, Frerichs, and Bidder and Schmidt. The parotid saliva is obtained in a state of purity from the dog by exposing the duct of Steno where it crosses the masseter muscle, and introducing into it, through an artificial opening, a fine silver canula. The parotid saliva then runs directly from its external orifice, without being mixed with that of the other salivary glands. It is clear, limpid, and watery, without the slightest viscidity, and has a faintly alkaline reaction. The submaxillary saliva is obtained in a similar manner, by inserting a canula into Wharton's duct. It differs from the parotid secretion, so far as its physical properties are concerned, chiefly in possessing a well-marked viscidity. It is alkaline in reaction. The sublingual saliva is also alkaline, colorless, and transparent, and possesses a greater degree of viscidity than that from the submaxillary. The mucous secretion of the follicles of the mouth, which forms properly a part of the saliva, is obtained by placing a ligature simultaneously on Wharton's and Steno's ducts, and on that of the sublingual gland, so as to shut out from the mouth all the glandular salivary secretions, and then collecting the fluid secreted by the buccal mucous membrane. This fluid is very scanty, and much more viscid than either of the other secretions; so much so, that it cannot be poured out in drops when received in a glass vessel, but adheres strongly to the surface of the glass.

We have obtained the *parotid saliva of the human subject* in a state of purity by introducing directly into the orifice of Steno's duct a silver canula $\frac{1}{25}$ to $\frac{1}{20}$ of an inch in diameter. The other extremity of the canula projects from the mouth, between the lips, and the saliva is collected as it runs from the open orifice. This method gives results much more valuable than observations made on salivary fistulæ and the like, since the secretion is obtained under perfectly healthy conditions, and unmixed with other animal fluids.

The result of many different observations, conducted in this way, is that the human parotid saliva, like that of the dog, is colorless, watery, and distinctly alkaline in reaction. It differs from the mixed saliva of the mouth, in being perfectly clear, without any turbidity or opalescence. Its flow is scanty while the cheeks and jaws remain at rest; but as soon as the movements of mastication are excited by the introduction of food, it runs in much greater abundance. We have collected, in this way, from the parotid duct of one side only, in a healthy man, 480 grains of saliva in the course of twenty minutes; and in seven successive observations, made on different days, comprising in all three hours and nine minutes, we have collected a little over 3000 grains.

The parotid saliva obtained in this way has been analyzed by Prof. Maurice Perkins, with the following result: —

Composition of Human Parotid Saliva.

Water	983.308
Organic matter precipitable by alcohol	7.352
Substance destructible by heat, but not precipitated by alcohol or acids	4.810
Sulpho-cyanide of sodium	0.330
Phosphate of lime	0.240
Chloride of potassium	0.900
Chloride of sodium and carbonate of soda	3.060
	1000.000

Prof. Perkins found, in accordance with our own observations, that the fresh parotid saliva, when treated with perchloride of iron, showed no evidences of sulpho-cyanogen; but after the organic matters had been precipitated by alcohol, the filtered fluid was found to contain an appreciable quantity of the sulpho-cyanide.

The *organic matter* in the parotid saliva is in rather large quantity as compared with the mineral ingredients. It is precipitable by alcohol, by a boiling temperature, by nitric acid, and by sulphate of soda in excess, but not by an acidulated solution of ferrocyanide of potassium. It bears some resemblance, accordingly, to albumen, but yet is not precisely identical with that substance.

The parotid saliva also differs from the mixed saliva of the mouth in containing some substance which masks the reaction of sulpho-cyanogen. For if the parotid saliva and that from the mouth be drawn from the same person within the same hour, the addition of perchloride of iron will produce a distinct red color in the latter, while no such change takes place in the former. And yet the parotid

saliva contains sulpho-cyanogen, which may be detected, as we have already seen, after the organic matters have been precipitated by alcohol.

A very curious fact has been observed by M. Colin, Professor of Anatomy and Physiology at the Veterinary School of Alfort,[1] viz., that in the horse and ass, as well as in the cow and other ruminating animals, the parotid glands of the two opposite sides, during mastication, are never in active secretion at the same time; but that they alternate with each other, one remaining quiescent while the other is active, and *vice versâ*. In these animals mastication is said to be *unilateral*, that is, when the animal commences feeding or ruminating, the food is triturated, for fifteen minutes or more, by the molars of one side only. It is then changed to the opposite side; and for the next fifteen minutes mastication is performed by the molars of that side only. It is then changed back again, and so on alternately, so that the direction of the lateral movements of the jaw may be reversed many times during the course of a meal. By establishing a salivary fistula simultaneously on each side, it is found that the flow of saliva corresponds with the direction of the masticatory movement. When the animal masticates on the right side, it is the right parotid which secretes actively, while but little saliva is supplied by the left; when mastication is on the left side, the left parotid pours out an abundance of fluid, while the right is nearly inactive.

We have observed a similar alternation in the flow of parotid saliva in the human subject, when the mastication is changed from side to side. In an experiment of this kind, the tube being inserted into the parotid duct of the left side, the quantity of saliva discharged during twenty minutes, while mastication was performed mainly on the opposite side of the mouth, was 127.5 grains; while the quantity during the same period, mastication being on the same side of the mouth, was 374.4 grains—being nearly three times as much in the latter case as in the former.

Owing to the variations in the rapidity of its secretion, and also to the fact that it is not so readily excited by artificial means as by the presence of food, it becomes somewhat difficult to estimate the *total quantity* of saliva secreted daily. The first attempt to do so was made by Mitscherlich,[2] who collected from two to three ounces in twenty-four hours from an accidental salivary fistula of Steno's

[1] Traité de Physiologie Comparée, Paris, 1854, p. 468.

[2] Simon's Chemistry of Man. Phila. ed., 1846, p. 295.

duct in the human subject; from which it was supposed that the total amount secreted by all the glands was from ten to twelve ounces daily. As this man was a hospital patient, however, and suffering from constitutional debility, the above calculation cannot be regarded as an accurate one, and accordingly Bidder and Schmidt[1] make a higher estimate. One of these observers, in experimenting upon himself, collected from the mouth in one hour, without using any artificial stimulus to the secretion, 1500 grains of saliva; and calculates, therefore, the amount secreted daily, making an allowance of seven hours for sleep, as not far from 25,000 grains, or about three and a half pounds avoirdupois.

On repeating this experiment, however, we have not been able to collect from the mouth, without artificial stimulus, more than 556 grains of saliva per hour. This quantity, however, may be greatly increased by the introduction into the mouth of any smooth unirritating substance, as glass beads or the like; and during the mastication of food, the saliva is poured out in very much greater abundance. The very sight and odor of nutritious food, when the appetite is excited, will stimulate to a remarkable degree the flow of saliva; and, as it is often expressed, "bring the water into the mouth." Any estimate, therefore, of the total quantity of saliva, based on the amount secreted in the intervals of mastication, would be a very imperfect one. We may make a tolerably accurate calculation, however, by ascertaining how much is really secreted during a meal, over and above that which is produced at other times. We have found, for example, by experiments performed for this purpose, that wheaten bread gains during complete mastication 55 per cent. of its weight of saliva; and that fresh cooked meat gains, under the same circumstances, 48 per cent. of its weight. We have already seen that the daily allowance of these two substances, for a man in full health, is 19 ounces of bread, and 16 ounces of meat. The quantity of saliva, then, required for the mastication of these two substances, is, for the bread 4,572 grains, and for the meat 3,360 grains. If we now calculate the quantity secreted between meals as continuing for 22 hours at 556 grains per hour, we have:—

Saliva required for mastication of bread =	4572 grains.
" " " " " meat =	3360 "
secreted in intervals of meals =	12232 "
Total quantity in twenty-four hours =	20164 grains;

or rather less than 3 pounds avoirdupois.

[1] Op. cit., p. 14.

The most important question, connected with this subject, relates to the *function of the saliva in the digestive process.* A very remarkable property of this fluid is that which was discovered by Leuchs in Germany, viz., that it possesses the power of converting boiled starch into sugar, if mixed with it in equal proportions, and kept for a short time at the temperature of 100° F. This phenomenon is one of catalysis, in which the starch is transformed into sugar by simple contact with the organic substance contained in the saliva. This organic substance, according to the experiments of Mialhe,[1] may even be precipitated by alcohol, and kept in a dry state for an indefinite length of time without losing the power of converting starch into sugar, when again brought in contact with it in a state of solution.

This action of ordinary human saliva on boiled starch takes place sometimes with great rapidity. Traces of glucose may occasionally be detected in the mixture in one minute after the two substances have been brought in contact; and we have even found that starch paste, introduced into the cavity of the mouth, if already at the temperature of 100° F., will yield traces of sugar at the end of half a minute. The rapidity however, with which this action is manifested, varies very much, as was formerly noticed by Lehmann, at different times; owing, in all probability, to the varying constitution of the saliva itself. It is often impossible, for example, to find any evidences of sugar, in the mixture of starch and saliva, under five, ten, or fifteen minutes; and it is frequently a longer time than this before the whole of the starch is completely transformed. Even when the conversion of the starch commences very promptly, it is often a long time before it is finished. If a thin starch paste, for example, which contains no traces of sugar, be taken into the mouth and thoroughly mixed with the buccal secretions, it will often, as already mentioned, begin to show the reaction of sugar in the course of half a minute; but some of the starchy matter still remains, and will continue to manifest its characteristic reaction with iodine, for fifteen or twenty minutes, or even half an hour.

This property of the saliva, however, is rather an incidental than an essential one; and although starchy substances are really converted into sugar, if mixed with saliva in a test-tube, yet they are not affected by it to the same degree in the natural process of digestion. We have already mentioned the extremely variable

[1] Chimie appliquée à la Physiologie et à la Thérapeutique, Paris, 1856, p. 43.

activity of the saliva, in this respect, at different times; and it must be recollected, also, that in digestion the food is not retained in the cavity of the mouth, but passes at once, after mastication, into the stomach. It might be supposed that the saccharine conversion of starch, after being commenced in the mouth, might continue and be completed in the stomach. We have convinced ourselves, however, by frequent experiments, that this is not the case. If a dog, with a gastric fistula, be fed with a mixture of meat and boiled starch, and portions of the fluid contents of the stomach withdrawn afterward through the fistula, the starch is easily recognizable by its reaction with iodine for ten, fifteen, and twenty minutes afterward. In forty-five minutes it is diminished in quantity, and in one hour has usually altogether disappeared; but no sugar is to be detected at any time. Sometimes the starch disappears more rapidly than this; but at no time, according to our observations, is there any indication of the presence of sugar in the gastric fluids. It is now generally acknowledged also, by most observers, that sugar cannot be detected in the stomach, after the introduction of starch in any form or by any method. In the ordinary process of digestion, in fact, starchy matters do not remain long enough in the mouth to be altered by the saliva, but pass at once into the stomach. Here they meet with the gastric fluids, which become mingled with them, and prevent the change which would otherwise be effected by the saliva. We have found that the gastric juice will interfere, in this manner, with the action of the saliva in the test-tube, as well as in the stomach. If two mixtures be made, one of starch and saliva, the other of starch, saliva, and gastric juice, and both kept for fifteen minutes at the temperature of 100° F., in the first mixture the starch will be promptly converted into sugar, while in the second no such change will take place. The above action, therefore, of saliva on starch, though a curious and interesting property, has no significance as to its physiological function, since it does not take place in the natural digestive process. We shall see hereafter that there are other means provided for the digestion of starchy matters, altogether independent of the action of the saliva.

The true function of the saliva is altogether a physical one. Its action is simply to moisten the food and facilitate its mastication, as well as to lubricate the triturated mass, and assist its passage down the œsophagus. Food which is hard and dry, like crusts, crackers, &c., cannot be masticated and swallowed with readiness, unless moistened by some fluid. If the saliva, therefore, be prevented

from entering the cavity of the mouth, its loss does not interfere directly with the chemical changes of the food in digestion, but only with its mechanical preparation. This is the result of direct experiments performed by various observers. Bidder and Schmidt,[1] after tying Steno's duct, together with the common duct of the submaxillary and sublingual glands on both sides in the dog, found that the immediate effect of such an operation was "a remarkable diminution of the fluids which exude upon the surfaces of the mouth; so that these surfaces retained their natural moisture only so long as the mouth was closed, and readily became dry on exposure to contact with the air. Accordingly, deglutition became evidently difficult and laborious, not only for dry food, like bread, but even for that of a tolerably moist consistency, like fresh meat. The animals also became very thirsty, and were constantly ready to drink."

Bernard[2] also found that the only marked effect of cutting off the flow of saliva from the mouth was a difficulty in the mechanical processes of mastication and deglutition. He first administered to a horse one pound of oats, in order to ascertain the rapidity with which mastication would naturally be accomplished. The above quantity of grain was thoroughly masticated and swallowed at the end of nine minutes. An opening had been previously made in the œsophagus at the lower part of the neck, so that none of the food reached the stomach; but each mouthful, as it passed down the œsophagus, was received at the œsophageal opening and examined by the experimenter. The parotid duct on each side of the face was then divided, and another pound of oats given to the animal. Mastication and deglutition were both found to be immediately retarded. The alimentary masses passed down the œsophagus at longer intervals, and their interior was no longer moist and pasty, as before, but dry and brittle. Finally, at the end of twenty-five minutes, the animal had succeeded in masticating and swallowing only about three-quarters of the quantity which he had previously disposed of in nine minutes.

It appears also, from the experiments of Magendie, Bernard, and Lassaigne, on horses and cows, that the quantity of saliva absorbed by the food during mastication is in direct proportion to its hardness and dryness, but has no particular relation to its chemical qualities. These experiments were performed as follows: The œso-

[1] Op. cit., p. 3.

[2] Leçons de Physiologie Expérimentale, Paris, 1856, p. 146.

phagus was opened at the lower part of the neck, and a ligature placed upon it, between the wound and the stomach. The animal was then supplied with a previously weighed quantity of food, and this, as it passed out by the œsophageal opening, was received into appropriate vessels and again weighed. The difference in weight, before and after swallowing, indicated the quantity of saliva absorbed by the food. The following table gives the results of some of Lassaigne's experiments,[1] performed upon a horse:—

Kind of Food employed.		Quantity of Saliva absorbed.		
For 100 parts of hay		there were absorbed	400	parts saliva.
"	barley meal	"	186	"
"	oats	"	113	"
"	green stalks and leaves	"	49	"

It is evident from the above facts, that the quantity of saliva produced has not so much to do with the chemical character of the food as with its physical condition. When the food is dry and hard, and requires much mastication, the saliva is secreted in abundance; when it is soft and moist, a smaller quantity of the secretion is poured out; and finally, when the food is taken in a fluid form, as soup or milk, or reduced to powder and moistened artificially with a very large quantity of water, it is not mixed at all with the saliva, but passes at once into the cavity of the stomach. The abundant and watery fluid of the parotid gland is most useful in assisting mastication; while the glairy and mucous secretion of the submaxillary gland and the muciparous follicles serve to lubricate the exterior of the triturated mass, and facilitate its passage through the œsophagus.

By the combined operation of the two processes which the food undergoes in the cavity of the mouth, its preliminary preparation is accomplished. It is triturated and disintegrated by the teeth, and, at the same time, by the movements of the jaws, tongue, and cheeks, it is intimately mixed with the salivary fluids, until the whole is reduced to a soft, pasty mass, of the same consistency throughout. It is then carried backward by the semi-involuntary movements of the tongue into the pharynx, and conducted by the muscular contractions of the œsophagus into the stomach.

Gastric Juice, and Stomach Digestion.—The mucous membrane of the stomach is distinguished by its great vascularity

[1] Comptes Rendus, vol. xxi. p. 362.

and the abundant glandular apparatus with which it is provided. Its entire thickness is occupied by certain glandular organs, the gastric tubules or follicles, which are so closely set as to leave almost no space between them except what is required for the capillary bloodvessels. The free surface of the gastric mucous membrane is not smooth, but is raised in minute ridges and projecting eminences. In the cardiac portion (Fig. 25), these ridges are reticulated with each other, so as to include between them polygonal interspaces, each of which is encircled by a capillary network. In the pyloric portion (Fig. 26), the eminences are more

Fig. 25. Fig. 26.

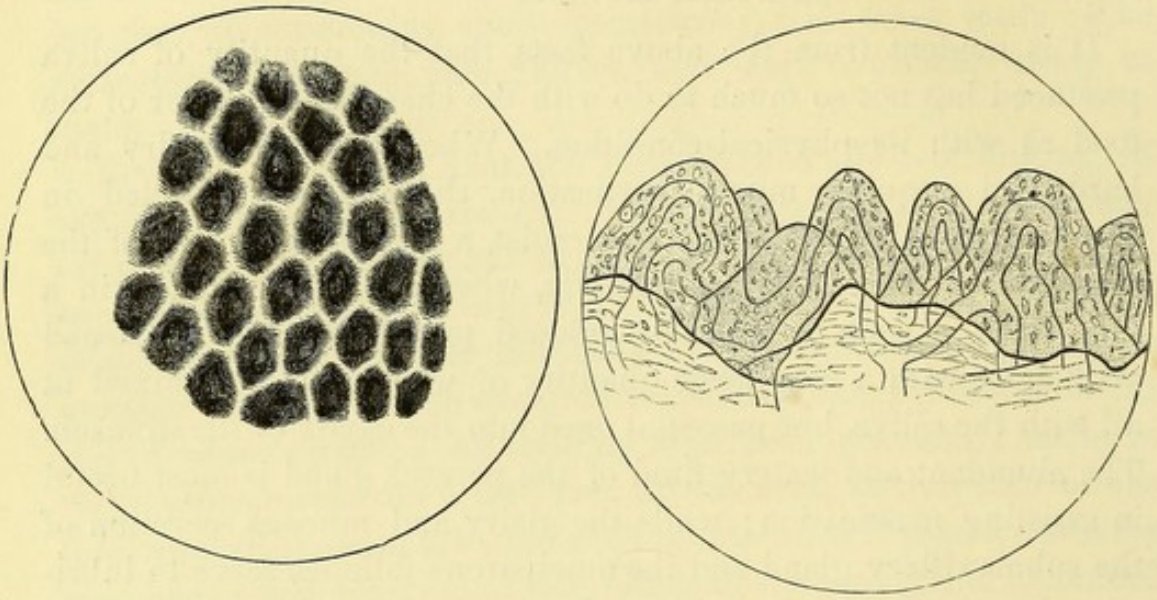


Fig. 25. Free surface of GASTRIC MUCOUS MEMBRANE, viewed from above; from Pig's Stomach, Cardiac portion. Magnified 70 diameters.

Fig. 26. Free surface of GASTRIC MUCOUS MEMBRANE, viewed in vertical section; from Pig's Stomach, Pyloric portion. Magnified 420 diameters.

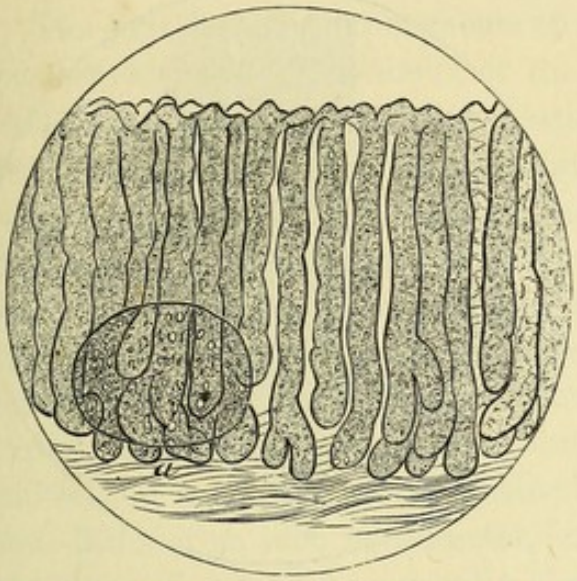
or less pointed and conical in form, and generally flattened from side to side. They contain each a capillary bloodvessel, which returns upon itself in a loop at the extremity of the projection, and communicates freely with adjacent vessels.

The gastric follicles are very different in different parts of the stomach.

In the *pyloric* portion of the pig's stomach (Fig. 27, next page), they are nearly straight or slightly tortuous tubules, $\frac{1}{4\,1\,0}$ of an inch in diameter, lined with small glandular epithelium cells, and terminating in blind extremities at the under surface of the mucous membrane. In their lower half they are often branched, two or more lateral diverticula passing off from the principal tubule, and forming a little mass or lobule of glandular tubes. At their upper

extremities, they open on the free surface of the mucous membrane, in the interspaces between the projecting folds or villi. Among these tubular glandules there is also found, in the gastric mucous membrane, another kind of glandular organ, consisting of closed follicles, similar to the solitary glands of the small intestine. These follicles, which are not very numerous, are seated in the lower part of the mucous membrane, and enveloped by the cæcal extremities of the tubules. (Fig. 27, *a*.)

Fig. 27.



MUCOUS MEMBRANE OF PIG'S STOMACH, from Pyloric portion; vertical section; showing gastric tubules, and, at *a*, a closed follicle. Magnified 70 diameters.

In the *cardiac* portion of the stomach the superficial part of the mucous membrane contains very wide circular tubes lined with large distinctly marked cylinder epithelium cells. (Fig. 29.) These tubes divide at a certain distance from the surface, and the tubules which result from their division become

Fig. 28.

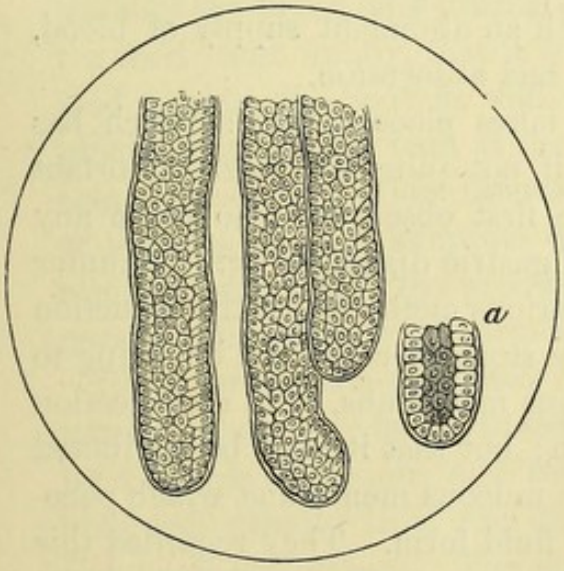


Fig. 29.

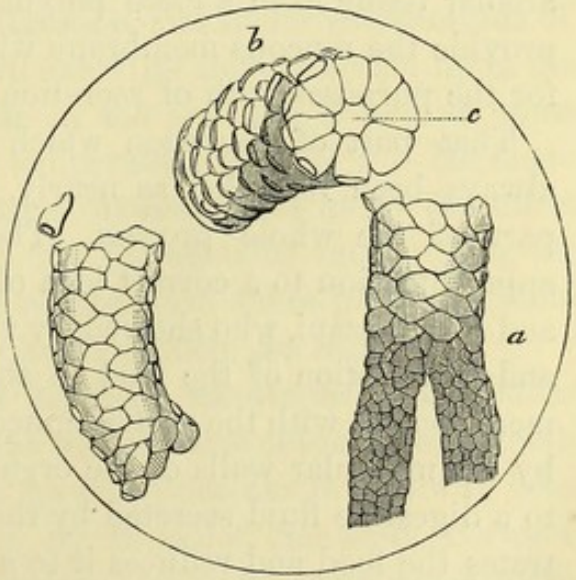
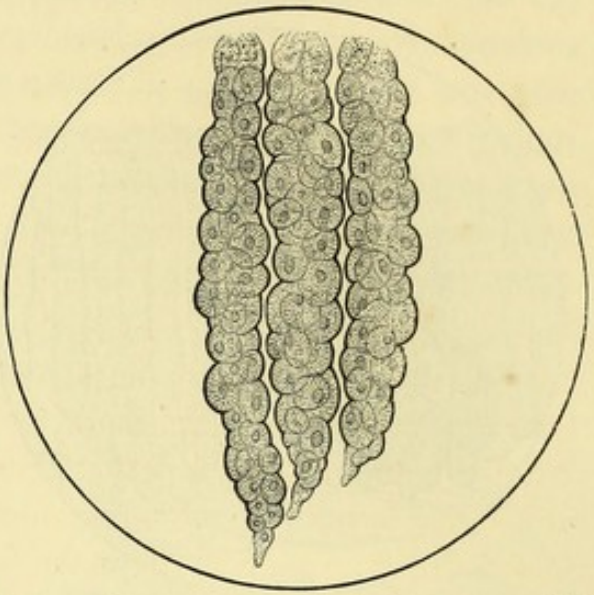


Fig. 28. GASTRIC TUBULES FROM PIG'S STOMACH, Pyloric portion, showing their Cæcal Extremities. At *a*, the torn extremity of a tubule, showing its cavity.

Fig. 29. GASTRIC TUBULES FROM PIG'S STOMACH; Cardiac portion. At *a*, a large tubule dividing into two small ones. *b*. Portion of a tubule, seen endwise. *c*. Its central cavity.

much reduced in size, and are lined with small rounded cells of glandular epithelium. They finally terminate, like the others, in rounded extremities at the bottom of the mucous membrane.

Fig. 30



Gastric Tubules from Pig's Stomach: middle portion.

In the *middle* portion of the stomach the tubules, which are here very long, in comparison both with those near the cardia and those near the pylorus, are also distinguished by being filled, in addition to the ordinary glandular epithelium, with very large, rounded, granular nucleated cells, which often seem to fill their entire cavity and project from their sides, giving them an irregularly tumefied or varicose appearance. These tubules, with large granular cells, are considered, by some authors, as the most important agents in the secretion of the gastric juice. All the gastric tubules, however, in the various parts of the stomach, probably combine to produce the digestive fluid.

The bloodvessels which come up from the submucous layer of areolar tissue form a close plexus around all these glandules, and provide the mucous membrane with an abundant supply of blood, for the purposes both of secretion and absorption.

That part of digestion which takes place in the stomach has always been regarded as nearly, if not quite, the most important part of the whole process. The first observers who made any approximation to a correct idea of gastric digestion were Reaumur and Spallanzani, who showed by various methods that the reduction and liquefaction of the food in the stomach could not be owing to mere contact with the gastric mucous membrane, or to compression by the muscular walls of the organ; but that it must be attributed to a digestive fluid secreted by the mucous membrane, which penetrates the food and reduces it to a fluid form. They regarded this process as a simple chemical solution, and considered the gastric juice as a universal solvent for all alimentary substances. They succeeded even in obtaining some of this gastric juice, mingled

probably with many impurities, by causing the animals upon which they experimented to swallow sponges attached to the ends of cords, by which they were afterward withdrawn, the fluids which they had absorbed being then expressed and examined.

The first decisive experiments on this point, however, were those performed by Dr. Beaumont, of the U. S. Army, on the person of Alexis St. Martin, a Canadian boatman, who had a permanent gastric fistula, the result of an accidental gunshot wound. The musket, which was loaded with buckshot at the time of the accident, was discharged, at the distance of a few feet from St. Martin's body, in such a manner as to tear away the integument at the lower part of the left chest, open the pleural cavity, and penetrate, through the lateral portion of the diaphragm, into the great pouch of the stomach. After the integument and the pleural and peritoneal surfaces had united and cicatrized, there remained a permanent opening, of about four-fifths of an inch in diameter, leading into the left extremity of the stomach, which was usually closed by a circular valve of protruding mucous membrane. This valve could be readily depressed at any time, so as to open the fistula and allow the contents of the stomach to be extracted for examination.

Dr. Beaumont experimented upon this person at various intervals from the year 1825 to 1832.[1] He established during the course of his examinations the following important facts: First, that the active agent in digestion is an acid fluid, secreted by the walls of the stomach; secondly, that this fluid is poured out by the glandular walls of the organ only during digestion, and under the stimulus of the food; and finally, that it will exert its solvent action upon the food outside the body as well as in the stomach, if kept in glass phials upon a sand bath at the temperature of 100° F. He made also a variety of other interesting investigations as to the effect of various kinds of stimulus on the secretion of the stomach, the rapidity with which the process of digestion takes place, the comparative digestibility of various kinds of food, &c. &c.

Since Dr. Beaumont's time it has been ascertained that similar gastric fistulæ may be produced at will on some of the lower animals by a simple operation; and the gastric juice has in this way been obtained, usually from the dog, by Blondlot, Schwann, Bernard, Lehmann and others. The simplest and most expeditious mode of doing the operation is the best. An incision should be made

[1] Experiments and Observations upon the Gastric Juice. Boston, 1834.

through the abdominal parietes in the median line, over the great curvature of the stomach. The anterior wall of the organ is then to be seized with a pair of hooked forceps, drawn out at the external wound, and opened with the point of a bistoury. A short silver canula, one-half to three-quarters of an inch in diameter, armed at each extremity with a narrow projecting rim or flange, is then inserted into the wound in the stomach, the edges of which are fastened round the tube with a ligature in order to prevent the escape of the gastric fluids into the peritoneal cavity. The stomach is then returned to its place in the abdomen, and the canula allowed to remain with its external flange resting upon the edges of the wound in the abdominal integuments, which are to be drawn together by sutures. The animal may be kept perfectly quiet, during the operation, by the administration of ether or chloroform. In a few days the ligatures come away, the wounded peritoneal surfaces are united with each other, and the canula is retained in a permanent gastric fistula; being prevented by its flaring extremities both from falling out of the abdomen and from being accidentally pushed into the stomach. It is closed externally by a cork, which may be withdrawn at pleasure, and the contents of the stomach withdrawn for examination.

Experiments conducted in this manner confirm, in the main, the results obtained by Dr. Beaumont. Observations of this kind are in some respects, indeed, more satisfactory when made upon the lower animals, than upon the human subject; since animals are entirely under the control of the experimenter, and all sources of deception or mistake are avoided, while the investigation is, at the same time, greatly facilitated by the simple character of their food.

The gastric juice, like the saliva, is secreted in considerable quantity only under the stimulus of recently ingested food. Dr. Beaumont states that it is entirely absent during the intervals of digestion; and that the stomach at that time contains no acid fluid, but only a little neutral or alkaline mucus. He was able to obtain a sufficient quantity of gastric juice for examination, by gently irritating the mucous membrane with a gum-elastic catheter, or the end of a glass rod, and by collecting the secretion as it ran in drops from the fistula. On the introduction of food, he found that the mucous membrane became turgid and reddened, a clear acid fluid collected everywhere in drops underneath the layer of mucus lining the walls of the stomach, and was soon poured out abundantly into its cavity. We have found, however, that the rule laid down

by Dr. Beaumont in this respect, though correct in the main, is not invariable. The truth is, the irritability of the gastric mucous membrane, and the readiness with which the flow of gastric juice may be excited, varies considerably in different animals; even in those belonging to the same species. In experimenting with gastric fistulæ on different dogs, for example, we have found in one instance, like Dr. Beaumont, that the gastric juice was always entirely absent in the intervals of digestion; the mucous membrane then presenting invariably either a neutral or slightly alkaline reaction. In this animal, which was a perfectly healthy one, the secretion could not be excited by any artificial means, such as glass rods, metallic catheters, and the like; but only by the natural stimulus of ingested food. We have even seen tough and indigestible pieces of tendon, introduced through the fistula, expelled again in a few minutes, one after the other, without exciting the flow of a single drop of acid fluid; while pieces of fresh meat, introduced in the same way, produced at once an abundant supply. In other instances, on the contrary, the introduction of metallic catheters, &c., into the empty stomach has produced a scanty flow of gastric juice; and in experimenting upon dogs that have been kept without food during various periods of time and then killed by section of the medulla oblongata, we have usually, though not always, found the gastric mucous membrane to present a distinctly acid reaction, even after an abstinence of six, seven, or eight days. There is at no time, however, under these circumstances, any considerable amount of fluid present in the stomach; but only just sufficient to moisten the gastric mucous membrane, and give it an acid reaction.

The gastric juice, which is obtained by irritating the stomach with a metallic catheter, is clear, perfectly colorless, and acid in reaction. A sufficient quantity of it cannot be obtained by this method for any extended experiments; and for that purpose, the animal should be fed, after a fast of twenty-four hours, with fresh lean meat, a little hardened by short boiling, in order to coagulate the fluids of the muscular tissue, and prevent their mixing with the gastric secretion. No effect is usually apparent within the first five minutes after the introduction of the food. At the end of that time the gastric juice begins to flow; at first slowly, and in drops. It is then perfectly colorless, but very soon acquires a slight amber tinge. It then begins to flow more freely, usually in drops, but often running for a few seconds in a continuous stream. In this way from ℥ij to ℥iiss may be collected in the course of fifteen

minutes. Afterward it becomes somewhat turbid with the debris of the food, which has begun to be disintegrated; but from this it may be readily separated by filtration. After three hours, it continues to run freely, but has become very much thickened, and even grumous in consistency, from the abundant admixture of alimentary debris. In six hours after the commencement of digestion it runs less freely, and in eight hours has become very scanty, though it continues to preserve the same physical appearances as before. It ceases to flow altogether in from nine to twelve hours, according to the quantity of food taken.

For purposes of examination, the fluid drawn during the first fifteen minutes after feeding should be collected, and separated by filtration from accidental impurities. Obtained in this way, the gastric juice is a clear, watery fluid, without any appreciable viscidity, very distinctly acid to test paper, of a faint amber color, and with a specific gravity of 1010. It becomes opalescent on boiling, owing to the coagulation of its organic ingredients. The following is the composition of the gastric juice of the dog, based on a comparison of various analyses by Lehmann, Bidder and Schmidt, and other observers: —

Composition of Gastric Juice.

Water	975.00
Organic matter	15.00
Lactic acid	4.78
Chloride of sodium	1.70
" " potassium	1.08
" " calcium	0.20
" " ammonium	0.65
Phosphate of lime	1.48
" " magnesia	0.06
" " iron	0.05
	1000.00

In place of lactic acid, Bidder and Schmidt found, in most of their analyses, hydrochloric acid. Lehmann admits that a small quantity of hydrochloric acid is present, but regards lactic acid as the most abundant and important ingredient of the two. Robin and Verdeil also regard the acid reaction of the gastric juice as due to lactic acid; and, finally, Bernard has shown,[1] by a series of well contrived experiments, that the free acid of the dog's gastric juice is undoubtedly the lactic; and that the hydrochloric acid obtained by distillation is really produced by a decomposition of the chlorides, which enter into the composition of the fresh juice.

[1] Leçons de Physiologie Expérimentale, Paris, 1856, p. 396.

Prof. C. Schmidt,[1] in Germany, has also had an opportunity of examining the human gastric juice in a case of gastric fistula, similar to that of Alexis St. Martin. This was the case of a healthy woman, 35 years of age, who, in consequence of a local inflammation, became affected with a gastric fistula situated below the left breast, in the ninth intercostal space. Prof. Schmidt found the gastric juice obtained from this fistula similar to that of the dog, except that it contained a smaller proportion of organic matter, of free acid, and of solid ingredients generally; — the whole secretion being, at the same time, more abundant in quantity.

From our own observations, already alluded to, we have no doubt that both the quantity and density of the gastric juice vary, within certain limits, in different individuals of the same species; — the proportion of solid ingredients being less when the secretion is more abundant, and greater when the secretion is in small quantity.

The *free acid* is an extremely important ingredient of the gastric secretion, and is, in fact, essential to its physiological properties; for the gastric juice will not exert its solvent action upon the food, after it has been neutralized by the addition of an alkali, or an alkaline carbonate.

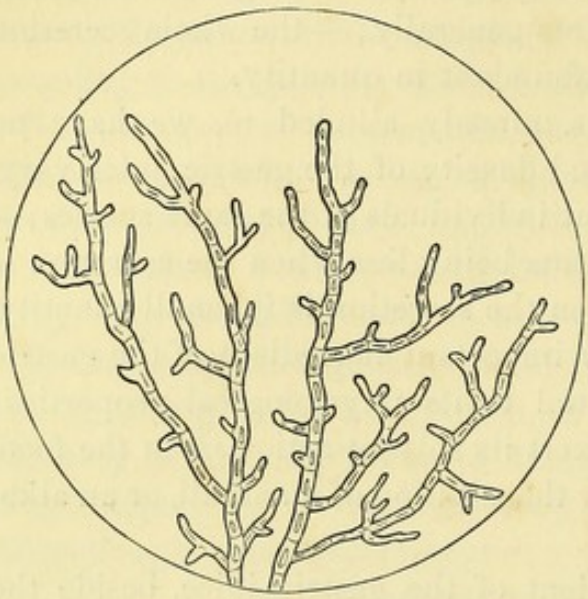
The most important ingredient of the gastric juice, beside the free acid, is its organic matter or "ferment," which is known under the name of *pepsine*. This name, "pepsine," was originally given by Schwann to a substance which he obtained from the mucous membrane of the pig's stomach, by macerating it in distilled water until a putrid odor began to be developed. The substance in question was precipitated from the watery infusion by the addition of alcohol, and dried; and if dissolved afterward in acidulated water, it was found to exert a solvent action on boiled white of egg. This substance, however, did not represent precisely the natural ingredient of the gastric secretion, and was probably a mixture of various matters, some of them the products of commencing decomposition of the mucous membrane itself. The name pepsine, if it be used at all, should be applied to the organic matter which naturally occurs in solution in the gastric juice. It is altogether unessential, in this respect, from what source it may be originally derived. It has been regarded by Bernard and others, on somewhat insufficient grounds, as a product of the alteration of the mucus of the stomach. But whatever be its source, since it is

[1] Annalen der Chemie und Pharmacie, 1854, p. 42.

always present in the secretion of the stomach, and takes an active part in the performance of its function, it can be regarded in no other light than as a real anatomical ingredient of the gastric juice, and as essential to its constitution.

Pepsine is precipitated from its solution in the gastric juice by absolute alcohol, and by various metallic salts, but is not affected by ferrocyanide of potassium. It is precipitated also, and coagulated, by a boiling temperature; and the gastric juice, accordingly, after being boiled, becomes turbid, and loses altogether its power of dissolving alimentary substances. Gastric juice is also affected in a remarkable manner by being mingled with *bile*. We have found that four to six drops of dog's bile precipitate completely with ʒj of gastric juice from the same animal; so that the whole of the biliary coloring matter is thrown down as a deposit, and the filtered fluid is found to have lost entirely its digestive power, though it retains an acid reaction.

Fig. 31.



CONFERVOID VEGETABLE, growing in the Gastric Juice of the Dog. The fibres have an average diameter of 1-7000 of an inch.

A very singular property of the gastric juice is its *inaptitude for putrefaction*. It may be kept for an indefinite length of time in a common glass-stoppered bottle without developing any putrescent odor. A light deposit generally collects at the bottom, and a confervoid vegetable growth or "mould" often shows itself in the fluid after it has been kept for one or two weeks. This growth has the form of white, globular masses, each of which is composed of delicate radiating branched filaments (Fig. 31); each filament consisting of a row of elongated cells, like other vegetable growths of a similar nature. These growths, however, are not accompanied by any putrefactive changes, and the gastric juice retains its acid reaction and its digestive properties for many months.

By experimenting artificially with gastric juice on various alimentary substances, such as meat, boiled white of egg, &c., it is found, as Dr. Beaumont formerly observed, to exert a solvent action

on these substances outside the body, as well as in the cavity of the stomach. This action is most energetic at the temperature of 100° F. It gradually diminishes in intensity below that point, and ceases altogether near 32°. If the temperature be elevated above 100° the action also becomes enfeebled, and is entirely suspended about 160°, or the temperature of coagulating albumen. Contrary to what was supposed, however, by Dr. Beaumont, and his predecessors, the gastric juice is not a universal solvent for all alimentary substances, but, on the contrary, affects only a single class of the proximate principles, viz., the albuminoid or organic substances. Neither starch nor oil, when digested in it at the temperature of the body, suffers the slightest chemical alteration. Fatty matters are simply melted by the heat, and starchy substances are only hydrated and gelatinized to a certain extent by the combined influence of the warmth and moisture. Solid and semi-solid albuminoid matters, however, are at once attacked and liquefied by the digestive fluid. Pieces of coagulated white of egg suspended in it, in a test-tube, are gradually softened on their exterior, and their edges become pale and rounded. They grow thin and transparent; and their substance finally melts away, leaving a light scanty deposit, which collects at the bottom of the test-tube. While the disintegrating process is going on, it may almost always be noticed that minute, opaque spots show themselves in the substance of the liquefying albumen, indicating that certain parts of it are less easily attacked than the rest; and the deposit which remains at the bottom is probably also composed of some ingredient, not soluble in the gastric juice. If pieces of fresh meat be treated in the same manner, the areolar tissue entering into its composition is first dissolved, so that the muscular bundles become more distinct, and separate from each other. They gradually fall apart, and a little brownish deposit is at last all that remains at the bottom of the tube. If the hard adipose tissue of beef or mutton be subjected to the same process, the walls of the fat vesicles and the intervening areolar tissue, together with the capillary bloodvessels, &c., are dissolved; while the oily matters are set free from their envelops, and collect in a white, opaque layer on the surface. In cheese, the casein is dissolved, and the oil which it contains set free. In bread the gluten is digested, and the starch left unchanged. In milk, the casein is first coagulated by contact with the acid gastric fluids, and afterward slowly liquefied, like other albuminoid substances.

The time required for the complete liquefaction of these substances varies with the quantity of matter present, and with its state of cohesion. The process is hastened by occasionally shaking up the mixture, so as to separate the parts already disintegrated, and bring the gastric fluid into contact with fresh portions of the digestible substance.

The liquefying process which the food undergoes in the gastric juice is not a simple solution. It is a catalytic transformation, produced in the albuminoid substances by contact with the organic matter of the digestive fluid. This organic matter acts in a similar manner to that of the catalytic bodies, or "ferments," generally. Its peculiarity is that, for its active operation, it requires to be dissolved in an acidulated fluid. In common with other ferments, it requires also a moderate degree of warmth; its action being checked, both by a very low, and a very high temperature. By its operation the albuminoid matters of the food, whatever may have been their original character, are all, without distinction, converted into a new substance, viz., *albuminose*. This substance has the general characters belonging to the class of organic matters. It is uncrystallizable, and contains nitrogen as an ultimate element. It is precipitated, like albumen, by an excess of alcohol, and by the metallic salts; but unlike albumen, is not affected by nitric acid or a boiling temperature. It is freely soluble in water, and after it is once produced by the digestive process, remains in a fluid condition, and is ready to be absorbed by the vessels. In this way, casein, fibrin, musculine, gluten, &c., are all reduced to the condition of albuminose. By experimenting as above, with a mixture of food and gastric juice in test-tubes, we have found that the casein of cheese is entirely converted into albuminose, and dissolved under that form. A very considerable portion of raw white of egg, however, dissolves in the gastric juice directly as albumen, and retains its property of coagulating by heat. Soft-boiled white of egg and raw meat are principally converted into albuminose; but at the same time, a small portion of albumen is also taken up unchanged.

The above process is a true liquefaction of the albuminoid substances, and not a simple disintegration. If fresh meat be cut into small pieces, and artificially digested in gastric juice in test-tubes, at 100° F., and the process assisted by occasional gentle agitation, the fluid continues to take up more and more of the digestible material for from eight to ten hours. At the end of that time if it be separated and filtered, the filtered fluid has a distinct, brownish

color, and is saturated with dissolved animal matter. Its specific gravity is found to have increased from 1010 to 1020; and on the addition of alcohol it becomes turbid, with a very abundant whitish precipitate (albuminose). There is also a peculiar odor developed during this process, which resembles that produced in the malting of barley.

Albuminose, in solution in gastric juice, has several peculiar properties. One of the most remarkable of these is that it interferes with the operation of Trommer's test for grape sugar (see page 68). We first observed and described this peculiarity in 1854,[1] but could not determine, at that time, upon what particular ingredient of the gastric juice it depended. A short time subsequently it was also noticed by M. Longet, in Paris, who published his observations in the *Gazette Hebdomadaire* for February 9th, 1855.[2] He attributed the reaction not to the gastric juice itself, but to the albuminose held in solution by it. We have since found this explanation to be correct. Gastric juice obtained from the empty stomach of the fasting animal, by irritation with a metallic catheter, which is clear and perfectly colorless, does not interfere in any way with Trommer's test; but if it be macerated for some hours in a test-tube with finely chopped meat, at a temperature of 100°, it will then be found to have acquired the property in a marked degree. The reaction therefore depends undoubtedly upon the presence of albuminose in solution. As the gastric juice, drawn from the dog's stomach half an hour or more after the introduction of food, already contains some albuminose in solution, it presents the same reaction. If such gastric juice be mixed with a small quantity of glucose, and Trommer's test applied, no peculiarity is observed on first dropping in the sulphate of copper; but on adding afterward the solution of potassa, the mixture takes a rich purple hue, instead of the clear blue tinge which is presented under ordinary circumstances. On boiling, the color changes to claret, cherry red, and finally to a light yellow; but no oxide of copper is deposited, and the fluid remains clear. If the albuminose be present only in small quantity, an incomplete reduction of the copper takes place, so that the mixture becomes opaline and cloudy, but still without any well marked deposit. This interference will take place when sugar is present in very large proportion. We have found that in a mix-

[1] American Journ. Med. Sci., Oct. 1854, p. 319.

[2] Nouvelles recherches relatives à l'action du suc gastrique sur les substances albuminoides.—*Gaz. Hebd.* 9 *Février*, 1855, p. 103.

ture of honey and gastric juice in equal volumes, no reduction of copper takes place on the application of Trommer's test. It is remarkable, however, that if such a mixture be previously diluted with an equal quantity of water, the interference does not take place, and the copper is deposited as usual.

Usually this peculiar reaction, now that we are acquainted with its existence, will not practically prevent the detection of sugar, when present; since the presence of the sugar is distinctly indicated by the change of color, as above mentioned, from purple to yellow, though the copper may not be thrown down as a precipitate. All possibility of error, furthermore, may be avoided by adopting the following precautions. The purple color, already mentioned, will, in the first place, serve to indicate the presence of the albuminoid ingredient in the suspected fluid. The mixture should then be evaporated to dryness, and extracted with alcohol, in order to eliminate the animal matters. After that, a watery solution of the sugar contained in the alcoholic extract will react as usual with Trommer's test, and reduce the oxide of copper without difficulty.

Another remarkable property of gastric juice containing albuminose, which is not, however, peculiar to it, but common to many other animal fluids, is that of interfering with the mutual reaction of starch and iodine. If ʒj of such gastric juice be mixed with ʒj of iodine water, and boiled starch be subsequently added, no blue color is produced; though if a larger quantity of iodine water be added, or if the tincture be used instead of the aqueous solution, the superabundant iodine then combines with the starch, and produces the ordinary blue color. This property, like that described above, is not possessed by pure, colorless, gastric juice, taken from the empty stomach, but is acquired by it on being digested with albuminoid substances.

Another important action which takes place in the stomach, beside the secretion of the gastric juice, is the *peristaltic movement* of the organ. This movement is accomplished by the alternate contraction and relaxation of the longitudinal and circular fibres of its muscular coat. The motion is minutely described by Dr. Beaumont, who examined it, both by watching the movements of the food through the gastric fistula, and also by introducing into the stomach the bulb and stem of a thermometer. According to his observations, when the food first passes into the stomach, and the secretion of the gastric juice commences, the muscular coat, which was before quiescent, is excited and begins to contract act-

ively. The contraction takes place in such a manner that the food, after entering the cardiac orifice of the stomach, is first carried to the left, into the great pouch of the organ, thence downward and along the great curvature to the pyloric portion. At a short distance from the pylorus, Dr. B. often found a circular constriction of the gastric parietes, by which the bulb of the thermometer was gently grasped and drawn toward the pylorus, at the same time giving a twisting motion to the stem of the instrument, by which it was rotated in his fingers. In a moment or two, however, this constriction was relaxed, and the bulb of the thermometer again released, and carried together with the food along the small curvature of the organ to its cardiac extremity. This circuit was repeated so long as any food remained in the stomach; but, as the liquefied portions were successively removed toward the end of digestion, it became less active, and at last ceased altogether when the stomach had become completely empty, and the organ returned to its ordinary quiescent condition.

It is easy to observe the muscular action of the stomach during digestion in the dog, by the assistance of a gastric fistula, artificially established. If a metallic catheter be introduced through the fistula when the stomach is empty, it must usually be held carefully in place, or it will fall out by its own weight. But immediately upon the introduction of food, it can be felt that the catheter is grasped and retained with some force, by the contraction of the muscular coat. A twisting or rotatory motion of its extremity may also be frequently observed, similar to that described by Dr. Beaumont. This peristaltic action of the stomach, however, is a gentle one. and not at all active or violent in character. We have never seen, in opening the abdomen, any such energetic or extensive contractions of the stomach, even when full of food, as may be easily excited in the small intestine by the mere contact of the atmosphere, or by pinching them with the blades of a forceps. This action of the stomach, nevertheless, though quite gentle, is sufficient to produce a constant churning movement of the masticated food, by which it is carried back and forward to every part of the stomach, and rapidly incorporated with the gastric juice which is at the same time poured out by the mucous membrane; so that the digestive fluid is made to penetrate equally every part of the alimentary mass, and the digestion of all its albuminous ingredients goes on simultaneously. This gentle and continuous movement of the stomach is one which cannot be successfully imitated in experi-

ments on artificial digestion with gastric juice in test-tubes; and consequently the process, under these circumstances, is never so rapid or so complete as when it takes place in the interior of the stomach.

The length of time which is required for digestion varies in different species of animals. In the carnivora, a moderate meal of fresh uncooked meat requires from nine to twelve hours for its complete solution and disappearance from the stomach. According to Dr. Beaumont, the average time required for digestion in the human subject is considerably less; varying from one hour to five hours and a half, according to the kind of food employed. This is probably owing to the more complete mastication of the food which takes place in man, than in the carnivorous animals. By examining the contents of the stomach at various intervals after feeding, Dr. Beaumont made out a list, showing the comparative digestibility of different articles of food, of which the following are the most important:—

Time required for digestion, according to Dr. Beaumont:—

Kind of Food.	Hours.	Minutes.
Pig's feet	1	00
Tripe	1	00
Trout (broiled)	1	30
Venison steak	1	35
Milk (boiled)	2	00
Roasted turkey	2	30
" beef	3	00
" mutton	3	15
Veal (broiled)	4	00
Salt beef (boiled)	4	15
Roasted pork	5	15

The comparative digestibility of different substances varies more or less in different individuals according to temperament; but the above list undoubtedly gives a correct average estimate of the time required for stomach digestion under ordinary conditions.

A very interesting question is that which relates to the *total quantity* of gastric juice secreted daily. Whenever direct experiments have been performed with a view of ascertaining this point, their results have given a considerably larger quantity than was anticipated. Bidder and Schmidt found that, in a dog weighing 34 pounds, they were able to obtain by separate experiments, consuming in all 12 hours, one pound and three-quarters of gastric juice. The total quantity, therefore, for 24 hours, in the same animal, would be 3½ pounds; and, by applying the same calculation to

a man of medium size, the authors estimate the total daily quantity in the human subject as but little less than 14 pounds (av.). This estimate is probably not an exaggerated one. Schmidt,[1] in his experiments on the gastric fistula of the human subject already alluded to, found the secretion of gastric juice even more abundant than the above; since, in a woman weighing only 117 pounds, he obtained, as the mean result of several observations, over one pound of gastric juice from the fistula in the course of an hour.

Owing, however, to the great variation in the secretion of the gastric juice at different times, according to the activity of digestion, we have endeavored to determine the question of its total daily quantity in a different manner, by experimenting as follows with the gastric juice of the dog.

It was first ascertained, by direct experiment, that the fresh lean meat of the bullock's heart loses, by complete desiccation, 78 per cent. of its weight. 300 grains of such meat, cut into small pieces, were then digested for ten hours, in ℥iss of gastric juice at 100° F.; the mixture being thoroughly agitated as often as every hour, in order to insure the digestion of as large a quantity of meat as possible. The meat remaining undissolved was then collected on a previously weighed filter, and evaporated to dryness. The dry residue weighed 55 grains. This represented, allowing for the loss by evaporation, 250 grains of the meat, in its natural moist condition; 50 grains of meat were then dissolved by ℥iss of gastric juice, or 33⅓ grains per ounce.

From these data we can form some idea of the large quantity of gastric juice secreted in the dog during the process of digestion. One pound of meat is only a moderate meal for a medium-sized animal, and the same amount, beside other articles of food, is often taken by the human subject in the course of a day; — and yet, to dissolve this quantity, no less than *thirteen pints* of gastric juice will be necessary. This quantity, or any approximation to it, would be altogether incredible if we did not recollect that the gastric juice, as soon as it has dissolved its quota of food, *is immediately reabsorbed,* and again enters the circulation, together with the alimentary substances which it holds in solution. The secretion and reabsorption of the gastric juice then go on simultaneously, and the fluids which the blood loses by one process are incessantly restored to it by the other. A very large quantity,

[1] Annalen der Chemie und Pharmacie, 1854, p. 42.

therefore, of the secretion may be poured out during the digestion of a meal, at an expense to the blood, at any one time, of only two or three ounces of fluid. The simplest investigation shows that the gastric juice does not accumulate in the stomach in any considerable quantity during digestion; but that it is gradually secreted so long as any food remains undissolved, each portion, as it is digested, being disposed of by reabsorption, together with its solvent fluid. There is accordingly, during digestion, a constant circulation of the digestive fluids from the bloodvessels to the alimentary canal, and from the alimentary canal back again to the bloodvessels.

That this circulation really takes place is proved by the following facts: First, if a dog be killed some hours after feeding, there is never more than a very small quantity of fluid found in the stomach, just sufficient to smear over and penetrate the half digested pieces of meat; and, secondly, in the living animal, gastric juice, drawn from the fistula five or six hours after digestion has been going on, contains little or no more organic matter in solution than that extracted fifteen to thirty minutes after the introduction of food. It has evidently been freshly secreted; and, in order to obtain gastric juice saturated with alimentary matter, it must be artificially digested with food in test-tubes, where this constant absorption and renovation cannot take place.

An unnecessary difficulty has sometimes been felt in understanding how it is that the gastric juice, which digests so readily all albuminous substances, should not destroy the walls of the stomach itself, which are composed of similar materials. This, in fact, was brought forward at an early day, as an insuperable objection to the doctrine of Reaumur and Spallanzani, that digestion was a process of chemical solution performed by a digestive fluid. It was said to be impossible that a fluid capable of dissolving animal matters should be secreted by the walls of the stomach without attacking them also, and thus destroying the organ by which it was itself produced. Since that time, various complicated hypotheses have been framed, in order to reconcile these apparently contradictory facts. The true explanation, however, as we believe, lies in this—that the process of digestion is not a simple solution, but a catalytic transformation of the alimentary substances, produced by contact with the pepsine of the gastric juice. We know that all the organic substances in the living tissues are constantly undergoing, in

the process of nutrition, a series of catalytic changes, which are characteristic of the vital operations, and which are determined by the organized materials with which they are in contact, and by all the other conditions present in the living organism. These changes, therefore, of nutrition, secretion, &c., necessarily exclude for the time all other catalyses, and take precedence of them. In the same way, any dead organic matter, exposed to warmth, air, and moisture, putrefies; but if immersed in gastric juice, at the same temperature, the putrefactive changes are stopped or altogether prevented, because the catalytic actions, excited by the gastric juice, take precedence of those which constitute putrefaction. For a similar reason the organic ingredient of the gastric juice, which acts readily on dead animal matter, has no effect on the living tissues of the stomach, because they are already subject to other catalytic influences, which exclude those of digestion, as well as those of putrefaction. As soon as life departs, however, and the peculiar actions taking place in the living tissues come to an end with the stoppage of the circulation, the walls of the stomach are really attacked by the gastric juice remaining in its cavity, and are more or less completely digested and liquefied. In the human subject, it is rare to make an examination of the body twenty-four or thirty-six hours after death, without finding the mucous membrane of the great pouch of the stomach more or less softened and disintegrated from this cause. Sometimes the mucous membrane is altogether destroyed, and the submucous cellular layer exposed; and occasionally, when death has taken place suddenly during active digestion, while the stomach contained an abundance of gastric juice, all the coats of the organ have been found destroyed, and a perforation produced leading into the peritoneal cavity. These post-mortem changes show that, after death, the gastric juice really dissolves the coats of the stomach without difficulty. But during life, the chemical changes of nutrition, which are going on in their tissues, protect them from its influence, and effectually preserve their integrity.

The secretion of the gastric juice is much influenced by nervous conditions. It was noticed by Dr. Beaumont, in his experiments upon St. Martin, that irritation of the temper, and other moral causes, would frequently diminish or altogether suspend the supply of the gastric fluids. Any febrile action in the system or any unusual fatigue, was liable to exert a similar effect. Every one is aware how readily any mental disturbance, such as anxiety, anger,

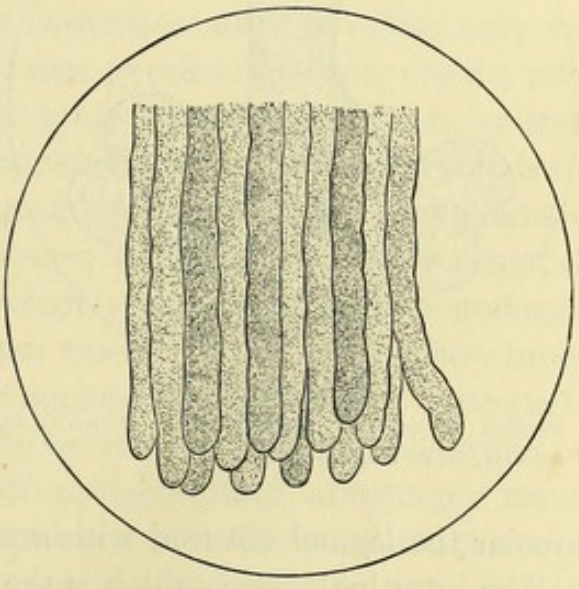
or vexation, will take away the appetite and interfere with digestion. Any nervous impression of this kind, occurring at the *commencement* of digestion, seems moreover to produce some change which has a lasting effect upon the process; for it is very often noticed that when any annoyance, hurry, or anxiety occurs soon after the food has been taken, though it may last only for a few moments, the digestive process is not only liable to be suspended for the time, but to be permanently disturbed during the entire day. In order that digestion, therefore, may go on properly in the stomach, food must be taken only when the appetite demands it; it should also be thoroughly masticated at the outset; and, finally, both mind and body, particularly during the commencement of the process, should be free from any unusual or disagreeable excitement.

Intestinal Juices, and the Digestion of Sugar and Starch. —From the stomach, those portions of the food which have not already suffered digestion pass into the third division of the alimentary canal, viz., the small intestine. As already mentioned, it is only the albuminous matters which are digested in the stomach. Cane sugar, it is true, is slowly converted by the gastric juice, outside the body, into glucose. We have found that ten grains of cane sugar, dissolved in ℥ss of gastric juice, give traces of glucose at the end of two hours; and in three hours, the quantity of this substance is considerable. It cannot be shown, however, that the gastric juice exerts this effect on sugar during ordinary digestion. If pure cane sugar be given to a dog with a gastric fistula, while digestion of meat is going on, it disappears in from two to three hours, without any glucose being detected in the fluids withdrawn from the stomach. It is, therefore, either directly absorbed under the form of cane sugar, or passes, little by little, into the duodenum, where the intestinal fluids at once convert it into glucose.

It is equally certain that starchy matters are not digested in the stomach, but pass unchanged into the small intestine. Here they meet with the mixed intestinal fluids, which act at once upon the starch, and convert it rapidly into sugar. The intestinal fluids, taken from the duodenum of a recently killed dog, exert this transforming action upon starch with the greatest promptitude, if mixed with it in a test-tube, and kept at the temperature of 100° F. Starch is converted into sugar by this means much more rapidly and certainly than by the saliva; and experiment shows that the

intestinal fluids are the active agents in its digestion during life. If a dog be fed with a mixture of meat and boiled starch, and killed a short time after the meal, the stomach is found to contain starch but no sugar; while in the small intestine there is an abundance of sugar, and but little or no starch. If some observers have failed to detect sugar in the intestine after feeding the animal with starch, it is because they have delayed the examination until too late. For it is remarkable how rapidly starchy substances, if previously disintegrated by boiling, are disposed of in the digestive process. If a dog, for example, be fed as above with boiled starch and meat, while some of the meat remains in the stomach for eight, nine, or ten hours, the starch begins immediately to pass into the intestine, where it is at once converted into sugar, and then as rapidly absorbed. The whole of the starch may be converted into sugar, and completely absorbed, in an hour's time. We have even found, at the end of three-quarters of an hour, after a tolerably full meal of boiled starch and meat, that all trace of both starch and sugar had disappeared from both stomach and intestine. The rapidity with which this passage of the starch into the duodenum takes place varies, to some extent, in different animals, according to the general activity of the digestive apparatus; but it is always a comparatively rapid process, when the starch is already liquefied and is administered in a pure form. There can be no doubt that the natural place for the digestion of starchy matters is the small intestine, and that it is accomplished by the action of the intestinal juices.

Fig. 32.



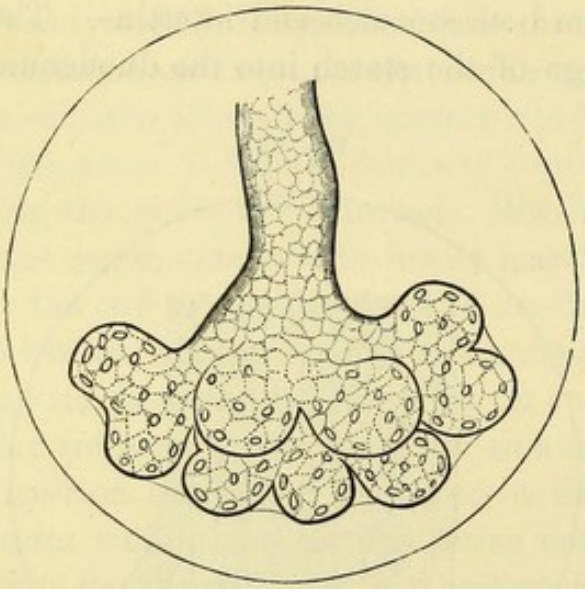
FOLLICLES OF LIEBERKUHN, from Small Intestine of dog.

Our knowledge is not very complete with regard to the exact nature of the fluids by which this digestion of the starch is accomplished. The juices taken from the duodenum are generally a mixture of three different secretions, viz., the bile, the pancreatic fluid, and the intestinal juice proper. Of these, the bile may be left out of the question; since it does not, when in a pure state,

exert any digestive action on starch. The pancreatic juice, on the other hand, has the property of converting starch into sugar; but it is not known whether this fluid be always present in the duodenum. The true *intestinal juice* is the product of two sets of glandular organs, seated in the substance of or beneath the mucous membrane, viz., the follicles of Lieberkühn and the glands of Brunner. The first of these, or Lieberkühn's follicles (Fig. 32), are the most numerous. They are simple, nearly straight tubules, lined with a continuation of the intestinal epithelium, and somewhat similar in their appearance to the follicles of the pyloric portion of the stomach. They occupy the whole thickness of the mucous membrane, and are found in great numbers throughout the entire length of the small and large intestine.

The glands of Brunner (Fig. 33), or the duodenal glandulæ, as they are sometimes called, are confined to the upper part of the duodenum, where they exist as a closely set layer, in the deeper portion of the mucous membrane, extending downward a short distance from the pylorus. They are composed of a great number of rounded follicles, clustered round a central excretory duct. Each follicle consists of a delicate membranous wall, lined with glandular epithelium, and covered on its surface with small, distinctly marked nuclei. The follicles collected around each duct are bound together by a thin layer of areolar tissue, and covered with a plexus of capillary bloodvessels.

Fig. 33.



Portion of one of Brunner's Duodenal Glands, from Human Intestine.

The intestinal juice, which is the secreted product of the above glandular organs, has been less successfully studied than the other digestive fluids, owing to the difficulty of obtaining it in a pure state. The method usually adopted has been to make an opening in the abdomen of the living animal, take out a loop of intestine, empty it by gentle pressure, and then to shut off a portion of it from the rest of the intestinal cavity by a couple of ligatures, situated six or eight inches apart; after which the loop is returned

into the abdomen, and the external wound closed by sutures. After six or eight hours the animal is killed, and the fluid, which has collected in the isolated portion of intestine, taken out and examined. The above was the method adopted by Frerichs. Bidder and Schmidt, in order to obtain pure intestinal juice, first tied the biliary and pancreatic ducts, so that both the bile and the pancreatic juice should be shut out from the intestine, and then established an intestinal fistula below, from which they extracted the fluids which accumulated in the cavity of the gut. From the great abundance of the follicles of Lieberkühn, we should expect to find the intestinal juice secreted in large quantity. It appears, however, in point of fact, to be quite scanty, as the quantity collected in the above manner by experimenters has rarely been sufficient for a thorough examination of its properties. It seems to resemble very closely, in its physical characters, the secretion of the mucous follicles of the mouth. It is colorless and glassy in appearance, viscid and mucous in consistency, and has a distinct alkaline reaction. It has the property when pure, as well as when mixed with other secretions, of rapidly converting starch into sugar, at the temperature of the living body.

PANCREATIC JUICE, AND THE DIGESTION OF FAT.—The only remaining ingredients of the food that require digestion are the oily matters. These are not affected, as we have already stated, by contact with the gastric juice; and examination shows, furthermore, that they are not digested in the stomach. So long as they remain in the cavity of this organ they are unchanged in their essential properties. They are merely melted by the warmth of the stomach, and set free by the solution of the vesicles, fibres, or capillary tubes in which they are contained, or among which they are entangled; and are still readily discernible by the eye, floating in larger or smaller drops on the surface of the semi-fluid alimentary mass. Very soon, however, after its entrance into the intestine, the oily portion of the food loses its characteristic appearance, and is converted into a white, opaque emulsion, which is gradually absorbed. This emulsion is termed the *chyle*, and is always found in the small intestine during the digestion of fat, entangled among the valvulæ conniventes, and adhering to the surface of the villi. The digestion of the oil, however, and its conversion into chyle, does not take place at once upon its entrance into the duodenum, but only after it has passed the orifices of the pancreatic and biliary ducts. Since

these ducts almost invariably open into the intestine at or near the same point, it was for a long time difficult to decide by which of the two secretions the digestion of the oil was accomplished. M. Bernard, however, first threw some light on this question by experimenting on some of the lower animals, in which the two ducts open separately. In the rabbit, for example, the biliary duct opens as usual just below the pylorus, while the pancreatic duct communicates with the intestine some eight or ten inches lower down. Bernard fed these animals with substances containing oil, or injected melted butter into the stomach; and, on killing them afterward, found that there was no chyle in the intestine between the opening of the biliary and pancreatic ducts, but that it was abundant immediately below the orifice of the latter. Above this point, also, he found the lacteals empty or transparent, while below it they were full of white and opaque chyle. The result of these experiments, which have since been confirmed by Prof. Samuel Jackson, of Philadelphia,[1] led to the conclusion that the pancreatic fluid is the active agent in the digestion of oily substances; and an examination of the properties of this secretion, when obtained in a pure state from the living animal, fully confirms the above opinion.

In order to obtain pancreatic juice from the dog, the animal must be etherized, an incision made in the upper part of the abdomen, a little to the right of the median line, and a loop of the duodenum, together with the lower extremity of the pancreas which lies adjacent to it, drawn out at the external wound. The pancreatic duct is then to be exposed and opened, and a small silver canula inserted into it and secured by a ligature. The whole is then returned into the abdomen and the wound closed by sutures, leaving only the end of the canula projecting from it. In the dog there are two pancreatic ducts, situated from half an inch to an inch apart. The lower one of these, which is usually the larger of the two, is the one best adapted for the insertion of the canula. When the effects of etherization have passed off, the animal may be fed, and soon after the digestive process has commenced, the pancreatic juice begins to run from the orifice of the canula, at first very slowly and in drops. Sometimes the drops follow each other with rapidity for a few moments, and then an interval occurs during which the secretion seems entirely suspended. After a time it recommences, and continues to exhibit similar fluctuations during the whole course of the experiment. Its flow, however, is at all times scanty, compared with that of the gastric juice; and we have

[1] American Journ. Med. Sci., Oct. 1854.

never been able to collect more than a little over two fluidounces and a half during a period of three hours, in a dog weighing not more than forty-five pounds. This is equivalent to about 364 grains per hour; but as the pancreatic juice in the dog is secreted with freedom only during digestion, and as this process is in operation not more than twelve hours out of the twenty-four, the entire amount of the secretion for the whole day, in the dog, may be estimated at 4,368 grains. This result, applied to a man weighing 140 pounds, would give, as the total daily quantity of the pancreatic juice, about 13,104 grains, or 1.872 pounds avoirdupois.

Pancreatic juice obtained by the above process is a clear, colorless, somewhat viscid fluid, with a specific gravity of 1008 or 1010, and a distinctly alkaline reaction. Its composition, according to the analysis of Bidder and Schmidt, is as follows: —

Composition of Pancreatic Juice.

Water		900.76
Organic matter (pancreatine)		90.38
Chloride of sodium		7.36
Free soda		0.32
Phosphate of soda		0.45
Sulphate of soda		0.10
Sulphate of potassa		0.02
Combinations of	Lime	0.54
	Magnesia	0.05
	Oxide of iron	0.02
		1000.00

The most important ingredient of the pancreatic juice is its organic matter, or *pancreatine*. It will be seen that this is much more abundant in proportion to the other ingredients of the secretion than the organic matter of any other digestive fluid. It is coagulable by heat; and the pancreatic juice often solidifies completely on boiling, like white of egg, so that not a drop of fluid remains after its coagulation. It is precipitated, furthermore, by nitric acid and by alcohol, and also by sulphate of magnesia in excess. After being precipitated by alcohol, the coagulated matter may be re-dissolved in water and thus regain all the original properties of pancreatine. By the last two characters, accordingly, it may be distinguished from albumen, which is not affected by sulphate of magnesia, and which is not soluble in water after being once precipitated by alcohol.

Fresh pancreatic juice, brought into contact with oily matters at the temperature of the body, exerts upon them, as was first noticed by Bernard, a marked effect. It disintegrates them, and reduces

them to a state of complete emulsion, so that the mixture is at once converted into a white, opaque, creamy-looking fluid. This effect is instantaneous and permanent, and only requires that the two substances be well mixed by gentle agitation. It is singular that some of the German observers should deny that the pancreatic juice possesses the property of emulsioning fat, to a greater extent than the bile and some other digestive fluids; and should state that although, when shaken up with oil, outside the body, it reduces the oily particles to a state of extreme minuteness, the emulsion is not permanent, and the oily particles "soon separate again on the surface."[1] We have frequently repeated this experiment with different specimens of pancreatic juice obtained from the dog, and have never failed to see that the emulsion produced by it is by far more prompt and complete than that which takes place with saliva, gastric juice, or bile. The effect produced by these fluids is in fact altogether insignificant, in comparison with the prompt and energetic action exerted by the pancreatic juice. The emulsion produced with the latter secretion may be kept, furthermore, for at least twenty-four hours, according to our observations, without any appreciable separation of the oily particles, or a return to their original condition.

The pancreatic juice, therefore, is peculiar in its action on oily substances, and reduces them at once to the condition of an emulsion. The oil, in this process, does not suffer any chemical alteration. It is not decomposed or saponified, to any appreciable extent. It is simply *emulsioned;* that is, it is broken up into a state of minute subdivision, and retained in suspension, by contact with the organic matter of the pancreatic juice. That its chemical condition is not altered is shown by the fact that it is still soluble in ether, which will withdraw the greater part of the fat from a mixture of oil and pancreatic juice, as well as from the chyle in the interior of the intestine. In a state of emulsion, the fat, furthermore, is capable of being absorbed, and its digestion may be then said to be accomplished.

We find, then, that the digestion of the food is not a simple operation, but is made up of several different processes, which commence successively in different portions of the alimentary canal. In the first place, the food is subjected in the mouth to the physical operations of mastication and insalivation. Reduced to a soft pulp and mixed abundantly with the saliva, it passes, secondly, into the stomach. Here it excites the secretion of the gastric juice,

[1] Lehmann's Physiological Chemistry. Philada. ed., vol. i. p. 507.

by the influence of which its chemical transformation and solution are commenced. If the meal consist wholly or partially of muscular flesh, the first effect of the gastric juice is to dissolve the intervening cellular substance, by which the tissue is disintegrated and the muscular fibres separated from each other. Afterward the muscular fibres themselves become swollen and softened by the imbibition of the gastric fluid, and are finally disintegrated and liquefied. In the small intestine, the pancreatic and intestinal juices convert the starchy ingredients of the food into sugar, and break up the fatty matters into a fine emulsion, by which they are converted into chyle.

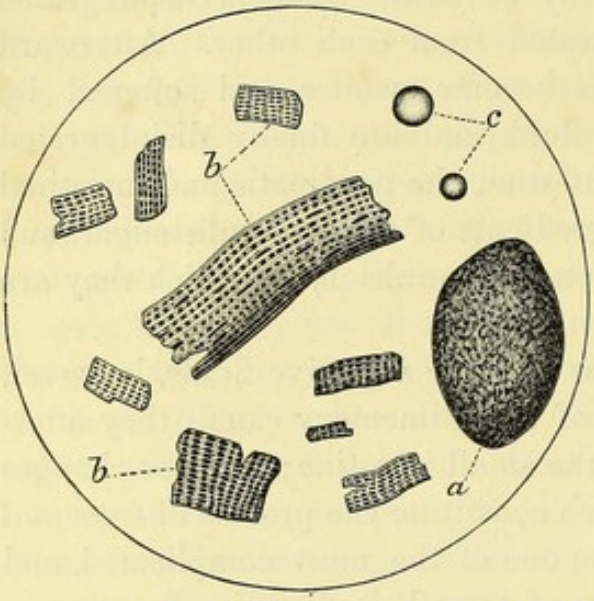
Although the separate actions of these digestive fluids, however, commence at different points of the alimentary canal, they afterward go on simultaneously in the small intestine; and the changes which take place here, and which constitute the process of *intestinal digestion*, form at the same time one of the most complicated, and one of the most important parts of the whole digestive function.

The phenomena of intestinal digestion may be studied, in the dog, by killing the animal at various periods after feeding, and examining the contents of the intestine. We have also succeeded, by establishing in the same animal an artificial intestinal fistula, in gaining still more satisfactory information on this point. The fistula may be established, for this purpose, by an operation precisely similar to that already described as employed for the production of a permanent fistula in the stomach. The silver tube having been introduced into the lower part of the duodenum, the wound is allowed to heal, and the intestinal secretions may then be withdrawn at will, and subjected to examination at different periods during digestion.

By examining in this way, from time to time, the intestinal fluids, it at once becomes manifest that the action of the gastric juice, in the digestion of albuminoid substances, is not confined to the stomach, but continues after the food has passed into the intestine. About half an hour after the ingestion of a meal, the gastric juice begins to pass into the duodenum, where it may be recognized by its strongly-marked acidity, and by its peculiar action, already described, in interfering with Trommer's test for grape sugar. It has accordingly already dissolved some of the ingredients of the food while still in the stomach, and contains a certain quantity of albuminose in solution. It soon afterward, as it continues to pass into the duodenum, becomes mingled with the debris of muscular

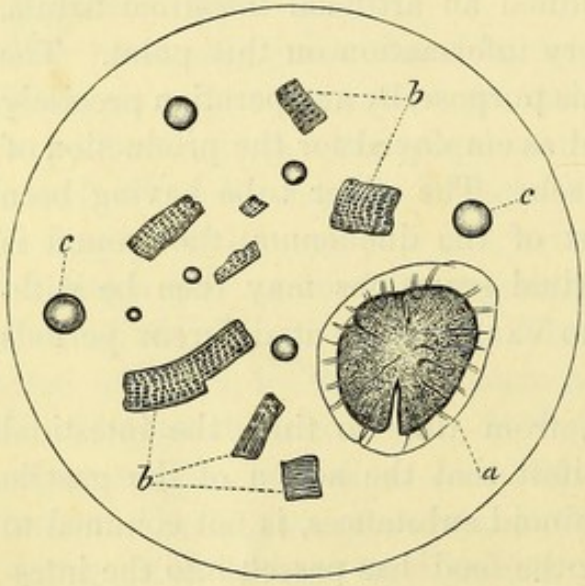
fibres, fat vesicles, and oil drops; recognizable under the microscope,

Fig. 34.



CONTENTS OF STOMACH DURING DIGESTION OF MEAT, from the Dog.—*a*. Fat Vesicle, filled with opaque, solid, granular fat. *b*, *b*. Bits of partially disintegrated muscular fibre. *c*. Oil globules.

Fig. 35.



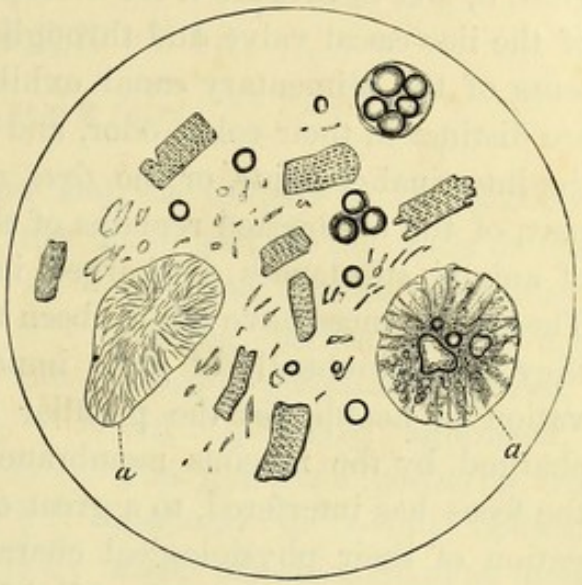
FROM DUODENUM OF DOG, DURING DIGESTION OF MEAT.—*a*. Fat Vesicle, with its contents diminishing. The vesicle is beginning to shrivel and the fat breaking up. *b*, *b*. Disintegrated muscular fibre. *c*, *c*. Oil Globules.

substances which are easily and which produce a grayish turbidity in the fluid drawn from the fistula. This turbid admixture grows constantly thicker from the second to the tenth or twelfth hour; after which the intestinal fluids become less abundant, and finally disappear almost entirely, as the process of digestion comes to an end.

The passage of disintegrated muscular tissue into the intestine may also be shown, as already mentioned, by killing the animal and examining the contents of the alimentary canal. During the digestion of muscular flesh and adipose tissue, the stomach contains masses of softened meat, smeared over with gastric juice, and also a moderate quantity of grayish, grumous fluid, with an acid reaction. This fluid contains muscular fibres, isolated from each other, and more or less disintegrated, by the action of the gastric juice. (Fig. 34.) The fat vesicles are but little or not at all altered in the stomach, and there are only a few free oil globules to be seen floating in the mixed fluids, contained in the cavity of the organ. In the duodenum the muscular fibres are further disintegrated. (Fig. 35.) They become very much broken up, pale and transparent, but can still be recognized by the granular markings and striations which are characteristic of them. The fat vesi-

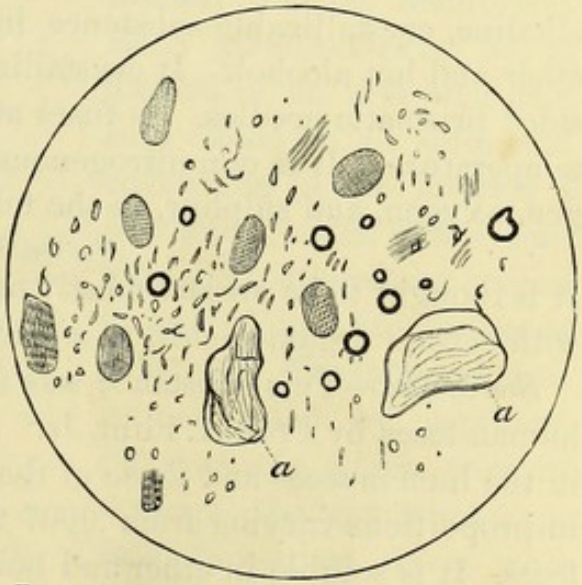
cles also begin to become altered in the duodenum. The solid granular fat of beef, and similar kinds of meat, becomes liquefied and emulsioned; and appears under the form of free oil drops and fatty molecules; while the fat vesicle itself is partially emptied, and becomes more or less collapsed and shrivelled. In the middle and lower parts of the intestine (Figs. 36 and 37) these changes continue. The muscular fibres become constantly more and more disintegrated, and a large quantity of granular debris is produced, which is at last also dissolved. The fat also progressively disappears, and the vesicles may be seen in the lower part of the intestine, entirely collapsed and empty.

Fig. 36.



From Middle of Small Intestine.—*a*, *a*. Fat vesicles, nearly emptied of their contents.

Fig. 37.



From last quarter of Small Intestine. —*a*, *a*. Fat vesicles, quite empty and shrivelled.

In this way the digestion of the different ingredients of the food goes on in a continuous manner, from the stomach throughout the entire length of the small intestine. At the same time, it results in the production of three different substances, viz: 1st. Albuminose, produced by the action of the gastric juice on the albuminoid matters; 2d. An oily emulsion, produced by the action of the pancreatic juice on fat; and, 3d. Sugar, produced from the transformation of starch by the mixed intestinal fluids. These substances are then ready to be taken up into the circulation; and as the mingled ingredients of the intestinal contents pass successively downward, through the duodenum, jejunum, and ileum, the products of digestion, together with the digestive secretions themselves, are gradually absorbed, one after another, by the vessels of the mucous membrane, and carried away by the current of the circulation.

THE LARGE INTESTINE AND ITS CONTENTS.—Throughout the small intestine, as we have just seen, the secretions are intended exclusively or mainly to act upon the food, to liquefy or disintegrate it, and to prepare it for absorption. But below the situation of the ileo-cæcal valve, and throughout the large intestine, the contents of the alimentary canal exhibit a different appearance, and are distinct in their color, odor, and consistency. This portion of the intestinal contents, or the *feces*, are not composed, for the most part, of the undigested remains of the food, but consist principally of animal substances discharged into the intestine by excretion. These substances have not all been fully investigated; for although they are undoubtedly of great importance in regard to the preservation of health, yet the peculiar manner in which they are discharged by the mucous membrane and united with each other in the feces has interfered, to a great extent, with a thorough investigation of their physiological characters. Those which have been most fully examined are the following:—

Excretine.—This was discovered and described by Dr. W. Marcet,[1] as a characteristic ingredient of the human feces. It is a slightly alkaline, crystallizable substance, insoluble in water, but soluble in ether and hot alcohol. It crystallizes in radiated groups of four-sided prismatic needles. It fuses at 204° F., and burns at a higher temperature. It is non-nitrogenous, and consists of carbon, hydrogen, oxygen, and sulphur, in the following proportions:—

$$C_{78}\,H_{78}\,O_2\,S.$$

It is thought to be present mostly in a free state, but partly in union with certain organic acids, as a saline compound.

Stercorine.—This substance was found to be an ingredient of the human feces by Prof. A. Flint, Jr.[2] It was found by Prof. Flint both in the human feces and those of the dog; and was obtained by him in proportions varying from .0007 to .003 of the whole mass of the feces. It is soluble in ether and boiling alcohol, and, like excretine, crystallizes in the form of radiating needles, but fuses at a much lower temperature. It is regarded by its discoverer as produced, by transformation, from cholesterine, one of the ingredients of the bile.

Beside these substances, the feces contain a certain amount of fat, fatty acids, and the remnants of undigested food. Vegetable cells and fibres may be detected, and some debris of the disintegrated muscular fibres may almost always be found after a meal composed of animal and vegetable substances. But little absorption, accordingly, takes place in the large intestine. Its office is mainly confined to the separation and discharge of certain excrementitious substances.

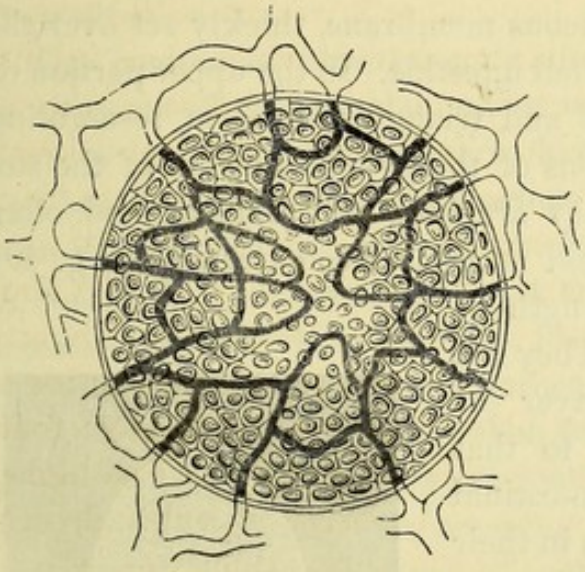
[1] Philos. Trans., Lond., 1857, p. 410. [2] Am. Journ. Med. Sci., Oct., 1862

CHAPTER VII.

ABSORPTION.

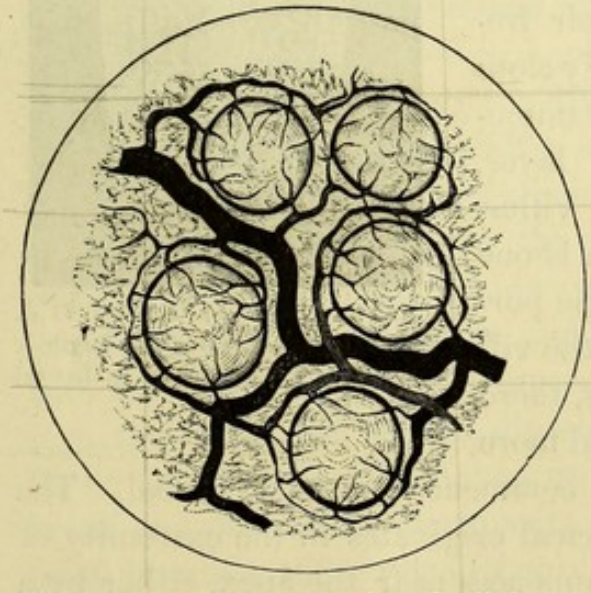
BESIDE the glands of Brunner and the follicles of Lieberkühn, already described, there are, in the inner part of the walls of the intestine, certain glandular-looking bodies which are termed "glandulæ solitariæ," and "glandulæ agminatæ." The glandulæ solitariæ are globular or ovoid bodies, about one-thirtieth of an inch in diameter, situated partly in and partly beneath the intestinal mucous membrane. Each glandule (Fig. 38) is formed of an investing capsule, closed on all sides, and containing in its interior a soft pulpy mass, which consists of minute cellular bodies, imbedded in a homogeneous substance. The inclosed mass is penetrated by capillary bloodvessels, which pass in through the investing capsule, inosculate freely with each other, and return upon themselves in loops near the centre of the glandular body. There is no external opening or duct; in fact, the contents of the vesicle, being pulpy and vascular, as already described, are not to be regarded as a secretion, but as constituting a kind of solid gland-

Fig. 38.



ONE OF THE CLOSED FOLLICLES OF PEYER'S PATCHES, from Small Intestine of Pig. Magnified 50 diameters.

Fig. 39.

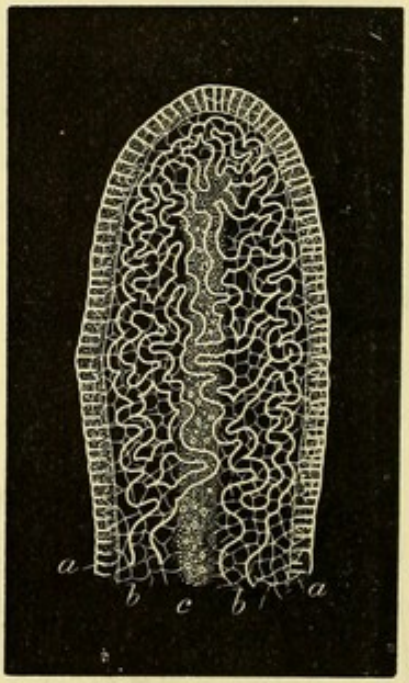


GLANDULÆ AGMINATÆ, from Small Intestine of Pig. Magnified 20 diameters.

tissue. The glandulæ agminatæ (Fig. 39), or "Peyer's patches," as they are sometimes called, consist of aggregations of similar globular or ovoid bodies, found most abundantly toward the lower extremity of the small intestine. Both the solitary and agminated glandules are evidently connected with the lacteals and the system of the mesenteric glands, which latter organs they resemble very much in their minute structure. They are probably to be regarded as the first row of mesenteric glands, situated in the walls of the intestinal canal.

Another set of organs, intimately connected with the process of absorption, are the *villi* of the small intestine. These are conical vascular eminences of the mucous membrane, thickly set over the whole internal surface of the small intestine. In the upper portion of the intestine, they are flattened and triangular in form, resembling somewhat the conical projections of the pyloric portion of the stomach. In the lower part they are long and filiform, and often slightly enlarged, or club-shaped at their free extremity (Fig. 40), and frequently attaining the length of one thirty-fifth of an inch. They are covered externally with a layer of columnar epithelium, similar to that which lines the rest of the intestinal mucous membrane, and contain in their interior two sets of vessels. The most superficial of these are the capillary bloodvessels, which are supplied in each villus by a twig of the mesenteric artery, and which form, by their frequent inosculation, an exceedingly close and abundant network, almost immediately beneath the epithelial layer. They unite at the base of the villus, and form a minute vein, which is one of the commencing rootlets of the portal vein. In the central part of the villus, and lying nearly in its axis, there is another vessel, with thinner and more transparent walls, which is the commencement of a lacteal. The precise manner in which the lacteal originates in the extremity of the villus is not known. It commences near the apex, either by a blind extremity, or by an irregular plexus, passes, in a straight or

Fig. 40.



EXTREMITY OF INTESTINAL VILLUS, from the Dog.—*a*. Layer of epithelium. *b*. Bloodvessel. *c*. Lacteal vessel.

somewhat wavy line, toward the base of the villus, and then becomes continuous with a small twig of the mesenteric lacteals.

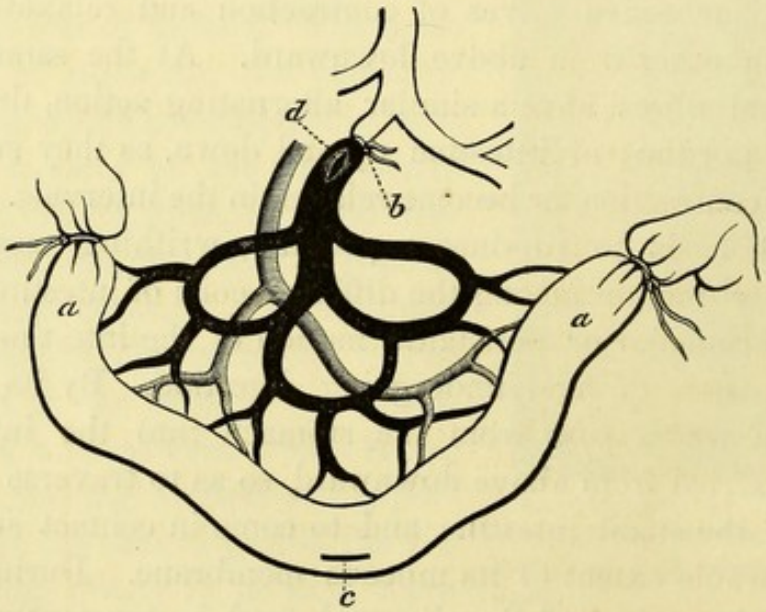
The villi are the active agents in the process of absorption. By their projecting form, and their great abundance, they increase enormously the extent of surface over which the digested fluids come in contact with the intestinal mucous membrane, and increase, also, to a corresponding degree, the energy with which absorption takes place. They hang out into the nutritious, semi-fluid mass contained in the intestinal cavity, as the roots of a tree penetrate the soil; and they imbibe the liquefied portions of the food, with a rapidity which is in direct proportion to their extent of surface, and the activity of their circulation.

The process of absorption is also hastened by the peristaltic movements of the intestine. The muscular layer here, as in other parts of the alimentary canal, is double, consisting of both circular and longitudinal fibres. The action of these fibres may be readily seen by pinching the exposed intestine with the blades of a forceps. A contraction then takes place at the spot irritated, by which the intestine is reduced in diameter, its cavity obliterated, and its contents forced onward into the succeeding portion of the alimentary canal. The local contraction then propagates itself to the neighboring parts, while the portion originally contracted becomes relaxed; so that a slow, continuous, creeping motion of the intestine is produced, by successive waves of contraction and relaxation, which follow each other from above downward. At the same time, the longitudinal fibres have a similar alternating action, drawing the narrowed portions of intestine up and down, as they successively enter into contraction, or become relaxed in the intervals. The effect of the whole is to produce a peculiar, writhing, worm-like, or "vermicular" motion, among the different coils of intestine. During life, the vermicular or peristaltic motion of the intestine is excited by the presence of food undergoing digestion. By its action, the substances which pass from the stomach into the intestine are steadily carried from above downward, so as to traverse the entire length of the small intestine, and to come in contact successively with the whole extent of its mucous membrane. During this passage, the absorption of the digested food is constantly going on. Its liquefied portions are taken up by the villi of the mucous membrane, and successively disappear; so that, at the termination of the small intestine, there remains only the undigestible portion of the food, together with the refuse of the intestinal secretions. These

pass through the ileo-cæcal orifice into the large intestine, and there become reduced to the condition of feces.

The absorption of the digested fluids is accomplished mainly by the bloodvessels. It was formerly supposed that the lacteals were the only agents in this process; but it has now been long known that this opinion was erroneous, and that the bloodvessels take at least an equal part in absorption, and are in some respects the most active and important agents of the two. Abundant experiments have demonstrated not only that soluble substances introduced into the intestine may be soon afterward detected in the blood of the portal vein, but that absorption takes place more rapidly and abundantly by the bloodvessels than by the lacteals. This was first shown by Magendie,[1] who found that the absorption of poisonous substances would take place, in the living animal, both from the cavity of the intestine and from the tissues of the lower extremity, notwithstanding that all communication through the lacteals and lymphatics was cut off, and the passage by the bloodvessels alone remained. These results were afterward corroborated by Panizza,[2] who succeeded in detecting the substance which had been absorbed in the venous blood returning from the part This observer opened the abdomen of a horse, and drew out a fold of the small intestine, eight or nine inches in length (Fig. 41, *a*, *a*), which

Fig. 41.



PANIZZA'S EXPERIMENT.—*aa*. Intestine. *b*. Point of ligature of mesenteric vein. *c*. Opening in intestine for introduction of poison. *d*. Opening in mesenteric vein behind the ligature.

[1] Journal de Physiologie, vol. i. p. 18.

[2] In Matteucci's Lectures on the Physical Phenomena of Living Beings, Pereira's edition, p. 83.

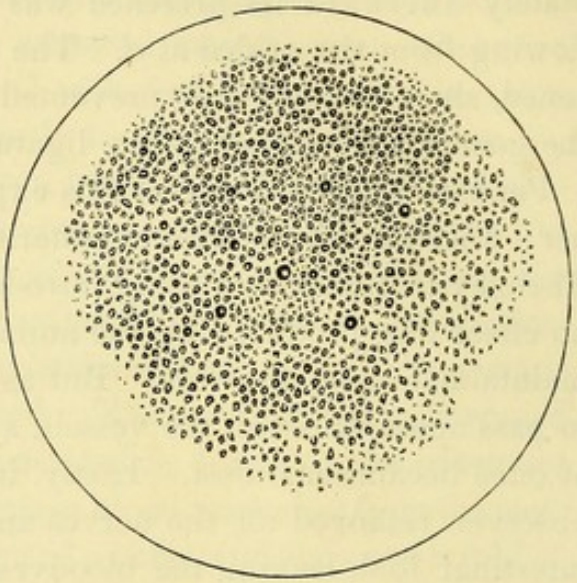
he included between two ligatures. A ligature was then placed (at *b*) upon the mesenteric vein receiving the blood from this portion of intestine; and, in order that the circulation might not be interrupted, an opening was made (at *d*) in the vein behind the ligature, so that the blood brought by the mesenteric artery, after circulating in the intestinal capillaries, passed out at the opening, and was collected in a vessel for examination. Hydrocyanic acid was then introduced into the intestine by an opening at *c*, and almost immediately afterward its presence was detected in the venous blood flowing from the orifice at *d*. The animal, however, was not poisoned, since the acid was prevented from gaining an entrance into the general circulation by the ligature at *b*.

Panizza afterward varied this experiment in the following manner: Instead of tying the mesenteric vein, he simply compressed it. Then, hydrocyanic acid being introduced into the intestine, as above, no effect was produced on the animal, so long as compression was maintained upon the vein. But as soon as the blood was allowed to pass again through the vessels, symptoms of general poisoning at once became manifest. Lastly, in a third experiment, the same observer removed all the nerves and lacteal vessels supplying the intestinal fold, leaving the bloodvessels alone untouched. Hydrocyanic acid now being introduced into the intestine, found an entrance at once into the general circulation, and the animal was immediately poisoned. The bloodvessels, therefore, are not only capable of absorbing fluids from the intestine, but take them up even more rapidly and abundantly than the lacteals.

Accordingly the products of digestion, on being taken up by the villi, are absorbed by the capillary bloodvessels and pass into the current of the abdominal venous circulation. After the digestion of food containing a mixture of albuminous and starchy ingredients, both albuminose and sugar are to be found in the blood of the portal vein. These substances, however, do not mingle at once with the general mass of the circulation, but, owing to the anatomical distribution of the portal vein, pass first through the capillary circulation of the liver. Soon after being introduced into the blood and coming in contact with its organic ingredients, they become altered and converted, by catalytic transformation, into other substances. The albuminose passes, in all probability, into the condition of ordinary albumen, while the sugar rapidly becomes decomposed, or transformed, and loses its characteristic properties; so that, on arriving at the entrance of the general circulation, both these newly absorbed ingredients have become already assimilated to those which previously existed in the blood.

The fatty matters of the digested food are also taken up by the bloodvessels and pass in this way into the circulation. We have already shown that these fatty ingredients, by the action of the pancreatic juice, are reduced to the condition of an emulsion, forming in the intestine a white milky fluid termed the "chyle." In chyle drawn from the lacteals or the thoracic duct, the fatty matter still presents itself in the same condition, and retains all the chemical properties of oil. Examined by the microscope, it is seen to exist under the form of fine granules and molecules, which present the ordinary appearances of oil in a state of minute subdivision. The chyle, therefore, does not represent the entire product of the digestive process, but contains only the fatty substances, suspended by emulsion in a serous fluid.

Fig. 42.



CHYLE FROM COMMENCEMENT OF THORACIC DUCT, from the Dog.—The molecules vary in size from 1-10,000th of an inch downward.

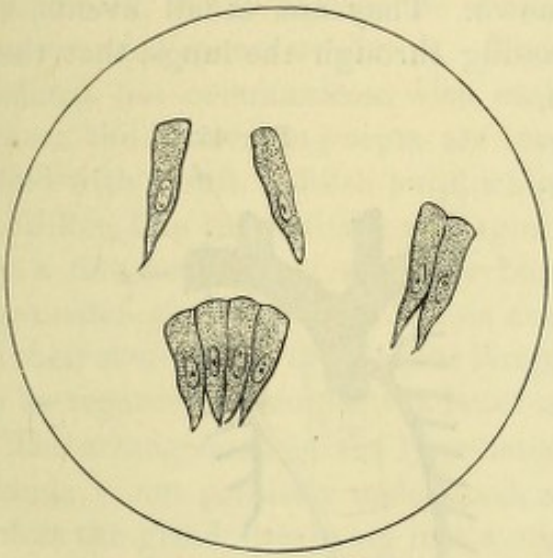
The oleaginous materials, thus prepared, are absorbed by the bloodvessels of the intestine. The blood of the portal vein during digestion, in the carnivorous animals, contains a considerable amount of fatty matter in a state of minute subdivision, often communicating a turbid or milky appearance to the serum after coagulation; other observers (Bernard,[1] Lehmann, Schultz, Simon) have noticed the same fact, and have found the blood of the portal vein to be considerably richer in fat, than that of other veins, particularly while intestinal digestion is going on with activity.

A difficulty has been experienced in accounting for the absorption of fat from the intestine, owing to its being considered as a non-endosmotic substance; that is, as incapable, in its free or undissolved condition, of penetrating and passing through an animal membrane by endosmosis. It is stated, indeed, that if a fine oily emulsion be placed on one side of an animal membrane in an endosmometer, and pure water on the other, the water will readily penetrate the substance of the membrane, while the oily particles cannot be made to pass, even under a high pressure. Though this be true, however, for pure water, it is not true for slightly alkaline fluids,

[1] Leçons de Physiologie Expérimentale. Paris, 1856, p. 325.

like the serum of the blood and the lymph. This has been demonstrated by the experiments of Matteucci, in which he made an emulsion with an alkaline fluid containing 43 parts per thousand of caustic potassa. Such a solution has no perceptible alkaline taste, and its action on reddened litmus paper is about equal to that of the lymph and chyle. If this emulsion were placed in an endosmometer, together with a watery alkaline solution of similar strength, it was found that the oily particles penetrated through the animal membrane without much difficulty, and mingled with the fluid on the opposite side. Although, therefore, we cannot explain the exact mechanism of absorption in the case of fat, still we know that it is not in opposition to the ordinary phenomena of endosmosis; for endosmosis will take place with a fatty emulsion, provided the fluids used in the experiment be slightly alkaline in reaction.

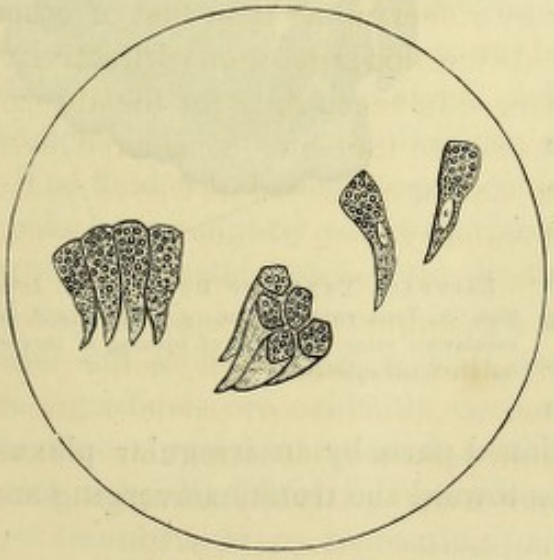
Fig. 43.



INTESTINAL EPITHELIUM; from the Dog, while fasting.

It is, accordingly, by a process of endosmosis, or imbibition, that the villi take up the digested fatty substances. There are no open orifices or canals, into which the oil penetrates; but it passes directly into and through the substance of the villi. The epithelial cells covering the external surface of the villus are the first active agents in this absorption. In the intervals of digestion (Fig. 43) these cells are but slightly granular and nearly transparent in appearance. But if examined during the digestion and absorption of fat (Fig. 44), their substance is seen to be crowded with oily particles, which they have taken up from the intestinal cavity by absorption. The

Fig. 44.



INTESTINAL EPITHELIUM; from the Dog, during the digestion of fat.

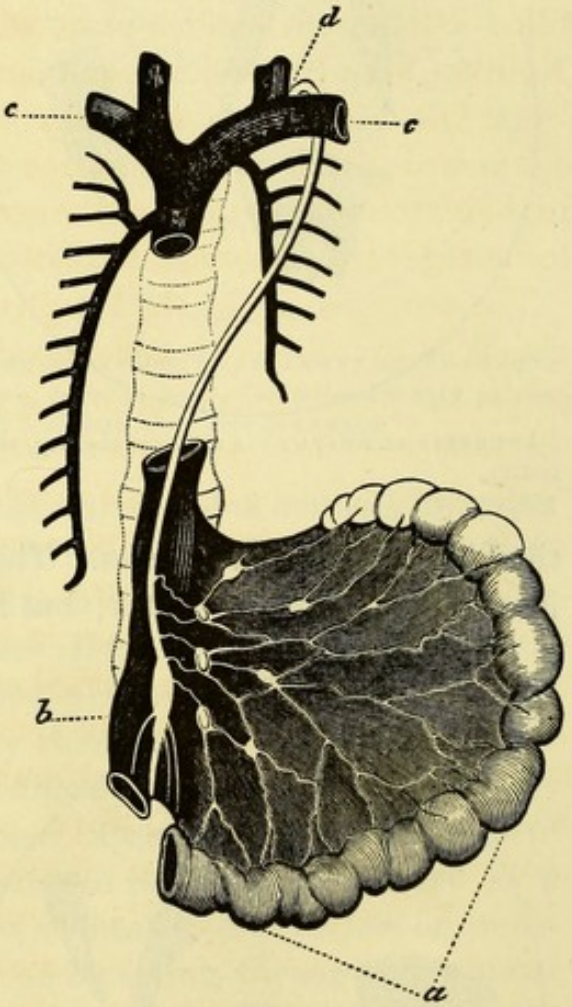
oily matter then passes onward, penetrating deeper and deeper into the substance of the villus, until it is at last received by the capillary vessels in its interior.

The fatty substances thus taken up by the portal vein, do not at once enter the general circulation, but pass first through the capillary system of the liver. Thence they are carried, with the blood of the hepatic vein, to the right side of the heart, and subsequently through the capillary system of the lungs. While passing through the pulmonary circulation, however, they disappear. Precisely what becomes of them, or what particular chemical changes they undergo, is not certainly known. They are, at all events, so altered in the blood, while passing through the lungs, that they lose the form of a fatty emulsion, and are no longer to be recognized by the usual tests for oleaginous substances.

The absorption of fatty matters is also accomplished by another set of capillary vessels of the intestine, namely, the "lacteals."

The lacteals, however, are not a special system of vessels by themselves, but are simply a part of the great system of "absorbent" or "lymphatic" vessels, which are to be found everywhere in the integuments of the head, the parietes of the trunk, the upper and lower extremities, and in the muscular tissues and mucous membranes throughout the body. The walls of these vessels are thinner and more transparent than those of the arteries and veins, and they are consequently less easily detected by ordinary dissection. They originate in the tissues of the above-mentioned parts by an irregular plexus. They pass from the extremities toward the trunk, converging and

Fig. 45.



LACTEALS, THORACIC DUCT, &c.—*a*. Intestine. *b*. Vena cava inferior. *c, c*. Right and left subclavian veins. *d*. Point of opening of thoracic duct into left subclavian.

uniting with each other like the veins, their principal branches taking usually the same direction with the nerves and bloodvessels, and passing, at various points in their course, through certain glandular bodies, the "lymphatic or "absorbent" glands. The lymphatic glands, among which are included the mesenteric glands, consist of an external layer of fibrous tissue and a contained pulp or parenchyma. The investing layer of fibrous tissue sends off thin septa or laminæ from its internal surface, which penetrate the substance of the gland in every direction and unite with each other at various points. In this way they form an interlacing laminated framework, which divides the substance of the gland into numerous rounded spaces or alveoli. These alveoli are not completely isolated, but communicate with each other by narrow openings, where the intervening septa are incomplete. These cavities are filled with a soft, reddish pulp, which is penetrated, according to Kölliker, like the solitary and agminated glands of the intestine, by a fine network of capillary bloodvessels. The solitary and agminated glands of the intestine are, therefore, closely analogous in their structure to those of the lymphatic system. The former are to be regarded as simple, the latter as compound vascular glands.

The arrangement of the lymphatic vessels in the interior of the glands is not precisely understood. Each lymphatic vessel, as it enters the gland, breaks up into a number of minute ramifications, the *vasa afferentia;* and other similar twigs, forming the *vasa efferentia,* pass off in the opposite direction, from the farther side of the gland; but the exact mode of communication between the two has not been definitely ascertained. The fluids, however, arriving by the vasa afferentia, must pass in some way through the tissue of the gland, before they are carried away again by the vasa efferentia. From the lower extremities the lymphatic vessels enter the abdomen at the groin and converge toward the receptaculum chyli, into which their fluid is discharged, and afterward conveyed, by the thoracic duct, to the left subclavian vein.

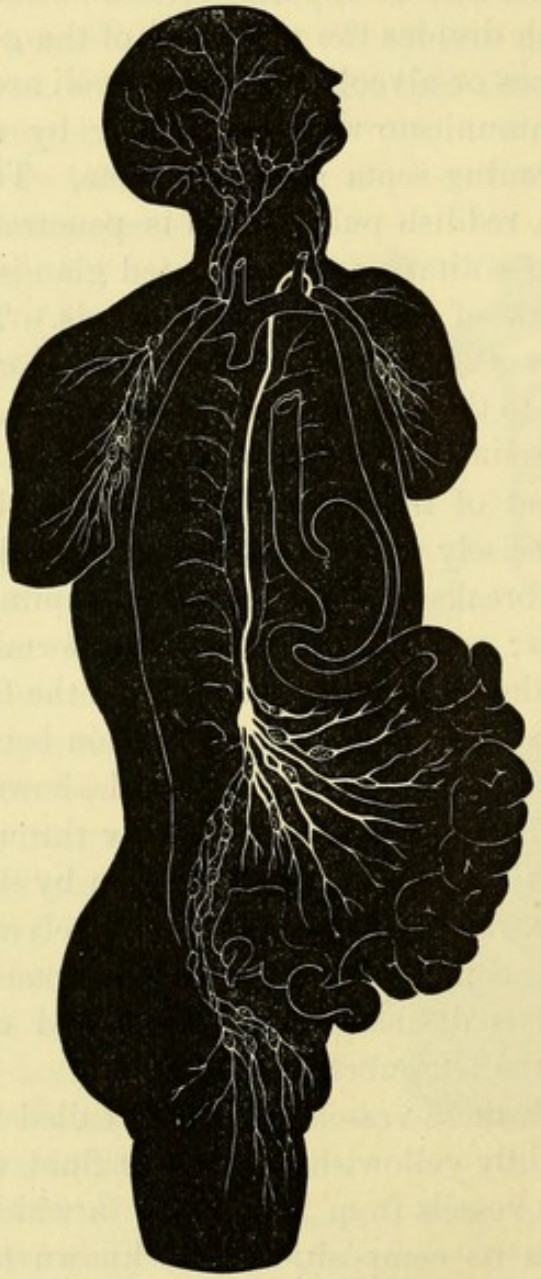
The fluid which these vessels contain is called the *lymph.* It is a colorless or slightly yellowish transparent fluid, which is absorbed by the lymphatic vessels from the tissues in which they originate. So far as regards its composition, it is known to contain, beside water and saline matters, a small quantity of fibrin and albumen. Its ingredients are evidently derived from the metamorphosis of the tissues, and are returned to the centre of the circulation in order to be eliminated by excretion, or in order to undergo some new transforming or renovating process. We are ignorant, how-

ever, with regard to the precise nature of their character and destination.

The lacteals are simply that portion of the absorbents which originate in the mucous membrane of the small intestine. During the intervals of digestion, these vessels contain a colorless and transparent lymph, entirely similar to that which is found in other parts of the absorbent system.

But while intestinal absorption is going on, after a meal contain-

Fig. 46.



LACTEALS AND LYMPHATICS.

ing fatty ingredients, the lacteals may be seen as white, opaque vessels, distended with milky chyle, passing through the mesentery,

and converging from its intestinal border toward the receptaculum chyli, near the spinal column. During their course, they pass through several successive rows of mesenteric glands, which also become turgid with chyle while the process of digestion is going on. The lacteals then conduct the chyle to the receptaculum chyli, whence it passes upward through the thoracic duct, and is finally discharged, at the termination of this canal, into the left subclavian vein. (Fig. 46.) It is then mingled with the returning current of venous blood, and passes into the right cavities of the heart.

The presence of chyle in the lacteals is, therefore, not a constant, but only a periodical phenomenon. The fatty substances constituting the chyle begin to be absorbed during the process of digestion, as soon as they have been disintegrated and emulsioned by the action of the intestinal fluids. As digestion proceeds, they accumulate in larger quantity, and gradually fill the whole lacteal system and the thoracic duct. As they are discharged into the subclavian vein, and mingled with the blood, they can still be distinguished in the circulating fluid, as a mixture of oily molecules, between the orifice of the thoracic duct and the right side of the heart; while passing through the lungs, however, they become altered in character as above described, and lose for the most part the distinguishing characteristics of oily matter before they have passed beyond the pulmonary circulation. The fatty substances thus introduced by the bloodvessels and the lacteals are in this way rapidly transformed and assimilated to the ordinary ingredients of the blood.

But as digestion proceeds, an increasing quantity of fatty matter finds its way, by these two passages, into the blood; and a time at last arrives when the whole of the fat so introduced is not destroyed during its passage through the lungs. Its absorption taking place at this time more rapidly than its decomposition, it begins to appear, in moderate quantity, in the blood of the general circulation; and, lastly, when the intestinal absorption is at its point of greatest activity, it is found in considerable abundance throughout the entire vascular system. At this period, some hours after the ingestion of food rich in oleaginous matters, the blood, not only of the portal vein, but also of the general circulation, everywhere contains a superabundance of fat, derived from the digestive process. If blood be then drawn from the veins or arteries in any part of the body, it will present the peculiar appearance known as that of "chylous" or "milky" blood. After the separation of the clot,

the serum presents a turbid appearance; and the fatty substances, which it contains, rise to the top after a few hours, and cover its surface with a partially opaque and creamy-looking pellicle. This appearance has been occasionally observed in the human subject, particularly in bleeding for apoplectic attacks occurring after a full meal, and has been mistaken, in some instances, for a morbid phenomenon. It is, however, a perfectly natural one, and depends simply on the rapid absorption, at certain periods of digestion, of oleaginous substances from the intestine. It can be produced at will, at any time, in the dog, by feeding him with fat meat, and drawing blood, seven or eight hours afterward, from the carotid artery or the jugular vein.

This state of things continues for a varying length of time, according to the amount of oleaginous matters contained in the food. When digestion is terminated, and the fat ceases to be introduced in unusual quantity into the circulation, its transformation and decomposition continuing to take place in the blood, it disappears gradually from the veins, arteries, and capillaries of the general system; and, finally, when the whole of the fat has been disposed of by the nutritive processes, the serum again becomes transparent, and the blood returns to its ordinary condition.

In this manner the nutritive elements of the food, prepared for absorption by the digestive process, are taken up into the circulation under the different forms of albuminose, sugar, and chyle, and accumulate as such, at certain times, in the blood. But these conditions are only temporary, or transitional. The nutritive materials soon pass, by catalytic transformation, into other forms, and become assimilated to the pre-existing elements of the circulating fluid. Thus they accomplish finally the whole object of digestion; which is to replenish the blood by a supply of new materials from without. There are, however, two other intermediate processes, taking place partly in the liver and partly in the intestine, at about the same time, and having for their object the final preparation and perfection of the circulating fluid. These two processes require to be studied, before we can pass on to the particular description of the blood itself. They are: 1st, the secretion and reabsorption of the bile; and 2d, the production of sugar in the liver, and its subsequent decomposition in the blood.

CHAPTER VIII.

THE BILE.

THE bile is more easily obtained in a state of purity than any other of the secretions which find their way into the intestinal canal, owing to the existence of a gall-bladder in which it accumulates, and from which it may be readily obtained without any other admixture than the mucus of the gall-bladder itself. Notwithstanding this, its study has proved an unusually difficult one. This difficulty has resulted from the peculiar nature of the biliary ingredients, and the readiness with which they become altered by chemical manipulation; and it is, accordingly, only quite recently that we have arrived at a correct idea of its real constitution.

The bile, as it comes from the gall-bladder, is a somewhat viscid and glutinous fluid, varying in color and specific gravity according to the species of animal from which it is obtained. Human bile is of a dark golden brown color, ox bile of a greenish yellow, pig's bile of a nearly clear yellow, and dog's bile of a deep brown. We have found the specific gravity of human bile to be 1018, that of ox bile 1024, that of pig's bile 1030 to 1036. The reaction of the bile with test-paper cannot easily be determined; since it has only a bleaching or decolorizing effect on litmus, and does not turn it either blue or red. It is probably either neutral or very slightly alkaline. A very characteristic physical property of the bile is that of frothing up into a soap-like foam when shaken in a test-tube, or when air is forcibly blown into it through a small glass tube or blowpipe. The bubbles of foam, thus produced, remain for a long time without breaking, and adhere closely to each other and to the sides of the glass vessel.

The following is an analysis of the bile of the ox, based on the calculations of Berzelius, Frerichs, and Lehmann:—

Composition of Ox Bile.

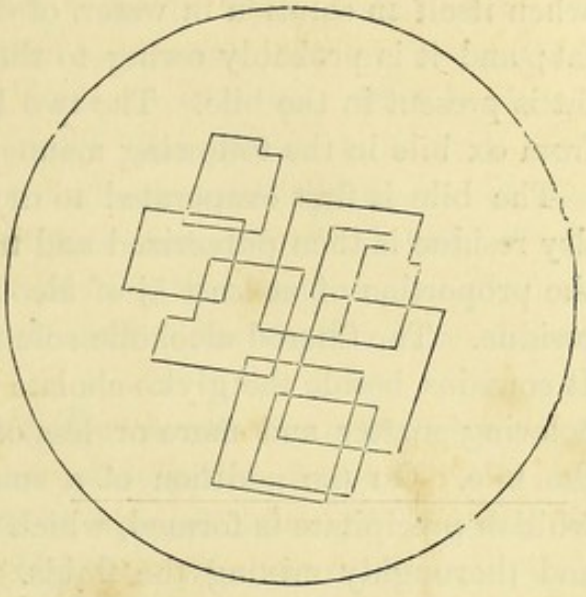
Water		880.00
Glyko-cholate of soda	90.00	
Tauro-cholate " "		
Biliverdine	13.42	
Fats		
Oleates, margarates, and stearates of soda and potassa		
Cholesterin		
Chloride of sodium	15.24	
Phosphate of soda		
" " lime		
" " magnesia		
Carbonates of soda and potassa		
Mucus of the gall-bladder		1.34
		1000.00

Biliverdine.—Of the above mentioned ingredients, *biliverdine* is peculiar to the bile, and therefore important, though not present in large quantity. This is the coloring matter of the bile. It is, like the other coloring matters, an uncrystallizable organic substance, containing nitrogen, and yielding to ultimate analysis a small quantity of iron. It exists in such small quantity in the bile that its exact proportion has never been determined. It is formed, so far as can be ascertained, in the substance of the liver, and does not pre-exist in the blood. It may, however, be reabsorbed in cases of biliary obstruction, when it circulates with the blood and stains nearly all the tissues and fluids of the body, of a peculiar lemon yellow color. This is the symptom which is characteristic of jaundice.

Cholesterin ($C_{25}H_{22}O$).—This is a crystallizable substance which resembles the fats in many respects; since it is destitute of nitrogen, readily inflammable, soluble in alcohol and ether, and entirely insoluble in water. It is not saponifiable, however, by the action of the alkalies, and is distinguished on this account from the ordinary fatty substances. It occurs, in a crystalline form, mixed with coloring matter, as an abundant ingredient in most biliary calculi; and is found also in different regions of the body, forming a part of various morbid deposits. We have met with it in the fluid of hydrocele, and in the interior of many encysted tumors. The crystals of cholesterin (Fig. 47) have the form of very thin, colorless, transparent, rhomboidal plates, portions of which are often cut out by lines of cleavage parallel to the sides of the crystal. They frequently occur deposited in layers, in which the outlines of

the subjacent crystals show very distinctly through the substance of those which are placed above. Cholesterin is not formed in the liver, but originates in the substance of the brain and nervous tissue, from which it may be extracted in large quantity by the action of alcohol. It has also been found, by Dr. W. Marcet,[1] to exist, in considerable abundance, in the tissue of the *spleen*. From all these tissues it is absorbed by the blood, then conveyed to the liver, and discharged with the bile.

Fig. 47.



CHOLESTERIN, from an Encysted Tumor.

This fact has been fully confirmed by the researches of Prof. A. Flint, Jr.,[2] who has found that there is nearly one-quarter part more cholesterin in the blood of the jugular vein, returning from the brain, than in that of the carotid artery, before its passage through that organ; and that, on the other hand, the blood of the hepatic artery, as well as that of the portal vein, loses cholesterin in passing through the liver, so that but a small quantity can be found in the blood of the hepatic vein.

Since cholesterin in a free state is insoluble in the animal fluids, it is probable that it exists in the blood and the bile, as well as in the nervous tissues from which it is derived, under some form of combination, as a lactate, oleate, or margarate; and that it is deposited in a crystalline form only after being liberated from this combination by the action of other substances.

The cholesterin, after being poured into the intestine with the bile, is decomposed or transformed into some other substance, since it is not discharged with the feces.[3] Its decomposition is probably effected by the contact of the intestinal fluids.

BILIARY SALTS.—By far the most important and characteristic ingredients of this secretion are the two saline substances mentioned

[1] Philosophical Transactions, London, 1857, p. 413.

[2] American Journ. Med. Sci., October, 1862.

[3] Prof. A. Flint, Jr., in Am. Journ. Med. Sci., Oct. 1862.

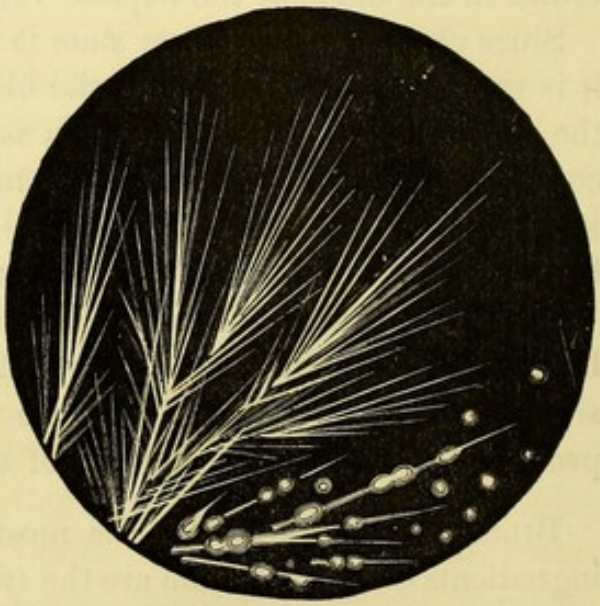
above as the *glyko-cholate* and *tauro-cholate of soda*. These substances were first discovered by Strecker, in 1848, in the bile of the ox. They are both freely soluble in water and in alcohol, but insoluble in ether. One of them, the tauro-cholate, has the property, when itself in solution in water, of dissolving a certain quantity of fat; and it is probably owing to this circumstance that some free fat is present in the bile. The two biliary substances are obtained from ox bile in the following manner:—

The bile is first evaporated to dryness by the water-bath. The dry residue is then pulverized and treated with absolute alcohol, in the proportion of at least ʒj of alcohol to every five grains of dry residue. The filtered alcoholic solution has a clear yellowish color. It contains, beside the glyko-cholate and tauro-cholate of soda, the coloring matter and more or less of the fats originally present in the bile. On the addition of a small quantity of ether, a dense, whitish precipitate is formed, which disappears again on agitating and thoroughly mixing the fluids. On the repeated addition of ether, the precipitate again falls down, and when the ether has been added in considerable excess, six to twelve times the volume of the alcoholic solution, the precipitate remains permanent, and the whole mixture is filled with a dense, whitish, opaque deposit, consisting of the glyko-cholate and tauro-cholate of soda, thrown down under the form of heavy flakes and granules, part of which subside to

Fig. 48.

Ox-bile, extracted with absolute alcohol and precipitated with ether.

Fig. 49.

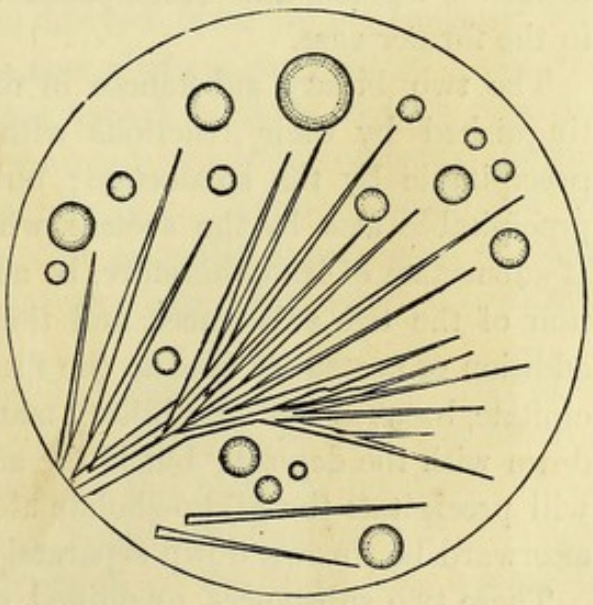


Glyko-cholate of Soda from Ox-bile, after two days' crystallization. At the lower part of the figure the crystals are melting into drops, from the evaporation of the ether and absorption of moisture.

the bottom of the test-tube, while part remain for a time in suspension. Gradually these flakes and granules unite with each other and fuse together into clear, brownish-yellow, oily, or resinous-looking drops. At the bottom of the test-tube, after two or three hours, there is usually collected a nearly homogeneous layer of this deposit, while the remainder continues to adhere to the sides of the glass in small, circular, transparent drops. The deposit is semi-fluid in consistency, and sticky, like Canada balsam or half-melted resin; and it is on this account that the ingredients composing it have been called the "resinous matters" of the bile. They have, however, no real chemical relation with true resinous bodies, since they both contain nitrogen, and differ from resins also in other important particulars.

At the end of twelve to twenty-four hours, the glyko-cholate of soda begins to crystallize. The crystals radiate from various points in the resinous deposit, and shoot upward into the supernatant fluid, in white, silky bundles. (Fig. 48.) If some of these crystals be removed and examined by the microscope, they are found to be of a very delicate acicular form, running to a finely pointed extremity, and radiating, as already mentioned, from a central point. (Fig. 49.) As the ether evaporates, the crystals absorb moisture from the air, and melt up rapidly into clear resinous drops; so that it is difficult to keep them under the microscope long enough for a correct drawing and measurement. The crystallization in the test-tube goes on after the first day, and the crystals increase in quantity for three or four, or even five or six days, until the whole of the glyko cholate of soda present has assumed the solid form. The tauro-cholate, however, is uncrystallizable, and remains in an amorphous condition. If a portion of the deposit be now removed and examined by the microscope, it is seen that the crystals of glyko-cholate of soda have increased considerably in thickness (Fig. 50), so that their trans-

Fig. 50.



GLYKO-CHOLATE AND TAURO-CHOLATE OF SODA, FROM OX-BILE, after six days' crystallization. The glyko-cholate is crystallized; the tauro-cholate is in fluid drops.

verse diameter may be readily estimated. The uncrystallizable tauro-cholate appears under the form of circular drops, varying considerably in size, clear, transparent, strongly refractive, and bounded by a dark, well-defined outline. *These drops are not to be distinguished, by any of their optical properties, from oil-globules,* as they usually appear under the microscope. They have the same refractive power, the same dark outline and bright centre, and the same degree of consistency. They would consequently be liable at all times to be mistaken for oil-globules, were it not for the complete dissimilarity of their chemical properties.

Both the glyko-cholate and tauro-cholate of soda are very freely soluble in water. If the mixture of alcohol and ether be poured off and distilled water added, the deposit dissolves rapidly and completely, with a more or less distinct yellowish color, according to the proportion of coloring matter originally present in the bile. The two biliary substances present in the watery solution may be separated from each other by the following means. On the addition of *acetate of lead,* the glyko-cholate of soda is decomposed, and precipitates as a glyko-cholate of lead. The precipitate, separated by filtration from the remaining fluid, is then decomposed in turn by carbonate of soda, and the original glyko-cholate of soda reproduced. The filtered fluid which remains, and which contains the tauro-cholate of soda, is then treated with *subacetate of lead,* which precipitates a tauro-cholate of lead. This is separated by filtration, washed, and decomposed again by carbonate of soda, as in the former case.

The two biliary substances in ox bile may, therefore, be distinguished by their reactions with the salts of lead. Both are precipitable by the subacetate; but the glyko-cholate of soda is precipitable also by the acetate, while the tauro-cholate is not so. If subacetate of lead, therefore, be added to the mixed watery solution of the two substances, and the whole filtered, the subsequent addition of acetate of lead to the filtered fluid will produce no precipitate, because both the biliary matters have been entirely thrown down with the deposit; but if the acetate of lead be first added, it will precipitate the glyko-cholate alone, and the tauro-cholate may afterward be thrown down separately by the subacetate.

These two substances, examined separately, have been found to possess the following properties:—

Glyko-cholate of soda ($NaO,C_{52}H_{42}NO_{11}$) crystallizes, when precipitated by ether from its alcoholic solution, in radiating bundles of fine white silky needles, as above described. It is composed of soda, united with a peculiar acid of organic origin, viz., *glyko-cholic*

acid ($C_{52}H_{42}NO_{11},HO$). This acid is crystallizable and contains nitrogen, as shown by the above formula, which is that given by Lehmann. If boiled for a long time with a dilute solution of potassa, glyko-cholic acid is decomposed with the production of two new substances; the first a non-nitrogenous acid body, *cholic acid* ($C_{48}H_{39}O_9,HO$); the second a nitrogenous neutral body, *glycine* ($C_4H_5NO_4$). Hence the name glyko-cholic acid, given to the original substance, as if it were a combination of cholic acid with glycine. In reality, however, these two substances do not exist originally in the glyko-cholic acid, but are rather new combinations of its elements, produced by long boiling, in contact with potassa and water. They are not, therefore, to be regarded as, in any way, natural ingredients of the bile, and do not throw any light on the real constitution of glyko-cholic acid.

Tauro-cholate of soda ($NaO,C_{52}H_{45}NS_2O_{14}$) is also a very abundant ingredient of the bile. It is said by Robin and Verdeil[1] that it is not crystallizable, owing probably to its not having been separated as yet in a perfectly pure condition. Lehmann states, on the contrary, that it may crystallize,[2] when kept for a long time in contact with ether. We have not been able to obtain this substance, however, in a crystalline form. Its acid constituent, *tauro-cholic acid*, is a nitrogenous body, like glyko-cholic acid, but differs from the latter by containing in addition two equivalents of sulphur. By long boiling in a dilute solution of potassa, it is decomposed with the production of two other substances; the first of them the same acid body mentioned above as derived from the glyko-cholic, viz., *cholic acid;* and the second a new nitrogenous neutral body, viz., *taurine* ($C_4H_7NS_2O_6$). The same remark holds good with regard to these two bodies, that we have already made in respect to the supposed constituents of glyko-cholic acid. Neither cholic acid nor taurine can be properly regarded as really ingredients of tauro-cholic acid, but only as artificial products resulting from its alteration and decomposition.

The glyko-cholates and tauro-cholates are formed, so far as we know, exclusively in the liver; since they have not been found in the blood, nor in any other part of the body, in healthy animals; nor even, in the experiments of Kunde, Moleschott, and Lehmann on frogs,[3] after the entire extirpation of the liver, and consequent

[1] Chimie Anatomique et Physiologique, vol. ii. p. 473.

[2] Physiological Chemistry, Phil. ed., vol. i. p. 209.

[3] Lehmann's Physiological Chemistry, Phil. ed., vol. i. p. 476.

suppression of the bile. These substances are, therefore, produced in the glandular cells of the liver, by transformation of some other of their ingredients. They are then exuded in a soluble form, as part of the bile, and finally discharged by the excretory hepatic ducts.

The two substances described above as the tauro-cholate and glyko-cholate of soda exist, properly speaking, only in the bile of the ox, where they were first discovered by Strecker. In examining the biliary secretions of different species of animals, Strecker found so great a resemblance between them, that he was disposed to regard their ingredients as essentially the same. Having established the existence in ox-bile of two peculiar substances, one crystallizable and non-sulphurous (glyko-cholate), the other uncrystallizable and sulphurous (tauro-cholate), he was led to consider the bile in all species of animals as containing the same substances, and as differing only in the relative quantity in which the two were present. The only exception to this was supposed to be pig's bile, in which Strecker found a peculiar organic acid, the "hyo-cholic" or "hyo-cholinic" acid, in combination with soda as a base.

Fig. 51.

Dog's Bile, extracted with absolute alcohol and precipitated with ether.

The above conclusion of his, however, was not entirely correct. It is true that the bile of all animals, so far as examined, contains peculiar substances, which resemble each other in being freely soluble in water, soluble in absolute alcohol, and insoluble in ether; and in giving also a peculiar reaction with Pettenkofer's test, to be described presently. But, at the same time, these substances present certain minor differences in different animals, which show them not to be identical.

In dog's bile, for example, there are, as in ox-bile, two substances precipitable by ether from their alcoholic solution; one crystallizable, the other not so. But the former of these substances crystallizes much more readily than the glyko-cholate of soda from ox-bile. Dog's bile will not unfrequently begin to crystallize freely in five to six hours after precipitation by ether (Fig. 51); while in ox-bile it is usually twelve, and often twenty-four or even forty-eight hours before crystallization is fully estab-

lished. But it is more particularly in their reaction with the salts of lead that the difference between these substances becomes manifest. For while the crystallizable substance of ox-bile is precipitated by acetate of lead, that of dog's bile is not affected by it. If dog's bile be evaporated to dryness, extracted with absolute alcohol, the alcoholic solution precipitated by ether, and the ether precipitate then dissolved in water, the addition of acetate of lead to the watery solution produces not the slighest turbidity. If subacetate of lead be then added in excess, a copious precipitate falls, composed of both the crystallizable and uncrystallizable substances. If the lead precipitate be then separated by filtration, washed, and decomposed, as above described, by carbonate of soda, the watery solution will contain the re-formed soda salts of the bile. The watery solution may then be evaporated to dryness, extracted with absolute alcohol, and the alcoholic solution precipitated by ether; when the ether precipitate crystallizes partially after a time as in fresh bile. Both the biliary matters of dog's bile are therefore precipitable by subacetate of lead, but neither of them by the acetate. Instead of calling them, consequently, glyko-cholate and tauro cholate of soda, we shall speak of them simply as the "crystalline" and "resinous" biliary substances.

In cat's bile, the biliary substances act very much as in dog's bile. The ether precipitate of the alcoholic solution contains here also a crystalline and a resinous substance; both of which are precipitable from their watery solution by subacetate of lead, but neither of them by the acetate.

In human bile there is also a crystallizable substance; but this substance, according to our own observations, is in much smaller quantity than in the foregoing cases. In the alcoholic extract of dried human bile, which has been precipitated by ether, the crystals which show themselves are of various forms and almost microscopic in size. (Fig. 52). Some of them are feathery in appearance, consisting of two or three diverging needles, with secondary needle-shaped crystals growing from their lateral edges. Others, which are larger and more abundant, are octohedral or diamond-shaped, sometimes with irregular sides and truncated angles. Others still

Fig. 52.

CRYSTALLINE AND RESINOUS BILIARY MATTERS from Human Bile, extracted with absolute alcohol and precipitated by ether. Magnified 25 diameters.

assume the form of rosettes, more or less perfect, consisting of short, fine, irregular, radiating fibres. These crystals are mingled with an abundant deposit of resinous drops, similar to those of the taurocholate of soda from ox-bile.

If the biliary deposit from human bile, thus prepared, be separated by decantation and dissolved in water, it precipitates from the watery solution by both the acetate and subacetate of lead. This might, perhaps, be attributed to the presence of two different substances, as in ox-bile, one precipitated by the acetate, the other by the subacetate of lead. Such, however, is not the case. For if the watery solution be precipitated by the acetate of lead and then filtered, the filtered fluid gives no precipitate afterward by the subacetate; and if first precipitated by the subacetate, it gives no precipitate after filtration by the acetate. The entire biliary ingredients, therefore, of human bile are precipitated by both or either of the salts of lead.

In pig's bile no crystallizable ingredient has been discovered, but the ether-precipitate is altogether resinous in appearance. Its watery solution, however, is abundantly precipitated, as in human bile, by both the acetate and subacetate of lead.

Different kinds of bile vary also in other respects; as, for example, their specific gravity, the depth and tinge of their color, the quantity of fat which they contain, &c. &c. We have already mentioned the variations in color and specific gravity. The alcoholic solution of dried ox-bile, furthermore, does not precipitate at all on the addition of water; while that of human bile, of pig's bile, and of dog's bile precipitate abundantly with distilled water, owing to the quantity of fat which they hold in solution. These variations, however, are of secondary importance compared with those which we have already mentioned, and which show that the crystalline and resinous substances in different kinds of bile, though resembling each other in very many respects, are yet in reality far from being identical.

Tests for Bile.—In investigating the physiology of any animal fluid it is, of course, of the first importance to have a convenient and reliable test by which its presence may be detected. For a long time the only test employed in the case of bile, was that which depended on *a change of color produced by oxidizing substances.* If the bile, for example, or a mixture containing bile, be exposed in an open glass vessel for a few hours, the upper layers of the fluid, which are in contact with the atmosphere, gradually assume a greenish tinge, which becomes deeper with the length of time which

elapses, and the quantity of bile existing in the fluid. Nitric acid, added to a mixture of bile and shaken up, produces a dense precipitate which takes a bright grass-green hue. Tincture of iodine produces the same change of color, when added in small quantity; and probably there are various other substances which would have the same effect. It is by this test that the bile has so often been recognized in the urine, serous effusions, the solid tissues, &c., in cases of jaundice. But it is very insufficient for anything like accurate investigation, since the appearances are produced simply by the action of an oxidizing agent on the coloring matter of the bile. A green color produced by nitric acid does not, therefore, indicate the presence of the biliary substances proper, but only of the biliverdine. On the other hand, if the coloring matter be absent, the biliary substances themselves cannot be detected by it. For if the biliary substances of dog's bile be precipitated by ether from an alcoholic solution, dissolved in water and decolorized by animal charcoal, the colorless watery solution will then give no green color on the addition of nitric acid or tincture of iodine, though it may precipitate abundantly by subacetate of lead, and give the other reactions of the crystalline and resinous biliary matters in a perfectly distinct manner.

Pettenkofer's Test.—This is undoubtedly the best test yet proposed for the detection of the biliary substances. It consists in mixing with a watery solution of the bile, or of the biliary substances, a little cane sugar, and then adding sulphuric acid to the mixture until a red, lake, or purple color is produced. A solution may be made of cane sugar, in the proportion of one part of sugar to four parts of water, and kept for use. One drop of this solution is mixed with the suspected fluid, and the sulphuric acid then immediately added. On first dropping in the sulphuric acid, a whitish precipitate falls, which is abundant in the case of ox-bile, less so in that of the dog. This precipitate redissolves in a slight excess of sulphuric acid, which should then continue to be added until the mixture assumes a somewhat syrupy consistency and an opalescent look, owing to the development of minute bubbles of air. A red color then begins to show itself at the bottom of the test-tube, and afterward spreads through the mixture, until the whole fluid is of a clear, bright, cherry red. This color gradually changes to a lake, and finally to a deep, rich, opaque purple. If three or four volumes of water be then added to the mixture, a copious precipitate falls down, and the color is destroyed.

Various circumstances modify, to some extent, the rapidity and

distinctness with which the above changes are produced. If the biliary substances be present in large quantity, and nearly pure, the red color shows itself at once after adding an equal volume of sulphuric acid, and almost immediately passes into a strong purple. If they be scanty, on the other hand, the red color may not show itself for seven or eight minutes, nor the purple under twenty or twenty-five minutes. If foreign matters, again, not of a biliary nature, be also present, they are apt to be acted on by the sulphuric acid, and, by becoming discolored, interfere with the clearness and brilliancy of the tinges produced. On this account it is indispensable, in delicate examinations, to evaporate the suspected fluid to dryness, extract the dry residue with absolute alcohol, precipitate the alcoholic solution with ether, and dissolve the ether-precipitate in water before applying the test. In this manner, all foreign substances which might do harm will be eliminated, and the test will succeed without difficulty.

It must not be forgotten, furthermore, that the sugar itself is liable to be acted on and discolored by sulphuric acid when added in excess, and may therefore by itself give rise to confusion. A little care and practice, however, will enable the experimenter to avoid all chance of deception from this source. When sulphuric acid is mixed with a watery solution containing cane sugar, after it has been added in considerable excess, a yellowish color begins to show itself, owing to the commencing decomposition of the sugar. This color gradually deepens until it has become a dark, dingy, muddy brown; but there is never at any time any clear red or purple color, unless biliary matters be present. If the bile be present in but small quantity, the colors produced by it may be modified and obscured by the dingy yellow and brown of the sugar; but even this difficulty may be avoided by paying attention to the following precautions. In the first place, only very little sugar should be added to the suspected fluid. In the second place, the sulphuric acid should be added very gradually, and the mixture closely watched to detect the first changes of color. If bile be present, the red color peculiar to it is always produced before the yellowish tinge which indicates the decomposition of the sugar. When the biliary matters, therefore, are present in small quantity, the addition of sulphuric acid should be stopped at that point, and the colors, though faint, will then remain clear, and give unmistakable evidence of the presence of bile.

The red color alone is not sufficient as an indication of bile. It is in fact only the commencement of the change which indicates the

biliary matters. If these matters be present, the color passes, as we have already mentioned, first into a lake, then into a purple; and it is this lake and purple color alone which can be regarded as really characteristic of the biliary reaction.

It is important to observe that Pettenkofer's reaction is produced by the presence of either or both of the biliary substances proper; and is not at all dependent on the coloring matter of the bile. For if the two biliary substances, crystalline and resinous, be extracted by the process above described, and, after being dissolved in water, decolorized with animal charcoal, the watery solution will still give Pettenkofer's reaction perfectly, though no coloring matter be present, and though no green tinge can be produced by the addition of nitric acid or tincture of iodine. If the two biliary substances be then separated from each other, and tested in distinct solutions, each solution will give the same reaction promptly and completely.

Various objections have been urged against this test. It has been stated to be uncertain and variable in its action. Robin and Verdeil[1] say that its reactions "do not belong exclusively to the bile, and may therefore give rise to mistakes." Some fatty substances and volatile oils (oleine, oleic acid, oil of turpentine, oil of caraway) have been stated to produce similar red and violet colors, when treated with sugar and sulphuric acid. These objections, however, have not much, if any, practical weight. The test no doubt requires some care and practice in its application, as we have already pointed out; but this is the case also, to a greater or less extent, with nearly all chemical tests, and particularly with those for substances of organic origin. No other substance is, in point of fact, liable to be met with in the intestinal fluids or the blood, which would simulate the reactions of the biliary matters. We have found that the fatty matters of the chyle, taken from the thoracic duct, do not give any coloration which would be mistaken for that of the bile. When the volatile oils (caraway and turpentine) are acted on by sulphuric acid, a red color is produced which afterward becomes brown and blackish, and a peculiar, tarry, empyreumatic odor is developed at the same time; but we do not get the lake and purple colors spoken of above. Finally, if the precaution be observed—first of extracting the suspected matters with absolute alcohol, then precipitating with ether and dissolving the precipitate in water, no ambiguity could result from the presence of any of the above substances.

[1] Op. cit., vol. ii. p. 468.

Pettenkofer's test, then, if used with care, is extremely useful, and may lead to many valuable results. Indeed, no other test than this can be at all relied on to determine the presence or absence of the biliary substances proper.

VARIATIONS AND FUNCTIONS OF BILE.—With regard to the *entire quantity of bile secreted daily*, we have had no very positive knowledge, until the experiments of Bidder and Schmidt, published in 1852.[1] These experiments were performed on cats, dogs, sheep, and rabbits, in the following manner. The abdomen was opened, and a ligature placed upon the ductus communis choledochus, so as to prevent the bile finding its way into the intestine. An opening was then made in the fundus of the gall-bladder, by which the bile was discharged externally. The bile, so discharged, was received into previously weighed vessels, and its quantity accurately determined. Each observation usually occupied about two hours, during which period the temporary fluctuations occasionally observable in the quantity of bile discharged were mutually corrected, so far as the entire result was concerned. The animal was then killed, weighed, and carefully examined, in order to make sure that the biliary duct had been securely tied, and that no inflammatory alteration had taken place in the abdominal organs. The observations were made at very different periods after the last meal, so as to determine the influence exerted by the digestive process upon the rapidity of the secretion. The average quantity of bile for twenty-four hours was then calculated from a comparison of the above results; and the quantity of its solid ingredients was also ascertained in each instance by evaporating a portion of the bile in the water bath, and weighing the dry residue.

Bidder and Schmidt found in this way that the daily quantity of bile varied considerably in different species of animals. It was very much greater in the herbivorous animals used for experiment than in the carnivora. The results obtained by these observers are as follows:—

For every pound weight of the entire body there is secreted during twenty-four hours

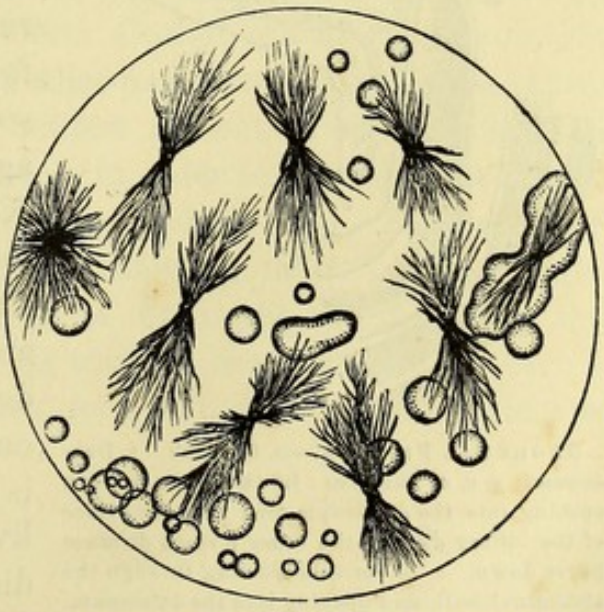
	Fresh Bile.	Dry Residue.
In the cat	102 grains.	5.712 grains.
" dog	140 "	6.916 "
" sheep	178 "	9.408 "
" rabbit	958 "	17.290 "

[1] Verdaungssaefte und Stoffwechsel. Leipzig, 1852.

Since, in the human subject, the digestive processes and the nutritive actions generally resemble those of the carnivora, rather than those of the herbivora, it is probable that the daily quantity of bile in man is very similar to that in the carnivorous animals. If we apply to the human subject the average results obtained by Bidder and Schmidt from the cat and dog, we find that, in an adult man, weighing 140 pounds, the daily quantity of the bile will be certainly not less than 16,940 grains, or very nearly 2½ pounds avoirdupois.

It is a matter of great importance, in regard to the bile, as well as the other intestinal fluids, to ascertain whether it be a *constant* secretion, like the urine and perspiration, or whether it be *intermittent*, like the gastric juice, and discharged only during the digestive process. In order to determine this point, we have performed the following series of experiments on dogs. The animals were kept confined, and killed at various periods after feeding, sometimes by the inoculation of woorara, sometimes by hydrocyanic acid, but most frequently by section of the medulla oblongata. The contents of the intestine were then collected and examined. In all instances, the bile was also taken from the gall-bladder, and treated in the same way, for purposes of comparison. The intestinal contents always presented some peculiarities of appearance when treated with alcohol and ether, owing probably to the presence of other substances than the bile; but they always gave evidence of the presence of biliary matters as well. The biliary substances could almost always be recognized by the microscope in the ether precipitate of the alcoholic solution; the resinous substance, under the form of rounded, oily-looking drops (Fig. 53), and the other, under the form of crystalline groups, generally presenting the appearance of double bundles of slender, radiating, slightly curved or wavy, needle-shaped crystals. These substances, dissolved in water, gave a purple

Fig. 53.

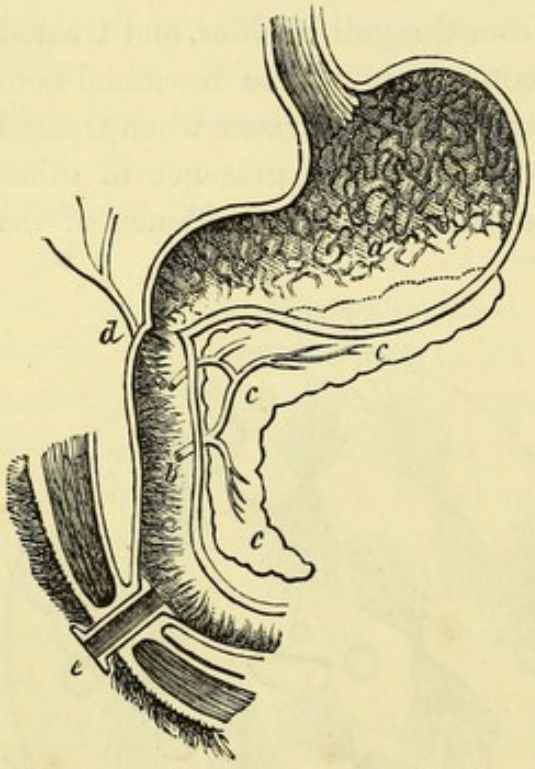


Crystalline and Resinous Biliary Substances; from Small Intestine of Dog, after two days fasting.

color with sugar and sulphuric acid. These experiments were tried after the animals had been kept for one, two, three, five, six, seven, eight, and twelve days without food. The result showed that, in all these instances, bile was present in the small intestine. It is, therefore, plainly not an intermittent secretion, nor one which is concerned exclusively in the digestive process; but its secretion is constant, and it continues to be discharged into the intestine for many days after the animal has been deprived of food.

The next point of importance to be examined relates to the *time after feeding at which the bile passes into the intestine in the greatest abundance.* Bidder and Schmidt have already investigated this point in the following manner. They operated, as above described, by tying the common bile-duct, and then opening the fundus of the gall-bladder, so as to produce a biliary fistula, by which the whole of the bile was drawn off. By doing this operation, and collecting and weighing the fluid discharged at different periods, they came to the conclusion that the flow of bile begins to increase within two and a half hours after the introduction of food into the stomach, but that it does not reach its maximum of activity till the end of twelve or fifteen hours. Other observers, however, have obtained different results. Arnold,[1] for example, found the quantity to be largest soon after meals, decreasing again after the fourth hour. Kölliker and Müller,[2] again, found it largest between the sixth and eighth hours. Bidder and Schmidt's experiments, indeed, strictly speaking, show only the time at which the bile is most actively secreted by the liver, but not when it is actually discharged into the intestine.

Fig. 54.



DUODENAL FISTULA.—*a.* Stomach. *b.* Duodenum. *c, c, c.* Pancreas; its two ducts are seen opening into the duodenum, one near the orifice of the biliary duct, *d*, the other a short distance lower down. *e.* Silver tube passing through the abdominal walls and opening into the duodenum.

Our own experiments, bear-

[1] In Am. Journ. Med. Sci., April, 1856.

[2] Ibid., April, 1857.

ing on this point, were performed on dogs, by making a permanent duodenal fistula, on the same plan that gastric fistulæ have so often been established for the examination of the gastric juice. (Fig. 54.) An incision was made through the abdominal walls, a short distance to the right of the median line, the floating portion of the duodenum drawn up toward the external wound, opened by a longitudinal incision, and a silver tube, armed at each end with a narrow projecting collar or flange, inserted into it by one extremity, five and a half inches below the pylorus, and two and a half inches below the orifice of the lower pancreatic duct. The other extremity of the tube was left projecting from the external opening in the abdominal parietes, the parts secured by sutures, and the wound allowed to heal. After cicatrization was complete, and the animal had entirely recovered his healthy condition and appetite, the intestinal fluids were drawn off at various intervals after feeding, and their contents examined. This operation, which is rather more difficult than that of making a permanent gastric fistula, is nevertheless exceedingly useful when it succeeds, since it enables us to study, not only the time and rate of the biliary discharge, but also, as mentioned in a previous chapter (Chap. VI.), many other extremely interesting matters connected with intestinal digestion.

In order to ascertain the absolute quantity of bile discharged into the intestine, and its variations during digestion, the duodenal fluids were drawn off, for fifteen minutes at a time, at various periods after feeding, collected, weighed, and examined separately, as follows: each separate quantity was evaporated to dryness, its dry residue extracted with absolute alcohol, the alcoholic solution precipitated with ether, and the ether-precipitate, regarded as representing the amount of biliary matters present, dried, weighed, and then treated with Pettenkofer's test, in order to determine, as nearly as possible, their degree of purity or admixture. The result of these experiments is given in the following table. At the eighteenth hour so small a quantity of fluid was obtained that the amount of its biliary ingredients was not ascertained. It reacted perfectly, however, with Pettenkofer's test, showing that bile was really present.

Time after feeding.	Quantity of fluid in 15 minutes.	Dry residue of same.	Quantity of biliary matters.	Proportion of biliary matters to dry residue.
Immediately	640 grains	33 grains	10 grains	.30
1 hour	1,990 "	105 "	4 "	.03
3 hours	780 "	60 "	4 "	.07
6 "	750 "	73 "	3½ "	.05
9 "	860 "	78 "	4¼ "	.06
12 "	325 "	23 "	3¾ "	.16
15 "	347 "	18 "	4 "	.22
18 "	—	—	—	—
21 "	384 "	11 "	1 "	.09
24 "	163 "	9½ "	3¼ "	.34
25 "	151 "	5 "	3 "	.60

From this it appears that the bile passes into the intestine in by far the largest quantity immediately after feeding, and within the first hour. After that time its discharge remains pretty constant; not varying much from four grains of solid biliary matters every fifteen minutes, or sixteen grains per hour. The animal used for the above observations weighed thirty-six and a half pounds.

The next point to be ascertained with regard to this question is the following, viz: *What becomes of the bile in its passage through the intestine?* Our experiments, performed with a view of settling this point, were tried on dogs. The animals were fed with fresh meat, and then killed at various intervals after the meals, the abdomen opened, ligatures placed upon the intestine at various points, and the contents of its upper, middle, and lower portions collected and examined separately. The results thus obtained show that, under ordinary circumstances, the bile, which is quite abundant in the duodenum and upper part of the small intestine, diminishes in quantity from above downward, and is not to be found in the large intestine. The entire quantity of the intestinal contents also diminishes, and their consistency increases, as we approach the ileo-cæcal valve; and at the same time their color changes from a light yellow to a dark bronze or blackish-green, which is always strongly pronounced in the last quarter of the small intestine.

The contents of the small and large intestine were furthermore evaporated to dryness, extracted with absolute alcohol, and the alcoholic solutions precipitated with ether; the quantity of ether-precipitate being regarded as representing approximately that of the biliary substances proper. The result showed that the quantity of this ether-precipitate is, both positively and relatively, very much less in the large intestine than in the small. Its proportion to the entire solid contents is only one-fifth or one-sixth as great in the

large intestine as it is in the small. But even this inconsiderable quantity, found in contents of the large intestine, does not consist of biliary matters; for the watery solutions being treated with sugar and sulphuric acid, those from both the upper and lower portions of the small intestine always gave Pettenkofer's reaction promptly and perfectly in less than a minute and a half; while in that from the large intestine no red or purple color was produced, even at the end of three hours.

The small intestine consequently contains, at all times, substances giving all the reactions of the biliary ingredients; while in the contents of the large intestine no such substances can be recognized by Pettenkofer's test.

The biliary matters, therefore, disappear in their passage through the intestine.

In endeavoring to ascertain what is the precise *function of the bile in the intestine*, our first object must be to determine what part, if any, it takes in the digestive process. As the liver is situated, like the salivary glands and the pancreas, in the immediate vicinity of the alimentary canal, and like them, discharges its secretion into the cavity of the intestine, it seems at first natural to regard the bile as one of the digestive fluids. We have previously shown, however, that the digestion of all the different elements of the food is provided for by other secretions; and furthermore, if we examine experimentally the digestive power of bile on alimentary substances, we obtain only a negative result. Bile exerts no special action upon either albuminoid, starchy, or oleaginous matters, when mixed with them in test-tubes and kept at the temperature of 100° F. It has therefore, apparently, no direct influence in the digestion of these substances.

It is a very remarkable fact, in this connection, that the bile *precipitates by contact with the gastric juice.* If four drops of dog's bile be added to ʒj of gastric juice from the same animal, a copious yellowish-white precipitate falls down, which contains the whole of the coloring matter of the bile which has been added; and if the mixture be then filtered, the filtered fluid passes through quite colorless. The gastric juice, however, still retains its acid reaction. This precipitation depends upon the presence of the biliary substances proper, viz., the glyko-cholate and tauro-cholate of soda, and not upon that of the incidental ingredients of the bile. For if the bile be evaporated to dryness and the biliary substances extracted

by alcohol and precipitated by ether, as above described, their watery solution will precipitate with gastric juice, in the same manner as fresh bile would do.

Although the biliary matters, however, precipitate by contact with fresh gastric juice, *they do not do so with gastric juice which holds albuminose in solution.* We have invariably found that if the gastric juice be digested for several hours at the temperature of 100° F., with boiled white of egg, the filtered fluid, which contains an abundance of albuminose, will no longer give the slightest precipitate on the addition of bile, or of a watery solution of the biliary substances, even in very large amount. The gastric juice and the bile, therefore, are not finally antagonistic to each other in the digestive process, though at first they produce a precipitate on being mingled together.

It appears, however, from the experiments detailed above, that the secretion of the bile and its discharge into the intestine are not confined to the periods of digestion, but take place constantly, and continue even after the animal has been kept for many days without food. These facts would lead us to regard the bile as simply an *excrementitious fluid;* containing only ingredients resulting from the waste and disintegration of the animal tissues, and not intended to perform any particular function, digestive or otherwise, but merely to be eliminated from the blood, and discharged from the system. The same view is more or less supported, also, by the following facts, viz:—

1st. The bile is produced, unlike all the other animal secretions, from venous blood; that is, the blood of the portal vein, which has already become contaminated by circulation through the abdominal organs, and may be supposed to contain disorganized and effete ingredients; and

2d. Its complete suppression produces, in the human subject, symptoms of poisoning of the nervous system, analogous to those which follow the suppression of the urine, or the stoppage of respiration, and the patient dies, usually in a comatose condition, at the end of ten or twelve days.

The above circumstances, taken together, would combine to make it appear that the bile is simply an excrementitious fluid, not necessary or useful as a secretion, but only destined, like the urine, to be eliminated and discharged. Nevertheless, experiment has shown that such is not the case; and that, in point of fact, it is necessary for the life of the animal, not only that the bile be secreted

and discharged, but furthermore that it be discharged into the intestine, and pass through the tract of the alimentary canal. The most satisfactory experiments of this kind are those of Bidder and Schmidt,[1] in which they tied the common biliary duct in dogs, and then established a permanent fistula in the fundus of the gall-bladder, through which the bile was allowed to flow by a free external orifice. In this manner the bile was effectually excluded from the intestine, but at the same time was freely and wholly discharged from the body, by the artificial fistula. If the bile therefore were simply an excrementitious fluid, its deleterious ingredients being all eliminated as usual, the animals would not suffer any serious injury from this operation. If, on the contrary, they were found to suffer or die in consequence of it, it would show that the bile has really some important function to perform in the intestinal canal, and is not simply excrementitious in its nature.

The result showed that the effects of such an experiment were fatal to the animal. Four dogs only survived the immediate effects of the operation, and were afterward frequently used for purposes of experiment. One of them was an animal from which the spleen had been previously removed, and whose appetite, as usual after this operation, was morbidly ravenous; his system, accordingly, being placed under such unnatural conditions as to make him an unfit subject for further experiment. In the second animal that survived, the communication of the biliary duct with the intestine became re-established after eighteen days, and the experiment consequently had no result. In the remaining two animals, however, everything was successful. The fistula in the gall-bladder became permanently established; and the bile-duct, as was proved subsequently by *post-mortem* examination, remained completely closed, so that no bile found its way into the intestine. Both these animals died; one of them at the end of twenty-seven days, the other at the end of thirty-six days. In both, the symptoms were nearly the same, viz., constant and progressive emaciation, which proceeded to such a degree that nearly every trace of fat disappeared from the body. The loss of flesh amounted, in one case, to more than two-fifths, and in the other to nearly one-half the entire weight of the animal. There was also a falling off of the hair, and an unusually disagreeable, putrescent odor in the feces and in the breath. Notwithstanding this, the appetite remained good. Digestion was not

[1] Op. cit., p. 103.

essentially interfered with, and none of the food was discharged with the feces; but there was much rumbling and gurgling in the intestines, and abundant discharge of flatus, more strongly marked in one instance than in the other. There was no pain; and death took place, at last, without any violent symptoms, but by a simple and gradual failure of the vital powers.

A similar experiment has been successfully performed by Prof. A. Flint, Jr.[1] In this instance the animal lived for thirty-eight days after the operation, and died finally of inanition; the symptoms agreeing in every important particular, with those reported by Bidder and Schmidt.

How is it, then, that although the bile be not an active agent in digestion, its presence in the alimentary canal is still essential to life? What office does it perform there, and how is it finally disposed of?

We have already shown that the bile disappears in its passage through the intestine. This disappearance may be explained in two different ways. First, the biliary matters may be actually reabsorbed from the intestine, and taken up by the bloodvessels; or secondly, they may be so altered and decomposed by the intestinal fluids as to lose the power of giving Pettenkofer's reaction with sugar and sulphuric acid, and so pass off with the feces in an insoluble form. Bidder and Schmidt[2] have finally determined this point in a satisfactory manner; and have demonstrated that the biliary substances are actually reabsorbed, by showing that the quantity of sulphur present in the feces is far inferior to that contained in the biliary ingredients as they are discharged into the intestine.

These observers collected and analyzed all the feces passed, during five days, by a healthy dog, weighing 17.7 pounds. The entire fecal mass during this period weighed 1508.15 grains,

Containing	Water	874.20 grains.
	Solid residue	633.95 "
		1508.15

[1] American Journ. Med. Sci., October, 1862.

[2] Op. cit., p. 217.

The solid residue was composed as follows:—

Neutral fat, soluble in ether . .	43.710 grains.	
Fat, with traces of biliary matter .	77.035 "	
Alcohol extract with biliary matter	58.900 containing	1.085 grs. of sulphur.
Substances not of a biliary nature extracted by muriatic acid and hot alcohol	148.800 containing	1.302 grs. of sulphur.
		2.387
Fatty acids with oxide of iron .	98.425	
Residue consisting of hair, sand, &c.,	207.080	
	633.950	

Now, as it has already been shown that the dog secretes, during 24 hours, 6.916 grains of solid biliary matter for every pound weight of the whole body, the entire quantity of biliary matter secreted in five days by the above animal, weighing 17.7 pounds, must have been 612.5 grains, or nearly as much as the whole weight of the dried feces. But furthermore, the natural proportion of sulphur in dog's bile (derived from the uncrystallizable biliary matter), is six per cent. of the dry residue. The 612.5 grains of dry bile, secreted during five days, contained, therefore, 36.75 grains of sulphur. But the entire quantity of sulphur, existing in any form in the feces, was 5.952 grains; and of this only 2.387 grains were derived from substances which could have been the products of biliary matters—the remainder being derived from the hairs which are always contained in abundance in the feces of the dog. That is, not more than one-fifteenth part of the sulphur, originally present in the bile, could be detected in the feces. As this is a simple chemical element, not decomposable by any known means, it must, accordingly, have been reabsorbed from the intestine.

We have endeavored to complete the evidence thus furnished by Bidder and Schmidt, and to demonstrate directly the reabsorption of the biliary matters, by searching for them in the ingredients of the portal blood. We have examined, for this purpose, the portal blood of dogs, killed at various periods after feeding. The animals were killed by section of the medulla oblongata, a ligature immediately placed on the portal vein, while the circulation was still active, and the requisite quantity of blood collected by opening the vein. The blood was sometimes immediately evaporated to dryness by the water bath. Sometimes it was coagulated by boiling in a porcelain capsule, over a spirit lamp, with water and an excess of sulphate of soda, and the filtered watery solution afterward examined. But most frequently the blood, after being col-

lected from the vein, was coagulated by the gradual addition of three times its volume of alcohol at ninety-five per cent., stirring the mixture constantly, so as to make the coagulation gradual and uniform. It was then filtered, the moist mass remaining on the filter subjected to strong pressure in a linen bag, by a porcelain press, and the fluid thus obtained added to that previously filtered. The entire spirituous solution was then evaporated to dryness, the dry residue extracted with absolute alcohol, and the alcoholic solution treated as usual, with ether, &c., to discover the presence of biliary matters. In every instance blood was taken at the same time from the jugular vein, or the abdominal vena cava, and treated in the same way for purposes of comparison.

We have examined the blood, in this way, one, four, six, nine, eleven and a half, twelve, and twenty hours after feeding. As the result of these examinations, we have found that in the venous blood, both of the portal vein and of the general circulation, there exists a substance soluble in water and absolute alcohol, and precipitable by ether from its alcoholic solution. This substance is often considerably more abundant in the portal blood than in that taken from the general venous system. It adheres closely to the sides of the glass after precipitation, so that it is always difficult, and often impossible, to obtain enough of it, mixed with ether, for microscopic examination. It dissolves, also, like the biliary substances, with great readiness in water; but in no instance have we ever been able to obtain from it such a satisfactory reaction with Pettenkofer's test, as would indicate the presence of bile. This is not because the reaction is masked, as might be suspected, by some of the other ingredients of the blood; for if at the same time, two drops of bile be added to half an ounce of blood taken from the abdominal vena cava, and the two specimens treated alike, the ether-precipitate may be considered more abundant in the case of the portal blood; and yet that from the blood of the vena cava, dissolved in water, will give Pettenkofer's reaction for bile perfectly, while that of the portal blood will give no such reaction.

Notwithstanding, then, the irresistible evidence afforded by the experiments of Bidder and Schmidt, that the biliary matters are really taken up by the portal blood, we have failed to recognize them there by Pettenkofer's test. They must accordingly undergo certain alterations in the intestine, previously to their absorption, so that they no longer give the ordinary reaction of the biliary substances. We cannot say, at present, precisely what these alterations

are; but they are evidently transformations of a catalytic nature, produced by the contact of the bile with the intestinal juices.

The bile, therefore, is a secretion which has not yet accomplished its function when it is discharged from the liver and poured into the intestine. On the contrary, during its passage through the intestine it is still in the interior of the body, in contact with glandular surfaces, and mingled with various organic substances, the ingredients of the intestinal fluids, which act upon it as catalytic bodies, and produce in it new transformations. This may account for the fact stated above, that the bile, though a constant and uninterrupted secretion, is nevertheless poured into the intestine in the greatest abundance immediately after a hearty meal. This is not because it is to take any direct part in the digestion of the food; but because the intestinal fluids, being themselves present at that time in the greatest abundance, can then act upon and decompose the greatest quantity of bile. At all events, the biliary ingredients, after being altered and transformed in the intestine, as they might be in the interior of a glandular organ, re-enter the blood under some new form, and are carried away by the circulation, to complete their function in some other part of the body.

CHAPTER IX.

FORMATION OF SUGAR IN THE LIVER.

Beside the secretion of bile, the liver performs also another exceedingly important function, viz., the *production of sugar* by a metamorphosis of some of its organic ingredients.

Under ordinary circumstances a considerable quantity of saccharine matter is introduced with the food, or produced from starchy substances, by the digestive process, in the intestinal canal. In man and the herbivorous animals, accordingly, an abundant supply of sugar is derived from these sources; and, as we have already shown, the sugar thus introduced is necessary for the proper support of the vital functions. For though the saccharine matter absorbed from the intestine is destroyed by decomposition soon after entering the circulation, yet the chemical changes by which its decomposition is effected are themselves necessary for the proper constitution of the blood, and the healthy nutrition of the tissues. Experiment shows, however, that the system does not depend, for its supply of sugar, entirely upon external sources; but that saccharine matter is also produced independently, in the tissue of the liver, whatever may be the nature of the food upon which the animal subsists.

This important function was first discovered by M. Claude Bernard[1] in 1848, and described by him under the name of the *glycogenic function of the liver.*

It has long been known that sugar may be abundantly secreted, under some circumstances, when no vegetable matters have been taken with the food. The milk, for example, of all animals, carnivorous as well as herbivorous, contains a notable proportion of sugar; and the quantity thus secreted, during lactation, is in some instances very great. In the human subject, also, when suffering from diabetes, the amount of saccharine matter discharged with the

[1] Nouvelle Fonction du Foie. Paris, 1853.

urine has often appeared to be altogether out of proportion to that which could be accounted for by the vegetable substances taken as food. The experiments of Bernard, the most important of which we have repeatedly confirmed, in common with other investigators, show that in these instances most of the sugar has an internal origin, and that it first makes its appearance in the tissue of the liver.

If a carnivorous animal, as, for example, a dog or a cat, be fed for several days exclusively upon meat, and then killed, the liver alone of all the internal organs is found to contain sugar among its other ingredients. For this purpose, a portion of the organ should be cut into small pieces, reduced to a pulp by grinding in a mortar with a little water, and the mixture coagulated by boiling with an excess of sulphate of soda, in order to precipitate the albuminous and coloring matters. The filtered fluid will then reduce the oxide of copper, with great readiness, on the application of Trommer's test. A decoction of the same tissue, mixed with a little yeast, will also give rise to fermentation, producing alcohol and carbonic acid, as is usual with saccharine solutions. On the contrary, the tissues of the spleen, the kidneys, the lungs, the muscles, &c., treated in the same way, give no indication of sugar, and do not reduce the salts of copper. Every other organ in the body may be entirely destitute of sugar, but the liver always contains it in considerable quantity, provided the animal be healthy. Even the blood of the portal vein, examined by a similar process, contains no saccharine element, and yet the tissue of the organ supplied by it shows an abundance of saccharine ingredients.

It is remarkable for how long a time the liver will continue to exhibit the presence of sugar, after all external supplies of this substance have been cut off. Bernard kept two dogs under his own observation, one for a period of three, the other of eight months,[1] during which period they were confined strictly to a diet of animal food (boiled calves' heads and tripe), and then killed. Upon examination, the liver was found, in each instance, to contain a proportion of sugar fully equal to that present in the organ under ordinary circumstances.

The sugar, therefore, which is found in the liver after death, is a normal ingredient of the hepatic tissue. It is not formed in other parts of the body, nor absorbed from the intestinal canal, but takes

[1] Nouvelle Fonction du Foie, p. 50.

its origin in the liver itself; it is produced, as a new formation, by a secreting process in the tissue of the organ.

The presence of sugar in the liver is common to all species of animals, so far as is yet known. Bernard found it invariably in monkeys, dogs, cats, rabbits, the horse, the ox, the goat, the sheep, in birds, in reptiles, and in most kinds of fish. It was only in two species of fish, viz., the eel and the ray (Muræna anguilla and Raia batis), that he sometimes failed to discover it; but the failure in these instances was apparently owing to the commencing putrescence of the tissue, by which the sugar had probably been destroyed. In the fresh liver of the human subject, examined after death from accidental violence, sugar was found to be present in the proportion of 1.10 to 2.14 per cent. of the entire weight of the organ.

The following list shows the average percentage of sugar present in the healthy liver of man and different species of animals, according to the examinations of Bernard:—

PERCENTAGE OF SUGAR IN THE LIVER.

In man	1.68	In ox	2.30
" monkey	2.15	" horse	4.08
" dog	1.69	" goat	3.89
" cat	1.94	" birds	1.49
" rabbit	1.94	" reptiles	1.04
" sheep	2.00	" fish	1.45

With regard to the nature and properties of the liver sugar, it resembles very closely glucose, or the sugar of starch, the sugar of honey, and the sugar of milk, though it is not absolutely identical with either one of them. Its solution reduces, as we have seen, the salts of copper in Trommer's test, and becomes colored brown when boiled with caustic potassa. It ferments very readily, also, when mixed with yeast and kept at the temperature of 70° to 100° F. It is distinguished from all the other sugars, according to Bernard,[1] by the readiness with which it becomes decomposed in the blood—since cane sugar and beet root sugar, if injected into the circulation of a living animal, pass through the system without sensible decomposition, and are discharged unchanged with the urine; sugar of milk and glucose, if injected in moderate quantity, are decomposed in the blood, but if introduced in greater abundance make their appearance also in the urine; while a solution of liver sugar, though injected in much larger quantity than either of the others, may dis-

[1] Leçons de Physiologie Experimentale. Paris, 1855, p. 213.

appear altogether in the circulation, without passing off by the kidneys.

This substance is therefore a sugar of animal origin, similar in its properties to other varieties of saccharine matter, derived from different sources.

The sugar of the liver is not produced in the blood by a direct decomposition of the elements of the circulating fluid in the vessels of the organ, but takes its origin in the *solid substance of the hepatic tissue,* as a natural ingredient of its organic texture. The blood which may be pressed out from a liver recently extracted from the body, it is true, contains sugar; but this sugar it has absorbed from the tissue of the organ in which it circulates. This is demonstrated by the singular fact that the fresh liver of a recently killed animal, though it may be entirely drained of blood and of the sugar which it contained at the moment of death, will still continue for a certain time to produce a saccharine substance. If such a liver be injected with water by the portal vein, and all the blood contained in its vessels washed out by the stream, the water which escapes by the hepatic vein will still be found to contain sugar. M. Bernard has found[1] that if all the sugar contained in a fresh liver be extracted in this manner by a prolonged watery injection, so that neither the water which escapes by the hepatic vein, nor the substance of the liver itself, contain any further traces of sugar, and if the organ be then laid aside for twenty-four hours, both the tissue of the liver and the fluid which exudes from it will be found at the end of that time to have again become highly saccharine. The sugar, therefore, is evidently not produced in the blood circulating through the liver, but in the substance of the organ itself. Once having originated in the hepatic tissue, it is absorbed thence by the blood, and transported by the circulation, as we shall hereafter show, to other parts of the body.

The sugar which thus originates in the tissue of the liver, is produced by a mutual decomposition and transformation of various other ingredients of the hepatic substance; these chemical changes being a part of the nutritive process by which the tissue of the organ is constantly sustained and nourished. There is probably a series of several different transformations which take place in this manner, the details of which are not yet known to us. It has been discovered, however, that one change at least precedes the final

[1] Gazette Hebdomadaire, Paris, Oct. 5, 1855.

production of saccharine matter; and that the sugar itself is produced by the transformation of another peculiar substance, of anterior formation. This substance, which precedes the formation of sugar, and which is itself produced in the tissue of the liver, is known by the name of *glycogenic matter*, or *glycogene*.

This glycogenic matter may be extracted from the liver in the following manner. The organ is taken immediately from the body of the recently killed animal, cut into small pieces, and coagulated by being placed for a few minutes in boiling water. This is in order to prevent the albuminous liquids of the organ from acting upon the glycogenic matter and decomposing it at a medium temperature. The coagulated tissue is then drained, placed in a mortar, reduced to a pulp by bruising and grinding, and afterward boiled in distilled water for a quarter of an hour, by which the glycogenic matter is extracted and held in solution by the boiling water.

The liquid of decoction, which should be as concentrated as possible, must then be expressed, strained, and filtered, after which it appears as a strongly opalescent fluid, of a slightly yellowish tinge. The glycogenic matter which is held in solution may be precipitated by the addition to the filtered fluid of five times its volume of alcohol. The precipitate, after being repeatedly washed with alcohol in order to remove sugar and biliary matters, may then be redissolved in distilled water. It may be precipitated from its watery solution either by alcohol in excess or by crystallizable acetic acid, in both of which it is entirely insoluble, and may be afterward kept in the dry state for an indefinite time without losing its properties.

The glycogenic matter, obtained in this way, is regarded as intermediate in its nature and properties between hydrated starch and dextrine. Its ultimate composition, according to M. Pelouze,[1] is as follows:—

$$C_{12}H_{12}O_{12}.$$

When brought into contact with iodine, it produces a coloration varying from violet to a deep, clear, maroon red. It does not reduce the salts of copper in Trommer's test, nor does it ferment when placed in contact with yeast at the proper temperature. It does not, therefore, of itself contain sugar. It may easily be converted into sugar, however, by contact with any of the animal ferments, as, for example, those contained in the saliva, or in the

[1] Journal de Physiologie, Paris, 1858, p. 552.

blood. If a solution of glycogenic matter be mixed with fresh human saliva, and kept for a few minutes at the temperature of 100° F., the mixture will then be found to have acquired the power of reducing the salts of copper and of entering into fermentation by contact with yeast. The glycogenic matter has therefore been converted into sugar by a process of catalysis, in the same manner as vegetable starch would be transformed under similar conditions.

The glycogenic matter which is thus destined to be converted into sugar, is formed in the liver by the processes of nutrition. It may be extracted, as we have seen above, from the hepatic tissue of carnivorous animals, and is equally present when they have been exclusively confined for many days to a meat diet. It is not introduced with the food; for the fleshy meat of the herbivora does not contain it in appreciable quantity, though these animals so constantly take starchy substances with their food. In them, the starchy matters are transformed into sugar by digestion, and the sugar so produced is rapidly destroyed after entering the circulation; so that usually neither saccharine nor starchy substances are to be discovered in the muscular tissue. M. Poggiale[1] found that in very many experiments, performed by a commission of the French Academy for the purpose of examining this subject, glycogenic matter was detected in ordinary butcher's meat only once. We have also found it to be absent from the fresh meat of the bullock's heart, when examined in the manner described above. Nevertheless, in dogs fed exclusively upon this food for eight days, glycogenic matter may be found in abundance in the liver, while it does not exist in other parts of the body, as the spleen, kidney, lungs, &c.

Furthermore, in a dog fed exclusively for eight days upon the fresh meat of the bullock's heart, and then killed four hours after a meal of the same food, at which time intestinal absorption is going on in full vigor, the liver contains, as above mentioned, both glycogenic matter and sugar; but neither sugar nor glycogenic matter can be found in the blood of the portal vein, when subjected to a similar examination.

The glycogenic matter, accordingly, does not originate from any external source, but is formed in the tissue of the liver; where it is soon afterward transformed into sugar, while still forming a part of the substance of the organ.

The formation of sugar in the liver is therefore a function com-

[1] Journal de Physiologie, Paris, 1858, p. 558.

posed of two distinct and successive processes, viz: first, the formation, in the hepatic tissue, of a glycogenic matter, having some resemblance to dextrine; and secondly, the conversion of this glycogenic matter into sugar, by a process of catalysis and transformation.

It has been doubted by some observers whether the sugar found in the liver after death really exists in the organ during life. This doubt, which was first raised by Pavy[1] in 1858, is based upon the fact that if the liver tissue, after death, be instantly subjected to the action of boiling water or strong alcohol, so as to arrest any further catalytic transformation of the glycogenic matter, the watery extract, when examined by the ordinary methods, has been found to yield no indication of sugar, or only slight traces of that substance. It was accordingly believed that the liver during life might contain only the glycogenic matter, but no sugar; and that the sugar, found a short time after death, was really produced by post-mortem fermentation during the interval which had elapsed.

The appearance of sugar under these circumstances must be admitted, at all events, to be exceedingly rapid. In a series of experiments performed in 1869, we have found that if a portion of the liver be excised from the abdomen of the living dog, and immediately cut into thin pieces and immersed in boiling water, when the preliminary operations are completed in so short a time as seventeen seconds or twenty-two seconds, the watery extract of the coagulated tissue, examined in the ordinary way by Trommer's test, gives no reduction of the copper oxide; but at the end of fifty seconds, a distinct though not abundant sugar reaction is manifest. This reaction is decided at the end of one minute, and becomes more and more marked at the end of two, three, four, five and seven minutes successively. It is only within fifty seconds, therefore, according to our own observations, that sugar fails to appear in the liver extract examined in the usual manner. Harley[2] has even found it, under these circumstances, within an interval of less than twenty seconds. But even within this short period the failure to detect sugar in the liver extract, thus examined, depends, as we believe, solely upon two causes: first, the small quantity of liver tissue employed; and secondly, the imperfect application of the copper test. In the first place, when a portion of liver,

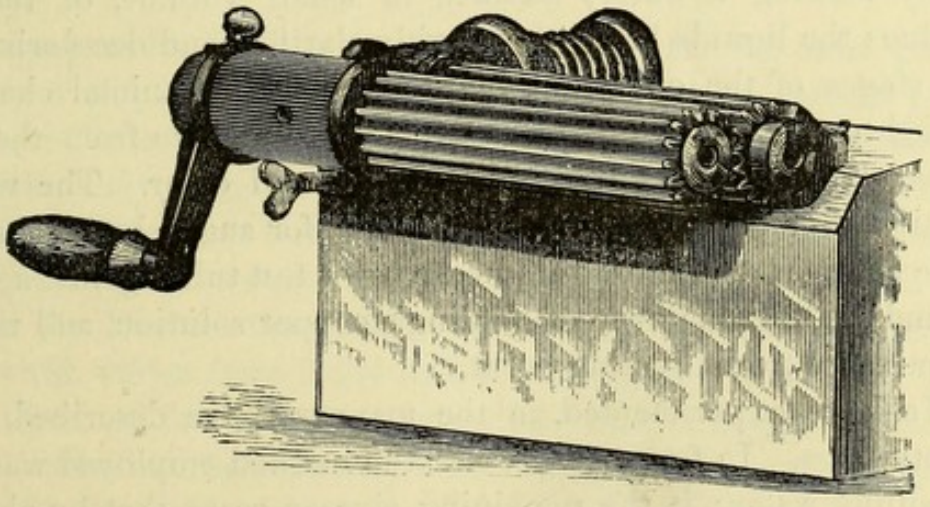
[1] Proceedings of the Royal Society of London, vol. ix. p. 300.

[2] Ibid., vol. x. p. 289.

removed from the body of the living or recently killed animal, is cut up by scissors into boiling water, only a small amount of the tissue can be treated in this way within a sufficiently short time. In the second place, the watery extract of the liver, as usually made, is more or less turbid and colored by various animal matters extracted at the same time; and the existence of these animal matters, when the sugar itself is present only in small amount, interferes in great measure with the reaction of the copper test. They must therefore be thoroughly removed by the free use of animal charcoal, and the watery extract of the liver tissue must be left absolutely clear and colorless, before we can apply the copper test with safety, to determine the presence or absence of sugar.

In order to avoid these two causes of error, we have adopted the following method of operating and of preparing the liver extract.[1] The animal is gently but firmly held upon a table by three assistants, the abdomen widely opened by a single stroke of a very sharp knife, the liver seized and drawn downward, and a portion instantly cut off and passed between the rollers of a comminuting machine into a vessel filled with strong alcohol or boiling water. The comminuting machine consists of two fluted brass cylinders placed horizontally side by side, and made to revolve rapidly toward each other by means of a crank-handle. The nearly

Fig. 55.



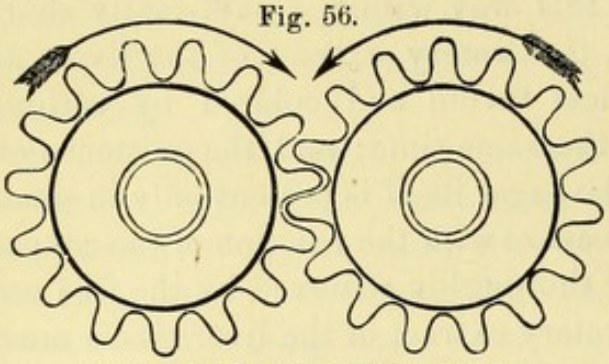
COMMINUTING MACHINE, used for grinding the liver substance.

parallel projections and depressions of the cylinders lock into each other, like the teeth of two cog-wheels; and their contiguous sur-

[1] All the details of this method are given in the New York Medical Journal for July, 1871.

faces, at the point of greatest proximity, are separated by a distance of not more than one sixteenth of an inch.

Fig. 56.



DIAGRAM, showing the revolving cylinders of the machine in profile.

When a portion of liver substance is passed between the rollers of this machine, it is disintegrated and comminuted in the most effectual manner; and no post-mortem fermentation can take place in any part of it, after it is once in contact with the alcohol, or boiling water. A large quantity of the liver tissue can, by this means, be used in a short time; from 1000 to 2000 grains being easily comminuted and immersed in the above mentioned liquids, within the space of ten seconds or even less.

Meanwhile, a fourth assistant marks the time consumed in the operation by means of a stop-watch, the second-hand of which is liberated at the instant the portion of liver is cut off, and again stopped when it is comminuted and immersed in alcohol or boiling water.

An extract is then made by slowly percolating the alcoholic liquor through the disintegrated liver tissue in a displacement apparatus, evaporating it to dryness over the water bath, and finally making a watery extract, in small volume, of the dry residue; the liquids being thoroughly clarified and decolorized, at two stages of the operation, by the free use of animal charcoal, carried to such an extent as completely to remove from the final watery solution every trace of turbidity and color. The watery solution, thus prepared, is then examined for sugar, by placing one cubic centimetre of the liquid in a narrow test tube against a black ground, adding one drop of Fehling's copper solution, and raising the mixture to the boiling-point.

We have experimented, in the manner above described, upon twenty dogs. In four of the cases, the method employed was that by boiling water; in the remaining sixteen cases, that by alcohol. The animals were examined four, eight, twelve, and twenty-four hours after feeding; the food consisting always of the fresh or cooked meat of the bullock's heart. The longest time which elapsed from the separation of the liver to its immersion in the alcohol or boiling water was thirteen seconds; the shortest time was three seconds. The average time was six and a quarter

seconds. In every instance the final watery solution gave a distinct and perfectly unmistakable sugar reaction by the copper test. In one half the cases, the presence of sugar alone was determined by this method; in the remainder, its proportion to one thousand parts of the liver tissue was also ascertained.

The following is a list of these experiments, with their results.

Experiment.	Time after Feeding.	Time consumed in taking out Liver.	Process of Treatment.	Proportion of Glucose in 1000 parts of Liver.
No. 1	4 hours	13 seconds	Alcohol	Glucose.
No. 2	4 hours	7 seconds	"	"
No. 3	4 hours	10 seconds	"	"
No. 4	4 hours	4 seconds	"	"
No. 5	8 hours	7 seconds	"	"
No. 6	8 hours	6 seconds	"	"
No. 7	4 hours	5 seconds	Boiling Water	"
No. 8	12 hours	6 seconds	" "	"
No. 9	12 hours	8 seconds	" "	"
No. 10	12 hours	5 seconds	" "	"
No. 11	4 hours	9 seconds	Alcohol	2.093
No. 12	4 hours	5 seconds	"	0.804
No. 13	8 hours	7 seconds	"	1.750
No. 14	8 hours	3 seconds	"	1.510
No. 15	12 hours	5 seconds	"	1.810
No. 16	12 hours	5 seconds	"	4.175
No. 17	12 hours	7 seconds	"	1.830
No. 18	12 hours	3 seconds	"	4.375
No. 19	24 hours	5 seconds	"	3.850
No. 20	24 hours	4 seconds	"	2.675

It appears from these results, that, when the requisite precautions are adopted, sugar is found in the liver at the earliest period at which it is possible to examine the organ after its separation from the body of the living animal; the average quantity of sugar existing in the liver tissue, at this time, being at least two and a half parts per thousand. The exact proportion of sugar thus present in the liver at the instant of death, or within a few seconds afterward, varies from 0.804 to 4.375 parts per thousand. These variations, so far as our observation extends, appear to depend upon individual differences in the animals employed for experiment; in the same manner as other ingredients of the tissues and fluids are found to vary, within physiological limits, in different individuals.

There is no doubt that the quantity of glucose in the liver increases immediately after death. This fact has been observed by all the recent experimenters upon the subject; and it was even shown by Bernard, as already mentioned, by experiments which

we have frequently verified, that sugar will be again produced in the liver, separated from the body, after it has once been entirely washed out by a continued watery injection of the hepatic blood-vessels. This is due to the fact that the sugar is produced by a transformation of the glycogenic matter; and this transformation will go on after death for a certain period, so long as the glycogenic matter remains unexhausted and the requisite temperature is kept up. Thus the sugar, no longer carried away by the current of the circulation, accumulates in the liver tissue at the expense of the glycogenic matter from which it is formed. This accumulation is at first very rapid, but subsequently diminishes in activity with the gradual deterioration of the liver substance.

In the following cases, the proportion of glucose per thousand parts was determined at various periods after death.

PROPORTION OF GLUCOSE IN THE LIVER.

	at the end of	*per thousand parts.*
Exp. No. 15.	5 seconds	1.810
	15 minutes	6.792
	1 hour	10.260
Exp. No. 19.	5 seconds	3.850
	6 hours	11.458
Exp. No. 20.	4 seconds	2.675
	1 hour	11.888
	4 hours	13.361
	12 hours	15.351

As sugar is found, under some circumstances, in minute quantity in the blood of the general circulation, there might perhaps be room for doubt whether the glucose, present in the liver at the moment of death, may not be due to the arterial blood with which the organ is supplied, rather than an ingredient of the hepatic tissue. This, however, is not the case. The question may be settled by examining, at the same time with the liver or immediately afterward, some other abdominal organ equally well supplied with arterial blood. In the series of experiments above described, the spleen was selected for this purpose, and in three cases was taken out within ten minutes after the excision of the liver, treated in precisely the same manner by the alcohol process, and examined for sugar, with the following result.

PROPORTION OF GLUCOSE PER THOUSAND PARTS.

	At the end of	*In the*	
Exp. No. 14.	3 seconds	Liver . .	1.510
	10 minutes	Spleen . .	0.
Exp. No. 19.	5 seconds	Liver . .	3.850
	10 minutes	Spleen . .	0.
Exp. No. 20.	4 seconds	Liver . .	2.675
	10 minutes	Spleen . .	0.

It is evident, accordingly, that the liver sugar does not belong to the arterial blood with which the organ is supplied, but is a normal ingredient of the hepatic tissue.

There is reason to believe that the sugar, produced in the substance of the liver, is absorbed from it by the circulating blood and carried away by the hepatic veins. A preponderance of sugar in the blood of the hepatic veins over that in other parts of the circulation was often recognized by Bernard and other observers, before it was considered as essential to make the examination within the first few seconds after death. Since that time the results of experimenters on this point have been conflicting, some observers, however, still finding a decided preponderance of sugar in the hepatic blood, within a very short period after death, or even during the life of the animal. Prof. A. Flint, Jr,[1] found sugar in the hepatic blood of the dog, obtained within a minute after death by ligature of the vena cava inferior; and Prof. Lusk[2] found that in five dogs, the blood of the right side of the heart, removed during life by catheterization through the jugular vein, contained a quantity of sugar from two to four times greater than that existing, in the same animals, in the blood of the jugular vein.

The sugar produced in the liver is accordingly to be regarded as a true secretion, formed by the glandular tissue of the organ, by a similar process to that of other glandular secretions. It differs from the latter, not in the manner of its production, but only in the mode of its discharge. For while the biliary matters produced in the liver are absorbed by the hepatic ducts and conducted downward to the gall-bladder and the intestine, the sugar is absorbed by the bloodvessels of the organ and carried upward, by the hepatic veins, toward the heart and the general circulation.

The production of sugar in the liver during health is a constant

[1] New York Medical Journal, January, 1869.

[2] Ibid., July, 1870.

process, continuing, in many cases, for several days after the animal has been altogether deprived of food. Its activity, however, like that of most other secretions, is subject to periodical augmentation and diminution. Under ordinary circumstances, the sugar, which is absorbed by the blood from the tissue of the liver, disappears very soon after entering the circulation. As the bile is transformed in the intestine, so the sugar is decomposed in the blood. We are not yet acquainted, however, with the precise nature of the changes which it undergoes after entering the vascular system. It is very probable, according to the views of Lehmann and Robin, that it is at first converted into lactic acid ($C_6H_6O_6$), which decomposes in turn the alkaline carbonates, setting free carbonic acid, and forming lactates of soda and potassa. But whatever be the exact mode of its transformation, it is certain that the sugar disappears rapidly; and while it exists in considerable quantity in the liver and in the blood of the hepatic veins and the right side of the heart, it is not usually to be found in the pulmonary veins nor in the blood of the general circulation.

About two and a half or three hours, however, after the ingestion of food, according to the investigations of Bernard, the circulation of blood through the portal system and the liver becomes considerably accelerated. A larger quantity of sugar is then produced in the liver and carried away from the organ by the hepatic veins; so that a portion of it then escapes decomposition while passing through the lungs, and begins to appear in the blood of the arterial system. Soon afterward it appears also in the blood of the capillaries; and from four to six hours after the commencement of digestion it is produced in the liver so much more rapidly than it is destroyed in the blood, that the surplus quantity circulates throughout the body, and the blood everywhere has a slightly saccharine character. It does not, however, in the healthy condition, make its appearance in any of the secretions.

After the sixth hour, this unusual activity of the sugar-producing function begins again to diminish; and, the transformation of the sugar in the circulation going on as before, it gradually disappears as an ingredient of the blood. Finally, the ordinary equilibrium between its production and its decomposition is re-established, and it can no longer be found except in the liver and in that part of the circulatory system which is between the liver and the lungs. There is, therefore, a periodical increase in the amount of undecomposed sugar in the blood, as we have already shown to be the

case with the fatty matter absorbed during digestion; but this increase is soon followed by a corresponding diminution, and during the greater portion of the time its decomposition keeps pace with its production, and it is consequently prevented from appearing in the blood of the general circulation.

There are produced, accordingly, in the liver, two different secretions, viz., bile and sugar. Both of them originate by transformation of the ingredients of the hepatic tissue, from which they are absorbed by two different sets of vessels. The bile is taken up by the biliary ducts, and by them discharged into the intestine; while the sugar is carried off by the hepatic veins, to be decomposed in the circulation, and become subservient to the nutrition of the blood.

CHAPTER X.

THE SPLEEN.

THE spleen is an exceedingly vascular organ, situated in the vicinity of the great pouch of the stomach and supplied abundantly by branches of the cœliac axis. Its veins, like those of the digestive abdominal organs, form a part of the great portal system, and conduct the blood which has passed through it to the liver, before it mingles again with the general current of the circulation.

The spleen is covered on its exterior by an investing membrane or capsule, which forms a protective sac, containing the soft pulp of which the greater part of the organ is composed. This capsule, in the spleen of the ox, is thick, whitish, and opaque, and is composed to a great extent of yellow elastic tissue. It accordingly possesses, in a high degree, the physical property of elasticity, and may be widely stretched without laceration; returning readily to its original size as soon as the extending force is relaxed.

In the carnivorous animals, on the other hand, the capsule of the spleen is thinner, and more colorless and transparent. It contains here but very little elastic tissue, being composed mostly of smooth, involuntary muscular fibres, connected in layers by a little intervening areolar tissue. In the herbivorous animals, accordingly, the capsule of the spleen is simply elastic, while in the carnivora it is contractile.

In both instances, however, the elastic and contractile properties of the capsule subserve a nearly similar purpose. There is every reason to believe that the spleen is subject to occasional and perhaps regular variations in size, owing to the varying condition of the abdominal circulation. Dr. William Dobson[1] found that the size of the organ increased, from the third hour after feeding up to the fifth; when it arrived at its maximum, gradually decreasing after that period. When these periodical congestions take place,

[1] In Gray, on the Structure and Uses of the Spleen. London, 1854, p. 40.

the organ becoming turgid with blood, the capsule is distended; and limits, by its resisting power, the degree of tumefaction to which the spleen is liable. When the disturbing cause has again passed away, and the circulation is about to return to its ordinary condition, the elasticity of the capsule in the herbivora, and its contractility in the carnivora, compress the soft vascular tissue within, and reduce the organ to its original dimensions. This contractile action of the invested capsule can be readily seen in the dog or the cat, by opening the abdomen while digestion is going on, exposing the spleen and removing it, after ligature of its vessels. When first exposed, the organ is plump and rounded, and presents externally a smooth and shining surface. But as soon as it has been removed from the abdomen and its vessels divided, it begins to contract sensibly, becomes reduced in size, stiff, and resisting to the touch; while its surface, at the same time, becomes uniformly wrinkled, by the contraction of its muscular fibres.

In its interior, the substance of the spleen is traversed everywhere by slender and ribbon-like cords of fibrous tissue, which radiate from the sheath of its principal arterial trunks, and are finally attached to the internal surface of its investing capsule. These fibrous cords, or *trabeculæ*, as they are called, by their frequent branching and mutual interlacement, form a kind of skeleton or framework by which the soft splenic pulp is embraced, and the shape and integrity of the organ maintained. They are composed of similar elements to those of the investing capsule, viz., elastic tissue and involuntary muscular fibres, united with each other by a varying quantity of the fibres of areolar tissue.

The interstices between the trabeculæ of the spleen are occupied by the splenic pulp; a soft, reddish substance, which contains, beside a few nerves and lymphatics, capillary bloodvessels in great profusion, and certain whitish globular bodies, which may be regarded as the distinguishing anatomical elements of the organ, and which are termed the *Malpighian bodies of the spleen.*

The Malpighian bodies are very abundant, and are scattered throughout the splenic pulp, being most frequently attached to the sides, or at the point of bifurcation of some small artery. They are readily visible to the naked eye in the spleen of the ox, upon a fresh section of the organ, as minute, whitish, rounded bodies, which may be separated, by careful manipulation, from the surrounding parts. In the carnivorous animals, on the other hand, and in the human subject, it is more difficult to distinguish them by the un-

aided eye, though they always exist in the spleen in a healthy condition. Their average diameter, according to Kölliker, is $\frac{1}{7}\frac{1}{2}$ of an inch. They consist of a closed sac, or capsule, containing in its interior a viscid, semi-solid mass of cells, cell-nuclei, and homogeneous substance. Each Malpighian body is covered, on its exterior, by a network of fine capillary bloodvessels; and it is now perfectly well settled, by the observations of various anatomists (Kölliker, Busk, Huxley, &c.), that bloodvessels also penetrate into the substance of the Malpighian body, and there form an internal capillary plexus.

The spleen is accordingly a glandular organ, analogous in its minute structure to the solitary and agminated glands of the small intestine, and to the lymphatic glands throughout the body. Like them, it is a gland without an excretory duct; and resembles, also, in this respect, the thyroid and thymus glands and the supra-renal capsules. All these organs have a structure which is evidently glandular in its nature, and yet the name of glands has been sometimes refused to them because they have, as above mentioned, no duct, and produce apparently no distinct secretion. We have already seen, however, that a secretion may be produced in the interior of a glandular organ, like the sugar in the substance of the liver, and yet not be discharged by its excretory duct. The veins of the gland, in this instance, perform the part of excretory ducts. They absorb the new materials, and convey them, through the medium of the blood, to other parts of the body, where they suffer subsequent alterations, and are finally decomposed in the circulation.

The action of such organs is consequently to modify the constitution of the blood. As the blood passes through their tissue, it absorbs from the glandular substance certain materials which it did not previously contain, and which are necessary to the perfect constitution of the circulating fluid. The blood, as it passes out from the organ, has therefore a different composition from that which it possessed before its entrance; and on this account the name of *vascular glands* has been applied to all the glandular organs above mentioned, which are destitute of excretory ducts, and is eminently applicable to the spleen.

The precise alteration, however, which is effected in the blood during its passage through the splenic tissue, has not yet been discovered. Various hypotheses have been advanced from time to time, as to the processes which go on in this organ; many of them

vague and indefinite in character, and some of them directly contradictory of each other. None, however, have yet been offered which are entirely satisfactory in themselves, or which rest on sufficiently reliable evidence.

A very remarkable fact with regard to the spleen is that it may be entirely removed in many of the lower animals, without its loss producing any serious permanent injury. This experiment has been frequently performed by various observers, and we have ourselves repeated it several times with similar results. The organ may be easily removed, in the dog or the cat, by drawing it out of the abdomen, through an opening in the median line, placing a few ligatures upon the vessels of the gastro-splenic omentum, and then dividing the vessels between the ligatures and the spleen. The wound usually heals without difficulty; and if the animal be killed some weeks afterward, the only remaining trace of the operation is an adhesion of the omentum to the inner surface of the abdominal parietes, at the situation of the original wound.

The most constant and permanent effect of a removal of the spleen is an unusual increase of the appetite. This symptom we have observed in some instances to be excessively developed; so that the animal would at all times throw himself, with an unnatural avidity, upon any kind of food offered him. We have seen a dog, subjected to this operation, afterward feed without hesitation upon the flesh of other dogs; and even devour greedily the entrails, taken warm from the abdomen of the recently killed animal. The food taken in this unusual quantity is, however, perfectly well digested; and the animal will often gain very perceptibly in weight. In one instance, a cat, in whom the unnatural appetite was marked though not excessive, increased in weight from five to six pounds, in the course of a little less than two months; and at the same time the fur became sleek and glossy, and there was a considerable improvement in the general appearance of the animal.

Another symptom, which usually follows removal of the spleen, is an unnatural ferocity of disposition. The animal will frequently attack others, of its own or a different species, without any apparent cause, and without any regard to the difference of size, strength, &c. This symptom is sometimes equally excessive with that of an unnatural appetite; while in other instances it shows itself only in occasional outbursts of irritability and violence.

Neither of the symptoms, however, which we have just described, appears to exert any permanently injurious effect upon the

animal which has been subjected to the operation; and life may be prolonged for an indefinite period without any serious disturbance of the nutritive process, after the spleen has been completely extirpated.

We must accordingly regard the spleen, not as a single organ, but as associated with others, which may completely, or to a great extent, perform its functions after its entire removal. We have already noticed the similarity in structure between the spleen and the mesenteric and lymphatic glands; a similarity which has led some writers to regard them as more or less closely associated with each other in function, and to consider the spleen as an unusually developed lymphatic or mesenteric gland. It is true that this organ is provided with a comparatively scanty supply of lymphatic vessels; and the chyle, which is absorbed from the intestine, does not pass through the spleen, as it passes through the remaining mesenteric glands. Still, the physiological action of the spleen may correspond with that of the other lymphatic glands, so far as regards its influence on the blood; and there can be little doubt that its function is shared, either by them or by some other glandular organs, which become unnaturally active, and more or less perfectly supply its place after its complete removal.

CHAPTER XI.

THE BLOOD.

THE blood, as it exists in its natural condition, while circulating in the vessels, is a thick opaque fluid, varying in different parts of the body from a brilliant scarlet to a dark purple or nearly black color. It has a slightly alkaline reaction, and a specific gravity of 1055. It is not, however, an entirely homogeneous fluid, but is found on microscopic examination to consist, first, of a nearly colorless, transparent, alkaline fluid, termed the *plasma*, containing water, fibrin, albumen, salts, &c., in a state of mutual solution; and, secondly, of a large number of distinct cells, or corpuscles, the *blood-globules*, swimming freely in the liquid plasma. The blood, taken as a whole, consists of blood-globules and plasma, in about equal proportions; that is, nearly one-half globules and one-half plasma. The specific gravity of these two ingredients is slightly different. That of the plasma is about 1030; that of the blood-globules, 1088. Nevertheless, the natural movement of the blood in the vessels keeps them thoroughly mingled together; and even when the blood is allowed to remain at rest in a glass jar, the globules subside only very slowly and imperfectly. Thus the globules, mingled abundantly and uniformly with the fluid plasma, give to the entire mass of the blood an opaque aspect and a deep red color.

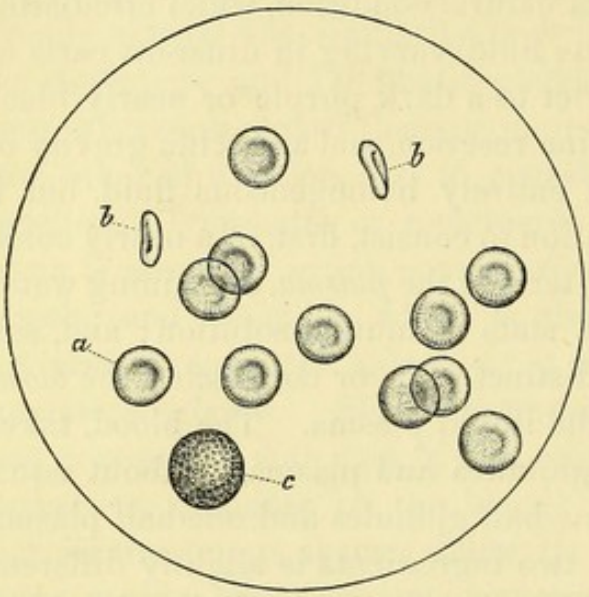
BLOOD-GLOBULES.—On microscopic examination it is found that the globules of the blood are of two kinds, viz., red and white; of these the red are by far the most abundant.

The *red globules* of the blood present, under the microscope, a perfectly circular outline and a smooth exterior. (Fig. 57.) Their size varies somewhat, in human blood, even in the same specimen. The greater number of them have a transverse diameter of $\frac{1}{3000}$ of an inch; but there are many smaller ones to be seen, which are not more than $\frac{1}{3500}$ or even $\frac{1}{4000}$ of an inch in diameter. Their form is that of a spheroid, very much flattened on its opposite surfaces, somewhat like a round biscuit, or a thick piece of money with rounded edges. The blood-globule accordingly, when seen flatwise, presents a comparatively broad surface and a circular outline (*a*); but if it be made to roll over, it will present itself edge-

wise during its rotation and assume the flattened form indicated at *b*. The thickness of the globule, seen in this position, is about $\frac{1}{16000}$ of an inch, or a little less than one-fifth of its transverse diameter.

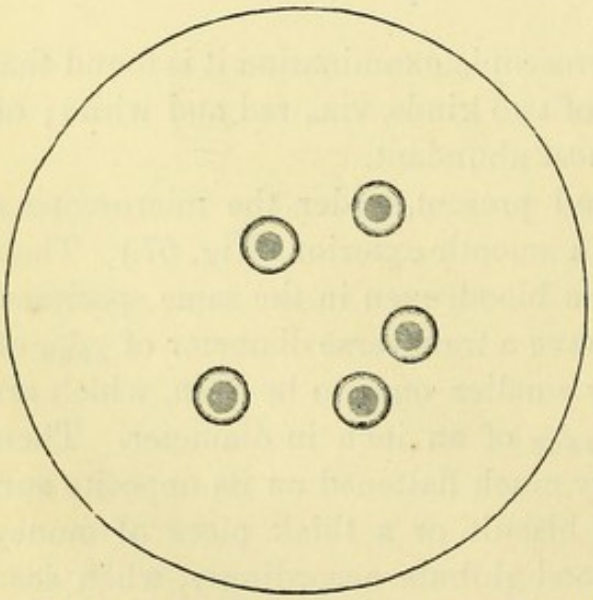
When the globules are examined lying upon their broad surfaces, it can be seen that these surfaces are not exactly flat, but that there is on each side a slight central depression, so that the rounded edges of the blood-globule are evidently thicker than its middle portion. This inequality produces a remarkable optical effect. The substance of which the blood-globule is composed refracts light more strongly than the fluid plasma. Therefore, when examined with the microscope, by transmitted light, the thick edges of the globules act as double convex lenses, and concentrate the light above the level of the fluid. Consequently, if the object-glass be carried upward by the adjusting screw of the microscope, and lifted away from the stage, so that the blood-globules fall beyond its focus, their edges will appear brighter. But the central portion of each globule, being excavated on both sides, acts as a double concave lens, and disperses the light from a point below the level of the fluid. It, therefore, grows brighter as the object-glass is carried downward, and the object falls within its focus. An alternating appearance of the blood-globules may, therefore, be produced by viewing them first beyond and then within the focus of the instrument.

Fig. 57.



HUMAN BLOOD-GLOBULES.—*a*. Red globules, seen flatwise. *b*. Red globules, seen edgewise. *c*. White globule.

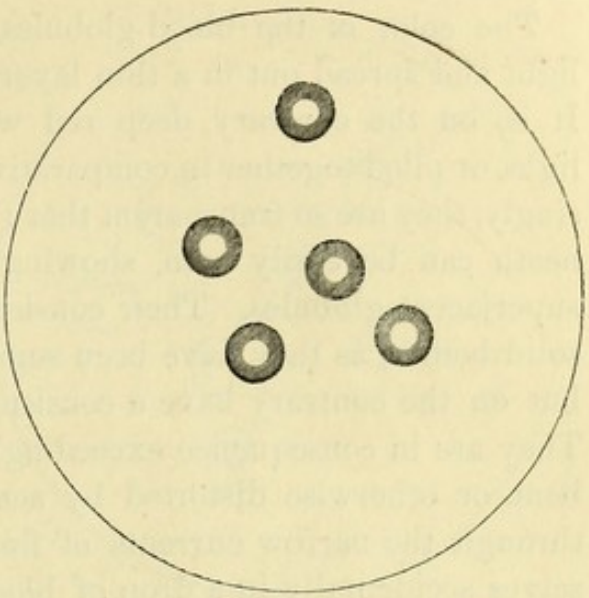
Fig. 58.



RED GLOBULES OF THE BLOOD, seen a little beyond the focus of the microscope.

When beyond the focus, the globules will be seen with a bright rim and a dark centre. (Fig. 58.) When within it they will appear with a dark rim and a bright centre. (Fig. 59.)

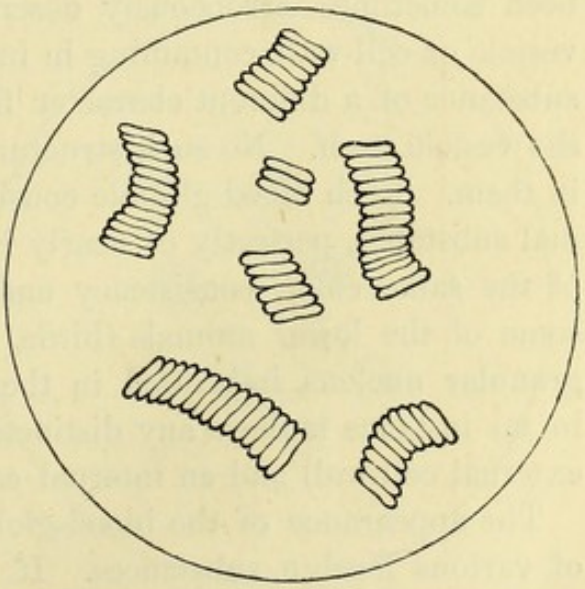
Fig. 59.



THE SAME, seen a little within the focus.

The blood-globules accordingly have the form of a thickened disk with rounded edges and a double central excavation. They have, consequently, been sometimes called "blood-disks," instead of blood-globules. The term 'disk," however, does not indicate their exact shape, any more than the other; and the term "blood-corpuscle," which is also sometimes used, does not indicate it at all. And although the term "blood-globule" may not be precisely a correct one, still it is the most convenient; and need not give rise to any confusion, if we remember the real shape of the bodies designated by it. This term will, consequently, be employed whenever we have occasion to speak of the blood-globules in the following pages.

Fig. 60.



BLOOD-GLOBULES adhering together, like rolls of coin.

Within a minute after being placed under the microscope, the blood-globules, after a fluctuating movement of short duration, very often arrange themselves in slightly curved rows or chains, in which they adhere to each other by their flat surfaces, presenting an appearance which has been aptly compared with that of rolls of coin. This is probably owing merely to the coagulation of the blood, which takes place very rapidly when it is spread out in thin layers and in contact with glass surfaces; and which, by

compressing the globules, forces them into such a position that they may occupy the least possible space. This position is evidently that in which they are applied to each other by their flat surfaces, as above described.

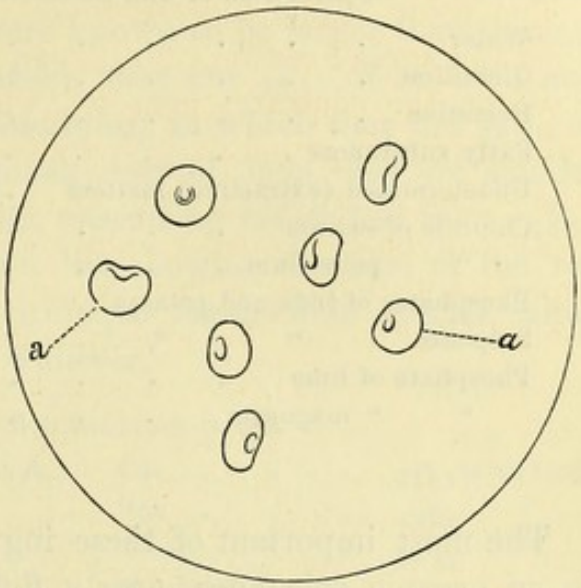
The color of the blood-globules, when viewed by transmitted light and spread out in a thin layer, is a light amber or pale yellow. It is, on the contrary, deep red when they are seen by reflected light, or piled together in comparatively thick layers. When viewed singly, they are so transparent that the outlines of those lying underneath can be easily seen, showing through the substance of the superjacent globules. Their consistency is peculiar. They are not solid bodies, as they have been sometimes inadvertently described; but on the contrary have a consistency which is *very nearly* fluid. They are in consequence exceedingly flexible, and easily elongated, bent, or otherwise distorted by accidental pressure, or in passing through the narrow currents of fluid which often establish themselves accidentally in a drop of blood under microscopic examination. This distortion, however, is only temporary, and the globules regain their original shape, as soon as the accidental pressure is taken off. The peculiar flexibility and elasticity thus noticed are characteristic of the red globules of the blood, and may always serve to distinguish them from any other free cells which may be found in the animal tissues or fluids.

In structure the blood-globules are homogeneous. They have been sometimes erroneously described as consisting of a closed vesicle or cell-wall, containing in its cavity some fluid or semi-fluid substance of a different character from that composing the wall of the vesicle itself. No such structure, however, is really to be seen in them. Each blood-globule consists of a mass of organized animal substance, perfectly or nearly homogeneous in appearance, and of the same color, consistency and composition throughout. In some of the lower animals (birds, reptiles, fish) it contains also a granular nucleus, imbedded in the substance of the globule; but in no instance is there any distinction to be made out between an external cell-wall and an internal cavity.

The appearance of the blood-globules is altered by the addition of various foreign substances. If water be added, so as to dilute the plasma, the globules absorb it by imbibition, swell, lose their double central concavity and become paler. If a larger quantity of water be added, they finally dissolve and disappear altogether. When a moderate quantity of water is mixed with the blood, the

edges of the globules, being thicker than the central portions, and absorbing water more abundantly, become turgid, and encroach gradually upon the central part. (Fig. 61.) It is very common to see the central depression under these circumstances, disappear on one side before it is lost on the other, so that the globule, as it swells up, curls over towards one side, and assumes a peculiar cup-shaped form (*a*). This form may often be seen in blood-globules that have been soaking for some time in the urine, or in any other animal fluid of a less density than the plasma of the blood. Dilute acetic acid dissolves the blood-globules more promptly than water, and solutions of the caustic alkalies more promptly still.

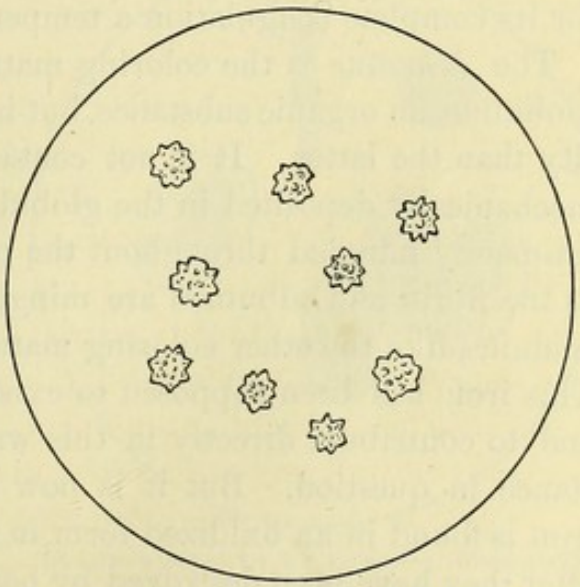
Fig. 61.



BLOOD-GLOBULES, swollen by the imbibition of water.

If a drop of blood be allowed partially to evaporate while under the microscope, the globules near the edges of the preparation often diminish in size, and at the same time present a shrunken and crenated appearance, as if minute granules were projecting from their surfaces (Fig. 62); an effect apparently produced by the evaporation of part of their watery ingredients. For some unexplained reason, however, a similar distortion is often produced in some of the globules by the addition of certain other animal fluids, as for example the saliva; and a few can even be seen in this condition after the addition of pure water.

Fig. 62.



BLOOD-GLOBULES, shrunken, with their margins crenated.

When separated from the other ingredients of the blood and examined by themselves, the globules are found, according to Lehmann, to present the following composition:—

Composition of the Blood-Globules in 1000 Parts.

Water		688.00
Globuline		282.22
Hematine		16.75
Fatty substances		2.31
Undetermined (extractive) matters		2.60
Chloride of sodium	8.12	
" potassium		
Phosphates of soda and potassa		
Sulphate " "		
Phosphate of lime		
" " magnesia		
		1000.00

The most important of these ingredients is the *globuline*. This is an organic substance, nearly fluid in its natural condition by union with water, and constituting the greater part of the mass of the blood-globules. It is soluble in water, but insoluble in the plasma of the blood, owing to the presence in that fluid of albumen and saline matters. If the blood be largely diluted, however, the globuline is dissolved, as already mentioned, and the blood-globules are destroyed. Globuline coagulates by heat; but, according to Robin and Verdeil, only becomes opalescent at 160°, and requires for its complete coagulation a temperature of 200° F.

The *hematine* is the coloring matter of the globules. It is, like globuline, an organic substance, but is present in much smaller quantity than the latter. It is not contained in the form of a powder, mechanically deposited in the globuline, but the two substances are intimately mingled throughout the mass of the blood-globule, just as the fibrin and albumen are mingled in the plasma. Hematine contains, like the other coloring matters, a small proportion of iron. This iron has been supposed to exist under the form of an oxide; and to contribute directly in this way to the red color of the substance in question. But it is now ascertained that although the iron is found in an oxidized form in the ashes of the blood-globules after they have been destroyed by heat, its oxidation probably takes place during the process of incineration. So far as we know, therefore, the iron exists originally in the hematine as an ultimate element, directly combined with the other ingredients of this substance, in the same manner as the carbon, the hydrogen, or the nitrogen.

The blood-globules of all the warm-blooded quadrupeds, with the exception of the family of the camelidæ, resemble those of the human species in shape and structure. They differ, however, somewhat in size, being usually rather smaller than in man. There are but two species in which they are known to be larger than in man, viz., the Indian elephant, in which they are $\frac{1}{2700}$ of an inch, and the two-toed sloth (*Bradypus didactylus*), in which they are $\frac{1}{2800}$ of an inch in diameter. In the musk deer of Java they are smaller than in any other known species, measuring rather less than $\frac{1}{12000}$ of an inch. The following is a list showing the size of the red globules of the blood in the principal mammalian species, taken from the measurement of Mr. Gulliver.[1]

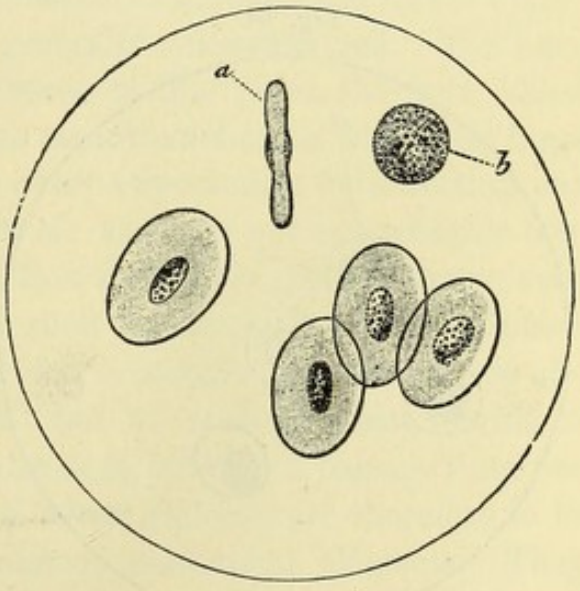
DIAMETER OF RED GLOBULES IN THE

Ape	$\frac{1}{3400}$ of an inch.	Cat	$\frac{1}{4400}$ of an inch.
Horse	$\frac{1}{4600}$ "	Fox	$\frac{1}{4100}$ "
Ox	$\frac{1}{4200}$ "	Wolf	$\frac{1}{3600}$ "
Sheep	$\frac{1}{3300}$ "	Elephant	$\frac{1}{2700}$ "
Goat	$\frac{1}{6300}$ "	Red deer	$\frac{1}{3000}$ "
Dog	$\frac{1}{3500}$ "	Musk deer	$\frac{1}{12000}$ "

In all these instances the form and general appearance of the globules are the same. The only exception to this rule among the mammalians is in the family of the camelidæ (camel, dromedary, llama), in which the globules present an oval out line instead of a circular one. In other respects they resemble the foregoing.

In the three remaining classes of vertebrate animals, viz., birds, reptiles, and fish, the blood-globules differ so much from the above that they can be readily distinguished by microscopic examination. They are oval in form, and contain a colorless granular nucleus imbedded in their

Fig. 63.



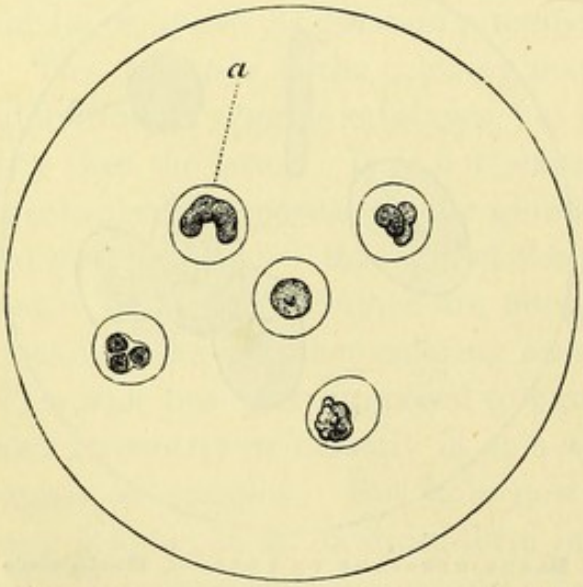
BLOOD-GLOBULES OF FROG.—*a*. Blood-globule seen edgewise. *b*. White globule.

[1] In Works of William Hewson, Sydenham edition, London, 1846, p. 327.

substance. They are also considerably larger than the blood-globules of the mammalians, particularly in the class of reptiles. In the frog (Fig. 63) they measure $\frac{1}{120}$ of an inch in their long diameter; and in *Menobranchus*, the great water-lizard of the northern lakes, $\frac{1}{400}$ of an inch. In *Proteus anguinus* they attain the size, according to Dr. Carpenter,[1] of $\frac{1}{337}$ of an inch.

Beside the corpuscles described above, there are globules of another kind to be found in the blood, viz., the *white globules*. These globules are much less numerous than the red; the proportion between the two, in human blood, being one white to about three hundred red globules. In reptiles, the relative quantity of the white globules is greater, but they are always considerably less abundant than the red. They differ also from the latter in shape, size, color, and consistency. They are globular in form, white or colorless, and instead of being homogeneous like the others, their substance is filled everywhere with minute dark molecules, which give them a finely granular appearance. (Fig. 57, *c*.) In size they are considerably larger than the red globules, being about $\frac{1}{2500}$ of an inch in diameter. They are also more consistent than the others, and do not so easily glide along in the minute currents of a drop of blood under examination, but adhere readily to the surfaces of the glass. If treated with dilute acetic acid, they swell up and become smooth and circular in outline; and at the same time a separation or partial coagulation seems to take place in the substance of which they are composed, so that an irregular collection of granular matter shows itself in their interior, becoming more divided and broken up as the action of the acetic acid upon the globule is longer continued. (Fig. 64.) This collection of granular matter often assumes a curved or crescentic form, as at *a*, and sometimes various other irregular shapes. It does not in-

Fig. 64.



White Globules of the Blood; altered by dilute acetic acid.

[1] The Microscope and its Revelations, Philadelphia edition, p. 600.

dicate the existence of a nucleus in the white globule, but it is merely an appearance produced by the coagulating and disintegrating action of acetic acid upon the substance of which it is composed.

The chemical constitution of the white globules, as distinguished from the red, has never been determined; owing to the small quantity in which they occur, and the difficulty of separating them from the others for purposes of analysis.

The two kinds of blood-globules, white and red, are to be regarded as distinct and independent anatomical forms. It has been sometimes supposed that the white globules were converted, by a gradual transformation, into the red. There is, however, no direct evidence of this; as the transformation has never been seen to take place, either in the human subject or in the mammalia, nor even its intermediate stages satisfactorily observed. When, therefore, in default of any such direct evidence, we are reduced to the surmise which has been adopted by some authors, viz., that the change "takes place too rapidly to be detected by our means of observation,"[1] it must be acknowledged that the above opinion has no solid foundation. It has been stated by some authors (Kölliker, Gerlach) that in the blood of the batrachian reptiles there are to be seen certain bodies intermediate in appearance between the white and the red globules, and which represent different stages of transition from one form to the other; but this is not a fact which is generally acknowledged. We have repeatedly examined, with reference to this point, the fresh blood of the frog, as well as that of the menobranchus, in which the large size of the globules would give every opportunity for detecting any such changes, did they really exist; and it is our unavoidable conclusion from these observations, that there is no good evidence, even in the blood of reptiles, of any such transformation taking place. There is simply, as in human blood, a certain variation in size and opacity among the red globules; but no such connection with, or resemblance to, the white globules as to indicate a passage from one form to the other. The red and white globules are therefore to be regarded as distinct and independent anatomical elements. They are mingled together in the blood, just as capillary bloodvessels and nerves are mingled in areolar tissue; but there is no other connection between them, so far as their formation is concerned, than that of juxtaposition.

[1] Kölliker, Handbuch der Gewebelehre, Leipzig, 1852, p. 582.

Neither is it at all probable that the red globules are produced or destroyed in any particular part of the body. One ground for the belief that these bodies were produced by a metamorphosis of the white globules was a supposition that they were continually and rapidly destroyed somewhere in the circulation; and as this loss must be as rapidly counterbalanced by the formation of new globules, and as no other probable source of their reproduction appeared, they were supposed to be produced by transformation of the white globules. But there is no reason for believing that the red globules of the blood are any less permanent, as anatomical forms, than the muscular fibres or the nervous filaments. They undergo, it is true, like all the constituent parts of the body, a constant interstitial metamorphosis. They absorb incessantly nutritious materials from the blood, and give up to the circulating fluid, at the same time, other substances which result from their internal waste and disintegration. But they do not, so far as we know, perish bodily in any part of the circulation. It is not the *anatomical forms*, anywhere, which undergo destruction and renovation in the nutritive process; but *only the proximate principles of which they are composed.* The effect of this interstitial nutrition, therefore, in the blood-globules as in the various solid tissues, is merely to maintain them in a natural and healthy condition of integrity. Their ingredients are incessantly altered, by transformation and decomposition, as they pass through various parts of the vascular system; but the globules themselves retain their form and texture, and still remain as constituent parts of the circulating fluid.

Plasma.—The *plasma* of the blood, according to Lehmann, has the following constitution:—

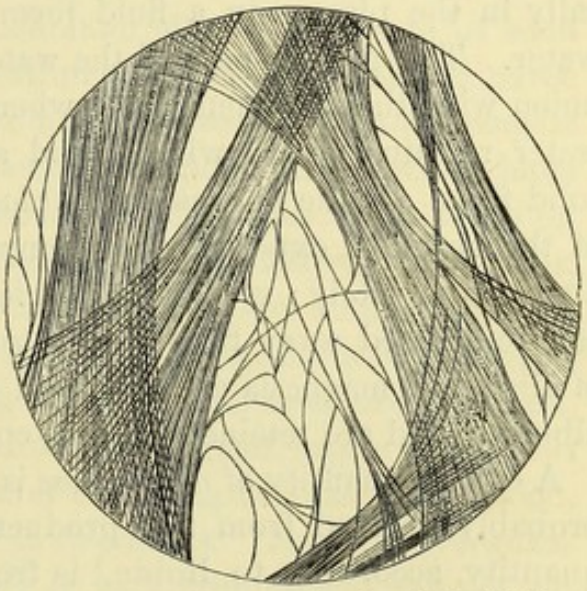
Composition of the Plasma in 1,000 parts.

Water		902.90
Fibrin		4.05
Albumen		78.84
Fatty matters		1.72
Undetermined (extractive) matters		3.94
Chloride of sodium		8.55
" potassium		
Phosphates of soda and potassa		
Sulphates " "		
Phosphate of lime		
" magnesia		
		1000.00

The above ingredients are all intimately mingled in the blood-plasma, in a fluid form, by mutual solution; but they may be separated from each other for examination by appropriate means. The two ingredients belonging to the class of organic substances are the fibrin and the albumen.

The *fibrin*, though present in small quantity, is evidently an important element in the constitution of the blood. It may be obtained in a tolerably pure form by gently stirring freshly drawn blood with a glass rod or a bundle of twigs; upon which the fibrin coagulates, and adheres to the twigs in the form of slender threads and flakes. The fibrin, thus coagulated, is at first colored red by the hæmatine of the blood-globules entangled in it; but it may be washed colorless by a few hours' soaking in running water. The fibrin then presents itself under the form of nearly white threads and flakes, having a semi-solid consistency, and a considerable degree of elasticity.

Fig. 65.



Coagulated Fibrin, showing its fibrillated condition.

The coagulation of fibrin takes place in a peculiar manner. It does not solidify in a perfectly homogeneous mass; but if examined by the microscope in thin layers it is seen to have a fibroid or filamentous texture. In this condition it is said to be "fibrillated." (Fig. 65.) The filaments of which it is composed are colorless and elastic, and when isolated are seen to be exceedingly minute, being not more than $\frac{1}{4000}$ or even $\frac{1}{5000}$ of an inch in diameter. They are in part arranged so as to lie parallel with each other; but are more generally interlaced in a kind of irregular network, crossing each other in every direction. On the addition of dilute acetic acid, they swell up and fuse together into a homogeneous mass, but do not dissolve. They are often interspersed everywhere with minute granular molecules, which render their outlines more or less obscure.

Once coagulated, fibrin is insoluble in water and can only be again liquefied by the action of an alkaline or strongly saline solution, or by prolonged boiling at a very high temperature. These

agents, however, produce a complete alteration in the properties of the fibrin, and after being subjected to them it is no longer the same substance as before.

The quantity of fibrin in the blood varies in different parts of the body. According to the observations of various writers, there is for the most part less fibrin in venous than in arterial blood. It is also more deficient in the blood of the large veins near the heart than of those at a distance. It disappears especially during the circulation through the liver and the kidneys; and, as a general rule, there is no fibrin in the blood of the hepatic or the renal veins.

The *albumen* is undoubtedly the most important ingredient of the plasma, judging both from its nature and the abundance in which it occurs. It coagulates at once on being heated to 160° F., or by contact with alcohol, the mineral acids, the metallic salts, or with ferrocyanide of potassium in an acidulated solution. It exists naturally in the plasma in a fluid form by reason of its union with water. The greater part of the water of the plasma, in fact, is in union with the albumen; and when the albumen coagulates, the water remains united with it, and assumes at the same time the solid form. If the plasma of the blood, therefore, after the removal of the fibrin, be exposed to the temperature of 160° F., it solidifies almost completely; so that only a few drops of water remain that can be drained away from the coagulated mass. The phosphates of lime and magnesia are also held in solution principally by the albumen, and are retained by it in coagulation.

A certain quantity of *albuminose* is also to be found in the blood, probably derived from the products of digestion. Its average quantity, according to Robin,[1] is from 2 to 3 parts per thousand. As it is absorbed in considerable quantities from the intestine during digestion, and neither accumulates in the blood nor appears in any of the excretions, it must be transformed into some other substance nearly as fast as it is taken into the blood.

The *fatty matters* exist in the blood mostly in a saponified form, excepting soon after the digestion of food rich in fat. At that period, as we have already mentioned, the emulsioned fat finds its way into the blood, and circulates for a time unchanged. Afterwards it disappears as free fat, and remains partly in the saponified condition.

The *saline ingredients* of the plasma are of the same nature with those existing in the globules. The chlorides of sodium and potas-

[1] Leçons sur les Humeurs, page 108.

sium, and the phosphates of soda and potassa are the most abundant in both, while the sulphates are present only in minute quantity. The proportions in which the various salts are present are very different, according to Lehmann,[1] in the blood-globules and in the plasma. Chloride of potassium is most abundant in the globules, while in the plasma chloride of sodium is the most abundant, forming rather more than one-half of all the saline ingredients taken together. The phosphates of soda and potassa are more abundant in the globules than in the plasma. On the other hand, the phosphates of lime and magnesia are more abundant in the plasma than in the globules.

The *alkalescence* of the plasma is due to the presence of the carbonate and basic phosphate of soda. It has already been mentioned, that, while the alkaline phosphates are most abundant in the blood of the carnivora, the carbonates are most abundant in that of the herbivora. Thus Lehmann[2] found carbonate of soda in the blood of the ox in proportion of 1.628 per thousand parts. The substances known under the name of *extractive matters* consist of a mixture of different ingredients, of organic origin, which have not yet been separated in a state of sufficient purity to admit of their being thoroughly examined and distinguished from each other. They do not exist in great abundance, but are undoubtedly of considerable importance in the constitution of the blood. There are also to be found, in solution in the blood, *urea, urate of soda, creatine, creatinine, sugar,* &c.; all of them crystallizable substances derived from the transformation of other ingredients of the blood, or of the tissues through which it circulates. The relative quantity, however, of these substances is very minute, and has not yet been determined with precision.

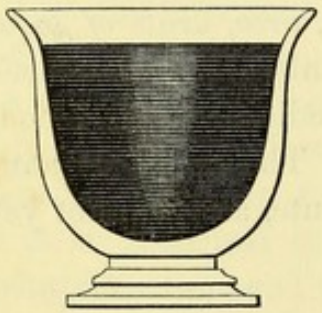
Coagulation of the Blood.—A few moments after the blood has been withdrawn from the vessels, a remarkable phenomenon presents itself, viz., its coagulation or clotting. This process commences at nearly the same time throughout the whole mass of the blood. The blood becomes first somewhat diminished in fluidity, so that it will not run over the edge of the vessel, when slightly inclined; and its surface may be gently depressed with the end of the finger or a glass rod. It then becomes rapidly thicker, and at last solidifies into a uniformly red, opaque, consistent, gelatinous mass, which takes the form of the vessel in which the blood was

[1] Op. cit., vol. i. p. 546. [2] Op. cit., vol. i. p. 393.

received. Its coagulation is then complete. The process usually commences, in the case of the human subject, in about fifteen minutes after the blood has been drawn, and is completed in about twenty minutes.

The coagulation of the blood is dependent entirely upon the presence of the fibrin. This fact has been demonstrated in various ways. In the first place, if frog's blood be filtered, so as to separate the globules and leave them upon the filter, while the plasma is allowed to run through, the colorless filtered fluid which contains the fibrin soon coagulates; while no coagulation takes place in the moist globules remaining on the filter. Again, if the freshly drawn blood be stirred with a bundle of rods, as we have already described above, the fibrin coagulates upon them by itself, while the rest of the plasma, mixed with the globules, remains perfectly fluid. It is the fibrin, therefore, which, by its own coagulation, induces the solidification of the entire blood. As the fibrin is uniformly distributed throughout the blood, when its coagulation takes place the minute filaments which make their appearance in it entangle in their meshes the globules and the albuminous fluids of the plasma. A very small quantity of fibrin, therefore, is sufficient to entangle by its solidification all the fluid and semi-fluid ingredients which were mingled with it, and convert the whole into a voluminous, trembling, jelly-like mass of coagulated or "clotted" blood. (Fig. 66.)

Fig. 66.

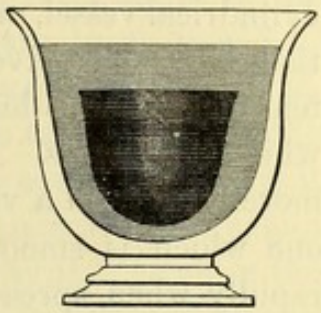


Bowl of recently Coagulated Blood, showing the whole mass uniformly solidified.

As soon as the clot has fairly formed, it begins to contract and diminish in size. Exactly how this contraction of the clot is produced, we are unable to say; but it is probably a continuation of the same process by which its solidification is at first accomplished, or at least one very similar to it. As the contraction proceeds, the albuminous fluids begin to be pressed out from the meshes in which they were entangled. A few isolated drops first appear on the surface of the clot. These drops soon increase in size and become more numerous. They run together and coalesce with each other, as more and more fluid exudes from the coagulated mass, until the whole surface of the clot is covered with a thin layer of fluid. The clot at first adheres pretty strongly to the sides of the vessel into which the blood was drawn; but as its contraction goes

on, its edges are separated, and the fluid continues to exude between it and the sides of the vessel. This exudation continues for ten or twelve hours; the clot growing constantly smaller and firmer, and the expressed fluid more and more abundant.

Fig. 67.



Bowl of Coagulated Blood, after twelve hours; showing the clot contracted and floating in the fluid serum.

The globules, owing to their greater consistency, do not escape with the albuminous fluids, but remain entangled in the fibrinous coagulum. Finally, at the end of ten or twelve hours the whole of the blood has usually separated into two parts, viz., the *clot* which is a red, opaque, dense and resisting semi-solid mass, consisting of the fibrin and the blood-globules; and the *serum*, which is a transparent, nearly colorless fluid, containing the water, albumen, and saline matters of the plasma. (Fig. 67.)

The change of the blood in coagulation may therefore be expressed as follows:—

Before coagulation the blood consists of

1st. Globules; and 2d. Plasma—containing { Fibrin, Albumen, Water, Salts.

After coagulation it is separated into

1st. Clot, containing { Fibrin and Globules; and 2d. Serum, containing { Albumen, Water, Salts.

The coagulation of the blood is hastened or retarded by various physical conditions, which have been studied with care by various observers, but more particularly by Robin and Verdeil. The conditions which influence the rapidity of coagulation are as follows: First, the rapidity with which the blood is drawn from the vein, and the size of the orifice from which it flows. If blood be drawn rapidly, in a full stream, from a large orifice, it remains fluid for a comparatively long time; if it be drawn slowly, from a narrow orifice, it coagulates quickly. Thus it usually happens that in the operation of venesection, the blood drawn immediately after the opening of the vein runs freely and coagulates slowly; while that which is drawn toward the end of the operation, when the tension of the veins has been relieved and the blood trickles slowly from the wound, coagulates quickly. Secondly, the shape of the vessel into which the blood is received and the condition of its internal

surface. The greater the extent of surface over which the blood comes in contact with the vessel, the more is its coagulation hastened. Thus, if the blood be allowed to flow into a tall, narrow, cylindrical vessel, or into a shallow plate, it coagulates more rapidly than if it be received into a hemispherical bowl, in which the extent of surface is less, in proportion to the entire quantity of blood which it contains. For the same reason, coagulation takes place more rapidly in a vessel with a roughened internal surface, than in one which is smooth and polished. The blood coagulates most rapidly when spread out in thin layers, and entangled among the fibres of cloth or sponges. For the same reason, also, hemorrhage continues longer from an incised wound than from a lacerated one; because the blood, in flowing over the ragged edges of the lacerated bloodvessels and tissues, solidifies upon them readily, and thus blocks up the wound.

In all these cases, there is an inverse relation between the rapidity of coagulation and the firmness of the clot. When coagulation takes place slowly, the clot afterward becomes small and dense, and the serum is abundant. When coagulation is rapid, there is but little contraction of the coagulum, an imperfect separation of the serum, and the clot remains large, soft, and gelatinous.

It is well known to practical physicians that a similar relation exists when the coagulation of the blood is hastened or retarded by disease. In cases of lingering and exhausting illness, or in diseases of a typhoid or exanthematous character, with much depression of the vital powers, the blood coagulates rapidly and the clot remains soft. In cases of active inflammatory disease, as pleurisy or pneumonia, occurring in previously healthy subjects, the blood coagulates slowly, and the clot becomes very firm. In every instance, the blood which has once coagulated liquefies again at the commencement of putrefaction.

The blood coagulates also in the interior of the vessels *after death and the stoppage of the circulation.* Under these circumstances coagulation takes place less rapidly than if the blood were wholly withdrawn from the body, owing probably to its remaining in contact with the smooth internal surfaces of the bloodvessels, and to the more gradual loss of its natural temperature. In man, as a general rule, the blood is found coagulated in the cavities of the heart and large vessels in from twelve to twenty-four hours after death. In the lower animals, coagulation occurs earlier than this, namely, from four to ten hours after death. The blood coagulates in the cavities

of the heart sooner than elsewhere, and the clot in the ventricles is often found to be so entangled with the valves and chordæ tendineæ as to be extricated from them with difficulty.

Coagulation of the blood takes place also in the interior of the body even during life, whenever, from any cause, there is a *local arrest or impediment of the circulation.* Thus, if blood be accidentally extravasated into the meshes of the areolar tissue, the substance of the brain or spinal cord, or into a serous cavity, it coagulates in these situations, after a short time, and forms a clot which takes the shape of the cavity occupied by it. Even in the vessels themselves, if the blood be arrested or imprisoned in any particular locality by pressure or ligatures, the same result follows. If a ligature be placed upon an artery in the living subject, the blood which stagnates above the ligatured spot coagulates as it would do if entirely removed from the circulation. The clot, under these circumstances, extends from the ligature backward to the situation of the next collateral arterial branch, that is, to the point at which the movement of the circulation still continues. In all cases, during life as after death, the stoppage or retardation of the circulatory movement induces, after a longer or shorter interval, the coagulation of the fibrin of the blood.

The coagulation of the fibrin is *not a commencement of organization;* it is merely its passage from the normal fluid condition to an unnatural state of solidity, as in the coagulation of the other organic substances. The filaments already described, which show themselves in the clot (Fig. 65), are not, properly speaking, organized fibres, and are entirely different in their character from the fibres of areolar tissue, or any other normal anatomical elements. They are simply the ultimate form which fibrin assumes in coagulating, just as albumen takes the form of granules under the same circumstances. The clot, therefore, when once formed, even in the interior of the system, as in cases of ligature, apoplexy or extravasation, becomes a foreign body, and is slowly reabsorbed by the neighboring parts during convalescence. This reabsorption of the clot is progressive, and is accompanied by various changes in its appearance and consistency. At first it is comparatively voluminous, soft, and of a deep red color. Its more fluid parts, or the serum, are then reabsorbed and the clot becomes smaller and denser. The red coloring matter then gradually diminishes, the whole mass becoming constantly more and more decolorized and reduced in size as absorption goes on, until it loses entirely its original ap-

pearance, and finally altogether disappears. The time required for complete reabsorption varies from a few days to several months, according to the size of the clot and the situation in which extravasation has taken place.

Fibrin, therefore, is distinguished from the other organic ingredients of the blood by its spontaneous coagulation. Its constitution is such, that, without the addition of heat or any chemical agent, it necessarily solidifies after a longer or shorter time, provided only that the movement of the blood in the circulation be arrested or seriously impeded. Why then does it not coagulate in the vessels during life, and while the circulation is actually going on?

The answer to this question is as follows:—The fibrin remains fluid during the natural state of the circulation, because, like the other ingredients of the blood, it is constantly undergoing changes which prevent its arriving at the state necessary for coagulation. We can easily understand how this should be the case when we remember, in the first place, the extreme rapidity with which the blood moves in the vessels of the living body. We shall see hereafter that from twenty-five seconds to half a minute is sufficient for the blood to accomplish the entire round of the circulation, so that during this time it visits the remotest organs and tissues and returns again to the right side of the heart.

Secondly, the fibrin of the blood *disappears while passing through the liver and the kidneys.* This fact is fully established by the observations of Simon,[1] Lehmann,[2] Bernard, and Brown-Séquard.[3] While there is an abundance of fibrin in both arterial and portal blood, none, or only feeble traces of it, can be found in that of the hepatic or the renal veins. It is, therefore, decomposed or transformed into some other substance while passing through these organs; and, its quantity in the blood remaining unimpaired, a fresh supply must be as constantly formed elsewhere. By calculating approximatively the quantity of blood contained in the whole body, and that passing daily through the liver and kidneys, it is easy to estimate that a quantity of fibrin equal to that in the entire blood is destroyed and reproduced several times over in the course of a single day. Thus the fibrin existing in the blood at any one time is that which has been recently formed; and before the time arrives at which

[1] Chemistry of Man. Day's Translation. Philadelphia, 1846, p. 178.

[2] Journal für praktische Chemie, 1851, p. 205.

[3] Journal de la Physiologie. Paris, April, 1858, p. 298.

it would naturally coagulate while still in the vessels, it has already been decomposed by its usual metamorphosis in the circulation, and has been replaced by a new supply of still more recent formation. But if any portion of the blood be shut off from the circulation, by ligature or otherwise, its fibrin remains unaltered, and in due time necessarily coagulates.

It is evident, therefore, that the spontaneous coagulation of the fibrin, though a property by which we recognize it when withdrawn from the vessels, is really an abnormal phenomenon, and never takes place in the natural state of the circulation.

Nevertheless, the coagulability of the blood is a very characteristic property, and becomes an exceedingly important one under many accidental circumstances. It is, in fact, the natural means by which hemorrhage is arrested, after a wound of any vascular tissue. If such a wound be compressed for a short time, a thin layer of blood coagulates between its edges, and the adherent clot thus formed acts as a temporary plug until the parts have permanently re-united by the slower growth of new tissue. A torn or contused wound bleeds less freely than an incised one, because the blood coagulates more rapidly upon the ragged edges of the lacerated tissues and thus blocks up the opening. When an artery of considerable size is wounded, and the surgeon places a ligature upon its divided extremity, the clot formed behind the ligature acts as a still more permanent plug and prevents hemorrhage even after the ligature has been thrown off by ulceration.

The *entire quantity* of blood existing in the body is difficult to ascertain with absolute precision. It is not possible to extract the whole of it by opening the large vessels, since a certain portion will always remain in the cavities of the heart, in the veins, and in the capillaries of the head and abdominal organs. The other methods which have been practised or proposed from time to time are, for the most part, liable to some practical objection. There is no doubt also that the quantity of blood varies within physiological limits according to the condition of fasting or digestion; since it will necessarily be more abundant after the digestion and absorption of a full meal, than in a state of prolonged abstinence. Bernard[1] has found, furthermore, that if a poisonous substance be injected in definite quantity into the veins of a living animal, it requires a considerably larger quantity to produce death if the animal be in digestion than if he be fasting, since the proportion

[1] Liquides de l'Organisme, Paris, 1859. Tome i., p. 419.

of the poison to the whole mass of the blood differs in the two cases. The most satisfactory method for ascertaining approximatively the entire quantity of blood in the human subject is that adopted by Weber and Lehmann.[1] These observers operated upon two criminals who suffered death by decapitation; in each of which instances both the methods and results were essentially similar. In one of them the quantities obtained were as follows:—The body weighed before decapitation 133 pounds avoirdupois. The blood which escaped from the vessels at the time of decapitation amounted to 12.27 pounds. In order to estimate the quantity of blood which remained in the vessels, the experimenters then injected the arteries of the head and trunk with water until it returned from the vessels of a pale red or yellow color, collected the fluid thus returned, and ascertained how much solid matter it held in solution. This amounted to 477.22 grains, which corresponded to 4.38 pounds of blood. The result of the experiment is therefore as follows:—

Blood which escaped from the vessels	12.27 pounds.
" remained in the body	4.38 "
Whole quantity of blood in the living body,	16.65

The weight of the blood, then, in proportion to the entire weight of the body, was as 1 : 8; and the body of a healthy man, weighing 145 pounds, will therefore contain on the average about 18 pounds of blood.

[1] Physiological Chemistry, vol. i. p. 638.

CHAPTER XII.

RESPIRATION.

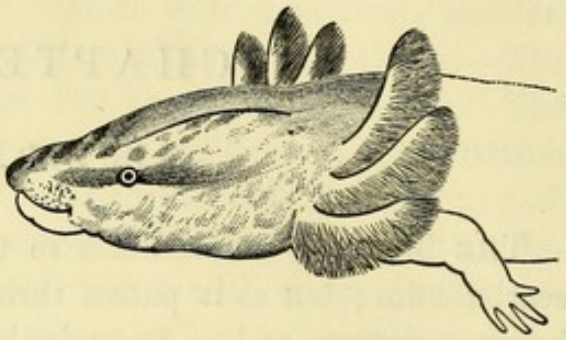
THE blood as it circulates in the arterial system has a bright scarlet color; but as it passes through the capillaries it gradually becomes darker, and on its arrival in the veins its color is a deep purple, and in some parts of the body nearly black. There are, therefore, two kinds of blood in the body; arterial blood, which is of a bright color, and venous blood, which is dark. Now it is found that the dark-colored venous blood, which has been contaminated by passing through the capillaries, is unfit for further circulation. It is incapable, in this state, of supplying the organs with their healthy stimulus and nutrition, and has lost its value as a circulating fluid. It is accordingly carried back to the heart by the veins, and thence sent to the lungs, where it is reconverted into arterial blood. The process by which the venous blood is thus arterialized and renovated, is known as the process of *respiration.*

This process takes place very actively in the higher animals, and probably does so to a greater or less extent in all animals without exception. Its essential conditions are that the circulating fluid should be exposed to the influence of atmospheric air, or of an aerated fluid; that is, of a fluid holding atmospheric air or oxygen in solution. The respiratory apparatus consists essentially of a moist and permeable animal membrane, the respiratory membrane, with the bloodvessels on one side of it, and the air or aerated fluid on the other. The blood and the air, consequently, do not come in direct contact with each other, but absorption and exhalation take place from one to the other through the thin membrane which lies between.

The special anatomical arrangement of the respiratory apparatus differs in different species of animals. In most of those inhabiting the water, the respiratory organs have the form of *gills* or *branchiæ;* that is, delicate filamentous prolongations of some part of the

integument or mucous membranes, which contain an abundant supply of bloodvessels, and which hang out freely into the surrounding water. In many kinds of aquatic lizards, as, for example, in *menobranchus* (Fig. 68), there are upon each side of the neck three delicate feathery tufts of thread-like prolongations from the mucous membrane of the pharynx, which pass out through fissures in the side of the neck. Each tuft is composed of a principal stem, upon which the filaments are arranged in a pinnated form, like the plume upon the shaft of a feather. Each filament, when examined by itself, is seen to consist of a thin, ribbon-shaped fold of mucous membrane, in the interior of which there is a plentiful network of minute bloodvessels. The dark blood, as it comes into the filament from the branchial artery, is exposed to the influence of the water in which the filament is bathed, and as it circulates through the capillary network of the gills is reconverted into arterial blood. It is then carried away by the branchial vein, and passes into the general current of the circulation. The apparatus is further supplied with a cartilaginous framework, and a set of muscles by which the gills are gently waved about in the surrounding water, and constantly brought into contact with fresh portions of the aerated fluid.

Fig. 68.



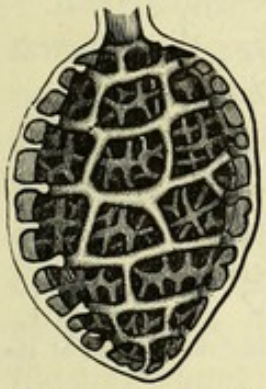
Head and Gills of Menobranchus.

Most of the aquatic animals breathe by gills similar in all their essential characters to those described above. In terrestrial and air-breathing animals, however, the respiratory apparatus is situated internally. In them, the air is made to penetrate into the interior of the body, into certain cavities or sacs called the lungs, which are lined with a vascular mucous membrane. In the salamanders, for example, which, though aquatic in their habits, are air-breathing animals, the lungs are two long cylindrical sacs, running nearly the entire length of the body, commencing anteriorly by a communication with the pharynx, and terminating by rounded extremities at the posterior part of the abdomen. These lungs, or air-sacs, have a smooth internal surface; and the blood which circulates through their vessels is arterialized by exposure to the air contained in their cavities. The air is forced into the lungs by a kind of

swallowing movement, and is after a time regurgitated and discharged, in order to make room for a fresh supply.

In frogs, turtles, serpents, &c., the structure of the lung is a little more complicated, since respiration is more active in these animals, and a more perfect organ is requisite to accomplish the arterialization of the blood. In these animals, the cavity of the lung, instead of being simple, is divided by incomplete partitions into a number of smaller cavities or "cells." The cells all communicate with the central pulmonary cavity; and the partitions, which join each other at various angles, are all composed of thin, projecting folds of the lining membrane, with bloodvessels ramifying between them. (Fig. 69.) By this arrangement, the extent of surface presented to the air by the pulmonary membrane is much increased, and the arterialization of the blood takes place with a corresponding degree of rapidity.

Fig. 69.

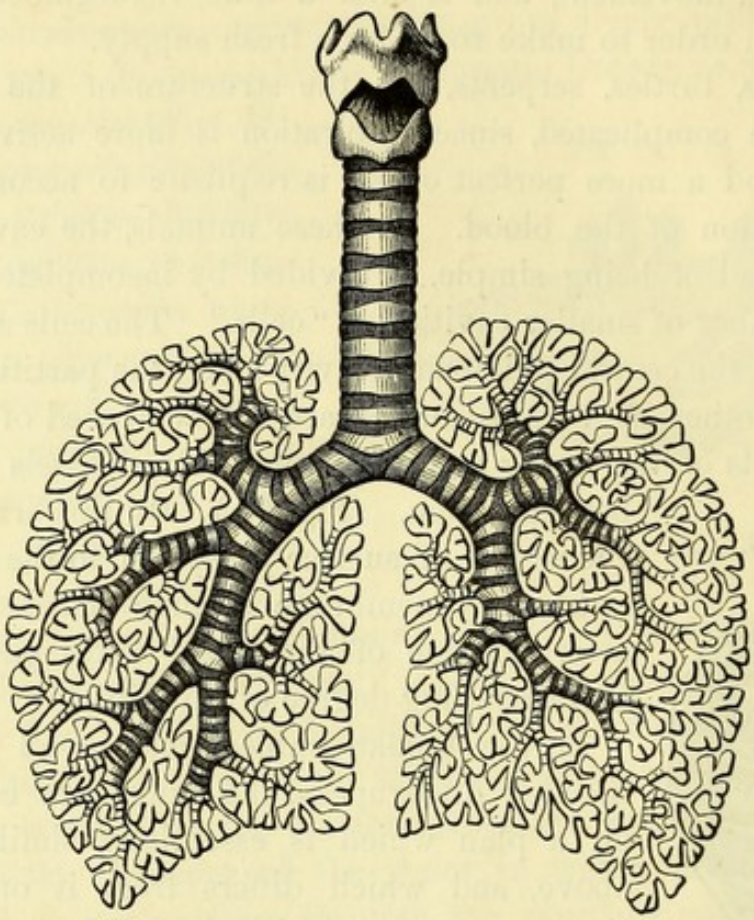


Lung of Frog, showing its internal surface.

In the human subject, and in all the warm-blooded quadrupeds, the lungs are constructed on a plan which is essentially similar to the above, and which differs from it only in the greater extent to which the pulmonary cavity is subdivided, and the surface of the respiratory membrane increased. The respiratory apparatus (Fig. 70) commences with the larynx, which communicates with the pharynx at the upper part of the neck. Then follows the trachea, a membranous tube with cartilaginous rings; which, upon its entrance into the chest, divides into the right and left bronchus. These again divide successively into secondary and tertiary bronchi; the subdivision continuing, while the bronchial tubes grow smaller and more numerous, and separate constantly from each other. As they diminish in size, the tubes grow more delicate in structure, and the cartilaginous rings and plates disappear from their walls. They are finally reduced, according to Kölliker, to the size of $\frac{1}{25}$ of an inch in diameter; and are composed only of a thin mucous membrane, lined with pavement epithelium, which rests upon an elastic fibrous layer. They are then known as the "ultimate bronchial tubes."

Each ultimate bronchial tube terminates in a division or islet of the pulmonary tissue, about $\frac{1}{12}$ of an inch in diameter, which is termed a "pulmonary lobule." Each pulmonary lobule resembles in its structure the entire frog's lung in miniature. It consists of a

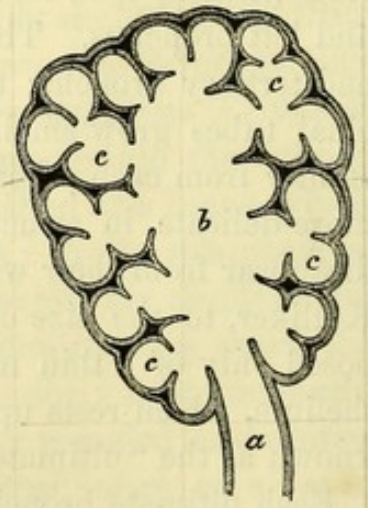
Fig. 70.



HUMAN LARYNX, TRACHEA, BRONCHI, AND LUNGS; showing the ramification of the bronchi, and the division of the lungs into lobules.

vascular membrane inclosing a cavity; which cavity is divided into a large number of secondary compartments by thin septa or partitions, which project from its internal surface. (Fig. 71.) These secondary cavities are the "pulmonary cells," or "vesicles." Each vesicle is about $\frac{1}{175}$ of an inch in diameter; and is covered on its exterior with a close network of capillary bloodvessels, which dip down into the spaces between the adjacent vesicles, and expose in this way a double surface to the air which is contained in their cavities. Between the vesicles, and in the interstices between the lobules, there is a large quantity of yellow elastic tissue, which gives firmness and resiliency to the pulmonary structure. The pulmonary vesicles, according to the observations of Kölliker, are lined everywhere with a layer of pavement epithelium, continuous with that in the

Fig. 71.



SINGLE LOBULE OF HUMAN LUNG.—*a*. Ultimate bronchial tube. *b*. Cavity of lobule. *c*, *c*, *c*. Pulmonary cells, or vesicles.

ultimate bronchial tubes. The whole extent of respiratory surface in both lungs has been calculated by Lieberkühn[1] at fourteen hundred square feet. It is plainly impossible to make a precisely accurate calculation of this extent; but there is every reason to believe that the estimate adopted by Lieberkühn, regarded as approximative, is not by any means an exaggerated one. The great multiplication of the minute pulmonary vesicles, and of the partitions between them, must evidently increase to an extraordinary degree the extent of surface over which the blood, spread out in a thin layer, is exposed to the action of the air. These anatomical conditions are, therefore, the most favorable for its rapid and complete arterialization.

Respiratory Movements of the Chest.—The air which is contained in the pulmonary lobules and vesicles becomes rapidly vitiated in the process of respiration, and requires therefore to be expelled and replaced by a fresh supply. This exchange or renovation of the air is effected by alternate movements of the chest, of expansion and collapse, which are termed the "respiratory movements of the chest." The expansion of the chest is effected by two sets of muscles, viz., first, the diaphragm, and, second, the intercostals. While the diaphragm is in a state of relaxation, it has the form of a vaulted partition between the thorax and abdomen, the edges of which are attached to the inferior extremity of the sternum, the inferior costal cartilages, the borders of the lower ribs and the bodies of the lumbar vertebræ, while its convexity rises high into the cavity of the chest, as far as the level of the fifth rib. When the fibres of the diaphragm contract, their curvature is necessarily diminished; and they approximate a straight line, exactly in proportion to the extent of their contraction. Consequently, the entire convexity of the diaphragm is diminished in the same proportion, and it descends toward the abdomen, enlarging the cavity of the chest from above downward. (Fig. 72.) At the same time the intercostal muscles enlarge it in a lateral direction. For the ribs, articulated behind with the bodies of the vertebræ, and joined in front to the sternum by the flexible and elastic costal cartilages, are so arranged that, in a position of rest, their convexities look obliquely outward and downward. When the movement of inspiration is about to commence, the first rib is fixed by the contraction of the

[1] In Simon's Chemistry of Man, Philada. ed., 1846, p. 109.

scaleni muscles, and the intercostal muscles then contracting simultaneously, the ribs are drawn upward. In this movement, as each rib rotates upon its articulation with the spinal column at one extremity, and with the sternum at the other, its convexity is necessarily carried outward at the same time that it is drawn upward, and the parietes of the chest are, therefore, expanded laterally. The sternum itself rises slightly with the same movement, and enlarges to some extent the antero-posterior diameter of the thorax. By the simultaneous action, therefore, of the diaphragm which descends, and of the intercostal muscles which lift the ribs and the sternum, the cavity of the chest is expanded in every direction, and the air passes inward, through the trachea and bronchial tubes, by the simple force of aspiration.

Fig. 72.

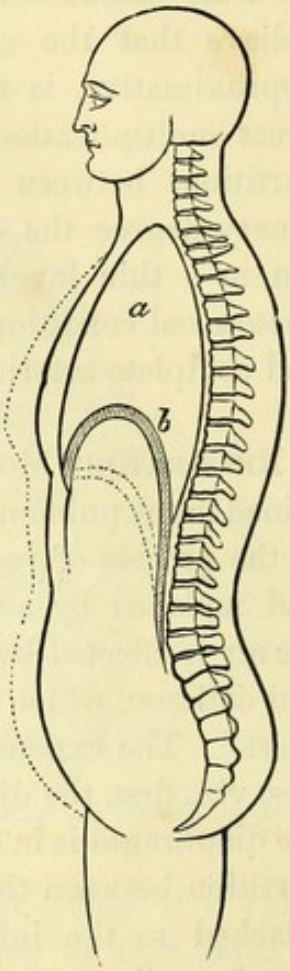


DIAGRAM ILLUSTRATING THE RESPIRATORY MOVEMENTS.—*a*. Cavity of the chest. *b*. Diaphragm. The dark outlines show the figure of the chest when collapsed; the dotted lines show the same when expanded.

After the movement of inspiration is accomplished, and the lungs are filled with air, the diaphragm and intercostal muscles relax, and a movement of expiration takes place, by which the chest is partially collapsed, and a portion of the air contained in the pulmonary cavity expelled. The movement of expiration is entirely a passive one, and is accomplished by the action of three different forces. First, the abdominal organs, which have been pushed out of their usual position by the descent of the diaphragm, fall backward by their own weight and carry upward the relaxed diaphragm before them. Secondly, the costal cartilages, which are slightly twisted out of shape when the ribs are drawn upward, resume their natural position as soon as the muscles are relaxed, and, drawing the ribs down again, compress the sides of the chest. Thirdly, the pulmonary tissue, as we have already remarked, is abundantly supplied with yellow elastic fibres, which retract by virtue of their own elasticity, in every part of the lungs, after they have been forcibly distended, and, compressing the pulmonary vesicles, drive out a portion of the air which they contained. By the constant

recurrence of these alternating movements of inspiration and expiration, fresh portions of air are constantly introduced into and expelled from the chest.

The average quantity of atmospheric air, taken into and discharged from the lungs with each respiratory movement, is, according to the results of various observers, twenty cubic inches. At eighteen respirations per minute, taken as the mean between the sleeping and waking hours, this amounts to 360 cubic inches of air inspired per minute, 21,600 cubic inches per hour, and 518,400 cubic inches per day. But as the movements of respiration are increased both in extent and rapidity by every muscular exertion, the entire quantity of air daily used in respiration is not less than 600,000 cubic inches, or 350 cubic feet.

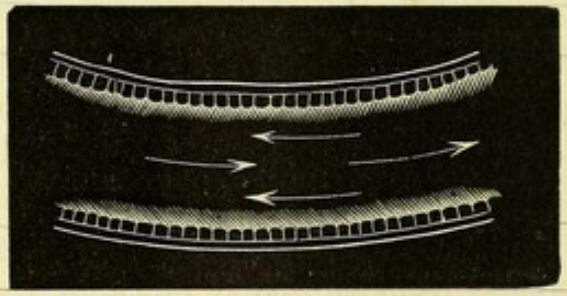
The whole of the air in the chest, however, is not changed at each movement of respiration. On the contrary, a very considerable quantity remains in the pulmonary cavity after the most complete expiration; and even after the lungs have been removed from the chest, they still contain a large quantity of air which cannot be entirely displaced by any violence short of disintegrating and disorganizing the pulmonary tissue. It is evident, therefore, that only a comparatively small portion of the air in the lungs passes in and out with each respiratory movement; and it will require several successive respirations before all the air in the chest can be entirely changed. It has not been possible to ascertain with certainty the exact proportion in volume which exists between the air which is alternately inspired and expired, or "tidal" air, and that which remains constantly in the chest, or "residual" air, as it is called. It has been estimated, however, by Dr. Carpenter,[1] from the reports of various observers, that the volume of inspired and expired air varies from 10 to 13 per cent. of the entire quantity contained in the chest. If this estimate be correct, it will require from eight to ten respirations to change the whole quantity of air in the cavity of the chest.

It is evident, however, from the foregoing, that the inspiratory and expiratory movements of the chest cannot be sufficient to change the air at all in the pulmonary lobules and vesicles. The air which is drawn in with each inspiration penetrates only into the trachea and bronchial tubes, until it occupies the place of that which was driven out by the last expiration. By the ordinary respiratory movements, therefore, only that small portion of the

[1] Human Physiology, Philada. ed., 1855, p. 300.

air lying nearest the exterior, in the trachea and large bronchi, would fluctuate backward and forward, without ever penetrating into the deeper parts of the lung, were there no other means provided for its renovation. There are, however, two other forces in play for this purpose. The first of these is the diffusive power of the gases themselves. The air remaining in the deeper parts of the chest is richer in carbonic acid and poorer in oxygen than that which has been recently inspired; and by the laws of gaseous diffusion there must be a constant interchange of these gases between the pulmonary vesicles and the trachea, tending to mix them equally in all parts of the lung. This mutual diffusion and intermixture of the gases will therefore tend to renovate, partially at least, the air in the pulmonary lobules and vesicles. Secondly, the trachea and bronchial tubes, down to those even of the smallest size, are lined with a mucous membrane which is covered with ciliated epithelium. The movement of those cilia is found to be directed always from below upward; and, like ciliary motion wherever it occurs, it has the effect of producing a current in the same direction, in the fluids covering the mucous membrane. The air in the tubes must participate, to a certain extent, in this current, and a double stream of air therefore is established in each bronchial tube; one current passing from within outward along the walls of the tube, and a return current passing from without inward, along the central part of its cavity. (Fig. 73.) By this means a kind of aerial circulation is constantly maintained in the interior of the bronchial tubes; which, combined with the mutual diffusion of the gases and the alternate expansion and collapse of the chest, effectually accomplishes the renovation of the air contained in all parts of the pulmonary cavity.

Fig. 73.

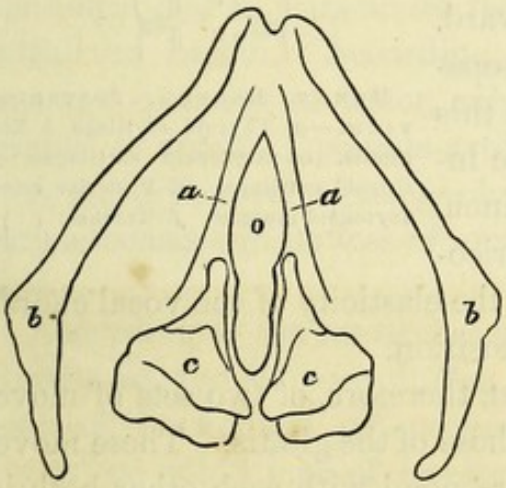


SMALL BRONCHIAL TUBE, showing outward and inward current, produced by ciliary motion.

RESPIRATORY MOVEMENTS OF THE GLOTTIS.—Beside the movements of expansion and collapse already described, belonging to the chest, there are similar respiratory movements which take place in the larynx. If the respiratory passages be examined after death, in the state of collapse in which they are usually found, it will be

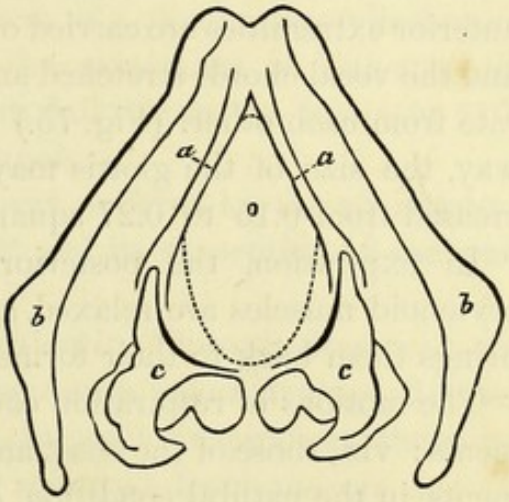
noticed that the opening of the glottis is very much smaller than the cavity of the trachea below. The glottis itself presents the appearance of a narrow chink, while the passage for the inspired air widens in the lower part of the larynx, and in the trachea constitutes a spacious tube, nearly cylindrical in shape, and over half an inch in diameter. We have found, for instance, that in the human subject the space included between the vocal chords has an area of only 0.15 to 0.17 square inch; while the calibre of the trachea in the middle of its length is 0.45 square inch. This disproportion, however, which is so evident after death, does not exist during life. While respiration is going on, there is a constant and regular movement of the vocal chords, synchronous with the inspiratory and expiratory movements of the chest, by

Fig. 74.



HUMAN LARYNX, viewed from above in its ordinary post-mortem condition.—*a*. Vocal chords. *b*. Thyroid cartilage. *cc*. Arytenoid cartilages. *o*. Opening of the glottis.

Fig. 75.

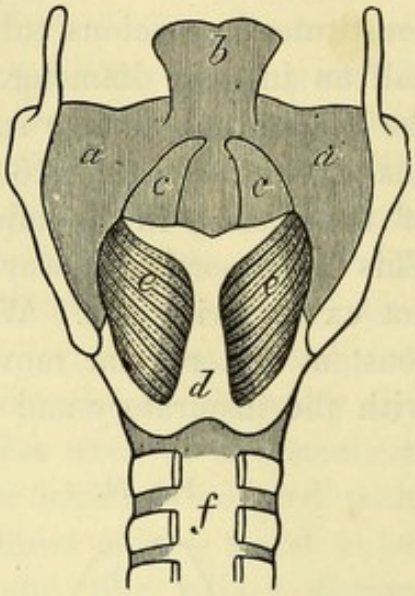


The same, with the glottis opened by separation of the vocal chords.—*a*. Vocal chords. *b*. Thyroid cartilage. *cc*. Arytenoid cartilages. *o*. Opening of the glottis.

which the size of the glottis is alternately enlarged and diminished. At every inspiration, the glottis opens and allows the air to pass freely into the trachea; at every expiration it collapses, and the air is driven out through it from below. These movements are called the "respiratory movements of the glottis." They correspond in every respect with those of the chest, and are excited or retarded by similar causes. Whenever the general movements of respiration are hurried and labored, those of the glottis become accelerated and increased in intensity at the same time; and when the movements of the chest are slower or fainter than usual, owing to debility, coma, or the like, those of the glottis are diminished in the same proportion.

In the respiratory motions of the glottis, as in those of the chest, the movement of inspiration is an active one, and that of expiration passive. In inspiration, the glottis is opened by contraction of the posterior crico-arytenoid muscles. (Fig. 76.) These muscles originate from the posterior surface of the cricoid cartilage, near the median line; and their fibres, running upward and outward, are inserted into the external angle of the arytenoid cartilages. By the contraction of these muscles, during the movement of inspiration, the arytenoid cartilages are rotated upon their articulations with the cricoid, so that their anterior extremities are carried outward, and the vocal chords stretched and separate from each other. (Fig. 75.) In this way, the size of the glottis may be increased from 0.15 to 0.27 square inch.

Fig. 76.



HUMAN LARYNX, POSTERIOR VIEW.—*a*. Thyroid cartilage. *b*. Epiglottis. *cc*. Arytenoid cartilages. *d*. Cricoid cartilage. *ee*. Posterior crico-arytenoid muscles. *f*. Trachea.

In expiration, the posterior crico-arytenoid muscles are relaxed, and the elasticity of the vocal chords brings them back to their former position.

The motions of respiration consist, therefore, of two sets of movements: viz., those of the chest and those of the glottis. These movements, in the natural condition, correspond with each other both in time and intensity. It is at the same time and by the same nervous influence, that the chest expands to inhale the air, while the glottis opens to admit it; and in expiration, the muscles of both chest and glottis are relaxed; while the elasticity of the tissues, by a kind of passive contraction, restores the parts to their original condition.

CHANGES IN THE AIR DURING RESPIRATION.—The atmospheric air, as it is drawn into the cavity of the lungs, is a mixture of oxygen and nitrogen, in the proportion of about 21 per cent., by volume, of oxygen, to 79 per cent. of nitrogen. It also contains about one-twentieth per cent. of carbonic acid, a varying quantity of watery vapor, and some traces of ammonia. The last named ingredients, however, are quite insignificant in comparison with the oxygen and nitrogen, which form the principal parts of its mass.

If collected and examined, after passing through the lungs, the

air is found to have become altered in the following essential particulars, viz:—

1st. It has lost oxygen.

2d. It has gained carbonic acid. And

3d. It has absorbed the vapor of water.

Beside the two latter substances, there are also exhaled with the expired air a very small quantity of nitrogen, over and above what was taken in with inspiration, and a little animal matter in a gaseous form, which communicates a slight but peculiar odor to the breath. The air is also somewhat elevated in temperature, by contact with the pulmonary mucous membrane.

The watery vapor, which is exhaled with the breath, is given off by the pulmonary mucous membrane, by which it is absorbed from the blood. At ordinary temperatures it is transparent and invisible; but in cold weather it becomes partly condensed, on leaving the lungs, and appears under the form of a cloudy vapor discharged with the breath. According to the researches of Valentin, the average quantity of water, exhaled daily from the lungs, is 8100 grains, or about $1\frac{1}{6}$ pounds avoirdupois.

A more important change, however, suffered by the air in respiration, consists in its loss of oxygen, and its absorption of carbonic acid.

According to the researches of Valentin, Vierordt, Regnault and Reiset, &c., the air loses during respiration, on an average, five per cent. of its volume of oxygen. At each inspiration, therefore, about one cubic inch of oxygen is removed from the air and absorbed by the blood; and as we have seen that the entire daily quantity of air used in respiration is about 350 cubic feet, the entire quantity of oxygen thus consumed in twenty-four hours is not less than seventeen and a half cubic feet. This is, by weight, 10,339 grains, or rather less than one pound and a half, avoirdupois.

The oxygen which thus disappears from the inspired air is not entirely replaced in the carbonic acid exhaled; that is, there is less oxygen in the carbonic acid which is returned to the air by expiration than has been lost during inspiration.

There is even more oxygen absorbed than is given off again in both the carbonic acid and aqueous vapor together, which are exhaled from the lungs.[1] There is, then, a constant disappearance of oxygen from the air used in respiration, and a constant accumulation of carbonic acid.

[1] Lehmann's Physiological Chemistry, Philada. ed., vol. ii. p. 432.

The proportion of oxygen which disappears in the interior of the body, over and above that which is returned in the breath under the form of carbonic acid, varies in different kinds of animals. In the herbivora, it is about 10 per cent. of the whole amount of oxygen inspired; in the carnivora, 20 or 25 per cent. and even more. It is a very remarkable fact, also, and an important one, as regards the theory of respiration, that, in the same animal, the proportion of oxygen absorbed, to that of carbonic acid exhaled, varies according to the quality of the food. In dogs, for instance, while fed on animal food, according to the experiments of Regnault and Reiset, 25 per cent. of the inspired oxygen disappeared in the body of the animal; but when fed on starchy substances, all but 8 per cent. reappeared in the expired carbonic acid. It is already evident, therefore, from these facts, that the oxygen of the inspired air is not altogether employed in the formation of carbonic acid.

Owing to the changes detailed above, the air which is used for breathing becomes rapidly deteriorated and unfit to sustain life. For as respiration goes on, the oxygen of the air constantly diminishes and the quantity of carbonic acid increases. It has been found that, as a general rule, the air is entirely unfit for respiration when its proportion of oxygen is reduced from 21 to 10 per cent.,[1] its composition remaining otherwise unchanged; and on the other hand it can no longer sustain life when it contains 20 per cent. of carbonic acid. Both these changes therefore combine to vitiate the respired air, unless it be constantly renewed from an external source.

Beside the carbonic acid, however, a certain amount of *organic matter* is also exhaled with the breath. It is this organic matter in a vaporous condition which causes the heavy and oppressive odor in the atmosphere of an ill-ventilated apartment, in which many persons are breathing at the same time. Although produced in comparatively small quantity, it is probably one of the most deleterious substances exhaled from the lungs in respiration; and, when allowed to accumulate in the atmosphere, gives rise to many of the injurious effects resulting from imperfect ventilation.

Changes in the Blood during Respiration.—If we pass from the consideration of the changes produced in the air by respiration to those which take place in the blood during the same process, we find, as might have been expected, that the latter correspond inversely with the former. The blood, in passing through the lungs, suffers the following alterations:—

1st. Its color is changed from venous to arterial.

[1] Longet, Traité de Physiologie, Paris, 1859, vol. i. p. 600.

2d. It absorbs oxygen. And

3d. It exhales carbonic acid and the vapor of water.

The interchange of gases, which takes place during respiration between the air and the blood, is a simple phenomenon of absorption and exhalation. The inspired oxygen does not, as Lavoisier once supposed, immediately combine with carbon in the lungs, and return to the atmosphere under the form of carbonic acid. On the contrary, almost the first fact of importance which has been established by the examination of the blood in this respect is the following, viz: that *carbonic acid exists ready formed in the venous blood before its entrance into the lungs;* and, on the other hand, that *the oxygen which is absorbed during respiration passes off in a free state with the arterial blood.* The real process, as it takes place in the lung, is, therefore, for the most part, as follows: The blood comes to the lungs already charged with carbonic acid. In passing through the pulmonary capillaries, it is exposed to the influence of the air in the cavity of the pulmonary cells, and a transudation of gases takes place through the moist animal membranes of the lung. Since the blood in the capillaries contains a larger proportion of carbonic acid than the air in the air-vesicles, a portion of this gas leaves the blood and passes out through the pulmonary membrane; while the oxygen, being more abundant in the air of the vesicles than in the circulating fluid, passes inward at the same time, and is condensed by the blood.

In this double phenomenon of exhalation and absorption, which takes place in the lungs, both parts of the process are equally necessary to life. It is essential for the constant activity and nutrition of the tissues that they be steadily supplied with oxygen by the blood; and if this supply be cut off, their functional activity ceases. On the other hand, the carbonic acid which is produced in the body by the processes of nutrition becomes a poisonous substance, if it be allowed to collect in large quantity. Under ordinary circumstances, the carbonic acid is removed by exhalation through the lungs as fast as it is produced in the interior of the body; but if respiration be suspended, or seriously impeded, since the production of carbonic acid continues, while its elimination is prevented, it accumulates in the blood and in the tissues, and becomes fatal by a rapid deterioration of the circulating fluid, and by its poisonous effect on the nervous system.

Examination of the blood shows furthermore that the interchange of gases in the lungs is not complete but partial in its extent. It results from the experiments of Magendie, Magnus, Bernard, and

others, that both oxygen and carbonic acid are contained in both venous and arterial blood. Their proportions, however, are different, since there is more oxygen in arterial than in venous blood, and more carbonic acid in venous blood than in arterial. Bernard found in a healthy dog[1] rather more than 18 per cent. by volume of oxygen in arterial, and only a little more than 8 per cent. in venous blood. He also found, in various analyses,[2] from 7 to 10 per cent. of carbonic acid in venous blood, while in arterial blood this gas was reduced to 3 per cent. or even a still smaller proportion. The venous blood, then, as it arrives at the lungs, still retains a remnant of the oxygen which it had previously absorbed; and in passing through the pulmonary capillaries it gives off only a part of the carbonic acid, with which it has become charged in the general circulation.

The oxygen and carbonic acid of the blood exist *in a state of solution* in the circulating fluid, and not in a state of intimate chemical combination. This is shown by the fact that both of these substances may be withdrawn from the blood by simple exhaustion with an air-pump, or by a stream of any other indifferent gas, such as hydrogen, which possesses sufficient physical displacing power. Magnus found[3] that freshly drawn arterial blood yielded by simple agitation with carbonic acid more than 10 per cent. of its volume of oxygen. The carbonic acid may also be expelled from venous blood by a current of pure oxygen, or of hydrogen, or, in great measure, by simple agitation with atmospheric air. There is some difficulty in determining, however, whether the carbonic acid of the blood be altogether in a free state, or whether it be partly in a state of loose chemical combination with a base, under the form of an alkaline bicarbonate. A solution of bicarbonate of soda itself will lose a portion of its carbonic acid, and become reduced to the condition of a carbonate by simple exhaustion under the air-pump, or by agitation with pure hydrogen at the temperature of the body. Lehmann has found[4] that after the expulsion of all the carbonic acid removable by the air-pump and a current of hydrogen, there still remains, in ox's blood, 0.1628 per cent. of carbonate of soda; and he estimates that this quantity is sufficient to have retained all the carbonic acid, previously given off, in the form of a bicarbonate.

[1] Liquides de l'organisme, vol. i. p. 367 *et seq.*

[2] In Robin, Leçons sur les Humeurs, p. 57.

[3] In Robin and Verdeil, op. cit., vol. ii. p. 34.

[4] Op. cit., vol. i. p. 393.

It makes little or no difference, however, so far as regards the process of respiration, whether the carbonic acid of the blood exist in an entirely free state, or under the form of an alkaline bicarbonate; since it may be readily removed from this combination, at the temperature of the body, by contact with an indifferent gas.

The oxygen of the blood is in solution principally *in the blood-globules*, and not in the plasma. The researches of Magnus have shown[1] that the blood holds in solution 2½ times as much oxygen as pure water could dissolve at the same temperature; and that while the serum of the blood, separated from the globules, exerts no more solvent power on oxygen than pure water, defibrinated blood, that is, the serum and globules mixed, dissolves quite as much oxygen as the fresh blood itself. The carbonic acid, on the other hand, is held in solution, not only in the blood-globules, but also by the plasma; for, the plasma, according to Robin,[2] owing to the presence of its alkaline phosphates and carbonates, has the power of dissolving no less than 48 per cent. of its volume of carbonic acid, a quantity much greater than is ever actually found in the blood.

Both the oxygen and carbonic acid, therefore, are present in solution in the blood-globules; and since the color of the blood depends entirely upon that of the globules, it is easy to understand why this color should be altered from purple to scarlet in passing through the lungs, where the globules give up carbonic acid, and absorb a fresh quantity of oxygen. The above change may readily be produced outside the body. If freshly drawn venous blood be shaken in a bottle with pure oxygen, its color changes at once from purple to red; and the same change will take place, though more slowly, if the blood be simply agitated with atmospheric air. It is for this reason that the surface of defibrinated venous blood, and the external parts of a dark-colored clot, exposed to the atmosphere, become rapidly reddened, while the internal portions retain their original color.

The process of respiration, so far as we have considered it, consists in an alternate interchange of carbonic acid and oxygen in the blood of the general and pulmonary circulations. In the pulmonary circulation, carbonic acid is given off and oxygen absorbed; while in the general circulation the oxygen gradually disappears, and is

[1] In Robin and Verdeil, op. cit., vol. ii. p. 28.

[2] Leçons sur les Humeurs, p. 67.

replaced, in the venous blood, by carbonic acid. The oxygen which thus disappears from the blood in the general circulation does not, for the most part, enter into direct combination in the blood itself. On the contrary, it exists there, as we have already stated, in the form of a simple solution. It is absorbed, however, from the blood of the capillary vessels, and becomes fixed in the substance of the vascular tissues. The blood may be regarded, therefore, in this respect, as a circulating fluid, destined to transport oxygen from the lungs to the tissues; for it is the tissues themselves which finally appropriate the oxygen, and fix it in their substance.

The next important question which presents itself in the study of the respiratory process relates to *the origin of the carbonic acid in the venous blood.* It was formerly supposed, when Lavoisier first discovered the changes produced in the air by respiration, that the production of the carbonic acid could be accounted for in a very simple manner. It was thought to be produced in the lungs by a direct union of the inspired oxygen with the carbon of the blood in the pulmonary vessels. It was found afterward, however, that this could not be the case; since carbonic acid exists already formed in the blood, previously to its entrance into the lungs. It was then imagined that the oxidation of carbon, and the consequent production of carbonic acid, took place in the capillaries of the general circulation, since it could not be shown to take place in the lungs, nor between the lungs and the capillaries. The truth is, however, that no direct evidence exists of such a direct oxidation taking place anywhere. The formation of carbonic acid, as it is now understood, takes place in three different modes: 1st, in the lungs; 2d, in the blood; and 3d, in the tissues.

First, *in the lungs.* There exists in the pulmonary tissue a peculiar acid substance, first described by Verdeil[1] under the name of "pneumic" or "pulmonic" acid. It is a crystallizable body, soluble in water, which is produced in the substance of the pulmonary tissue by transformation of some of its other ingredients, in the same manner as sugar is produced in the tissue of the liver. It is on account of the presence of this substance that the fresh tissue of the lung has usually an acid reaction to test-paper, and that it has also the property, which has been noticed by several observers, of decomposing the metallic cyanides, with the production of hydrocyanic acid; a property not possessed by sections of areolar tissue,

[1] Robin and Verdeil, op. cit., vol. ii. p. 460.

the internal surface of the skin, &c. &c. When the blood, therefore, comes in contact with the pulmonary tissue, which is permeated everywhere by pneumic acid in a soluble form, its alkaline carbonates and bicarbonates, if any be present, are decomposed with the production on the one hand of the pneumates of soda and potassa, and on the other of free carbonic acid, which is exhaled. M. Bernard has found[1] that if a solution of bicarbonate of soda be rapidly injected into the jugular vein of a rabbit, it becomes decomposed in the lungs with so rapid a development of carbonic acid, that the gas accumulates in the pulmonary tissue, and even in the pulmonary vessels and the cavities of the heart, to such an extent as to cause immediate death by stoppage of the circulation. In the normal condition, however, the carbonates and bicarbonates of the blood arrive so slowly at the lungs that as fast as they are decomposed there, the carbonic acid is readily exhaled by expiration, and produces no deleterious effect on the circulation.

Secondly, *in the blood.* There is little doubt, although the fact has not been directly proved, that some of the oxygen definitely disappears, and some of the carbonic acid is also formed, in the substance of the blood-globules during their circulation. Since these globules are anatomical elements, and since they undoubtedly go through with nutritive processes analogous to those which take place in the elements of the solid tissues, there is every reason for believing that they also require oxygen for their support, and that they produce carbonic acid as one of the results of their interstitial decomposition. While the oxygen and carbonic acid, therefore, contained in the globules, are for the most part transported by these bodies from the lungs to the tissues, and from the tissues back again to the lungs, they probably take part, also, to a certain extent, in the nutrition of the blood-globules themselves.

Thirdly, *in the tissues.* This is by far the most important source of the carbonic acid in the blood. From the experiments of Spallanzani, W. Edwards, Marchand and others, the following very important fact has been established, viz., that *every organized tissue and even every organic substance, when in a recent condition, has the power of absorbing oxygen and of exhaling carbonic acid.* G. Liebig, for example,[2] found that frog's muscles, recently prepared and completely freed from blood, continued to absorb oxygen and discharge

[1] Archives Générales de Médecine, xvi. 222.

[2] In Lehmann, op. cit., vol. ii. p. 474.

carbonic acid. Similar experiments with other tissues have led to a similar result. The interchange of gases, therefore, in the process of respiration, takes place mostly in the tissues themselves. It is in their substance that the oxygen becomes fixed and assimilated, and that the carbonic acid takes its origin. As the blood in the lungs gives up its carbonic acid to the air, and absorbs oxygen from it, so in the general circulation it gives up its oxygen to the tissues, and absorbs from them carbonic acid.

We come lastly to examine the exact mode by which the carbonic acid originates in the animal tissues. Investigation shows that even here it is *not produced by a process of oxidation, or direct union of oxygen with the carbon of the tissues, but in some other and more indirect mode.* This is proved by the fact that animals and fresh animal tissues will continue to exhale carbonic acid in an atmosphere of hydrogen or of nitrogen, or even when placed in a vacuum. Marchand found[1] that frogs would live for from half an hour to an hour in pure hydrogen gas; and that during this time they exhaled even more carbonic acid than in atmospheric air, owing probably to the superior displacing power of hydrogen for carbonic acid. For while 15,500 grains' weight of frogs exhaled about 1.13 grain of carbonic acid per hour in atmospheric air, they exhaled during the same time in pure hydrogen as much as 4.07 grains. The same observer found that frogs would recover on the admission of air after remaining for nearly half an hour in a nearly complete vacuum; and that if they were killed by total abstraction of the air, 15,500 grains' weight of the animals were found to have eliminated 9.3 grains of carbonic acid. The exhalation of carbonic acid by the tissues does not, therefore, depend directly upon the access of free oxygen. It cannot go on, it is true, for an indefinite time, any more than the other vital processes, without the presence of oxygen. But it may continue long enough to show that the carbonic acid exhaled is not a direct product of oxidation, but that it originates, on the contrary, in all probability, by a decomposition of the organic ingredients of the tissues, resulting in the production of carbonic acid on the one hand, and of various other substances on the other, with which we are not yet fully acquainted; in very much the same manner as the decomposition of sugar during fermentation gives rise to alcohol on the one hand and to carbonic acid on the other. The fermentation of sugar, when it has

[1] In Lehmann, op. cit., vol. ii. p. 442.

once commenced, does not require the continued access of air. It will go on in an atmosphere of hydrogen, or even when confined in a close vessel over mercury; since its carbonic acid is not produced by direct oxidation, but by a decomposition of the sugar already present. For the same reason, carbonic acid will continue to be exhaled by living or recently dead animal tissues, even in an atmosphere of hydrogen, or in a vacuum.

Carbonic acid makes its appearance, accordingly, in the tissues, as one product of their decomposition in the nutritive process. From them it is taken up by the blood, either in simple solution or in loose combination as a bicarbonate, transported by the circulation to the lungs, and finally exhaled from the pulmonary mucous membrane in a gaseous form.

The carbonic acid exhaled from the lungs should accordingly be studied by itself as one of the products of the animal organism, and its quantity ascertained in the different physiological conditions of the body. The expired air usually contains about four per cent. of its volume of carbonic acid. Rather less than one cubic inch is accordingly given off with each ordinary expiration; and as we have already found that no less than 350 cubic feet of air are inhaled and discharged during twenty-four hours, this would give fourteen cubic feet of carbonic acid expired per day. This quantity is, by weight, 11,433 grains, or a little over one pound and a half.

The amount of carbonic acid exhaled, however, varies from time to time, according to many different circumstances. These variations have been very fully investigated by Andral and Gavarret,[1] who found that the principal conditions modifying the amount of this gas produced were age, sex, constitution and development. The variations were very marked in different individuals, notwithstanding that the experiments were made at the same period of the day, and with the subject as nearly as possible in the same condition. Thus they found that the quantity of carbonic acid exhaled per hour in five different individuals was as follows:—

Quantity of Carbonic Acid per hour.

In subject	No.	1	.	.	.	.	.	1207	cubic	inches.
"	"	"	2	.	.	.	.	.	970	"	"
"	"	"	3	.	.	.	.	.	1250	"	"
"	"	"	4	.	.	.	.	.	1250	"	"
"	"	"	5	.	.	.	.	.	1591	"	"

[1] Annales de Chimie et de Physique, 1843, 3d series, vol. viii. p. 129.

With regard to the difference produced by age, it was found that from the period of eight years up to puberty the quantity of carbonic acid increases constantly with the age. Thus a boy of eight years exhales, on the average, 564 cubic inches per hour; while a boy of fifteen years exhales 981 cubic inches in the same time. Boys exhale during this period more carbonic acid than girls of the same age. In males this augmentation of the quantity of carbonic acid continues till the twenty-fifth or thirtieth year, when it reaches, on the average, 1398 cubic inches per hour. Its quantity then remains stationary for ten or fifteen years; then diminishes slightly from the fortieth to the sixtieth year; and after sixty years diminishes in a marked degree, so that it may fall so low as 1038 cubic inches. In one superannuated person, 102 years of age, Andral and Gavarret found the hourly quantity of carbonic acid to be only 665 cubic inches.

In women, the increase of carbonic acid ceases at the period of puberty; and its production then remains constant until the cessation of menstruation, about the fortieth or forty-fifth year. At that time it increases again until after fifty years, when it subsequently diminishes with the approach of old age, as in men. Pregnancy, occurring at any time in the above period, immediately produces a temporary increase in the quantity of carbonic acid.

The strength of the constitution, and more particularly *the development of the muscular system*, was found to have a very great influence in this respect; increasing the quantity of carbonic acid very much in proportion to the weight of the individual. The largest production of carbonic acid observed was in a young man, 26 years of age, whose frame presented a remarkably vigorous and athletic development, and who exhaled 1591 cubic inches per hour. This large quantity of carbonic acid, moreover, in well developed persons, is not owing simply to the size of the entire body, but particularly to the development of the muscular system, since an unusually large skeleton, or an abundant deposit of adipose tissue, is not accompanied by any such increase of the carbonic acid.

Andral and Gavarret finally sum up the results of their investigations as follows:—

1. The quantity of carbonic acid exhaled from the lungs in a given time varies with the age, the sex, and the constitution of the subject.
2. In the male, as well as in the female, the quantity of carbonic

acid varies according to the age; and that independently of the weight of the individual subjected to experiment.

3. During all the periods of life, from that of eight years up to the most advanced age, the male and female may be distinguished by the different quantities of carbonic acid which they exhale in a given time. Other things being equal, the male exhales always a larger quantity than the female. This difference is particularly marked between the ages of 16 and 40 years, during which period the male usually exhales twice as much carbonic acid as the female.

4. In the male, the quantity of carbonic acid increases constantly from eight to thirty years; and the rate of this increase undergoes a rapid augmentation at the period of puberty. Beyond thirty years the exhalation of carbonic acid begins to decrease, and its diminution is more marked as the individual approaches extreme old age, so that near the termination of life, the quantity of carbonic acid produced may be no greater than at the age of ten years.

5. In the female, the exhalation of carbonic acid increases according to the same law as in the male, from the age of eight years until puberty. But at the period of puberty, at the same time with the appearance of menstruation, the exhalation of carbonic acid, contrary to what happens in the male, ceases to increase; and it afterward remains stationary so long as the menstrual periods recur with regularity. At the cessation of the menses, the quantity of carbonic acid exhaled increases in a notable manner; then it decreases again, as in the male, as the woman advances toward old age.

6. During the whole period of pregnancy, the exhalation of carbonic acid rises, for the time, to the same standard as in women whose menses have ceased.

7. In both sexes, and at all ages, the quantity of carbonic acid is greater as the constitution is stronger, and the muscular system more fully developed.

Prof. Scharling, in a similar series of investigations,[1] found that the quantity of carbonic acid exhaled was greater during the digestion of food than in the fasting condition. It is greater, also, in the waking state than during sleep; and in a state of activity than in one of quietude. It is diminished, also, by fatigue, and by most conditions which interfere with perfect health.

[1] Annales de Chimie et de Physique, vol. viii. p. 490.

The process of respiration is not altogether confined to the lungs, but the discharge of carbonic acid takes place also, to a slight extent, both by the urine and the perspiration. M. Morin[1] has found that the urine always contains gases in solution, of which carbonic acid is considerably the most abundant. The mean result of fifteen observations showed that urine excreted during the night contains about 1.96 per cent. of its volume of carbonic acid. During the day the quantity of this gas contained in the urine varied considerably, according to the condition of muscular repose or activity; since after remaining quiet for an hour or two, it was only 1.19 per cent. of the volume of the urine, while after continued exertion for the same space of time, not only was the urine augmented in quantity, but the proportion of carbonic acid contained in it was nearly doubled, amounting to 2.29 per cent. of its volume.

An equal or even greater activity of gaseous exhalation takes place by the skin. It has been found, by inclosing one of the limbs in an air-tight case, that the air in which it is confined loses oxygen and gains in carbonic acid. By an experiment of this sort, performed by Prof. Scharling, it was ascertained that the carbonic acid given off from the whole cutaneous surface, in the human subject, is from one-sixtieth to one-thirtieth of that discharged during the same period from the lungs. A certain amount of odoriferous organic matter is also given off by the skin as well as by the lungs. In the truly amphibious animals, that is, those which breathe by lungs, and can yet remain under water for a long period without injury (as frogs and salamanders), the respiratory function of the skin is very active. In these animals, the integument is very vascular, moist, and flexible; and is covered, not with dry cuticle, but with a very thin and delicate layer of epithelium. It therefore presents all the conditions necessary for the accomplishment of respiration; and while the animal remains beneath the surface, and the lungs are in a state of comparative inactivity, the exhalation and absorption of gases continue to take place through the skin, and the process of respiration goes on without interruption.

[1] Recherches sur les gaz libres de l'urine. Journal de Pharmacie et de Chimie, Paris, 1864, vol. xlv. p. 396.

CHAPTER XIII.

ANIMAL HEAT.

One of the most important phenomena presented by animals and vegetables is the property which they possess of maintaining, more or less constantly, a standard temperature, notwithstanding the external vicissitudes of heat and cold to which they may be subjected. If a bar of iron, or a jar of water, be heated up to 100° or 200° F., and then exposed to the air at 50° or 60°, it will immediately begin to lose heat by radiation and conduction; and this loss of heat will steadily continue, until, after a certain time, the temperature of the heated body has become reduced to that of the surrounding atmosphere. It then remains stationary at this point, unless the temperature of the atmosphere should happen to rise or fall: in which case, a similar change takes place in the inorganic body, its temperature remaining constant, or varying with that of the surrounding medium.

With living animals the case is different. If a thermometer be introduced into the stomach of a dog, or placed under the tongue of the human subject, it will indicate a temperature of 100° F., very nearly, whatever may be the condition of the surrounding atmosphere at the time. This internal temperature is the same in summer and in winter. If the individual upon whom the experiment has been tried be afterward exposed to a cold of zero, or even of 20° or 30° below zero, the thermometer introduced into the interior of the body will still stand at 100° F. As the body, during the whole period of its exposure, must have been losing heat by radiation and conduction, like any inorganic mass, and has, notwithstanding, maintained a constant temperature, it is plain that a certain amount of heat has been generated in the interior of the body by means of the vital processes, sufficient to compensate for the external loss. The internal heat, so produced, is known by the name of *vital* or *animal heat.*

There are two classes of animals in which the production of vital

heat takes place with such activity that their blood and internal organs are nearly always very much above the external temperature; and which are therefore called "warm-blooded animals." These are mammalia and birds. Among the birds, some species, as the gull, have a temperature as low as 100° F.; but in most of them, it is higher, sometimes reaching as high as 110° or 111°. In the mammalians, to which class man belongs, the animal temperature is never far from 100°. In the seal and the Greenland whale, it has been found to be 104°; and in the porpoise, which is an air-breathing animal, 99.5°. In the human subject, if the bulb of a delicate thermometer be held for some minutes between the folds of skin in the palm of the hand, it will stand at 97.5°: in the axilla, at 98°; under the tongue, and protected from contact with the breath, it will reach 99°; and in the deeper parts of the internal organs, the temperature is no doubt 100°. When the temperature of the air is below this, the external parts of the body, being most exposed to the cooling influences of radiation and conduction, fall a little below the standard, and may indicate a temperature of 97°, or even several degrees below this point. Thus, on a very cold day, the thinner and more exposed parts, such as the nose, the ears, and the ends of the fingers, may be cooled down considerably below the standard temperature, and may even be congealed, if the cold be severe; but the temperature of the internal organs and of the blood still remains the same under all ordinary exposures.

If the cold, however, be so intense and long continued as to affect the general temperature of the blood, it becomes fatal. Every warm-blooded animal has the power of resisting the depressing influence of external cold, both by the internal heat which is constantly generated, and by its external covering of fur or feathers, by which this heat is prevented from being too rapidly lost. But when the exposure is so great that the loss of heat is more rapid than its production, the internal temperature begins to fall, and the animal becomes gradually torpid and insensible in proportion as the warmth of the body is exhausted. As a general rule, death results, in the warm-blooded animals, if the temperature of the blood be reduced to about 80°. These animals, accordingly, have a natural internal temperature, at which the blood must be maintained in order to sustain life; and even the different species belonging to the same class, have each a specific temperature which is characteristic of them, and which cannot be raised or lowered, to any considerable extent, without producing death.

While in the birds and mammalians, however, the internal production of heat is so active that their temperature is nearly always considerably above that of the surrounding media, and suffers but little variation; in reptiles and fish, on the other hand, its production is much less rapid, and the temperature of their bodies differs but little from that of the air or water which they inhabit. Birds and mammalians are therefore called "warm-blooded," and reptiles and fish "cold-blooded" animals. There is, however, no other distinction between them, in this respect, than one of degree. In reptiles and fish there is also an internal source of heat; only this is not so active as in the other classes. Even in these animals a difference is usually found to exist between the temperature of their bodies and that of the surrounding media. John Hunter, Sir Humphrey Davy, Czermak, and others,[1] have found the temperature of Proteus anguinus to be 63.5°, when that of the air was 55.4°; that of a frog 48°, in water at 44.4°; that of a serpent 88.46°, in air at 81.5°; that of a tortoise 84°, in air at 79.5°; and that of fish to be from 1.7° to 2.5° above that of the surrounding water.

The following list[2] shows the mean temperature belonging to animals of different classes and species, according to the results obtained by various observers.

	Animal.	Mean Temperature.
Birds.	Swallow	111.25°
	Heron	111.2°
	Raven	108.5°
	Pigeon	107.6°
	Fowl	106.7°
	Gull	100.0°
Mammalia.	Squirrel	105°
	Goat	102.5°
	Cat	101.3°
	Hare	100.4°
	Dog	100.3°
	Ox	99.5°
	Horse	98.2°
	Ape	95.9°
Reptile.	Toad	51.6°
Fish.	Carp	51.25°
	Tench	52.10°

In the invertebrate animals, as a general rule, the internal heat is produced in too small quantity to be readily estimated. In some

[1] Simon's Chemistry of Man, Philadelphia edition, p. 124.

[2] Ibid., pp. 123—126.

of the more active kinds, however, such as insects and arachnida, it is occasionally generated with such activity that it may be appreciated by the thermometer. Thus, the temperature of the butterfly, when in a state of excitement, is from 5° to 9° above that of the air; and that of the humble-bee from 3° to 10° higher than the exterior. According to the experiments of Mr. Newport,[1] the interior of a hive of bees may have a temperature of 48°.5. when the external atmosphere is at 34°.5, even while the insects are quiet; but if they be excited, by tapping on the outside of the hive, it may rise to 102°. In all cases, while the insect is at rest, the temperature is very moderate; but if kept in rapid motion in a confined space, it may generate heat enough to affect the thermometer sensibly, in the course of a few minutes.

Even in vegetables a certain degree of heat-producing power is occasionally manifest. Usually, the exposed surface of a plant is so extensive in proportion to its mass, that whatever caloric may be generated is too rapidly lost by radiation and evaporation, to be appreciated by ordinary means. Under some circumstances, however, it may accumulate to such an extent as to become readily perceptible. In the process of malting, for example, when a large quantity of germinating grain is piled together in a mass, its elevated temperature may be readily distinguished, both by the hand and the thermometer. During the flowering process, also, an unusual evolution of heat takes place in plants. The flowers of the geranium have been found to have a temperature of 87°, while that of the air was 81°; and the thermometer, placed in the centre of a clump of blossoms of arum cordifolium, has been seen to rise to 111°, and even 121°, while the temperature of the external air was only 66°.[2]

Dutrochet has moreover found, by a series of very ingenious and delicate experiments,[3] that nearly all parts of a living plant generate a certain amount of heat. The proper heat of the plant is usually so rapidly dissipated by the continuous evaporation of its fluids, that it is mostly imperceptible by ordinary means; but if this evaporation be prevented, by keeping the air charged with watery vapor, the heat becomes sensible and can be appreciated by a delicate thermometer. Dutrochet used for this purpose a thermo-

[1] Carpenter's General and Comparative Physiology, Philadelphia, 1851, p. 852.

[2] Carpenter's Gen. and Comp. Physiology, p. 846.

[3] Annales des Sciences Naturelles, 2d series, xii. p. 277.

electric apparatus, so constructed that an elevation of temperature of 1° F., in the substances examined, would produce a deviation in the needle of nearly nine degrees. By this means he found that he could appreciate, without difficulty, the proper temperature of the plant. A certain amount of heat was constantly generated, during the day, in the green stems, the leaves, the buds, and even the roots and fruit. The maximum temperature of these parts, above that of the surrounding atmosphere, was sometimes a little over one-half a degree Fahrenheit; though it was often considerably less than this.

The different parts of the vegetable fabric, therefore, generate different quantities of caloric. In the same manner, the heat-producing power is not equally active in different species of animals; but its existence is nevertheless common to both animals and vegetables.

With regard to the *mode of generation* of this internal or vital heat, we may start with the assertion that its production depends upon changes of a chemical nature, and is so far to be regarded as a chemical phenomenon. The sources of heat which we meet with in nature are of various kinds. Sometimes the heat is of a physical origin; as, for example, that derived from the rays of the sun, the friction of solid substances, or the passage of electric currents. In other instances it is produced by chemical changes; and the most abundant and useful source of artificial heat is the oxidation, or combustion, of carbon and carbonaceous compounds. Wood and coal, substances rich in carbon, are mostly used for this purpose; and charcoal, which is nearly pure carbon, is frequently employed by itself. These substances, when burned, or oxidized, evolve a large amount of heat; and produce, as the result of their oxidation, carbonic acid. In order that the process may go on, it is of course necessary that oxygen, or atmospheric air, should have free access to the burning body; otherwise the combustion and evolution of heat cease, for want of a necessary agent in the chemical combination. In all these instances, the quantity of heat generated is in direct proportion to the amount of oxidation; and may be measured, either by the quantity of carbon consumed, or by that of carbonic acid produced. It may be made to go on, also, either slowly or rapidly, according to the abundance and purity in which oxygen is supplied to the carbonaceous substance. Thus, if charcoal be ignited in an atmosphere of pure oxygen, it burns rapidly and violently, raises the temperature to a high point, and is soon

consumed. On the other hand, if it be shut up in a close stove, to which the air is admitted slowly, it produces only a slight elevation of temperature, and may require a much longer time for its complete disappearance. Nevertheless, for the same quantity of carbon consumed, the amount of heat generated, as well as that of carbonic acid produced, will be equal in the two cases. In one instance we have a rapid combustion, in the other a slow combustion; the total effect being the same in both.

Such is the mode in which heat is commonly produced by artificial means. its evolution is here dependent upon two principal conditions, which are essential to it, and by which it is always accompanied, viz., the consumption of oxygen, and the production of carbonic acid.

Now, since the two phenomena just mentioned are presented also by the living body, and since they are accompanied here, too, by the production of animal heat, it was very natural to suppose that in the animal organization, as well as elsewhere, the internal heat might be owing to an oxidation or combustion of carbon. According to Lavoisier, the oxygen taken into the lungs was supposed to combine immediately with the carbon of the pulmonary tissues and fluids, producing carbonic acid, and to be at once returned under that form to the atmosphere; the same quantity of heat resulting from the above process as would have been produced by the oxidation of a similar quantity of carbon in wood or coal. Accordingly, he regarded the lungs as a sort of stove or furnace, by which the rest of the body was warmed, through the medium of the circulating blood.

It was soon found, however, that this view was altogether erroneous; for the slightest examination shows that the lungs are not perceptibly warmer than the rest of the body; and that the heat-producing power, whatever it may be, does not reside exclusively in the pulmonary tissue. Furthermore, subsequent investigations showed the following very important facts, which we have already mentioned, viz., that the carbonic acid is not formed in the lungs, but exists in the blood before its arrival in the pulmonary capillaries; and that the oxygen of the inspired air, so far from combining with carbon in the lungs, is taken up in solution by the blood-globules, and carried away by the current of the general circulation. It is evident, therefore, that this oxidation or combustion of the blood must take place, if at all, not in the lungs, but in the capillaries of the various organs and tissues of the body.

Liebig accordingly adopted Lavoisier's theory of the production of animal heat, with the above modification. He believed the heat of the animal body to be produced by the oxidation or combustion of certain elements of the food while still circulating in the blood; these substances being converted into carbonic acid and water by the oxidation of their carbon and hydrogen, and immediately expelled from the body without ever having formed a part of the solid tissues. He therefore divided the food into two different classes of alimentary substances; viz., 1st, the *nitrogenous* or *plastic elements*, which are introduced in comparatively small quantity, and which are to be actually converted into the substance of the tissues, such as albumen, muscular flesh, &c.; and 2d, the *hydro-carbons* or *respiratory elements*, such as sugar, starch, and fat; which, according to his view, are taken into the blood solely to be burned, never being assimilated or converted into the tissues, but only oxidized in the circulation, and immediately expelled, as above, under the form of carbonic acid and water. He therefore regarded these elements of the food only as so much fuel; destined simply to maintain the heat of the body, but taking no part in the proper function of nutrition.

The above theory of animal heat has been very generally adopted and acknowledged by the medical profession until within a recent period. A few years ago, however, some of its deficiencies and inconsistencies were pointed out, by Lehmann in Germany, and by Robin and Verdeil in France; and since that time it has begun to lose ground and give place to a different mode of explanation, more in accordance with the present state of physiological science. We believe it, in fact, to be altogether erroneous; and incapable of explaining, in a satisfactory manner, the phenomena of animal heat, as exhibited by the living body. We shall now proceed to pass in review the principal objections to the theory of combustion, considered as a physiological doctrine.

I. It is not at all necessary to regard the evolution of heat as dependent solely on direct oxidation. This is only one of its sources, as we constantly see in external nature. The sun's rays, mechanical friction, electric currents, and more particularly a great variety of chemical actions, such as various saline combinations and decompositions, are all capable of producing heat; and even simple solutions, such as the solution of caustic potassa in water, the mixture of sulphuric acid and water, or of alcohol and water, will often produce a very sensible elevation of temperature. Now we know that

in the interior of the body many different actions of this nature are constantly going on; solutions, combinations and decompositions in endless variety, all of which, taken together, are no doubt sufficient to account for the production of animal heat, provided the theory of combustion be found insufficient or improbable.

II. In vegetables there is an internal production of heat, as well as in animals; a fact which has been fully demonstrated by the experiments of Dutrochet and others, already described. In vegetables, however, the absorption of oxygen and exhalation of carbonic acid do not take place; excepting, to some extent, during the night. On the contrary, the diurnal process in vegetables, it is well known, is exactly the reverse of this. Under the influence of the solar light they absorb carbonic acid and exhale oxygen. And it is exceedingly remarkable that, in Dutrochet's experiments, he found that the evolution of heat by plants was always accompanied by the disappearance of carbonic acid and the exhalation of oxygen. Plants which, in the daylight, exhale oxygen and evolve heat, if placed in the dark, immediately begin to absorb oxygen and exhale carbonic acid; and, at the same time, the evolution of heat is suspended. Dutrochet even found that the evolution of heat by plants presented a regular diurnal variation; and that its maximum of intensity was about the middle of the day, *just at the time when the absorption of carbonic acid and the exhalation of oxygen are going on with the greatest activity.* The proper heat of plants, therefore, cannot be the result of oxidation or combustion, but must be dependent on a different process.

III. In animals, the quantities of oxygen absorbed and of carbonic acid exhaled do not correspond with each other. Most frequently a certain amount of oxygen disappears in the body, over and above that which is returned in the breath under the form of carbonic acid. This overplus of oxygen has been said to unite with the hydrogen of the food, so as to form water which also passes out by the lungs; but this is a pure assumption, resting on no direct evidence, for we have no experimental proof that any more watery vapor is exhaled from the lungs than is supplied by the fluids taken into the stomach. It is superfluous, therefore, to assume that any of it is produced by the oxidation of hydrogen.

Furthermore, the proportion of overplus oxygen which disappears in the body, beside that which is exhaled in the carbonic acid of the breath, varies greatly in the same animal according to the

quality of the food. Regnault and Reiset[1] found, that in dogs fed on meat, the oxygen which reappeared under the form of carbonic acid was only 75 per cent. of the whole quantity absorbed; while in dogs fed on vegetable substances it amounted to over 90 per cent. In some instances,[2] where the animals (rabbits and fowls) were fed on bread and grain exclusively, the proportion of expired oxygen amounted to 101 or even 102 per cent.; that is, *more oxygen was actually contained in the carbonic acid exhaled, than had been absorbed in a free state from the atmosphere.* A portion, at least, of the carbonic acid must therefore have been produced by other means than direct oxidation.

IV. It has already been shown, in a previous chapter, that the carbonic acid which is exhaled from the lungs is not primarily formed in the blood, but makes its appearance in the substance of the tissues themselves; and furthermore, that even here it does not originate by a direct oxidation, but rather by a process of decomposition, similar to that by which it is produced from sugar in the alcoholic fermentation. We understand from this how to explain the singular fact alluded to in the last paragraph, viz., the abundant production of carbonic acid, under some circumstances, with a comparatively small supply of free oxygen. The statement made by Liebig, therefore, that starchy and oily matters taken with the food are immediately oxidized in the circulation without ever being assimilated by the tissues, is without foundation. It never, in fact, rested on any other ground than a supposed probability; and as we see that carbonic acid is abundantly produced in the body by other means, we have no longer any reason for assuming, without direct evidence, the existence of a combustive process in the blood.

V. The evolution of heat in the animal body is not general, as it would be if it resulted from a combustion of the blood; but local, since it takes place primarily in the substance of the tissues themselves. Various causes will therefore produce a local elevation or depression of temperature, by modifying the nutritive changes which take place in the tissues. Local inflammations increase very sensibly the temperature of the part in which they are seated, while that of the general mass of the blood is not altered. Finally it has been demon

[1] Annales de Chimie et de Physique, 3d series, xxvi. p. 428.
[2] Ibid. pp. 409–451.

strated by Bernard that in the natural state of the system there is a marked difference in the temperature of the different organs and of the blood returning from them.[1] The method adopted by this experimenter was to introduce, in the living animal, the bulb of a fine thermometer successively into the bloodvessels entering and those leaving the various internal organs. The difference of temperature in these two situations showed whether the blood had lost or gained in heat while traversing the capillaries of the organ. Bernard found, in the first place, that the blood in passing through the lungs, so far from increasing, was absolutely diminished in temperature; the blood on the left side of the heart being sometimes a little more and sometimes a little less than one-third of a degree Fahr. lower than on the right side. This slight cooling of the blood in the lungs is owing simply to its exposure to the air through the pulmonary membrane, and to the vaporization of water which takes place in these organs. In the abdominal viscera, on the contrary, the blood is increased in temperature. It is sensibly warmer in the portal vein than in the aorta; and very considerably warmer in the hepatic vein than in either the portal vein or vena cava. As the result of many observations,[2] Bernard found that in the dog the temperature of the blood in the abdominal aorta varied from 99.5° to 105.5° F.; in the portal vein, from 100° to 106°; and in the hepatic vein, from 101° to 106.8°. The warmest blood in the body, accordingly, is that of the hepatic vein, which has already passed through two successive capillary circulations since leaving the arterial system. The greatest increase in temperature, however, according to the above observations, takes place in the liver itself; for, while the average increase between the blood of the aorta and that of the portal vein was rather less than a quarter of a degree, that between the portal vein and the hepatic vein was over half a degree.

Furthermore, it is Bernard's conclusion that animal heat is produced in the substance of the tissues, since these are often warmer than the venous blood coming from them. Thus the stomach and duodenum were found to have a temperature of from half a degree to one degree higher than that of the blood in the portal vein in their vicinity. The blood accordingly receives its heat in great measure from tissue of the organs through which it circulates; and as the chemical processes of nutrition are necessarily different

[1] Gazette Hebdomadaire, Aug. 29 and Sept. 26, 1856.

[2] Leçons sur les Liquides de l'organisme, Paris, 1859, vol. i. p. 84.

in the different tissues and organs, it is easy to understand why a specific amount of heat should be produced in each of them. A similar fact, it will be recollected, was noticed by Dutrochet, in regard to the different parts of the vegetable organism.

VI. Animal heat has been supposed to stand in a special relation to the production of carbonic acid, because in warm-blooded animals the respiratory process is more active than in those of a lower temperature; and because, in the same animal, an increase or diminution in the evolution of heat is accompanied by a corresponding increase or diminution in the products of respiration. But this is also true of all the other excretory products of the body. An elevation of temperature is accompanied by an increased activity of *all* the nutritive processes. Not only carbonic acid, but the ingredients of the urine and the perspiration are discharged in larger quantity than usual. An increased supply of food also is required, as well as a larger quantity of oxygen; and the digestive and secretory processes both go on, at the same time, with unusual activity.

Animal heat, then, is a phenomenon which results from the simultaneous activity of many different processes, taking place in many different organs, and dependent, undoubtedly, on different chemical changes in each one. The introduction of oxygen and the exhalation of carbonic acid have no direct connection with each other, but are only the beginning and the end of a long series of changes, in which all the tissues of the body successively or simultaneously take part. Their relation is precisely that which exists between the food introduced into the stomach, and the urine discharged by the kidneys. The tissues require for their nutrition a constant supply of solid and liquid food which is introduced through the stomach, and of oxygen which is introduced through the lungs. The disintegration and decomposition of the tissues give rise, on the one hand, to urea, uric acid, &c., which are discharged with the urine, and on the other hand to carbonic acid, which is exhaled from the lungs. But the oxygen is not directly converted into carbonic acid, any more than the food is directly converted into urea and the urates.

Animal heat is not to be regarded, therefore, as the result of a combustive process. There is no reason for believing that the greater part of the food is "burned" in the circulation. It is, on the contrary, assimilated by the substance of the tissues; and these,

in their subsequent disintegration, give rise to several excretory products, one of which is carbonic acid.

The numerous combinations and decompositions which follow each other incessantly during the nutritive process, result in the production of an internal or vital heat, which is present in both animals and vegetables, and which varies in amount in different species, in the same individual at different times, and even in different parts and organs of the same body.

CHAPTER XIV.

THE CIRCULATION.

THE blood may be regarded as a nutritious fluid, holding in solution all the ingredients necessary for the formation of the tissues. In some animals and vegetables, of the lowest organization, such as infusoria, polypes, algæ, and the like, neither blood nor circulation is required; since all parts of the body, having a similar structure, absorb nourishment equally from the surrounding media, and carry on nearly or quite the same chemical processes of growth and assimilation. In the higher animals and vegetables, however, as well as in the human subject, the case is different. In them, the structure of the body is compound. Different organs, with widely different functions, are situated in different parts of the frame; and each of these functions is more or less essential to the continued existence of the whole. In the intestine, for example, the process of digestion is accomplished; and the prepared ingredients of the food are thence absorbed into the bloodvessels, by which they are transported to distant tissues and organs. In the lungs, again, the blood absorbs oxygen which is afterward to be appropriated by the tissues; and the carbonic acid, first produced in the tissues, is finally exhaled from the lungs. In the liver, the kidneys, and the skin, other substances still are produced or eliminated, and these local processes are all necessary to the preservation of the general organization. The circulating fluid is, therefore, in the higher animals, a *means of transportation*, by which the substances produced in particular organs are dispersed throughout the body, or by which substances produced generally in the tissues are conveyed to particular organs, in order to be eliminated.

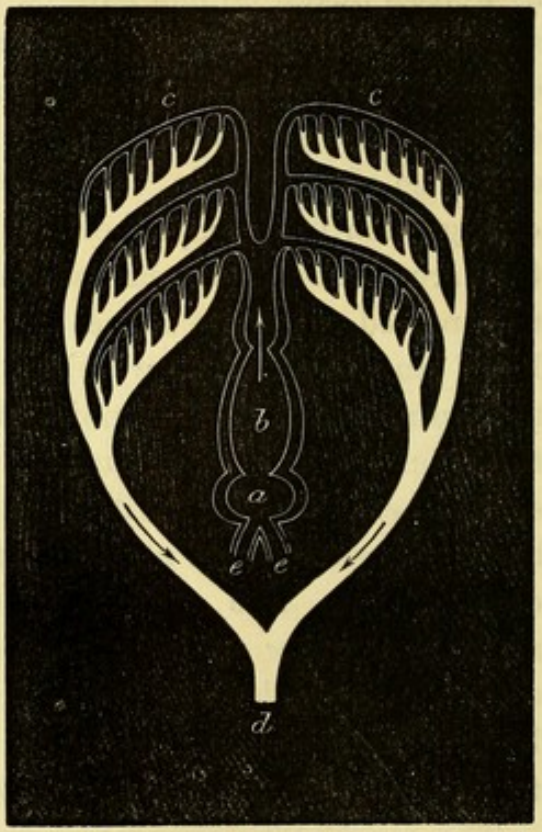
The circulatory apparatus consists of four different parts, viz: 1st. The heart; a hollow, muscular organ, which receives the blood at one orifice and drives it out, in successive impulses, at another. 2d. The arteries; a series of branching tubes, which convey the blood from the heart to the different tissues and organs of the body.

3d. The capillaries; a network of minute inosculating tubules which are interwoven with the substance of the tissues, and which bring the blood into intimate contact with their component parts; and 4th. The veins; a set of converging vessels, destined to collect the blood from the capillaries, and return it to the heart. In each of these different parts of the circulatory apparatus, the movement of the blood is peculiar and dependent on special conditions. It will therefore require to be studied in each one separately.

THE HEART.

The structure of the heart, and of the adjacent vessels, varies in different classes of animals, owing to the different arrangement of the respiratory organs. For the respiratory apparatus being one of the most important in the body, and the one most closely connected by anatomical relations with the organs of circulation, the latter are necessarily modified in structure to correspond with the former. In fish, for example (Fig. 77), the heart is an organ consisting of two principal cavities; an auricle (*a*) into which the blood is received from the central extremity of the vena cava, and a ventricle (*b*) into which the blood is driven by the contraction of the auricle. The ventricle is considerably larger and more powerful than the auricle, and by its contraction drives the blood into the main artery supplying the gills. In the gills (*cc*) the blood is arterialized; after which it is collected by the branchial veins. These veins unite upon the median line to form the aorta (*d*) by which the blood is finally distributed throughout the frame. In

Fig. 77.

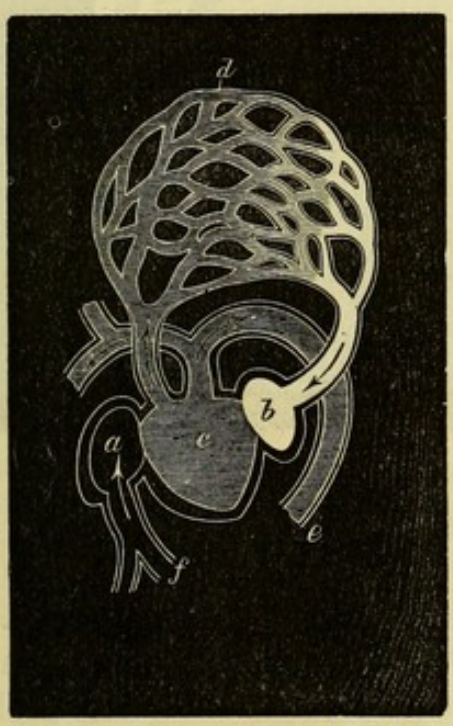


Circulation of Fish.—*a*. Auricle. *b*. Ventricle. *cc*. Gills. *d*. Aorta. *ee*. Venæ cavæ.

these animals the respiratory process is not a very active one; but the gills, which are of small size, being the only respiratory organs, all the blood requires to pass through them for purposes of aeration. The heart here is a single organ, destined only to drive the blood from the termination of the venous system to the capillaries of the gills.

In reptiles the heart is composed of two auricles and one ventricle. (Fig. 78.) The venæ cavæ discharge their blood into the right auricle (*a*), whence it passes into the ventricle (*c*). From the ventricle, a part of it is carried into the aorta and distributed throughout the body, while a part is sent to the lungs through the pulmonary artery. The arterialized blood, returning from the lungs by the pulmonary vein, is discharged into the left auricle (*b*), and thence into the ventricle (*c*), where it mingles with the venous blood which has just arrived by the venæ cavæ. In the reptile, therefore, the ventricle is a common organ of propulsion, both for the lungs and for the general circulation. In these animals the aeration of the blood in the lungs is only partial; a certain portion of the blood being carried to the lungs by the pulmonary artery, just as in the human subject it is only a portion of the blood which is carried to the kidney by the renal artery. This arrangement is sufficient for the reptiles, because in many of them, such as serpents and turtles, the lungs are much more extensive and efficient, as respiratory organs, than the gills of fish; while in others, such as frogs and water-lizards, the integument itself, which is moist, smooth, and naked, also takes an important share in the aeration of the blood.

Fig. 78.

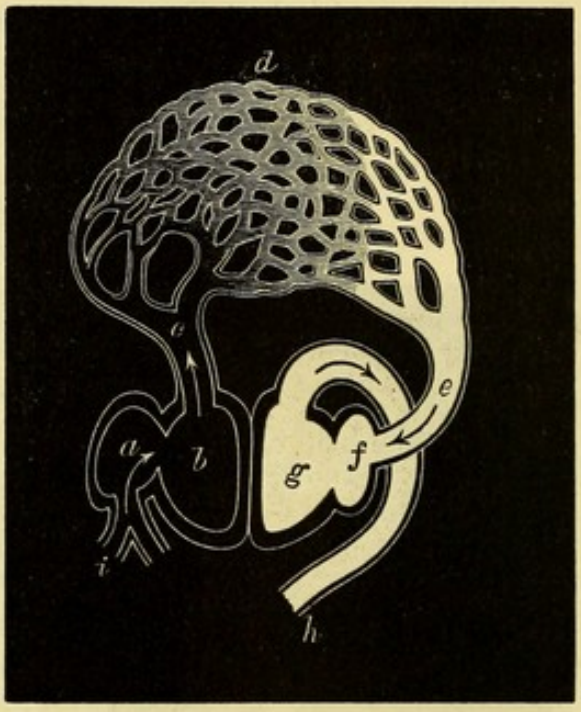


Circulation of Reptiles.—*a*. Right auricle. *b*. Left auricle. *c*. Ventricle. *d*. Lungs. *e*. Aorta. *f*. Vena cava.

In quadrupeds and the human species, however, the respiratory process is not only exceedingly active, but the lungs are, at the same time, the only organs in which the aeration of the blood is fully accomplished. Here, accordingly, we find the two circulations, general and pulmonary, distinct from each other. (Fig. 79.) All

the blood returning from the body by the veins must pass through the lungs before it is again distributed through the arterial system. We have therefore a double circulation and a double heart; the two sides of the organ, though united externally, being separate internally. The mammalian heart consists of a right auricle and ventricle (*a*, *b*), receiving the blood from the vena cava (*i*), and driving it to the lungs; and a left auricle and ventricle (*f*, *g*) receiving the blood from the lungs and driving it outward through the arterial system.

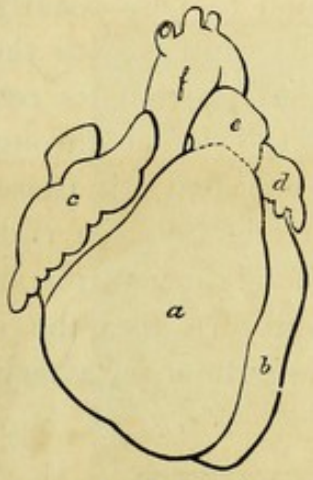
Fig. 79.



CIRCULATION IN MAMMALIANS.—*a*. Right auricle. *b*. Right ventricle. *c*. Pulmonary artery. *d*. Lungs. *e*. Pulmonary vein. *f*. Left auricle. *g* Left ventricle. *h*. Aorta. *i*. Vena cava.

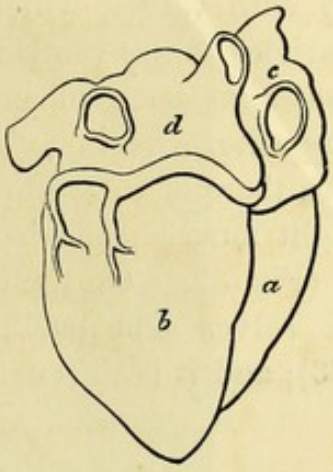
In the complete or double mammalian heart, the different parts of the organ present certain peculiarities and bear certain relations to each other, which it is necessary to understand before we can properly appreciate its action and movements. The entire organ has a more or less conical form, its base being situated on the median line, directed upward and backward; the whole being suspended in the chest, and loosely fixed to the spinal column, by the great vessels which enter and leave it at this point. The apex, on the contrary, is directed downward, forward, and to the left, surrounded by the pericardium, but capable of a certain degree of lateral and rotatory motion. The auricles, which have a smaller capacity and thinner walls than the ventricles, are situated at the upper and posterior part of the organ (Figs. 80 and 81); while the ventricles occupy its anterior and lower portions. The two ventricles, moreover, are not situated on the same plane, but the right ventricle occupies a position somewhat in front and above that of the left; so that in an anterior view of the heart the greater portion of the left ventricle is concealed by the right (Fig. 80), and in a posterior view the greater portion of the right ventricle is concealed by the left (Fig. 81); while in both positions the apex of the heart is constituted altogether by the point of the left ventricle.

Fig. 80.



HUMAN HEART, anterior view.—*a*. Right ventricle. *b*. Left ventricle. *c*. Right auricle. *d*. Left auricle. *e*. Pulmonary artery. *f*. Aorta.

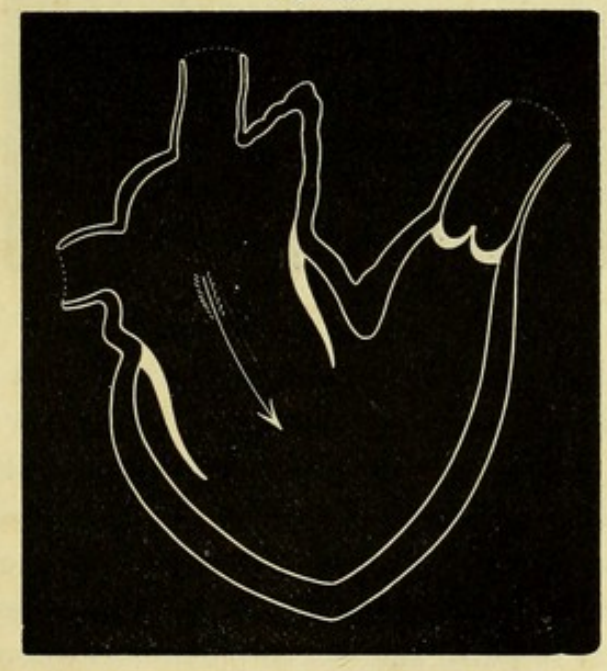
Fig. 81.



HUMAN HEART, posterior view.—*a*. Right ventricle. *b*. Left ventricle. *c*. Right auricle. *d*. Left auricle.

The different cavities of the heart and of the adjacent bloodvessels on each side, though continuous with each other, are partially separated by certain constrictions. These constricted orifices, by which the different cavities communicate, are known by the names of the

Fig. 82.

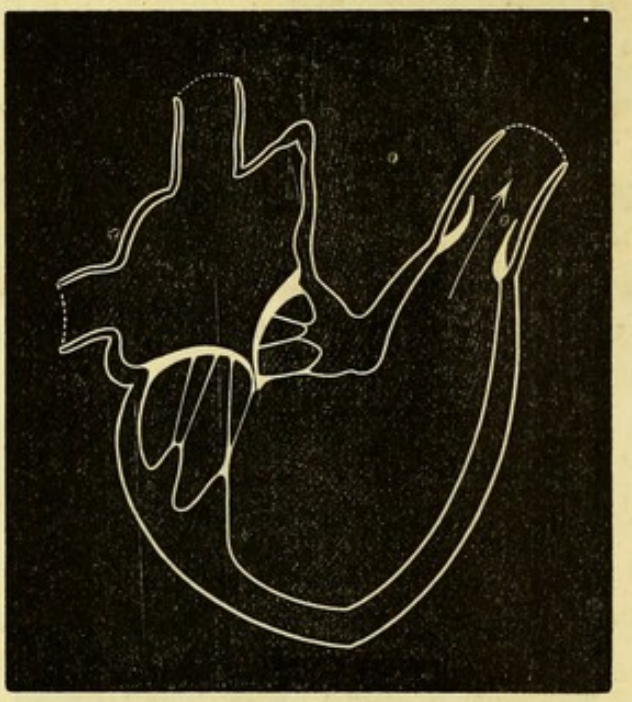


RIGHT AURICLE AND VENTRICLE; Auriculo-ventricular Valves open, Arterial Valves closed.

auricular, auriculo-ventricular, and aortic and pulmonary orifices; the auricular orifices being the passages from the venæ cavæ and pulmonary veins into the right and left auricles; the auriculo-ventricular orifices leading from the auricles into the ventricles; and the aortic and pulmonary orifices leading from the ventricles into the aortic and pulmonary arteries respectively.

The auriculo-ventricular, aortic, and pulmonary orifices are furnished with valves, which allow the blood to pass readily from the auricles to the ventricles, and from the ventricles to the arteries, but shut back in such a manner as to prevent its return in the opposite direction. The course of the blood through the heart is, therefore, as follows. From the vena cava it passes into the right auricle; and from the right auricle into the right ventricle. (Fig. 82.) On the contraction of the right ventricle, the tricuspid valves shut back, preventing its return into the auricle (Fig. 83); and it is thus driven through the pulmonary artery to the

Fig. 83.

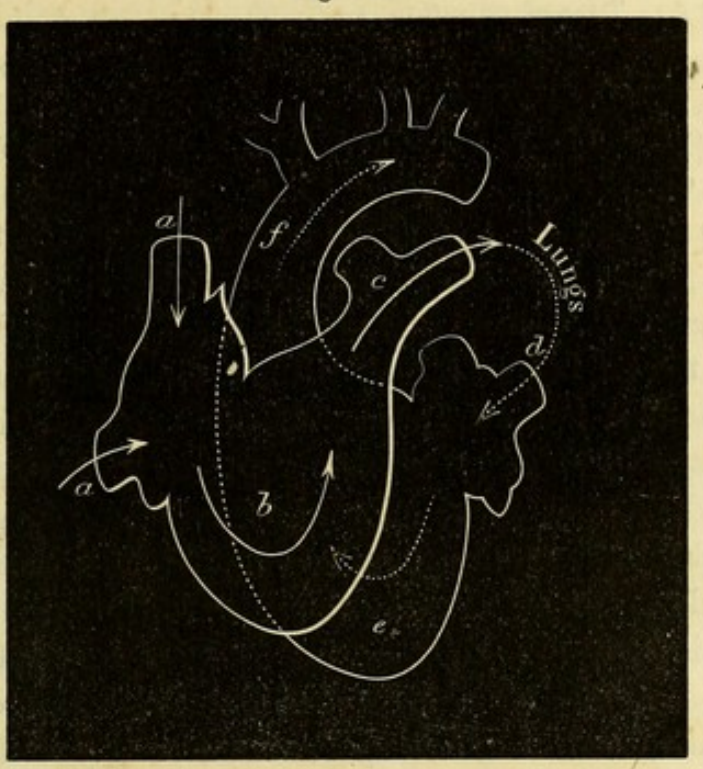


Right Auricle and Ventricle; Auriculo-ventricular Valves closed, Arterial Valves open

lungs. Returning from the lungs, it enters the left auricle, thence passes into the left ventricle, from which it is finally delivered into the aorta, and distributed throughout the body. (Fig. 84.) This movement of the blood, however, through the cardiac cavities, is not a continuous and steady flow, but is accomplished by alternate contractions and relaxations of the muscular parietes of the heart so that with every impulse, successive portions of blood are received by the auricles, delivered into the ventricles, and by them discharged into the arteries. Each one of these successive actions is called a beat, or *pulsation* of the heart.

Each pulsation of the heart is accompanied by certain important phenomena, which require to be studied in detail. These are the *sounds*, the *movements*, and the *impulse*.

Fig. 84.



Course of Blood through the Heart.—*a*, *a*. Vena cava, superior and inferior. *b*. Right ventricle. *c*. Pulmonary artery. *d*. Pulmonary vein. *e*. Left ventricle. *f*. Aorta.

The *sounds* of the heart are two in number. They can readily be heard by applying the ear over the cardiac region, when they are found to be quite different from each other in position, in tone, and in duration. They are distinguished as the *first* and *second* sounds of the heart. The first sound is heard with the greatest intensity over the anterior surface of the heart, and more particularly over the fifth rib and the fifth intercostal space. It is long, dull, and smothered in tone, and occupies one-half the entire duration of a single beat. It corresponds in time with the impulse of the heart in the precordial region, and the stroke of the large arteries in the immediate vicinity of the chest. The second sound follows immediately upon the first. It is heard most distinctly at the situation of the aortic and pulmonary valves, viz., over the sternum at the level of the third costal cartilage. It is short, sharp, and distinct in tone, and occupies only about one-quarter of the whole time of a pulsation. It is followed by an equal interval of silence; after which the first sound again recurs. The whole time of a cardiac pulsation may then be divided into four quarters, of which the first two are occupied by the first sound, the third by the second sound, and the fourth by an interval of silence, as follows:—

Time of pulsation.
- 1st quarter } First sound.
- 2d " }
- 3d " Second sound.
- 4th " Interval of silence.

The *cause* of the second sound is universally acknowledged to be the sudden closure and tension of the aortic and pulmonary valves. This fact is established by the following proofs: 1st, this sound is heard with perfect distinctness, as we have already mentioned, directly over the situation of the above-mentioned valves; 2d, the farther we recede in any direction from this point, the fainter becomes the sound; and 3d, in experiments upon the living animal, often repeated by different observers, it has been found that if a curved needle be introduced into the base of the large vessels, so as to hook back the semilunar valves, the second sound at once disappears, and remains absent until the valve is again liberated. These valves consist of fibrous sheets, covered with a layer of endocardial epithelium. They have the form of semilunar festoons, the free edge of which is directed away from the cavity of the ventricle, while the attached edge is fastened to the inner surface of the base of the artery. While the blood is passing from the ventricle to the artery, these valves are thrown forward and relaxed; but when the artery reacts upon its contents they shut back, and their fibres, becoming suddenly tense, yield a clear, characteristic, snapping sound.

The production of the *first* sound has been attributed to a variety of causes; such as the rush of blood through the cardiac orifices, the muscular contraction of the parietes of the heart, the tension of the auriculo-ventricular valves, the collision of the particles of blood with each other and with the surface of the ventricle, &c. &c. We believe, however, with Andry[1] and some others, that the first sound of the heart has, for the most part, a similar origin with the second; and that it is *dependent mainly on the closure of the auriculo-ventricular valves.* The reasons for this conclusion are the following: —

1st. The second sound is undoubtedly caused by the closure of the semilunar valves, and in the action of the heart the movements of the two sets of valves alternate with each other precisely as do the first and second sounds; and the sudden tension of the valvular fibres is calculated to produce a similar effect in each instance.

[1] Diseases of the Heart, Kneeland's Translation, Boston, 1846.

2d. The first sound is heard most distinctly over the anterior surface of the ventricles, where the tendinous cords supporting the auriculo-ventricular valves are inserted, and where the sound produced by the tension of these valves is most readily conducted to the ear.

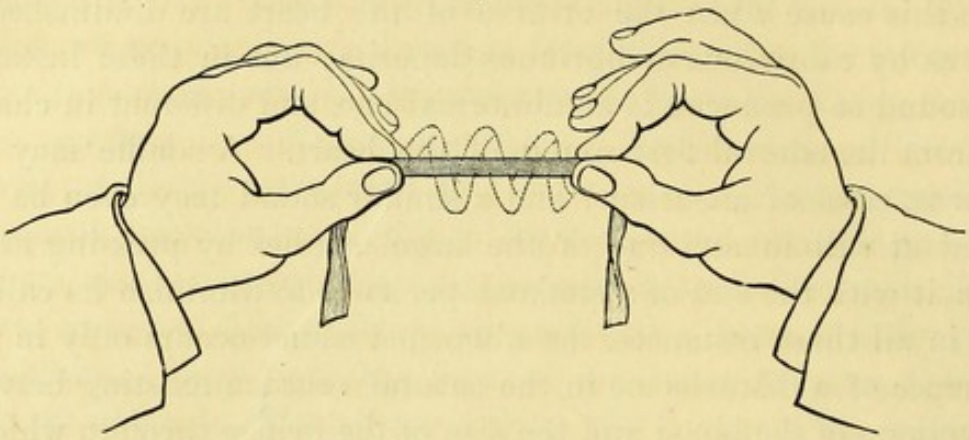
3d. There is no reason to believe that the current of blood through the cardiac orifices could give rise to an appreciable sound, so long as these orifices, and the cavities to which they lead, have their normal dimensions. An unnatural souffle may indeed originate from this cause when the orifices of the heart are diminished in size, as by calcareous or fibrinous deposits; but in these instances the sound so produced is an abnormal one, and different in character from the natural first sound of the heart. A souffle may also occur in cases of aneurism; and a similar sound may even be produced at will in any one of the large arteries by pressing firmly upon it with the end of a stethoscope, so as to diminish its calibre. But in all these instances, the abnormal sound occurs only in consequence of a disturbance in the natural relation existing between the volume of the blood and the size of the orifice through which it passes. In the healthy heart, the size of the different orifices is in proportion to the quantity of the circulating fluid; and there is no more reason for believing that the passage of the blood should give rise to a sound in the cardiac cavities than in the larger arteries or veins.

4th. The difference in character between the two sounds of the heart probably depends, in great measure, on the different arrangement of the two sets of valves. The second sound is short, sharp, and distinct, because the semilunar valves are short and narrow, superficial in their situation, and supported by the dense and fibrous bases of the aortic and pulmonary arteries. The first sound is dull and prolonged, because the auriculo-ventricular valves are broad and deep-seated, and are attached, by their long chordæ tendineæ, to the comparatively soft and yielding fleshy columns of the heart. The difference between the first and second sounds can, in fact, be easily imitated, by simply snapping between the fingers two pieces of tape or ribbon, of the same texture but of different lengths. (Fig. 85.) The short one will give out a distinct and sharp sound; the long one a comparatively dull and prolonged sound.

Together with the first sound of the heart there is also heard a friction sound, or sound of impulsion, produced by the collision of the point of the heart with the parietes of the chest. This sound, which is most distinctly heard in the fifth intercostal space, is min-

gled with the valvular sound which occurs at the same time. It is different, however, in character from the latter, and may usually be distinguished from it by careful examination. It has been observed by Prof. Austin Flint,[1] that it may be more or less completely eliminated, by ausculting the heart at a distance from its apex, so that the first sound may then be heard purely valvular in quality, and entirely similar to the second sound in all its essential characters.

Fig. 85.



The *movements* of the heart during the time of a pulsation are of a peculiar character, and have been very often erroneously described. In fact altogether the best description of the movements of the heart which has yet appeared, is that given by William Harvey, in his celebrated work on the *Motion of the Heart and Blood*, published in 1628. He examined the motion of the heart by opening the chest of the living animal; and though the same or similar experiments have been frequently performed since his time, the descriptions given by subsequent observers have been for the most part singularly inferior to his, both in clearness and fidelity. The method which we have adopted for examining the motions of the heart in the dog is as follows: The animal is first rendered insensible by ether, or by the inoculation of woorara. The latter mode is preferable, since a long-continued etherization seems to exert a sensibly depressing effect on the heart's action, which is not the case with woorara. The trachea is then exposed and opened just below the larynx, and the nozzle of a bellows inserted and secured by ligature. Finally, the chest is opened on the median line, its two sides widely separated, so as to expose the heart and lungs, the pericardium slit up and carefully cut away from its attachments, and the lungs inflated by insufflation through the trachea. By keeping up a steady artificial respiration, the move-

[1] Heart-Sounds in Health and Disease. Prize Essay of the American Medical Association. Transactions of 1858, p. 825.

ments of the heart may be made to continue, in favorable cases, for more than an hour; and its actions may be studied by direct observation, like those of any external organ.

The examination, however, requires to be conducted with certain precautions, which are indispensable to success. When the heart is first exposed, its movements are so complicated, and recur with such rapidity, that it is difficult to distinguish them perfectly from each other, and to avoid a certain degree of confusion. Singular as it may seem, it is even difficult at first to determine what period in the heart's pulsation corresponds to contraction, and what to relaxation of the organ. We have even seen several medical men, watching together the pulsations of the same heart, unable to agree upon this point. It is very evident, indeed, that several English and continental observers have mistaken, in their examinations, the contraction for the relaxation, and the relaxation for the contraction. The first point, therefore, which it is necessary to decide, in examining the successive movements of a cardiac pulsation, is the following, viz: *Which is the contraction and which the relaxation of the ventricles?* The method which we have adopted is to pass a small silver canula directly through the parietes of the left ventricle into its cavity. The blood is then driven from the external orifice of the canula in interrupted jets; each jet indicating the time at which the ventricle contracts upon its contents. The canula is then withdrawn, and the different muscular layers of the ventricular walls, crossing each other obliquely, close the opening, so that there is little or no subsequent hemorrhage.

When the successive actions of contraction and relaxation have by this means been fairly recognized and distinguished from each other, the cardiac pulsations are seen to be characterized by the following phenomena. The changes in form and position of the entire heart are mainly dependent on those of the ventricles, which contract simultaneously with each other, and which constitute much the largest portion of the entire mass of the organ.

1. At the time of its contraction the heart hardens. This phenomenon is exceedingly well marked, and is easily appreciated by placing the finger upon the ventricles, or by grasping them between the finger and thumb. The muscular fibres become swollen and indurated, and, if grasped by the hand, communicate the sensation of a somewhat sudden and powerful shock. It is this forcible induration of the heart, at the time of contraction, which has been mistaken by some writers for an active dilatation, and described as

such. It is, however, a phenomenon precisely similar to that which takes place in the contraction of a voluntary muscle, which becomes swollen and indurated at the same moment and in the same proportion that it diminishes in length.

2. At the time of contraction, the point of the heart protrudes, and, coming in contact with the walls of the chest, produces the cardiac impulse. This action was well described by Dr. Harvey.[1] "The heart," he says, "is erected, and rises upward to a point, so that at this time it strikes against the chest and the pulse is felt externally." This phenomenon is due to an elongation of the ventricle, by which its point is thrown forward at the same time that its sides are drawn together. The elongation of the heart, however, has often been denied by physiological writers. The only modern observers, so far as we are aware, who have recognized its existence, are Drs. C. W. Pennock and Edward M. Moore, who performed a series of very careful and interesting experiments on the action of the heart, in Philadelphia, in the year 1839.[2] These experimenters operated upon calves, sheep, and horses, by stunning the animal with a blow upon the head, opening the chest, and keeping up artificial respiration. They observed an elongation of the ventricle at the time of contraction, and were even able to measure its extent by applying a shoemaker's rule to the heart while in active motion. We are able to corroborate the statement of these observers by the result of our own experiments on dogs, rabbits and frogs. The appearances presented by the heart, in active motion, are somewhat modified by the direction in which it is examined. If viewed anteriorly, the right ventricle with the conus arteriosus, situated over the front of the organ, comes prominently into view; and its fibres, running from above downward and from right to left, tilt the apex of the heart, at the time of contraction, diagonally forward and to the right side. But if the heart be turned upward, so as to expose the posterior surface of the organ, which is constituted almost altogether by the left ventricle, the elongation of its figure, at the moment of contraction, may be distinctly seen. At this time, the sides of the ventricle approximate each other and its point protrudes; so that the transverse diameter of the heart is diminished, and its longitudinal diameter increased. This does not appear to be due to a recoil of the entire heart, but is a real elonga-

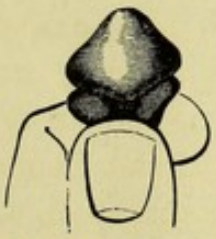
[1] Works of William Harvey, M.D. Sydenham ed., London, 1847, p. 21.

[2] Philadelphia Medical Examiner, No. 44.

tion of its figure; since it takes place also when the base of the organ is seized with a pair of forceps, at its junction with the large vessels, and held in an immovable position. The above action can also be readily felt by grasping the base of the heart and the origin of the large vessels gently between the first and middle fingers, and allowing the end of the thumb of the same hand to rest lightly upon its apex. With every contraction the thumb is sensibly lifted and separated from the fingers, by a somewhat forcible elevation of the point of the heart.

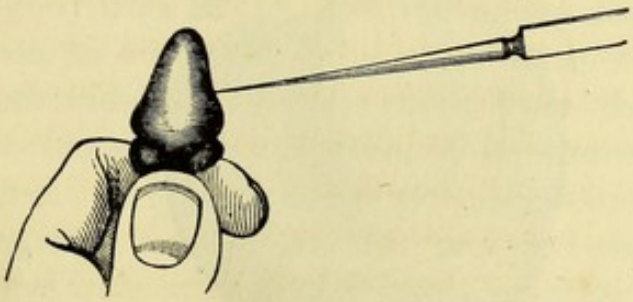
The contraction of the heart is an active movement, its relaxation entirely a passive one. The difference between these two conditions of the heart, and the forcible character of its contraction, may be seen in the following manner. If the heart of the frog, or even of any small warm-blooded animal, as the rabbit, be rapidly removed from the chest, it will continue to beat for some minutes afterward; and when the rhythmical pulsations have finally ceased, contractions can still be readily excited by touching the heart with the point of a steel needle. If the heart be now held by its base between the thumb and finger, with its point directed upward, it will be seen to have a pyramidal or conical form, representing very nearly in its outline an equilateral triangle (Fig. 86); its base, while in a condition of rest, bulging out laterally, while the apex is comparatively obtuse.

Fig. 86.



HEART OF FROG in a state of relaxation.

Fig. 87.



HEART OF FROG in contraction.

When the heart, held in this position, is touched with the point of a needle (Fig. 87), it starts up, becomes instantly narrower and longer, its sides approximating and its point rising to an acute angle. This contraction is immediately followed by a relaxation; the point of the heart sinks down, and its sides again bulge outward.

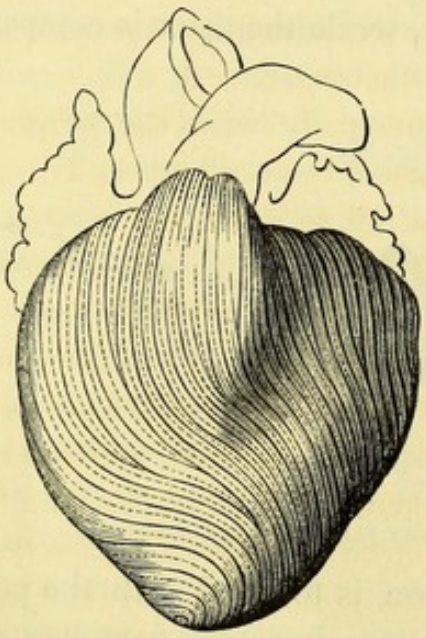
Let us now see in what manner this change in the figure of the ventricles during contraction is produced. If the muscular fibres

Fig. 88.

Diagram of SIMPLE LOOPED FIBRES, in relaxation and contraction.

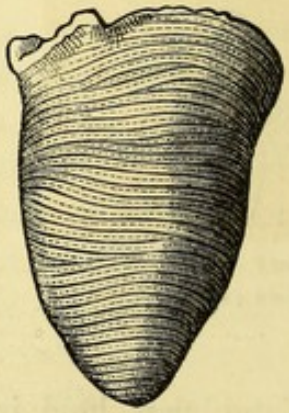
of the heart were arranged in the form of simple loops, running parallel with the axis of the organ, the contraction of these fibres would merely have the effect of diminishing the size of the heart in every direction. This effect can be seen in the accompanying hypothetical diagram (Fig. 88), where the white outline represents such simple looped fibres in a state of relaxation, and the dotted internal line indicates the form which they would take in contraction. In point of fact, however, none of the muscular fibres of the heart run throughout parallel to its longitudinal axis. They are disposed, on the contrary. in a direction partly spiral and partly circular. The most superficial fibres start from the base of the ventricles, and pass toward the apex, curling round the heart in such a manner as to pass over its anterior surface in an obliquely spiral direction, from above downward, and from right to left. (Fig. 89.) They converge toward the point of the heart, curling round the centre of its apex, and then, changing their direction, become deep-seated, run upward along

Fig. 89.



BULLOCK'S HEART, anterior view, showing the superficial muscular fibres.

Fig. 90.



LEFT VENTRICLE OF BULLOCK'S HEART, showing the deep fibres.

the septum and internal surface of the ventricles, and terminate in the columnæ carneæ, and in the inner border of the auriculo-ventricular ring. The deeper layers of fibres, on the contrary, are wrapped round the ventricles in a nearly circular direction (Fig.

90); their points of origin and attachment being still the auriculo-ventricular ring, and the points of the fleshy columns. The entire arrangement of the muscular bundles may be readily seen in a heart which has been boiled for six or eight hours, so as to soften the connecting areolar tissue, and enable the fibrous layers to be easily separated from each other.

By far the greater part of the mass of the fibres have therefore a circular instead of a longitudinal direction. When they contract, their action tends to draw the lateral walls of the ventricles together, and thus to diminish the transverse diameter of the heart; but as each muscular fibre becomes thickened in direct proportion to its contraction, their combined lateral swelling necessarily pushes out the apex of the ventricle, and the heart elongates at the same time that its sides are drawn together. This effect is illustrated in the accompanying diagram (Fig. 91), where the white lines show the figure of the heart during relaxation, with the course of its circular fibres, while the dotted line shows the narrowed and elongated figure necessarily produced by their contraction. This phenomenon, therefore, of the protrusion of the apex of the heart at the time of contraction, is not only fully established by observation, but is readily explained by the anatomical structure of the organ.

Fig. 91.

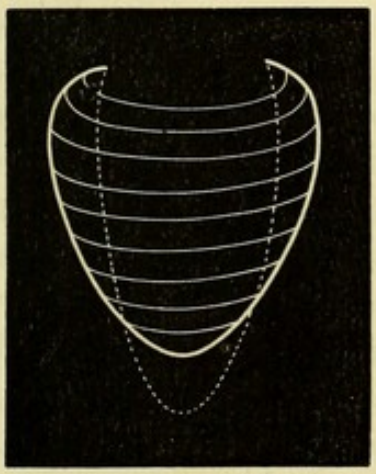


Diagram of CIRCULAR FIBRES OF THE HEART, and their contraction.

3. Simultaneously with the hardening and elongation of the heart, its apex moves slightly from left to right, and rotates also upon its own axis in the same direction. Both these movements result from the peculiar spiral arrangement of the cardiac fibres. If we refer again to the preceding diagrams, we shall see that, provided the fibres were arranged in simple longitudinal loops (Fig. 88), their contraction would merely have the effect of drawing the point of the heart directly upward in a straight line toward its base. On the other hand, if they were arranged altogether in a circular direction (Fig. 91), the apex would be simply protruded, also in a direct line, without deviating, or twisting either to the right or to the left. But in point of fact, the superficial fibres, as we have already described, run spirally, and, curling round the point of the heart turn inward toward its base; so that if the apex of the organ be

viewed externally, it will be seen that the superficial fibres converge toward its central point in curved lines, as in Fig. 92. It is well known that every curved muscular fibre, at the time of its shortening, necessarily approximates more or less to a straight line. Its curvature is diminished in exact proportion to the extent of its contraction; and if arranged in a spiral form, its contraction tends in the same degree to untwist the spiral. During the contraction of the heart, therefore, its apex rotates on its own axis in the direction indicated by the arrows in Fig. 92, viz., from left to right anteriorly, and from right to left posteriorly. This produces a twisting movement of the apex in the above direction, which is very perceptible to the eye at each pulsation of the heart, when exposed in the living animal.

Fig. 92

Converging Fibres at the Apex of the Heart.

4. The protrusion of the point of the heart at the time of contraction, together with its rotation upon its axis from left to right, brings the apex of the organ in contact with the parietes of the chest, and produces the shock or *impulse* of the heart, which is readily perceptible externally, both to the eye and to the touch. In the human subject, when in an erect position, the heart strikes the chest in the fifth intercostal space, midway between the edge of the sternum and a line drawn perpendicularly through the left nipple. In a supine position of the body, the heart falls away from the anterior parietes of the chest so much that the impulse may disappear for the time altogether. This alternate recession and advance of the point of the heart, in relaxation and contraction, is provided for by the anatomical arrangement of the pericardium, and the existence of the pericardial fluid. As the heart plays backward and forward, the pericardial fluid constantly follows its movements, receding as the heart advances, and advancing as the heart recedes. It fulfils, in this respect, the same purpose as the synovial fluid, and the folds of adipose tissue in the cavity of the large articulations; and allows the cardiac movements to take place to their full extent without disturbing or injuring in any way the adjacent organs.

5. The *rhythm* of the heart's pulsations is peculiar and somewhat complicated. Each pulsation is made up of a double series of contractions and relaxations. The two auricles contract together, and

afterward the two ventricles; and in each case the contraction is immediately followed by a relaxation. The auricular contraction is short and feeble, and occupies the first part of the time of a pulsation. The ventricular contraction is longer and more powerful, and occupies the latter part of the same period. Following the ventricular contraction there comes a short interval of repose, after which the auricular contraction agains recurs. The auricular and ventricular contractions, however, do not alternate so distinctly with each other (like the strokes of two pistons) as we should be led to believe from the accounts which have been given by some observers. On the contrary, they are connected and continuous. The contraction, which commences at the auricle, is immediately propagated to the ventricle, and runs rapidly from the base of the heart to its apex, very much in the manner of a *peristaltic* motion, except that it is more sudden and vigorous.

William Harvey, again, gives a better account of this part of the heart's action than has been published by any subsequent writer. The following exceedingly graphic and appropriate description, taken from his book, shows that he derived his knowledge, not from any secondary or hypothetical sources, but from direct and careful study of the phenomena in the living animal.

"First of all," he says,[1] "the auricle contracts, and in the course of its contraction throws the blood (which it contains in ample quantity as the head of the veins, the storehouse and cistern of the blood) into the ventricle, which being filled, the heart raises itself straightway, makes all its fibres tense, contracts the ventricles, and performs a beat, by which beat it immediately sends the blood supplied to it by the auricle, into the arteries; the right ventricle sending its charge into the lungs by the vessel which is called vena arteriosa, but which, in structure and function, and all things else, is an artery; the left ventricle sending its charge into the aorta, and through this by the arteries to the body at large.

"These two motions, one of the ventricles, another of the auricles, take place consecutively, but in such a manner that there is a kind of harmony or rhythm preserved between them, the two concurring in such wise that but one motion is apparent, especially in the warmer blooded animals, in which the movements in question are rapid. Nor is this for any other reason than it is in a piece of machinery, in which, though one wheel gives motion to another,

[1] Op. cit., p. 31.

yet all the wheels seem to move simultaneously; or in that mechanical contrivance which is adapted to fire-arms, where the trigger being touched, down comes the flint, strikes against the steel, elicits a spark, which falling among the powder, it is ignited, upon which the flame extends, enters the barrel, causes the explosion, propels the ball, and the mark is attained; all of which incidents, by reason of the celerity with which they happen, seem to take place in the twinkling of an eye."

The above description indicates precisely the manner in which the contraction of the ventricle follows successively and yet continuously upon that of the auricle. The entire action of the auricles and ventricles during a pulsation is accordingly as follows: The contraction begins, as we have already stated, at the auricle. Thence it runs immediately forward to the apex of the heart. The entire ventricle contracts vigorously, its walls harden, its apex protrudes, strikes against the walls of the chest, and twists from left to right, the auriculo-ventricular valves shut back, the first sound is produced, and the blood is driven into the aorta and pulmonary artery. These phenomena occupy about one-half the time of an entire pulsation. Then the ventricle is immediately relaxed, and a short period of repose ensues. During this period the blood flows in a steady stream from the large veins into the auricle, and through the auriculo-ventricular orifice into the ventricle; filling the ventricle, by a kind of passive dilatation, about two-thirds or three-quarters full. Then the auricle contracts with a quick sharp motion, forces the last drop of blood into the ventricle, distending it to its full capacity, and then the ventricular contraction follows, as above described, driving the blood into the large arteries. These movements of contraction and relaxation continue to alternate with each other, and form, by their recurrence, the successive cardiac pulsations.

THE ARTERIES AND THE ARTERIAL CIRCULATION.

The arteries are a series of branching tubes which commence with the aorta and ramify throughout the body, distributing the blood to all the vascular organs. They are composed of three coats, viz: an internal homogeneous tunic, continuous with the endocardium; a middle coat, composed of elastic and muscular fibres; and an external or "cellular" coat, composed of condensed layers of areolar tissue. The essential anatomical difference be-

tween the larger and the smaller arteries consists in the structure of their middle coat. In the smaller arteries this coat is composed exclusively of smooth muscular fibres, arranged in a circular manner around the vessel, like the circular fibres of the muscular coat of the intestine. In arteries of medium size the middle coat contains both muscular and elastic fibres; while in those of the largest calibre it consists of elastic tissue alone. The large arteries, accordingly, possess a remarkable degree of elasticity and little or no contractility; while the smaller are contractile, and less distinctly elastic.

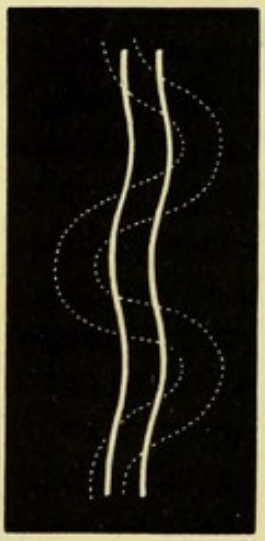
It is found, by measuring the diameters of the successive arterial ramifications, that the combined area of all the branches given off from a trunk is somewhat greater than that of the original vessel; and therefore that the combined area of all the small arteries must be considerably larger than that of the aorta, from which they originate. As the blood, consequently, in its passage from the heart outward, flows successively through larger and larger spaces, the rapidity of its circulation must necessarily be diminished, in the same proportion as it recedes from the heart. It is driven rapidly through the larger trunks, more slowly through those of medium size, and more slowly still as it approaches the termination of the arterial system and the commencement of the capillaries.

The *movement of the blood through the arteries* is primarily caused by the contractions of the heart; but it is, at the same time, regulated and modified by the elasticity of the vessels. The mode in which the arterial circulation takes place is as follows. The arterial system is, as we have seen, a vast and connected ramification of tubular canals, which may be regarded as a great vascular cavity, divided and subdivided from within outward by the successive branching of its vessels, but communicating freely with the heart and aorta at one extremity, and with the capillary plexus at the other; and this vascular system is filled everywhere with the circulating fluid. At the time of the heart's contraction, the muscular walls of the ventricle act powerfully upon its fluid contents. The auriculo-ventricular valves at the same time shutting back and preventing the blood from regurgitating into the auricle, it is forced out through the aortic orifice. A charge of blood is therefore driven into the arterial ramifications, distending their walls by the additional quantity of fluid forced into their cavities. When the ventricle immediately afterward relaxes, the active distending force is removed; and the elastic arterial walls, reacting upon their contents,

would force the blood back again into the heart, were it not for the semilunar valves, which shut together and close the aortic orifice. The blood is therefore urged onward, under the pressure of the arterial elasticity, into the capillary system. When the arteries have thus again partially emptied themselves, and returned to their original dimensions, they are again distended by another contraction of the heart. In this manner a succession of impulses or distensions is produced, which alternates with the reaction or subsidence of the vessels, and which can be felt throughout the body, wherever the arterial ramifications penetrate. This phenomenon is known by the name of the arterial *pulse*.

When the blood is thus driven by the cardiac pulsations into the arteries, the vessels are not only distended laterally, but are elongated as well as widened, and enlarged in every direction. Particularly when the vessel takes a curved or serpentine course, its elongation and the increase of its curvatures may be observed at every pulsation. This may be seen, for example, in the temporal, or even in the radial arteries, in emaciated persons. It is also very well seen in the mesenteric arteries, when the abdomen is opened in the living animal. At every contraction of the heart the curves of the artery on each side become more strongly pronounced. (Fig. 93.) The vessel even rises up partially out of its bed, particularly where it runs over a bony surface, as in the case of the radial artery. In old persons the curves of the vessels become permanently enlarged from frequent distension; and all the arteries tend to assume, with the advance of age, a more serpentine and even spiral course.

Fig. 93.



Elongation and curvature of an ARTERY IN PULSATION.

But the arterial pulse has certain other peculiarities which deserve a special notice. In the first place, if we place one finger upon the chest at the situation of the apex of the heart, and another upon the carotid artery at the middle of the neck, we can distinguish little or no difference in time between the two impulses. The distension of the carotid seems to take place at the same instant with the contraction of the heart. But if the second finger be placed upon the temporal artery, instead of the carotid, there is a perceptible interval between the two beats. The impulse of the temporal artery is felt to be a little later than that of the heart. In the same way the pulse of the radial artery at the wrist seems a little later than that of the carotid, and that of the

posterior tibial at the ankle joint a little later than that of the radial. So that, the greater the distance from the heart at which the artery is examined, the later is the pulsation perceived by the finger laid upon the vessel.

But it has been conclusively shown, particularly by the investigations of M. Marey,[1] that this difference in time of the arterial pulsations, in different parts of the body, is rather relative than absolute. By the contraction of the heart, the impulse is communicated at the same instant to all parts of the arterial system; but the apparent difference between them, in this respect, depends upon the fact, that, although all the arteries *begin* to be distended at the same moment, yet those nearest the heart are distended suddenly and rapidly, while for those at a distance, the distension takes place more slowly and gradually. Thus the impulse given to the finger, which marks the condition of maximum distension of the vessel, occurs a little later at a distance from the heart, than in its immediate proximity.

This modification of the arterial pulse is produced in the following way:—

The contraction of the left ventricle is a brisk, vigorous and sudden motion. The charge of blood, thus driven into the arterial system, meeting with a certain amount of resistance from the fluid already filling the vessels, does not instantly displace and force onward a quantity of blood equal to its own mass, but a certain proportion of its force is used in expanding the distensible walls of the vessels. In the immediate neighborhood, therefore, the expansion of the arteries is sudden and momentary, like the contraction of the heart itself. But this expansion requires for its completion a certain expenditure, both of force and time; so that at a little distance farther on, the vessel is neither distended to the same degree nor with the same rapidity. At the more distant point, accordingly, the arterial impulse is less powerful and arrives more slowly at its maximum.

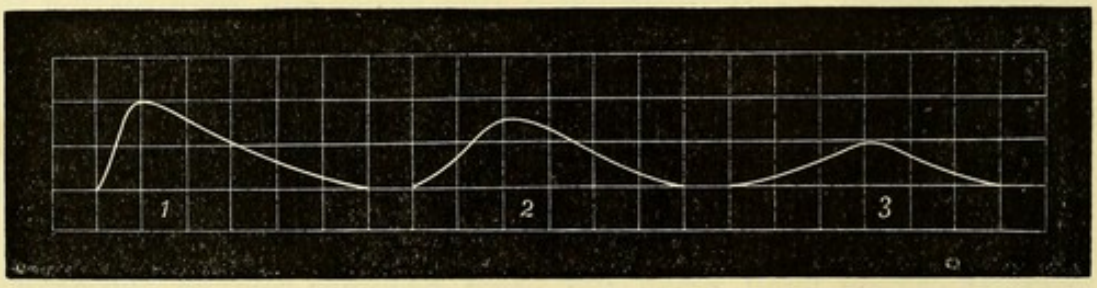
On the other hand, when the heart becomes relaxed, the artery in its immediate neighborhood contracts upon the blood by its own elasticity; and as its contraction at this time meets with no other resistance than that of the blood in the smaller vessels beyond, it drives a portion of its own blood into them, and thus supplies these vessels with a certain degree of distending force even in the inter-

[1] Journal de la Physiologie. Paris, April, 1859.

vals of the heart's action. Thus the difference in size of the carotid artery, at the two periods of the heart's contraction and its relaxation, is very marked; for the degree of its distension is great when the heart contracts, and its own reaction afterward empties it of blood to a very considerable extent. But in the small branches of the radial or ulnar artery, there is less distension at the time of the cardiac contraction, because this force has been partly expended in overcoming the elasticity of the larger vessels; and there is less emptying of the vessel afterward, because it is still kept partially filled by the reaction of the aorta and its larger branches. In other words, there is progressively less variation in size, at the periods of distension and collapse, for the smaller and distant arteries than for those which are larger and nearer the heart.

M. Marey has illustrated these facts by an exceedingly ingenious and effectual contrivance. He attached to the pipe of a small forcing pump, to be worked by alternate strokes of the piston, a long elastic tube open at the farther extremity. At different points upon this tube there rested little movable levers, which were raised by the distension of the tube whenever water was driven into it by the forcing pump. Each lever carried upon its extremity a small pencil, which marked upon a strip of paper, moving with uniform rapidity, the lines produced by its alternate elevation and depression. By these curves, therefore, both the extent and rapidity of distension of different parts of the elastic tube were accurately registered. The curves thus produced are as follows:—

Fig. 94.



CURVES OF PULSATION IN AN ELASTIC TUBE, as illustrated by M. Marey's experiment.—1. Near the distending force. 2. At a distance from it. 3. Still farther removed.

It will be seen that the whole time of pulsation is everywhere of equal length, and that the distension everywhere begins at the same moment. But at the beginning of the tube the expansion is wide and sudden, and occupies only a sixth part of the entire pulsation, while all the rest is taken up by a slow reaction. At the more

remote points, however, the period of expansion becomes longer and that of collapse shorter; until at 3 the two periods are completely equalized, and the amount of expansion is at the same time reduced one-half. Thus, the farther the blood passes from the heart outward, the more uniform is its flow, and the more moderate the distension of the arteries.

Owing to the alternating contractions and relaxations of the heart, accordingly, the blood passes through the arteries, not in a steady stream, but in a series of welling impulses; and the hemorrhage from a wounded artery is readily distinguished from venous or capillary hemorrhage by the fact that the blood flows in successive jets, as well as more rapidly and abundantly. If a puncture be made in the walls of the ventricle, and a slender canula introduced, the flow of the blood through it is seen to be entirely intermittent. A strong jet takes place at each ventricular contraction, and at each relaxation the flow is completely interrupted. If the puncture be made, however, in any of the large arteries near the heart, the flow of blood through the orifice is no longer intermittent, but is continuous; only it is very much stronger at the time of ventricular contraction, and diminishes, though it does not entirely cease, at the time of relaxation. If the blood were driven through a series of perfectly rigid and unyielding tubes, its flow would be everywhere intermittent; and it would be delivered from an orifice situated at any point, in perfectly interrupted jets. But the arteries are yielding and elastic; and this elasticity, as we have already explained, moderates the force of the separate arterial pulsations, and gradually fuses them with each other. The interrupted or pulsating character of the arterial current, therefore, which is strongly pronounced in the immediate vicinity of the heart, becomes gradually lost and equalized, during its passage through the vessels, until in the smallest arteries it is nearly imperceptible.

The same effect of an elastic medium in equalizing the force of an interrupted current may be shown by fitting to the end of a common syringe a long glass or metallic tube. Whatever be the length of the inelastic tubing, the water which is thrown into one extremity of it by the syringe will be delivered from the other end in distinct jets, corresponding with the strokes of the piston; but if the metallic tube be replaced by one of India rubber, of sufficient length, the elasticity of this substance merges the force of the separate impulses into each other, and the water is driven out from the farther extremity in a continuous stream.

The elasticity of the arteries, however, never entirely equalizes the force of the separate cardiac pulsations, since a pulsating character can be seen in the flow of the blood through even the smallest arteries, under the microscope; but this pulsating character diminishes very considerably from the heart outward, and the current becomes much more continuous in the smaller vessels than in the larger arteries or those of medium size.

M. Marey has still further developed his contrivance of a moveable lever, registering its own oscillations, in such a manner that it may be adapted to any of the superficial arteries in the living body. The instrument thus perfected is the *sphygmograph*. It consists of a small ivory plate which presses gently upon the artery by means of a fine spring, and which thus rises and falls with each alternate expansion and collapse of the arterial tube. The motion of the ivory plate is, in its turn, communicated to a vertical metallic rod, which touches the under surface of the horizontal registering lever near its attached extremity. The oscillating extremity of the lever, when the instrument is in operation, thus follows the movements of the ivory plate, and registers faithfully upon the strip of paper, the frequency and form of the arterial pulsations.

The advantage of this instrument is, that, in the first place, the length of the lever magnifies to the eye the extent of the arterial oscillations, and thus enables us to perceive movements too delicate to be distinguished by the touch alone; and, secondly, that, each part of the pulsations being permanently registered upon paper, the most rapid and evanescent changes in the form of the artery may be afterward studied at leisure, and compared with each other.

By the use of the sphygmograph it is shown, that, while there is a general resemblance in the form of pulsation of different arteries, nearly every vessel to which the instrument can be applied presents certain peculiarities dependent on its size, position, and distance from the heart. In the radial artery at the wrist, each pulsation consists of a sudden expansion of the vessel, indicated by a rapid upward movement of the lever, making, in the trace, a straight, nearly vertical line. This is followed by a gradual descent of the lever, accompanying the systole of the artery, until it reaches the lowest point of the trace, when the movement of ascension again takes place, and so on alternately. The line of descent, however, is not straight, like that of ascension, but is almost always marked by one, and sometimes two or even three slight undulations, giving it a wavy character, and indicating a

corresponding variation in the tension of the artery during the period of its systole. (Fig. 95.)

Fig. 95.

TRACE OF THE RADIAL PULSE, taken by the Sphygmograph.

There can be no doubt that the undulations in the line of descent are due to an oscillation in the mass of the blood, subsequent to its impulse by the heart, and during the reaction of the arterial system. Marey has shown, by a series of well-conducted experiments,[1] that similar oscillations are produced when any incompressible liquid is driven by a sudden impulse into an elastic tube; and that these oscillations are indicated by a similar movement of the index of the sphygmograph applied to its surface. When the heart's impulse is moderate, and the tension of the arterial system fully developed, the undulations in the descending line of the pulse are only slightly perceptible; but when the heart's impulse is more rapid, and the arterial tension diminished, the undulations become more marked. Marey found that he could procure upon his own person traces of different form, in this respect, by simply increasing the temperature of the body by the addition of warmer clothing. The following (Figs. 96, 97, 98), are three traces of the radial

Fig. 96.

Fig. 97

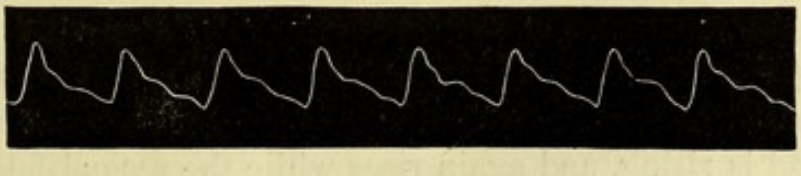
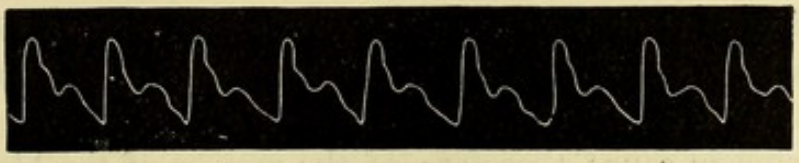


Fig. 98.



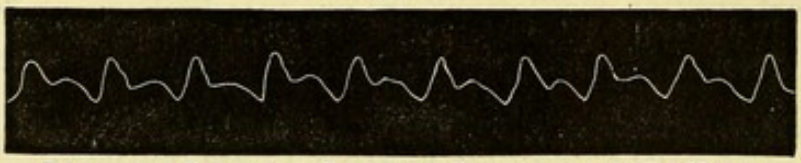
VARIATIONS OF THE RADIAL PULSE, under the influence of increased temperature; after Marey.

[1] Marey. Physiologie médicale de la circulation du sang. Paris, 1863, p. 266.

pulse obtained in this way, by increasing the quantity of clothing at intervals of twenty minutes.

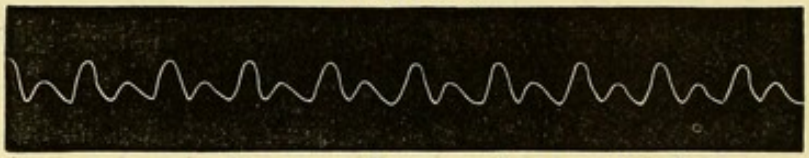
In certain diseased conditions, accompanied by rapid pulsation of the heart with greatly diminished arterial tension, the rebound or oscillation of the artery becomes so marked, in proportion to the original impulse, that it is easily perceived by the finger, and thus the pulse is apparently reduplicated; that is, there are two pulsations of the artery for each contraction of the heart, viz.: one due to the original impulse, and another due to the oscillation of the blood in the feebly distended artery. This is the *dicrotic* pulse which is often present in diseases of a typhoid character.

Fig. 99.



Dicrotic Pulse of Typhoid Pneumonia; after Marey.

Fig. 100.



Dicrotic Pulse of Typhoid Fever; after Marey.

It is evident that the dicrotic character of the pulse is not, in reality, peculiar to diseased conditions, since the sphygmograph shows that it exists more or less perfectly in a state of health; only it is usually too slight in degree to be appreciated by the finger.

Koschlakoff[1] has also succeeded in verifying the results obtained from the sphygmograph, and in demonstrating the mechanism of the dicrotic pulse. He shows that if a liquid be driven by a rapid impulse through an elastic tube, which is connected with two pressure gauges, one near the point of entrance of the liquid, the other near its point of exit, the liquid will rise in the first gauge before the increased pressure reaches the second; that it then falls, while the second is rising, and again rises while the second falls; showing an alternate increase and diminution of pressure in the two extremities of the elastic tube. This alternation continues until the pressure is equalized throughout, or until the tube is again distended by a new impulse.

The primary cause, therefore, of the motion of the blood in the

[1] In *Lorain*, Etudes de Médecine clinique. Paris, 1870, page 75.

arteries is the contraction of the heart, which, by driving out the blood in interrupted impulses, distends at every stroke the whole arterial system. But the arterial pulse is not exactly synchronous everywhere with the beat of the heart; since a certain amount of time is required to propagate the blood-wave from the centre of the circulation outward. The pulse of the radial artery at the wrist is perceptibly later than that of the heart; and the pulse of the posterior tibial at the ankle, again, perceptibly later than that at the wrist. The arterial circulation, accordingly, is not an entirely simple phenomenon; but is made up of the combined effects of two different physical forces. It is due, in the first place, to the intermittent action of the heart, by which the blood is driven in successive impulses from within outward; and, secondly, to the elasticity of the entire arterial system, by which it is subjected to an unceasing pressure, during the relaxation as well as during the contraction of the heart.

The passage of the blood through the arterial system takes place, accordingly, everywhere under a certain degree of pressure. For these vessels being everywhere elastic, and filled with blood, they constantly tend to react, more or less vigorously, and to compress the circulating fluid which they contain. If any one of the arteries, accordingly, be opened in the living animal, and a glass tube inserted, the blood will immediately be seen to rise in the tube to a height of about five and a half or six feet, and will remain at or about that level; thus indicating the pressure to which it was subjected in the interior of the vessels. The pressure, which is thus due to the reaction of the entire arterial system, is known as the *arterial pressure.*

The degree of arterial pressure may be easily measured by connecting the open artery, by a flexible tube, with a small reservoir of mercury, which is provided with a narrow upright glass tube, open at its upper extremity. When the blood, therefore, urged by the reaction of the arterial walls, presses upon the surface of the mercury in the receiver, the mercury rises in the upright tube, to a corresponding height. By the use of this instrument it is seen, in the first place, that the arterial pressure is nearly the same all over the body. Since the cavity of the arterial system is everywhere continuous, the pressure must necessarily be communicated, by the blood in its interior, equally in all directions. Accordingly, the constant pressure is the same, or nearly so, in the larger and the smaller arteries, in those nearest the heart, and those at a distance.

This constant pressure averages, in the higher quadrupeds, six inches of mercury, which is equivalent to from five and a half to six feet of blood.

It is also seen, however, in employing such an instrument, that the level of the mercury, in the upright tube, is not perfectly steady, but rises and falls with the pulsations of the heart. Thus, at every contraction of the ventricle, the mercury rises for about half an inch, and at every relaxation it falls to its previous level. Thus the instrument becomes a measure, not only for the constant pressure of the arteries, but also for the intermitting pressure of the heart; and on that account it has received the name of the *cardiometer*. It is seen, accordingly, that each contraction of the heart is superior in force to the reaction of the arteries by about one-twelfth; and these vessels are kept filled by a succession of cardiac pulsations, and discharge their contents in turn into the capillaries, by their own elastic reaction.

The *rapidity* with which the blood circulates through the arterial system is very great. Its velocity is greatest in the immediate neighborhood of the heart, and diminishes somewhat as the blood recedes farther and farther from the centre of the circulation. This diminution in the rapidity of the arterial current is due to the successive division of the aorta and its primary branches into smaller and smaller ramifications, by which the total calibre of the arterial system, as we have already mentioned, is somewhat increased. The blood, therefore, flowing through a larger space as it passes outward, necessarily moves more slowly. At the same time the increased extent of the arterial parietes with which the blood comes in contact, as well as the mechanical obstacle arising from the division of the vessels and the separation of the streams, undoubtedly contributes more or less to retard the currents. The mechanical obstacle, however, arising from the friction of the blood against the walls of the vessels, which would be very serious in the case of water or any similar fluid flowing through glass or metallic tubes, has comparatively little effect on the rapidity of the arterial circulation. This can readily be seen by microscopic examination of any transparent and vascular tissue. The internal surface of the arteries is so smooth and yielding, and the consistency of the circulating fluid so accurately adapted to that of the vessels which contain it, that the retarding effects of friction are reduced to a minimum, and the blood in flowing through the vessels meets with the least possible resistance.

Fig. 101.

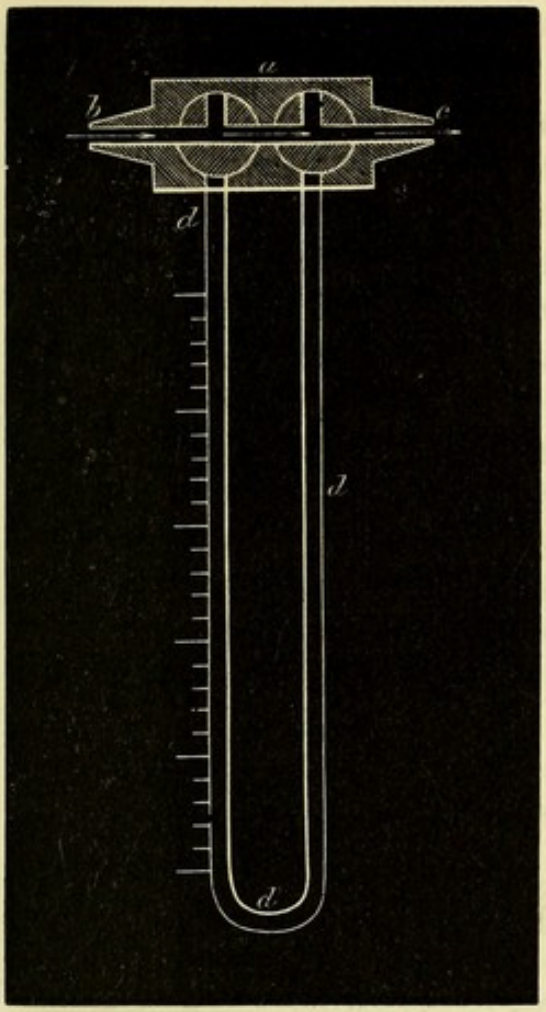
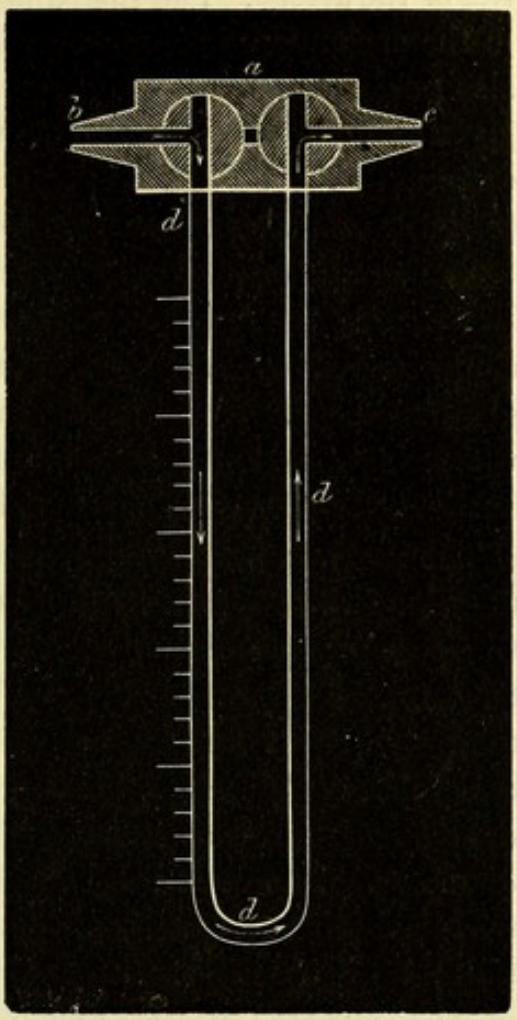


Fig. 102.



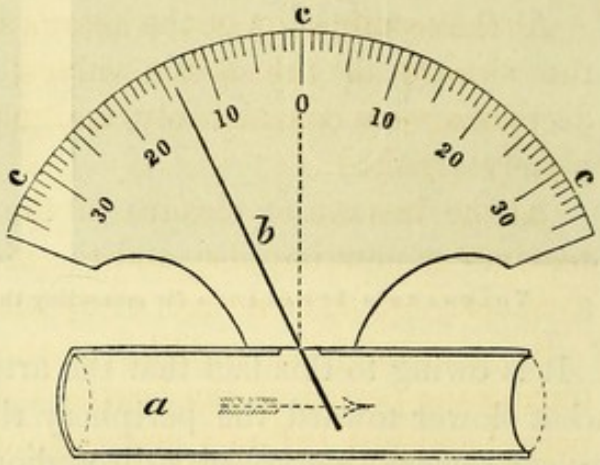
VOLKMANN'S APPARATUS for measuring the rapidity of the arterial circulation.

It is owing to this fact that the arterial circulation, though somewhat slower toward the periphery than near the heart, yet retains a very remarkable velocity throughout; and even in arteries of the minutest size it is so rapid that the shape of the blood-globules cannot be distinguished in it on microscopic examination, but only a mingled current shooting forward with increased velocity at every cardiac pulsation. Volkmann, in Germany, has determined, by a very ingenious contrivance, the velocity of the current of blood in some of the large sized arteries in dogs, horses, and calves. The instrument which he employed (Fig. 101) consisted of a metallic cylinder (*a*), with a perforation running from end to end, and corresponding in size with the artery to be examined. The artery was divided transversely, and its cardiac extremity fastened to the upper end (*b*) of the instrument, while its peripheral extremity was fastened in the same manner to the lower end (*c*). The blood accordingly still kept on its usual course; cnly passing for a short

distance through the artificial tube (*a*), between the divided extremities of the artery. The instrument, however, was provided, as shown in the accompanying figures, with two transverse cylindrical plugs, also perforated; and arranged in such a manner, that when, at a given signal, the two plugs were suddenly turned in opposite directions, the stream of blood would be turned out of its course (Fig. 102), and made to traverse a long bent tube of glass (*d*, *d*, *d*), before again finding its way back to the lower portion of the artery. In this way the distance passed over by the blood in a given time could be readily measured upon a scale attached to the side of the glass tube. Volkmann found, as the average result of his observations, that the blood moves in the carotid arteries of warm-blooded quadrupeds with a velocity of 12 inches per second.

The most exact experiments on the velocity and movement of the blood in the larger arteries and their branches, are those of Chauveau.[1] He experimented by introducing into the carotid artery of the horse a brass tube with thin walls, about two inches long and a little over one-third of an inch in diameter. The tube was introduced through a longitudinal incision in the walls of the exposed vessel, and secured in position by a ligature near each extremity, so that the arterial current would then pass, without any perceptible obstruction, through the tube forming, for the time, a part of the arterial walls. In the side of the tube was a small opening, one eighth of an inch long by one sixteenth of an inch wide, which was closed by a thin membrane properly secured so as to prevent the escape of the blood. Through the centre of the elastic membrane there was passed a very light metallic needle, the inner extremity of which, somewhat flattened in shape, projected into the interior of the vessel, and received the impulse of the ar-

Fig. 103.



CHAUVEAU'S INSTRUMENT, for measuring the rapidity of the arterial current.—*a*. Brass tube, introduced into the calibre of the artery.—*b*. Index-needle passing through the elastic membrane in the side of the brass tube, and moving by the impulse of the blood-current.—*c* Graduated scale, for measuring the extent of the oscillations of the needle.

[1] Journal de la Physiologie, Paris, October 1860, p. 695.

terial blood; while the outer portion, prolonged into a slender index, marked upon a semicircular graduated scale the oscillations of the movable inner extremity, and consequently the varying rapidity of the arterial current.

The actual velocity, indicated by any given oscillation of the needle, was ascertained beforehand by attaching the apparatus to an elastic tube and passing through it a stream of warm water of known rapidity. The deviation of the needle under these circumstances being noted, it becomes afterward an exact register for the velocity of the blood in the arterial circulation.

Chauveau found, as the result of these experiments, that the details of the circulatory movement differ somewhat in the larger arteries near the heart, and in the smaller branches farther removed.

a. In the carotid artery, at the instant of the systole of the heart, the blood is suddenly put in motion with a comparatively high degree of rapidity, amounting on the average to 20 inches per second.

At the termination of the heart's systole, and immediately before the closure of the aortic valves, the movement of the blood decreases very considerably, and may even, for the time, be completely arrested.

At the instant of closure of the aortic valves, the circulation receives a new impulse, and the blood again moves forward with a velocity, on the average, of 8½ inches per second.

Subsequently the rapidity of the current diminishes gradually during the period of the heart's inaction, until, at the end of this period and just before a new systole, it is reduced, on the average, to a little less than 6 inches per second.

b. In the smaller arterial branches, such as the facial, the movement of the arterial current is more uniform than the above. It is considerably less rapid at the moment of the heart's systole; and on the other hand, it is always comparatively more active during the period of ventricular repose.

The secondary impulse, following the closure of the aortic valves, is much less perceptible than in the larger arteries, and may even be altogether absent.

VENOUS CIRCULATION.

The veins, which collect the blood from the tissues and return it to the heart, are composed, like the arteries, of three coats; an inner, middle, and exterior. In structure, they differ from the arteries in containing a much smaller quantity of muscular and elastic fibres, and a larger proportion of simple condensed areolar tissue. They are consequently more flaccid and compressible than the arteries, and less elastic and contractile. They are furthermore distinguished, throughout the limbs, neck, and external portions of the head and trunk, by being provided with valves, consisting of fibrous sheets arranged in the form of festoons, and so placed in the cavity of the vein as to allow the blood to pass readily from the periphery toward the heart, while they prevent altogether its reflux in an opposite direction.

Although the veins are provided with walls which are very much thinner and less elastic than those of the arteries, yet, contrary to what we might expect, their capacity for *resistance to pressure* is equal, or even superior, to that of the arterial tubes. Milne Edwards has collected the results of various experiments, which show that the veins will sometimes resist a pressure which is sufficient to rupture the walls of the arteries.[1] In one instance the jugular vein supported, without breaking, a pressure equal to a column of water 148 feet in height; and in another, the iliac vein of a sheep resisted a pressure of more than four atmospheres. The portal vein was found capable of resisting a pressure of six atmospheres; and in one case, in which the aorta of a sheep was ruptured by a pressure of 158 pounds, the vena cava of the same animal supported a pressure equal to 176 pounds.

This resistance of the veins is to be attributed to the large proportion of white fibrous tissue which enters into their composition; the same tissue which forms nearly the whole of the tendons and fasciæ, and which is distinguished by its density and unyielding nature.

The *elasticity* of the veins, however, is much less than that of the arteries. When they are filled with blood, they enlarge to a certain size, and collapse again when the pressure is taken off; but they do not react by virtue of an elastic resilience, or, at least, only to a slight extent, as compared with the arteries. Accordingly, when

[1] Leçons sur la Physiologie, &c., vol. iv. p. 301.

the arteries are cut across, and emptied of blood, they still remain open and pervious, retaining the tubular form, on account of the elasticity of their walls; while, if the veins be treated in the same way, their sides simply fall together and remain in contact with each other.

Another peculiarity of the venous system is the *abundance of the separate channels*, which it affords, for the flow of blood from the periphery towards the centre. The arteries pass directly from the heart outward, each separate branch, as a general rule, going to a separate region, and supplying that part of the body with all the blood which it requires; so that the arterial system is kept constantly filled to its entire capacity with the blood which passes through it. But that is not the case with the veins. In injected preparations of the vascular system, we have often two, three, four, or even five veins, coming together from the same region of the body. There are also abundant inosculations between the different veins. The deep veins which accompany the brachial artery inosculate freely with each other, and also with the superficial veins of the arm. In the veins coming from the head, we have the external jugular communicating with the thyroid veins, the anterior jugular, and the brachial veins. The external and internal jugulars communicate with each other, and the two thyroid veins also form an abundant plexus in front of the trachea.

Thus the blood, coming from the extremities toward the heart, flows, not in a single channel, but in many channels; and as these channels communicate freely with each other, the blood passes sometimes through one of them, and sometimes through another.

The flow of blood through the veins is less powerful and regular than that through the arteries. It depends on the combined action of three different forces.

1. *The force of aspiration of the thorax.*—When the chest expands by the lifting of the ribs and the descent of the diaphragm, its movement, of course, tends to diminish the pressure exerted upon its contents, and so has the effect of drawing into the thoracic cavity all the fluids which can gain access to it. The expanded cavity is principally filled by the air, which passes in through the trachea and fills the bronchial tubes and the pulmonary vesicles. But the blood in the veins is also drawn into the chest at the same time and by the same force. This force of aspiration, exerted by the expansion of the chest, is gentle and uniform in character, like the movements of respiration themselves. Accordingly its influence is ex-

tended, without doubt, to the farthest extremities of the venous system, the blood being gently solicited toward the heart, at each expansion of the chest, without any visible alteration in the size of the veins, which are filled up from behind as fast as they are emptied in front.

But if the movement of inspiration be sudden and violent, instead of gentle and easy, a different effect is produced. For then the walls of the veins, which are thin and flaccid, cannot retain their position, but collapse under the external pressure too rapidly to allow the blood to flow in from behind. In this case, therefore, the vein is simply emptied in the immediate neighborhood of the chest, but the entire venous circulation is not assisted by the movement.

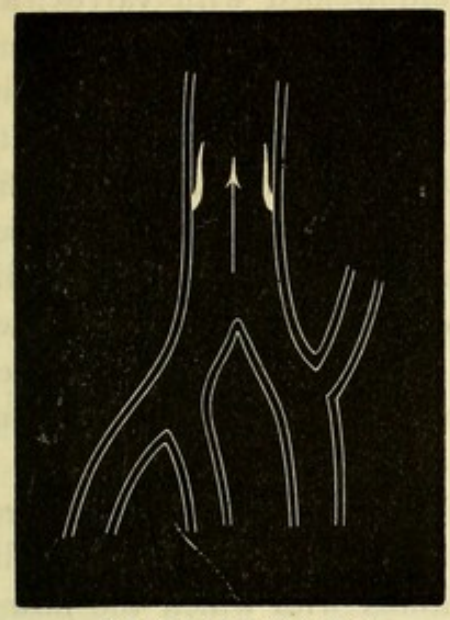
The same difference in the effect of an easy and a violent suction movement, may be readily shown by attaching to the nozzle of an air-tight syringe a flexible elastic tube with thin walls, and placing the other extremity of the tube under water. If the piston of the syringe be now withdrawn with a gentle and gradual motion, the water will be readily drawn up into the tube, while the tube itself suffers no visible change; but if the suction movement be made rapid and violent, the tube will collapse instantly under the pressure of the air, and will fail to draw the water into its cavity.

A similar effect shows itself in the living body. If the jugular or subclavian vein be exposed in a dog or cat, it will be seen that while the movements of respiration are natural and easy no fluctuation in the vein can be perceived. But as soon as the respiration becomes disturbed and laborious, then at each inspiration the vein is collapsed and emptied; while during expiration, the chest being strongly compressed and the inward flow of the blood arrested, the vein becomes turgid with blood which accumulates in it from behind. In young children, also, the spasmodic movements of respiration in crying produce a similar turgescence and engorgement of the large veins during expiration, while they are momentarily emptied during the hurried and forcible inspiration.

In natural and quiet respiration, therefore, the movements of the chest hasten and assist the venous circulation; but in forced or laborious respiration, they do not assist and may even retard its flow.

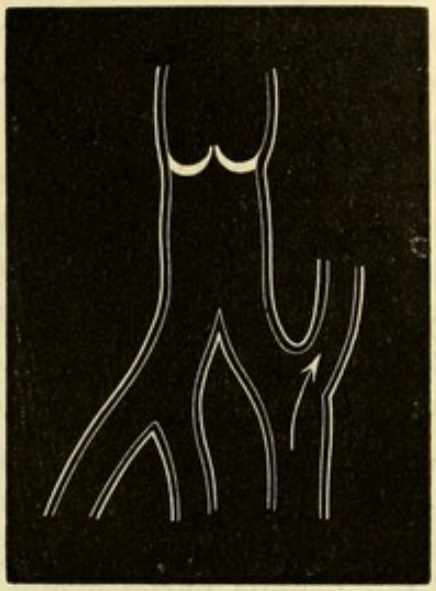
2. *The contraction of the voluntary muscles.*—The veins which convey the blood through the limbs, and the parietes of the head and trunk, lie among voluntary muscles, which are more or less constantly in a state of alternate contraction and relaxation. At every contraction these muscles become swollen laterally, and, of course, compress the veins which are situated between them. The

Fig. 104.



Vein with valves open.

Fig. 105.



Vein with valves closed; stream of blood passing off by a lateral channel.

blood, driven out from the vein by this pressure, cannot regurgitate toward the capillaries, owing to the valves, already described, which shut back and prevent its reflux. It is accordingly forced onward toward the heart; and when the muscle relaxes and the vein is liberated from pressure, it again fills up from behind, and the circulation goes on as before. This force is a very efficient one in producing the venous circulation; since the voluntary muscles are more or less active in every position of the body, and the veins constantly liable to be compressed by them. It is on this account that the veins, in the external parts of the body, communicate so freely with each other by transverse branches; in order that the current of blood, which is momentarily excluded from one vein by the pressure of the muscles, may readily find a passage through others, which communicate by cross branches with the first. (Figs. 104 and 105.)

3. *The force of the capillary circulation.*—This last cause of the motion of the blood through the veins is the most important of all, as it is the only one which is constantly and universally active. In fish, for example, respiration is performed altogether by gills; and in reptiles the air is forced down into the lungs by a kind of deglutition, instead of being drawn in by the expansion of the chest. In neither of these classes, therefore, can the movements of respiration assist mechanically in the circulation of the blood. In the splanchnic cavities, again, of all the vertebrate animals, the veins coming

from the internal organs, as, for example, the cerebral, pulmonary, portal, hepatic, and renal veins, are unprovided with valves; and the passage of the blood through them cannot therefore be effected by any lateral pressure. The circulation, however, constantly going on in the capillaries, everywhere tends to crowd the radicles of the veins with blood; and this *vis a tergo*, or pressure from behind, fills the whole venous system by a constant and steady accumulation. So long, therefore, as the veins are relieved of blood at their cardiac extremity by the regular pulsations of the heart, there is no backward pressure to oppose the impulse derived from the capillary circulation; and the movement of the blood through the veins continues in a steady and uniform course.

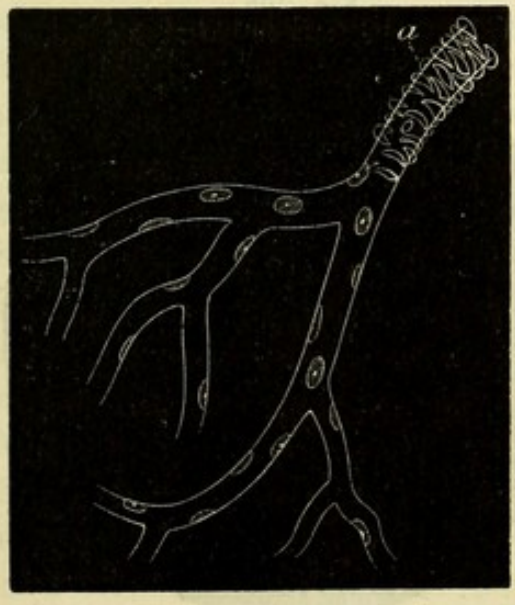
With regard to the *rapidity of the venous circulation*, no direct results have been obtained by experiment. Owing to the flaccidity of the venous parietes, and the readiness with which the flow of blood through them is disturbed, it is not possible to determine this point for the veins, in the same manner as it has been determined for the arteries. The only calculation which has been made in this respect is based upon a comparison of the total capacity of the arterial and venous systems. As the same blood which passes outward through the arteries, passes inward again through the veins, the rapidity of its flow in each must be in inverse proportion to the capacity of the two sets of vessels. That is to say, a quantity of blood which would pass in a given time, with a velocity of x, through an opening equal to one square inch, would pass during the same time through an opening equal to two square inches, with a velocity of $\frac{x}{2}$; and would require, on the other hand, a velocity of $2\ x$, to pass in the same time through an opening equal to one-half a square inch. Now the capacity of the entire venous system, when distended by injection, is about twice as great as that of the entire arterial system. During life, however, the venous system is at no time so completely filled with blood as is the case with the arteries, and, making allowance for this difference, we find that the entire quantity of venous blood is to the entire quantity of arterial blood nearly as three to two. The velocity of the venous blood, as compared with that of the arterial, is therefore as two to three; or about 8 inches per second. It will be understood, however, that this calculation is altogether approximative, and not exact; since the venous current varies, according to many different circumstances, in different parts of the body; being slower near the capillaries, and more rapid near the heart. It expresses, however, with suffi-

cient accuracy, the relative velocity of the arterial and venous currents, at corresponding parts of their course.

THE CAPILLARY CIRCULATION.

The capillary bloodvessels are minute inosculating tubes, which permeate the vascular organs in every direction, and bring the blood into intimate contact with the substance of the tissues. They are continuous with the terminal ramifications of the arteries on the one hand, and with the commencing rootlets of the veins on the other. They vary somewhat in size in different organs, and in different species of animals; their average diameter in the human subject being a little over $\frac{1}{3000}$ of an inch. They are composed of a single, transparent, homogeneous, somewhat elastic, tubular membrane, which is provided at various intervals with flattened, oval nuclei. As the smaller arteries approach the capillaries, they diminish constantly in size by successive subdivision, and lose first their external or fibrous tunic. They are then composed only of the internal or homogeneous coat, and the middle or muscular. (Fig. 106, *a*.) The middle coat then diminishes in thickness, until it is reduced to a single layer of circular, fusiform, unstriped, muscular fibres, which in their turn disappear altogether, as the artery merges at last in the capillaries; leaving only, as we have already mentioned, a simple, homogeneous, nucleated, tubular membrane, which is continuous with the internal arterial tunic.

Fig. 106.

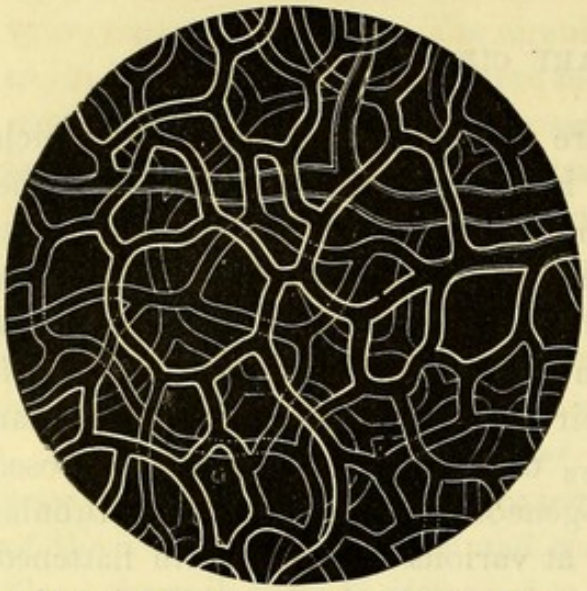


SMALL ARTERY, with its muscular tunic (*a*), breaking up into capillaries. From the *pia mater*.

The capillaries are further distinguished from both arteries and veins by their frequent inosculation. The arteries constantly divide and subdivide, as they pass from within outward; while the veins as constantly unite with each other to form larger and less numerous branches and trunks, as they pass from the circumference toward the centre. But the capillaries simply inosculate with each other in every direction, in such a manner as to form an interlacing network or plexus, the *capillary plexus* (Fig.

107), which is exceedingly rich and abundant in some organs, less so in others. The spaces included between the meshes of the capillary network vary also, in shape as well as in size, in different parts of the body. In the muscular tissue they form long parallelograms; in the areolar tissue, irregular shapeless figures, corresponding with the direction of the fibrous bundles of which the tissue is composed. In the mucous membrane of the large intestine, the capillaries include hexagonal or nearly circular spaces, enclosing the orifices of the follicles. In the papillæ of the tongue and of the skin, and in the tufts of the placenta, they are arranged in long spiral loops, and in the adipose tissue in wide meshes, among which the fat vesicles are entangled.

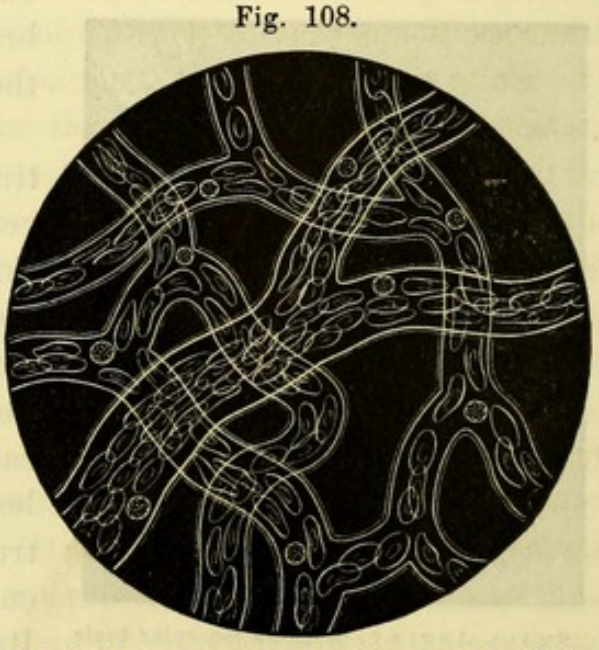
Fig. 107.



CAPILLARY NETWORK from web of frog's foot.

The *motion of the blood in the capillaries* may be studied by examining under the microscope any transparent tissue, of a sufficient degree of vascularity. One of the most convenient parts for this purpose is the web of the frog's foot. When properly prepared and kept moistened by the occasional addition of water to the integument, the circulation will go on in its vessels for an indefinite length of time. The blood can be seen entering the field by the smaller arteries, shooting through them with great rapidity and in successive impulses, and flowing off again by the veins at a somewhat slow rate. In the capillaries themselves the circulation is considerably less rapid than in either the arteries

Fig. 108.



CAPILLARY CIRCULATION in web of frog's foot.

or the veins. It is also perfectly steady and uninterrupted in its flow. The blood passes along in a uniform and continuous current, without any apparent contraction or dilatation of the vessels, very much as if it were flowing through glass tubes. Another very remarkable peculiarity of the capillary circulation is that it has no definite direction. The numerous streams of which it is composed (Fig. 108) do not tend to the right or to the left, nor toward any one particular point. On the contrary, they pass above and below each other, at right angles to each other's course, or even in opposite directions; so that the blood, while in the capillaries, merely circulates promiscuously among the tissues, in such a manner as to come intimately in contact with every part of their substance.

The motion of the white and red globules in the circulating blood is also peculiar, and shows very distinctly the difference in their consistency and other physical properties. In the larger vessels the red globules are carried along in a dense column, in the central part of the stream; while near the edges of the vessel there is a transparent space occupied only by the clear plasma of the blood, in which no red globules are to be seen. In the smaller vessels the globules pass along in a narrower column, two by two, or following each other in single file. The flexibility and semi-fluid consistency of these globules are here very apparent, from the readiness with which they become folded up, bent or twisted in turning corners, and the ease with which they glide through minute branches of communication, smaller in diameter than themselves. The white globules, on the other hand, flow more slowly and with greater difficulty through the vessels. They drag along the exter nal portions of the current, and are sometimes momentarily arrested; apparently adhering for a few seconds to the internal surface of the vessel. Whenever the current is obstructed or retarded in any manner, the white globules accumulate in the affected portion, and become more numerous there in proportion to the red.

It is during the capillary circulation that the blood serves for the nutrition of the vascular organs. Its fluid portions slowly transude through the walls of the vessels, and are absorbed by the tissues in such proportion as is requisite for their nourishment. The saline substances enter at once into the composition of the surrounding parts, generally without undergoing any change. The phosphate of lime, for example, is taken up in large quantity by the bones and cartilages, and in smaller quantity by the softer parts;

while the chlorides of sodium and potassium, the carbonates, sulphates, &c., are appropriated in special proportions by the different tissues, according to the quantity necessary for their organization. The albuminous ingredients of the blood, on the other hand, are not only absorbed in a similar manner by the animal tissues, but at the same time are transformed by catalysis, and converted into new materials, characteristic of the different tissues. In this way are produced the musculine of the muscles, the osteine of the bones, the cartilagine of the cartilages, &c. &c. It is probable that this transformation does not take place in the interior of the vessels themselves; but that the organic ingredients of the blood are absorbed by the tissues, and at the same moment converted into new materials, by contact with their substance. The blood in this way furnishes, directly or indirectly, all the materials necessary for the nutrition of the body.

The physical conditions which influence the movement of the blood in the capillaries, are somewhat different from those which regulate the arterial and venous circulations. We must remember that, as the arteries pass from the heart outward, they subdivide and ramify to such an extent that the surface of the arterial walls is very much increased in proportion to the quantity of blood which they contain. It is on this account that the arterial pulsation is so much equalized at a distance from the heart, since the influence of the elasticity of the arterial coats is thus constantly increased from within outward. But as these vessels finally reach the confines of the arterial system, having already been very much increased in number and diminished in size, they suddenly break up into a terminal ramification of still smaller and more numerous vessels, and so lose themselves at last in the capillary network.

By this final increase of the vascular surface, the equalization of the heart's action is completed. There is no longer any intermitting or pulsatile character in the force which acts upon the circulating fluid; and the blood, as it is delivered from the arteries, moves through the capillary vessels under a perfectly continuous and uniform pressure.

This pressure is sufficient to cause the blood to pass with considerable rapidity, through the capillary plexus, into the commencement of the veins. This fact was first demonstrated by Prof. Sharpey,[1] of London, who employed an injecting syringe with a

[1] Todd and Bowmann, Physiological Anatomy and Physiology of man, vol. ii. p. 350.

double nozzle, one extremity of which was connected with a mercurial gauge, while the other was inserted into the artery of a recently killed animal. When the syringe, filled with defibrinated blood, was fixed in this position and the vessels of the animal injected, the defibrinated blood would press with equal force upon the mercury in the gauge and upon the fluid in the bloodvessels; and thus it was easy to ascertain the exact amount of pressure required to force the defibrinated blood through the capillaries of the animal, and to make it return by the corresponding vein. In this way Prof. Sharpey found that when the free end of the injecting tube was attached to the mesenteric artery of the dog, a pressure of 90 millimetres of mercury caused the blood to pass through the capillaries of the intestine and of the liver; and that under a pressure of 130 millimetres, it flowed in a full stream from the divided extremity of the vena cava.

We have also performed a similar experiment on the vessels of the lower extremity. A full grown healthy dog was killed, and the lower extremity immediately injected with defibrinated blood, by the femoral artery, in order to prevent coagulation in the smaller vessels. A syringe with a double flexible nozzle was then filled with defibrinated blood, and one extremity of its injecting tube attached to the femoral artery, the other to the mouthpiece of a cardiometer. By making the injection, it was then found that the defibrinated blood ran from the femoral vein in a continuous stream under a pressure of 120 millimetres, and that it was discharged very freely under a pressure of 130 millimetres.

Since, as we have already seen, the arterial pressure upon the blood is equal to six inches, or 150 millimetres, of mercury, it is evident that this pressure is sufficient to propel the blood through the capillary circulation.

Beside, the blood is not altogether relieved from the influence of elasticity, after it has left the arteries. For the capillaries themselves are elastic, notwithstanding the delicate texture of their walls; and even the tissues of the organs which they traverse possess, in many instances, a considerable share of elasticity, owing to the minute elastic fibres which are scattered through their substance. These elastic fibres are found in considerable quantity in the lungs, the spleen, the skin, the lobulated glands, and more or less in the mucous membranes. They are abundant, of course, in the fibrous tissues of the extremities, in the fasciæ, the tendons, and the intermuscular substance.

In the experiment of injecting the vessels of the lower extremity with defibrinated blood, if the injection be stopped, the blood does not instantly cease flowing from the extremity of the femoral vein, but continues for a short time, until the elasticity of the intervening parts is exhausted.

The same thing may be observed even in the liver. If the end of a water-pipe be inserted into the portal vein, and the liver injected with water under the pressure of a hydrant, the liquid will distend the vessels of the organ, and pass out by the hepatic veins. But if the portal vein be suddenly tied or compressed, so as to shut off the pressure from behind, the stream will continue to run, for several seconds afterward, from the hepatic vein, owing to the reaction of the organ itself upon the fluid contained in its vessels.

As a general rule, also, the capillaries do not suffer any backward pressure from the venous system. On the contrary, as soon as the blood has been delivered into the veins, it is hurried onward toward the heart by the compression of the muscles and the action of the venous valves. The right side of the heart itself continues the same process, by its regular contractions, and by the action of its own valvular apparatus; so that the blood is constantly lifted away from the capillaries, by the muscular action of the surrounding parts.

These are the most important of the mechanical influences under which the blood moves through the continuous round of the circulation. The heart, by its alternating contractions and relaxations, and by the backward play of its valves, continually urges the blood forward into the arterial system. The arteries, by their dilatable and elastic walls, convert the cardiac pulsations into a uniform and steady pressure. Under this pressure, the blood passes through the capillary vessels; and it is then carried backward to the heart through the veins, assisted by the action of the muscles and the respiratory movements of the chest.

The *rapidity* of the circulation in the capillary vessels is much less than in the arteries or the veins. It may be measured, with a tolerable approach to accuracy, during the microscopic examination of transparent and vascular tissues, as, for example, the web of the frog's foot, or the mesentery of the rat. The results obtained in this way by different observers (Valentine, Weber, Volkmann, &c.) show that the rate of movement of the blood through the capillaries is rather less than one-thirtieth of an inch per second; or not quite two inches per minute. Since the rapidity of the current, as we have mentioned above, must be in inverse ratio to the entire

calibre of the vessels through which it moves, it follows that the united calibre of all the capillaries of the body must be from 350 to 400 times greater than that of the arteries. It must not be supposed from this, however, that the whole quantity of blood contained in the capillaries at any one time is so much greater than that in the arteries; since, although the united *calibre* of the capillaries is very large, their *length* is very small. The effect of the anatomical structure of the capillary system is, therefore, to disseminate a comparatively small quantity of blood over a very large space, so that the chemico-physiological reactions, necessary to nutrition, may take place with promptitude and energy. For the same reason, although the rate of movement of the blood in these vessels is very slow, yet as the distance to be passed over between the arteries and veins is very small, the blood requires but a short time to traverse the capillary system, and to commence its returning passage by the veins.

GENERAL RAPIDITY OF THE CIRCULATION.

The rapidity with which the blood passes through the *entire round of the circulation* is a point of great interest, and one which has received a considerable share of attention. The results of such experiments, as have been tried, show that this rapidity is much greater than would have been anticipated. Hering, Poisseuille, and Matteucci,[1] have all experimented on this subject in the following manner. A solution of ferrocyanide of potassium was injected into the right jugular vein of a horse, at the same time that a ligature was placed upon the corresponding vein on the left side, and an opening made in it above the ligature. The blood flowing from the left jugular vein was then received in separate vessels, which were changed every five seconds, and the contents afterward examined. It was thus found that the blood drawn from the first to the twentieth second contained no traces of the ferrocyanide; but that which escaped from the vein at the end of from twenty to twenty-five seconds, showed unmistakable evidence of the presence of the foreign salt. The ferrocyanide of potassium must, therefore, during this time, have passed from the point of injection to the right side of the heart, thence to the lungs and through the pulmonary circulation, returned to the heart, passed out again through the arteries to the capillary system of the head and neck, and

[1] Physical Phenomena of Living Beings, Pereira's translation, Philada. ed., 1848, p. 317.

thence have commenced its returning passage to the right side of the heart, through the jugular vein.

By extending these investigations to different animals, it was found that the duration of the circulatory movement varied, to some extent, with the size and species. In the larger quadrupeds, as a general rule, it was longer; in the smaller, the time required was less.

In the Horse,[1]	the	mean	duration	was	28	seconds.
" Dog	"	"	"	"	15	"
" Goat	"	"	"	"	13	"
" Fox	"	"	"	"	12½	"
" Rabbit	"	"	"	"	7	"

When these results were first published, it was thought to be doubtful whether the circulation were really as rapid as they would make it appear. It was thought that the saline matter which was injected, "travelled faster than the blood;" that it became "diffused" through the circulating fluid; that it transuded through dividing membranes; or passed round to the point at which it was detected, by some short and irregular route.

But none of these explanations have ever been found to be correct. They are all really more improbable than the fact which they are intended to explain. The physical diffusion of liquids does not take place with such rapidity as that manifested by the circulation; and there is no other route so likely to give passage to the injected fluid, as the bloodvessels and the movement of the blood itself. Beside, the first experiments of Poisseuille and others have not been since invalidated, in any essential particular. It was found, it is true, that certain other substances, injected at the same time with the saline matter, might hasten or retard the circulation to a certain degree. But these variations were not very marked, and never exceeded the limits of from eighteen to forty-five seconds. There is no doubt that the blood itself makes the same circuit in very nearly the same interval of time.

The truth is, however, that we cannot fix upon any absolutely uniform rate which shall express the time required by the entire blood to pass the round of the whole vascular system, and return to a given point. The circulation of the blood, far from being a simple phenomenon, like a current of water through a circular tube, is, on the contrary, extremely complicated in all its anatomical and physiological conditions; and it differs in rapidity, as well as in its

[1] In Milne Edwards, Leçons sur la Physiologie, &c., vol. iv. p. 364.

physical and chemical phenomena, in different parts of the circulatory apparatus. We have already seen how much the form of the capillary plexus varies in different organs. In some the vascular network is close, in others comparatively open. In some its meshes are circular in shape, in others polygonal, in others rectangular. In some the vessels are arranged in twisted loops, in others they communicate by irregular but abundant inosculations. The mere distance from the heart at which an organ is situated must modify to some extent the time required for its blood to return again to the centre of the circulation. The blood which passes through the coronary arteries and the capillaries of the heart, for example, must be returned to the right auricle in a comparatively short time; while that which is carried by the carotids into the capillary system of the head and neck, to return by the jugulars, will require a longer interval. That, again, which descends by the abdominal aorta and its divisions to the lower extremities, and which, after circulating through the tissues of the leg and foot, mounts upward through the whole course of the saphena, femoral, iliac, and abdominal veins, must be still longer on its way; while that which circulates through the abdominal digestive organs and is then collected by the portal system, to be again dispersed through the glandular tissue of the liver, requires undoubtedly a longer period still to perform its double capillary circulation. The blood, therefore, arrives at the right side of the heart, from different parts of the body, at successive intervals; and may pass several times through the capillaries of the heart while performing a single circulation through a more distant organ.

LOCAL VARIATIONS IN THE CAPILLARY CIRCULATION.

An important class of phenomena connected with this part of the subject consists of the *local variations* in the capillary circulation. These variations are often very marked, and show themselves in many different parts of the body. The pallor or suffusion of the face under mental emotion, the congestion of the mucous membranes during the digestive process, and the local and defined redness of the skin produced by any irritating application, are all instances of this sort. These changes are due to the contraction and dilatation of the more minute arterial branches which supply the part with blood, under the influence of nervous action. We have already seen that these smaller arteries are provided with organic muscular fibres; and that in their smallest branches, which immediately com-

municate with the capillaries, the middle coat is composed exclusively of such muscular fibres. These vessels, therefore, by their state of comparative contraction and dilatation, regulate, to a certain extent, the quantity of blood admitted to a part. When contracted, they resist more strongly the impulsive force of the arterial current, and the blood enters the capillaries in smaller quantity. When dilated, they allow a freer access to the capillaries and admit the blood in greater abundance.

The alterations in the calibre of the smaller arteries, and the consequent variations in the capillary circulation, are caused by different nervous influences, some of which are occasional and accidental, while others recur with a certain degree of regularity, as in the periodical excitement of the digestive organs.

These changes are most distinctly manifested in the periodical congestion of the glandular organs. We have already shown that all the glands and mucous membranes connected with the digestive apparatus are in a state of unusual vascular excitement while secretion and digestion are going on. This periodical congestion, which accompanies the functional activity of the organs, can readily be seen, in the living animal, in the pancreas, and in the mucous membranes of the stomach and small intestine; the tissues of these parts being visibly redder and more turgid during digestion and absorption than in the fasting condition.

A similar variation of the circulation has been more particularly studied by Bernard in the submaxillary gland of the dog. During the ordinary condition of glandular repose he found that it required sixty-five seconds to obtain five cubic centimetres of blood from the submaxillary vein; but, when the gland was excited to functional activity by galvanizing the tympanico-lingual nerve distributed to its tissue, the same quantity of blood was discharged by the vein in fifteen seconds.[1] Thus the quantity of blood passing through the organ in a given time was rather more than four times as great while the gland was in a state of active secretion, as while in a condition of repose.

This increased flow of blood in a secreting glandular organ is accompanied also by a remarkable change in its appearance. During repose the blood, which enters the submaxillary gland by the arteries of a bright red color, is changed in its tissue, as elsewhere, from arterial to venous, and passes out by the veins of a

[1] Leçons sur les Liquides de l'Organisme, Paris, 1859, vol. ii. p. 272.

dark purple color. But at the moment when the secretion of the gland is excited, either by galvanization of its nerve or by introducing a little vinegar into the mouth of the animal, the blood is not only discharged in larger quantity, but passes out red by the veins, so as hardly to be distinguished in color from arterial blood.[1] When the secretion of the gland is suspended, the blood in its vein again becomes dark-colored as before. The veins returning from the mucous membrane of the mouth have also been observed to become red during the active secretion of the buccal follicles, and to resume their venous color after its cessation. There is little doubt that the same thing is true of most, if not all, the secreting glands, and that the blood circulating in their capillaries is changed from red to blue only during the repose of the glandular organ; while at the time of active secretion it not only passes through the vessels in greater abundance, but retains its ruddy color even in the veins.

This is because, during the period of glandular repose, the blood performs in its tissues the usual functions of nutrition, supplying the materials for the glandular structure and also for the peculiar substance characteristic of its secretion, which is stored up in its follicles. It therefore undergoes the ordinary changes and becomes altered in color from arterial to venous. But the period of active discharge from the gland is simply a period of vascular congestion, when the blood passes in larger quantity, and its watery and saline ingredients exude into the secretory ducts, bringing with them at the same time the peculiar materials already accumulated in the intervals of repose. There is nothing in this process which should produce a change in the blood from arterial to venous, and it consequently passes into the veins with its color unaltered. In other words, the gland is alternately in two different conditions: first, a condition of repose, in which the small quantity of blood which it contains is entirely used for purposes of nutrition, and is completely changed from red to blue; and, secondly, a condition of activity, in which the blood in its vessels is suddenly increased to three or four times its previous quantity, this increased amount of blood being employed simply to supply the fluids of the secretion, and therefore passing through the vessels unchanged in color.

The blood in the renal veins is also of a ruddy hue, nearly identical with that of arterial blood. This fact, which we have often

[1] Bernard, op. cit., vol. i. chap. xiv.

verified, was also first noticed by Bernard.[1] The ruddy hue of the blood in the renal veins of the living animal is readily distinguished from the dark color of that in the vena cava inferior, or in the muscular veins of the neighborhood. The blood circulates through the kidneys for the double purpose of nourishing their tissue and of discharging the watery and excrementitious matters of the urine. But by far the larger proportion is employed in the latter process, and accordingly the greater part of the blood returns by the renal veins unaltered in color.

On the other hand, the venous blood coming from a muscle in a state of contraction is exceedingly dark-colored. The greater the activity of the muscular system, the deeper the color of the blood returning from the extremities. When the muscles are in a state of repose or complete relaxation, on the contrary, the change is much less marked. This has often been observed in cases of syncope, and in the relaxation produced by abundant bleeding, both in man and in the lower animals. As a general rule, the blood drawn from a vein is at first dark-colored; but as the hemorrhage goes on it grows lighter in color, and, if the bleeding be excessive, it may become nearly as bright as arterial blood.

The color of the venous blood, as we have already shown, depends on the disappearance of its oxygen and the presence of carbonic acid. These changes take place generally in the process of nutrition throughout the body, and in the muscles during contraction. In the lungs, on the other hand, the change is directly the reverse. Here the carbonic acid is discharged and oxygen is absorbed; and consequently the color of the blood changes from venous to arterial. In the kidneys, again, while the discharge of urine is going on with activity, and in the glands during secretion, the disappearance of oxygen and the production of carbonic acid are secondary in importance to other and more active changes; and the blood of these organs accordingly retains, in great measure, its arterial hue.

Both the physical and chemical phenomena, therefore, of the circulation vary at different times and in different organs. The actions of transformation and decomposition, of nutrition and secretion, of endosmosis and exosmosis, which go on simultaneously throughout the body, are yet extremely varied in their character, and produce a similar variation in the phenomena of the circula-

[1] Op. cit., vol. i. p. 257.

tion. In one organ the blood loses more fluid than it absorbs; in another it absorbs more than it loses. The venous blood, consequently, has a different composition as it returns from different organs. In the brain and spinal cord it gives up the ingredients necessary for the nutrition of the nervous matter, and absorbs cholesterine and other materials resulting from its waste; in the muscles it loses the substances necessary for the supply of the muscular tissue, and in the bones those which are requisite for the osseous system. In the parotid gland it yields the ingredients of the saliva; in the kidneys, those of the urine. In the intestine it absorbs in large quantity the nutritious elements of the digested food; and in the liver it gives up substances destined finally to produce the bile, while it absorbs the sugar which has been produced in the hepatic tissue. In the lungs it changes from blue to red, and in the capillaries of the general system, from red to blue; while its temperature, as we have already remarked, varies in different veins, according to the peculiar chemical and nutritive changes going on in the organs from which they originate.

Fig. 109.

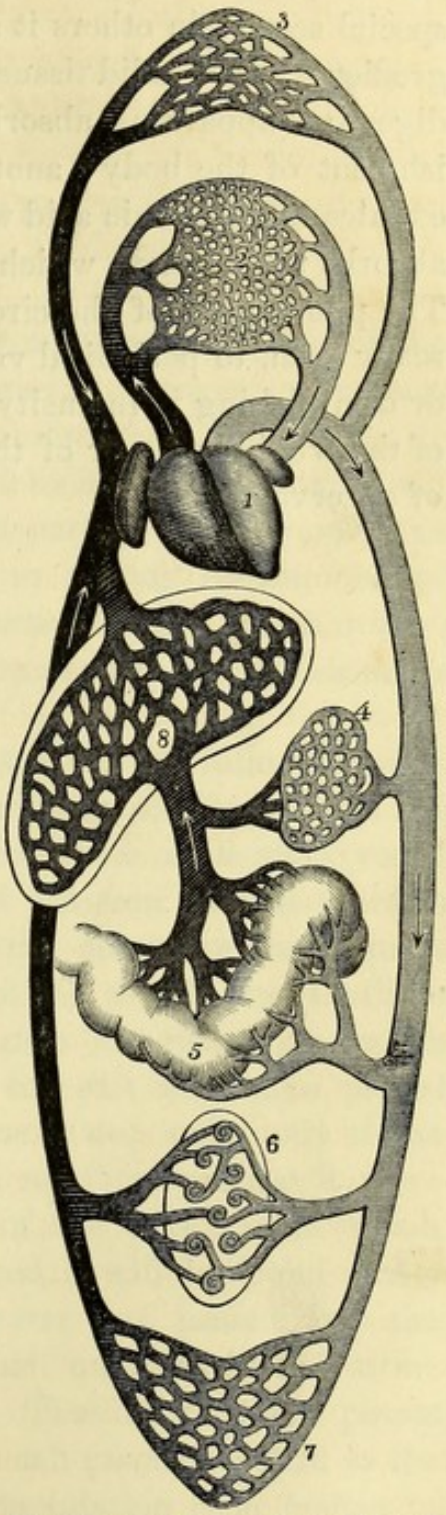


Diagram of the CIRCULATION.—1. Heart. 2. Lungs. 3. Head and upper extremities. 4. Spleen. 5. Intestine. 6. Kidney. 7. Lower extremities. 8. Liver.

We must regard the circulation of the blood, therefore, not as a simple process, but as made up of many different circulations, going on simultaneously in different organs. This may be represented in diagram, as in Fig. 109, where the variations of the circulation, in different parts of the body, are indicated in such a manner as to show, in some degree, the complicated char-

acter of its phenomena. The circulation is modified in these different parts, not only in its mechanism, but also in its rapidity and quantity, and in the nutritive functions performed by the blood. In one part, it stimulates the nervous centres and the organs of special sense; in others it supplies the fluid secretions, or the ingredients of the solid tissues. One portion, in passing through the digestive apparatus, absorbs the materials requisite for the nourishment of the body; another, in circulating through the lungs, exhales the carbonic acid which it has accumulated elsewhere, and absorbs the oxygen which is to be transported to distant tissues. The phenomena of the circulation are even liable, as we have already seen, to periodical variations in the same organ; increasing or diminishing in intensity with the condition of rest or activity of the whole body, or of the particular organ which is the subject of observation.

CHAPTER XV.

IMBIBITION AND EXHALATION.—THE LYMPHATIC SYSTEM.

During the passage of the blood through the capillaries of the circulatory system, a very important series of changes takes place by which its ingredients are partly transferred to the tissues by exhalation, and at the same time replaced by others which the blood derives by absorption from the adjacent parts. These phenomena depend upon the property, belonging to animal membranes, of imbibing or absorbing certain fluid substances in a peculiar way. They are known more particularly as the phenomena of *endosmosis* and *exosmosis*.

These phenomena may be demonstrated in the following way. If we take two different liquids, for example a solution of salt and a quantity of distilled water, and inclose them in a glass vessel with a fresh animal membrane stretched between, so that there is no direct communication from one to the other, the two liquids being in contact with opposite sides of the membrane, it will be found after a time that they have become mingled, to a certain extent, with each other. A part of the salt will have passed into the distilled water, giving it a saline taste; and a part of the water will have passed into the saline solution, making it more dilute than before. If the quantities of the two liquids, which have become so transferred, be measured, it will be found that a comparatively large quantity of the water has passed into the saline solution, and a comparatively small quantity of the saline solution has passed out into the water. That is, the water passes inward to the salt more rapidly than the salt passes outward to the water. The consequence is, that an accumulation soon begins to show itself on the side of the salt. The saline solution is increased in volume and diluted, while the water is diminished in volume, and acquires a saline ingredient. This abundant passage of the water, through the membrane, to the salt, is called *endosmosis;* and

the more scanty passage of the salt outward to the water is called *exosmosis.*

The mode usually adopted for measuring the rapidity of endosmosis is to take a glass vessel, shaped somewhat like an inverted funnel, wide at the bottom and narrow at the top. The bottom of the vessel is closed by a thin animal membrane, like the mucous membrane of an ox-bladder, which is stretched tightly over its edge and secured by a ligature. From the top of the vessel there rises a very narrow glass tube, open at its upper extremity. When the instrument is thus prepared, it is filled with a solution of sugar and placed in a vessel of distilled water, so that the animal membrane, stretched across its mouth, shall be in contact with pure water on one side and with the saccharine solution on the other. The water then passes in through the membrane, by endosmosis, faster than the saccharine solution passes out. An accumulation therefore takes place inside the vessel, and the level of the fluid rises in the upright tube. The height to which the fluid thus rises in a given time is a measure of the intensity of the endosmosis, and of its excess over exosmosis. By varying the constitution of the two liquids, the arrangement of the membrane, &c., the variation in endosmotic action under different conditions may be easily ascertained. Such an instrument is called an *endosmometer.*

If the extremity of the upright tube be bent over, so as to point downward, as endosmosis continues to go on after the tube has become entirely filled by the rising of the fluid, the saccharine solution will be discharged in drops from the end of the tube, and fall back into the vase of water. A steady circulation will thus be kept up for a time by the force of endosmosis. The water still passes through the membrane, and accumulates in the endosmometer; but, as this is already full of fluid, the surplus immediately falls back into the outside vase, and thus a current is established which will go on until the two liquids have become intimately mingled.

The conditions which influence the rapidity and extent of endosmosis have been most thoroughly investigated by Dutrochet, who was the first to make a systematic examination of the subject.

The first of these conditions is the *freshness of the animal membrane.* This is an indispensable requisite for the success of the experiment. A membrane that has been dried and moistened again, or one that has begun to putrefy, will not produce the desired effect. It has been also found that if the membrane of the endosmometer be

allowed to remain and soak in the fluids, after the column has risen to a certain height in the upright tube, it begins to descend again as soon as putrefaction commences, and the two liquids finally sink to the same level.

The next condition is the *extent of contact* between the membrane and the two liquids. The greater the extent of this contact, the more rapid and forcible is the current of endosmosis. An endosmometer with a wide mouth will produce more effect than with a narrow one, though the volume of the liquid contained in it may be the same in both instances. The action takes place at the surface of the membrane, and is proportionate to its extent.

Another very important circumstance is the *constitution of the two liquids*, and their relation to each other. As a general thing, if we use water and a saline solution in our experiments, endosmosis is more active, the more concentrated is the solution in the endosmometer. A larger quantity of water will pass inward toward a dense solution than toward one which is dilute. But the force of endosmosis varies with different liquids, even when they are of the same density. Dutrochet measured the force with which water passes through the mucous membrane of the ox-bladder into different solutions of the same density. He found that the force varies with different substances, as follows:[1] —

Endosmosis of water, with a solution of albumen . .	12
" " " sugar . . .	11
" " " gum . . .	5
" " " gelatine . .	3

The *position of the membrane* also makes a difference. With some fluids, endosmosis is more rapid when the membrane has its mucous surface in contact with the dense solution, and its dissected surface in contact with the water. With other substances the more favorable position is the reverse. Matteucci found that, in using the mucous membrane of the ox-bladder with water and a solution of sugar, if the mucous surface of the membrane were in contact with the saccharine solution, the liquid rose in the endosmometer between four and five inches. But if the same surface were turned outward toward the water, the column of fluid was less than three inches in height. Different membranes also act with different degrees of force. The effect produced is not the same with the integument of different animals, nor with mucous membranes taken from different parts of the body.

[1] In Matteucci's Lectures on the Physical Phenomena of Living Beings. Philada., 1848, p. 48.

Generally speaking, endosmosis is more active when the *temperature* is moderately elevated. Dutrochet noticed that an endosmometer, containing a solution of gum, absorbed only one volume of water at a temperature of 32° Fahr., but absorbed three volumes at a temperature a little above 90°. Variations of temperature will sometimes even change the direction of the endosmosis altogether, particularly with dilute solutions of hydrochloric acid. Dutrochet found, for example,[1] that when the endosmometer was filled with dilute hydrochloric acid and placed in distilled water, at the temperature of 50° F., endosmosis took place from the acid to the water, if the density of the acid solution were less than 1.020; but that it took place from the water to the acid, if its density were greater than this. On the other hand, at the temperature of 72° F., the current was from within outward when the density of the acid solution was below 1.003, and from without inward when it was above that point.

Finally, the *pressure* which is exerted upon the fluids and the membrane favors their endosmosis. Fluids that pass slowly under a low pressure will pass more rapidly with a higher one. Different liquids, too, require different degrees of pressure to make them pass the same membrane. Liebig[2] has measured the pressure required for several different liquids, in order to make them pass through the same membrane. He found that this pressure was

	Inches of Mercury.
For alcohol	52
For oil	37
For solution of salt	20
For water	13

There are some cases in which endosmosis takes place without being accompanied by exosmosis. This occurs when we use water and albumen as the two liquids. For while water readily passes in through the animal membrane, the albumen does not pass out. If an opening be made, for example, in the large end of an egg, so as to expose the shell-membrane, and the whole be then placed in a goblet of water, endosmosis will take place very freely from the water to the albumen, so as to distend the shell-membrane and make it protrude, like a hernia, from the opening in the shell. But the albumen does not pass outward through the membrane, and the water in the goblet remains pure. After a time,

[1] In Milne Edwards, Leçons sur la Physiologie, &c., vol. v. p. 164.

[2] In Longet's Traité de Physiologie, vol. i. p. 384.

however, the accumulation of fluid in the interior becomes so excessive as to burst the shell-membrane, and then the two liquids become mingled with each other.

These are the principal conditions by which endosmosis is influenced and regulated. Let us now see what is the nature of the process, and upon what its phenomena depend.

Endosmosis is not dependent upon the simple force of diffusion or admixture of two different liquids. For sometimes, as in the case of albumen and water, all the fluid passes in one direction and none in the other. It is true that the activity of the process depends very much, as we have already seen, upon the difference in constitution of the two liquids. With water and a saline solution, for instance, the stronger the solution of salt, the more rapid is the endosmosis of the water. And if two solutions of salt be used, with a membranous septum between them, endosmosis takes place from the weaker solution to the stronger, and is proportionate in activity to the difference in their densities. From this fact, Dutrochet was at first led to believe that the direction of endosmosis was determined by the difference in density of the two liquids, and that the current of accumulation was always directed from the lighter liquid to the denser. But we now know that this is not the case. For though, with solutions of salt, sugar, and the like, the current of endosmosis is from the lighter to the denser liquid; in other instances it is the reverse. With water and alcohol, for example, endosmosis takes place, not from the alcohol to the water, but from the water to the alcohol; that is, from the denser liquid to the lighter. The difference in density of the liquids, therefore, is not the only condition which regulates the direction of the endosmotic current. In point of fact, the process of endosmosis does not depend principally upon the attraction of the two liquids for each other, but upon *the attraction of the animal membrane for the two liquids.* The membrane is not a passive filter through which the liquids mingle, but is the active agent which determines their passage. The membrane has the power of absorbing liquids, and of taking them up into its own substance. This power of absorption, belonging to the membrane, depends upon the organic or albuminous ingredients of which it is composed; and, with different animal substances, the power of absorption is different. The tissue of cartilage, for example, will absorb more water, weight for weight, than that of the tendons; and the tissue of the cornea will absorb nearly twice as much as that of cartilage.

Beside, the power of absorption of an animal membrane is different for different liquids. Nearly all animal membranes absorb pure water more freely than a solution of salt. If a membrane, partly dried, be placed in a saturated saline solution, it will absorb the water in larger proportion than the salt, and a part of the salt will, therefore, be deposited in the form of crystals on the surface of the membrane.

Oily matters, on the other hand, are usually absorbed less readily than either water or saline solutions.

Chevreuil has investigated the absorbent power of different animal substances for different liquids, by taking definite quantities of the animal substance and immersing it for twenty-four hours in different liquids. At the end of that time, the substance was removed and weighed. Its increase in weight showed the quantity of liquid which it had absorbed. The results which were obtained are given in the following table:—[1]

100 Parts of		Water.	Saline Solution.	Oil.
Cartilage,	absorb in 24 hours,	231 parts.	125 parts.	
Tendon,		178 "	114 "	8.6 parts.
Elastic ligament,		148 "	30 "	7.2 "
Cornea,		461 "	370 "	9.1 "
Cartilaginous ligament,		319 "		3.2 "
Dried fibrin,		301 "	154 "	

The same substance, therefore, will take up different quantities of water, saline solutions, and oil.

Accordingly, when an animal membrane is placed in contact with two different liquids, it absorbs one of them more abundantly than the other; and that which is absorbed in the greatest quantity is also diffused most abundantly into the liquid on the opposite side of the membrane. A rapid endosmosis takes place in one direction, and a slow exosmosis in the other. Consequently, the least absorbable fluid increases in volume by the constant admixture of that which is taken up more rapidly.

The process of endosmosis, therefore, is essentially one of imbibition or absorption of the liquid by an animal membrane, composed of organic ingredients. We have already shown, in describing the organic proximate principles in a previous chapter, that these substances have the power of absorbing watery and serous fluids in a peculiar way. In endosmosis, accordingly, the

[1] In Longet's Traité de Physiologie, vol. i. p. 383.

imbibed fluid penetrates the membrane by a kind of chemical combination, and unites intimately with the substance of which its tissues are composed.

It is in this way that all imbibition and transudation take place in the living body. Under the most ordinary conditions, the transudation of certain fluids is accomplished with great rapidity. It has been shown by M. Gosselin,[1] that if a watery solution of iodide of potassium be dropped upon the cornea of a living rabbit, the iodine passes into the cornea, aqueous humor, iris, lens, sclerotic and vitreous body, in the course of eleven minutes; and that it will penetrate through the cornea into the aqueous humor in three minutes, and into the substance of the cornea in a minute and a half. In these experiments it was evident that the iodine actually passed into the deeper portions of the eye by simple endosmosis, and was not transported by the vessels of the general circulation; since no trace of it could be found in the tissues of the opposite eye, examined at the same time.

The same observer showed that the active principle of belladonna penetrates the tissues of the eyeball in a similar manner. M. Gosselin applied a solution of sulphate of atropine to both eyes of two rabbits. Half an hour afterward, the pupils were dilated. Three quarters of an hour later, the aqueous humor was collected by puncturing the cornea with a trocar; and this aqueous humor, dropped upon the eye of a cat, produced dilatation and immobility of the pupil in half an hour. These facts show that the aqueous humor of the affected eye actually contains atropine, which it absorbs from without through the cornea, and this atropine then acts directly and locally upon the muscular fibres of the iris.

But in all the vascular organs, the processes of endosmosis and exosmosis are very much accelerated by two important conditions, viz., first, the *movement* of the blood circulating in the vessels, and secondly, the minute *dissemination* and distribution of these vessels through the tissue of the organs.

The movement of a fluid in a continuous current always favors endosmosis through the membrane with which it is in contact. For if the two liquids be stationary, on the opposite sides of an animal membrane, as soon as endosmosis commences they begin to approximate in constitution to each other by mutual admixture; and, as this admixture goes on, endosmosis of course becomes less active,

[1] Gazette Hebdomadaire, Sept. 7, 1855.

and ceases entirely when the two liquids have become perfectly alike in composition. But if one of the liquids be constantly renewed by a continuous current, those portions of it which have become contaminated are immediately carried away by the stream, and replaced by fresh portions in a state of purity. Thus the difference in constitution of the two liquids is preserved, and transudation will continue to take place between them with unabated rapidity.

Matteucci demonstrated the effect of a current in facilitating endosmosis by attaching to the stopcock of a glass reservoir filled with water, a portion of a vein also filled with water. The vein was then immersed in a very dilute solution of hydrochloric acid. So long as the water remained stationary in the vein it did not give any indications of the presence of the acid, or did so only very slowly; but if a current were allowed to pass through the vein by opening the stopcock of the reservoir, then the fluid running from its extremity almost immediately showed an acid reaction.

The same thing may be shown even more distinctly upon the living animal. If a solution of the extract of nux vomica be injected into the subcutaneous areolar tissue of the hind leg of two rabbits, in one of which the bloodvessels of the extremity have been left free, while in the other they have been previously tied, so as to stop the circulation in that part—in the first rabbit, the poison will be absorbed and will produce convulsions and death in the course of a few minutes; but in the second animal, owing to the stoppage of the local circulation, absorption will be much retarded, and the poison will find its way into the general circulation so slowly, and in such small quantities, that its specific effects will show themselves only at a late period, or even may not be produced at all.

The anatomical arrangement of the bloodvessels and adjacent tissues is the second important condition regulating endosmosis and exosmosis. We have already seen that the network of capillary bloodvessels results from the excessive division and ramification of the smaller arteries. The blood, therefore, as it leaves the arteries and enters the capillaries, is constantly divided into smaller and more numerous currents, which are finally disseminated in the most intricate manner throughout the substance of the organs and tissues. Thus, the blood is brought into intimate contact with the surrounding tissues, over a comparatively large surface. It has already been stated, as the result of Dutrochet's investigations, that the activity of endosmosis is in direct proportion to

the extent of surface over which the two liquids come in contact with the intervening membrane. It is very evident, therefore, that it will be very much facilitated by the anatomical distribution of the capillary bloodvessels.

It is in some of the glandular organs, however, that the transudation of fluids can be shown to take place with the greatest rapidity. For in these organs the exhaling and absorbing surfaces are arranged in the form of minute ramifying tubes and follicles, which penetrate everywhere through the glandular substance; while the capillary bloodvessels form an equally complicated and abundant network, situated between the adjacent follicles and ducts. In this way, the union and interlacement of the glandular membrane, on the one hand, and the bloodvessels on the other, become exceedingly intricate and extensive; and the ingredients of the blood are almost instantaneously subjected, over a very large surface, to the influence of the glandular membrane.

The rapidity of transudation through the glandular membranes has been shown in a very striking manner by Bernard.[1] This observer injected a solution of iodide of potassium into the duct of the parotid gland on the right side, in a living dog, and immediately afterward found iodine to be present in the saliva of the corresponding gland on the opposite side. In the few instants, therefore, required to perform the experiment, the salt of iodine must have been taken up by the glandular tissue on one side, carried by the blood of the general circulation to the opposite gland, and there transuded through the secreting membrane.

We have also found the transudation of iodine through the glandular tissue to be exceedingly rapid, by the following experiment. The parotid duct is exposed and opened, upon one side, in a living dog, and a canula inserted into it, and secured by ligature. The secretion of the parotid saliva is then excited, by introducing a little vinegar into the mouth of the animal, and the saliva, thus obtained, found to be entirely destitute of iodine. A solution of iodide of potassium being then injected into the jugular vein, and the parotid secretion again immediately excited by the introduction of vinegar, as before, the saliva first discharged from the canula shows evident traces of iodine, by striking a blue color on the addition of starch and nitric acid.

The processes of exosmosis and endosmosis, therefore, in the living

[1] Leçons de Physiologie Expérimentale, Paris, 1856, p. 107.

body, are regulated by the same conditions as in artificial experiments, but they take place with infinitely greater rapidity, owing to the movement of the circulating blood, and the extent of contact existing between the bloodvessels and adjacent tissues. We have already seen that the absorption of the same fluid is accomplished with different degrees of rapidity by different animal substances. Accordingly, though the arterial blood is everywhere the same in composition, yet its different ingredients are imbibed in varying quantities by the different tissues. Thus, the cartilages absorb from the circulating fluid a larger proportion of phosphate of lime than the softer tissues, and the bones a larger proportion than the cartilages; and the watery and saline ingredients generally are found in different quantities in different parts of the body. The same animal membrane, also, as is shown by experiment, will imbibe different substances with different degrees of facility. Thus, the blood contains more chloride of sodium than chloride of potassium; but the muscles, which it supplies with nourishment, contain more chloride of potassium than chloride of sodium. In this way, the proportion of each ingredient derived from the blood is determined, in each separate tissue, by its special absorbing or endosmotic power.

Furthermore, we have seen that albumen, under ordinary conditions, is not endosmotic; that is, it will not pass by transudation through an animal membrane. For the same reason, the albumen of the blood, in the natural state of the circulation, is not exhaled from the secreting surfaces, but is retained within the circulatory system, while the watery and saline ingredients transude in varying quantities. But the degree of *pressure* to which a fluid is subjected has great influence in determining its endosmotic action. A substance which passes but slowly under a low pressure, may pass more rapidly if the force be increased. Accordingly, we find that if the pressure upon the blood in the vessels be increased, by obstruction to the venous current and backward congestion of the capillaries, then not only the saline and watery parts of the blood pass out in larger quantities, but the albumen itself transudes, and infiltrates the neighboring parts. It is in this way that albumen makes its appearance in the urine, in consequence of obstruction to the renal circulation, and that local œdema or general anasarca may follow upon venous congestion in particular regions, or upon general disturbance of the circulation.

The processes of imbibition and exudation, which thus take

place incessantly throughout the body, are intimately connected with the action of the great absorbent or *lymphatic* system of vessels, which is to be considered as secondary or complementary to that of the sanguiferous circulation.

The lymphatics may be regarded as a system of vessels, commencing in the substance of the various tissues and organs, and endowed with the property of absorbing certain of their ingredients. Their commencement has been demonstrated by injections, more particularly in the membranous parts of the body; viz., in the skin, the mucous membranes, the serous and synovial surfaces, and the inner tunic of the arteries and veins. They originate in these situations by vascular networks, not very unlike those of the capillary bloodvessels. Notwithstanding this resemblance in form between the capillary plexuses of the lymphatics and the bloodvessels, it is most probable that they are anatomically distinct from each other. It has been supposed, at various times, that there might be communications between them, and even that the lymphatic plexus might be a direct continuation of that originating from the smaller arteries; but this has never been demonstrated, and it is now generally conceded that the anatomical evidence is in favor of a complete separation between the two vascular systems.

Commencing in this way in the substance of the tissues, by a vascular network, the minute lymphatics unite gradually with each other to form larger vessels; and, after continuing their course for a certain distance from without inward, they enter and are distributed to the substance of the lymphatic glands. According to M. Colin,[1] beside the more minute and convoluted vessels in each gland, there are always some larger branches which pass directly through its substance, from the afferent to the efferent vessels; so that only a portion of the lymph is distributed to its ultimate glandular plexus. This portion, however, in passing through the organ, is evidently subjected to some glandular influence, which may serve to modify its composition.

After passing through these glandular organs, the lymphatic vessels unite into two great trunks (Fig. 46): the *thoracic duct*, which collects the fluid from the absorbents of the lower extremities, the intestines and other abdominal organs, the chest, the left upper extremity, and the left side of the head and neck, and terminates in the left subclavian vein, at the junction of the internal jugular; and the *right lymphatic duct*, which collects the fluid from the right

[1] Physiologie comparée des Animaux domestiques, Paris, 1856, vol. ii. p. 68.

upper extremity and right side of the head and neck, and joins the right subclavian vein at its junction with the corresponding jugular. Thus nearly all the lymph from the external parts, and the whole of that from the abdominal organs, passes, by the thoracic duct, into the left subclavian vein.

We already know that the lymphatic vessels are not to be regarded as the exclusive agents of absorption. On the contrary, absorption takes place by the bloodvessels even more rapidly and abundantly than by the lymphatics. Even the products of digestion, including the chyle, are taken up from the intestine in large proportion by the bloodvessels, and are only in part absorbed by the lymphatics. But the main peculiarity of the lymphatic system is that its vessels all pass in one direction, viz., from without inward, and none from within outward. Consequently there is no *circulation* of the lymph, strictly speaking, like that of the blood, but it is all supplied by exudation and absorption from the tissues.

The lymph has been obtained, in a state of purity, by various experimenters, by introducing a canula into the thoracic duct, at the root of the neck, or into large lymphatic trunks in other parts of the body. It has been obtained by Rees from the lacteal vessels and the lymphatics of the leg in the ass, by Colin from the lacteals and thoracic duct of the ox, and from the lymphatics of the neck in the horse. We have also obtained it, on several different occasions, from the thoracic duct of the dog and of the goat.

The lymph, thus obtained, is an opalescent or nearly transparent, alkaline fluid, usually of a light amber color, and having a specific gravity of 1022. Its analysis shows a remarkable similarity in constitution between it and the plasma of the blood. It contains water, fibrin, albumen, fatty matters, and the usual saline substances of the animal fluids. At the same time, the lymph is very much poorer in albuminous ingredients than the blood. The following is an analysis by Lassaigne,[1] of the fluid obtained from the thoracic duct of the cow:—

	Parts per thousand.
Water	964.0
Fibrin	0.9
Albumen	28.0
Fat	0.4
Chloride of sodium	5.0
Carbonic, Phosphate and Sulphate of soda	1.2
Phosphate of lime	0.5
	1000.0

[1] Colin, Physiologie comparée des Animaux domestiques, vol. ii. p. 111.

It thus appears that both the fibrin and the albumen of the blood actually transude to a certain extent from the bloodvessels, even in the ordinary condition of the circulatory system. But this transudation takes place in so small a quantity that the albuminous matters are all taken up again by the lymphatic vessels, and do not appear in the excreted fluids.

The first important peculiarity which is noticed in regard to the fluid of the lymphatic system, especially in the carnivorous animals, is that it varies very much, both in appearance and constitution, at different times. In the ruminating and graminivorous animals, such as the sheep, ox, goat, horse, &c., it is either opalescent in appearance, with a slight amber tinge, or nearly transparent and colorless. In the carnivorous animals, such as the dog and cat, it is also opaline and amber colored, in the intervals of digestion, but soon after feeding becomes of a dense, opaque, milky white, and continues to present that appearance until the processes of digestion and intestinal absorption are complete. It then regains its original aspect, and remains opaline or semi-transparent until digestion is again in progress.

The cause of this variable constitution of the fluid discharged by the thoracic duct is the absorption of fatty substances from the intestine during digestion. Whenever fatty substances exist in considerable quantity in the food, they are reduced, by the process of digestion, to a white, creamy mixture of molecular fat, suspended in an albuminous menstruum. The mixture is then absorbed by the lymphatics of the mesentery, and transported by them through the thoracic duct to the subclavian vein. While this absorption is going on, therefore, the fluid of the thoracic duct alters its appearance, becomes white and opaque, and is then called *chyle;* so that there are two different conditions, in which the contents of the great lymphatic trunks present different appearances. In the fasting condition, these vessels contain a semi-transparent, or opaline and nearly colorless lymph; and during digestion, an opaque, milky chyle. It is on this account that the lymphatics of the mesentery are called "lacteals."

The chyle, accordingly, is nothing more than the lymph which is constantly absorbed by the lymphatic system everywhere, with the addition of more or less fatty ingredients taken up from the intestine during the digestion of food.

The results of analysis show positively that the varying appearance of the lymphatic fluids is really due to this cause; for though

the chyle is also richer than the lymph in albuminous matters, the principal difference between them consists in the proportion of fat. This is shown by the following comparative analysis of the lymph and chyle of the ass, by Dr. Rees:[1]—

	Lymph.	Chyle.
Water	965.36	902.37
Albumen	12.00	35.16
Fibrin	1.20	3.70
Spirit extract	2 40	3.32
Water extract	13.19	12.33
Fat	traces.	36.01
Saline matter	5 85	7.11
	1,000.00	1,000.00

When a canula, accordingly, is introduced into the thoracic duct at various periods after feeding, the fluid which is discharged varies considerably, both in appearance and quantity. We have found that, in the dog, the fluid of the thoracic duct never becomes quite transparent, but retains a very marked opaline tinge even so late as eighteen hours after feeding, and at least three days and a half after the introduction of fat food. Soon after feeding, however, as we have already seen, it becomes whitish and opaque, and remains so while digestion and absorption are in progress. It also becomes more abundant soon after the commencement of digestion, but diminishes again in quantity during its latter stages. We have found the lymph and chyle to be discharged from the thoracic duct, in the dog, in the following quantities per hour, at different periods of digestion. The quantities are calculated in proportion to the entire weight of the animal.

	Per Thousand Parts.
3¼ hours after feeding	2.45
7 " " "	2.20
13 " " "	0.99
18 " " "	1.15
18½ " " "	1.99

It would thus appear that the hourly quantity of lymph, after diminishing during the latter stages of digestion, increases again somewhat, about the eighteenth hour, though it is still considerably less abundant than while digestion was in active progress.

The lymph obtained from the thoracic duct at all periods coagulates soon after its withdrawal, owing to the fibrin which it contains

[1] In Colin, op. cit., vol. ii. p. 18.

in small quantity. After coagulation, a separation takes place between the clot and serum, precisely as in the case of blood.

The *movement* of the lymph in the lymphatic vessels, from the extremities toward the heart, is accomplished by various forces. The first and most important of these forces is that by which the fluids are originally absorbed by the lymphatic capillaries. Throughout the entire extent of the lymphatic system, an extensive process of endosmosis is incessantly going on, by which the ingredients of the lymph are imbibed from the surrounding tissues, and compelled to pass into the lymphatic vessels. The lymphatics are thus filled at their origin; and, by mere force of accumulation, the fluids are then compelled, as their absorption continues, to discharge themselves into the large veins in which the lymphatic trunks terminate.

The movement of the fluids through the lymphatic system is also favored by the contraction of the voluntary muscles and the respiratory motions of the chest. For as the lymphatic vessels are provided with valves, arranged like those of the veins, opening toward the heart and shutting backward toward the extremities, the alternate compression and relaxation of the adjacent muscles, and the expansion and collapse of the thoracic parietes, must have the same effect upon the movement of the lymph as upon that of the venous blood. By these different influences the chyle and lymph are incessantly carried from without inward, and discharged, in a slow but continuous stream, into the returning current of the venous blood.

The entire quantity of the lymph and chyle has been found, by direct experiment, to be very much larger than was previously anticipated. M. Colin[1] measured the chyle discharged from the thoracic duct of an ox during twenty-four hours, and found it to exceed *eighty pounds*. In other experiments of the same kind, he obtained still larger quantities.[2] From two experiments on the horse, extending over a period of twelve hours each, he calculates the quantity of chyle and lymph in this animal as from twelve to fifteen thousand grains per hour, or between forty and fifty pounds per day. But in the ruminating animals, according to his observations, the quantity is considerably greater. In an ordinary-sized cow, the smallest quantity obtained in an experiment extending over

[1] Gazette Hebdomadaire, April 24, 1857, p. 285.

[2] Colin, op. cit., vol. ii. p. 100.

a period of twelve hours, was a little over 9,000 grains in fifteen minutes; that is, five pounds an hour, or 120 pounds per day. In another experiment, with a young bull, he actually obtained a little over 100 pounds from a fistula of the thoracic duct, in twenty-four hours.

We have also obtained similar results by experiments upon the dog and goat. In a young kid, weighing fourteen pounds, we have obtained from the thoracic duct 1890 grains of lymph in three hours and a half. This quantity would represent 540 grains in an hour, and 12,690 grains, or 1.85 pounds in twenty-four hours; and in a ruminating animal weighing 1000 pounds, this would correspond to 132 pounds of lymph and chyle discharged by the thoracic duct in the course of twenty-four hours.

The average of all the results obtained by us, in the dog, at different periods after feeding, gives very nearly four and a half per cent. of the entire weight of the animal, as the total daily quantity of lymph and chyle. This is substantially the same result as that obtained by Colin, in the horse; and for a man weighing 140 pounds, it would be equivalent to between six and six and a half pounds of lymph and chyle per day.

But of this quantity a considerable portion consists of the chyle which is absorbed from the intestines during the digestion of fatty substances. If we wish, therefore, to ascertain the total amount of the lymph, separate from that of the chyle, the calculation should be based upon the quantity of fluid obtained from the thoracic duct in the intervals of digestion, when no chyle is in process of absorption. We have seen that in the dog, eighteen hours after feeding, the lymph, which is at that time opaline and semi-transparent, is discharged from the thoracic duct, in the course of an hour, in a quantity equal to 1.15 parts per thousand of the entire weight of the animal. In twenty-four hours this would amount to 27.6 parts per thousand; and for a man weighing 140 pounds this would give 3.864 pounds as the total daily quantity of the lymph alone.

It will be seen, therefore, that the processes of exudation and absorption, which go on in the interior of the body, produce a very active interchange or *internal circulation* of the animal fluids, which may be considered as secondary to the circulation of the blood. For all the digestive fluids, as we have found, together with the bile discharged into the intestine, are reabsorbed in the natural process of digestion and again enter the current of the circulation. These fluids, therefore, pass and repass through the mucous membrane of

the alimentary canal and adjacent glands, becoming somewhat altered in constitution at each passage, but still serving to renovate alternately the constitution of the blood and the ingredients of the digestive secretions. Furthermore the elements of the blood itself also transude in part from the capillary vessels, and are again taken up, by absorption, by the lymphatic vessels, to be finally restored to the returning current of the venous blood, in the immediate neighborhood of the heart.

The daily quantity of all the fluids, thus secreted and reabsorbed during twenty-four hours, will enable us to estimate the activity with which endosmosis and exosmosis go on in the living body. In the following table, the quantities are all calculated for a man weighing 140 pounds.

SECRETED AND REABSORBED DURING 24 HOURS.

Saliva	20,164	grains,	or	2.880	pounds.
Gastric juice	98,000	"	"	14.000	"
Bile	16.940	"	"	2.420	"
Pancreatic juice	13,104	"	"	1.872	"
Lymph	27,048	"	"	3.864	"
				25.036	

A little over twenty-five pounds, therefore, of the animal fluids transude through the internal membranes and are restored to the blood by reabsorption in the course of a single day. It is by this process that the natural constitution of the parts, though constantly changing, is still maintained in its normal condition by the movement of the circulating fluids, and the incessant renovation of their nutritious materials.

CHAPTER XVI.

SECRETION.

We have already seen, in a previous chapter, how the elements of the blood are absorbed by the tissues during the capillary circulation, and assimilated by them or converted into their own substance. In this process, the inorganic or saline matters are mostly taken up unchanged, and are merely appropriated by the surrounding parts in particular quantities; while the organic substances are transformed into new compounds, characteristic of the different tissues by which they are assimilated. In this way the various tissues of the body, though they have a different chemical composition from the blood, are nevertheless supplied by it with appropriate ingredients, and their nutrition constantly maintained.

Beside this process, which is known by the name of "assimilation," there is another somewhat similar to it, which takes place in the different glandular organs, known as the process of *secretion*. It is the object of this function to supply certain fluids, differing in chemical constitution from the blood, which are required to assist in various physical and chemical actions going on in the body. These secreted fluids, or "secretions," as they are called, vary in consistency, density, color, quantity, and reaction. Some of them are thin and watery, like the tears and the perspiration; others are viscid and glutinous, like mucus and the pancreatic fluid. They are alkaline like the saliva, acid like the gastric juice, or neutral like the bile. Each secretion contains water and the inorganic salts of the blood; and these ingredients, in varying proportions, are common to all, or nearly all, of the secreted fluids. But each secretion is also distinguished by the presence of some peculiar animal substance which does not exist in the blood, but which is produced by the secreting action of the glandular organ. Thus the gastric juice contains pepsine, which is formed only in the tubules of the gastric mucous membrane; the pancreatic juice contains pancreatine, formed only in the pancreas; and the bile contains tauro-cholate of soda, formed only in the liver. As the blood circulates through the capillaries of the gland, its watery and saline constitu-

ents transude in certain quantities, and are discharged into the excretory duct. At the same time, the glandular cells, which have themselves been nourished by the blood, produce a new substance by the catalytic transformation of their organic constituents; and this new substance is discharged also into the excretory duct and completes the constitution of the secreted fluid. A true secretion, therefore, is produced only in its own particular gland, and cannot be formed elsewhere; since the glandular cells of that organ are the only ones capable of producing its most characteristic ingredient.

One secreting gland, consequently, can never perform vicariously the office of another. Those instances which have been from time to time reported of such an unnatural action are not, properly speaking, instances of "vicarious secretion;" but only cases in which certain substances, already existing in the blood, have made their appearance in secretions to which they do not naturally belong. Thus cholesterine, which is produced in the brain and is taken up from it by the blood, usually passes out with the bile; but it may also appear in the fluid of hydrocele, or in inflammatory exudations. The sugar, again, which is produced in the liver and taken up by the blood, when it accumulates in large quantity in the circulating fluid, may pass out with the urine. The coloring matter of the bile, in cases of biliary obstruction, may be reabsorbed, and so make its appearance in the serous fluids, or even in the perspiration. In these instances, however, the unnatural ingredient is not actually produced by the kidneys, or the perspiratory glands, but is merely supplied to them, already formed, by the blood. Cases of "vicarious menstruation" are simply capillary hemorrhages which take place from various mucous membranes, owing to the general disturbance of the circulation in amenorrhœa. A true secretion, however, is always confined to the gland in which it naturally originates.

The force by which the different secreted fluids are prepared in the glandular organs, and discharged into their ducts, is a peculiar one, and resident only in the glands themselves. It is not simply a process of filtration, in which the ingredients of the secretion exude from the bloodvessels by exosmosis under the influence of pressure; since the most characteristic of these ingredients, as we have already mentioned, do not pre-exist in the blood, but are formed in the substance of the gland itself. Substances, even, which already exist in the blood in a soluble form, may not have the power of passing out through the glandular tissue. Bernard

has found[1] that ferrocyanide of potassium, when injected into the jugular vein, though it appears with great facility in the urine, does not pass out with the saliva; and even that a solution of the same salt, injected into the duct of the parotid gland, is absorbed, taken up by the blood, and discharged with the urine; but does not appear in the saliva, even of the gland into which it has been injected. The force with which the secreted fluids accumulate in the salivary ducts has also been shown by Ludwig's experiments[2] to be sometimes greater than the pressure in the bloodvessels. This author found, by applying mercurial gauges at the same time to the duct of Steno and to the artery of the parotid gland, that the pressure in the duct from the secreted saliva was considerably greater than that in the artery from the circulating blood; so that the passage of the secreted fluids had really taken place in a direction contrary to that which would have been caused by the simple influence of pressure.

The process of secretion, therefore, is one which depends upon the peculiar anatomical and chemical constitution of the glandular tissue and its secreting cells. These cells have the property of absorbing and transmitting from the blood certain inorganic and saline substances, and of producing, by chemical metamorphosis, certain peculiar animal matters from their own tissue. These substances are then mingled together, dissolved in the watery fluids of the secretion, and discharged simultaneously by the excretory duct.

All the secreting organs vary in activity at different periods. Sometimes they are nearly at rest; while at certain periods they become excited, under the influence of an occasional or periodical stimulus, and then pour out their secretion with great rapidity and in large quantity. The perspiration, for example, is usually so slowly secreted that it evaporates as rapidly as it is poured out, and the surface of the skin remains dry; but under the influence of unusual bodily exercise or mental excitement it is secreted much faster than it can evaporate, and the whole integument becomes covered with moisture. The gastric juice, again, in the intervals of digestion, is either not secreted at all, or is produced in a nearly inappreciable quantity; but on the introduction of food into the stomach, it is immediately poured out in such abundance, that between two and three ounces may be collected in a quarter of an hour.

[1] Leçons de Physiologie Expérimentale. Paris, 1856, tome ii. p. 96 *et seq.*

[2] Ibid., p. 106.

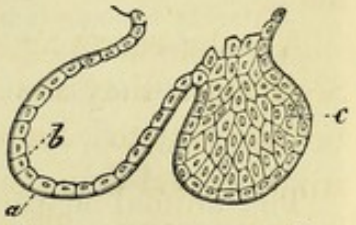
The principal secretions met with in the animal body are as follows:—

1. Mucus.
2. Sebaceous matter.
3. Perspiration.
4. The tears.
5. The milk.
6. Saliva.
7. Gastric juice.
8. Pancreatic juice.
9. Intestinal juice.
10. Bile.

The last five of these fluids have already been described in the preceding chapters. We shall therefore only require to examine at present the five following, viz., mucus, sebaceous matter, perspiration, the tears, and the milk, together with some peculiarities in the secretion of the bile.

1. MUCUS.—Nearly all the mucous membranes are provided with follicles or glandulæ, in which the mucus is prepared. These follicles are most abundant in the lining membrane of the mouth, nares, pharynx, œsophagus, trachea and bronchi, vagina, and male urethra. They are generally of a compound form, consisting of a number of secreting sacs or cavities, terminating at one end in a blind extremity, and opening by the other into a common duct by which the secreted fluid is discharged. Each ultimate secreting sac or follicle is lined with glandular epithelium (Fig. 110), and surrounded on its external surface by a network of capillary bloodvessels. These vessels, penetrating deeply into the interstices between the follicles, bring the blood nearly into contact with the epithelial cells lining its cavity. It is these cells which prepare the secretion, and discharge it afterward into the commencement of the excretory duct.

Fig. 110.



FOLLICLES OF A COMPOUND MUCOUS GLANDULE. From the human subject. (After Kölliker.)—*a*. Membrane of the follicle. *b*, *c*. Epithelium of the same.

The mucus, produced in the manner above described, is a clear, colorless fluid, which is poured out in larger or smaller quantity on the surface of the mucous membranes. It is distinguished from other secretions by its viscidity, which is its most marked physical property, and which depends on the presence of a peculiar animal matter, known under the name of *mucosine*. When unmixed with other animal fluids, this viscidity is so great that the mucus has nearly a semi-solid or gelatinous consistency. Thus, the mucus of the mouth, when obtained unmixed with the secretions of the salivary glands, is so

tough and adhesive that the vessel containing it may be turned upside down without its running out. The mucus of the cervix uteri has a similar firm consistency, so as to block up the cavity of this part of the organ with a semi-solid gelatinous mass. Mucus is at the same time exceedingly smooth and slippery to the touch, so that it lubricates readily the surfaces upon which it is exuded, and facilitates the passage of foreign substances, while it defends the mucus membrane itself from injury.

The composition of pulmonary mucus, that is, the fluid secreted by the follicles of the trachea and bronchial tubes, is as follows:—[1]

Composition of Pulmonary Mucus.

Water	955.52
Animal matter	33.57
Fat	2.89
Chloride of sodium	5.83
Phosphates of soda and potassa	1.05
Sulphates " "	0.65
Carbonates " "	0.49
	1000.00

The following is the composition of the mucus of the gall-bladder:—[2]

Mucus of the Gall-bladder.

Water	985.00
Mucosine	6.25
Extractive matters	5.44
Chloride of sodium, Chloride of potassium, Carbonate of soda	3.06
Phosphates of lime and magnesia	0.25
	1000.00

The animal matter of mucus is insoluble in water, though it absorbs this fluid to some extent, becoming slowly more fluid in consistency. Consequently, a concentrated and viscid mucus, when dropped into water, does not mix with it, but is merely broken up by agitation into gelatinous threads and flakes, which subside after a time to the bottom. It is miscible, however, to some extent, with other animal fluids, and may be incorporated with them, so as to become thinner and more dilute. Mucus readily takes on putrefactive changes, and communicates them to other organic substances with which it may be in contact.

The varieties of mucus found in different parts of the body are probably not identical in composition, but differ a little in the char-

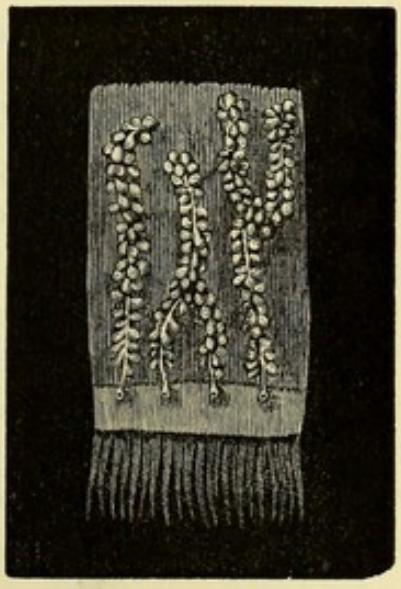
[1] Simon's Chemistry of Man, Philadelphia, 1846, p. 352.

[2] Robin, Leçons sur les Humeurs. Paris, 1867, p. 475.

acter of their principal organic ingredient, as well as in the proportion of their saline constituents. Its function is for the most part a physical one, viz., to lubricate the mucous surfaces, to defend them from injury, and to facilitate the passage of foreign substances through their cavities.

2. SEBACEOUS MATTER.—The sebaceous matter is distinguished by containing a very large proportion of fatty or oily ingredients. There are three varieties of this secretion met with in the body, viz., one produced by the sebaceous glands of the skin, another by the ceruminous glands of the external auditory meatus, and a third by the Meibomian glands of the eyelid. The sebaceous glands of the skin are found most abundantly in those parts which are thickly covered with hairs, as well as on the face, the labia minora of the female generative organs, the glans penis, and the prepuce. They consist sometimes of a simple follicle, or flask-shaped cavity, opening by a single orifice; but more frequently of a number of such follicles grouped round a common excretory duct. The duct nearly always opens just at the root of one of the hairs, which is smeared more or less abundantly with its secretion. Each follicle, as in the case of the mucous glandules, is lined with epithelium, and its cavity is filled with the secreted sebaceous matter.

Fig. 111.



MEIBOMIAN GLANDS, after Ludovic.

In the Meibomian glands of the eyelid (Fig. 111), the follicles are ranged along the sides of an excretory duct, situated just beneath the conjunctiva, on the posterior surface of the tarsus, and opening upon its free edge, a little behind the roots of the eyelashes. The ceruminous glands of the external auditory meatus, again, have the form of long tubes, which terminate, at the lower part of the integument lining the meatus, in a globular coil, or convolution, covered externally by a network of capillary bloodvessels.

The sebaceous matter of the skin has the following composition according to Esenbeck.[1]

[1] Simon's Chemistry of Man, p. 379.

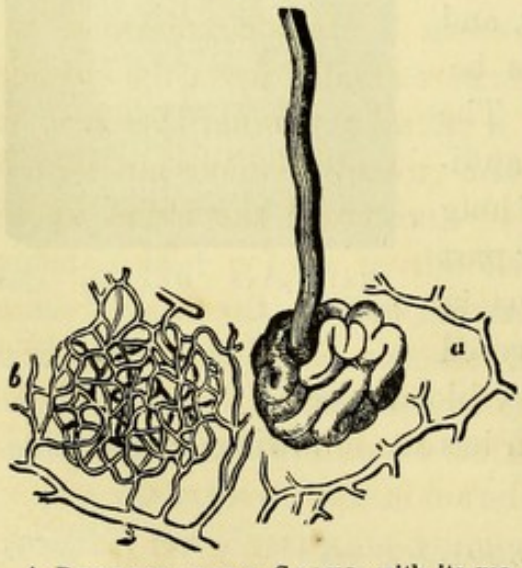
Composition of Sebaceous Matter.

Animal substances	358
Fatty matters	368
Phosphate of lime	200
Carbonate of lime	21
Carbonate of magnesia	16
Chloride of sodium, Acetate of soda, &c.	37
	1000

Owing to the large proportion of stearine in the fatty ingredients of the sebaceous matters, they have a considerable degree of consistency. Their office is to lubricate the integument and the hairs, to keep them soft and pliable, and to prevent their drying up by too rapid evaporation. When the sebaceous glands of the scalp are inactive or atrophied, the hairs become dry and brittle, are easily split or broken off, and finally cease growing altogether. The ceruminous matter of the ear is intended without doubt partly to obstruct the cavity of the meatus, and by its glutinous consistency and strong odor to prevent small insects from accidentally introducing themselves into the meatus. The secretion of the Meibomian glands, by being smeared on the edges of the eyelids, prevents the tears from running over upon the cheeks, and confines them within the cavity of the lachrymal canals.

3. Perspiration.—The perspiratory glands of the skin are scattered everywhere throughout the integument, being most abundant on the anterior portions of the body. They consist each of a slender tube, about $\frac{1}{400}$ of an inch in diameter, lined with glandular epithelium, which penetrates nearly through the entire thickness of the skin, and terminates below in a globular coil, very similar in appearance to that of the ceruminous glands of the ear. (Fig. 112.) A network of capillary vessels envelops the tubular coil and supplies the gland with the materials necessary to its secretion.

Fig. 112.



A Perspiratory Gland, with its vessels; magnified 35 times. (After Todd and Bowman.)—*a*. Glandular coil. *b*. Plexus of vessels.

These glands are very abundant in some parts. On the posterior portion of the trunk, the cheeks,

and the skin of the thigh and leg, there are, according to Krause,[1] about 500 to the square inch; on the anterior part of the trunk, the forehead, the neck, the forearm, and the back of the hand and foot, 1000 to the square inch; and on the sole of the foot and the palm of the hand, about 2700 in the same space. According to the same observer, the whole number of perspiratory glands is not less than 2,300,000, and the length of each tubular coil, when unravelled, about $\frac{1}{15}$ of an inch. The entire length of the glandular tubing must therefore be not less than 153,000 inches, or about two miles and a half.

The fluid derived from this extensive glandular apparatus is the perspiration. It is a clear, colorless, watery liquid, with a distinctly acid reaction, and a specific gravity of 1003 or 1004. Its constitution, according to the average of estimates given by various authors, is as follows:—

Composition of the Perspiration.

Water	995.50
Chloride of sodium	2.23
Chloride of potassium	0.24
Sulphates of soda and potassa	0.01
Salts of organic acids with soda and potassa	2.02
	1000.00

In addition to the above ingredients, there are present in the perspiration traces of an organic substance similar to albumen, and also a free acid of a volatile nature, which gives to the fluid its acid reaction and odor, but whose specific characters have not been more fully determined. It is known to be volatile since the perspiration, when subjected to evaporation by heat, soon loses its acid reaction and becomes neutral or alkaline.

The perspiration is a constant secretion. In a condition of repose or of moderate bodily activity, it is exuded upon the surface of the skin in so continuous and gradual a manner that it is at once carried off by evaporation. Consequently it does not appear in the liquid form, and has, therefore, received the name, under these circumstances, of the *insensible transpiration*. The entire quantity of fluid discharged from the skin in this way during twenty-four hours, according to the observations of Lavoisier and Seguin,[2] amounts to 13,500 grains, or nearly two pounds avoirdupois. It appears that the exhalation of watery vapor from the lungs, during the same space of time, amounts to over 8000 grains;

[1] Kölliker, Handbuch der Gewebelehre, Leipzig, 1852, p. 147.

[2] Milne Edwards, Leçons sur la Physiologie, &c., vol. ii. p. 623.

so that from the lungs and skin combined, the watery exhalation amounts, on the average, to rather more than three pounds per day.

But the cutaneous secretion may be greatly increased by temporary causes. An elevated temperature or unusual muscular exertion, or, still more, a combination of the two, will increase the circulation through the skin and largely augment the amount of fluid discharged. It then exudes more rapidly than it can be carried off by evaporation, and collects upon the skin as a visible moisture, whence it is known as the *sensible* perspiration. The amount of perspiration discharged during violent exercise has been known to rise as high as 5000 or 6000 grains per hour; and Dr. Southwood Smith[1] found that the laborers employed in heated gas-works sometimes lost, by both cutaneous and pulmonary exhalation, as much as 3½ pounds' weight in less than an hour.

The office of the cutaneous perspiration is principally to regulate the temperature of the body. We have already seen, in a preceding chapter, that the living body will maintain the temperature of 100° F., though subjected to a much lower temperature by the surrounding atmosphere, in consequence of the continued generation of heat which takes place in its interior; and that if, by long continued or severe exposure, the blood become cooled down much below its natural standard, death inevitably results. But the temperature of the body is regulated also in the opposite direction, and is prevented from rising above the natural standard as well as falling below it. The temperature of the skin is never so high as that of the internal organs, being slightly cooled by contact with the external atmosphere, so that it rarely, if ever, in the normal state, rises above 97° or 98°. This moderate temperature is undoubtedly essential to the healthy action of the skin itself, and even the partial cooling of the blood in the cutaneous capillaries is important in regulating the temperature of the whole mass of the circulating fluid. But when, in consequence of unusual muscular exertion, the circulation is quickened, animal heat is more rapidly generated in the internal organs and a larger volume of warm blood is brought to the cutaneous capillaries, the simple contact with the atmosphere is no longer sufficient to keep down its temperature to the usual standard. Then the perspiration is exuded in increased abundance, and its evaporation provides for the requisite cooling of the skin and of the blood circulating in its vessels.

Even if exposed to the influence of an atmosphere warmer than 100° F., the body does not become heated up to the temperature

[1] Philosophy of Health, London, 1838, chap. xiii.

of the air, but remains at its natural standard. This is provided for by the action of the cutaneous glands, which are excited to unusual activity, and pour out a large quantity of watery fluid upon the skin. This fluid immediately evaporates, and in assuming the gaseous form appropriates so much heat that the cutaneous surfaces are reduced to their natural temperature.

So long as the air is dry, so that evaporation from the surface can go on rapidly, a very elevated temperature can be borne with impunity. The workmen of the sculptor Chantrey were in the habit, according to Dr. Carpenter, of entering a furnace in which the air was heated up to 350°; and other instances have been known in which a temperature of 400° to 600° has been borne for a time without much inconvenience. But if the air be saturated with moisture, and evaporation from the skin in this way retarded, the body soon becomes unnaturally warm; and if the exposure be long continued, death is the result. It is easily seen that horses, when fast driven, suffer much more from a warm and moist atmosphere than from a warm and dry one. The experiments of Magendie and others have shown[1] that quadrupeds confined in a dry atmosphere suffer at first but little inconvenience, even when the temperature is much above that of their own bodies; but as soon as the atmosphere is loaded with moisture, or the supply of perspiration is exhausted, the blood becomes heated, and the animal dies. Death follows in these cases as soon as the blood has become heated up to 10° or 13° F., above its natural standard. The temperature of 113°, which is but little above the natural temperature of birds, is fatal to quadrupeds; and we have found that frogs, whose natural temperature is 50° or 60°, die very soon if they are kept in water at 100° F.

The amount of perspiration is liable to variation, as we have already intimated, from the variations in temperature of the surrounding atmosphere. It is excited also by unusual muscular exertion, and increased or diminished by various nervous conditions, such as anxiety, irritation, lassitude, or excitement.

4. THE TEARS.—The tears are produced by the lachrymal glands, which are lobulated glandular organs, situated at the upper and outer part of the orbit of the eye, and opening, by from six to twelve ducts, upon the surface of the conjunctiva, in the fold between the eyeball and the outer portion of the upper lid. The secretion is a clear, alkaline, watery fluid, containing an organic

[1] Bernard, Lectures on the Blood. Atlee's translation, Phila., 1854, p. 25.

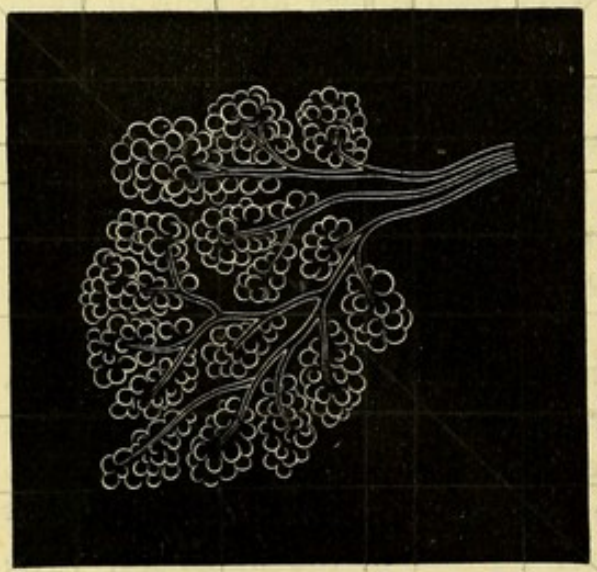
substance similar to albumen, and saline matters consisting, for the most part, of chloride of sodium. Its composition is as follows:—[1]

Composition of the Tears.

Water	982.0
Albuminous matter	5.0
Chloride of sodium	13.0
Other mineral salts	0.2
	1000.2

The office of the lachrymal secretion is simply to keep the surfaces of the cornea and conjunctiva moist and polished, and to preserve in this way the transparency of the parts. For the evaporation taking place from the exposed surface of the conjunctiva tends to dry the membrane, and would thus destroy its transparency, were not the loss of fluid constantly replaced by the watery film supplied from the lachrymal glands. After death, the eyeball at once loses its brilliancy, and its surface becomes dull and tarnished from the stoppage of the lachrymal secretion. During life, as the tears are secreted, they are spread out uniformly over the anterior part of the eyeball by the movement of the lids in winking, and are gradually conducted to the inner angle of the eye. Here they are taken up by the puncta lachrymalia, pass through the lachrymal canals, and are finally discharged into the nasal passages beneath the inferior turbinated bones. A constant supply of fresh fluid is thus kept passing over the transparent parts of the eyeball, and the bad results avoided which would follow from its accumulation and putrefactive alteration.

Fig. 113.



Glandular Structure of Mamma.

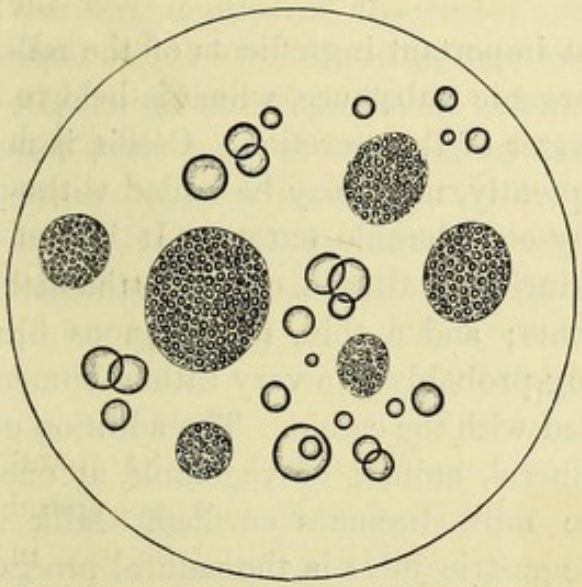
5. The Milk.—The mammary glands are lobulated organs, resembling closely in their structure the pancreas, the salivary, and the lachrymal glands. They consist of numerous secreting sacs or follicles, grouped together in lobules; each lobule being supplied with a common excretory duct, which joins those coming from adjacent parts of the gland. (Fig. 113.) In this way, by their successive union, they

[1] Robin, Leçons sur les Humeurs, Paris, 1867, p. 492.

form larger branches and trunks, until they are reduced in number to some 15 or 20 cylindrical ducts, the *lactiferous ducts*, which open finally, by as many minute orifices, upon the extremity of the nipple.

The secretion of the milk becomes fairly established at the end of two or three days after delivery, though the breasts often contain a milky fluid during the latter part of pregnancy. At first the fluid discharged from the nipple is a yellowish turbid mixture, which is called the *colostrum*. It has the appearance of being thinner than the milk, but chemical examinations have shown[1] that it really contains a larger amount of solid ingredients than the perfect secretion. When examined under the microscope it is seen to contain, beside the milk-globules proper, a large amount of irregularly globular or oval bodies, from $\frac{1}{175}$ to $\frac{1}{50}$ of an inch in diameter, which are termed the "colostrum corpuscles." (Fig. 114.) These bodies are more yellow and opaque than the true milk-globules, as well as being very much larger. They have a well defined outline, and consist apparently of a group of minute oily granules or globules, imbedded in a mass of organic substance. The milk-globules at this time are less abundant than afterward, and of larger size, measuring mostly from $\frac{1}{200}$ to $\frac{1}{150}$ of an inch in diameter.

Fig. 114.



Colostrum Corpuscles, with milk-globules; from a woman, one day after delivery.

At the end of a day or two after its first appearance, the colostrum ceases to be discharged, and is replaced by the true milky secretion.

The milk, as it is discharged from the nipple, is a white, opaque fluid, with a slightly alkaline reaction, and a specific gravity of

[1] Lehmann, op. cit., vol. ii. p. 63.

about 1030. Its proximate chemical constitution, according to Pereira and Lehmann, is as follows:—

Composition of Cow's Milk.

Water	870.2
Casein	44.8
Butter	31.3
Sugar	47.7
Soda	6.0
Chlorides of sodium and potassium	
Phosphates of soda and potassa	
Phosphate of lime	
" " magnesia	
" " iron	
Alkaline carbonates	
Iron, &c.	
	1000.0

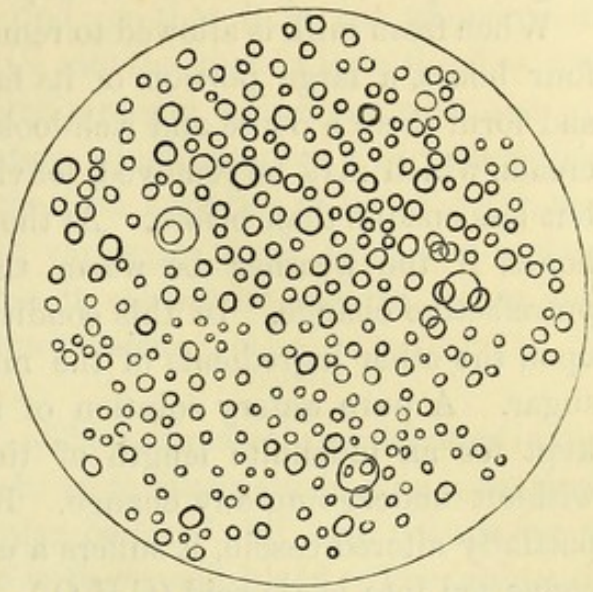
Human milk is distinguished from the above by containing less casein, and a larger proportion of oily and saccharine ingredients. The entire amount of solid ingredients is also somewhat less than in cow's milk.

The *casein* is one of the most important ingredients of the milk. It is an extremely nutritious organic substance, which is held in a fluid form by union with the water of the secretion. Casein is not coagulable by heat, and consequently, milk may be boiled without changing its consistency to any considerable extent. It becomes a little thinner and more fluid during ebullition, owing to the melting of its oleaginous ingredients; and a thin, membranous film forms upon its surface, consisting probably of a very little albumen, which the milk contains, mingled with the casein. The addition of any of the acids, however, mineral, animal, or vegetable, at once coagulates the casein, and the milk becomes curdled. Milk is coagulated, furthermore, by the gastric juice in the natural process of digestion, immediately after being taken into the stomach; and if vomiting occur soon after a meal containing milk, it is thrown off in the form of semi-solid, curd-like flakes.

The mucous membrane of the calves' stomach, or rennet, also has the power of coagulating casein; and when milk has been curdled in this way, and its watery, saccharine, and inorganic ingredients separated by mechanical pressure, it is converted into cheese. The peculiar flavor of the different varieties of cheese depends on the quantity and quality of the oleaginous ingredients which have been entangled with the coagulated casein, and on the

alterations which these substances have undergone by the lapse of time and exposure to the atmosphere.

Fig. 115.



MILK-GLOBULES; from same woman as above, four days after delivery. Secretion fully established.

The sugar and saline substances of the milk are in solution, together with the casein and water, forming a clear, colorless, homogeneous, serous fluid. The butter, or oleaginous ingredient, however, is suspended in this serous fluid in the form of minute granules and globules, the true "milk-globules." (Fig. 115.) These globules are nearly fluid at the temperature of the body, and have a perfectly circular outline. In the perfect milk, they are very much more abundant and smaller in size than in the colostrum; as the largest of them are not over $\frac{1}{2000}$ of an inch in diameter, and the greater number about $\frac{1}{10000}$ of an inch.

The following is the composition of the butter of cow's milk, according to Robin and Verdeil:—

Margarine	68
Oleine	30
Butyrine	2
	100

It is the last of these ingredients, the butyrine, which gives the peculiar flavor to the butter of milk.

The milk-globules have sometimes been described as if each one were separately covered with a thin layer of coagulated casein or albumen. No such investing membrane, however, is to be seen. The milk-globules are simply small masses of semi-fluid fat, suspended by admixture in the watery and serous portions of the secretion, so as to make an opaque, whitish emulsion. They do not fuse together when they come in contact under the microscope, simply because they are not quite fluid, but contain a large proportion of margarine, which is solid at ordinary temperatures of the body, and is only retained in a partially fluid form by the oleine with which it is associated. The globules may be made to fuse with

each other, however, by simply heating the milk and subjecting it to gentle pressure between two slips of glass.

When fresh milk is allowed to remain at rest for twelve to twenty-four hours, a large portion of its fatty matters rise to the surface, and form there a dense and rich-looking yellowish-white layer, the cream, which may be removed, leaving the remainder still opaline, but less opaque than before. At the end of thirty-six to forty-eight hours, if the weather be warm, the casein begins to take on a putrefactive change. In this condition it exerts a catalytic action upon the other ingredients of the milk, and particularly upon the sugar. A pure watery solution of milk-sugar ($C_{24}H_{24}O_{24}$) may be kept for an indefinite length of time, at ordinary temperatures, without undergoing any change. But if kept in contact with the partially altered casein, it suffers a catalytic transformation, and is converted into lactic acid ($C_6H_6O_6$). This unites with the free soda, and decomposes the alkaline carbonates, forming lactates of soda and potassa. After the neutralization of these substances has been accomplished, the milk loses its alkaline reaction and begins to turn sour. The free lactic acid then coagulates the casein, and the milk is curdled. The altered organic matter also acts upon the oleaginous ingredients, which are partly decomposed; and the milk begins to give off a rancid odor, owing to the development of various volatile fatty acids, among which are butyric acid, and the like. These changes are very much hastened by a moderately elevated temperature, and also by a highly electric state of the atmosphere.

The production of the milk, like that of other secretions, is liable to be much influenced by nervous impressions. It may be increased or diminished in quantity, or vitiated in quality by sudden emotions; and it is even said to have been sometimes so much altered in this way as to produce indigestion, diarrhœa, and convulsions in the infant.

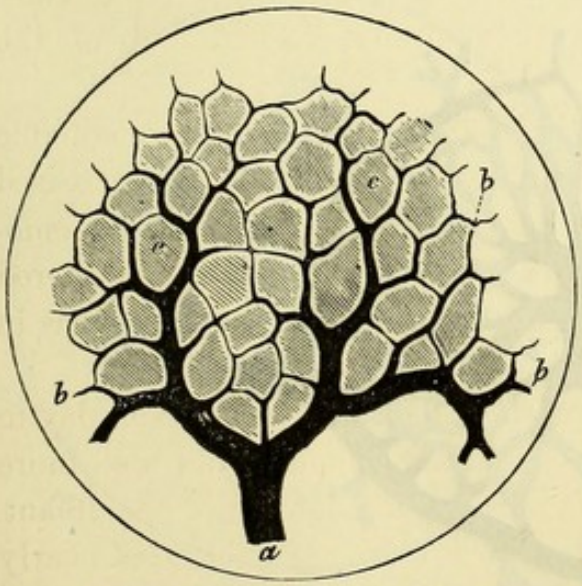
Simon found[1] that the constitution of the milk varies from day to day, owing to temporary causes; and that it undergoes also more permanent modifications, corresponding with the age of the infant. He analyzed the milk of a nursing woman during a period of nearly six months, commencing with the second day after delivery, and repeating his examinations at intervals of eight or ten days. It appears, from these observations, that the casein is at first in small quantity; but that it increases during the first two months, and

[1] Op. cit., p. 337.

then attains a nearly uniform standard. The saline matters also increase in a nearly similar manner. The sugar, on the contrary, diminishes during the same period; so that it is less abundant in the third, fourth, fifth and sixth months, than it is in the first and second. These changes are undoubtedly connected with the increasing development of the infant, which requires a corresponding alteration in the character of the food supplied to it. Finally, the quantity of butter in the milk varies so much from day to day, owing to incidental causes, that it cannot be said to follow any regular course of increase or diminution.

6. SECRETION OF THE BILE.—The anatomical peculiarities in the structure of the liver are such as to distinguish it in a marked degree from the other glandular organs. Its first peculiarity is that it is furnished principally with venous blood. For, although it receives its blood from the hepatic artery as well as from the portal vein, the quantity of arterial blood with which it is supplied is extremely small in comparison with that which it receives from the portal system. The blood which has circulated through the capillaries of the stomach, spleen, pancreas, and intestine is collected by the roots of the corresponding veins, and discharged into the portal vein, which enters the liver at the great transverse fissure of the organ. Immediately upon its entrance, the portal vein divides into two branches, right and left, which supply the corresponding portions of the liver; and these branches successively subdivide into smaller twigs and ramifications, until they are reduced to the size, according to Kölliker, of $\frac{1}{1200}$ of an inch in diameter. These veins, with their terminal branches, are arranged in such a manner as to include between them pentagonal or hexagonal spaces, or portions of the hepatic substance, $\frac{1}{36}$ to $\frac{1}{12}$ of an inch in diameter in the human subject, which can readily be distinguished by the naked eye, both on

Fig. 116.

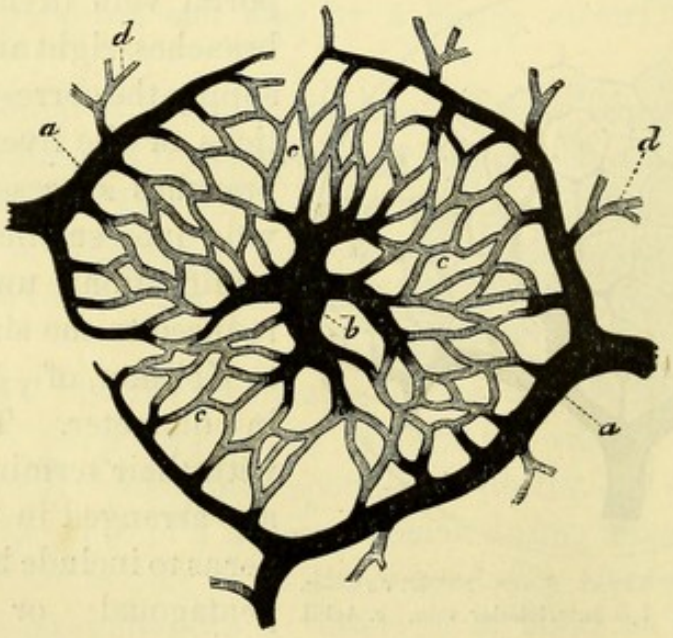


Ramification of PORTAL VEIN IN LIVER.—*a*. Twig of portal vein. *b*, *b*. Interlobular vein. *c*. Acini.

the exterior of the organ and by the inspection of cut surfaces. The portions of hepatic substance included in this way between the terminal branches of the portal vein (Fig. 116) are termed the "acini" or "lobules" of the liver; and the terminal venous branches, occupying the spaces between the adjacent lobules, are the "interlobular" veins. In the spaces between the lobules we also find the minute branches of the hepatic artery, and the commencing rootlets of the hepatic ducts. As the portal vein, the hepatic artery, and the hepatic duct enter the liver at the transverse fissure, they are closely invested by a fibrous sheath, termed Glisson's capsule, which accompanies them in their divisions and ramifications. In some of the lower animals, as in the pig, this sheath extends even to the interlobular spaces, inclosing each lobule in a thin fibrous investment, by which it is distinctly separated from the neighboring parts. In the human subject, however, Glisson's capsule becomes gradually thinner as it penetrates the liver, and disappears altogether before reaching the interlobular spaces; so that here the lobules are nearly in contact with each other by their adjacent surfaces, being separated only by the interlobular veins and the minute branches of the hepatic artery and duct previously mentioned.

From the sides of the interlobular veins, and also from their

Fig. 117.



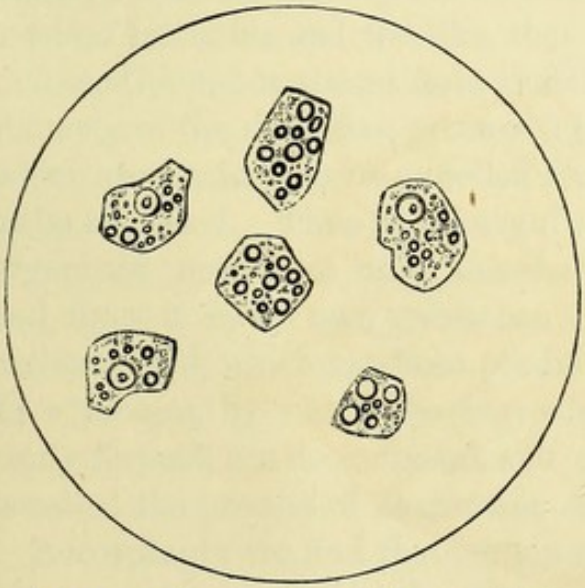
LOBULE OF LIVER, showing distribution of bloodvessels; magnified 22 diameters.—*a, a.* Interlobular veins. *b.* Intralobular vein. *c, c, c.* Lobular capillary plexus. *d, d.* Twigs of interlobular vein passing to adjacent lobules.

terminal extremities, there are given off capillary vessels, which penetrate the substance of each lobule and converge from its circumference toward its centre, inosculating at the same time freely with each other, so as to form a minute vascular plexus, the "lobular" capillary plexus. (Fig. 117.) At the centre of each lobule, the converging capillaries unite into a small vein (*b*), the "intralobular" vein, which is one of the commencing rootlets of the hepatic vein. These rootlets, uniting successively with each other, so as to form larger and larger branches, finally leave the liver at its posterior edge, to empty into the ascending vena cava.

Beside the capillary bloodvessels of the lobular plexus, each acinus is made up of an abundance of minute cellular bodies, about $\frac{1}{1200}$ of an inch in diameter, the "hepatic cells." (Fig. 118.) These cells have an irregularly pentagonal figure, and a soft consistency. They are composed of a homogeneous organic substance, in the midst of which are imbedded a large number of minute granules and generally several well defined oil-globules. There is also a round or oval nucleus, with a nucleolus, imbedded in the substance of the cell, sometimes more or less obscured by the granules and oil drops with which it is surrounded.

The exact mode in which these cells are connected with the hepatic duct was for a long time the most obscure point in the minute anatomy of the liver. It has now been ascertained, however, by the researches of Dr. Leidy, of Philadelphia,[1] and Dr. Beale, of London,[2] that they are really contained in the interior of secreting tubules, which pass off from the smaller hepatic ducts, and penetrate everywhere the substance of the lobules. The cells fill nearly or completely the whole cavity of the tubules, and the tubules, themselves lie in close proximity with each other, so as

Fig. 118.



HEPATIC CELLS. From the human subject.

[1] American Journal Med. Sci., January, 1848.

[2] On Some Points in the Minute Anatomy of the Liver. London, 1856.

to leave no space between them except that which is occupied by the capillary bloodvessels of the lobular plexus.

These cells are the active agents in accomplishing the function of the liver. It is by their influence that the blood which is brought in contact with them suffers certain changes which give rise to the secreted products of the organ. The ingredients of the bile first make their appearance in the substance of the cells. They are then transuded from one to the other, until they are at last discharged into the small biliary ducts seated in the interlobular spaces. Each lobule of the liver must accordingly be regarded as a mass of secreting tubules, lined with glandular cells, and invested with a close network of capillary bloodvessels. It follows, therefore, from the abundant inosculation of the lobular capillaries, and the manner in which they are entangled with the hepatic tissue, that the blood, in passing through the circulation of the liver, comes into the most intimate relation with the glandular cells of the organ, and gives up to them the nutritious materials which are afterward converted into the ingredients of the bile.

CHAPTER XVII.

EXCRETION.

We have now come to the last division of the great nutritive function, viz., the process of *excretion*. In order to understand fairly the nature of this process we must remember that all the component parts of a living organism are necessarily in a state of constant change. It is one of the essential conditions of their existence and activity that they should go through with this incessant transformation and renewal of their component substances. Every living animal and vegetable, therefore, constantly absorbs certain materials from the exterior, which are modified and assimilated by the process of nutrition, and converted into the natural ingredients of the organized tissues. But at the same time with this incessant growth and supply, there goes on in the same tissues an equally incessant process of waste and decomposition. For though the elements of the food are absorbed by the tissues, and converted into musculine, osteine, hæmatine and the like, they do not remain permanently in this condition, but almost immediately begin to pass over, by a continuance of the alterative process, into new forms and combinations, which are destined to be expelled from the body, as others continue to be absorbed. Thus Spallanzani and Edwards found that every organized tissue not only absorbs oxygen from the atmosphere and fixes it in its own substance; but at the same time exhales carbonic acid, which has been produced by internal metamorphosis. This process, by which the ingredients of the organic tissues, already formed, are decomposed and converted into new substances, is called the process of *Destructive Assimilation.*

Accordingly we find that certain substances are constantly making their appearance in the tissues and fluids of the body, which did not exist there originally, and which have not been introduced with the food, but which have been produced by the process of internal metamorphosis. These substances represent the waste, or physiological detritus of the animal organism. They are the forms

under which those materials present themselves, which have once formed a part of the living tissues, but which have become altered by the incessant changes characteristic of organized bodies, and which are consequently no longer capable of exhibiting vital properties, or of performing the vital functions. They are, therefore, destined to be removed and discharged from the animal frame, and are known accordingly by the name of *Excrementitious Substances.*

These excrementitious substances have peculiar characters by which they may be distinguished from the other ingredients of the living body; and they might, therefore, be made to constitute a fourth class of proximate principles, in addition to the three which we have enumerated in the preceding chapters. They are all substances of definite chemical composition, and all susceptible of crystallization. Some of the most important of them contain nitrogen, while a few are non-nitrogenous in their composition. They originate in the interior of living bodies, and are not found elsewhere, except occasionally as the result of decomposition. They are nearly all soluble in water, and are soluble without exception in the animal fluids. They are formed in the substance of the tissues, from which they are absorbed by the blood, to be afterward conveyed by the circulating fluid to certain excretory organs, particularly the kidneys, from which they are finally discharged and expelled from the body. This entire process, made up of the production of the excrementitious substances, their absorption by the blood, and their final elimination, is known as the process of *excretion.*

The importance of this process to the maintenance of life is readily shown by the injurious effects which follow upon its disturbance. If the discharge of the excrementitious substances be in any way impeded or suspended, these substances accumulate, either in the blood or in the tissues, or in both. In consequence of this retention and accumulation, they become poisonous, and rapidly produce a derangement of the vital functions. Their influence is principally exerted upon the nervous system, through which they produce most frequent irritability, disturbance of the special senses, delirium, insensibility, coma, and finally death. The readiness with which these effects are produced depends on the character of the excrementitious substance, and the rapidity with which it is produced in the body. Thus, if the elimination of carbonic acid be stopped, by overloading the atmosphere with an abundance of the same gas, death takes place at the end of a few minutes; but if the elimination of urea by the kidneys be checked, it requires three or

four days to produce a fatal result. A fatal result, however, is certain to follow, at the end of a longer or shorter time, if any one of these substances be compelled to remain in the body, and accumulate in the animal tissues and fluids.

The principal excrementitious substances known to exist in the human body are as follows:—

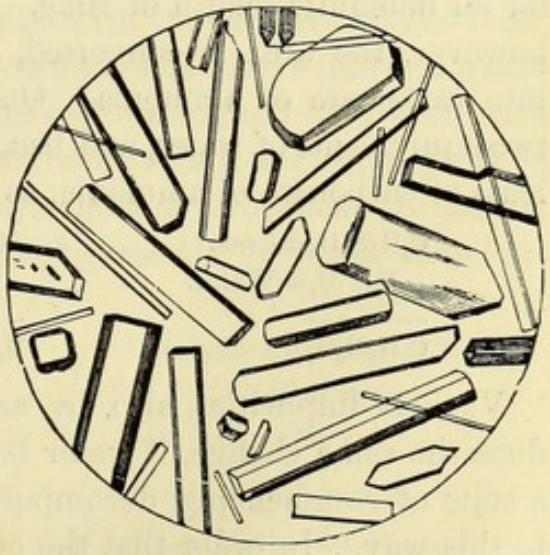
1. Carbonic acid	CO_2
2. Urea	$C_2H_4N_2O_2$
3. Creatine	$C_8H_9N_3O_4$
4. Creatinine	$C_8H_7N_3O_2$
5. Urate of soda	$NaO,C_5HN_2O_2+HO$
6. Urate of potassa	$KO,C_5HN_2O_2$
7. Urate of ammonia	$NH_4O,2C_5HN_2O_2+HO$

The physiological relations of carbonic acid have already been studied, at sufficient length, in the preceding chapters.

The remaining excrementitious substances may be examined together with the more propriety, since they are all ingredients of a single excretory fluid, viz., the urine.

UREA.—This is a neutral, crystallizable, nitrogenous substance, very readily soluble in water, and easily decomposed by various external influences. It occurs in the urine in the proportion of 30 parts per thousand; in the blood, in the normal condition, according to Picard,[1] in the proportion of 1.6 per ten thousand. The blood, however, is the source from which this substance is supplied to the urine; and it exists, accordingly, in but small quantity in the circulating fluid, for the reason that it is constantly drained off by the kidneys. But if the kidneys be extirpated, or the renal arteries tied, so that the excretion of urine is suspended, the urea then accumu-

Fig. 119.



UREA, prepared from urine, and crystallized by slow evaporation. (After Lehmann.)

[1] In Milne Edwards, Leçons sur la Physiologie, &c., vol. i. p. 297.

lates in the blood,[1] and presents itself there in considerable quantity. It has also been found in the blood, in the human subject, in cases of disease of the kidney, in unnatural proportions, amounting, in some instances, to 1.5 parts per thousand.[2] It is not yet known from what source the urea is originally derived; whether it is produced in the blood itself, or whether it is formed in some of the solid tissues, and thence taken up by the blood. It has been found, however, by Zalesky,[3] in the muscles of the healthy dog, in the exceedingly minute proportion of from one to two parts per hundred thousand.

Urea is obtained most readily from the urine. For this purpose the fresh urine is evaporated in the water bath until it has a syrupy consistency. It is then mixed with an equal volume of nitric acid, which forms nitrate of urea. This salt, being less soluble than pure urea, rapidly crystallizes, after which it is separated by filtration from the other ingredients. It is then dissolved in water and decomposed by carbonate of lead, forming nitrate of lead which remains in solution, and carbonic acid which escapes. The solution is then evaporated, the urea dissolved out by alcohol, and finally crystallized in a pure state.

Urea has no tendency to spontaneous decomposition, and may be kept, when perfectly pure, in a dry state or dissolved in water, for an indefinite length of time. If the watery solution be boiled, however, the urea is converted, during the process of ebullition, into carbonate of ammonia. One equivalent of urea unites with two equivalents of water, and becomes transformed into two equivalents of carbonate of ammonia, as follows:—

$C_2H_4N_2O_2$=Urea.	NH_3,CO_2=Carbonate of ammonia.
$H_2\ O_2$=Water.	2
$C_2H_6N_2O_4$	$N_2H_6C_2O_4$

Various impurities, also, by acting as catalytic bodies, will induce the same change, if water be present. Animal substances in a state of commencing decomposition are particularly liable to act in this way. In order that the conversion of the urea be thus pro-

[1] Prevost and Dumas. Annales de Chimie et de Physique, 1823, tome xxiii. p. 90.—Ségalas. Journal de Physiologie, tome ii. p. 354.—Mitscherlich, Tiedemann, and Gmelin. Poggendorf's Annalen, tome xxxi. p. 303.—Cl. Bernard. Liquides de l'organisme. Paris, 1859, tome ii., Deuxième Leçon.

[2] In Milne Edwards, op. cit., vol. i. p. 298.

[3] Untersuchungen über den Urämischen Process. Tübingen, 1865, Table iii.

duced, it is necessary that the temperature of the mixture be not far from 70° to 100° F.

The quantity of urea produced and discharged daily by a healthy adult is, according to the experiments of Lehmann and others, about 500 grains. It varies to some extent, like all the other secreted and excreted products, with the size and development of the body. Lehmann, in experiments on his own person, found the average daily quantity to be 501 grains. Bischoff, who was a man above the average size and weight, by similar experiments[1] found it to be 540 grains. Prof. William A. Hammond,[2] whose weight was 205 pounds, found it to be 670 grains. Prof. John C. Draper,[3] whose weight was 145 pounds, found it 408 grains.

It has been shown by Prof. John C. Draper[4] that there is also a *diurnal* variation in the normal quantity of urea. A smaller quantity is produced during the night than during the day; and this difference exists even in patients who are confined to the bed during the whole twenty-four hours, as in the case of a man under treatment for fracture of the leg. This is probably owing to the greater activity, during the waking hours, of both the mental and digestive functions. More urea is produced in the latter half than in the earlier half of the day; and the greatest quantity is discharged during the four hours from 6½ to 10½ P. M.

The quantity of urea varies also with the nature of the food. Lehmann, by experiments on his own person, found that the quantity was larger while living exclusively on animal food than with a mixed or vegetable diet; and that its quantity was smallest when confined to a diet of purely non-nitrogenous substances, as starch, sugar, and oil. The following table[5] gives the result of these experiments.

Kind of Food.	Daily Quantity of Urea.
Animal	821 grains.
Mixed	501 "
Vegetable	347 "
Non-nitrogenous	237 "

These experiments have since been abundantly confirmed; so much so as to induce the belief, with some writers, that the variations in the daily quantity of urea are principally, if not altogether, connected with the amount of nitrogenous food consumed.

[1] Bernard. Leçons de Physiologie. Paris, 1859, vol. ii. p. 31.
[2] American Journal Med. Sci., Jan., 1855, and April, 1850.
[3] New York Journal of Medicine, March, 1856.
[4] Loc. cit. [5] Lehmann, op. cit., vol. ii. p. 163.

Finally, the daily quantity of urea varies with the degree of bodily activity. Both Lehmann and Hammond found it very sensibly increased by muscular exertion and diminished by repose. The most recent and conclusive investigations on this subject are those of Prof. A. Flint, Jr.,[1] on the excretions of the pedestrian E. P. Weston, while walking an average distance of nearly 64 miles per day for five consecutive days. These experiments have the advantage, in the first place, of being carried out in an instance where an unusual amount of muscular work was performed, while the food taken did not differ essentially from that of an ordinary diet; and secondly, of being continued for a sufficiently long time, before, during, and after the exertion, to secure results more reliable than those previously obtained.

The pedestrian was under observation for fifteen days; namely, five days previous to the walk, five days during its continuance, and five days immediately afterward. For the period preceding the walk, the average exercise was about eight miles per day; for that subsequent to the walk, it was a little over two miles per day. The results obtained during the three periods showed, accordingly, the normal amount of urea excreted by the pedestrian under ordinary conditions, the amount discharged during an unusual and nearly continuous muscular exertion, and the subsequent effects of the exertion on the general condition of the system.

The nitrogenous ingredients of the food, during all three periods, were also accurately recorded, so that the influence of the food itself on the amount of urea may be estimated at the same time with that of the muscular exertion.

The following table gives the main results of these experiments, so far as they are connected with our present subject.

Daily Quantity of	First Period. Five days before the walk.	Second Period. Five days during the walk.	Third Period. Five days after the walk.
Urea	628.24 grains.	722 16 grains.	726.79 grains.
Nitrogen in food	339.46 "	234.76 "	440.93 "
Nitrogen in urea	293.18 "	337.01 "	339.17 "
Total nitrogen in urea and feces	315.09 "	361.52 "	373.15 "
Nitrogen in urea and feces per 100 parts of nitrogen in food.	95.53	174.81	91.93

It is evident, therefore, that during the time of unusual muscular exertion the daily quantity of urea was increased by nearly fifteen per cent. over that of the previous ordinary condition, the

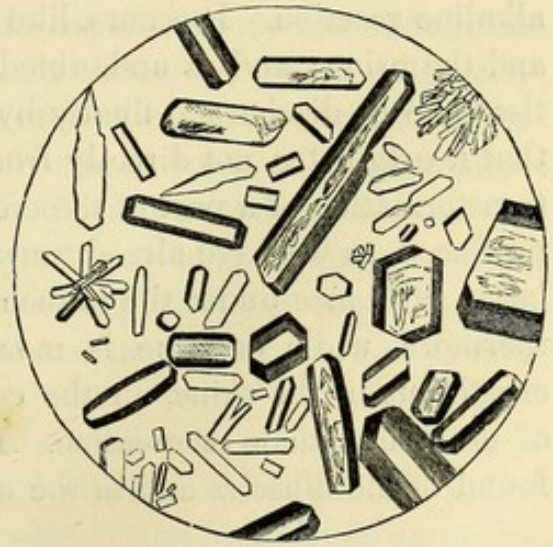
[1] New York Medical Journal, June, 1871.

nitrogenous elements of the food being at the same time considerably diminished; and that, during the period of exertion, the total quantity of nitrogen discharged by the urea and feces combined was nearly seventy-five per cent. greater than that introduced with the food, while in both the previous and subsequent periods it was from about four and a half to eight per cent. less. During the period of exertion there was a loss of nearly three and a half pounds of bodily weight, and an increase of a similar amount during the subsequent period of rest. The author fairly explains the above loss of weight by the disintegration of muscular tissue, and the subsequent increase by a retention of nitrogenous constituents in the body, to repair the waste thus produced.

"During the five days of the walk,[1] Mr. Weston consumed in all 1,173.80 grains of nitrogen in his food. During the same period he eliminated 1,807.60 grains of nitrogen, in the urine and feces. This leaves 633.80 grains of nitrogen, over and above the nitrogen of the food, which must be attributed to the waste of his tissues, and probably almost exclusively to the waste of his muscular tissue. According to the best authorities, lean meat uncooked, or muscular tissue, contains 3 per cent. of nitrogen. The loss of 633.80 grains of nitrogen would then represent a loss of 21,127.00 grains, or 3.018 lbs. of muscular tissue. The actual loss of weight was 3.450 lbs. This allows about 0.43 lb. of loss unaccounted for, which might be fat or water."

Urea exists in the urine of both the carnivorous and herbivorous quadrupeds; but, as a general rule, there is little or none to be found in that of birds, reptiles, or fish.

Fig. 120.



CREATINE, crystallized from hot water. (After Lehmann.)

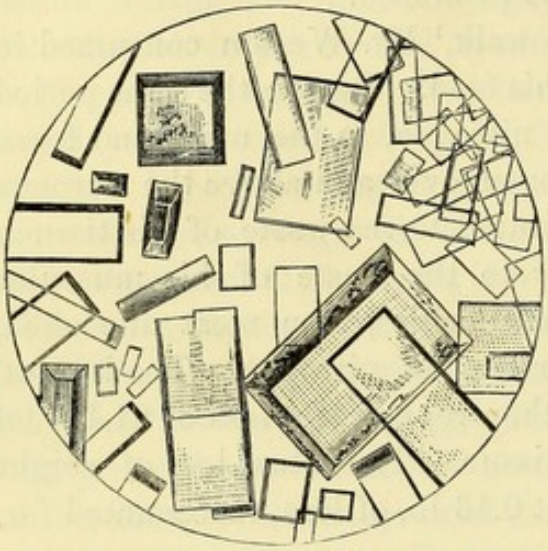
CREATINE.—This is a neutral crystallizable substance, found in the muscles, the blood, and the urine. It is soluble in water, very slightly soluble in alcohol, and not at all so in ether. By boiling with an alkali, it is either converted into carbonic acid and ammonia, or is decomposed with the production of urea and

[1] Op. cit., p. 669.

an artificial nitrogenous crystallizable substance, termed sarcosine. By being heated with strong acids, it loses two equivalents of water, and is converted into the substance next to be described, viz., creatinine.

Creatine exists in the urine, in the human subject, in the proportion of about 1.25 parts, and in the muscles in the proportion of 0.67 parts per thousand. Its quantity in the blood has not been determined. In the muscular tissue it is simply in solution in the interstitial fluid of the parts, so that it may be extracted by simply cutting the muscle into small pieces, treating it with distilled water, and subjecting it to pressure. Creatine evidently originates in the muscular tissue, is absorbed thence by the blood, and is finally discharged with the urine.

Fig. 121.



CREATININE, crystallized from hot water. (After Lehmann.)

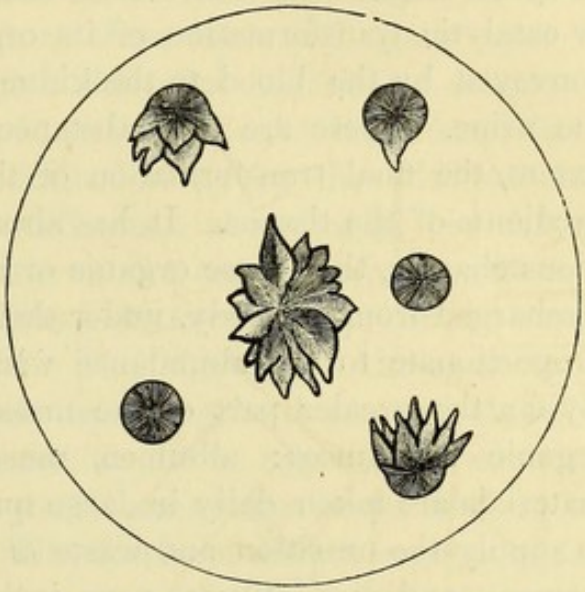
CREATININE.—This is also a crystallizable substance. It differs in composition from creatine by containing two equivalents less of the elements of water. It is more soluble in water and in spirit than creatine, and dissolves slightly also in ether. It has a distinctly alkaline reaction. It occurs, like creatine, in the muscles, the blood, and the urine; and is undoubtedly first produced in the muscular tissue, to be discharged finally by the kidneys. It is very possible that it originates, not directly from the muscles, but indirectly, by transformation of a part of the creatine; since it may be artificially produced, as we have already mentioned, by transformation of the latter substance under the influence of strong acids, and since, furthermore, while creatine is more abundant in the muscles than creatinine, in the urine, on the contrary, there is a larger quantity of creatinine than of creatine. Both these substances have been found in the muscles and in the urine of the lower animals.

URATE OF SODA.—As its name implies, this substance is a neutral salt, formed by the union of soda, as a base, with a nitrogenous animal acid, viz., *uric acid* ($C_5HN_2O_2HO$). Uric acid is sometimes

spoken of as though it were itself a proximate principle, and a constituent of the urine; but it cannot properly be regarded as such, since it never occurs in a free state, in a natural condition of the fluids. When present, it has always been produced by decomposition of the urates.

Urate of soda is readily soluble in hot water, from which a large portion again deposits on cooling. It is slightly soluble in alcohol, and insoluble in ether. It crystallizes in small globular masses, with projecting, curved, conical, wart-like excrescences. (Fig. 122.) It dissolves readily in the alkalies; and by most acid solutions it is decomposed, with the production of free uric acid.

Fig. 122.



URATE OF SODA; from a urinary deposit.

Urate of soda is a constant ingredient of human urine, in which it is next in importance to the urea; being present in the proportion of rather more than one part per thousand. It has not yet been detected in normal human blood, but has often been found both in the blood and exudations in cases of gouty and rheumatic disease. It is therefore undoubtedly either produced originally in the blood, or else formed in some of the solid tissues, and absorbed from them by the circulating fluid. It is constantly eliminated by the kidneys, in company with the other ingredients of the urine. The average daily quantity of urate of soda discharged by the healthy human subject is, according to Lehmann, about 25 grains. This substance exists in the urine of the carnivorous and omnivorous animals, but not in that of the herbivora. In the latter, it is replaced by another substance, differing somewhat from it in composition and properties, viz., hippurate of soda. The urine of herbivora, however, while still very young and living upon the milk of the mother, has been found to contain urates. But when the young animal is weaned, and becomes herbivorous, the urate of soda disappears, and is replaced by the hippurate.

The *urates of potassa and ammonia* resemble the preceding salt very closely in their physiological relations. They are formed in much smaller quantity than the urate of soda, and appear like it as ingredients of the urine.

Formation and General Characters of the Urine.—The substances above enumerated closely resemble each other in their most striking and important characters. They all contain nitrogen, are all crystallizable, and all readily soluble in water. They all originate in the interior of the body by the decomposition or catalytic transformation of its organic ingredients, and are all conveyed by the blood to the kidneys, to be finally expelled with the urine. These are the substances which represent, to a great extent, the final transformation of the organic or albuminoid ingredients of the tissues. It has already been mentioned, in a previous chapter, that these organic or albuminoid substances are not discharged from the body, under their own form, in quantity at all proportionate to the abundance with which they are introduced. By far the greater part of the mass of the frame is made up of organic substances: albumen, musculine, osteine, &c. Similar materials are taken daily in large quantity with the food, in order to supply the nutrition and waste of those already composing the tissues; and yet only a very insignificant quantity of similar material is expelled with the excretions. A minute proportion of volatile animal matter is exhaled with the breath, and a minute proportion also with the perspiration. A very small quantity is discharged under the form of mucus and coloring matter, with the urine and feces; but all these taken together are entirely insufficient to account for the constant and rapid disappearance of organic matters in the interior of the body. These matters, in fact, before being discharged, are converted by catalysis and decomposition into new substances. Carbonic acid, under which form 3500 grains of carbon are daily expelled from the body, is one of these substances; the others are urea, creatine, creatinine, and the urates.

We see, then, in what way the organic matters, in ceasing to form a part of the living body, lose their characteristic properties, and are converted into crystallizable substances, of definite chemical composition. It is a kind of retrograde metamorphosis, by which they return more or less to the condition of ordinary inorganic

materials. These excrementitious matters are themselves decomposed, after being expelled from the body, under the influence of the atmospheric air and moisture; so that the decomposition and destruction of the organic substances are at last complete.

It will be seen, consequently, that the urine has a character altogether peculiar, and one which distinguishes it completely from every other animal fluid. All the others are either nutritive fluids, like the blood and milk, or are destined, like the secretions generally, to take some direct and essential part in the vital operations. Many of them, like the gastric and pancreatic juices, are reabsorbed after they have done their work, and again enter the current of the circulation. But the urine is merely a solution of excrementitious substances. Its materials exist beforehand in the circulation, and are simply drained away by the kidneys from the blood. There is a wide difference, accordingly, between the action of the kidneys and that of the true glandular organs, in which certain new and peculiar substances are produced by the action of the glandular tissue. The kidneys, on the contrary, do not secrete anything, properly speaking, and are not, therefore, glands. In their mode of action, so far as regards the excretory function, they have more resemblance to the lungs than to any other of the internal organs. But this resemblance is not complete. For, in the first place, the lungs are adapted, by their anatomical structure, to the absorption and exhalation of gases; while the matters discharged by the kidneys are in a liquid form, the solid substances being dissolved in the water of the urine. Furthermore, the lungs perform a double function, absorbing oxygen at the same time that they exhale carbonic acid; while the kidneys are exclusively occupied in the discharge of the urine, absorbing nothing in return. The kidneys alone, therefore, of all the organs in the body, are purely excretory in their office. The urine is not intended to fulfil any function, mechanical, chemical, or otherwise; but is destined only to be eliminated and expelled. Since it possesses so peculiar and important a character, it will require to be carefully studied in detail.

The *urine* is a clear, watery, amber-colored fluid, with a distinctly acid reaction. It has, while still warm, a peculiar odor, which disappears more or less completely on cooling, and returns when the urine is gently heated. The ordinary quantity of urine discharged daily by a healthy adult is about 35 fluid ounces, and its mean specific

gravity, 1024. Both its total quantity, however, and its mean specific gravity are liable to vary somewhat from day to day, owing to the different proportions of water and solid ingredients entering into its constitution. Ordinarily the water of the urine is more than sufficient to hold all the solid matters in solution; and its proportion may therefore be diminished by accidental causes without the urine becoming turbid by the formation of a deposit. Under such circumstances, it merely becomes deeper in color, and of a higher specific gravity. Thus, if a smaller quantity of water than usual be taken into the system with the drink, or if the fluid exhalations from the lungs and skin, or the intestinal discharges, be increased, a smaller quantity of water will necessarily pass off by the kidneys; and the urine will be diminished in quantity, while its specific gravity is increased. We have observed the urine to be reduced in this way to eighteen or twenty ounces per day, its specific gravity rising at the same time to 1030. On the other hand, if the fluid ingesta be unusually abundant, or if the perspiration be diminished, the surplus quantity of water will pass off by the kidneys; so that the amount of urine in twenty-four hours may be increased to forty-five or forty-six ounces, and its specific gravity reduced at the same time to 1020 or even 1017. Under these conditions the total amount of solid matter discharged daily remains about the same. The changes above mentioned depend simply upon the fluctuating quantity of water, which may pass off by the kidneys in larger or smaller quantity, according to accidental circumstances. In these purely normal or physiological variations, therefore, the entire quantity of the urine and its mean specific gravity vary always in an inverse direction with regard to each other; the former increasing while the latter diminishes, and *vice versâ*. If, however, it should be found that both the quantity and specific gravity of the urine were increased or diminished at the same time, or if either one were increased or diminished while the other remained stationary, such an alteration would show an actual change in the total amount of solid ingredients, and would indicate an unnatural and pathological condition. This actually takes place in certain forms of disease.

The amount of variation in the quantity of water, even, may be so great as to constitute by itself a pathological condition. Thus, in hysterical attacks there is sometimes a very abundant flow of limpid, nearly colorless urine, with a specific gravity not over 1005 or 1006. On the other hand, in the onset of febrile attacks, the

quantity of water is often so much diminished that it is no longer sufficient to retain in solution all the solid ingredients of the urine, and the urate of soda is thrown down, after cooling, as a fine red or yellowish sediment. So long, however, as the variation is confined within strictly physiological limits, all the solid ingredients are held in solution, and the urine remains clear.

There is also, in a state of health, a *diurnal variation* of the urine, both in regard to its specific gravity and its degree of acidity. The urine is generally discharged from the bladder five or six times during the twenty-four hours, and at each of these periods shows more or less variation in its physical characters. We have found that the urine which collects in the bladder during the night, and is first discharged in the morning, is usually dense, highly colored, of a strongly acid reaction, and a high specific gravity. That passed during the forenoon is pale, and of a low specific gravity, sometimes not more than 1018 or even 1015. It is at the same time neutral or slightly alkaline in reaction. Toward the middle of the day, its density and depth of color increase, and its acidity returns. All these properties become more strongly marked during the afternoon and evening, and toward night the urine is again deeply colored and strongly acid, and has a specific gravity of 1028 or 1030.

The following instances will serve to show the general characters of this variation:—

OBSERVATION FIRST. *March 20th.*

Urine of	1st	discharge,	acid,	sp. gr.	1025.
"	2d	"	alkaline,	"	1015.
"	3d	"	neutral,	"	1018.
"	4th	"	acid,	"	1018.
"	5th	"	acid,	"	1027.

OBSERVATION SECOND. *March 21st.*

Urine of	1st	discharge,	acid,	sp. gr.	1029.
"	2d	"	neutral,	"	1022.
"	3d	"	neutral,	"	1025.
"	4th	"	acid,	"	1027.
"	5th	"	acid,	"	1030.

These variations do not always follow the perfectly regular course manifested in the above instances, since they are somewhat liable, as we have already mentioned, to temporary modification from accidental causes during the day; but their general tendency nearly always corresponds with that given above.

It is evident, therefore, that whenever we wish to test the specific

gravity and acidity of the urine in cases of disease, it will not be sufficient to examine any single specimen taken at random; but all the different portions discharged during the day should be collected and examined together. Otherwise, we should incur the risk of regarding as a permanently morbid symptom what might be nothing more than a purely accidental and temporary variation.

The *chemical constitution* of the urine as it is discharged from the bladder, according to the analyses of Berzelius, Lehmann, Becquerel, and others, is as follows:—

COMPOSITION OF THE URINE.

Water	938.00
Urea	30.00
Creatine	1.25
Creatinine	1.50
Urate of soda " potassa " ammonia	1.80
Coloring matter and Mucus	.30
Biphosphate of soda Phosphate of soda " potassa " magnesia " lime	12.45
Chlorides of sodium and potassium	7.80
Sulphates of soda and potassa	6.90
	1000.00

We need not repeat that the proportionate quantity of these different ingredients, as given above, is not absolute, but only approximative; and that they vary, from time to time, within certain physiological limits, like the ingredients of all other animal fluids.

The urea, creatine, creatinine and urates have all been sufficiently described above. The mucus and coloring matter, unlike the other ingredients of the urine, belong to the class of organic substances proper. They are both present, as may be seen by the analysis quoted above, in a very small quantity. The coloring matter, or *urosacine*, is in solution in a natural condition of the urine, but it is apt to be entangled by any accidental deposits which may be thrown down, and more particularly by those consisting of the urates. These deposits, from being often strongly colored red or pink by the urosacine thus thrown down with them, are known under the name of "brick-dust" sediments.

The *mucus* of the urine comes from the lining membrane of the

urinary bladder. When first discharged it is not visible, owing to its being uniformly disseminated through the urine by mechanical agitation; but if the fluid be allowed to remain at rest for some hours in a cylindrical glass vessel, the mucus collects at the bottom, and may then be seen as a light cottony cloud, interspersed often with minute semi-opaque points. It plays, as we shall hereafter see, a very important part in the subsequent fermentation and decomposition of the urine.

Biphosphate of soda exists in the urine by direct solution, since it is readily soluble in water. It is this salt which gives to the urine its acid reaction, as there is no free acid present, in the recent condition. It is probably derived from the neutral phosphate of soda in the blood which is decomposed by the uric acid at the time of its formation; producing, on the one hand, a urate of soda, and converting a part of the neutral phosphate of soda into the acid biphosphate.

The *phosphates of lime and magnesia,* or the "earthy phosphates," as they are called, exist in the urine by indirect solution. Though insoluble, or very nearly so, in pure water, they are held in solution in the urine by the acid phosphate of soda, above described. They are derived from the blood, in which they exist in considerable quantity. When the urine is alkaline, these phosphates are deposited as a light-colored precipitate, and thus communicate a turbid appearance to the fluid. When the urine is neutral, they may still be held in solution, to some extent, by the chloride of sodium, which has the property of dissolving a small quantity of phosphate of lime.

The remaining ingredients, phosphates of soda and potassa, sulphates and chlorides, are all derived from the blood, and are held directly in solution by the water of the urine.

The urine, constituted by the above ingredients, forms, as we have already described, a clear amber-colored fluid, with a reaction for the most part distinctly acid, sometimes neutral, and occasionally slightly alkaline. In its healthy condition it is affected by chemical and physical reagents in the following manner.

Boiling the urine does not produce any visible change, provided its reaction be acid. If it be neutral or alkaline, and if, at the same time, it contain a larger quantity than usual of the earthy phosphates, it will become turbid on boiling; since these salts are less soluble at a high than at a low temperature.

The addition of nitric or other mineral acid produces at first only

a slight darkening of the color, owing to the action of the acid upon the organic coloring matter of the urine. If the mixture, however, be allowed to stand for some time, the urates will be decomposed, and pure uric acid, which is very insoluble, will be deposited in a crystalline form upon the sides and bottom of the glass vessel. It must be remembered that uric acid does not normally exist in the urine under its own form, but in combination with the alkalies, as the urate of soda, potassa, &c. It is only when this combination is destroyed by the addition of a free acid, that the uric acid is liberated, and, owing to its insolubility, appears as a crystalline deposit. Its crystals have most frequently the form of transparent rhomboidal plates, or oval laminæ with pointed extremities. They are usually tinged of a yellowish hue by the coloring matter of the urine which is united with them at the time of their deposit. They are frequently arranged in radiated clusters, or small spheroidal masses, so as to present the appearance of minute calculous concretions. (Fig. 123.) The crystals vary very much in size and regularity, according to the time occupied in their formation.

Fig. 123.

Uric Acid; deposited from urine.

If a free alkali, such as potassa or soda, be added to the urine so as to neutralize its acid reaction, it becomes immediately turbid from a deposit of the earthy phosphates, which are insoluble in alkaline fluids.

The addition of nitrate of baryta, chloride of barium or subacetate of lead to healthy urine, produces a dense precipitate, owing to the presence of the alkaline sulphates.

Nitrate of silver produces a precipitate with the chlorides of sodium and potassium.

Subacetate of lead and nitrate of silver precipitate also the organic substances, mucus and coloring matter, present in the urine.

All the above reactions, it will be seen, are owing to the presence of the natural ingredients of the urine, and do not, therefore, indicate any abnormal condition of the excretion.

Beside the properties mentioned above, the urine has several others which are of some importance, and which have not been usually noticed in previous descriptions. It contains, among other ingredients, certain organic substances which have the power of interfering with the mutual reaction of starch and iodine, and even of decomposing the iodide of starch, after it has once been formed. This peculiar action of the urine was first noticed and described by us in 1856.[1] If ʒj of iodine water be mixed with a solution of starch, it strikes an opaque blue color; but if ʒj of fresh urine be afterward added to the mixture, the color is entirely destroyed at the end of four or five seconds. If fresh urine be mixed with four or five times its volume of iodine water, and starch be subsequently added, no union takes place between the starch and iodine, and no blue color is produced. In these instances, the iodine unites with the animal matters of the urine in preference to combining with the starch, and is consequently prevented from striking its ordinary blue color with the latter. This interference occurs whether the urine be acid or alkaline in reaction. In all cases in which iodine exists in the urine, as for example where it has been administered as a medicine, it is under the form of an organic combination; and in order to detect its presence by means of starch, a few drops of nitric acid must be added at the same time, so as to destroy the organic matters, after which the blue color immediately appears, if iodine be present. This reaction with starch and iodine belongs also, to some extent, to most of the other animal fluids, as the saliva, gastric and pancreatic juices, serum of the blood, &c.; but it is most strongly marked in the urine.

Another remarkable property of the urine, also dependent on its organic ingredients, is that of interfering with Trommer's test for grape sugar. If clarified honey be mixed with fresh urine, and sulphate of copper with an excess of potassa be afterward added, the mixture takes a dingy, grayish-blue color. On boiling, the color turns yellowish or yellowish-brown, but the suboxide of copper is not deposited. In order to remove the organic matter and detect the sugar, the urine must be first treated with an excess of animal charcoal and filtered. By this means the organic substances are retained upon the filter, while the sugar passes through in solution, and may then be detected as usual by Trommer's test.

[1] American Journal Med. Sci., April, 1856.

Accidental Ingredients of the Urine.—Since the urine, in its natural state, consists of materials which are already prepared in the blood, and which merely pass out through the kidneys by a kind of filtration, it is not surprising that most medicinal and poisonous substances, introduced into the circulation, should be expelled from the body by the same channel. Those substances which tend to unite strongly with the animal matters, and to form with them insoluble compounds, such as the preparations of iron, lead, silver, arsenic, mercury, &c., are least liable to appear in the urine. They may occasionally be detected in this fluid when they have been given in large doses, but when administered in moderate quantity are not usually to be found there. Most other substances, however, accidentally present in the circulation, pass off readily by the kidneys, either in their original form, or after undergoing certain chemical modifications.

The salts of the organic acids, such as *lactates, acetates, malates,* &c., of soda and potassa, when introduced into the circulation, are replaced by the carbonates of the same bases, and appear under that form in the urine. The urine accordingly becomes alkaline from the presence of the carbonates, whenever the above salts have been taken in large quantity, or after the ingestion of fruits and vegetables which contain them. We have already spoken (Chap. II.) of the experiments of Lehmann, in which he found the urine exhibiting an alkaline reaction, a very few minutes after the administration of lactates and acetates. In one instance, by experimenting upon a person with congenital extroversion of the bladder, in whom the orifices of the ureters were exposed,[1] he found that the urine became alkaline in the course of seven minutes after the ingestion of half an ounce of acetate of potassa.

The *pure alkalies and their carbonates,* according to the same observer, produce a similar effect. Bicarbonate of potassa, for example, administered in doses of two or three drachms, causes the urine to become neutral in from thirty to forty-five minutes, and alkaline in the course of an hour. It is in this way that certain "anti-calculous" or "anti-lithic" nostrums operate, when given with a view of dissolving concretions in the bladder. These remedies, which are usually strongly alkaline, pass into the urine, and by giving it an alkaline reaction, produce a precipitation of the earthy phosphates. Such a precipitate, however, so far from indicating the

[1] Physiological Chemisty, vol. ii. p. 133.

successful disintegration and discharge of the calculus, can only tend to increase its size by additional deposit.

Ferrocyanide of potassium, when introduced into the circulation, appears readily in the urine. Bernard[1] observed that a solution of this salt, after being injected into the duct of the submaxillary gland, could be detected in the urine at the end of twenty minutes.

Iodine, in all its combinations, passes out by the same channel. We have found that after the administration of half a drachm of the syrup of iodide of iron, iodine appears in the urine at the end of thirty minutes, and continues to be present for nearly twenty-four hours. In the case of two patients who had been taking iodide of potassium freely, one of them for two months, the other for six weeks, the urine still contained iodine at the end of three days after the suspension of the medicine. In three days and a half, however, it was no longer to be detected. Iodine appears also, after being introduced into the circulation, both in the saliva and the perspiration.

Quinine, when taken as a remedy, has also been detected in the urine. *Ether* passes out of the circulation in the same way. We have observed the odor of this substance very perceptibly in the urine, after it had been inhaled for the purpose of producing anæsthesia. The *bile-pigment* passes into the urine in great abundance in some cases of jaundice, so that the urine may have a deep yellow or yellowish brown tinge, and may even stain linen clothes, with which it comes in contact, of a similar color. The *saline biliary substances*, viz., glyko-cholate and tauro-cholate of soda, have occasionally, according to Lehmann, been also found in the urine. In these instances the biliary matters are reabsorbed from the hepatic ducts, and afterward conveyed by the blood to the kidneys.

Sugar.—When sugar exists in unnatural quantity in the blood, it passes out with the urine. We have repeatedly found that if sugar be artificially introduced into the circulation in rabbits, or injected into the subcutaneous areolar tissue so as to be absorbed by the blood, it is soon discharged by the kidneys. It has been shown by Bernard[2] that the rapidity with which this substance appears in the urine under these circumstances varies with the quantity injected and the kind of sugar used for the experiment. If a solution of 15 grains of glucose be injected into the areolar tissue of a rabbit

[1] Leçons de Physiologie Expérimentale, 1856, p. 111.

[2] Ibid., 1855, p. 214 *et seq.*

weighing a little over two pounds, it is entirely destroyed in the circulation, and does not pass out with the urine. A dose of 23 grains, however, injected in the same way, appears in the urine at the end of two hours, 30 grains in an hour and a half, 38 grains in an hour, and 188 grains in fifteen minutes. Again, the kind of sugar used makes a difference in this respect. For while 15 grains of glucose may be injected without passing out by the kidneys, 7½ grains of cane sugar, introduced in the same way, fail to be completely destroyed in the circulation, and may be detected in the urine. In certain forms of disease (diabetes), where sugar accumulates in the blood, it is eliminated by the same channel; and a saccharine condition of the urine, accompanied by an increase in its quantity and specific gravity, constitutes the most characteristic feature of the disease.

Finally, *albumen* sometimes shows itself in the urine in consequence of various morbid conditions. Most acute inflammations of the internal organs, as pneumonia, pleurisy, &c., are liable to be accompanied, at their outset, by a congestion of the kidneys, which produces a temporary exudation of the albuminous elements of the blood. Albumen has been found in the urine, according to Simon, Becquerel, and others, in pericarditis, pneumonia, pleurisy, bronchitis, hepatitis, inflammation of the brain, peritonitis, metritis, &c. We have observed it, as a temporary condition, in pneumonia and after amputation of the thigh. Albuminous urine also occurs frequently in pregnant women, and in those affected with abdominal tumors, where the pressure upon the renal veins is sufficient to produce passive congestion of the kidneys. When the renal congestion is spontaneous in its origin, and goes on to produce actual degeneration of the tissue of the kidneys, as in Bright's disease, the same symptom occurs, and remains as a permanent condition. In all such instances, however, as the above, where foreign ingredients exist in the urine, these substances do not originate in the kidneys themselves, but are derived from the blood, in the same manner as the natural ingredients of the excretion.

Changes in the Urine during Decomposition.—When the urine is allowed to remain exposed, after its discharge, at ordinary temperatures, it becomes decomposed, after a time, like any other animal fluid; and this decomposition is characterized by certain changes which take place in a regular order of succession, as follows:—

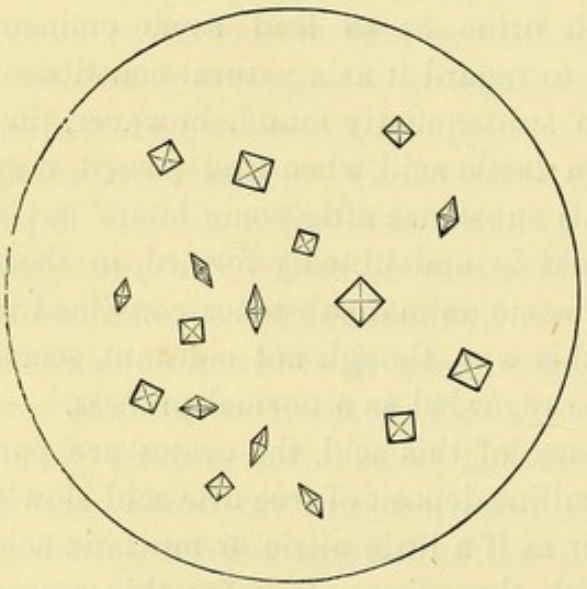
After a few hours of repose, the mucus of the urine, as we have mentioned above, collects near the bottom of the vessel as a light, nearly transparent, cloudy layer. This mucus, being an organic substance, is liable to putrefaction; and if the temperature to which it is exposed be between 60° and 100° F., it soon becomes altered, and communicates these alterations more or less rapidly to the supernatant fluid. The first of these changes is called the *acid fermentation* of the urine. It consists in the production of a free acid, usually lactic acid, from some of the undetermined animal matters contained in the excretion. This fermentation takes place very early; within the first twelve, twenty-four, or forty-eight hours, according to the elevation of the surrounding temperature. Perfectly fresh urine, as we have already stated, contains no free acid, its acid reaction with test paper being dependent entirely on the presence of biphosphate of soda. Lactic acid nevertheless has been so frequently found in nearly fresh urine as to lead some eminent chemists (Berzelius, Lehmann) to regard it as a natural constituent of the excretion. It has been subsequently found, however, that urine, though entirely free from lactic acid when first passed, may frequently present traces of this substance after some hours' exposure to the air. The lactic acid is undoubtedly formed, in these cases, by the decomposition of some animal substance contained in the urine. Its production in this way, though not constant, seems to be sufficiently frequent to be regarded as a normal process.

In consequence of the presence of this acid, the urates are partially decomposed; and a crystalline deposit of free uric acid slowly takes place, in the same manner as if a little nitric or muriatic acid had been artificially mixed with the urine. It is for this reason that urine which is abundant in the urates frequently shows a deposit of crystallized uric acid some hours after it has been passed, though it may have been perfectly free from deposit at the time of its emission.

During the period of the "acid fermentation," there is reason to believe that oxalic acid is also sometimes produced, in a similar manner with the lactic. It is very certain that the deposit of oxalate of lime, far from being a dangerous or even morbid symptom, as it was at one time regarded, is frequently present in perfectly normal urine after a day or two of exposure to the atmosphere. We have often observed it, under these circumstances, when no morbid symptom could be detected in connection either with the kidneys or with any other bodily organ. Now, whenever oxalic

acid is formed in the urine, it must necessarily be deposited under the form of oxalate of lime; since this salt is entirely insoluble both in water and in the urine, even when heated to the boiling point. It is difficult to understand, therefore, when oxalate of lime is found as a deposit in the urine, how it can previously have been held in solution. Its oxalic acid is in all probability gradually formed, as we have said, in the urine itself; uniting, as fast as it is produced, with the lime previously in solution, and thus appearing as a crystalline deposit of oxalate of lime. It is much more probable that this is the true explanation, since, in the cases to which we allude, the crystals of oxalate of lime grow, as it were, in the cloud of mucus which collects at the bottom of the vessel, while the supernatant fluid remains clear. These crystals are of minute size, transparent, and colorless, and have the form of regular octohedra, or double quadrangular pyramids, united base to base. (Fig. 124.) They make their appearance usually about the commencement of the second day, the urine at the same time continuing clear and retaining its acid reaction. This deposit is of frequent occurrence when no substance containing oxalic acid or oxalates has been taken with the food.

Fig. 124.



Oxalate of Lime; deposited from healthy urine, during the acid fermentation.

The precise source from which the oxalic acid, under these circumstances, is derived has not been fully determined. The most probable explanation is that it is produced from a metamorphosis of a small portion of the uric acid of the urine. It is known that if uric acid be boiled in twenty parts of water with peroxide of lead, it is decomposed and oxidized with the production, among other substances, of urea and oxalic acid; and it is supposed that some similar change may take place in the urine, causing the appearance of a minute quantity of oxalic acid, which at once decomposes a portion of the lime-salts, and thus appears as a crystalline deposit of oxalate of lime.

At the end of some days the changes above described

come to an end, and are succeeded by a different process known as the *alkaline fermentation.* This consists essentially in the decomposition or metamorphosis of urea into carbonate of ammonia. As the alteration of the mucus advances, it loses the power of producing lactic and oxalic acids, and becomes a ferment capable of acting by catalysis upon the urea, and of exciting its decomposition as above. We have already mentioned that urea may be converted into carbonate of ammonia by prolonged boiling or by contact with decomposing animal substances. In this conversion, the urea unites with the elements of two equivalents of water; and consequently it is not susceptible of the transformation when in a dry state, but only when in solution or supplied with a sufficient quantity of moisture. The presence of mucus, in a state of incipient decomposition, is also necessary, to act the part of a catalytic body. Consequently if the urine, when first discharged, be passed through a succession of close filters, so as to separate its mucus, it may be afterward kept, for an indefinite time, without alteration. But under ordinary circumstances, the mucus, as soon as its putrefaction has commenced, excites the decomposition of the urea, and carbonate of ammonia begins to be developed.

The first portions of the ammoniacal salt thus produced neutralize a corresponding quantity of the biphosphate of soda, so that the acid reaction of the urine diminishes in intensity. This reaction gradually becomes weaker, as the fermentation proceeds, until it at last disappears altogether, and the urine becomes neutral. The production of carbonate of ammonia still continuing, the reaction of the fluid then becomes alkaline, and its alkalescence grows more strongly pronounced with the constant accumulation of the ammoniacal salt.

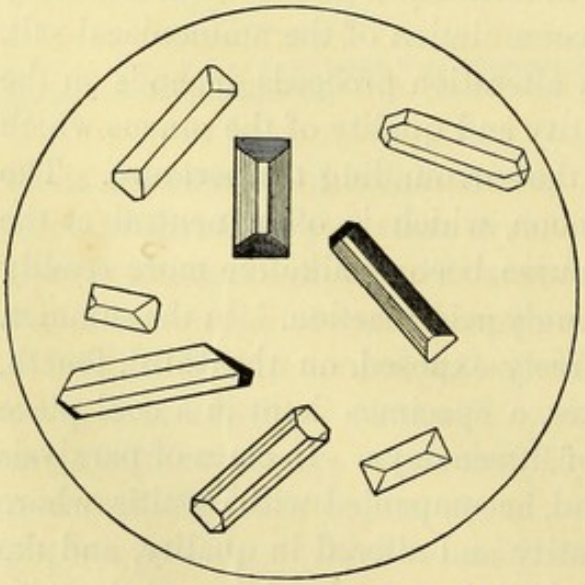
The rapidity with which this alteration proceeds depends on the character of the urine, the quantity and quality of the mucus which it contains, and the elevation of the surrounding temperature. The urine passed early in the forenoon, which is often neutral at the time of its discharge, will of course become alkaline more readily than that which has at first a strongly acid reaction. In the summer, urine will become alkaline, if freely exposed, on the third, fourth, or fifth day; while in the winter, a specimen kept in a cool place may still be neutral at the end of fifteen days. In cases of paralysis of the bladder, on the other hand, accompanied with cystitis, where the mucus is increased in quantity and altered in quality, and the urine is retained in the bladder for ten or twelve hours at the temperature of the body, the change may go on much more rapidly, so

that the urine may be distinctly alkaline and ammoniacal at the time of its discharge. In these cases, however, it is really acid when first secreted by the kidneys, and becomes alkaline while retained in the interior of the bladder.

The first effect of the alkaline condition of the urine, thus produced, is the precipitation of the earthy phosphates. These salts, being insoluble in neutral and alkaline fluids, begin to precipitate as soon as the natural acid reaction of the urine has fairly disappeared, and thus produce in the fluid a whitish turbidity. This precipitate slowly settles upon the sides and bottom of the vessel, or is partly entangled with certain animal matters which rise to the surface and form a thin, opaline scum upon the urine. There are no crystals to be seen at this time, but the deposit is entirely amorphous and granular in character.

The next change consists in the production of two new double salts by the action of carbonate of ammonia on the phosphates of soda and magnesia. One of these is the "triple phosphate," phosphate of magnesia and ammonia ($2MgO,NH_4O,PO_5+2HO$). The other is the phosphate of soda and ammonia (NaO,NH_4O,HO,PO_5+8HO). The phosphate of magnesia and ammonia is formed from the phosphate of magnesia in the urine ($3MgO,PO_5+7HO$) by the replacement of one equivalent of magnesia by one of ammonia. The crystals of this salt are very elegant and characteristic. They show themselves throughout all parts of the mixture; growing gradually in the mucus at the bottom, adhering to the sides of the glass, and scattered abundantly over the film which collects upon the surface. By their refractive power, they give to this film a peculiar glistening and iridescent appearance, which is nearly always visible at the end of six or seven days. The crystals are perfectly colorless and transparent, and have the form of triangular prisms, generally with bevelled extremities. (Fig. 125.) Frequently, also, their edges and angles are

Fig. 125.



PHOSPHATE OF MAGNESIA AND AMMONIA; deposited from healthy urine, during alkaline fermentation.

replaced by secondary facets. They are insoluble in alkalies, but are easily dissolved by acids, even in a very dilute form. At first they are of minute size, but gradually increase, so that after seven or eight days they may become visible to the naked eye.

The phosphate of soda and ammonia is formed, in a similar manner to the above, by the union of ammonia with the phosphate of soda previously existing in the urine. Its crystals resemble very much those just described, except that their prisms are of a quadrangular form, or some figure derived from it. They are intermingled with the preceding in the putrefying urine, and are affected in a similar way by chemical reagents.

As the putrefaction of the urine continues, the carbonate of ammonia which is produced, after saturating all the other ingredients with which it is capable of entering into combination, begins to be given off in a free form. The urine then acquires a strong ammoniacal odor; and a piece of moistened test paper, held a little above its surface, will have its color immediately turned by the alkaline gas escaping from the fluid. This is the source of the ammoniacal vapor which is so freely given off from stables and from dung heaps, or wherever urine is allowed to remain and decompose. This process continues until all the urea has been destroyed, and until the products of its decomposition have either united with other substances, or have finally escaped in a gaseous form.

Renovation of the Body by the Nutritive Process.—We can now estimate, from the foregoing details, the entire quantity of material assimilated and decomposed by the living body. For we have already seen how much food is taken into the alimentary canal and absorbed by the blood after digestion, and how much oxygen is appropriated from the atmosphere in the process of respiration. We have also learned the amount of carbonic acid evolved with the breath, and that of the various excretory substances discharged from the body. The following table shows, in an approximative manner, the quantity of these different ingredients of the ingesta and egesta, as compiled from the results of experiment already given in the foregoing pages.

Absorbed during 24 hours.		Discharged during 24 hours.	
Oxygen	1.470 lbs.	Carbonic acid	1.630 lbs.
Water	4.535 "	Aqueous vapor	1.155 "
Albuminous matter	.305 "	Perspiration	1.930 "
Starch	.660 "	Water of the urine	2.020 "
Fat	.220 "	Urea and salts	.137 "
Salts	.040 "	Feces	.358 "
	7.230		7.230

Rather more than seven pounds, therefore, are absorbed and discharged daily by the healthy adult human subject; and, for a man having the average weight of 140 pounds, a quantity of material, equal to the weight of the entire body, thus passes through the system in the course of twenty days.

It is evident, also, that this is not a simple phenomenon of the passage, or filtration, of foreign substances through the animal frame. The materials which are absorbed actually combine with the tissues, and form a part of their substance; and it is only after undergoing subsequent decomposition, that they finally make their appearance in the excretions. None of the solid ingredients of the food are discharged under their own form in the urine, viz., as starch, fat, or albumen; but they are replaced by urea and other crystallizable substances, of a different nature. Even the carbonic acid exhaled by the breath, as experience has taught us, is not produced by a direct oxidation of carbon; but originates by a process of decomposition, throughout the tissues of the body, somewhat similar to that by which it is generated in the decomposition of sugar by fermentation. These phenomena, therefore, indicate an actual change in the substance of which the body is composed, and show that its entire ingredients are incessantly renewed under the influence of the vital operations.

SECTION II.

NERVOUS SYSTEM.

CHAPTER I.

GENERAL STRUCTURE AND FUNCTIONS OF THE NERVOUS SYSTEM.

In entering upon the study of the nervous system, we commence the examination of an entirely different order of phenomena from those which have thus far engaged our attention. Hitherto we have studied the physical and chemical actions taking place in the body and constituting together the process of nutrition. We have seen how the lungs absorb and exhale different gases; how the stomach dissolves the food introduced into it, and how the tissues produce and destroy different substances by virtue of the varied transformations which take place in their interior. In all these instances, we have found each organ and each tissue possessing certain properties and performing certain functions, of a physical or chemical nature, which belong exclusively to it, and are characteristic of its action.

The functions of the nervous system, however, are neither physical nor chemical in their nature. They do not correspond, in their mode of operation, with any known phenomena belonging to these two orders. The nervous system, on the contrary, acts only upon other organs, in some unexplained manner, so as to excite or modify the functions peculiar to them. It is not therefore an apparatus which acts for itself, but is intended entirely for the purpose of influencing, in an indirect manner, the action of other organs. Its object is to connect and associate the functions of different

parts of the body, and to cause them to act in harmony with each other.

This object may be more fully exemplified as follows:—

Each organ and tissue in the body has certain properties peculiar to it, which may be called into activity by the operation of a stimulus or exciting cause. This capacity, which all the organs possess, of reacting under the influence of a stimulus, is called their excitability, or *irritability*. We have often had occasion to notice this property of irritability, in experiments related in the foregoing pages. We have seen, for example, that if the heart of a frog, after being removed from the body, be touched with the point of a needle, it immediately contracts, and repeats the movement of an ordinary pulsation. If the leg of a frog be separated from the thigh, its integument removed, and the poles of a galvanic battery brought in contact with the exposed surface of the muscles, a violent contraction takes place every time the electric circuit is completed. In this instance, the stimulus to the muscles is supplied by the electric discharge, as, in the case of the heart above mentioned, it is supplied by the contact of the steel needle; and in both, a muscular contraction is the immediate consequence. If we introduce a metallic catheter into the empty stomach of a dog through a gastric fistula, and gently irritate with it the mucous membrane, a secretion of gastric juice at once begins to take place; and if food be introduced the fluid is poured out in still greater abundance. We know also that if the integument be exposed to contact with a heated body, or to friction with an irritating liquid, an excitement of the circulation is at once produced, which again passes away after the removal of the irritating cause.

In all these instances we find that the organ which is called into activity is excited by the direct application of some stimulus to its own tissues. But this is not usually the manner in which the different functions are excited during life. The stimulus which calls into action the organs of the living body is usually not direct, but indirect in its operation. Very often, two organs which are situated in distant parts of the body are connected with each other by such a sympathy, that the activity of one is influenced by the condition of the other. The muscles, for example, are almost never called into action by an external stimulus operating directly upon their own fibres, but by one which is applied to some other organ, either adjacent or remote. Thus the peristaltic action of the muscular coat of the intestine commences when the food is brought in

contact with its mucous membrane. The lachrymal gland is excited to increased activity by anything which causes irritation of the conjunctiva. In all such instances, the physiological connection between two different organs is established through the medium of the nervous system.

The function of the nervous system may therefore be defined, in the simplest terms, as follows: *It is intended to associate the different parts of the body in such a manner, that stimulus applied to one organ may excite the activity of another.*

The instances of this mode of action are exceedingly numerous. Thus, the light which falls upon the retina produces a contraction of the pupil. The presence of food in the stomach causes the gall-bladder to discharge its contents into the duodenum. The expulsive efforts of coughing, by the thoracic and abdominal muscles, are excited by a foreign body entangled in the glottis.

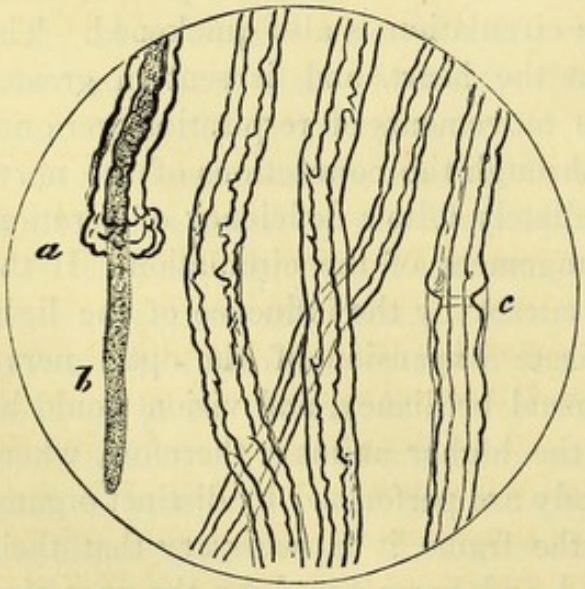
It is easy to understand the great importance of this function, particularly in the higher animals and in man, whose organization is a complicated one. For the different organs of the body, in order to preserve the integrity of the whole frame, must not only act and perform their functions, but they must act in harmony with each other, and at the right time, and in the right direction. The functions of circulation, of respiration, and of digestion, are so mutually dependent, that if their actions do not take place harmoniously, and in proper order, a serious disturbance must inevitably follow. When the muscular system is excited by unusual exertion, the circulation is also quickened. The blood arrives more rapidly at the heart, and is sent in greater quantity to the lungs. If the movements of respiration were not accelerated at the same time, through the connections of the nervous system, there would immediately follow deficiency of aeration, vascular congestion, and derangement of the circulation. If the iris were not stimulated to contract by the influence of the light falling on the retina, the delicate expansion of the optic nerve would be dazzled by any unusual brilliancy, and vision would be obscured or confused. In all the higher animals, therefore, where the different functions of the body are performed by distinct organs, situated in different parts of the frame, it is necessary that their action should be thus regulated and harmonized by the operation of the nervous system.

The nervous system consists of two kinds of nervous tissue, differing from each other in appearance, structure, and physiological endowments. One of these is the *white substance*, composed of nervous filaments; the other is the *gray substance*, which contains granular matter and ganglionic cells. The white substance is found in all the trunks and branches of the nerves, on the exterior of the spinal cord and in the internal parts of the brain. The gray substance, on the other hand, forms the external layer or convolutions of the brain, as well as various deposits about its base and central parts, the interior of the spinal cord, and a large number of small detached masses, called the sympathetic ganglia, in different parts of the body. The filaments and cells constituting these two kinds of nervous tissue are so different in their properties and function as to require for each a separate description.

Nervous filaments of the white substance. — The white substance of the nervous system, when examined by the microscope, is seen to be composed everywhere of minute fibres or filaments, the "ultimate nervous filaments," running in a direction very nearly parallel with each other. These filaments are cylindrical in shape, and vary considerably in size. Those which are met with in the spinal cord and the brain are the smallest, and have an average diameter of $\frac{1}{10000}$ of an inch. In the trunks and branches of the nerves they average $\frac{1}{2000}$ of an inch.

The structure of the ultimate nervous filament is as follows: The exterior of each filament consists of a colorless, transparent tubular membrane, which is seen with some difficulty in the natural condition of the fibre, owing to the extreme delicacy of its texture, and to its cavity being completely filled with a substance very similar to it in refractive power. It may, however, be distinguished where the outlines of the nervous filament are strongly curved or indented, as at *c* in Fig. 126. In the interior of this tubular membrane there is a layer of thick, fluid, highly refractive substance which is called the

Fig. 126.

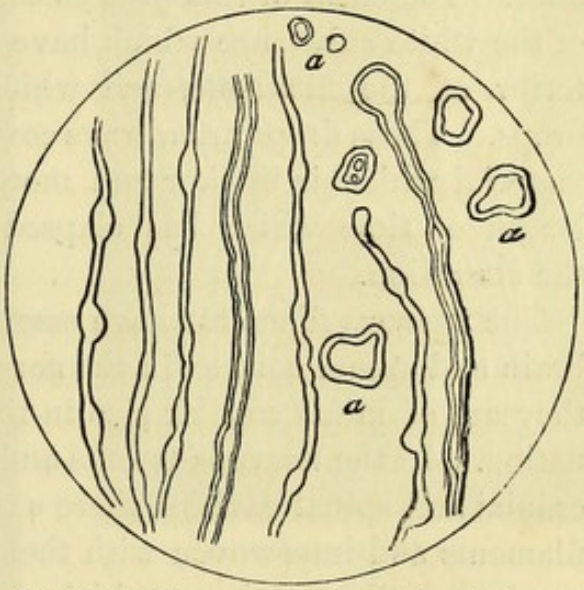


NERVOUS FILAMENTS from sciatic nerve. — At *a*, the torn extremity of a nervous filament with the axis cylinder (*b*) protruding from it. At *c*, the medullary layer is nearly separated by accidental compression, but the axis cylinder passes across the ruptured portion. The outline of the tubular membrane is also seen at *c* on the outside of the nervous filament.

"medullary layer." It is this medullary layer which causes the opaque white color of the nervous tissue. Owing to its highly refractive power, it appears, in a microscopic view, as a strongly marked double outline on each border of the nervous filament. Finally, there is, inclosed in the medullary layer, and forming the central part of the filament, a delicate cylindrical or flattened cord, of a finely granulated appearance, known as the "axis cylinder."

When white nervous tissue, from the brain or spinal cord, is prepared for the microscope and examined by transmitted light, two remarkable appearances are observed in its filaments, produced by the contact of foreign substances. In the first place the unequal pressure, to which the filaments are accidentally subjected in the process of dissection and preparation, produces an irregularly bulging or varicose appearance in them at various points, owing to the readiness with which the fluid substance in their interior is displaced in different directions. (Fig. 127.) Sometimes spots may be seen here and there, where the nervous matter has been entirely pressed apart in the centre of a filament, so that there appears to be an entire break in its continuity, while the external layers may be still seen, passing across from one portion to the other. When a nervous filament is torn across under the microscope and subjected to pressure, a certain quantity of the fluid substance is pressed out from its torn extremity, and may be entirely separated from it, so as to present itself under the form of irregularly rounded drops of various sizes (*a*, *a*, *a*), scattered over the field of the microscope. The varicose appearance above alluded to is more frequently seen in the smaller nervous filaments from the brain and spinal cord, owing to their soft consistency and the readiness with which they yield to pressure.

Fig. 127.



NERVOUS FILAMENTS from white substance of brain.— *a*, *a*, *a*. Soft substance of the filaments pressed out, and floating in irregularly rounded drops.

The second effect produced by the artificial preparation of the nervous matter is an alteration or partial coagulation of the fluid

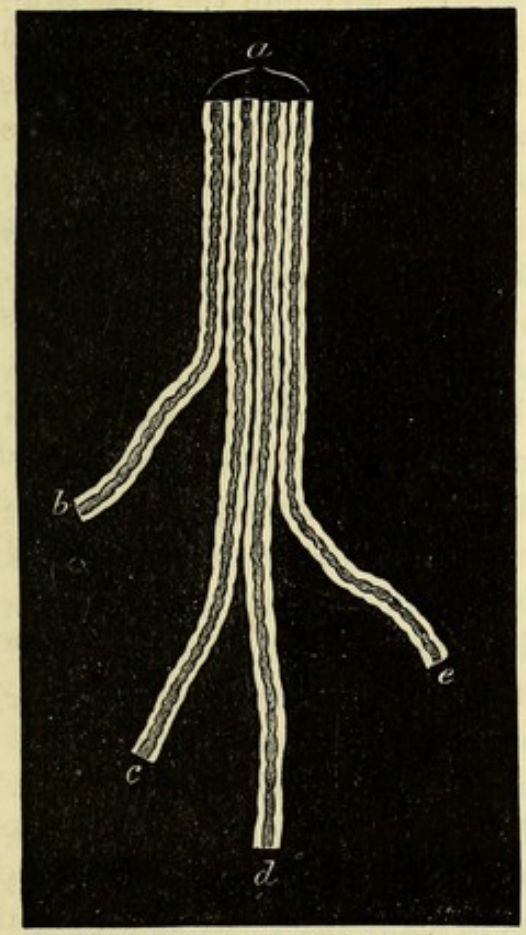
substance of the medullary layer. In its natural condition this substance has the same consistency throughout, and appears perfectly transparent and homogeneous by transmitted light. As soon, however, as the nervous filament is removed from its natural situation, and brought in contact with air, water, or other unnatural fluids, the soft substance immediately under the investing membrane begins to coagulate. It increases in consistency, and at the same time becomes more highly refractive; so that it presents on each side, immediately underneath the investing membrane, a thin layer of a peculiar glistening aspect. At first, this change takes place only in the outer portions of the medullary layer. The coagulating process, however, subsequently goes on, and gradually advances from the edges of the filament toward its centre, until its entire thickness after a time presents the same appearance. The effect of this process can also be seen in those portions of the white substance which have been pressed out from the interior of the filaments, and which float about in the form of drops. These drops are always covered with a layer of coagulated material which is thicker and more opaque in proportion to the length of time which has elapsed since the commencement of the alteration.

The nervous filaments have essentially the same structure in the brain and spinal cord as in the nervous trunks and branches; only they are of much smaller size in the former than in the latter situation. In the nervous trunks and branches, however, outside the cranial and spinal cavities, there exists, superadded to the nervous filaments and interwoven with them, a large amount of condensed areolar or fibrous tissue, which protects them from injury, and gives to this portion of the nervous system a peculiar density and resistance. This difference in consistency between the white matter of the nerves and that of the brain and spinal cord is owing, therefore, exclusively to the presence of ordinary fibrous tissue in the nerves, while it is wanting in the brain and spinal cord. The consistency of the nervous filaments themselves is the same in each situation.

A *Nerve*, accordingly, consists of a bundle or collection of ultimate nervous filaments, associated with each other in larger or smaller packets, and bound together by the investing layers of fibrous tissue which form its sheath, or "neurilemma." The neurilemma sends prolongations of fibrous tissue into the interior of the nerve, dividing its filaments into secondary and tertiary

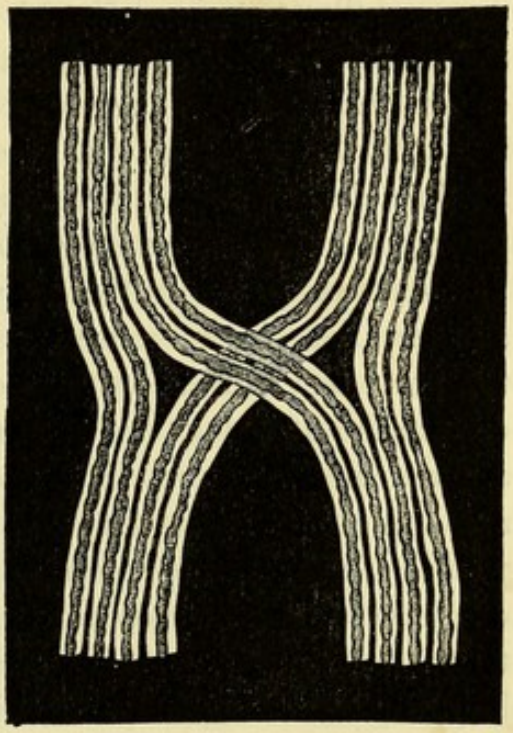
bundles, and containing the small bloodvessels destined for the nutrition of the nerve. When a nerve, therefore, divides during its course into several branches, this does not imply that the filaments themselves become branched or divided at this point, but only that some of them leave the bundles with which they were previously associated, and pursue a different direction. (Fig. 128.) A

Fig. 128.



Division of a NERVE, showing portion of nervous trunk (*a*), and the separation of its filaments (*b*, *c*, *d*, *e*).

Fig. 129.



Inosculation of NERVES.

nerve which originates, for example, from the spinal cord in the region of the neck, and runs down the upper extremity, dividing and subdividing, to be finally distributed to the integument and muscles of the hand, contains at its point of origin all the filaments into which it is afterward divided, and which are merely separated at successive points from the main bundle. The ultimate filaments themselves divide, and even form sometimes minute plexuses, when they have finally arrived at their destination and are about to terminate in the sensitive or muscular parts; but during the whole previous transit of the nerve, between its origin and its termination, they remain distinct and anatomically independent of

each other, each filament by itself remaining continuous throughout.

When a nerve, furthermore, is said to "inosculate" with another nerve, as when the infra-orbital inosculates with the facial, or the cervical nerves inosculate with each other, this means simply that some of the filaments composing the first nervous bundle separate from it, and cross over to form a part of the second, while some of those belonging to the second cross over and join the first (Fig. 129); but the individual filaments in each instance remain continuous and preserve their identity throughout. Accordingly the nervous filaments in different nerves, or in the adjacent parts of inosculating nerves, still remain separate and distinct from each other; and, however they may be associated in the nervous trunks and branches, they may still act independently and preserve their specific characters and functions in every part of their course.

Origin and termination of the nervous filaments.—The nervous filaments originate in the gray substance of the nervous centres and terminate in the muscular tissues and sensitive membranes of the periphery. Both at their origin and termination, they present certain modifications in their appearance and structure which deserve a special notice. The most important of these modifications are a diminution in size and a disappearance of their external parts. Thus in the gray matter of the brain and spinal cord, many of them are very much smaller than elsewhere, and are also destitute both of the external tubular envelope and of the medullary layer; being reduced simply to the central cord or axis cylinder. The naked axis cylinder, to which the nerve filament is thus reduced, becomes continuous in many instances, as we shall hereafter see, with the ganglionic cells of the gray matter, the substance of which resembles its own in appearance and consistency. This fact has led many anatomists to regard the axis cylinder as the most essential constituent part of the nervous filament, since it continues throughout its entire length; while the medullary layer and the tubular envelope, though superadded during the greater part of its extent, nevertheless cease to exist at a short distance both from its origin and its termination.

It is now fully established that the nervous filaments terminate at the periphery by free extremities. Just previous to the final distribution of the nerves, both in the skin and in the muscles, two peculiarities are to be seen in their anatomical arrangement. First, the small nervous branches divide and subdivide with unusual

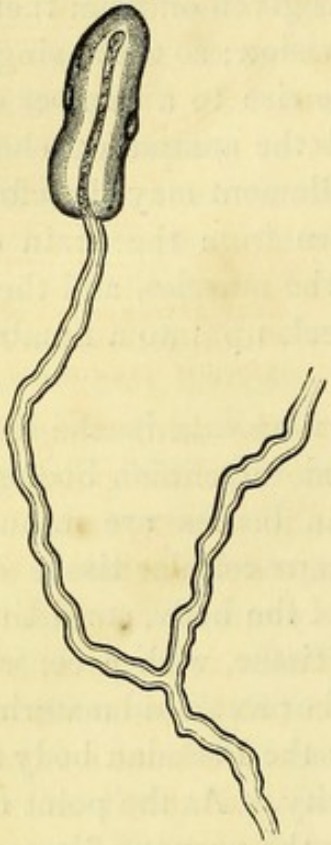
rapidity; and their subdivisions, uniting with each other by inosculation, form abundant and closely set plexuses, while from these plexuses the nervous filaments are given off which immediately, or soon after, terminate in the substance of the tissues. Secondly, both in these plexuses and in the ramifications given off from them, the nervous filaments themselves undergo division; so that a single nervous filament, in this situation, may give rise to a number of different branches, each branch retaining all the anatomical characters of the original filament. A nervous filament may therefore run undivided throughout the long distance from the brain or spinal cord until its arrival at the skin or the muscles, and then, immediately before its final distribution, break up into a number of separate but closely adjacent branches.

The ultimate termination of the nervous filaments in the skin has been most distinctly seen in the so-called "Pacinian bodies" and the "tactile corpuscles." The Pacinian bodies are minute ovoid-shaped masses found in the subcutaneous cellular tissue of the hands and feet, and various other parts of the body, consisting of a series of concentric laminæ of fibrous tissue, with a central cavity, enclosing a transparent, colorless, fluid or semifluid material. A single ultimate nervous filament penetrates the Pacinian body at one extremity and passes into its central cavity. At the point of entrance the external tubular envelope leaves the nervous filament and becomes continuous with the fibrous laminæ of the Pacinian body. The medullary layer also disappears, and the nervous filament, thus reduced to its axis cylinder, runs longitudinally through the greater part of the central cavity and terminates, toward its farther end, in either one or several slightly rounded extremities. The "tactile corpuscles" are much smaller than the Pacinian bodies, but are of similar form. They are situated in the substance of the sensitive papillæ of the skin and elsewhere. They consist each of an ovoid mass, marked externally with transverse elongated nuclei and striations. Each corpuscle has attached to its surface sometimes two, but frequently only a single nervous filament, which loses its external envelopes, as in the Pacinian body, and terminates in some way, not yet fully determined, in the substance of the corpuscle.

The simplest form of tactile corpuscle is supposed to be that known under the name of the "terminal corpuscles of the sensitive nerves," found in the conjunctiva, the lips, the tongue, and the soft palate. They are round or elongated ovoid bodies, consisting of

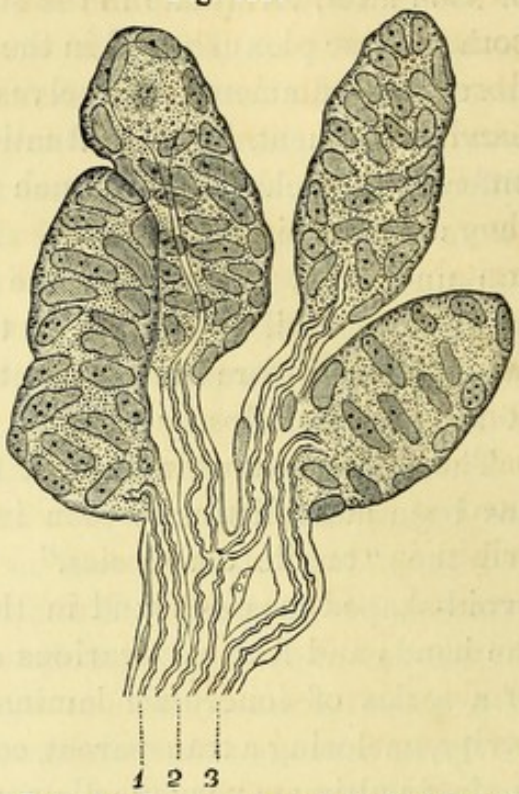
a closed sac of connective tissue, sometimes marked with abundant transverse nuclei, and containing a homogeneous or finely granular substance. Into this body is received the ultimate branch of

Fig. 130.



TERMINAL CORPUSCLE of sensitive nerve; from the conjunctiva of the calf. (After Frey.)

Fig. 131.



TACTILE CORPUSCLES, from the (edge of the) tongue of the sparrow. 1,2,3. Medullated nerve filaments supplying four tactile corpuscles. One filament divides into two branches; and one of them is traced to near the extremity of the corresponding corpuscle, where it ends in a cell-like expansion. (After Ihlder.)

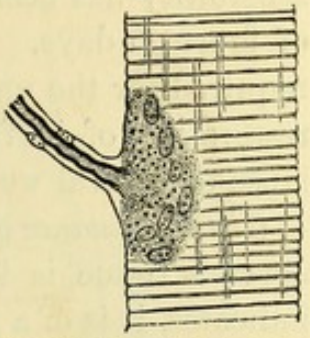
a nervous filament, which is reduced to its axis-cylinder, and in many cases may be seen to terminate in the interior by a single free extremity.

In the muscles, as a rule, each muscular fibre has, connected with it, at least one nervous filament, and sometimes more than one. The ultimate filament, produced by the branching and subdivision of the original filament, approaches the muscular fibre, usually at right angles, and penetrates its exterior, — the tubular membrane of the filament becoming continuous with the sarcolemma. At the same time its medullary layer ceases abruptly, and the axis-cylinder spreads out into a thin oval expansion of granular matter, interspersed with nuclei, called the "terminal plate," and lying in immediate contact with the contractile substance of the muscular fibre. Some variations have been described in the form and disposition of the axis-cylinder in the terminal plate, in some of the inferior classes; but the above represents the essential characters

of the nervous termination in the muscles of man and most of the vertebrate animals.

Physiological properties of the nervous filaments.—The nervous filaments are organs of communication. They serve as connecting fibres between the nervous centres on the one hand, and the sensitive and muscular tissues on the other. In order to accomplish this, they are endowed with a peculiar power of irritability, by which, when called into action at either extremity, they become excited throughout their entire length, and produce a corresponding effect at their opposite termination. Thus, those which are distributed to the skin, when excited at their peripheral extremities, produce at their point of origin in the brain a sensation corresponding to the external impression. On the other hand, those which are distributed to the muscles, when excited at their origin by the impulse of the will, produce immediately a contraction in the muscular fibres at the periphery. This state of physiological action produces no visible change in the nervous filament itself. Its effects are manifest only at the extremities of the nerve, in the organs in which it has its termination. Nevertheless, it is evident that the nervous filament serves to communicate in some way an action from one of its extremities to the other; since, if it be divided in any part of its course, the communication at once ceases, and sensations can no longer be perceived in the skin, nor any voluntary contraction excited in the muscles.

Fig. 132.



TERMINATION OF NERVOUS FILAMENT in muscular fibre of the fowl. (After Rouget.)

The nervous filaments however, like the elements of other tissues, have the power of reuniting after they have been divided by section, and may recover in this way the functions which had been temporarily lost. When a nerve which is distributed both to the skin and muscles is divided in the middle of its course, the reunion of its filaments is indicated, after a time, by the reappearance of sensation and voluntary motion in the parts below. Even when a portion of the nerve-trunk has been cut out, the lost fibres may be regenerated and the functions of the nerve restored. In dogs, cats, and rats, according to the observations of Vulpian and others,—especially when the experiment is performed upon young animals,—the nerve may be regenerated and its function restored when even a little more than two inches of its length have been removed.

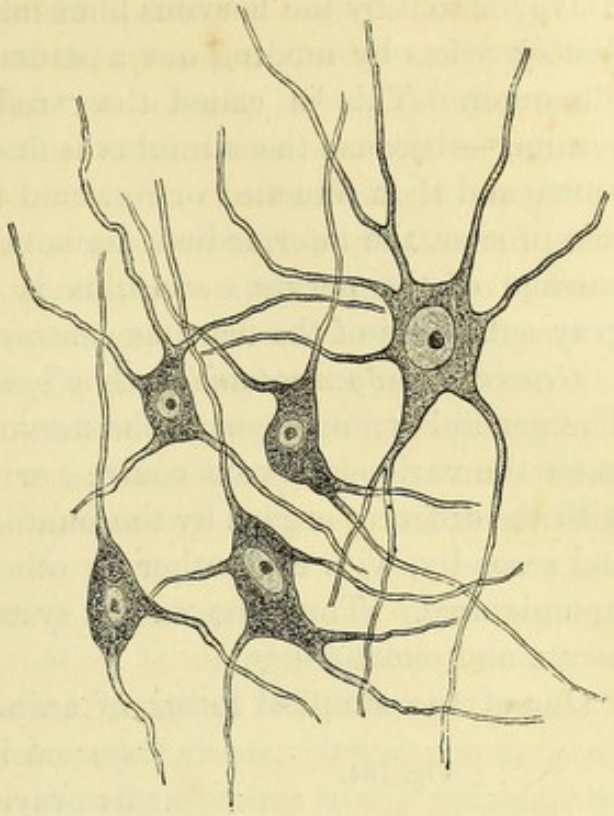
Vulpian[1] found the sciatic nerve regenerated, in very young rats, after the excision of two inches and one-third, in seventeen days; and in young cats, after excision of one inch of the lingual nerve, sensibility has been found to reappear in the tongue in the course of fourteen days. In man and in adult animals a longer time is required for the union or regeneration of a divided nerve, and the restoration of its functions is sometimes completed only after the lapse of several weeks or even months.

Gray substance of the nervous tissue. — The second variety of nervous tissue is known as the "gray substance." As its name indicates, it is of a grayish or ashen hue, by which it is readily distinguished from its contrast with the dead white color of the fibrous matter. It consists of a granular intercellular material with nuclei and pigment grains, and containing, imbedded in its substance, beside an abundance of slender nervous filaments, numerous ganglionic *cells*, of great variety in form and size, termed the "nerve cells." As these cells are the most characteristic elements recognizable by the microscope in the gray nervous tissue, its peculiar properties are regarded as principally dependent upon them. Their average size varies in different parts from $\frac{1}{2000}$ to $\frac{1}{250}$ of an inch in diameter. They usually have a very distinct oval nucleus and a nucleolus, while the substance of the cell is composed of a finely granular material, of soft consistency. They are sometimes of an ovoid or generally rounded form, as in the ganglia of the sympathetic nerve, with a long process or extension of the substance of the cell frequently running out in the form of a filament, resembling the axis-cylinder of a nerve-fibre. In the ganglia of the posterior roots of the spinal nerves they are usually also rounded or oval in form; often with two similar processes, extending from the cell in two opposite directions. The above two varieties have received the names respectively of "unipolar" and "bi-polar" cells. In the gray matter at the base of the brain, and in the interior of the spinal cord, are to be found the most remarkable of the nerve cells, both for form and size. (Fig. 133.) The largest of them measure, according to Kölliker, $\frac{1}{200}$ of an inch in diameter. They present frequently three or four, and even five or six, processes or prolongations running in various directions, and are therefore called "multi-polar" cells. Most of these fibre-like prolongations, as they recede from the border of the cell, become branched and subdivided, and are thus finally reduced

[1] Leçons sur la physiologie du système nerveux. Paris, 1866, p. 256.

to filaments of such minute size that they can no longer be followed by the microscope. One of the prolongations, however, instead of breaking up into branches, pursues an undivided course, and becomes continuous with the axis-cylinder of a nervous filament. In this way the nervous filaments may be said, in many instances at least, to have their origin and termination in the ganglionic cells of the gray substance.

Fig. 133.



NERVE CELLS of the gray substance; from the medulla oblongata. (After Dr. J. Dean.)

Physiological properties of the gray substance. — Every collection of gray nervous substance, whatever may be its form or size, is called a "nervous centre," or a "ganglion." Its function is to receive impressions conveyed to it by the nervous filaments, and to send out by them impulses, which are to be transmitted to distant organs. The nervous centres, accordingly, originate nervous power, so to speak, while the filaments and nerves only transmit it. The mode in which this function of the nervous centres is performed is still more unknown to us than that of the filaments and the nerves. The action which takes place in them, during the period of their excitement, is not accompanied by any visible changes, and can only be explained as the operation of a peculiar power dependent on their physiological constitution. It is evident that they are essential to the general action of the nervous system, for neither sensation nor movement is ever excited, in the natural condition, by aid of the nervous filaments, unless these are in communication with the gray matter of the nervous centres.

We have already seen that the function of the nervous system, as a whole, is to associate the different parts of the body in such a manner that a stimulus applied to one organ may excite the activity of another. Now this communication between the two

organs is not direct, but circuitous. It passes, in all cases, through an intermediate nervous centre, which receives the impression conveyed to it by the nervous filaments from one organ, and immediately reacts by sending out a stimulus which calls into activity the other. This is called the "reflex action" of the nervous system, — because the stimulus is first sent inward to the nervous centre and then returned or reflected in the opposite direction. In this process, the intermediate act between the inward and outward passage of the nervous stimulus is always accomplished in the gray substance of the nervous centres.

General arrangement and mode of operation of the nervous system.— The general arrangement of the nervous system is such that in all cases the various nervous centres, or ganglia, are connected, first, with the different organs by the bundles of filaments called nerves; and secondly, with each other by other bundles which are termed commissures. Thus the entire system is made up of *ganglia*, *nerves*, and *commissures*.

One of the simplest forms of animal life in which a nervous system is to be found is probably the five-rayed starfish. This animal belongs to the type known as *radiata;* that is, animals whose organs radiate from a central point, so as to form a circular series of similar parts, each organ being repeated at different points of the circumference. The starfish (Fig. 134) consists of a central mass, with five arms or limbs radiating from it. In the centre is the mouth, and immediately beneath it the stomach or digestive cavity, which sends prolongations into every one of the projecting limbs. There is also contained in each limb a portion of the glandular and muscular systems, and the whole is covered by a sensitive integument. The nervous system consists of five similar ganglia, situated in the central portion, at the base of the arms. These ganglia are connected with each other by commissures, so as to form a nervous collar or chain, surrounding the orifice of the digestive cavity. Each ganglion also sends off nerves, the filaments of which are distributed to the organs contained in the corresponding limb.

Fig. 134.

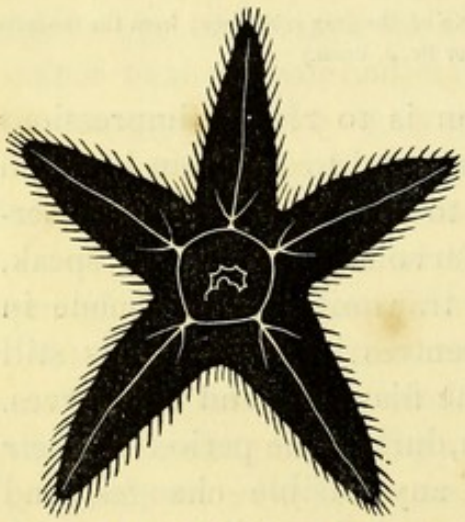


Diagram of Nervous System of Starfish.

When any stimulus or irritation is applied to the integument of one of the arms, it is transmitted by the nerves of the integument to the ganglion situated near the mouth. Arrived here, it is received by the gray matter of the ganglion, and immediately converted into an impulse which is sent out by other filaments to the muscles of the corresponding limb; and a muscular contraction and movement consequently take place. The muscles therefore contract in consequence of an irritation which has been applied to the skin. It must be recollected that this action does not necessarily indicate any sensation or volition, nor even any consciousness on the part of the animal. The function of the gray matter is simply to receive the impulse conveyed to it, and to reflect or send back another; and this may be accomplished altogether involuntarily, and without the existence of any conscious perception. It is the simplest form of reflex action.

Where the irritation applied to the integument is of an ordinary character and not very intense, it is simply reflected, as above described, from the corresponding ganglion back to the same limb. But if it be of a peculiar character, or of greater intensity than usual, it may be also transmitted by the commissures to the neighboring ganglia; and so two, three, four, or even all five of the limbs may be set in motion by a stimulus applied to the integument of one of them. Now, as all the limbs of the animal have the same structure and contain the same organs, their action will also be the same; and the effects of this communication of the stimulus from one to the other by means of commissures will be a repetition, or rather a simultaneous production of similar movements in different parts of the body. According to the character and intensity, therefore, of the original stimulus, it will be followed by a response from one, several, or all of the different parts of the animal frame.

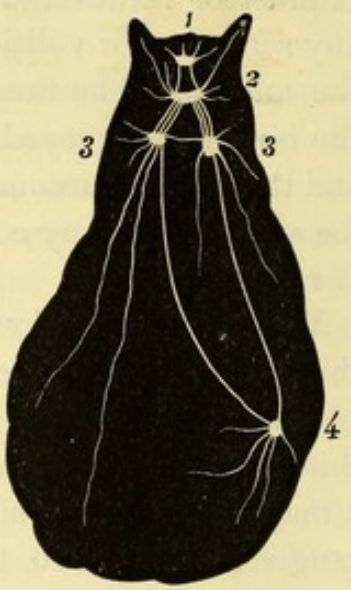
It will be seen also that there are two sets of nervous filaments, differing essentially in their functions. One set of these fibres run from the sensitive surfaces to the ganglion, and convey the nervous impression inward. These are called *sensitive* fibres. The other set run from the ganglion to the muscles, and carry the nervous impression outward. These are called *motor* fibres.

In the starfish, where the body is composed of a repetition of similar parts arranged round a common centre, and where all the limbs are precisely alike in structure, the several ganglia composing the nervous system are also similar to each other, and act in the same

way. But in animals which are constructed upon a different plan, and whose bodies are composed of distinct organs, situated in different regions, we find that the nervous ganglia, presiding over the function of these organs, present a corresponding degree of dissimilarity.

In *Aplysia*, for example, which belongs to the type of "mollusca," or soft-bodied animals, the digestive apparatus consists of a mouth, an œsophagus, a triple stomach, and a somewhat convoluted intestine. The liver is large, and placed on one side of the body, while the gills, in the form of vascular laminæ, occupy the opposite side. There are both testicles and ovaries in the same animal, the male and female functions coexisting, as in many other invertebrate species. All the organs, furthermore, are here arranged without reference to a regular or symmetrical plan. The body is covered with a muscular mantle, which expands at the ventral surface into a tolerably well-developed "foot," or organ of locomotion, by which the animal is enabled to change its position and move from one locality to another.

Fig. 135.

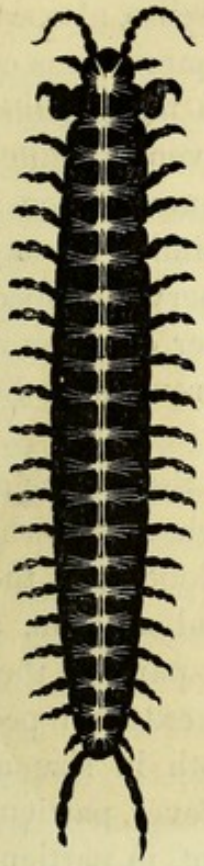


Nervous System of Aplysia. — 1. Digestive or œsophageal ganglion. 2. Cerebral ganglion. 3, 3. Pedal or locomotory ganglia. 4. Respiratory ganglion.

The nervous system of this animal is constructed upon a plan corresponding with that of the entire body. (Fig. 135.) There is a small ganglion (1) situated anteriorly, which sends nerves to the commencement of the digestive apparatus, and is regarded as the œsophageal or digestive ganglion. Immediately behind it is a larger one (2) called the cephalic or cerebral ganglion, which sends nerves to the organs of special sense, and which is regarded as the seat of volition and general sensation for the entire body. Following this is a pair of ganglia (3, 3), the pedal or locomotory ganglia, which supply the muscular mantle and its foot-like expansion, and which regulate the movement of these organs. Finally, another ganglion (4), situated at the posterior part of the body, sends nerves to the branchiæ or gills, and is termed the branchial or respiratory ganglion. All these nervous centres are connected by commissures with the central or cerebral ganglion, and may therefore act either independently or in association with each other, by means of these connecting fibres.

In the third type of animals, again, viz., the *articulata*, the general plan of structure of the body is different from the foregoing, and the nervous system is accordingly modified to correspond with it. In these animals, the body is composed of a number of rings or sections, which are articulated with each other in linear series. A very good example of this type may be found in the common centipede, or *scolopendra*. Here the body is composed of twenty-two successive and nearly similar articulations, each of which has a pair of legs attached, and contains a portion of the glandular, respiratory, digestive and reproductive apparatuses. The animal, therefore, consists of a repetition of similar compound parts, arranged in a longitudinal chain or series. The only exceptions to this similarity are in the first and last articulations. The first is large, and contains the mouth; the last is small, and contains the anus. The first articulation, which is called the "head," is also furnished with eyes, with antennæ, and with a pair of jaws, or mandibles.

Fig. 136.



Nervous System of Centipede.

The nervous system of the centipede (Fig. 136), corresponding in structure with the above plan, consists of a linear series of nearly equal and similar ganglia arranged in pairs, situated upon the median line, along the ventral surface of the alimentary canal. Each pair of ganglia is connected with the integument and muscles of its own articulation by sensitive and motor filaments; and with those which precede and follow by a double cord of longitudinal commissural fibres. In the first articulation, moreover, or the head, the ganglia are larger than elsewhere, and send nerves to the antennæ and to the organs of special sense. This pair is termed the cerebral ganglion, or the "brain."

A reflex action may take place, in these animals, through either one or all of the ganglia composing the nervous chain. An impression received by the integument of any part of the body may be transmitted inward to its own ganglion and thence reflected immediately outward, so as to produce a movement of the limbs belonging to that articulation alone; or it may be propagated through the longitudinal commissures, forward or backward, and produce simultaneous movements in several neighboring articula-

tions; or, finally, it may be propagated quite up to the anterior pair of ganglia or "brain," where its reception will be accompanied with consciousness, and a voluntary movement reflected back upon any or all of the limbs at once. The organs of special sense, also, communicate directly with the cerebral ganglia; and impressions conveyed through them may accordingly give rise to movements in any distant part of the body. In these animals the ventral ganglia, or those which simply stand as a medium of communication between the integument and the muscles, are nearly similar throughout; while the first pair, or those which receive the nerves of special sense, and which exercise a general controlling power over the rest of the nervous system, are distinguished from the remainder by a well-marked preponderance in size.

In the centipede it will be noticed that nearly all the organs and functions are distributed in an equal degree throughout the whole length of the body. The organs of special sense alone, with those of mastication and the functions of perception and volition, are confined to the head. The ganglia occupying this part are therefore the only ones which are distinguished by any external peculiarities; the remainder being nearly uniform both in size and activity. In some kinds of articulated animals, however, particular functions are concentrated, to a greater or less extent, in particular parts of the body; and the nervous ganglia which preside over them are modified in a corresponding manner. In the insects, for example, the body is divided into three distinct sections, viz: the head, containing the organs of prehension, mastication, tact and special sense; the chest, upon which are concentrated the organs of locomotion, the legs and wings; and the abdomen, containing the greater part of the alimentary canal, together with the glandular and generative organs. As the insects have a greater amount of intelligence and activity than the centipedes and other worm-like articulata, and as the organs of special sense are more perfect in them, the cerebral ganglia are also unusually developed, and are evidently composed of several pairs, connected by commissures so as to form a compound mass. As the organs of locomotion, furthermore, instead of being distributed, as in the centipede, throughout the entire length of the animal, are concentrated upon the chest, the locomotory ganglia also preponderate in size in this region of the body; while the ganglia which preside over the secretory and generative functions are situated together, in the cavity of the abdomen.

All the above parts, however, are connected, in the same manner as previously described, with the anterior or cerebral pair of ganglia. In all articulate animals, moreover, the general arrangement of the body is symmetrical. The right side is, for the most part, precisely like the left, as well in the internal organs as in the external covering and the locomotory appendages. The only marked variation between different parts of the body is in an antero-posterior direction; owing to different organs being concentrated, in some cases, in the head, chest, and abdomen.

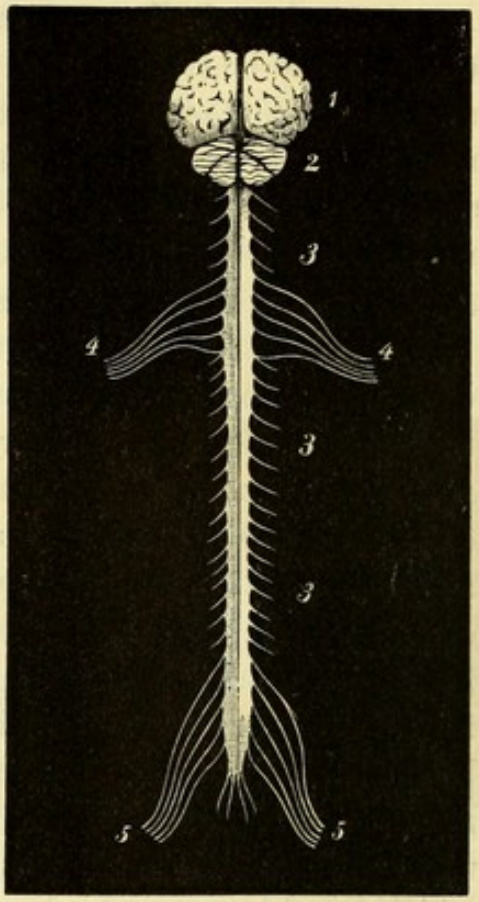
Finally, in the *vertebrate* type of animals, comprising man, the quadrupeds, birds, reptiles, and fish, the external parts of the body, together with the locomotory apparatus and the organs of special sense, are symmetrical, as in the articulata; but the internal organs, especially those concerned in the digestive and secretory functions, are unsymmetrical and irregular, as in the molluscs. The organs of respiration, however, are nearly symmetrical in the vertebrata, for the reason that the respiratory movements, upon which the function of these organs is immediately dependent, are performed by muscles belonging to the general locomotory apparatus. The nervous system of the vertebrata partakes, accordingly, of the structural arrangement of the organs under its control. That portion which presides over the locomotory, respiratory, sensitive, and intellectual functions forms a system by itself, called the *cerebro-spinal system*. This system is arranged in a manner very similar to that of the articulata. It is composed of two equal and symmetrical halves, running along the median line of the body, the different parts of which are connected by transverse and longitudinal commissures. Its ganglia occupy the cavities of the cranium and the spinal canal, and send out their nerves through openings in the bony walls of these cavities.

The other portion of the nervous system of vertebrata is that which presides over the functions of vegetative life. It is called the *ganglionic* or *great sympathetic system*. Its ganglia are situated anteriorly to the spinal column, in the visceral cavities of the body, and are connected, like the others, by transverse and longitudinal commissures. This part of the nervous system is symmetrical in the neck and thorax, but is unsymmetrical in the abdomen, where it attains its largest size and its most complete development.

The vertebrate animals, as a general rule, are very much superior to the other classes, in intelligence and activity, as well as in the variety and complicated character of their motions; while their

nutritive or vegetative functions, on the other hand, are not particularly well developed. Accordingly we find that in these animals the cerebro-spinal system of nerves preponderates very much, in importance and extent, over that of the great sympathetic. The quantity of nervous matter contained in the brain and spinal cord is, even in the lowest vertebrate animal, very much greater than that contained in the system of the great sympathetic; and this preponderance increases, in the higher classes, just in proportion to their superiority in intelligence, sensation, power of motion, and other functions of a purely animal character.

Fig. 137.



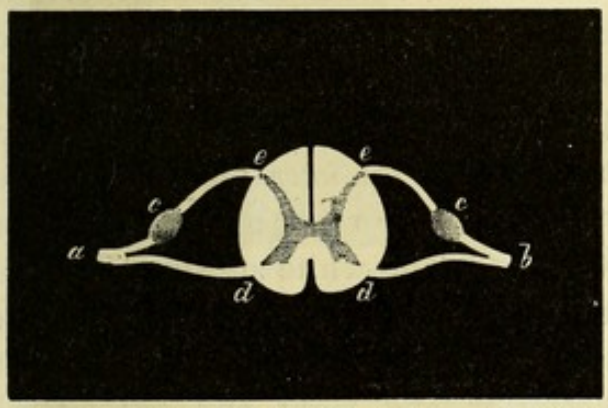
Cerebro-spinal System of Man.—1. Cerebrum. 2. Cerebellum. 3,3,3. Spinal cord and nerves. 4, 4. Brachial nerves 5, 5. Sacral nerves.

The spinal cord is very nearly alike in the different classes of vertebrate animals. It is a nearly cylindrical cord, running from one end of the spinal canal to the other, and connected at its anterior extremity with the ganglia of the brain. (Fig. 137.) It is divided, by an anterior and posterior median fissure, into two lateral halves, which still remain connected with each other by a central mass or commissure. Its inner portions are occupied by gray matter, which forms a continuous ganglionic chain, running from one extremity of the cord to the other. Its outer portions are composed of white substance, the filaments of which run for the most part in a longitudinal direction, connecting the different parts of the cord with each other, and the cord itself with the ganglia of the brain.

The spinal nerves are given off from the spinal cord at regular intervals, and in symmetrical pairs; one pair to each successive portion of the body. Their filaments are distributed to the integument and muscles of the corresponding regions. In serpents, where locomotion is performed by simple, alternate, lateral movements of the spinal column, the spinal cord and its nerves are of the same size throughout. But in the other vertebrate classes, where

there exist special organs of locomotion, such as fore and hind legs, wings, and the like, the spinal cord is increased in size at the points where the nerves of these organs are given off; and the nerves themselves, which supply the limbs, are larger than those originating from other parts of the spinal cord. Thus, in the human subject (Fig. 137), the cervical nerves, which go to the arms, and the sacral nerves, which are distributed to the legs, are larger than the dorsal and lumbar nerves. They form, also, by frequent inosculation, two remarkable plexuses, before entering their corresponding limbs, viz., the brachial plexus above, and the sacral plexus below. The cord itself, moreover, presents two enlargements at the point of origin of these nerves, viz., the cervical enlargement from which the brachial nerves (4, 4) are given off, and the lumbar enlargement from which the sacral nerves (5, 5) originate.

Fig. 138.



Transverse Section of SPINAL CORD.—*a*, *b*. Spinal nerves of right and left sides, showing their two roots. *d*. Origin of anterior root. *e*. Origin of posterior root. *c*. Ganglion of posterior root.

If the spinal cord be examined in transverse section (Fig. 138), it will be seen that the gray matter in its central portion forms a double crescentic-shaped mass, with the concavity of the crescents turned outward. These crescentic masses of gray matter, occupying the two lateral halves of the cord, are united with each other by a transverse band of the same substance, which is called the *gray commissure of the cord.* Their anterior and posterior portions, in front and behind the gray commissure, are called, respectively, the anterior and posterior *horns* of gray matter. Directly in front of the gray commissure is a transverse band of white substance, connecting in a similar manner the white portions of the two lateral halves. It is called the *white commissure of the cord.*

The spinal nerves originate from the cord on each side by two distinct roots; one anterior, and one posterior. The anterior root (Fig. 138, *d*) arises from the surface of the cord near the extremity of the anterior horn of gray matter. The posterior root (*e*) originates at the point corresponding with the posterior horn of gray matter. Both roots are composed of a considerable number of ultimate nervous filaments, united with each other in parallel

bundles. The posterior root is distinguished by the presence of a small ganglion (*c*), which appears to be incorporated with it, and through which its fibres pass. There is no such ganglion on the anterior root. The two roots unite with each other shortly after leaving the cavity of the spinal canal, and mingle their filaments in a single trunk.

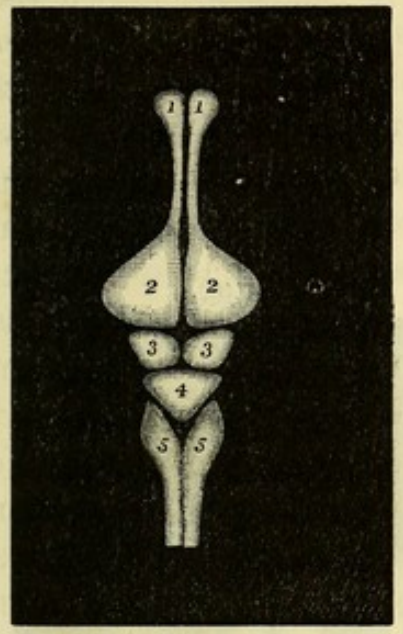
It will be seen, on referring to the diagram (Fig. 138), that each lateral half of the spinal cord is divided into two portions, an anterior and a posterior portion. The posterior horn of gray matter comes quite up to the surface of the cord, and it is just at this point (*e*) that the posterior roots of the nerves have their origin. The whole of the white substance included between this point and the posterior median fissure is called the *posterior column of the cord.* That which is included between the origins of the posterior and those of the anterior roots is called the *lateral column;* while that which is included between the anterior roots and the anterior median fissure is the *anterior column.* The white substance of the cord may then be regarded as consisting for the most part of six longitudinal bundles of nervous filaments, viz., the right and left anterior, the right and left posterior, and right and left lateral columns. The posterior median fissure penetrates deeply into the substance of the cord, quite down to the gray matter, so that the posterior columns appear entirely separated from each other in a transverse section; while the anterior median fissure is more shallow and stops short of the gray matter, so that the anterior columns are connected with each other by the white commissure above mentioned.

By the *encephalon* we mean the whole of that portion of the cerebro-spinal system which is contained in the cranial cavity. It is divided into three principal parts, viz., the cerebrum, cerebellum, and medulla oblongata. The anatomy of these parts, though somewhat complicated, can be readily understood if it be recollected that they are simply *a double series of nervous ganglia, connected with each other and with the spinal cord by transverse and longitudinal commissures.* The number and relative size of these ganglia, in different kinds of animals, depend upon the perfection of the bodily organization in general, and more especially on that of the intelligence and the special senses. They are most readily described by commencing with the simpler forms and terminating with the more complex.

The brain of the *Alligator* (Fig. 139) consists of five pair of ganglia, ranged one behind the other in the interior of the cranium.

The first of these are two rounded masses (1), lying just above and behind the nasal cavities, which distribute their nerves upon the Schneiderian mucous membrane. These are the *olfactory ganglia.* They are connected with the rest of the brain by two long and slender commissures, the "olfactory commissures." The next pair (2) are somewhat larger and of a triangular shape, when viewed from above downward. They are termed the "cerebral ganglia," or the *hemispheres.* Immediately following them are two quadrangular masses (3) which give origin to the optic nerves, and are therefore called the *optic ganglia.* They are termed also the "optic tubercles;" and in some of the higher animals, where they present an imperfect division into four nearly equal parts, they are known as the "tubercula quadrigemina." Behind them, we have a single triangular collection of nervous matter (4), which is called the *cerebellum.* Finally, the upper portion of the cord, just behind and beneath the cerebellum, is seen to be enlarged and spread out laterally, so as to form a broad oblong mass (5), the *medulla oblongata.* It is from this latter portion of the brain that the pneumogastric or respiratory nerves originate, and its ganglia are therefore sometimes termed the "pneumogastric" or "respiratory" ganglia.

Fig. 139.



BRAIN OF ALLIGATOR.—1. Olfactory ganglia. 2. Hemispheres. 3. Optic tubercles. 4. Cerebellum. 5. Medulla oblongata.

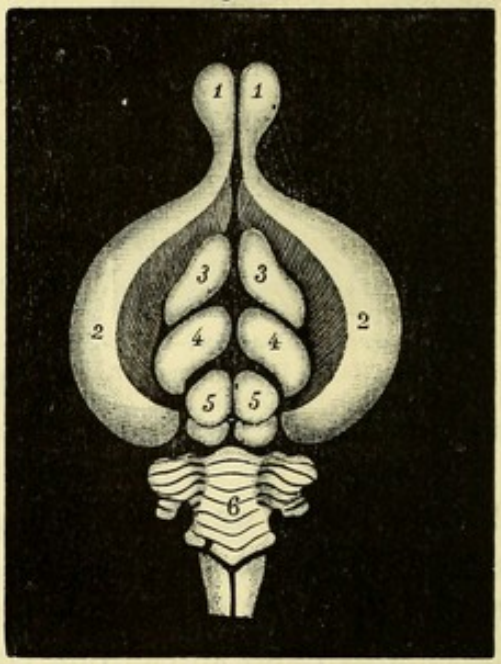
It will be seen that the posterior columns of the cord, as they diverge laterally in order to form the medulla oblongata, leave between them an open space, which is continuous with the posterior median fissure of the cord. This space is known as the "fourth ventricle." It is partially covered in by the backward projection of the cerebellum, but in the alligator is still somewhat open posteriorly, presenting a kind of chasm or gap between the two lateral halves of the medulla oblongata.

The successive ganglia which compose the brain, being arranged in pairs as above described, are separated from each other on the two sides by a longitudinal median fissure, which is continuous with the posterior median fissure of the cord. In the brain of the alligator this fissure appears to be interrupted at the cerebellum;

but in the higher classes, where the lateral portions of the cerebellum are more highly developed, as in the human subject (Fig. 137), they are also separated from each other posteriorly on the median line, and the longitudinal median fissure is complete throughout.

In *birds*, the hemispheres are of much larger size than in reptiles, and partially conceal the optic ganglia. The cerebellum, also, is very well developed in this class, and presents on its surface a number of transverse foldings or convolutions by which the quantity of gray matter which it contains is considerably increased. The cerebellum here extends so far backward as almost completely to conceal the medulla oblongata and the fourth ventricle.

Fig. 140.



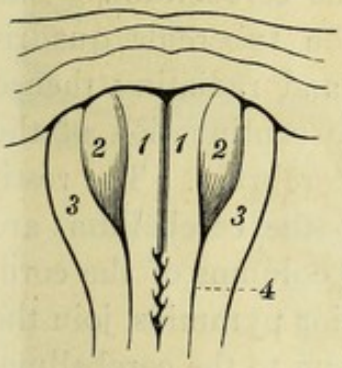
BRAIN OF RABBIT, viewed from above.—1. Olfactory ganglia. 2 Hemispheres, turned aside. 3. Corpora striata. 4 Optic thalami. 5. Tubercula quadrigemina 6. Cerebellum.

In the *quadrupeds*, the hemispheres and cerebellum attain a still greater size in proportion to the remaining parts of the brain. There are also two other pairs of ganglia, situated beneath the hemispheres, and between them and the tubercula quadrigemina. These are the *corpora striata* in front and the *optic thalami* behind. In Fig. 140 is shown the brain of the rabbit, with the hemispheres laid open and turned aside, so as to show the internal parts in their natural situation. The olfactory ganglia are seen in front (1) connected with the remaining parts by the olfactory commissures. The separation of the hemispheres (2, 2) shows the corpora striata (3) and the optic thalami (4). Then come the tubercula quadrigemina (5), which are here composed, as above mentioned, of four rounded masses nearly equal in size. The cerebellum (6) is considerably enlarged by the development of its lateral portions, and shows an abundance of transverse convolutions. It conceals from view the fourth ventricle and most of the medulla oblongata.

In other species of quadrupeds the hemispheres increase in size so as to project entirely over the olfactory ganglia in front, and to cover in the tubercula quadrigemina and the cerebellum behind. The surface of the hemispheres also becomes covered with nume-

rous convolutions, which are curvilinear and somewhat irregular in form and direction, instead of being transverse, like those of the cerebellum. In man, the development of the hemispheres reaches its highest point; so that they preponderate altogether in size over the rest of the ganglia constituting the brain. In the human brain, accordingly, when viewed from above downward, there is nothing to be seen but the convex surfaces of the hemispheres; and even in a posterior view, as seen in Fig. 137, they conceal everything but a portion of the cerebellum. All the remaining parts, however, exist even here, and have the same connections and relative situation as in other instances. They may best be studied in the following order.

Fig. 141.



MEDULLA OBLONGATA OF HUMAN BRAIN, anterior view —1, 1. Anterior pyramids. 2, 2. Olivary bodies. 3, 3. Restiform bodies. 4. Decussation of the anterior columns. The medulla oblongata is seen terminated above by the transverse fibres of the pons Varolii.

As the spinal cord, in the human subject, passes upward into the cranial cavity, it enlarges into the medulla oblongata as already described. The medulla oblongata presents on each side three projections, two anterior and one posterior. The middle projections on its anterior surface (Fig. 141, 1, 1), which are called the *anterior pyramids*, are the continuation of the anterior columns of the cord. They pass onward, underneath the transverse fibres of the pons Varolii, run upward to the corpora striata, pass through these bodies, and radiate upward and outward from their external surface, to terminate in the gray matter of the hemispheres. The projections immediately on the outside of the anterior pyramids, in the medulla oblongata, are the *olivary bodies* (2, 2). Each contains in its interior a thin layer of gray matter folded upon itself, forming a convoluted ganglion, which is connected, by longitudinal, radiating and transverse fibres, with other parts of the medulla above and below, and with the corresponding ganglion of the opposite side.

The anterior columns of the cord present, at the lower part of the medulla oblongata, a remarkable interchange or crossing of their fibres (4), known as the *decussation of the anterior pyramids*. This decussation, as shown by Mr. J. L. Clarke,[1] consists of fibres derived from the lateral columns of the cord, which cross obliquely at the median line, and pass over to be incorporated with the sub

[1] Researches on the Intimate Structure of the Brain, &c. London, Phil. Trans., 1858.

stance of the opposite anterior columns, thus increasing their mass at this point, and forming the rounded prominences known as the anterior pyramids. Thus the right side of the brain is connected with the left side of the spinal cord, and the right side of the spinal cord with the left side of the brain.

The posterior columns of the cord, as they diverge on each side of the fourth ventricle, form the posterior and lateral projections of the medulla oblongata (3, 3). They are sometimes called the "restiform bodies," and are extremely important parts of the brain. They consist in great measure of the longitudinal filaments of the posterior columns, which pass upward and outward, and are distributed partly to the gray matter of the cerebellum. The remainder then pass forward, underneath the tubercula quadrigemina, into and through the optic thalami; and radiating thence upward and outward, are distributed, like the continuation of the anterior columns, to the gray matter of the cerebrum. The restiform bodies, however, in passing upward to the cerebellum, are supplied with some fibres from the anterior columns of the cord, which, leaving the lower portion of the anterior pyramids, join the restiform bodies, and are distributed with them to the cerebellum. From this description it will be seen that both the cerebrum and the cerebellum are supplied with filaments from both the anterior and posterior columns of the cord.

In the substance of each restiform body, moreover, there is imbedded a ganglion which gives origin to the pneumogastric nerve, and presides over the functions of respiration. This ganglion is surrounded and covered by the longitudinal fibres passing upward from the cord to the cerebellum, but may be discovered by cutting into the substance of the restiform body, in which it is buried. It is the first important ganglion met with, in dissecting the brain from below upward.

While the anterior columns are passing beneath the pons Varolii, they form, together with the continuation of the posterior columns and the transverse fibres of the pons itself, a rounded prominence or tuberosity, which is known by the name of the *tuber annulare*. In the deeper portions of this protuberance there is situated, among the longitudinal fibres, another collection of gray matter, which though not of large size, has very important functions and connections. This is known as the *ganglion of the tuber annulare*.

Situated almost immediately above these parts we have the corpora striata in front, and the optic thalami behind, nearly equal in

size, and giving passage, as above described, to the fibres of the anterior and posterior columns. Behind them still, and on a little lower level, are the tubercula quadrigemina, giving origin to the optic nerves. The olfactory ganglia rest upon the cribriform plate of the ethmoid bone, and send the olfactory filaments through the perforations in this plate, to be distributed upon the mucous membrane of the upper and middle turbinated bones. The cerebellum covers in the fourth ventricle and the posterior surface of the medulla oblongata; and finally the cerebrum, which has attained the size of the largest ganglion in the cranial cavity, extends so far in all directions, forward, backward, and laterally, as to form a convoluted arch or vault, completely covering all the remaining parts of the encephalon.

Fig. 142.

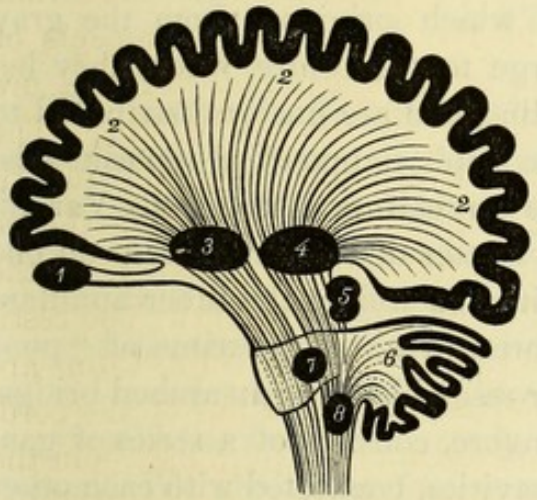


Diagram of HUMAN BRAIN, in vertical section; showing the situation of the different ganglia, and the course of the fibres. 1. Olfactory ganglion. 2. Hemisphere. 3. Corpus striatum. 4. Optic thalamus. 5. Tubercula quadrigemina. 6. Cerebellum. 7. Ganglion of tuber annulare. 8. Ganglion of medulla oblongata.

The entire brain may therefore be regarded as a connected series of ganglia, the arrangement of which is shown in the accompanying diagram. (Fig. 142.) These ganglia occur in the following order, counting from before backward: 1st. The olfactory ganglia. 2d. The cerebrum or hemispheres. 3d. The corpora striata. 4th. The optic thalami. 5th. The tubercula quadrigemina. 6th. The cerebellum. 7th. The ganglion of the tuber annulare. And 8th. The ganglion of the medulla oblongata. Of these ganglia, only the hemispheres and cerebellum are convoluted, while the remainder are smooth and rounded or somewhat irregular in shape. The course of the fibres coming from the anterior and posterior columns of the cord is also to be seen in the accompanying figure. A portion of the anterior fibres, we have already observed, pass upward and backward, with the restiform bodies, to the cerebellum; while the remainder run forward through the tuber annulare and the corpus striatum, and then radiate to the gray matter of the cerebrum. The posterior fibres, constituting the restiform body, are distributed partly to the cerebellum, and then pass forward, as previously described, under-

neath the tubercula quadrigemina to the optic thalmi, whence they are also finally distributed to the gray matter of the cerebrum.

The cerebrum and cerebellum, each of which is divided into two lateral halves or "lobes," by the great longitudinal fissure, are both provided with transverse commissures, by which a connection is established between their right and left sides. The great transverse commissure of the cerebrum is that layer of white substance which is situated at the bottom of the longitudinal fissure, and which is generally known by the name of the "corpus callosum." It consists of nervous filaments, which originate from the gray matter of one hemisphere, converge to the centre, where they become parallel, cross the median line, and are finally distributed to the corresponding parts of the hemisphere upon the opposite side. The transverse commissure of the cerebellum is the pons Varolii. Its fibres converge from the gray matter of the cerebellum on one side, and pass across to the opposite; encircling the tuber annulare with a band of parallel curved fibres, to which the name of "pons Varolii" has been given from their resemblance to an arched bridge.

The cerebro-spinal system, therefore, consists of a series of ganglia situated in the cranio-spinal cavities, connected with each other by transverse and longitudinal commissures, and sending out nerves to the corresponding parts of the body. The spinal cord supplies the integument and muscles of the neck, trunk, and extremities; while the ganglia of the brain, besides supplying the corresponding parts of the head, preside also over the organs of special sense, and perform various other functions of a purely nervous character.

CHAPTER II.

OF NERVOUS IRRITABILITY AND ITS MODE OF ACTION.

We have already mentioned, in a previous chapter, that every organ in the body is endowed with the property of *irritability;* that is, the property of reacting in some peculiar manner when subjected to the action of a direct stimulus. Thus the irritability of a gland shows itself by increased secretion, that of the capillary vessels by congestion, that of the muscles by contraction. Now the irritability of the muscles, indicated as above by their contraction, is extremely serviceable as a means of studying and exhibiting nervous phenomena. We shall therefore commence this chapter by a study of some of the more important facts relating to muscular irritability.

The irritability of the muscles is a property inherent in the muscular fibre itself. The existence of muscular irritability cannot be explained by any known physical or chemical laws, so far as they relate to inorganic substances. It must be regarded simply as a peculiar property, directly dependent on the structure and constitution of the muscular fibre; just as the property of emitting light belongs to phosphorus, or that of combining with metals to oxygen. This property may be called into action by various kinds of stimulus; as by pinching the muscular fibre, or pricking it with the point of a needle, the application of an acid or alkaline solution, or the discharge of a galvanic battery. All these irritating applications are immediately followed by contraction of the muscular fibre. This contraction will even take place under the microscope, when the fibre is entirely isolated, and removed from contact with any other tissue; showing that the properties of contraction and irritability reside in the fibre itself, and are not communicated to it by other parts.

Muscular irritability continues for a certain time after death. The stoppage of respiration and circulation does not at once destroy the vital properties of the tissues, but nearly all of them retain

these properties to a certain extent for some time afterward. It is only when the constitution of the tissues has become altered by being deprived of blood, and by the consequent derangement of the nutritive process, that their characteristic properties are finally lost. Thus, in the muscles, irritability and contractility may be easily shown to exist for a short time after death by applying to the exposed muscular fibre the same kind of stimulus that we have already found to affect it during life. It is easy to see, in the muscles of the ox, after the animal has been killed, flayed, and eviscerated, different bundles of muscular fibres contracting irregularly for a long time, where they are exposed to the contact of the air. Even in the human subject the same phenomenon may be seen in cases of amputation; the exposed muscles of the amputated limb frequently twitching and quivering for many minutes after their separation from the body.

The duration of muscular irritability, after death, varies considerably in different classes of animals. It disappears most rapidly in those whose circulation and respiration are naturally the most active; while it continues for a longer time in those whose circulation and respiration are sluggish. Thus in birds the muscular irritability continues only a few minutes after the death of the animal. In quadrupeds it lasts somewhat longer; while in reptiles it remains, under favorable circumstances, for many hours. The cause of this difference is probably that, in birds and quadrupeds, the tissues being very vascular, and the molecular changes of nutrition going on with rapidity, the constitution of the muscular fibre becomes so rapidly altered after the circulation has ceased, that its irritability soon disappears. In reptiles, on the other hand, the tissues are less vascular than in birds and quadrupeds, and all the nutritive changes go on more slowly. Respiration and circulation can therefore be dispensed with for a longer period, before the constitution of the tissues becomes so much altered as to destroy altogether their vital properties.

Fig. 143.

Frog's Leg, with poles of galvanic battery applied to the muscles at *a*, *b*.

Owing to this peculiarity of the cold-blooded animals, their tissues may be used with great advantage for purposes of experiment. If a frog's leg, for example, be separated from the body of the animal (Fig. 143), the skin

removed, and the poles of a galvanic apparatus applied to the surface of the muscle (*a*, *b*), a contraction takes place every time the circuit is completed and a discharge passed through the tissues of the limb. The leg of the frog, prepared in this way, may be employed for a long time for the purpose of exhibiting the effect of various kinds of stimulus upon the muscles. All the mechanical and chemical irritants which we have mentioned, pricking, pinching, cauterization, galvanism, &c., act with more or less energy and promptitude, though the most efficient of all is the electric discharge.

Continued irritation exhausts the irritability of the muscles. It is found that the irritability of the muscles wears out after death more rapidly if they be artificially excited, than if they be allowed to remain at rest. During life, the only habitual excitant of muscular contraction is the peculiar stimulus conveyed by the nerves. After death this stimulus may be replaced or imitated, to a certain extent, by other irritants; but their application gradually exhausts the contractility of the muscle and hastens its final disappearance. Under ordinary circumstances, the post-mortem irritability of the muscle remains until the commencement of cadaveric rigidity. When this has become fairly established, the muscles will no longer contract under the application of an artificial stimulus.

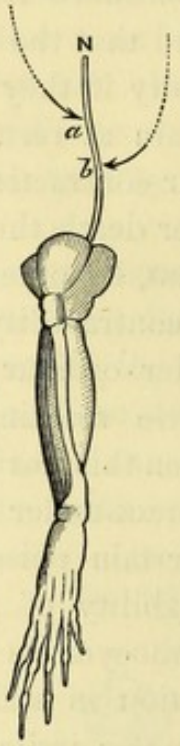
Certain poisonous substances have the power of destroying the irritability of the muscles by a direct action upon their tissue. Sulphocyanide of potassium, for example, introduced into the circulation in sufficient quantity to cause death, destroys entirely the muscular irritability, so that no contraction can afterward be produced by the application of an external stimulant.

Nervous Irritability.—The irritability of the nerves is the property by which they may be excited by an external stimulus, so as to be called into activity and excite in their turn other organs to which their filaments are distributed. When a nerve is irritated, therefore, its power of reaction, or its irritability, can only be estimated by the degree of excitement produced in the organ to which the nerve is distributed. A nerve running from the integument to the brain produces, when irritated, a painful sensation; one distributed to a glandular organ produces increased secretion; one distributed to a muscle produces contraction. Of all these effects, muscular contraction is found to be the best test and measure of nervous irritability, for purposes of experiment. Sensation cannot of course be relied on for this purpose, since both consciousness and volition are abolished at the time of death. The activity of the

glandular organs, owing to the stoppage of the circulation, disappears also very rapidly, or at least cannot readily be demonstrated. The contractility of the muscles, however, lasts, as we have seen, for a considerable time after death, and may accordingly be employed with great readiness as a test of nervous irritability. The manner of its employment is as follows:—

The leg of a frog is separated from the body and stripped of its integument; the sciatic nerve having been previously dissected out and cut off at its point of emergence from the spinal canal, so that a considerable portion of it remains in connection with the separated limb. (Fig. 144.) If the two poles of a galvanic apparatus be now placed in contact with different points (*a b*) of the exposed nerve, and a discharge allowed to pass between them, at the moment of discharge a sudden contraction takes place in the muscles below. It will be seen that this experiment is altogether different from the one represented in Fig. 143. In that experiment the galvanic discharge passes through the muscles themselves, and acts upon them by direct stimulus. Here, however, the discharge passes only from *a* to *b* through the tissues of the nerve, and acts directly upon the nerve alone; while the nerve, acting upon the muscles by its own peculiar agency, causes in this way a muscular contraction. It is evident that in order to produce this effect, two conditions are equally essential: 1st. The irritability of the muscles; and 2d. The irritability of the nerve. So long, therefore, as the muscles are in a healthy condition, their contraction, under the influence of a stimulus applied to the nerve, demonstrates the irritability of the latter, and may be used as a convenient measure of its intensity.

Fig. 144.



Frog's Leg, with sciatic nerve (N) attached.—*a b*. Poles of galvanic battery, applied to nerve.

The irritability of the nerve continues after death. The knowledge of this fact follows from what has just been said with regard to experimenting upon the frog's leg, prepared as above. The irritability of the nerve, like that of the muscle, depends directly upon its anatomical structure and constitution; and so long as these remain unimpaired, the nerve will retain its vital properties, though respiration and circulation may have ceased. For the same reason,

also, as that given above with regard to the muscles, nervous irritability lasts much longer after death in the cold-blooded than in the warm-blooded animals. Various artificial irritants may be employed to call it into activity. Pinching or pricking the exposed nerve with steel instruments, the application of caustic liquids, and the passage of galvanic discharges, all have this effect. The electric current, however, is much the best means to employ for this purpose, since it is more delicate in its operation than the others, and will continue to succeed for a longer time.

The nerve is, indeed, so exceedingly sensitive to the electric current, that it will respond to it when insensible to all other kinds of stimulus. A frog's leg freshly prepared with the nerve attached, as in Fig. 144, will react so readily whenever a discharge is passed through the nerve, that it forms an extremely delicate instrument for detecting the presence of electric currents of low intensity, and has even been used for this purpose by Matteucci, under the name of the "galvanoscopic frog." It is only necessary to introduce the nerve as part of the electric circuit; and if even a very feeble current be present, it is at once betrayed by a muscular contraction.

The superiority of electricity over other means of exciting nervous action, such as mechanical violence or chemical agents, probably depends upon the fact that the latter necessarily alter and disintegrate more or less the substance of the nerve, so that its irritability soon disappears. The electric current, on the other hand, excites the nervous irritability without any marked injury to the substance of the nervous fibre. Its action may, therefore, be continued for a longer period.

Nervous irritability, like that of the muscles, is exhausted by repeated excitement. If a frog's leg be prepared as above, with the sciatic nerve attached, and allowed to remain at rest in a damp and cool place, where its tissue will not become altered by desiccation, the nerve will remain irritable for many hours; but if it be excited, soon after its separation from the body, by repeated galvanic shocks, it soon begins to react with diminished energy, and becomes gradually less and less irritable, until it at last ceases to exhibit any further excitability. If it be now allowed to remain for a time at rest, its irritability will be partially restored; and muscular contraction will again ensue on the application of a stimulus to the nerve. Exhausted a second time, and a second time allowed to repose, it will again recover itself; and this may even be repeated several times in succession. At each repetition, however, the recovery of

nervous irritability is less complete, until it finally disappears altogether, and can no longer be recalled.

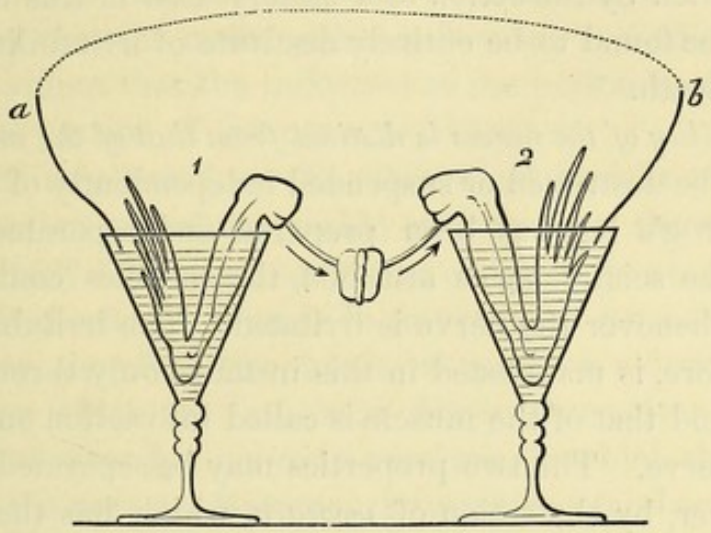
Various accidental circumstances tend to diminish or destroy nervous irritability. The action of the *woorara* poison, for example, destroys at once the irritability of the nerves; so that in animals killed by this substance, no muscular contraction takes place on irritating the nervous trunk. Severe and sudden mechanical injuries often have the same effect; as where death is produced by violent and extensive crushing or laceration of the body or limbs. Such an injury produces a general disturbance, or *shock* as it is called, which affects the entire nervous system, and destroys or suspends its irritability. The effects of such a nervous shock may frequently be seen in the human subject after railroad accidents, where the patient, though very extensively injured, may remain for some hours without feeling the pain of his wounds. It is only after reaction has taken place, and the activity of the nerves has been restored, that the patient begins to be sensible of pain.

It will often be found, on preparing the frog's leg for experiment as above, that immediately after the limb has been separated from the body and the integument removed, the nerve is destitute of irritability. Its vitality has been suspended by the violence inflicted in the preparatory operation. In a few moments, however, if kept under favorable conditions, it recovers from the shock, and regains its natural irritability.

The action of the galvanic current upon the nerves, as first shown by the experiments of Matteucci, is in many respects peculiar. If the current be made to traverse the nerve in the natural direction of its fibres, viz., from its origin towards its distribution, as from *a* to *b* in Fig. 144, it is called the *direct* current. If it be made to pass in the contrary direction, as from *b* to *a*, it is called the *inverse* current. When the nerve is fresh and exceedingly irritable, a muscular contraction takes place at both the commencement and termination of the current, whether it be direct or inverse. But very soon afterward, when the activity of the nerve has become somewhat diminished, it will be found that contraction takes place only at the *commencement* of *the direct* and at the *termination* of *the inverse* current. This may readily be shown by preparing the two legs of the same frog in such a manner that they remain connected with each other by the sciatic nerves and that portion of the spinal column from which these nerves take their origin. The two legs, so prepared, should be placed each in a vessel of water, with the

nervous connection hanging between. (Fig. 145.) If the positive pole, *a*, of the battery be now placed in the vessel which holds leg No. 1, and the negative pole, *b*, in that containing leg No. 2, it will be seen that the galvanic current will traverse the two legs in opposite directions. In No. 1, it will pass in a direction contrary to the course of its nervous fibres, that is, it will be for this leg an

Fig. 145.



inverse current; while in No. 2 it will pass in the same direction with that of the nervous fibres, that is, it will be for this leg a *direct* current. It will now be found that at the moment when the circuit is completed, a contraction takes place in No. 2 by the direct current, while No. 1 remains at rest; but at the time the circuit is broken, a contraction is produced in No. 1 by the inverse current, but no movement takes place in No. 2. A succession of alternate contractions may thus be produced in the two legs by repeatedly closing and opening the circuit. If the position of the poles, *a*, *b*, be reversed, the effects of the current will be changed in a corresponding manner.

After a nerve has become exhausted by the direct current, it is still sensitive to the inverse; and after exhaustion by the inverse, it is still sensitive to the direct. It has even been found by Matteucci that after a nerve has been exhausted for the time by the direct current, the return of its irritability is hastened by the subsequent passage of the inverse current; so that it will become again sensitive to the direct current sooner than if allowed to remain at rest. Nothing, accordingly, is so exciting to a nerve as the passage of direct and inverse currents, alternating with each other in rapid succession. Such a mode of applying the electric stimulus is that

usually adopted in the galvanic machines used in medical practice, for the treatment of certain paralytic affections. In these machines, the electric circuit is alternately formed and broken with great rapidity, thus producing the greatest effect upon the nerves with the smallest expenditure of electricity. Such alternating currents, however, if very powerful, exhaust the nervous irritability more rapidly and completely than any other kind of irritation; and in an animal killed by the action of a battery used in this manner, the nerves may be found to be entirely destitute of irritability from the moment of death.

The irritability of the nerves is distinct from that of the muscles; and the two may be destroyed or suspended independently of each other. When the frog's leg has been prepared and separated from the body, with the sciatic nerve attached, the muscles contract, as we have seen, whenever the nerve is irritated. The irritability of the nerve, therefore, is manifested in this instance only through that of the muscle, and that of the muscle is called into action only through that of the nerve. The two properties may be separated from each other, however, by the action of *woorara*, which has the power, as first pointed out by Bernard,[1] of destroying the irritability of the nerve without affecting that of the muscles. If a frog be poisoned by this substance, and the leg prepared as above, the poles of a galvanic battery applied to the nerve will produce no effect; showing that the nervous irritability has ceased to exist. But if the galvanic discharge be passed directly through the muscles, contraction at once takes place. The muscular irritability has survived that of the nerves, and must therefore be regarded as essentially distinct from it.

It is found, moreover, that the action of woorara, in these cases, is especially exerted, not upon the entire length of the motor filaments, but upon their peripheral extremities, at the point where they join the muscular fibres. If the trunk of the sciatic nerve, for example, be exposed to the influence of the poison, while its terminal ramifications are protected from it by a ligature of the bloodvessels,[2] galvanization of the nerve above the ligature will still produce contraction in the muscles below. Bernard[3] has shown this peculiarity in the action of woorara on the motor nerves by a still more striking experiment. He prepared two gastrocnemii

[1] Leçons sur la physiologie du système nerveux. Paris, 1858, vol. i. p. 199.

[2] Vulpian, Système nerveux. Paris, 1866, p. 208.

[3] Substances toxiques et médicamenteuses. Paris, 1857, p. 329.

muscles of the frog, each one having about an inch of its nervous trunk attached. In one, the exposed portion of the nerve is immersed for some time in a watch-glass containing an aqueous solution of woorara; and notwithstanding the direct contact of the poison with the nervous trunk, galvanization of the nerve at this point still causes a muscular contraction in the gastrocnemius. In the other, the muscle itself is immersed in the solution of woorara, and the nerve is then found to have lost all signs of irritability. As we know that the muscles themselves are not affected by woorara, it is evident that the influence of the poison is exerted upon the terminal portion of the nervous filaments.

It will be recollected, on the other hand, that in cases of death from the action of sulphocyanide of potassium, the muscular irritability is itself destroyed; so that no contractions occur, even when the galvanic discharge is made to traverse the muscular tissue.

There are, therefore, two kinds of paralysis: first, a muscular paralysis, in which the muscular fibres themselves are directly affected; and second, a nervous paralysis, in which the affection is confined to the nervous filaments, the muscles retaining their natural properties, and being still capable of contracting under the influence of a direct stimulus.

Rapidity of the Nervous Force.—Some very ingenious experiments have been performed by Helmholtz,[1] in order to determine the rapidity with which a stimulus is transmitted through the nervous fibre. These experiments not only show that a certain interval of time is required for this transmission, but indicate also in an approximate manner the measurement of its rapidity for different distances. Helmholtz exposed the muscle of a recently killed animal with the nerve attached. He first passed an electric discharge through the muscle itself, and found that only $\frac{1}{100}$ of a second intervened between the electric discharge and the muscular contraction. He then applied the electric stimulus to the nerve in the immediate neighborhood of the muscle, and found that the previous interval was not perceptibly increased. But if the poles of the battery were applied to the nerve at various distances from the muscle, the interval between the electric discharge and the muscular contraction became longer, as the length of the nervous branch transmitting the impulse was increased. Helmholtz ascertained in this way that the rapidity of transmission of the motor impulse in the nerves of the frog was a little over eighty-five feet

[1] Comptes Rendus de l'Académie des Sciences. Vol. xxxiii. p. 262.

per second. Similar investigations were subsequently carried out by Baxt, in the laboratory of Helmholtz, in order to determine the rate of transmission of the motor nervous influence in man.[1] This was done by passing a galvanic discharge between two electrodes placed directly above the nerve at varying distances from the muscles to which its filaments were distributed. Thus the galvanic stimulus was applied to the median nerve at the wrist, at the elbow, and at the upper arm near the lower extremities of the coraco-brachialis and deltoid muscles; and the effect of the stimulation was marked by the contraction of the muscles of the ball of the thumb. By accurate measurement it was found that the interval of time between the galvanic discharge and the muscular contraction was greater when the stimulus was applied to the nerve at the upper arm, than when applied at the wrist; this increased interval being evidently the time required for the propagation of the nervous impulse from one point to the other. The rapidity of transmission, as ascertained by these experiments, was found to vary considerably according to the varying conditions of cold and warmth; the lowest rate of transmission in the median nerve, from the middle of the upper arm to the wrist, being a little over one hundred feet per second, the highest two hundred and ninety-three feet. The average rate, as deduced from the entire series, cannot be estimated at less than two hundred feet per second.

If we regard this as representing the usual rate of transmission in the human motor nerves, and if we estimate the distance from the origin of the motor filaments in the brain to their termination in the muscles of the foot as five feet, the time required to transmit the nervous impulse from the brain to these muscles would be one-fortieth of a second.

Nature of the Nervous Force.—The special endowment by which a nerve acts and manifests its vitality is a peculiar one, inherent in the anatomical structure and constitution of the nervous tissue. It is manifested, in the foregoing experiments, by its effect upon the contractile muscles. But we shall hereafter see that this is, in reality, only one of its results, and that it shows itself, during life, by a variety of other influences. Thus it produces, in one case, sensation; in another, muscular contraction; in another, increased or modified glandular activity; in another, alterations in the phenomena of the circulation. The force, however, which is exerted by

[1] Monatsbericht der Königlichen Preussischen Academie. April, 1867, and March, 1870.

a nerve in a state of activity, and which brings about these changes, is not directly appreciable in any way by the senses, and can be judged of only by its secondary effects. We understand enough of its mode of operation, to know that it is not identical with the forces of chemical affinity, of mechanical action, or of electricity.

And yet, by acting upon the organs to which the nerves are distributed, it will finally produce phenomena of all these different kinds. By the intervention of the muscles, it results in mechanical action; and by its influence upon the glands and bloodvessels, it causes chemical alterations in the animal fluids of the most important character.

It will even produce well-marked electrical phenomena, which in some cases are so decided, as to have long attracted the attention of physiologists.

It has been fully demonstrated that certain fish (gymnotus and torpedo) have the power of generating electricity, and of producing electric discharges, which are often sufficiently powerful to kill small animals that may come within their reach. That the force generated by these animals is in reality electricity, is beyond a doubt. It is conducted by the same bodies which serve as conductors for electricity, and is stopped by those which are non-conductors of the same. All the ordinary phenomena produced by the electric current, viz: the heating and melting of a fine conducting wire, the induction of secondary currents and of magnetism, the decomposition of saline solutions, and even the electric spark, have all been produced by the force generated by these animals. There is, accordingly, no room for doubt as to its nature.

The electrical phenomena, in these cases, are produced by certain organs which are called into activity by the nervous influence.

The electrical organs of the gymnotus and torpedo occupy a considerable portion of the body, and are largely supplied with nerves which regulate their function. If these nerves be divided, tied, or injured in any way, the electrical organ is weakened or paralyzed, just as the muscles would suffer if the nerves distributed to them were subjected to a similar violence. The electricity produced by these animals, accordingly, is not supplied by the nerves, but by a special generating organ, the action of which is regulated by nervous influence.

CHAPTER III.

THE SPINAL CORD.

We have already seen that the spinal cord is a long ganglion, covered with longitudinal bundles of nervous filaments, and occupying the cavity of the spinal canal. It sends out nerves which supply the muscles and integument of at least nine-tenths of the whole body, viz., those of the neck, trunk, and extremities. All these parts of the body are endowed with two very remarkable properties, the exercise of which depends, directly or indirectly, upon the integrity and activity of the spinal cord, viz., the power of sensation and the power of motion. Both these properties are said to reside in the nervous system, because they are so readily influenced by its condition, and are so closely connected with its physiological action. We shall therefore commence the study of the spinal cord with an examination of these two functions, and of the situation which they occupy in the nervous system.

Sensation.—The power of sensation, or *sensibility*, is the power by which we are enabled to receive impressions from external objects. These impressions are usually of such a nature that we can derive from them some information in regard to the qualities of external objects and the effect which they may produce upon our own systems. Thus, by bringing a foreign body into contact with the skin, we feel that it is hard or soft, rough or smooth, cold or warm. We can distinguish the separate impressions produced by several bodies of a similar character, and we can perceive whether either one of them, while in contact with the skin, be at rest or in motion. This power, which is generally distributed over the external integument, is dependent on the nervous filaments ramifying in its tissue. For if the nerves distributed to any part of the body be divided, the power of sensation in the corresponding region is immediately lost.

The sensibility, thus distributed over the integument, varies in its acuteness in different parts of the body. Thus, the extremities of the fingers are more sensitive to external impressions than the general surface of the limbs and trunk. The surfaces of the fingers which lie in contact with each other are more sensitive than their dorsal or palmar surfaces. The point of the tongue, the lips, and the orifices of most of the mucous passages are endowed with a sensibility which is more acute than that of the general integument.

If the impression to which these parts are subjected be harsh or violent in its character, or of such a nature as to injure the texture of the integument or its nerves, it then produces a sensation of *pain*. It is essential to notice, however, that the sensation of pain is not a mere exaggeration of ordinary sensitive impressions, but is one of quite a different character, which is superadded to the others, or takes their place altogether. Just in proportion as the contact of a foreign body becomes painful, our ordinary perceptions of its physical properties are blunted, and the sense of suffering predominates over ordinary sensibility. Thus if the integument be gently touched with the blade of a knife we easily feel that it is hard, cold, and smooth; but if an incision be made with it in the skin, we lose all distinct perception of these qualities, and feel only the suffering produced by the incision. We perceive, also, the difference in temperature between cold and warm substances brought in contact with the skin, so long as this difference is moderate in degree; but if a foreign body be excessively cold or excessively hot, we can no longer appreciate its temperature by the touch, but only its injurious and destructive effect. Thus the sensation caused by touching frozen carbonic acid is the same with that produced by a red-hot metal. Both substances blister the surface, but their actual temperatures cannot be distinguished.

It is, therefore, a very important fact in this connection, that *the sensibility to pain is distinct from the power of ordinary sensation*. This distinction was first fully established by M. Beau, of Paris, who has shown conclusively that the sensibility to pain may be diminished or suspended, while ordinary sensation remains. This is often seen in patients who are partially under the influence of ether or chloroform. The etherization may be carried to such an extent that the patient may be quite insensible to the pain of a surgical operation, and yet remain perfectly conscious, and even capable of feeling the incisions, ligatures, &c., though he does not suffer from them. It not unfrequently happens, also, when opium has been adminis-

tered for the relief of neuralgia, that the pain is completely abolished by the influence of the drug, while the patient retains completely his consciousness and his ordinary sensibility.

In all cases, however, if the influence of the narcotic be pushed to its extreme, both kinds of sensibility are suspended together, and the patient becomes entirely unconscious of external impressions.

Motion.—Wherever muscular tissue exists, in any part of the body, we find the power of motion, owing to the contractility of the muscular fibres. But this power of motion, as we have already seen, is dependent on the nervous system. The excitement which causes the contraction of the muscles is transmitted to them by the nervous filaments; and if the nerve supplying a muscle or a limb be divided or seriously injured, these parts are at once paralyzed and become incapable of voluntary movement. A nerve which, when irritated, acts directly upon a muscle, producing contraction, is said to be *excitable;* and its excitability, acting through the muscle, produces motion in the part to which it is distributed.

The excitability of various nerves, however, often acts during life upon other organs, beside the muscles; and the ultimate effect varies, of course, with the properties of the organ which is acted upon. Thus, the nervous excitement transmitted to a muscle produces contraction, while that transmitted to a gland produces an increased secretion, and that conveyed to a vascular surface causes congestion. In all such instances, the effect is produced by an influence transmitted by the nerve directly to the organ which is called into activity.

But in all the external parts of the body muscular contraction is the most marked and palpable effect produced by the direct influence of nervous excitement. We find, therefore, that so far as we have yet examined it, the nervous action shows itself principally in two distinct and definite forms; first, as *sensibility*, or the power of sensation, and second, as *excitability* or the power of producing motion.

Distinct Seat of Sensation and Motion in the Nervous System.—Sensation and motion are usually the first functions which suffer by any injury inflicted on the nervous system. As a general rule, they are both suspended or impaired at the same time, and in a nearly equal degree. In a fainting fit, an attack of apoplexy, concussion or compression of the brain or spinal cord, or a

wound of any kind involving the nerves or nervous centres, insensibility and loss of motion usually appear simultaneously. It is difficult, therefore, under ordinary conditions, to trace out the separate action of these two functions, or to ascertain the precise situation occupied by each.

This difficulty, however, may be removed by examining separately different parts of the nervous system. In the instances mentioned above, the injury which is inflicted is comparatively an extensive one, and involves at the same time many adjacent parts. But instances sometimes occur in which the two functions, sensation and motion, are affected independently of each other, owing to the peculiar character and situation of the injury inflicted. Sensation may be impaired without loss of motion, and loss of motion may occur without injury to sensation. In tic douloureux, for example, we have an exceedingly painful affection of the sensitive parts of the face, without any impairment of its power of motion; and in facial paralysis we often see a complete loss of motion affecting one side of the face, while the sensibility of the part remains altogether unimpaired.

The above facts first gave rise to the belief that sensation and motion might occupy distinct parts of the nervous system; since it would otherwise be difficult to understand how the two could be affected independently of each other by anatomical lesions. It has accordingly been fully established by the labors of Sir Charles Bell, Magendie, Müller, Panizza, and Longet, that the two functions do in reality occupy distinct parts of the nervous system.

If any one of the spinal nerves, in the living animal, after being exposed at any part of its course outside the spinal canal, be divided, ligatured, bruised, or otherwise seriously injured, paralysis of motion and loss of sensation are immediately produced in that part of the body to which the nerve is distributed. If, on the other hand, the same nerve be pricked, galvanized, or otherwise gently irritated, a painful sensation and convulsive movements are produced in the same parts. The nerve is therefore said to be both *sensitive* and *excitable;* sensitive, because irritation of its fibres produces a painful sensation, and excitable, because the same irritation causes muscular contraction in the parts below.

The result of the experiment, however, will be different if it be tried upon the parts situated inside the spinal canal, and particularly upon the anterior and posterior roots of the spinal nerves. If an irritation be applied, for example, to the anterior root of a spinal

nerve in the living animal, convulsive movements are produced in the parts below, but there is no painful sensation. The anterior root accordingly is said to be excitable, but not sensitive. If the posterior root, on the other hand, be irritated, acute pain is produced, but no convulsive movements. The posterior root is therefore sensitive, but not excitable.

The above facts show the different properties manifested by the two roots of a spinal nerve, when subjected to artificial irritation. Still more important results, as showing what are actually the natural functions of the parts, are derived from the experiment of dividing separately each of the two roots and observing the effect upon the parts below. These experiments, first performed by Magendie[1] in 1822, have been frequently repeated since, and their results fully confirmed. If the posterior root of a spinal nerve, in the living animal, be divided by a transverse section, (as in Fig. 146, *a*, *b*,) without injuring the anterior root, it is found that the sensibility of the integument, in the corresponding part of the body, has disappeared, while the power of voluntary motion remains unimpaired in the muscles of the same region. On the other hand, if the anterior root be alone divided (Fig. 146, *c*, *d*), leaving the posterior untouched, the power of voluntary motion is abolished in the corresponding muscles, but at the same time the skin retains its sensibility.

Thus it is evident that the impressions of sensibility pass to the nervous centres exclusively by the posterior roots, while the stimulus which excites the muscles to contraction is conveyed only by the anterior roots. We have therefore a separate localization of sensation and motion in this part of the nervous system; and it is easy accordingly to understand how one may be impaired without injury to the other, or how both may be simultaneously affected, according to the situation and extent of the anatomical lesion.

In the two roots of a spinal nerve, furthermore, the nervous action is manifested in two opposite directions. If the posterior root be divided (Fig. 146) at *a*, *b*, and an irritation applied to the separated extremity (*a*), no effect will be produced, because the nerve at this point is cut off from its communication with the nervous centres; but if the irritation be applied to the attached extremity (*b*), a painful sensation is immediately the result. The nervous action, therefore, in the posterior root, is manifested in a direction from without inward. If the anterior root, on the other hand, be

[1] Journal de Physiologie Expérimentale, vol. ii. p. 276.

divided at *c, d,* and its attached extremity (*d*) be irritated, no effect follows, because the nervous filaments here are no longer in communication with the muscles; but if the separated extremity (*c*)

Fig. 146.

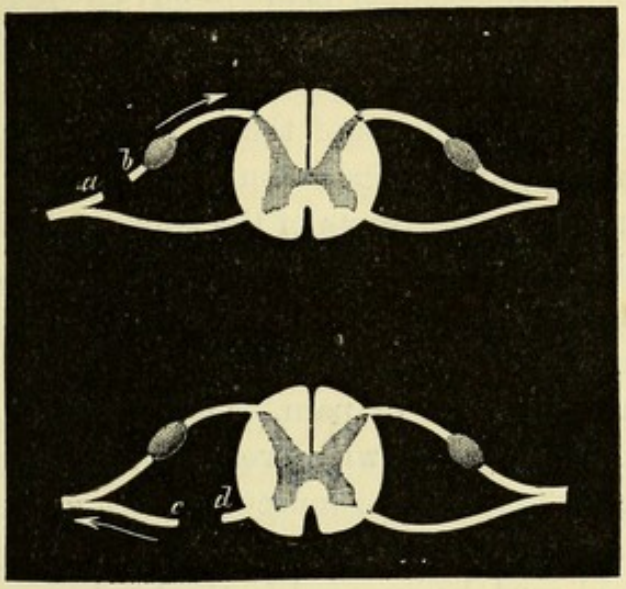


Diagram of SPINAL CORD AND NERVES. The posterior root is seen divided at *a, b,* the anterior at *c, d.*

be irritated, convulsive movements instantly take place. The nervous action, consequently, passes, in the anterior root, in a direction from within outward.

The same thing is true with regard to the transmission of sensation and motion in the spinal nerves outside the spinal canal. If one of these nerves be divided in the living animal, and its attached extremity irritated, pain is produced, but no convulsive motion; if the irritation be applied to its separated extremity, muscular contractions follow, but no painful sensation.

There are therefore in the spinal nerves, as elsewhere, two sets of nervous filaments adapted to the performance of two different functions; viz., the "sensitive" filaments, or those which convey sensation, and the "motor" filaments, or those which excite movement. In the roots of the spinal nerves these two sets of fibres are separated from each other, the anterior root being exclusively motor, and the posterior exclusively sensitive. At the point of junction, however, of the two roots, the spinal nerve, as it emerges from the spinal canal, contains both motor and sensitive fibres intimately mingled in a common trunk. It is therefore called a *mixed* nerve, serving at the same time, by the two sets of fibres which it contains, for the conveyance of both sensibility and motive power. At the periphery the two sets of filaments again separate,

the sensitive fibres passing to the integument, and the motor fibres to the muscles.

Distinct Seat of Sensibility and Excitability in the Spinal Cord.—Various experimenters have demonstrated the fact that different parts of the spinal cord, like the two roots of the spinal nerves, are separately endowed with sensibility and excitability. The anterior columns of the cord, like the anterior roots of the spinal nerves, are excitable but not sensitive; the posterior columns, like the posterior roots of the spinal nerves, are sensitive but not excitable. Accordingly, when the spinal canal is opened in the living animal, an irritation applied to the anterior columns of the cord produces immediately convulsions in the limbs below; but there is no indication of pain. On the other hand, signs of acute pain become manifest whenever the irritation is applied to the posterior columns; but no muscular contractions follow, other than those of a voluntary or reflex character. Longet has found[1] that if the spinal cord be exposed in the lumbar region and completely divided at that part by transverse section, the application of any irritant to the anterior surface of the separated portion produces convulsions below; while if applied to the posterior columns behind the point of division, it has no sensible effect whatever. The anterior and posterior columns of the cord are accordingly, so far, analogous in their properties to the anterior and posterior roots of the spinal nerves.

The route through which motor and sensitive impulses are transmitted, in the spinal cord, has also been ascertained with tolerable success, by the researches of Magendie, Longet, Brown-Sequard, and Vulpian.[2] The impulse which gives rise to voluntary motion is transmitted by the white substance of the anterior and lateral columns; for if these antero-lateral columns be divided in the living animal by a transverse section, all power of voluntary motion is abolished in the parts below. The stimulus to sensation, on the other hand, seems to traverse the deeper portions of the cord by filaments which pass through the gray substance. For, according to the experiments of Brown-Sequard, confirmed by Vulpian and Philippeaux,[3] sensibility is destroyed by division of the gray substance and the anterior portions of the cord, even though the posterior columns be left untouched. The

[1] Traité de Physiologie, vol. ii. part 2, p. 8.

[2] Vulpian. Physiologie du Système nerveux. Paris, 1866, p. 369.

[3] Ibid. p. 373.

posterior columns, accordingly, though sensitive to artificial irritation, are not the portions through which sensitive impressions are directly conveyed from the posterior roots of the nerves. It is possible that they may serve, according to the opinion entertained by Vulpian, as longitudinal commissures, connecting with each other different portions of the length of the spinal cord.

An irritation accordingly, applied to any part of the integument, is conveyed, along the sensitive filaments of the nerve and its posterior root, to the spinal cord; then upward, along the communicating fibres of the cord, to the brain, where it produces a sensation corresponding in character with the original irritation. A motor impulse, on the other hand, originating in the brain, is transmitted downward, along the longitudinal fibres of the antero-lateral columns, passes outward by the anterior root of the spinal nerve, and, following the motor filaments of the nerve through its trunk and branches, produces at last a muscular contraction at the point of its final distribution.

Crossed Action of the Spinal Cord.—As the anterior columns of the cord pass upward to join the medulla oblongata, a decussation takes place between the two sides, as we have already mentioned, at the level of the anterior pyramids. The fibres of the right lateral column pass over to the left side of the medulla oblongata, and so upward to the left side of the brain; while the fibres of the left lateral column pass over to the right side of the medulla oblongata, and so upward to the right side of the brain. This decussation may be readily shown (as in Fig. 141) by gently separating the anterior pyramids from each other, at the lower extremity of the medulla oblongata, where the decussating bundles may be seen crossing obliquely from side to side, at the bottom of the anterior median fissure. Below this point, the anterior columns remain distinct from each other so far as regards any external decussation; but there is still reason for believing that their fibres continue to cross from side to side, in the anterior commissure, throughout the cervical portion of the spinal cord.

The final result of this interchange is a complete decussation of the motor fibres, and a crossed action of the spinal cord, as a medium of communication for motor impulses. Apoplexy, softening, or mechanical injury, on the right side of the brain, will pro-

duce paralysis of the left side of the body; and injury of the left side of the brain will be followed by paralysis of the right side of the body. If the seat of the injury, on the other hand, be lower down, at the level of the medulla oblongata, or at any point where the crossing of the fibres is taking place, it will cause a partial paralysis, on both the same and opposite sides of the body; while if it be seated in one lateral half of the cord, below the level of complete decussation, the paralysis which results will be manifested only on the corresponding side of the body.

If the anterior columns of the spinal cord, therefore, be wounded at any point in the dorsal or lumbar region, a paralysis of voluntary motion is produced in the limbs below, on the same side with the injury. But if a similar lesion occur in the brain, the paralysis which results is on the opposite side of the body. Thus it has long been known that an abscess or an apoplectic hemorrhage on the right side of the brain will produce paralysis of the left side of the body; and injury of the left side of the brain will be followed by paralysis of the right side of the body.

The spinal cord has also a crossed action in transmitting sensitive as well as motor impulses. It has been demonstrated by Dr. Brown-Sequard,[1] that the crossing of the sensitive fibres in the spinal cord does not take place, like that of the motor fibres, at its upper portion only, but throughout its entire length; so that the sensitive fibres of the right spinal nerves, very soon after their entrance into the cord, pass over to the left side, and those of the left spinal nerves pass over to the right side. For if one lateral half of the spinal cord of a dog be divided in the dorsal region, the power of sensation remains upon the corresponding side of the body, but is lost upon the opposite side. It has been shown, furthermore, by the same observer,[2] that the sensitive fibres of the spinal nerves, when they first enter the cord, join the posterior columns, which are everywhere extremely sensitive; but that they very soon leave the posterior columns, and, passing through the central parts of the gray matter, reach the opposite side of the spinal cord. If the posterior columns, accordingly, be alone divided at any part of the cord, sensibility is not destroyed in all the nerves behind the seat of injury, but only in those which enter the cord at the point of

[1] Experimental Researches applied to Physiology and Pathology. New York, 1853.

[2] Mémoirs sur la Physiologie de la Moelle épinière; Gazette Médicale de Paris, 1855.

section; since the posterior columns consist of different nervous filaments, joining them constantly on one side from below, and leaving them on the other to pass upward toward the brain.

There are certain important facts which still remain to be noticed regarding the mode of action of the spinal cord and its nerves. They are as follows:—

1. *An irritation applied to a spinal nerve at the middle of its course produces the same effect as if it traversed its entire length.* Thus, if the sciatic or median nerve be irritated at any part of its course, contraction is produced in the muscles to which these nerves are distributed, just as if the impulse had originated as usual from the brain. This fact depends upon the character of the nervous filaments, as simple conductors. Wherever the impulse may originate, the final effect is manifested only at the termination of the nerve. As the impulse in the motor nerves travels always in an outward direction, the effect is always produced at the muscular termination of the filaments, no matter how small or how large a portion of their length may have been engaged in transmitting the stimulus.

If the irritation, again, be applied to a sensitive nerve in the middle of its course, the painful sensation is felt, not at the point of the nerve directly irritated, but in that portion of the integument to which its filaments are distributed. Thus, if the ulnar nerve be accidentally struck at the point where it lies behind the inner condyle of the humerus, a sensation of tingling and numbness is produced in the last two fingers of the corresponding hand. It is common to hear patients who have suffered amputation complain of painful sensations in the amputated limb for weeks or months, and sometimes even for years after the operation. They assert that they can feel the separated parts as distinctly as if they were still attached to the body. This sensation, which is a real one and not fictitious, is owing to some irritation operating upon the divided extremities of the nerves in the cicatrized wound. Such an irritation, conveyed to the brain by the sensitive fibres, will produce precisely the same sensation as if the amputated parts were still present, and the irritation actually applied to them.

It is on this account also that division of the trifacial nerve is not always effectual for the cure of tic douloureux. If the cause of the difficulty be seated upon the trunk of the nerve, between its point of emergence from the bones and its origin in the brain, it is evident that division of the nerve upon the face will be of no avail; since the cause of irritation will still exist behind the point

of section, and the same painful sensations will still be produced in the brain.

2. *The irritability of the motor filaments disappears from within outward, that of the sensitive filaments from without inward.* According to the researches of Longet,[1] the irritability of the motor fibres, in an animal recently killed, ceases to manifest itself first in the central and afterward in the peripheral portions; disappearing successively in the anterior columns of the spinal cord, the anterior roots of the nerves, the nervous trunks, and lastly their branches and ramifications. Thus immediately after the separation of the frog's leg from the body, irritation of the nerve at any point produces muscular contraction in the limb below. As time elapses, however, and the irritability of the nerve diminishes, the galvanic current, in order to produce contraction, must be applied at a point nearer its termination. Subsequently, the irritability of the nerve is entirely lost in its upper portions, but is retained in the parts situated lower down, from which also, in turn, it afterward disappears; receding in this manner farther and farther toward the terminal distribution of the nerve, where it finally disappears altogether.

On the other hand the signs of irritability in the sensitive nerves disappear first at their extremities. This fact, established by both Longet and Bernard,[2] and confirmed by most other observers, shows that sensibility at the time of death recedes from the circumference toward the centre. The skin may have already become insensible while the trunk of the nerve still retains its sensibility; and sensibility continues to be manifested in the spinal cord after it has already disappeared from the nerve itself.

3. *Each nervous filament acts independently of the rest throughout its entire length, and does not communicate its irritation to those which are in proximity with it.* It is evident that this is true with regard to the nerves of sensation, from the fact that if the integument be touched with the point of a needle, the sensation is referred to that spot alone. Since the nervous filaments coming from it and the adjacent parts are all bound together in parallel bundles, to form the trunk of the nerve, if any irritation were communicated from one sensitive filament to another, the sensation produced would be indefinite and diffused, whereas it is really confined to the spot irri-

[1] Physiologie, vol. ii. part 2, p. 52.

[2] Substances Toxiques et Médicamenteuses, p. 330.

tated. If a frog's leg, furthermore, be prepared, with the sciatic nerve attached, a few of the fibres separated laterally from the nervous trunk for a portion of its length, and the poles of a galvanic battery applied to the separated portion, the contractions which follow in the leg will not be general, but will be confined to those muscles in which the galvanized nervous fibres especially have their distribution. There are also various instances, in the body, of antagonistic muscles, which must act independently of each other, but which are supplied with nerves from a common trunk. The superior and inferior straight muscles of the eyeball, for example, are both supplied by the motor oculi communis nerve. Extensor and flexor muscles, as, for example, those of the fingers, are often supplied by the same nerve, and yet act alternately without mutual interference. It is easy to see that if this were not the case, confusion would constantly arise, both in the perception of sensations, and in the execution of movements.

4. There are certain sensations which are excited simultaneously by the same causes, and which are termed *associated sensations;* and there are also certain movements which take place simultaneously, and are called *associated movements.* In the former instance, one of the associated sensations is called up immediately upon the perception of the other, without requiring any direct impulse of its own. Thus, tickling the soles of the feet produces a peculiar sensation at the epigastrium. Nausea is occasioned by certain disagreeable odors, or by rapid rotation of the body, so that the landscape seems to turn round. A striking example of associated movements, on the other hand, may be found in the action of the muscles of the eyeball. The eyeballs always accompany each other in their lateral motions, turning to the right or the left side simultaneously. It is evident, however, that in producing this correspondence of motion, the left internal rectus muscle must contract and relax together with the right external; while a similar harmony of action must exist between the right internal and the left external. The explanation of such singular correspondences cannot be found in the anatomical arrangement of the muscles themselves, nor in that of the nervous filaments by which they are directly supplied, but must be looked for in some special endowment of the nervous centres from which they originate.

Reflex Action of the Spinal Cord.—The spinal cord, as we have thus far examined it, may be regarded simply as a great nerve; that is, as a bundle of motor and sensitive filaments, connecting the muscles and integument below with the brain above, and assisting, in this capacity, in the production of conscious sensation and voluntary motion. Beside its nervous filaments, however, it contains also a large quantity of gray matter, and is, therefore, itself a ganglionic centre, and capable of independent action as such. We shall now proceed to study it in its second capacity, as a distinct nervous centre.

If a frog be decapitated, and the body allowed to remain at rest for a few moments, so as to recover from the depressing effects of shock upon the nervous system, it will be found that, although sensation and consciousness are destroyed, the power of motion still remains. If the skin of one of the feet be irritated by pinching it with a pair of forceps, the leg is immediately drawn up toward the body, as if to escape the cause of irritation. If the irritation applied to the foot be of slight intensity, the corresponding leg only will move; but if it be more severe in character, motions will often be produced in the posterior extremity of the opposite side, and even in the two fore legs, at the same time. These motions, it is important to observe, are never spontaneous. The decapitated frog remains perfectly quiescent if left to himself. It is only when some cause of irritation is applied externally, that movements occur as above described.

It will be seen that the character of these phenomena indicates the active operation of some part of the nervous system, and particularly of some ganglionic centre. The irritation is applied to the skin of the foot, and the muscles of the leg contract in consequence; showing evidently the intermediate action of a nervous connection between the two.

The effect in question is due to the activity of the spinal cord, operating as a nervous centre. In order that the movements may take place as above, it is essential that both the integument and the muscles should be in communication with the spinal cord by nervous filaments, and that the cord itself be in a state of integrity. If the sciatic nerve be divided in the upper part of the thigh, irritation of the skin below is no longer followed by any muscular contraction. If either the anterior or posterior roots of the nerve be divided, the same want of action results; and finally, if, the nerve and its roots remaining entire, the spinal cord itself be broken up

by a needle introduced into the spinal canal, the integument may then be irritated or mutilated to any extent, without exciting the least muscular contraction. It is evident, therefore, that the spinal cord acts, in this case, as a nervous centre, through which the irritation applied to the skin is communicated to the muscles. The irritation first passes upward, as shown in the accompanying diagram (Fig. 147), along the sensitive fibres of the posterior root (*a*) to the gray matter of the cord, and is then reflected back, along the motor fibres of the anterior root (*b*), until it finally reaches the muscles, and produces a contraction. This action is known, accordingly, as the *reflex action of the spinal cord.*

Fig. 147.

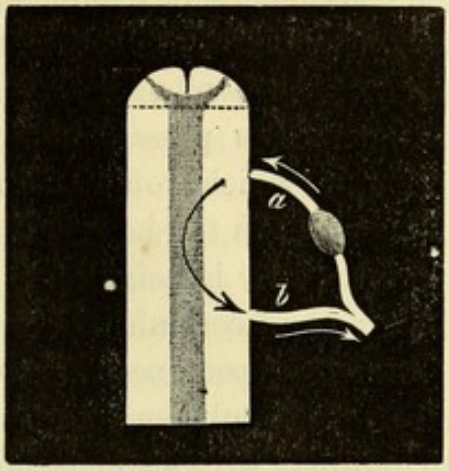


Diagram of SPINAL CORD IN VERTICAL SECTION, showing reflex action. —*a*. Posterior root of spinal nerve. *b* Anterior root of spinal nerve.

It will be remembered that this reflex action of the cord is not accompanied by volition, nor even by any conscious sensation.

The function of the spinal cord as a nervous centre is simply to convert an impression, received from the skin, into a motor impulse which is sent out again to the muscles. There is absolutely no farther action than this; no exercise of will, consciousness, or judgment. This action will therefore take place perfectly well after the brain has been removed, and after the entire sympathetic system has also been taken away, provided only that the spinal cord and its nerves remain in a state of integrity.

The existence of this reflex action after death is accordingly an evidence of the continued activity of the spinal cord, just as contractility is an evidence of the activity of the muscles, and irritability of that of the nerves. Like the two last-mentioned properties, also, it continues for a longer time after death in cold-blooded than in warm-blooded animals. It is for this reason that frogs and other reptiles are the most useful subjects for the study of these phenomena, as for that of most others belonging to the nervous system.

The irritability of the spinal cord, as manifested by its reflex action, may be very much exaggerated by certain diseases, and by the operation of poisonous substances. Tetanus and poisoning by strychnine both act in this way, by heightening the irritability of the spinal cord, and causing it to produce convulsive movements

on the application of external stimulus. It has been observed that the convulsions in tetanus are rarely, if ever, spontaneous, but that they always require to be excited by some external cause, such as the accidental movement of the bedclothes, the shutting of a door, or the sudden passage of a current of air. Such slight causes of irritation, which would be entirely inadequate to excite involuntary movements in the healthy condition, act upon the spinal cord, when its irritability is heightened by disease, in such a manner as to produce violent convulsions.

Similar appearances are to be seen in animals poisoned by strychnine. This substance acts upon the spinal cord and increases its irritability, without materially affecting the functions of the brain. Its effects will show themselves, consequently, without essential modification, after the head has been removed. If a decapitated frog be poisoned with a moderate dose of strychnine, the body and limbs will remain quiescent so long as there is no external source of excitement; but the limbs are at once thrown into convulsions by the slightest irritation applied to the skin, as, for example, the contact of a hair or a feather, or even the jarring of the table on which the animal is placed. That the convulsions in cases of poisoning by strychnine are always of a reflex character, and never spontaneous, is shown by the following fact first noticed by Bernard,[1] viz., that if a frog be poisoned after division of the posterior roots of all the spinal nerves, while the anterior roots are left untouched, death takes place as usual, but is not preceded by any convulsions. In this instance the convulsions are absent simply because, owing to the division of the posterior roots, external irritations cannot be communicated to the cord.

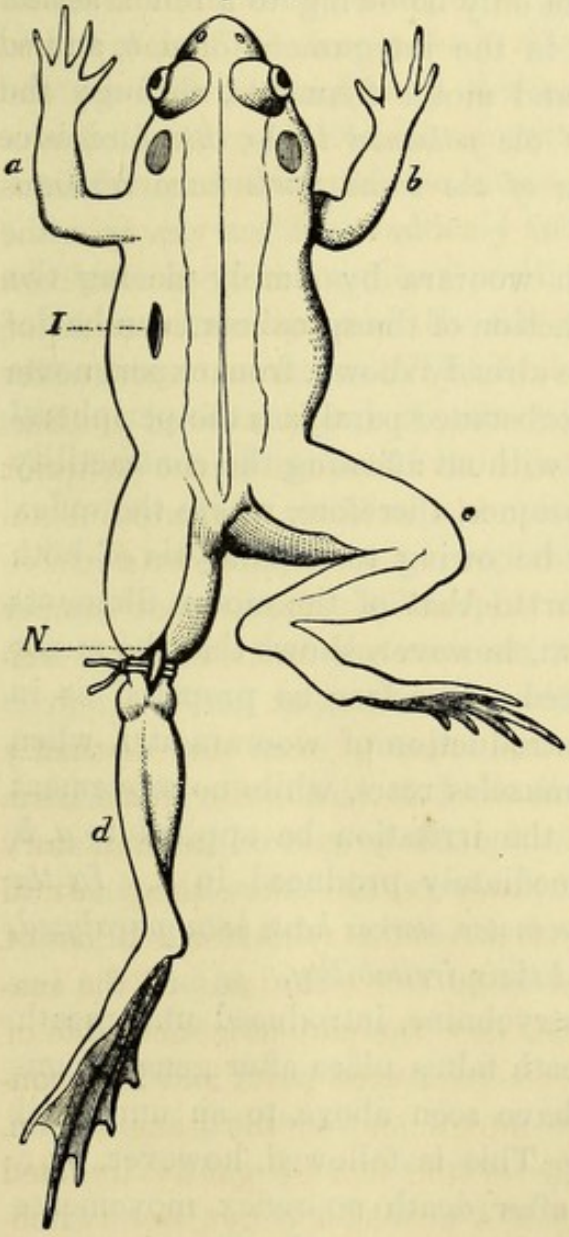
The reflex action, above described, may be seen very distinctly in the human subject, in certain cases of disease of the spinal cord. If the upper portion of the cord be disintegrated by inflammatory softening, so that its middle and lower portions lose their natural connection with the brain, paralysis of voluntary motion and loss of sensation ensue in all parts of the body below the seat of the anatomical lesion. Under these conditions, the patient is incapable of making any muscular exertion in the paralyzed parts, and is unconscious of any injury done to the integument in the same region. Notwithstanding this, if the soles of the feet be gently irritated with a feather, or with the point of a needle, a convulsive twitch-

[1] Leçons sur les effets des Substances toxiques et médicamenteuses, Paris, 1857, p. 357.

ing of the toes will often take place, and even retractile movements of the leg and thigh, altogether without the patient's knowledge. Such movements may frequently be excited by simply allowing the cool air to come suddenly in contact with the lower extremities. We have repeatedly witnessed these phenomena, in a case of disease of the spinal cord, where the paralysis and insensibility of the lower extremities were complete. Many other similar instances are reported by various authors.

The existence of this reflex action of the cord has enabled the physiologist to ascertain several other important facts concerning the mode of operation of the nervous system. M. Bernard has demonstrated,[1] by a series of extremely ingenious experiments on the action of poisonous substances: 1st, that the irritability of the muscles may be destroyed, while that of the nerves remains unaltered; and 2d, that the motor and sensitive nervous filaments may be paralyzed independently of each other. The above facts are shown by the three following experiments: —

Fig. 148.



1. In a living frog (Fig. 148), the sciatic nerve (*N*) is exposed in the back part of the thigh, after which a ligature is passed underneath it and drawn tight around the bone and the remaining soft parts. In this way the circulation is entirely cut off from the limb (*d*), which remains in connection with the trunk only by means of the sciatic nerve. A solution of sulphocyanide of potassium is then introduced beneath the skin of the back, at *I*, in suf-

[1] Leçons sur les effets des substances toxiques et médicamenteuses, Paris, 1857, chaps. 23 and 24.

ficient quantity to produce its specific effect. The poison is then absorbed, and is carried by the circulation throughout the trunk and the three extremities *a*, *b*, *c*; while it is prevented from entering the limb *d*, by the ligature which has been placed about the thigh. Sulphocyanide of potassium produces paralysis, as we have previously mentioned, by acting directly upon the muscular tissue. Accordingly, a galvanic discharge passed through the limbs *a*, *b*, and *c*, produces no contraction in them, while the same stimulus, applied to *d*, is followed by a strong and healthy reaction. But at the moment when the irritation is applied to the poisoned limbs *a*, *b*, and *c*, though no visible effect is produced in them, an active movement takes place in the healthy limb, *d*. This can only be owing to a reflex action of the spinal cord, originating in the integument of *a*, *b*, and *c*, and transmitted, by sensitive and motor filaments, through the cord to *d*. *While the muscles of the poisoned limbs, therefore, have been directly paralyzed, the nerves of the same parts have retained their irritability.*

2. If a frog be poisoned with woorara by simply placing the poison under the skin, no reflex action of the spinal cord can be demonstrated after death. We have already shown, from experiments detailed in chapter II., that this substance paralyzes the peripheral extremities of the motor nerves, without affecting the contractility of the muscles. In the above instance, therefore, where the reflex action is abolished, its loss may be owing to a paralysis of both motor and sensitive filaments, or to that of the motor filaments alone. The following experiment, however, shows that the motor filaments are the only ones affected. If a frog be prepared as in Fig. 148, and poisoned by the introduction of woorara at *I*, when the limb *d* is irritated, its own muscles react, while no movement takes place in *a*, *b*, or *c*; but if the irritation be applied to *a*, *b*, or *c*, reflex movements are immediately produced in *d*. *In the poisoned limbs, therefore, while the motor nerves have been paralyzed, the sensitive filaments have retained their irritability.*

3. If a frog be poisoned with strychnine, introduced underneath the skin in sufficient quantity, death takes place after general convulsions, which are due, as we have seen above, to an unnatural excitability of the reflex action. This is followed, however, by a paralysis of sensibility, so that after death no reflex movements can be produced by irritating the skin or even the posterior roots of the spinal nerves. But if the anterior roots, or the motor nerves

themselves be galvanized, contractions immediately take place in the corresponding muscles. *In this case, therefore, the sensitive filaments have been paralyzed, while the motor filaments and the muscles have retained their irritability.*

We now come to investigate the reflex action of the spinal cord, as it takes place in a healthy condition during life. This action readily escapes notice, unless our attention be particularly directed to it, because the sensations which we are constantly receiving, and the many voluntary movements which are continually executed, serve naturally to mask those nervous phenomena which take place without our immediate knowledge, and over which we exert no voluntary control. Such phenomena, however, do constantly take place, and are of extreme physiological importance. If the surface of the skin, for example, be at any time unexpectedly brought in contact with a heated body, the injured part is often withdrawn by a rapid and convulsive movement, long before we feel the pain, or even fairly understand the cause of the involuntary act. If the body by any accident suddenly and unexpectedly loses its balance, the limbs are thrown into a position calculated to protect the exposed parts, and to break the fall, by a similar involuntary and instantaneous movement. The brain does not act in these cases, for there is no intentional character in the movement, nor even any complete consciousness of its object. Everything indicates that it is the immediate result of a simple reflex action of the spinal cord.

The cord exerts also an important and constant influence upon the *sphincter muscles.* The sphincter ani is habitually in a state of contraction, so that the contents of the intestine are not allowed to escape. When any external irritation is applied to the anus, or whenever the feces present themselves internally, the sphincter contracts involuntarily, and the discharge of the feces is prevented. This habitual closure of the sphincter depends on the reflex action of the spinal cord. It is entirely an involuntary act, and will continue, in the healthy condition, during profound sleep, as complete and efficient as in the waking state.

When the rectum, however, has become filled by the accumulation of feces from above, the nervous action changes. Then the impression produced on the mucous membrane of the distended rectum, conveyed to the spinal cord, causes at the same time relaxation of the sphincter and contraction of the rectum itself; so that a discharge of the feces consequently takes place.

Now all these actions are to some extent under the control of

sensation and volition. The distended state of the rectum is usually accompanied by a distinct sensation, and the resistance of the sphincter may be voluntarily prolonged for a certain period, just as the respiratory movements, which are usually involuntary, may be intentionally hastened or retarded, or even temporarily suspended. But this voluntary power over the sphincter and the rectum is limited. After a time the involuntary impulse, growing more urgent with the increased distension of the rectum, becomes irresistible; and the discharge finally takes place by the simple reflex action of the spinal cord.

If the spinal cord be injured in its middle or upper portions, the sensibility and voluntary action of the sphincter are lost, because its connection with the brain has been destroyed. The evacuation then takes place at once, by the ordinary mechanism, as soon as the rectum is filled, but without any knowledge on the part of the patient. The discharges are then said to be "involuntary and unconscious."

If the irritability of the cord, on the other hand, be exaggerated by disease, while its connection with the brain remains entire, the distension of the rectum is announced by the usual sensation, but the reflex impulse to evacuation is so urgent that it cannot be controlled by the will, and the patient is compelled to allow it to take place at once. The discharges are then said to be simply "involuntary."

Finally, if the substance of the spinal cord be extensively destroyed by accident or disease, the sphincter is permanently relaxed. The feces are then evacuated almost continuously, without any knowledge or control on the part of the patient, as fast as they descend into the rectum from the upper portions of the intestine.

Injury of the spinal cord produces a somewhat different effect on the urinary bladder. Its muscular fibres are directly paralyzed; and the organ, being partially protected by elastic fibres, both at its own orifice and along the urethra, becomes gradually distended by urine from the kidneys. The urine then overcomes the elasticity of the protecting fibres, by simple force of accumulation, and afterward dribbles away as fast as it is excreted by the kidneys. Paralysis of the bladder, therefore, first causes a permanent distension of the organ, which is afterward followed by a continuous, passive, and incomplete discharge of its contents.

Injury of the spinal cord produces also an important, though probably an indirect effect on nutrition, secretion, animal heat, &c.,

in the paralyzed parts. Diseases of the cord which result in its softening or disintegration, are notoriously accompanied by constipation, often of an extremely obstinate character. In complete paraplegia, also, the lower extremities become emaciated. The texture and consistency of the muscles are altered, and the animal temperature is considerably reduced. All such disturbances of nutrition, however, which almost invariably follow upon local paralysis, are no doubt immediately owing to the inactive condition of the muscles; a condition which naturally induces debility of the circulation, and consequently of all those functions which are dependent upon it.

It is less easy to explain the connection between injury of the spinal cord and inflammation of the urinary passages. It is, however, a matter of common observation among pathologists, that injury or disease of the cord, particularly in the dorsal and upper lumbar regions, is soon followed by catarrhal inflammation of the urinary passages. This gives rise to an abundant production of altered mucus, which in its turn, by causing an alkaline fermentation of the urine contained in the bladder, converts it into an irritating and ammoniacal liquid, which reacts upon the mucous membrane and aggravates the previous inflammation.

We find, therefore, that the spinal cord, in its character of a nervous centre, exerts a general protective action over the whole body. It presides over the involuntary movements of the limbs and trunk; it regulates the action of the sphincters, the rectum, and the bladder; while at the same time it exerts an indirect influence on the nutritive changes in those parts which it supplies with nerves.

CHAPTER IV.

THE BRAIN.

By the brain, or *encephalon*, as it is sometimes called, we mean all that portion of the nervous system which is situated within the cavity of the cranium. It consists, as we have already shown, of a series of different ganglia, connected with each other by transverse and longitudinal commissures.

Since we have found the functions of sensation and motion, or sensibility and excitability, so distinctly separated in the spinal cord, we should expect to find the same distinction in the interior of the brain. These two properties have indeed been found to be distinct from each other, so far as they exist at all, in the encephalic mass; but most observers are agreed that they are both confined to very small portions of the brain, in comparison with its entire bulk. According to the investigations of Longet, neither the olfactory ganglia, the corpora striata, the optic thalami, the tubercula quadrigemina, nor the white or gray substance of the cerebrum or the cerebellum, are in the least degree excitable. Mechanical irritation of these parts does not produce the slightest convulsive movement in the muscles below. The application of caustic liquids and the passage of galvanic currents are equally without effect. The only portions of the brain in which irritation is followed by convulsive movements are the anterior surface of the medulla oblongata, the tuber annulare, and the lower part of the crura cerebri; that is, the lower and central parts of the brain, containing continuations of the anterior columns of the cord. On the other hand, neither the olfactory ganglia, the corpora striata, the tubercula quadrigemina, nor the white or gray substance of the cerebrum or cerebellum, give rise, on being irritated, to any painful sensation. The only sensitive parts are the posterior surface of the medulla oblongata, the restiform bodies, the processus e cerebello ad testes, and the upper part of the crura cerebri; that is, those portions of the base of the brain which contain prolongations of the posterior columns of the cord.

The most central portions of the nervous system, therefore, and particularly the gray matter, are usually regarded as destitute of both excitability and sensibility. It is only those portions which serve to *conduct* sensations and nervous impulses that can be excited by mechanical irritation; not the ganglionic centres themselves, which receive and originate the nervous impressions.

We shall now study in succession the different ganglia of which the brain is composed.

OLFACTORY GANGLIA.—These ganglia, which in some of the lower animals are very large, corresponding in size with the extent of the olfactory membrane and the acuteness of the sense of smell, are very small in the human subject. They are situated on the cribriform plate of the ethmoid bone, on each side of the crista galli, just beneath the anterior lobes of the cerebrum. They send their nerves through the numerous perforations which exist in the ethmoid bone at this part, and are connected with the base of the brain by two longitudinal commissures. The olfactory ganglia with their commissures are sometimes spoken of as the "olfactory nerves." They are not nerves, however, but ganglia, since they are mostly composed of gray matter; and the term "olfactory nerves" can be properly applied only to the filaments which originate from them, and which are afterward spread out in the substance of the olfactory membrane.

It has been found difficult to determine the function of these ganglia by direct experiment on the lower animals. They may be destroyed by means of a strong needle introduced through the bones of the cranium; but the signs of the presence or absence of the sense of smell, after such an operation, are too indefinite to allow us to draw from them a decided conclusion. The anatomical distribution of their nerves, however, and the evident correspondence which exists, in different species of animals, between their degree of development and that of the external olfactory organs, leaves no doubt as to their true function. They are the ganglia of the special sense of smell, and are not connected, in any appreciable degree, with ordinary sensibility, nor with the production of voluntary movements.

OPTIC THALAMI.—These bodies are not, as their name would imply, the ganglia of vision. Longet has found that the power of sight and the sensibility of the pupil both remain, in birds, after

the optic thalami have been thoroughly disorganized; and that artificial irritation of the same ganglia has no effect in producing either contraction or dilatation of the pupil. The optic thalami, however, according to the same observer, have a peculiar crossed action upon the voluntary movements. If both hemispheres and both optic thalami be removed in the rabbit, the animal is still capable of standing and of using his limbs in progression. But if the right optic thalamus alone be removed, the animal falls at once upon his left side; and if the left thalamus be destroyed, a similar debility is manifest on the right side of the body. In these instances there is no absolute paralysis of the side upon which the animal falls, but rather a simple want of balance between the two opposite sides. The exact mechanism of this peculiar functional disturbance is not well understood; and but little light has yet been thrown, either by direct experiment or by the facts of comparative anatomy, on the real function of the optic thalami.

Corpora Striata.—The function of these ganglia is equally uncertain with that of the preceding. They are traversed, as we have already seen, by fibres coming from the anterior columns of the cord; and they are connected, by the continuation of these fibres, with the gray substance of the hemispheres. They have therefore, in all probability, like the optic thalami, some connection with sensation and volition; but the precise nature of this connection is at present altogether unknown.

Hemispheres.—The hemispheres, or the cerebral ganglia, constitute in the human subject about nine-tenths of the whole mass of the brain. Throughout their whole extent they are entirely destitute, as we have already mentioned, of both sensibility and excitability. Both the white and gray substance may be wounded, burned, lacerated, crushed, or galvanized in the living animal, without exciting any convulsive movement or any apparent sensation. In the human subject a similar insensibility has been observed when the substance of the hemispheres has been exposed by accidental violence, or in the operation of trephining.

Very severe mechanical injuries may also be inflicted upon the hemispheres, even in the human subject, without producing any directly fatal result. One of the most remarkable instances of this fact is a case reported by Prof. William Detmold, of New York,[1] in

[1] Am. Journ. of Med. Sci., January, 1850.

which an abscess in the anterior lobe of the brain was opened by an incision passing through the cerebral substance, not only without any immediate bad effect, but with great temporary relief to the patient. This was the case of a laborer who was struck on the left side of the forehead by a piece of falling timber, which produced a compound fracture of the skull at this part. One or two pieces of bone afterward became separated and were removed, and the wound subsequently healed. Nine weeks after the accident, however, headache and drowsiness came on; and the latter symptom, becoming rapidly aggravated, soon terminated in complete stupor. At this time, the existence of an abscess being suspected, the cicatrix, together with the adherent portion of the dura mater, was dissected away, several pieces of fractured bone removed, and the surface of the brain exposed. A knife was then passed into the cerebral substance, making a wound one inch in length and half an inch in depth, when the abscess was reached and over two ounces of pus discharged. The patient immediately aroused from his comatose condition, so that he was able to speak; and in a few days recovered, to a very considerable extent, his cheerfulness, intelligence, and appetite. Subsequently, however, the collection of pus returned, accompanied by a renewal of the previous symptoms; and the patient finally died at the end of seven weeks from the time of opening the abscess.

Another and still more striking instance of recovery from severe injury of the brain is reported by Prof. H. J. Bigelow in the *American Journal of Medical Sciences* for July, 1850. In this case, a pointed iron bar, three feet and a half in length, and one inch and a quarter in diameter, was driven through the patient's head by the premature blasting of a rock. The bar entered the left side of the face, just in front of the angle of the jaw, and passed obliquely upward, inside the zygomatic arch and through the anterior part of the cranial cavity, emerging from the top of the frontal bone on the median line, just in front of the point of union of the coronal and sagittal sutures. The patient was at first stunned, but soon recovered himself so far as to be able to converse intelligently, rode home in a common cart, and with a little assistance walked up stairs to his room. He became delirious within two days after the accident, and subsequently remained partly delirious and partly comatose for about three weeks. He then began to improve, and at the end of rather more than two months from the date of the injury, was able to walk about. At the end of sixteen months he was in perfect health, with the wounds healed, and with the mental and

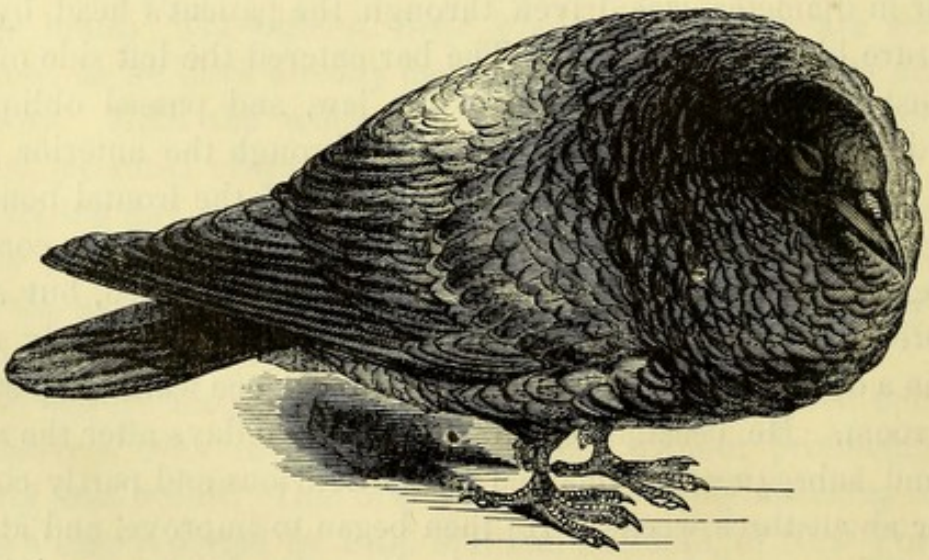
bodily functions entirely unimpaired, except that sight was permanently lost in the eye of the injured side.

This patient survived the injury for a little over twelve years, being able for a great part of the time to do the ordinary work of an ostler, coachman, and farm-laborer, in all of which occupations he was employed at various intervals. He finally died in 1861, after a short illness accompanied by convulsions. The skull, which was subsequently obtained and deposited in the Warren Anatomical Museum,[1] shows the openings corresponding with the points of entrance and exit of the iron bar.

The hemispheres, furthermore, may not only be seriously injured without destroying life, but in many of the lower animals they may be entirely removed without abolishing the powers of sensation and volition. In quadrupeds, the complete removal of the hemispheres is attended with so much hemorrhage that the operation is generally fatal from this cause within a few minutes. In birds, however, it may be performed without any immediate danger to life. Longet has removed the hemispheres in pigeons and fowls, and has kept these animals afterward for several days, with most of the organic functions unimpaired. We have frequently performed the same experiment upon pigeons, with a similar favorable result.

The effect of this mutilation is simply to plunge the animal into a state of profound stupor, in which he is almost entirely inattentive to surrounding objects. The bird remains sitting motionless upon his perch, or standing upon the ground, with the eyes closed, and the head sunk between the shoulders. (Fig. 149.) The plu-

Fig. 149.



Pigeon, after Removal of the Hemispheres

[1] J. B. S. Jackson, Descriptive Catalogue of the Warren Anatomical Museum, Boston, 1870, p. 145.

mage is smooth and glossy, but is uniformly expanded, by a kind of erection of the feathers, so that the body appears somewhat puffed out, and larger than natural. Occasionally the bird opens his eyes with a vacant stare, stretches his neck, perhaps shakes his bill once or twice, or smooths down the feathers upon his shoulders, and then relapses into his former apathetic condition. This state of immobility, however, is not accompanied by the loss of sight, of hearing, or of ordinary sensibility. All these functions remain, as well as that of voluntary motion. If a pistol be discharged behind the back of the animal, he at once opens his eyes, moves his head half round, and gives evident signs of having heard the report; but he immediately becomes quiet again, and pays no farther attention to it. Sight is also retained, since the bird will sometimes fix its eye on a particular object, and watch it for several seconds together. Longet has even found that by moving a lighted candle before the animal's eyes in a dark place, the head of the bird will often follow the movements of the candle from side to side or in a circle, showing that the impression of light is actually perceived by the sensorium. Ordinary sensation also remains, after removal of the hemispheres, together with voluntary motion. If the foot be pinched with a pair of forceps, the bird becomes partially aroused, moves uneasily once or twice from side to side, and is evidently annoyed at the irritation.

The animal is still capable, therefore, after removal of the hemispheres, of receiving sensations from external objects. But these sensations appear to make upon him no lasting impression. He is incapable of connecting with his perceptions any distinct succession of ideas. He hears, for example, the report of a pistol, but he is not alarmed by it; for the sound, though distinctly enough perceived, does not suggest any idea of danger or injury. There is accordingly no power of forming mental associations, nor of perceiving the relation between external objects. The memory, more particularly, is altogether destroyed, and the recollection of sensation is not retained from one moment to another. The limbs and muscles are still under the control of the will; but the will itself is inactive, because apparently it lacks its usual mental stimulus and direction. The powers which have been lost, therefore, by destruction of the cerebral hemispheres, are altogether of a mental or intellectual character; that is, the power of comparing with each other different ideas, and of perceiving the proper relation between them.

The same result is well known to follow, in the human subject,

from injury or disease of these parts. A disturbance of the mental powers has long been recognized as the ordinary consequence of lesions of the brain. In cases of impending apoplexy, for example, or of softening of the cerebral substance, among the earliest and most constant phenomena is a loss or impairment of the memory. The patient forgets the names of particular objects or of particular persons; or he is unable to calculate numbers with his usual facility. His mental derangement is often shown in the undue estimate which he forms of passing events. He is no longer able to appreciate the true relation between different objects and different phenomena. Thus, he will show an exaggerated degree of solicitude about a trivial occurrence, and will pay no attention to other matters of real importance. As the difficulty increases, he becomes careless of the directions and advice of his attendants, and must be watched and managed like a child or an imbecile. After a certain period, he no longer appreciates the lapse of time, and even loses the distinction between day and night. Finally, when the injury to the hemispheres is complete, the senses may still remain active and impressible, while the patient is completely deprived of intelligence, memory, and judgment.

If we examine the comparative development of the hemispheres in different species of animals, and in different races of men, we shall find that the size of these ganglia corresponds very closely with the degree of intelligence possessed by the individual. We have already traced, in a preceding chapter, the gradual increase in size of the hemispheres in fish, reptiles, birds, and quadrupeds: four classes of animals which may be arranged, with regard to the amount of intelligence possessed by each, in precisely the same order of succession. Among quadrupeds, the elephant has much the largest and most perfectly formed cerebrum, in proportion to the size of the entire body; and of all quadrupeds he is proverbially the most intelligent and the most teachable. It is important to observe in this connection, that the kind of intelligence which characterizes the elephant and some other of the lower animals, and which most nearly resembles that of man, is a *teachable* intelligence; a very different thing from the intelligence which depends upon instinct, such as that of insects, for example, or birds of passage. Instinct is unvarying, and always does the same thing in the same manner, with endless repetition; but intelligence is a power which adapts itself to new circumstances, and enables its possessor, by comprehending and retaining new ideas, to profit by experience.

It is this quality which distinguishes the higher classes of animals from the lower; and which, in a very much greater degree. constitutes the intellectual superiority of man himself. The size of the cerebrum in man is accordingly very much greater, in proportion to that of the entire body, than in any of the lower animals; while other parts of the brain, on the contrary, such as the olfactory ganglia or the optic tubercles, are frequently smaller in him than in them. For while man is superior in general intelligence to all the lower animals, he is inferior to many of them in the acuteness of the special senses.

As a general rule, also, the size of the cerebrum in different races and in different individuals corresponds with the grade of their intelligence. The size of the cranium, as compared with that of the face, is smallest in the savage negro and Indian tribes; larger in the civilized or semi-civilized Chinese, Malay, Arab, and Japanese; while it is largest of all in the enlightened European races. This difference in the development of the brain is not probably an effect of long-continued civilization or otherwise; but it is, on the contrary, the superiority in cerebral development which makes some races readily susceptible of civilization, while others are either altogether incapable of it, or can only advance in it to a certain limit. Although all races therefore may, perhaps, be said to start from the same level of absolute ignorance, yet after the lapse of a certain time one race will have advanced farther in civilization than another, owing to a superior capacity for improvement, dependent on original organization.

The same thing is true with regard to different individuals. At birth, all men are equally ignorant; and yet at the end of a certain period one will have acquired a very much greater intellectual power than another, even under similar conditions of training, education, &c. He has been able to accumulate more information from the same sources, and to use the same experience to better advantage than his associates; and the result of this is a certain intellectual superiority, which becomes still greater by its own exercise. This superiority, it will be observed, lies not so much in the power of perceiving external objects and events, and of recognizing the connection between them, as in that of drawing conclusions from one fact to another, and of adapting to new combinations the knowledge which has already been acquired.

It is this particular kind of intellectual difference, existing in a marked degree, between animals, races, and individuals, which cor-

responds with the difference in development of the cerebral hemispheres. We have, therefore, evidence from three different sources that the cerebral hemispheres are the seat of the reasoning powers, or of the intellectual faculties proper. First, when these ganglia are removed in the lower animals, the intellectual faculties are the only ones which are lost. Secondly, injury to these ganglia, in the human subject, is followed by a corresponding impairment of the same faculties. Thirdly, in different species of animals, as well as in different races of men and in different individuals, the development of these faculties is in proportion to that of the cerebral hemispheres.

When we say, however, that the hemispheres are the seat of the intellectual faculties, of memory, reason, judgment, and the like, we do not mean that these faculties are, strictly speaking, located in the substance of the hemispheres, or that they belong directly to the matter of which the hemispheres are composed. The hemispherical ganglia are simply the instruments through which the intellectual powers manifest themselves, and which are accordingly necessary to their operation. If these instruments be imperfect in structure, or be damaged in any manner by violence or disease, the manifestations of intelligence are affected in a corresponding degree. So far, therefore, as the mental faculties are the subject of physiological research and experiment, they are necessarily connected with the hemispherical ganglia; and the result of investigation shows this connection to be extremely intimate and important in its character.

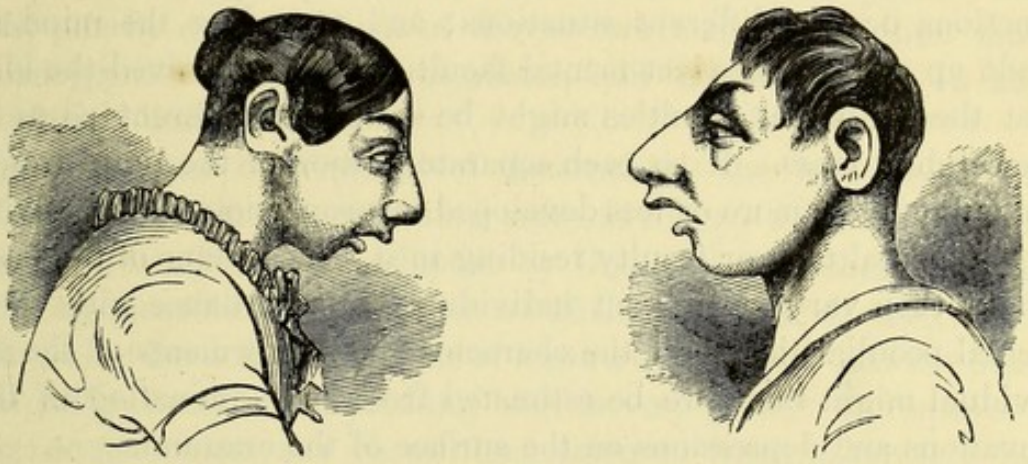
There are, however, various circumstances which modify, in particular cases, the general rule given above, viz., that the larger the cerebrum the greater the intellectual superiority. The functional activity of the brain is modified, no doubt, by its texture as well as by its size; and an increased excitability may compensate, partially or wholly, for a deficiency in bulk. This fact is sometimes illustrated in the case of idiots. There are instances where idiotic children with small brains are less imbecile and helpless than others with a larger development, owing to a certain vivacity and impressibility of organization which take the place, to a certain extent, of the purely intellectual faculties.

This was the case, in a marked degree, with a pair of dwarfed and idiotic Central American children, who were exhibited some years ago in various parts of the United States, under the name of the "Aztec children." They were a boy and a girl, aged respectively

about seven and five years. The boy was 2 feet 9¾ inches high, and weighed a little over 20 pounds. The girl was 2 feet 5½ inches high, and weighed 17 pounds. Their bodies were tolerably well proportioned, but the cranial cavities, as shown by the accompanying portraits, were extremely small.

The antero-posterior diameter of the boy's head was only 4½ inches, the transverse diameter less than 4 inches. The antero-posterior diameter of the girl's head was 4⅓ inches, the transverse diameter only 3¾ inches. The habits of these children, so far as regards feeding and taking care of themselves, were those of chil-

Fig. 150.



AZTEC CHILDREN.—Taken from life, at five and seven years of age.

dren two or three years of age. They were incapable of learning to talk, and could only repeat a few isolated words. Notwithstanding, however, the extremely limited range of their intellectual powers, these children were remarkably vivacious and excitable. While awake they were in almost constant motion, and any new object or toy presented to them immediately attracted their attention, and evidently awakened a lively curiosity. They were accordingly easily influenced by proper management, and understood readily the meaning of those who addressed them, so far as this meaning could be conveyed by gesticulation and the tones of the voice. Their expression and general appearance, though decidedly idiotic, were not at all disagreeable or repulsive; and they were much less troublesome to the persons who had them in charge than is often the case with idiots possessing a larger cerebral development.

It may also be observed that the purely intellectual or reasoning powers are not the only element in the mental superiority of certain races or of particular individuals over their associates. There is

also a certain rapidity of perception and strength of will which may sometimes overbalance greater intellectual acquirements and more cultivated reasoning powers. These, however, are different faculties from the latter; and occupy, as we shall hereafter see, different parts of the encephalon.

A very remarkable physiological doctrine, dependent partly on the foregoing facts, was brought forward some years ago by Gall and Spurzheim, under the name of *Phrenology*. These observers recognized the fact that the intellectual powers are undoubtedly seated in the brain, and that the development of the brain is, as a general rule, in correspondence with the activity of these powers. They noticed also that in other parts of the nervous system, different functions occupy different situations; and regarding the mind as made up of many distinct mental faculties, they conceived the idea that these different faculties might be seated in different parts of the cerebral mass. If so, each separate portion of the brain would undoubtedly be more or less developed in proportion to the activity of the mental trait or faculty residing in it. The shape of the head would then vary in different individuals, in accordance with their mental peculiarities; and the character and endowments of the individual might therefore be estimated from an examination of the elevations and depressions on the surface of the cranium.

Accordingly, the authors of this doctrine endeavored, by examining the heads of various individuals whose character was already known, to ascertain the location of the different mental faculties. In this manner they finally succeeded, as they supposed, in accomplishing their object; after which they prepared a chart, in which the surface of the cranium was mapped out into some thirty or forty different regions, corresponding with as many different mental traits or faculties. With the assistance of this chart it was thought that phrenology might be practised as an art; and that, by one skilled in its application, the character of a stranger might be discovered by simply examining the external conformation of his head.

We shall not expend much time in discussing the claims of phrenology to rank as a science or an art, since we believe that it has of late years been almost wholly discarded by scientific men, owing to the very evident deficiencies of the basis upon which it was founded. Passing over, therefore, many minor details, we will merely point out, as matters of physiological interest, the principal defects which must always prevent the establishment of phrenology as a science, and its application as an art.

First, though we have no reason for denying that different parts of the brain may be occupied by different intellectual faculties, there is no direct evidence which would show this to be the case. Phrenologists include, in those parts of the brain which they employ for examination, both the cerebrum and cerebellum; and they justly regard the external parts of these bodies, viz., the layer of gray matter which occupies their surface, as the ganglionic portion in which must reside more especially the nervous functions which they possess. But this layer of gray matter, in each principal portion of the brain, is continuous throughout. There is no anatomical division or limit between its different parts, like those between the different ganglia in other portions of the nervous system; and consequently such divisions of the cerebrum and cerebellum must be altogether arbitrary in character, and not dependent on any anatomical basis.

Secondly, the only means of ascertaining the location of the different mental traits, supposing them to occupy different parts of the brain, would be that adopted by Gall and Spurzheim, viz., to make an accurate comparison, in a sufficient number of cases, of the form of the head in individuals of known character. But the practical difficulty of accomplishing this is very great. It requires a long acquaintance and close observation to learn accurately the character of a single person; and it is in this kind of observation, more than in any other, that we are proverbially liable to mistakes. It is extremely improbable, therefore, that either Gall or Spurzheim could, in a single lifetime, have accomplished this comparison in so many instances as to furnish a reliable basis for the construction of a phrenological chart.

Fig. 151.

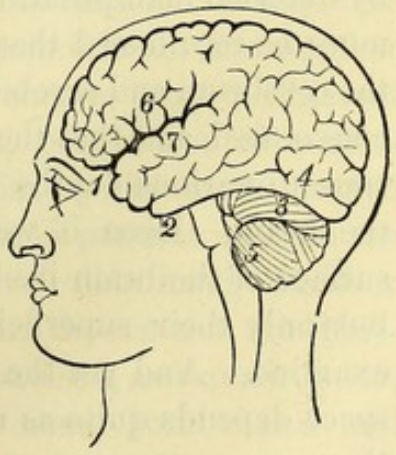
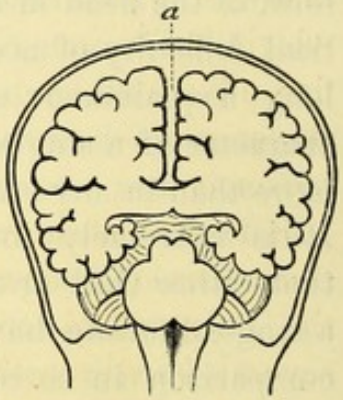


Diagram of the BRAIN IN SITU, showing those portions which are exposed to examination.

A still more serious practical difficulty, however, is the following. The different intellectual faculties being supposed to reside in the layer of gray substance constituting the surfaces of the cerebrum and cerebellum, they must of course be distributed throughout this layer, wherever it exists. Gall and Spurzheim located all the mental faculties in those parts of the brain which are accessible to external exploration.

An examination of different sections of the brain will show, however, that the greater portion of the gray substance is so placed, that its quantity cannot be estimated by an external examination through the skull. The only portions which are exposed to such an examination are the upper and lateral portions of the convexities of the hemispheres, together with the posterior edge and part of the under surface of the cerebellum. (Fig. 151.) A very extensive portion of the cerebral surface, however, remains concealed in such a manner that it cannot possibly be subjected to examination, viz., the entire base of the brain, with the under surface of the anterior and middle lobes (1, 2); the upper surface of the cerebellum (3) and the inferior surface of the posterior lobe of the cerebrum which covers it (4); that portion of the cerebellum situated above the medulla oblongata (5); and the two opposite convoluted surfaces in the fissure of Sylvius (6, 7), where the anterior and middle lobes of the cerebrum lie in contact with each other. The whole extent, also, of the cerebral surfaces which are opposed to each other in the great longitudinal fissure (Fig. 152), throughout its entire length, are equally protected by their position, and concealed from external examination. The whole of the convoluted surface of the brain must, however, be regarded as of equal importance in the distribution of the mental qualities; and yet it is evident that not more than one-third or one-quarter of this surface is so placed that it can be examined by external manipulation. It must furthermore be recollected that the gray matter of the cerebrum and cerebellum is everywhere convoluted, and that the convolutions penetrate to various depths in the substance of the brain. Even if we were able to feel, therefore, the external surface of the brain itself, it would not be the entire convolutions, but only their superficial edges, that we should really be able to examine. And yet the amount of gray matter contained in a given space depends quite as much upon the depth to which the convolutions penetrate, as upon the prominence of their edges.

Fig. 152.



Transverse section of BRAIN, showing depth of great longitudinal fissure, at *a*.

While phrenology, therefore, is partially founded upon acknowledged physiological facts, there are yet essential deficiencies in its scientific basis, as well as insurmountable difficulties in the way of its practical application.

CEREBELLUM.—The cerebellum is the second ganglion of the encephalon, in respect to size. If it be examined, moreover, in regard to the form and disposition of its convolutions, it will be seen that these are much more complicated and more numerous than in the cerebrum, and penetrate much deeper into its substance. Though the cerebellum therefore is smaller, as a whole, than the cerebrum, it contains, in proportion to its size, a much larger quantity of gray matter.

In examining the comparative development of the brain, also, in different classes and species of animals, we find that the cerebellum nearly always keeps pace, in this respect, with the cerebrum. These facts would lead us to regard it as a ganglion hardly secondary in importance to the cerebrum itself.

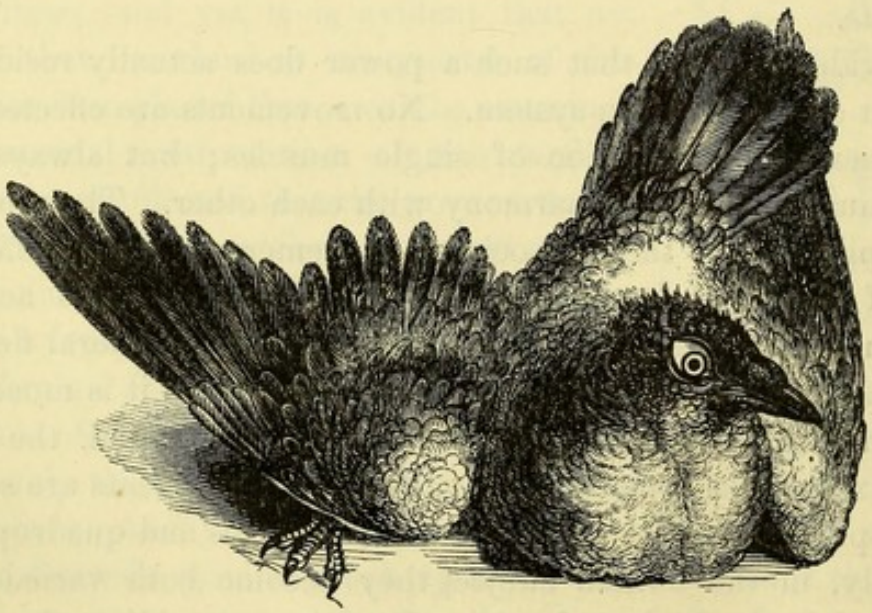
Physiologists, however, have thus far failed to demonstrate the nature of its function with the same degree of precision as that of many other parts of the brain. The opinion of Gall, which located in the cerebellum the sexual impulse and instincts, is at the present day generally abandoned; for the reason that it has not been found to be sufficiently supported by anatomical and experimental facts, many of which are indeed directly opposed to it. The opinion which has of late years been received with the most favor is that first advocated by Flourens, which attributes to the cerebellum the power of associating or "co-ordinating" the different voluntary movements.

It is evident, indeed, that such a power does actually reside in some part of the nervous system. No movements are effected by the independent contraction of single muscles; but always by several muscles acting in harmony with each other. The number and complication of these associated movements vary in different classes of animals. In fish, for example, progression is accomplished in the simplest possible manner, viz., by the lateral flexion and extension of the vertebral column. In serpents it is much the same. In frogs, lizards, and turtles, on the other hand, the four jointed extremities come into play, and the movements are somewhat complicated. They are still more so in birds and quadrupeds; and finally, in the human subject they become both varied and complicated in the highest degree. Even in maintaining the ordinary postures of standing and sitting, there are many different muscles acting together, in each of which the degree of contraction, in order to preserve the balance of the body, must be accurately proportioned to that of the others. In the motions of walking and

running, or in the still more delicate movements of the hands and fingers, this harmony of muscular action becomes still more evident, and is seen also to be absolutely indispensable to the efficiency of the muscular apparatus.

The opinion which locates the above harmonizing or associating power in the cerebellum was first suggested by the effects observed after experimentally injuring or destroying this part of the brain. If the cerebellum be exposed in a living pigeon, and a portion of its substance removed, the animal exhibits at once a peculiar uncertainty in his gait, and in the movement of his wings. If the injury be more extensive, he loses altogether the power of flight, and can walk, or even stand, only with great difficulty. This is not owing to any actual paralysis, for the movements of the limbs are exceedingly rapid and energetic; but is due to a peculiar want of control over the muscular contractions, precisely similar to that which is seen in a man in a state of intoxication. The movements of the legs and wings, though forcible and rapid, are confused and blundering; so that the animal cannot direct his steps to any particular spot, nor support himself in the air by flight. He reels and tumbles, but can neither walk nor fly.

Fig. 153.



Pigeon, after Removal of the Cerebellum.

The senses and intelligence at the same time are unimpaired. It is extremely curious, as first remarked by Longet, to compare the

different phenomena produced by removal of the cerebrum and that of the cerebellum. If we do these operations upon two different pigeons, and place the animals side by side, it will be seen that the first pigeon, from whom the cerebrum only has been removed, remains standing firmly upon his feet, in a condition of complete repose; and that when aroused and compelled to stir, he moves sluggishly and unwillingly, but otherwise acts in a perfectly natural manner. The second pigeon, on the other hand, from whom the cerebellum only has been taken away, is in a constant state of agitation. He is easily terrified, and endeavors, frequently with violent struggles, to escape the notice of those who are watching him; but his movements are sprawling and unnatural, and are evidently no longer under the effectual control of the will. (Fig. 153.) If the entire cerebellum be destroyed, the animal is no longer capable of assuming or retaining any natural posture. His legs and wings are almost constantly agitated with ineffectual struggles, which are evidently voluntary in character, but are at the same time altogether irregular and confused. Death generally takes place after this operation within twenty-four hours.

We have often performed the above operation, and always with the same effect. Indeed there are few experiments that have been tried upon the nervous system, which give results so uniform and so constant as this. Taken by themselves, these results would invariably sustain the theory of Flourens, which, indeed, is founded entirely upon them.

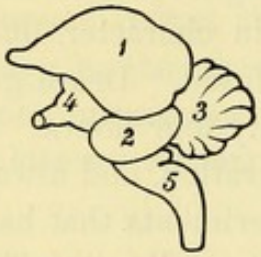
But we have met with another very important fact, in this respect, which for a long time escaped notice. That is, that birds, which have lost their power of muscular co-ordination from injury of the cerebellum, may *recover this power in process of time*, notwithstanding that a large portion of the cerebellum has been permanently removed. Usually such an operation upon the cerebellum, as we have mentioned above, is fatal within twenty-four hours, probably on account of the close proximity of the medulla oblongata. But in some instances, the pigeons upon which we have operated have survived, and in these cases the co-ordinating power became re-established.

In the first of these instances, about two-thirds of the cerebellum was taken away, by an opening in the posterior part of the cranium. Immediately after the operation, the animal showed all the usual effects of the operation, being incapable of flying, walking, or even standing still, but reeled and sprawled about in a perfectly helpless manner. In the course of five or six days, however, he had regained

a very considerable control over the voluntary movements, and at the end of sixteen days his power of muscular co-ordination was so nearly perfect, that its deficiency, if any existed, was imperceptible. He was then killed; and on examination, it was found that his cerebellum remained in nearly the same condition as immediately after the operation; about two-thirds of its substance being deficient, and no attempt having been made at regeneration of the lost parts. The accompanying figures, 154 to 157, show the appearances, in this case, as compared with the brain of a healthy pigeon.

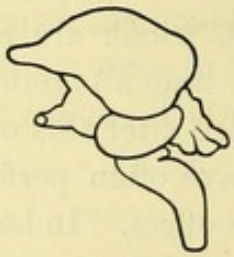
We have also met with three other cases, similar to the above, in which about one-half of the cerebellum was removed by operation. The loss of co-ordinating power, immediately after the operation, though less complete than in the instance above mentioned, was perfectly well marked in character; and in little more than a fort-

Fig. 154.



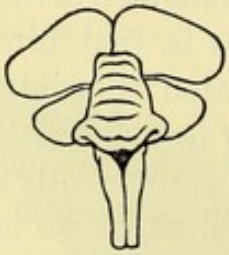
BRAIN OF HEALTHY PIGEON—Profile view.—1. Hemisphere. 2. Optic tubercle. 3. Cerebellum. 4. Optic nerve. 5. Medulla oblongata.

Fig. 155.



BRAIN OF OPERATED PIGEON—Profile view—showing the mutilation of cerebellum.

Fig. 156.



BRAIN OF HEALTHY PIGEON—Posterior view.

Fig. 157.

BRAIN OF OPERATED PIGEON—Posterior view—showing the mutilation of cerebellum.

night the animals had nearly or quite recovered the natural control of their motions.

It is evident that in these cases, if the theory of Flourens be correct, two different effects are produced simultaneously by the operation, which ought to be carefully distinguished from each other. The first of these effects is the shock due to the *sudden injury of the cerebellum as a whole.* This effect is temporary, and may be re-

covered from in time, provided the animal be sufficiently strong to survive the immediate results of the operation. The remaining effect is that due simply to *the loss of the nervous substance;* and this second effect must of course be permanent, unless the nervous matter be regenerated. In the cases detailed above, the greatest amount of disturbance seems to have depended upon the sudden injury to the nervous centre as a whole; and as the immediate effect of this injury passed off, the animals recovered, to a very great extent, their power of muscular co-ordination, notwithstanding that from one-half to two-thirds of the substance of the cerebellum had been permanently lost. It must be remembered, however, that birds, when confined to the limited space of a laboratory, have no opportunity of exercising the more complicated and active movements which are natural to them in a condition of freedom; and accordingly, they might not show any great deficiency of muscular co-ordination while in a state of confinement, and might still be quite incapable of executing the rapid and various movements of natural flight.

In birds, therefore, the simpler motions may continue to be performed with only a part of the cerebellum remaining; but we are not sure that, even in these cases, a portion of the co-ordinating power, corresponding with the destruction of nervous substance, has not been permanently lost.

Furthermore, there are many facts derived from comparative anatomy which seem to favor the opinion of Flourens. If we compare different classes of animals with each other, as fish with reptiles, or birds with quadrupeds, in which the development and activity of the entire nervous system vary extremely, the results of the comparison will be often contradictory. But if the comparison be made between different species in which the general structure and plan of organization are similar, we often find the development of the cerebellum to correspond very closely with the perfection and variety of the voluntary movements. The frog, for example, is an aquatic reptile, provided with anterior and posterior extremities; but its movements, though rapid and vigorous, are exceedingly simple in character, consisting of little else than flexion and extension of the posterior limbs. The cerebellum in this animal is exceedingly small, as compared with the rest of the brain; being nothing more than a thin, narrow ribbon of nervous matter, stretched across the upper part of the fourth ventricle. In the common turtle we have another aquatic reptile, where the movements of swimming, diving,

progression, &c., are accomplished by the consentaneous action of anterior and posterior extremities, and where the motions of the head and neck are also much more varied than in the frog. In this instance the cerebellum is very much more highly developed than in the former. In the alligator, again, a reptile whose motions, both of the head, limbs, and tail, approach very closely to those of the quadrupeds, the cerebellum is still larger in proportion to the remaining ganglia of the encephalon.

On the other hand, morbid alterations of the cerebellum, particularly of a chronic nature, such as slow inflammations, abscesses, tumors, &c., have often been observed in the human subject, without giving rise to any marked disturbance of the voluntary movements.

The complete function of the cerebellum, accordingly, as a nervous centre, cannot be regarded as positively ascertained; but so far as we may rely on the results of direct experiment, this organ has evidently such an intimate and peculiar connection with the voluntary movements, that a sudden injury inflicted upon its substance is always followed by an immediate and strongly marked disturbance of the co-ordinating power.

Tubercula Quadrigemina. — These bodies, notwithstanding their small size, are very important in regard to their function. They give origin to the optic nerves, and preside, as ganglia, over the sense of sight; on which account they are also known by the name of the "optic ganglia." Their development corresponds very closely with that of the external organs of vision. Thus, they are large in fish, reptiles, and birds, in which the eyeball is for the most part very large in proportion to the entire head; and are small in quadrupeds and in man, where the eyeball is, comparatively speaking, of insignificant size. Direct experiment also shows the close connection between the tubercula quadrigemina and the sense of sight. Section of the optic nerve at any point between the retina and the tubercles, produces complete blindness; and destruction of the tubercles themselves has the same effect. But if the division be made between the tubercles and the cerebrum, or if the cerebrum itself be taken away while the tubercles are left untouched, vision, as we have already seen, still remains. It is the tubercles, therefore, in which the impression of light is perceived. So long as these ganglia are uninjured and retain their connection with the eye, vision remains. As soon as this connection is cut

off, or the ganglia themselves are injured, the power of vision is destroyed.

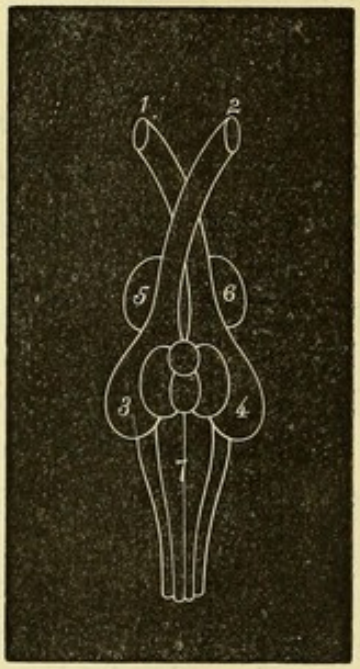
The tubercula quadrigemina not only serve as nervous centres for the perception of light, but a reflex action also takes place through them, by which the quantity of light admitted to the eye is regulated to suit the sensibility of the pupil. In darkness and in twilight, or wherever the light is feeble, the pupil is enlarged by relaxation of its circular fibres, so as to admit as large a quantity of light as possible. On first coming into a dark room, accordingly, everything is nearly invisible; but gradually, as the pupil dilates and as more light is admitted, objects begin to show themselves with greater distinctness, and at last we can see tolerably well in a place where we were at first unable to perceive a single object. On the other hand, when the eye is exposed to an unusually brilliant light, the pupil contracts and shuts out so much of it as would be injurious to the retina.

The above is a reflex action, in which the impression received by the retina is transmitted along the optic nerve to the tubercula quadrigemina. From the tubercles, a motor impulse is then sent out through the motor nerves of the eye and the filaments distributed to the iris, and a contraction of the pupil takes place in consequence. The optic nerves act here as sensitive fibres, which convey the impression from the retina to the ganglion; and if they be irritated in any part of their course with the point of a needle, the result is a contraction of the pupil. This influence is not communicated directly from the nerve to the iris, but is first sent inward to the tubercles, to be afterward reflected outward by the motor nerves. So long as the eyeball remains in connection with the brain, mechanical irritation of the optic nerve, as we have shown above, causes contraction of the pupil; but if the nerve be divided, and the extremity which remains in connection with the eyeball be subjected to irritation, no effect upon the pupil is produced.

The anatomical arrangement of the optic nerves, and the connections of the optic tubercles, are modified in a remarkable degree in different animals, to correspond with the position of the two eyes. In fish, for example, the eyes are so placed, on opposite sides of the head, that their axes cannot be brought into parallelism with each other, and the two eyes can never be directed together at the same object. In these animals, the optic nerves cross each other at the base of the brain without any intermixture of their fibres; that

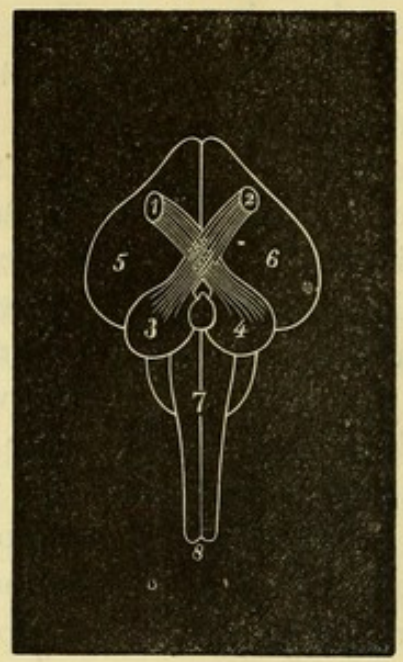
from the right optic tubercle passing to the left eye, and that from the left optic tubercle passing to the right eye. (Fig. 158.) The two

Fig. 158.



Inferior Surface of Brain of Cod.—1. Right optic nerve. 2. Left optic nerve. 3. Right optic tubercle. 4. Left optic tubercle. 5, 6. Hemispheres. 7. Medulla oblongata.

Fig. 159.

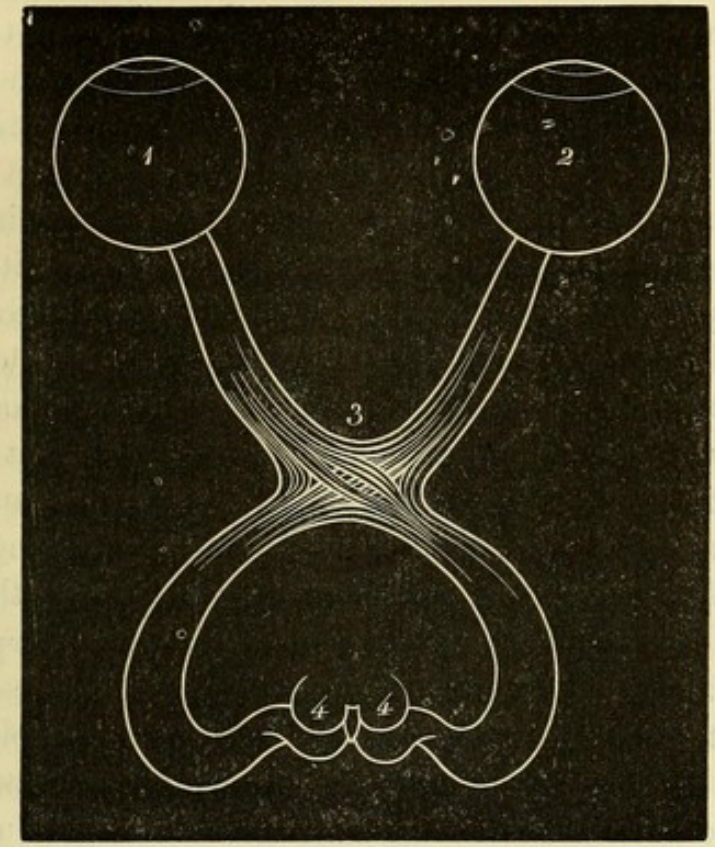


Inferior Surface of Brain of Fowl.—1. Right optic nerve. 2 Left optic nerve. 3. Right optic tubercle 4. Left optic tubercle. 5, 6 Hemispheres. 7. Medulla oblongata.

nervous cords are here totally distinct from each other throughout their entire length; and are only connected, at the point of crossing, by intervening areolar tissue. Impressions made on the right eye must therefore be perceived on the left side of the brain; while those which enter the left eye are conveyed to the right side of the brain.

In birds, also, the axes of the two eyes are so widely divergent that near objects cannot probably be in exact focus for both of them at the same time. The optic nerves are here united, and apparently soldered together, at their point of crossing; but the decussation of their fibres is nevertheless complete. (Fig. 159.) The nervous filaments coming from the left side pass altogether over to the right; and those coming from the right side pass over to the left. The result of direct experiment on the crossed action of the tubercles in these animals corresponds with the anatomical arrangement of the nervous fibres. If one of the optic tubercles be destroyed in the pigeon, complete blindness is at once produced in the eye of the opposite side; but vision remains unimpaired in the eye of the side on which the injury was inflicted.

Fig. 160.



COURSE OF OPTIC NERVES IN MAN.—1, 2. Right and left eyeballs. 3. Decussation or optic nerves. 4, 4. Tubercula quadrigemina.

In the human subject, on the other hand, where the visual axes are parallel, and where both eyes are simultaneously directed toward the same object, the optic nerves decussate with each other in such a manner as to form a connection between the two opposite sides, as well as between each tubercle and retina of the same side. (Fig. 160.) This decussation, which is somewhat complicated, takes place in the following manner. From each optic tubercle three different bundles or "tracts" of nervous fibres are given off. One set passes across transversely at the point of decussation, and, turning backward, terminates in the tubercle of the opposite side; another, crossing diagonally, continues onward to the opposite eyeball; while a third passes directly forward to the eyeball of the same side. A fourth set of fibres, still, passes across in front of the decussation, from the retina of one eye to that of the opposite side. We have, therefore, by this arrangement, the two retinæ, as well as the two optic tubercles, connected with each other by commissural fibres; while each tubercle is, at the same time, connected both with its own retina, and with that of the opposite side. It is undoubtedly owing to these connections that when, in the human subject, the eyes are directed in their proper axes, the two retinæ, as well as the two optic tubercles, act as a single organ. Vision is single,

therefore, though there are two images upon the retinæ. Double, vision occurs only when the eyeballs are turned out of their proper direction, so that the parallelism of their axes is lost, and the image no longer falls upon corresponding parts of the two retinæ.

Tuber Annulare.—The collection of gray matter imbedded in the deeper portions of the tuber annulare occupies a situation near the central part of the brain, and lies directly in the course of the ascending fibres of the anterior and posterior columns of the cord. This ganglion is immediately connected with the functions of sensation and voluntary motion. We have already seen that these functions are not destroyed by taking away the cerebrum, and that they also remain after removal of the cerebellum. According to the experiments of Longet, even after complete removal of the olfactory ganglia, the cerebrum, cerebellum, optic tubercles, corpora striata and optic thalami, and when nothing remains in the cavity of the cranium but the tuber annulare and the medulla oblongata, the animal is still sensitive to external impressions, and will still endeavor by voluntary movements to escape from a painful irritation. The same observer has found, however, that as soon as the ganglion of the tuber annulare is broken up, all manifestations of sensation and volition cease, and even consciousness no longer appears to exist. The only movements which then follow external irritation are the occasional convulsive motions which are due to reflex action of the spinal cord, and which may be readily distinguished from those of a voluntary character. The animal, under these circumstances, is to all appearance reduced to the condition of a dead body, except for the movements of respiration and circulation, which still go on for a certain time. The tuber annulare must therefore be regarded as the ganglion by which impressions, conveyed inward through the nerves, are first converted into conscious sensations; and in which the voluntary impulses originate, which stimulate the muscles to contraction.

We must carefully distinguish, however, in this respect, a simple sensation from the ideas to which it gives origin in the mind, and the mere act of volition from the train of thought which leads to it. Both these purely mental operations take place, as we have seen, in the cerebrum; for mere sensation and volition may exist independently of any intellectual action, as they may exist after the cerebrum has been destroyed. A sensation may be felt, for example, without our having the power of thoroughly appreciating

it, or of referring it to its proper source. This condition is often experienced in a state of deep sleep, when, the body being exposed to cold, or accidentally placed in a constrained position, we feel a sense of suffering without being able to understand its cause. We may even, under such circumstances, execute voluntary movements to escape the cause of annoyance; but these movements, not being directed by any active intelligence, fail of accomplishing their object. We therefore remain in a state of discomfort until, on awakening, the activity of the reason and judgment is restored, when the offending cause is at once removed.

We distinguish, then, between the simple power of sensation, and the power of fully appreciating a sensitive impression and of drawing a conclusion from it. We distinguish also between the intellectual process which leads us to decide upon a voluntary movement, and the act of volition itself. The former must precede, the latter must follow. The former takes place, so far as experiment can show, in the cerebral hemispheres; the latter, in the ganglion of the tuber annulare.

MEDULLA OBLONGATA.—The last remaining division of the encephalon is the medulla oblongata. The most important ganglion contained in this part is the "pneumogastric ganglion," or "nucleus," imbedded in the substance of the restiform body, and occupying the middle and posterior portions of the medulla, where the fibres of the pneumogastric nerve take their origin. This portion of the brain has long been known to be particularly essential to the preservation of life; so that it has received the name of the "vital point," or the "vital knot." All the other parts of the brain may be injured or removed, as we have already seen, without the immediate and necessary destruction of life; but so soon as the medulla oblongata is broken up, and its ganglion destroyed, respiration ceases instantaneously, and the circulation also soon comes to an end. Removal of the medulla oblongata produces, therefore, as its immediate and direct result, a stoppage of respiration: and death takes place principally as a consequence of this fact.

Flourens and Longet have determined, with considerable accuracy, the precise limits of this vital spot in the medulla oblongata. Flourens ascertained that in rabbits it extended from just above the origin of the pneumogastric nerve, to a level situated three lines and a half below this origin. In larger animals, its extent is proportionally increased. Longet ascertained, furthermore, that the properties of the medulla were not the same throughout its entire

thickness; but that its posterior and anterior parts might be destroyed with comparative impunity, the peculiarly vital spot being confined to the intermediate portions. This vital point accordingly is situated in the layer of gray matter, imbedded in the thickness of the restiform bodies, which has been previously spoken of as giving origin to the pneumogastric nerves.

The precise nature of the connection between this ganglion and the function of respiration may be described as follows. The movements of respiration, which follow each other with incessant regularity through the whole period of life, are not voluntary movements. We may to a certain extent, hasten or retard them at will, but our power over them, even in this respect, is extremely limited; and in point of fact they are performed, during the greater part of the time, in a perfectly quiet and regular manner, without our volition and even without our consciousness. They continue uninterruptedly through the deepest slumber, and even in a condition of insensibility from accident or disease.

These movements are the result of a reflex action taking place through the medulla oblongata. The impression which gives rise to them originates principally in the lungs, from the accumulation of carbonic acid in the pulmonary vessels and air-cells, is transmitted by the pneumogastric nerves to the medulla, and is thence reflected along the motor nerves to the respiratory muscles. These muscles are then called into action, producing an expansion of the chest. The impression so conveyed to the medulla is usually unperceived by the consciousness. It is generally converted directly into a motor impulse, without attracting our attention or giving rise to any conscious sensation. Respiration, accordingly, goes on perfectly well without our interference and without our knowledge. The nervous impression, however, conveyed to the medulla, though usually imperceptible, may be made evident at any time by voluntarily suspending the respiration. As the carbonic acid begins to accumulate in the blood and in the lungs, a peculiar sensation makes itself felt, which grows stronger and stronger with every moment, and impels us to recommence the movements of inspiration. This peculiar sensation, entirely different in character from any other, is designated by the French under the name of "besoin de respirer." It becomes more urgent and distressing, the longer respiration is suspended, until finally the impulse to expand the chest can no longer be resisted by any effort of the will.

During ordinary respiration, therefore, each inspiratory move-

ment is excited by the partial vitiation of the air contained in the lungs. As soon as a new supply has been inhaled, the impulse to respire is satisfied, the muscles relax, and the chest collapses. In a few seconds the previous condition recurs and the same movements are repeated, producing in this way a regular alternation of inspirations and expirations.

Since the movements of respiration are performed partly by the diaphragm and partly by the intercostal muscles, they will be differently modified by injuries of the nervous system, according to the spot at which the injury is inflicted. If the spinal cord, for example, be divided or compressed in the lower part of the neck, all the intercostal muscles will be necessarily paralyzed, and respiration will then be performed entirely by the diaphragm. The chest in these cases remaining motionless, and the abdomen alone rising and falling with the movements of the diaphragm, such respiration is called "abdominal" or "diaphragmatic" respiration. It is a common symptom of fracture of the spine in the lower cervical region. If the phrenic nerve, on the other hand, be divided, the diaphragm will be paralyzed, and respiration will then be performed altogether by the rising and falling of the ribs. It is then called "thoracic" or "costal" respiration. If the injury inflicted upon the spinal cord be above the origin of the second and third cervical nerves, both the phrenic and intercostal nerves are at once paralyzed, and death necessarily takes place from suffocation. The attempt at respiration, however, still continues in these cases, showing itself by ineffectual inspiratory movements of the mouth and nostrils. Finally, if the medulla itself be broken up by a steel instrument introduced through the foramen magnum, so as to destroy the nervous centre in which the above reflex action takes place, both the power and the desire to breathe are at once taken away. No attempt is made at inspiration, there is no struggle, and no appearance of suffering. The animal dies simply by a want of aeration of the blood, which leads in a few moments to an arrest of the circulation.

It is owing to the above action of the medulla oblongata that injuries of this part are so promptly and constantly fatal. When the "neck is broken," as in hanging or by sudden falls upon the head, a rupture takes place of the transverse ligament of the atlas; the head, together with the first cervical vertebra, is allowed to slide forward, and the medulla is compressed between the odontoid process of the axis in front and the posterior part of the arch of the

atlas behind. In cases of apoplexy, where any part of the hemispheres, corpora striata, or optic thalami, is the seat of the hemorrhage, the patient generally lives at least twelve hours; but if the hemorrhage takes place in the medulla itself, or at the base of the brain in its immediate neighborhood, so as to compress its substance, death follows instantaneously, and by the same mechanism as where the medulla is intentionally destroyed.

An irregularity or want of correspondence in the movements of respiration is accordingly found to be one of the most threatening of all symptoms in affections of the brain. A disturbance or suspension of the intellectual powers does not indicate necessarily any immediate danger to life. Even sensation and volition may be impaired without serious and direct injury to the organic functions. These symptoms only indicate the threatening progress of the disease, and show that it is gradually approaching the vital centre. It is common to see, however, as the medulla itself begins to be implicated, a paralysis first showing itself in the respiratory movements of the nostrils and lips, while those of the chest and abdomen still go on as usual. The cheeks are then drawn in with every inspiration and puffed out sluggishly with every expiration, the nostrils themselves sometimes participating in these unnatural movements. A still more threatening symptom, and one which frequently precedes death, is an irregular, hesitating respiration, which sometimes attracts the attention of the physician, even before the remaining cerebral functions are seriously impaired. These phenomena depend on the connection between the respiratory movements and the reflex action of the medulla oblongata.

We have now, in studying the functions of various parts of the cerebro-spinal system, become familiar with three different kinds of reflex action.

The first is that of the spinal cord. Here, there is no proper sensation and no direct consciousness of the act which is performed. It is simply a nervous impression, coming from the integument, and transformed by the gray matter of the spinal cord into a motor impulse destined for the muscles. This action will take place after the removal of the hemispheres and the abolition of consciousness, as well as in the ordinary condition. The respiratory action of the medulla oblongata is of the same general character; that is, it is not necessarily connected with either volition or consciousness. The only peculiarity in this instance is that the original nervous impression is of a special character, and its influence is finally

exerted upon a special muscular apparatus. Actions of this nature are termed, par excellence, *reflex* actions.

The second kind of reflex action takes place in the tuber annulare. Here the nervous impression, which is conveyed inward from the integument, instead of stopping at the spinal cord, passes onward to the tuber annulare, where it first gives rise to a conscious sensation; and this sensation is immediately followed by a voluntary act. Thus, if a crumb of bread fall into the larynx, the sensation produced by it excites the movement of coughing. The sensations of hunger and thirst excite a desire for food and drink. The sexual impulse acts in precisely the same manner; the perception of particular objects giving rise immediately to special desires of a sexual character.

It will be observed, in these instances, that in the first place, the nervous sensation must be actually perceived, in order to produce its effect; and in the second place that the action which follows is wholly voluntary in character. But the most important peculiarity, in this respect, is that the voluntary impulse follows *directly* upon the receipt of the sensation. There is no intermediate reasoning or intellectual process. We do not cough because we know that this is the most effectual way to clear the larynx; but simply because we are impelled to do so by the sensation which is felt at the time. We do not take food or drink because we know that they are necessary to support life, much less because we understand the mode in which they accomplish this object; but merely because we desire them whenever we feel the sensation of hunger and thirst.

All actions of this nature are termed *instinctive*. They are voluntary in character, but are performed blindly; that is, without any idea of the ultimate object to be accomplished by them, and simply in consequence of the receipt of a particular sensation. Accordingly experience, judgment, and adaptation have nothing to do with these actions. Thus the bee builds his cell on the plan of a mathematical figure, without performing any mathematical calculation. The silkworm wraps himself in a cocoon of his own spinning, certainly without knowing that it is to afford him shelter during the period of his metamorphosis. The fowl incubates her eggs and keeps them at the proper temperature for development, simply because the sight of them creates in her a desire to do so. The habits of these animals, it is true, are so arranged by nature, that such instinctive actions are always calculated to accomplish an

ultimate object. But this calculation is not made by the animal himself, and does not form any part of his mental operations. There is consequently no improvement in the mode of performing such actions, and but little deviation under a variety of circumstances.

The third kind of reflex action requires the co-operation of the hemispheres. Here, the nervous impression is not only conveyed to the tuber annulare and converted into a sensation, but, still following upward the course of the fibres to the cerebrum, it there gives rise to a special train of ideas. We understand then the external source of the sensation, the manner in which it is calculated to affect us, and how by our actions we may turn it to our advantage or otherwise. The action which follows, therefore, in these cases, is not simply voluntary but *reasonable*. It does not depend directly upon the external sensation, but upon an intellectual process which intervenes between the sensation and the volition. These actions are distinguished, accordingly, by a character of definite contrivance, and a conscious adaptation of means to ends; characteristics which do not belong to any other operations of the nervous system.

The possession of this kind of intelligence and reasoning power is not confined to the human species. We have already seen that there are many purely instinctive actions in man, as well as in animals. It is no less true that in the higher animals there is often the same exercise of reasoning power as in man. The degree of this power is much less in them than in him, but its nature is the same. Whenever, in an animal, we see any action performed with the evident intention of accomplishing a particular object, to which it is properly adapted, such an act is plainly the result of reasoning powers, not essentially different from our own. The establishment of sentinels by gregarious animals, to warn the herd of the approach of danger, the recollection of punishment inflicted for a particular action, and the subsequent avoidance or concealment of that action, the teachability of many animals, and their capacity of forming new habits or of improving the old ones, are all instances of the same kind of intellectual power, and are quite different from instinct, strictly speaking. It is this faculty which especially predominates over the others in the higher classes of animals, and which finally attains its maximum of development in the human species.

CHAPTER V.

THE CRANIAL NERVES.

In examining the cranial nerves, we shall find that although they at first seem quite different in their distribution and properties from the spinal nerves, yet they are in reality arranged for the most part on the same plan, and may be studied in a similar manner.

At the outset, however, we find that there are three of the cranial nerves, commonly so called, which must be arranged in a class by themselves; since they have no character in common with the other nerves originating either from the brain or the spinal cord. These are the three nerves of special sense; viz., the Olfactory, Optic, and Auditory. They are, properly speaking, not so much nerves as commissures, connecting different parts of the encephalic mass with each other. They are neither sensitive nor motor, in the ordinary meaning of these terms; but are capable of conveying only the special sensation characteristic of the organ with which they are connected.

Olfactory Nerves.—We have already described the so-called olfactory nerves as being in reality commissures, connecting the olfactory ganglia with the central parts of the brain. The masses situated upon the cribriform plate of the ethmoid bone are composed of gray matter; and even the filaments which they send outward to be distributed in the Schneiderian mucous membrane, are gray and gelatinous in their texture, and quite different from the fibres of ordinary nerves. The olfactory nerves are not very well adapted for direct experiment. It is, however, at least certain with regard to them that they serve to convey the special sensation of smell; that their mechanical irritation does not give rise to either pain or convulsions; and finally that their destruction, together with that of the olfactory ganglia, does not occasion any paralysis nor loss of ordinary sensibility.

Optic Nerves.—We have already given some account of these nerves and their decussations, in connection with the history of the tubercula quadrigemina. They consist of rounded bundles of white fibres, running between the tubercles and the retinæ. As the retinæ themselves are membranous expansions consisting mostly of vesicular or cellular nervous matter, the optic nerves, or "tracts," must be regarded as commissures connecting the retinæ with the tubercles. We have also seen that they serve, by some of their fibres, to connect the two retinæ with each other, as well as the two tubercles with each other.

The optic nerves convey only the special impression of light from without inward, and give origin to the reflex action of the optic tubercles, by which the pupil is made to contract. According to Longet, the optic nerves are absolutely insensible to pain throughout their entire length. When a galvanic current is passed through the eyeball, or when the retina is touched in operations upon the eye, the irritation has been found to produce the impression of luminous sparks and flashes, instead of an ordinary painful sensation. The impression of colored rings or spots may be easily produced by compressing the eye in particular directions; and a sudden stroke upon the eyeball will often give rise to an apparent discharge of brilliant sparks. Division of the optic nerves produces complete blindness, but does not destroy ordinary sensibility in any part of the eye, nor occasion any muscular paralysis.

Auditory Nerves.—The nervous expansion in the cavity of the internal ear contains, like the retina, vesicles or cells as well as fibres; and the auditory nerves are therefore to be regarded, like the optic and olfactory, as commissural in their character. They are also, like the preceding, destitute of ordinary sensibility. According to Longet, they may be injured or destroyed without giving rise to any sensation of pain. They serve to convey to the brain the special sensation of sound, and seem incapable of transmitting any other. Longet[1] relates an experiment performed by Volta, in which, by passing a galvanic current through the ears, the observer experienced the sensation of an interrupted hissing noise, so long as the connection of the wires was maintained. Inflammations within the ear, or in its neighborhood, are often accompanied by the perception of various noises, like the ringing of bells, the

[1] Traité de Physiologie, vol. ii. p 286.

washing of the waves, the humming of insects; sounds which have no external existence, but which are simulated by the morbid irritation of the auditory nerve.

It is evident, from the facts detailed above, that the nerves of special sense are neither motor or sensitive, properly speaking; and that they are distinct in their nature from the ordinary spinal nerves.

The remainder of the cranial nerves, however, present the ordinary qualities belonging to the spinal nerves. Some of them are exclusively motor in character, others exclusively sensitive; while most of them exhibit the two properties, to a certain extent, as mixed nerves. They may be conveniently arranged in three pairs, according to the regions in which they are distributed, corresponding very closely with the motor and sensitive roots of the spinal nerves. According to such a plan, the arrangement of the cranial nerves would be as follows:—

CRANIAL NERVES.

Nerves of Special Sense.

1. Olfactory. 2. Optic. 3. Auditory.

	Motor nerves.	Sensitive Nerves.	Distributed to
1st PAIR.	Motor oculi com. Patheticus Motor oc. externus Small root of 5th pair Facial	Large root of 5th pair.	Face.
2d PAIR.	Hypoglossal	Glosso-pharyngeal.	Tongue.
3d PAIR.	Spinal accessory	*Pneumogastric.	Neck, &c.

The above arrangement of the cranial nerves is not absolutely perfect in all its details. Thus, while the hypoglossal supplies the muscles of the tongue alone, the glosso-pharyngeal sends part of its sensitive fibres to the tongue and part to the pharynx; and while the large root of the 5th pair is mostly distributed in the face, one of its branches, viz., the gustatory, is distributed to the tongue. Notwithstanding these irregularities, however, the above division of the cranial nerves is in the main correct, and will be found extremely useful as an assistant in the study of their functions.

There is no impropriety, moreover, in regarding all the motor branches distributed upon the face as one nerve; since even the anterior roots of the spinal nerves originate from the spinal cord, each by several distinct filaments, which are associated into a single

bundle only at a certain distance from their point of origin. The mere fact that two nerves leave the cavity of the cranium by the same foramen does not indicate that they have the same or even a similar function. Thus the facial and auditory both escape from the cavity of the cranium by the foramen auditorium internum, and yet we do not hesitate to regard them as entirely distinct in their nature and functions. It is the ultimate distribution of a nerve, and not its course through the bones of the skull, that indicates its physiological character and position. For while the ultimate distribution of any particular nerve is always the same, its arrangement as to trunk and branches may vary, in different species of animals, with the anatomical arrangement of the bones of the skull. This is well illustrated by a fact first pointed out by Prof. Jeffries Wyman[1] in the anatomy of the nervous system of the bullfrog. In this animal, both the facial nerve and motor oculi externus, instead of arising as distinct nerves, are actually given off as branches of the 5th pair; while their ultimate distribution is the same as in other animals. All the motor and sensitive nerves distributed to the face are accordingly to be regarded as so many different branches of the same trunk; varying sometimes in their course, but always the same in their ultimate distribution.

The *motor* nerves of the head are in all respects identical in their properties with the anterior roots of the spinal nerves. For, in the first place, they are distributed to muscles, and not to the integument or to mucous membranes; secondly, their division causes muscular paralysis; and thirdly, mechanical irritation applied at their origin produces muscular contraction in the parts to which they are distributed, but does not give rise to a painful sensation. In several instances, nevertheless, the motor nerves, though insensible at their origin, show a certain degree of sensibility when irritated after their exit from the skull, owing to fibres of communication which they receive from the purely sensitive nerves. In this respect they resemble the spinal nerves, the motor and sensitive filaments of which are at first distinct in the anterior and posterior roots, but afterward mingle with each other, on leaving the cavity of the spinal canal.

The three *sensitive* nerves originating from the brain are the

[1] Nervous System of Rana pipiens; published by the Smithsonian Institution. Washington, 1853.

large root of the fifth pair, the glosso-pharyngeal, and the pneumogastric. It will be observed that, in all their essential properties, they correspond with the posterior roots of the spinal nerves. Like them they are inexcitable, but extremely sensitive. Irritated at their point of origin, they give rise to acutely painful sensations, but to no convulsive movements. Secondly, if divided at the same situation, the operation is followed by loss of sensibility in the parts to which they are distributed, without any disturbance of the motive power. Each of these nerves, furthermore, like the posterior root of a spinal nerve, is provided with a ganglion through which its fibres pass: the fifth pair, with the Casserian ganglion, situated near the inner extremity of the petrous portion of the temporal bone; the glosso-pharyngeal, with the ganglion of Andersch, situated in the jugular fossa; while the pneumogastric presents, just before its passage through the jugular foramen, a ganglion known as the ganglion of the pneumogastric nerve. Finally, the sensitive fibres of all these nerves, beyond the situation of their ganglia, are intermingled with others of a motor origin. The large root of the fifth pair, which is exclusively sensitive, is accompanied by the fibres of the small root, which are exclusively motor. The glosso-pharyngeal receives motor filaments from the facial and spinal accessory, becoming consequently a mixed nerve outside the cranial cavity; while the pneumogastric is joined by fibres from the spinal accessory and various other nerves of a motor character. These nerves, accordingly, are exclusively sensitive only at their point of origin. Though they afterward retain the predominating character of sensitive nerves, they are yet found, if irritated in the middle of their course, to be intermingled with motor fibres, and to have consequently acquired, to a certain extent, the character of mixed nerves.

The resemblance, therefore, between the cranial and spinal nerves is complete.

Motor Oculi Communis.—This nerve, which is sometimes known by the more convenient name of the *oculo-motorius*, emerges from the encephalon at the inner edge of the crus cerebri, passes into the cavity of the orbit by the sphenoidal fissure, and is distributed to the levator palpebræ superioris, and to all the muscles moving the eyeball, except the external rectus and the superior oblique. Its irritation accordingly produces convulsive movements in these

parts, and its division has the effect of paralyzing the muscles to which it is distributed. The superior eyelid falls down over the pupil, and cannot be raised, owing to the inaction of its levator muscle, so that the eye appears constantly half shut. This condition is known by the name of "ptosis." The movements of the eyeball are also nearly suspended, and permanent external strabismus takes place, owing to the paralysis of the internal rectus muscle, while the external rectus, animated by a different nerve, preserves its activity.

Patheticus.—This nerve, which supplies the superior oblique muscle of the eyeball, is similar in its general properties to the preceding. Its section causes paralysis of the above muscle, without any loss of sensibility.

Motor Externus.—This nerve, the sixth pair, or "abducens oculi," according to the usual anatomical nomenclature, emerges from the medulla oblongata just behind the lower border of the pons Varolii; but its fibres have been shown, by Dr. John Dean,[1] to originate, in the deeper part of the medulla, from a collection of gray matter, which is a continuation of the anterior horn of the gray matter of the cord. From its point of origin, the nerve passes forward, through the sphenoidal fissure, into the orbit of the eye, and is exclusively distributed to the external rectus muscle of the eyeball. Its division or injury by disease is followed by internal strabismus, owing to the unopposed action of the internal rectus muscle.

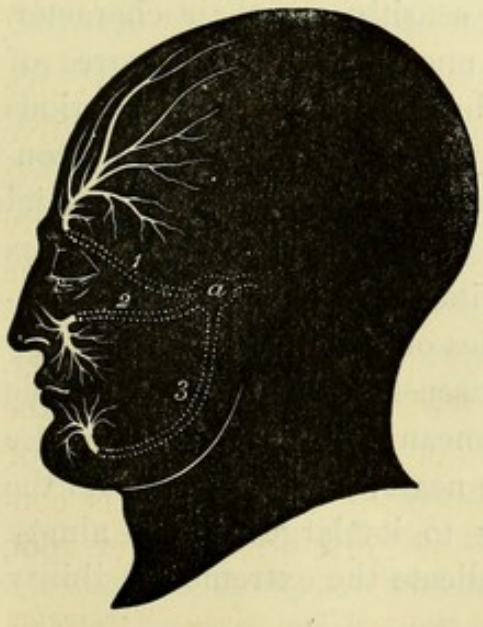
Fifth Pair.—This is one of the most important and remarkable in its properties of all the cranial nerves. It is the great sensitive nerve of the face, and of the adjoining mucous membranes. It arises by two roots, a larger and a smaller, which emerge, nearly side by side, from the lateral portion of the pons Varolii. The fibres of these roots, however, have been traced[2] through the substance of the pons to two "nuclei," or collections of gray matter, in the deeper parts of the medulla. The nucleus with which the larger root is connected is a continuation of the posterior horn of gray matter of the cord; that with which the smaller root is connected is a continuation of the anterior horn. The larger root,

[1] The Gray Substance of the Medulla Oblongata and Trapezium. Washington City, 1864, (Smithsonian Contributions to Knowledge,) p. 61.

[2] The Gray Substance of the Medulla Oblongata, &c., by Dr. John Dean, p. 49.

after emerging from the outer and under surface of the pons Varolii, passes forward over the inner extremity of the petrous portion of the temporal bone. It there expands into a crescentic-shaped swelling, containing a quantity of gray matter with which its fibres are intermingled, and which is known as the Gasserian ganglion. The fibres of the smaller root, passing forward in company with the others, do not take any part in the formation of this ganglion, but may be seen passing beneath it as a distinct bundle, and continuing their course forward to the foramen ovale, through which they emerge from the skull. In front of the anterior and external border of the Gasserian ganglion, the fifth nerve separates into three principal divisions, viz., the ophthalmic, the superior maxillary, and the inferior maxillary. The first of these divisions, viz., the ophthalmic, is so called because it passes through the orbit of the eye. It enters the sphenoidal fissure, and runs along the upper portion of the orbit, sending branches to the ophthalmic ganglion of the sympathetic, to the lachrymal gland, the conjunctiva, and the mucous membrane of the lachrymal sac. It also sends off a small branch (nasal branch) which penetrates into the nasal passages and supplies the Schneiderian mucous membrane. It then emerges upon the face by the supra-orbital foramen, and is distributed to the integument of the forehead and side of the head as far back as the vertex.

Fig. 161.



DISTRIBUTION OF FIFTH NERVE UPON THE FACE.—*a*. Gasserian ganglion. 1. Ophthalmic division. 2. Superior maxillary division. 3. Inferior maxillary division.

The second division of this nerve, or the superior maxillary, passes out by the foramen rotundum, and runs along the longitudinal canal in the floor of the orbit, giving off branches during its passage to the teeth of the upper jaw and to the mucous membrane of the antrum maxillare. It finally emerges upon the middle of the face by the infra-orbital foramen, and is distributed to the integument of the lower eyelid, nose, cheek, and upper lip.

The third, or inferior maxillary division of the fifth pair, which is the largest of the three, leaves the cavity of the cranium by the foramen ovale. It comprises a con-

siderable portion of the large root of the nerve, and all the fibres of the small root. This division is therefore a mixed nerve, containing both motor and sensitive fibres, while the two former are exclusively sensitive. It is distributed, accordingly, both to muscles and to the sensitive surfaces. Soon after emerging from the foramen ovale it sends branches to the temporal muscle, to the masseter, the buccinator, and to the internal and external pterygoids; that is, to the muscles which are particularly concerned in the movements of the lower jaw. It also sends sensitive filaments to the integument of the temple, to that of a portion of the external ear and external auditory meatus. The third division of the fifth pair, then passing downward and forward, gives off a branch of considerable size, the *lingual* branch, which is distributed to the mucous membrane of the anterior two-thirds of the tongue, and which also sends filaments to the arches of the palate and to the mucous membrane of the cheek. The remaining portion of the third division, after giving a few branches to the mylo-hyoid muscle and to the anterior belly of the digastric, then enters the inferior dental canal, sends filaments to the teeth of the lower jaw, emerges at the mental foramen, and is finally distributed to the integument of the chin, lower lip, and inferior part of the face.

This nerve is accordingly distributed to the sensitive surfaces, that is, the integument and mucous membranes about the face, and to the muscles of mastication. A few of its fibres are sent also to the superficial muscles of the face, such as the buccinator and the orbicularis oris; but these fibres are sensitive in their character, and serve merely to impart to the muscles a certain degree of sensibility. It has been ascertained by Longet that if the various branches of this nerve be irritated by a galvanic current, no convulsive movements whatever are produced in those superficial muscles of the face, which it supplies with filaments; but if its smaller or non-ganglionic root be irritated in the same way, contractions instantly follow in the muscles of mastication.

The fifth pair is the most acutely sensitive nerve in the whole body. Its irritation by mechanical means always causes intense pain, and even though the animal be nearly unconscious from the influence of ether, any severe injury to its large root is almost invariably followed by cries which indicate the extreme sensibility of its fibres.

If this nerve be completely divided, in the living animal, within the cranium, at the situation of the Gasserian ganglion, the operation

is followed by total loss of sensibility in the skin of the face and in the adjacent mucous membranes. The conjunctiva, upon the affected side, is then completely insensible, and may be touched with the point of a needle or the blade of a knife, without exciting any uneasiness, and even without the consciousness of the animal. Probes and needles may be passed into the nostril, and the lips or the cheek may be pinched, pierced or cut, without exciting the least sign of sensibility. The animal is entirely indifferent to all mechanical injuries upon the affected side, though upon the opposite side the parts retain their natural sensibility.

Owing to the paralysis of the *lingual nerve*, also, after this operation, the tongue, in its anterior two-thirds, becomes insensible to ordinary irritations, and loses, beside, the power of taste.

Another peculiar effect of the division of the fifth pair depends upon the paralysis of its motor fibres, which are distributed, as we have seen, to the muscles of mastication. In many of the lower animals, consequently, the movements of mastication become exceedingly enfeebled upon the affected side. In the cat, for example, an animal in which mastication is usually very thoroughly performed, this process becomes excessively laborious, so that the animal after this operation cannot masticate solid meat, but requires to be fed with that which has already been cut in pieces.

The fifth pair, beside supplying the sensibility of the integument of the face, has a peculiar and important influence on the organs of special sense. This influence appears to consist in some connection between the action of the fifth pair and the processes of nutrition; so that when the former is injured, the latter very soon become deranged. For the perfect action of any one of the organs of special sense, two conditions are necessary: first, the sensibility of the special nerve belonging to it, and secondly, the integrity of the component parts of the organ itself. Now as the nutrition of the organ is, to a certain extent, under the control of the fifth pair, any serious injury to this nerve produces a derangement in the tissues of the organ, and consequently interferes with the due performance of its function.

The mucous membrane of the nasal passages, for example, is supplied by two different nerves; first, the olfactory, distributed throughout its upper portion, by which it is endowed with the special sense of smell; and, secondly, the nasal branch of the fifth pair, distributed throughout its middle and lower portions, by which it is supplied with ordinary sensibility.

Since the fifth pair, accordingly, supplies general sensibility to the nasal passages, this property will remain after the special sense of smell has been destroyed. If, however, the fifth pair itself be divided, not only is general sensibility destroyed in the Schneiderian mucous membrane, but a disturbance begins to take place in the nutrition of its tissue, by which it is gradually rendered unfit for the performance of its special function, and the power of smell is finally lost. The mucous membrane, under these circumstances, becomes injected and swollen, and the nasal passage is obstructed by an accumulation of puriform mucus. According to Longet, the mucous membrane also assumes a fungous consistency, and is liable to bleed at the slightest touch. The effect of this alteration is to blunt or altogether destroy the sense of smell. It is owing to a similar unnatural condition of the mucous membrane that the power of smell is always more or less impaired in cases of coryza and influenza. The olfactory nerves become inactive in consequence of the morbid alteration in their mucous membrane, and in the secretions which cover it.

The influence of this nerve over the organ of vision is still more remarkable. It has been known for many years that division of the fifth pair within the cranium, or of its ophthalmic branch, is followed by an inflammation of the corresponding eye, which usually goes on to complete and permanent destruction of the organ. Immediately after the operation, the pupil becomes contracted and the conjunctiva loses its sensibility. At the end of twenty-four hours, the cornea begins to become opaline, and by the second day the conjunctiva is already inflamed and begins to discharge a purulent secretion. The inflammation, after commencing in the conjunctiva, increases in intensity and soon spreads to the iris, which becomes covered with a layer of inflammatory exudation. The cornea grows constantly more opaque, until it is at last altogether impermeable to light, and vision is consequently suspended. Blindness, therefore, does not result in these instances from any direct affection of the optic nerve or of the retina, but is owing simply to opacity of the cornea. Sometimes the diseased action goes on until it results in ulceration of the cornea and discharge of the humors of the eye; sometimes, after the lapse of several days, the inflammatory appearances subside, and the eye is finally restored to its natural condition.

It has been observed, however, that although the above consequences always follow division of the fifth pair, when performed at

the level of the Gasserian ganglion, or between it and the eyeball, they are either much diminished in intensity or altogether wanting when the division is made at a point posterior to the ganglion. This circumstance has led to the belief that the influence of the fifth pair on the nutrition of the eyeball does not reside in its own proper fibres, but in some filaments of the sympathetic nerve which join the fifth pair at the level of the Gasserian ganglion. If the section accordingly be made at this point, or in front of it, the fibres of the sympathetic will be divided with the others, and inflammation of the eye will result; but if the section be made behind the ganglion, the fibres of the sympathetic will escape division, and the injurious effects upon the eye will be absent. It is certain that inflammation of the eye sometimes follows division of the fifth nerve, and sometimes is wanting; but the precise reason of this variation is not fully understood.

Division of the fifth pair destroys also the general sensibility of the external auditory meatus, the lining membrane of which is supplied by its filaments. Inflammation of this membrane and its consequent alterations, it is well known, interfere seriously with the sense of hearing. It is no uncommon occurrence for an accumulation of cerumen to take place after inflammation of this part, so as to block up the auditory canal and produce partial or complete deafness. It has not been ascertained, however, whether division of the fifth pair is usually followed by similar changes in this part.

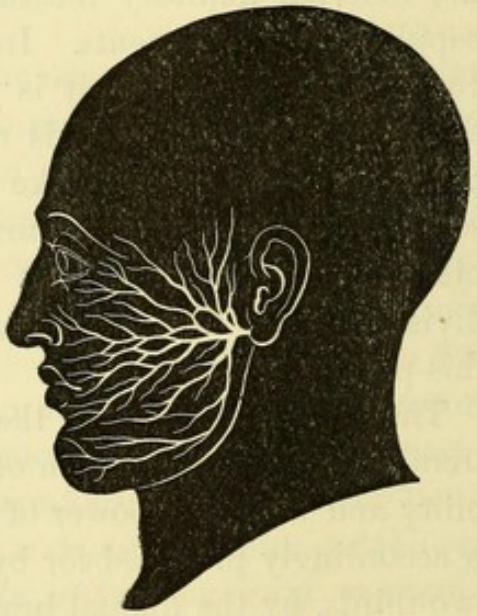
The lingual branch of the fifth pair supplies the anterior extremity and middle portion of the tongue both with general sensibility and with the power of taste. The sensibility of the tongue is accordingly provided for by two different nerves; in its anterior two-thirds, by the lingual branch of the fifth pair; in its posterior third, by the fibres of the glosso-pharyngeal.

The facial branches of the fifth pair are the ordinary seat of tic douloureux. This affection is not unfrequently confined to either the supra-orbital, the infra-orbital, or the mental branch; and the pain may be accurately traced in the direction of their diverging fibres. It has already been mentioned that the painful sensations sometimes also follow the course of the facial, owing to some sensitive filaments which that nerve receives from the fifth pair.

FACIAL.—This nerve, the "seventh pair," according to the modern enumeration of the cranial nerves, leaves the side of the me-

dulla oblongata, just behind the pons Varolii. Its fibres are traced to a collection of gray matter in the upper part of the medulla continuous with that from which the roots of the sixth pair originate. The facial nerve, after leaving the side of the medulla, passes onward through the petrous portion of the temporal bone, emerges at the stylo-mastoid foramen, bends round beneath the external ear, and passes forward through the substance of the parotid gland, forming a plexus called the "pes anserinus," by the abundant inosculation of its different branches. It then sends its filaments forward in a diverging course, and is finally distributed to the muscles of the external ear, to the frontalis and superciliaris muscles, to the orbicularis oculi, the compressors and dilators of the nares, the orbicularis oris, and to the elevators and depressors of the lips; that is, to the superficial muscles of the face, which are concerned in the production of expression. (Fig. 162.)

Fig. 162.



Facial Nerve.

The facial, consequently, is the motor nerve of the face. It has nothing to do with transmitting sensitive impressions, since it has been frequently shown that after section of the fifth pair, the facial remaining entire, the sensibility of the face is completely lost; so that the integument may be cut, pricked, pierced, or lacerated, without any sign of pain being exhibited by the animal. The facial, therefore, does not transmit sensation from these parts; and its division, which was formerly resorted to in cases of tic douloureux, is accordingly altogether incapable of relieving neuralgic pains.

This nerve, however, is directly connected with muscular action, since mechanical or galvanic irritation of its fibres produces convulsive twitching in the ears, nostrils, lips, and cheeks.

If the facial nerve be divided in one of the lower animals, as, for example, in the cat, immediately after its emergence from the stylo-mastoid foramen, it will be found that complete muscular paralysis has occurred in all those parts to which the nerve is distributed, while the power of sensation remains unimpaired. The animal is incapable of moving the ear, which remains constantly in

the same position. There is also incapacity of closing the eyelids, owing to paralysis of the orbicularis oculi, and the eye accordingly remains constantly open, even when the opposite eye is closed; as during sleep, or in the act of winking. If the conjunctiva be touched, the animal feels the irritation, and endeavors to escape from it; but the eyeball is only drawn partially backward into the socket by the action of the recti muscles, and the third eyelid pushed partly across the cornea. The complete closure of the eye is impossible. It will be observed, accordingly, that precisely opposite effects are produced upon the eyelids by paralysis of the oculomotorius nerve, and by that of the facial. In the former instance, owing to the paralysis of the levator palpebræ superioris, the eye is always partially closed; in the latter, owing to paralysis of the orbicularis, it is always partially open. The movements of the nares are also suspended on the side of the injury, and if the angle of the mouth be examined on that side, it will be found to hang down lower than on the opposite side, and to be constantly partly open, owing to the paralysis of the orbicularis oris and the elevators of the angle of the mouth.

These are the only inconveniences which follow the division of the facial nerve in the cat, but in some other of the lower animals, where various muscular organs in this region are particularly developed, the consequences are more troublesome. Thus, in the rabbit, the ear, upon the affected side, falls down, and cannot be raised or pointed in different directions; and as the movements of the ear are important in these animals, as aids to the hearing, the perfection of this sense must be considerably impaired by paralysis of the facial nerve. In the horse, it has been noticed by Bernard,[1] that division of the facial on both sides is fatal by suffocation. For this animal breathes exclusively through the nostrils, which open widely at the time of inspiration, to allow the admission of air. If these movements be suspended, by paralysis of the facial nerve, the nostrils immediately collapse, and the animal dies by suffocation.

In the human subject, the facial nerve is occasionally paralyzed upon one side, sometimes from sympathetic irritation, sometimes from organic disease in the petrous portion of the temporal bone, or within the cranial cavity near the origin of the nerve. In either case, an extremely well-marked affection is the result, known as

[1] Leçons sur la Physiologie et la Pathologie du Système Nerveux, Paris, 1858, vol. ii. p. 38.

"facial paralysis." This condition is chiefly characterized by an entire absence of expression on the affected side of the face. The lower eyelid sinks downward, from paralysis of the orbicularis muscle, and cannot be closed.

The corner of the mouth also falls downward, and the whole lower part of the face is drawn over to the opposite side, by the force of the antagonistic muscles. The lips are unable to retain the fluids of the mouth; and the saliva dribbles away from between them, giving to that side of the face a remarkably vacant and helpless appearance.

The principal inconvenience, however, suffered by the human subject in facial paralysis, depends upon the want of action of the muscles about the lips and cheek. In drinking, the fluids escape by the corner of the mouth, and in mastication the food has partly a tendency to escape by the same opening, and partly accumulates, on the affected side, between the gums and the cheek, owing to the paralysis of the buccinator muscle, which receives its motor filaments from the facial nerve. Thus, the action of all the superficial facial muscles is suspended, the expression of the face is destroyed, and the movements of the lips and the prehension of the food seriously interfered with.

Though the facial, however, be essentially a motor nerve, yet its principal branches distributed to the face have a certain degree of sensibility; that is, when these branches are irritated in the middle of their course, the animal immediately gives evidence of a painful sensation. Longet has shown, by an extremely ingenious mode of experiment,[1] that this sensibility of the branches of the facial does not depend on any sensitive fibres of their own, but upon those which they derive *from inosculation with the fifth pair.* He exposes, for example, the facial nerve in the dog, and, irritating its principal branches one after the other, at each application of the irritant there are evident signs of pain. He then divides the facial nerve at its point of exit from the stylo-mastoid foramen, and finds that, after this operation, the sensibility of its branches still remains. The fibres, accordingly, upon which this sensibility depends, do not pass out with the trunk of the nerve, but are derived from some other source. The experimenter, then, upon another animal, divides the fifth pair within the skull, leaving the facial untouched; and afterward, on irritating as before the ex-

[1] Traité de Physiologie, vol. ii. pp. 354–357.

posed branches of the latter nerve, he finds that its sensibility has entirely disappeared. It is by filaments, accordingly, derived from the fifth pair, that a certain degree of sensibility is communicated to the branches of the facial.

These facts account for the peculiar circumstance that, in cases of tic douloureux, the spasmodic pain sometimes follows exactly the course of the facial nerve, viz: from behind the ear forward upon the side of the face; and yet the section of this nerve does not put an end to the neuralgia, but only causes paralysis of the facial muscles.

GLOSSO-PHARYNGEAL.—This nerve originates from the gray matter of the upper and posterior portion of the medulla oblongata, emerges from the side of the medulla, and enters the posterior foramen lacerum in company with the pneumogastric and spinal accessory. While in the jugular fossa it presents a gangliform enlargement, called the ganglion of Andersch, below the level of which it receives branches of communication from the facial and the spinal accessory. It then runs downward and forward, and is distributed to the mucous membrane of the base of the tongue, pillars of the fauces, soft palate, middle ear, and upper part of the pharynx. It also sends some branches to the constrictors of the pharynx and the neighboring muscles. Longet has found this nerve at its origin to be exclusively sensitive; but below the level of its ganglion it has been found by him, as well as by various other observers, to be both sensitive and motor, owing to the fibres of communication received from the motor nerves mentioned above. Its final distribution is, however, as we have seen, principally to sensitive surfaces. The principal office of this nerve is to impart the sense of taste to the posterior third of the tongue, to which it is distributed. It also presides over the general sensibility of this part of the tongue, as well as that of the fauces and pharynx.

Dr. John Reid,[1] who has performed a great variety of experiments upon this nerve, comes to the following conclusions in regard to it. First, that it is essentially a sensitive nerve, since there are unequivocal signs of pain when it is pricked, pinched, or cut. Second, that irritation of this nerve produces convulsive movements of the throat and lower part of the face; but that these movements are, in great measure, not direct, but reflex in their character, since they

[1] In Todd's Cyclopædia of Anatomy and Physiology, article *Glosso-pharyngeal Nerve.*

will take place equally well after the glosso-pharyngeal has been divided, if the irritation be applied to its cranial extremity. Third, that this nerve supplies the special sensibility of taste to a portion of the tongue; but that it is not the *exclusive* nerve of this sense, since the power of taste remains, after it has been divided on both sides.

There are certain reflex actions, furthermore, which take place through the medium of the glosso-pharyngeal nerve. After the food has been thoroughly masticated, it is carried, by the movements of the tongue and sides of the mouth, through the fauces, and brought in contact with the mucous membrane of the pharynx. This produces an impression which, conveyed to the medulla oblongata by the filaments of the glosso-pharyngeal, excites the muscles of the fauces and pharynx by reflex action. The food is consequently grasped by these muscles, without the concurrence of the will, and the process of deglutition is commenced. This action is not only involuntary, but it will frequently take place even in opposition to the will. The food, once past the isthmus of the fauces, is beyond the control of volition, and cannot be returned except by convulsive action, equally involuntary in its character.

Natural stimulants, therefore, applied to the mucous membrane of the pharynx, excite deglutition; unnatural stimulants, applied to the same part, excite vomiting. If the finger be introduced into the fauces and pharynx, or if the mucous membrane of these parts be irritated by prolonged tickling with the end of a feather, the sensation of nausea, conveyed through the glosso-pharyngeal nerve, is sometimes so great as to produce immediate and copious vomiting. This method may often be successfully employed in cases of poisoning, when it is desirable to excite vomiting rapidly, and when emetic medicines are not at hand.

Pneumogastric.—Owing to the numerous connections of the pneumogastric with other nerves, its varied and extensive distribution, and the important character of its functions, this is properly regarded as one of the most remarkable nerves in the whole body. Owing to the wandering course of its fibres, which are distributed to no less than four different vital organs, viz., the heart, lungs, stomach and liver, as well as to several other parts of secondary importance, it has been often known by the name of the *par vagum*. The pneumogastric arises from a collection of gray matter in the posterior and middle portions of the medulla oblongata, already

spoken of as the "nucleus" of the pneumogastric nerve. It emerges, by a number of separate filaments, from the lateral portion of the medulla, in the groove between the olivary and restiform bodies. These filaments unite into a single trunk, which passes out of the cranium through the jugular canal, where it is provided with a ganglionic swelling, the "jugular ganglion of the pneumogastric nerve." Immediately below the level of this ganglion the nerve receives an important branch of communication from the spinal accessory, and afterward from the facial, the hypoglossal, and the anterior branches of the first and second cervicals.

Fig. 163.

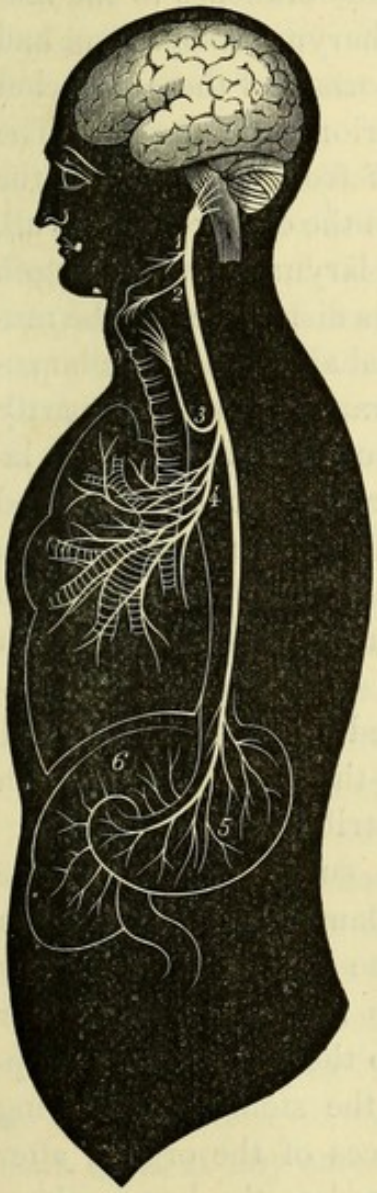


Diagram of PNEUMOGASTRIC NERVE, with its principal branches. —1. Pharyngeal branch. 2. Superior laryngeal. 3. Inferior laryngeal. 4. Pulmonary branches. 5. Stomach. 6. Liver.

According to the results obtained by Longet, whose experiments appear to be the most conclusive on this point, the pneumogastric is, at its origin, exclusively a sensitive nerve. Galvanic irritation applied to the roots of the nerve, when carefully separated from the medulla and from all adjacent filaments, is not found to produce any muscular contractions; but if the stimulus be applied to the trunk of the nerve, below the level of the jugular ganglion, muscular contractions are excited, owing to the motor filaments which have already joined it from the above-mentioned sources. The pneumogastric therefore becomes, after emerging from the cranial cavity, a mixed nerve; and has accordingly, in nearly all its branches, a double distribution, viz., to the mucous membranes and the muscular coat of the organs to which it belongs.

The ordinary sensibility of the pneumogastric nerve, however, as all experimenters have observed, is exceedingly dull, in comparison with that of the other sensitive cranial nerves. We have often divided this nerve in the middle of the neck, without any distinct manifestation of pain being

given by the animal; and though Bernard has found that at some times its sensibility is well marked, while at others it is very indistinct, he is not able to say upon what special physiological conditions this difference depends. While the pneumogastric, however, is decidedly deficient, as a general rule, in ordinary sensibility, it possesses, as we shall see hereafter, a sensibility of a peculiar kind, which is exceedingly important for the maintenance of the vital functions.

In passing down the neck, this nerve sends branches to the mucous membrane and muscular coat of the pharynx, œsophagus, and respiratory passages. Among the most important of these branches are the two laryngeal nerves, viz., the superior and inferior. The superior laryngeal nerve, which is given off from the trunk of the pneumogastric just after it has emerged from the cavity of the skull, passes downward and forward, penetrates the larynx by an opening in the side of the thyro-hyoid membrane, and is distributed to the mucous membrane of the larynx and glottis, and also to a single laryngeal muscle, viz., the crico-thyroid. This branch is therefore partly muscular, but mostly sensitive in its distribution. The inferior laryngeal branch is given off just after the pneumogastric has entered the cavity of the chest. It curves round the subclavian artery on the right side and the arch of the aorta on the left, and ascends in the groove between the trachea and œsophagus, to the larynx. It then enters the larynx between the cricoid cartilage and the posterior edge of the thyroid, and is distributed to all the muscles of the larynx, with the exception of the crico-thyroid. This branch is, therefore, exclusively muscular in its distribution.

The trunk of the pneumogastric, after supplying the above branches, as well as sending numerous filaments to the trachea and œsophagus in the neck, gives off in the chest its pulmonary branches, which follow the bronchial tubes in the lungs to their minutest ramifications. It then passes into the abdomen and supplies the muscular and mucous layers of the stomach, ramifying over both the anterior and posterior surfaces of the organ; after which its fibres spread out and are distributed to the liver, spleen, pancreas, and gall-bladder.

The functions of the pneumogastric will now be successively studied in the various organs to which it is distributed.

Pharynx and Œsophagus.—The reflex act of deglutition, which has already been described as commencing in the upper part of the pharynx, by means of the glosso-pharyngeal, is continued in the

lower portion of the pharynx and throughout the œsophagus by the aid of the pneumogastric. As the food is compressed by the superior constrictor muscle of the pharynx and forced downward, it excites the mucous membrane with which it is brought in contact and gives rise to another contraction of the middle constrictor. The lower constrictor is then brought into action in its turn in a similar manner; and a wave-like or peristaltic contraction is thence propagated throughout the entire length of the œsophagus, by which the food is carried rapidly from above downward, and conducted at last to the stomach. Each successive portion of the mucous membrane, in this instance, receives in turn the stimulus of the food, and excites instantly its own muscles to contraction; so that the food passes rapidly from one end of the œsophagus to the other, by an action which is wholly reflex in character and entirely withdrawn from the control of the will. Section of the pneumogastric, or of its pharyngeal and œsophageal branches, destroys therefore at the same time the sensibility and the motive power of these parts. The food is no longer conveyed readily to the stomach, but accumulates in the paralyzed œsophagus, into which it is forced by the voluntary movements of the mouth and fauces, and by the continued action of the upper part of the pharynx.

It must be remembered that the general sensibility of the œsophagus is very slight, as compared with that of the integument, or even of the mucous membranes near the exterior. It is a general rule, in fact, that the sensibility of the mucous membranes is most acute at the external orifices of their canals; as, for example, at the lips, anterior nares, anus, orifice of the urethra, &c. It diminishes constantly from without inward, and disappears altogether at a certain distance from the surface. The sensibility of the pharynx is less acute than that of the mouth, but is still sufficient to enable us to perceive the contact of ordinary substances; while in the œsophagus we are not usually sensible of the impression of the food as it passes from above downward. The reflex action takes place here without any assistance from the consciousness; and it is only when substances of an unusually pungent or irritating nature are mingled with the food, that its passage through the œsophagus produces a distinct sensation.

Larynx.—We have already described the course and distribution of the two laryngeal branches of the pneumogastric. The superior laryngeal nerve is principally the sensitive nerve of the larynx. Its division destroys sensibility in the mucous membrane of this

organ, but paralyzes only one of its muscles, viz: the crico-thyroid. Galvanization of this nerve has also been found to induce contractions in the crico-thyroid, but in none of the other muscles belonging to the larynx. The inferior laryngeal, on the other hand, is a motor nerve. Its division paralyzes all the muscles of the larynx except the crico-thyroid; and irritation of its divided extremity produces contraction in the same muscles. The muscles and mucous membrane of the larynx are therefore supplied by two different branches of the same trunk, viz., the superior laryngeal nerve for the mucous membrane, and the inferior laryngeal nerve for the muscles.

The larynx, in man and in all the higher animals, performs a double function; one part of which is connected with the voice, the other with respiration.

The formation of the *voice* in the larynx takes place as follows. If the glottis be exposed in the living animal, by opening the pharynx and œsophagus on one side, and turning the larynx forward, it will be seen that so long as the vocal chords preserve their usual relaxed condition during expiration, no sound is heard, except the ordinary faint whisper of the air passing gently through the cavity of the larynx. When a vocal sound, however, is to be produced, the chords are suddenly made tense and applied closely to each other, so as to diminish very considerably the size of the orifice; and the air, driven by an unusually forcible expiration through the narrow opening of the glottis, in passing between the vibrating vocal chords, is itself thrown into vibrations which produce the sound required. The tone, pitch, and intensity of this sound, vary with the conformation of the larynx, the degree of tension and approximation of the vocal chords, and the force of the expiratory effort. The narrower the opening of the glottis, and the greater the tension of the chords, under ordinary circumstances, the more acute the sound; while a wider opening and a less degree of tension produce a graver note. The quality of the sound is also modified by the length of the column of air included between the glottis and the mouth, the tense or relaxed condition of the walls of the pharynx and fauces, and the state of dryness or moisture of the mucous membrane lining the aerial passages.

Articulation, on the other hand, or the division of the vocal sound into vowels and consonants, is accomplished entirely by the lips, tongue, teeth, and fauces. These organs, however, are under the

control of other nerves, and the mechanism of their action need not occupy us here.

Since the production of a vocal sound, therefore, depends upon the tension and position of the vocal chords, as determined by the action of the laryngeal muscles, it is not surprising that division of the inferior laryngeal nerves, by paralyzing these muscles, should produce a loss of voice. It has been sometimes found that in very young animals the crico-thyroid muscles, which are the only ones not affected by division of the inferior laryngeal nerves, are still sufficient to give some degree of tension to the vocal chords, and to produce in this way an imperfect sound; but usually the voice is entirely lost after such an operation.

It is a very remarkable fact, however, in this connection, that all the motor filaments of the pneumogastric, which are concerned in the formation of the voice, are derived from a single source. It will be remembered that the pneumogastric, itself originally a sensitive nerve, receives motor filaments, on leaving the cranial cavity, from no less than five different nerves. Of these filaments, however, those coming from the spinal accessory are the only ones necessary to the production of vocal sounds. For it has been found by Bischoff and by Bernard[1] that if all the roots of the spinal accessory be divided at their origin, or if the nerve itself be torn away at its exit from the skull, all the other cranial nerves remaining untouched, the voice is lost as completely as if the inferior laryngeal itself had been destroyed. All the motor fibres of the pneumogastric, therefore, which act in the formation of the voice are derived, by inosculation, from the spinal accessory nerve.

In *respiration*, again, the larynx performs another and still more important function. In the first place, it stands as a sort of guard, or sentinel, at the entrance of the respiratory passages, to prevent the intrusion of foreign substances. If a crumb of bread accidentally fall within the aryteno-epiglottidean folds, or upon the edges of the vocal chords, or upon the posterior surface of the epiglottis, the sensibility of these parts immediately excites a violent expulsive cough, by which the foreign body is dislodged. The impression received and conveyed inward by the sensitive fibres of the superior laryngeal nerve, is reflected back upon the expiratory muscles of the chest and abdomen, by which the instinctive movements of coughing are accomplished. Touching the above parts with the point of a needle, or pinching them with the blades of a forceps,

[1] Recherches Expérimentales sur les fonctions du nerf spinal. Paris, 1851.

will produce the same effect. This reaction is essentially dependent on the sensibility of the laryngeal mucous membrane; and it can no longer be produced after section of the pneumogastric nerve, or of its superior laryngeal branch.

In the second place, the *respiratory movements of the glottis*, already described in a previous chapter, are of the greatest importance to the preservation of life. We have seen that at the moment of inspiration the vocal chords are separated from each other, and the glottis opened, by the action of the posterior crico-arytenoid muscles; and that in expiration the muscles and the vocal chords are both relaxed, and the air allowed to pass out readily through the glottis. The opening of the glottis in inspiration, therefore, is an active movement, while its partial closure or collapse in expiration is a passive one. Furthermore, the opening of the glottis in inspiration is necessary in order to afford a sufficiently wide passage for the air, in its way to the trachea, bronchi, and pulmonary vesicles.

Now we have found, as Budge and Longet had previously noticed, that if the inferior laryngeal nerve on the right side be divided while the glottis is exposed as above, the respiratory movements of the right vocal chord instantly cease, owing to the paralysis of the posterior crico-arytenoid muscle on that side. If the inferior laryngeal nerve on the left side be also divided, the paralysis of the glottis is then complete, and its respiratory movements cease altogether. A serious difficulty in respiration is the immediate consequence of this operation. For the vocal chords, being no longer stretched and separated from each other at the moment of inspiration, but remaining lax and flexible, act as a double valve, and are pressed inward by the column of inspired air; thus partially blocking up the passage and impeding the access of air to the lungs. If the pneumogastrics be divided in the middle of the neck, the larynx is of course paralyzed precisely as after section of the inferior laryngeal nerves, since these nerves are given off only after the main trunks have entered the cavity of the chest. The immediate effect of either of these operations is to produce a difficulty of inspiration, accompanied by a peculiar wheezing or *sucking* noise, evidently produced in the larynx and dependent on the falling together of the vocal chords. In very young animals, as, for example, in pups a few days old, in whom the glottis is smaller and the larynx less rigid than in adult dogs, this difficulty is much more strongly marked. Legallois[1] has even seen a pup

[1] In Longet's Traité de Physiologie, vol. ii. p. 324.

two days old almost instantly suffocated after section of the two inferior laryngeal nerves. We have found that, in pups two weeks old, division of the inferior laryngeals is followed by death at the end of from thirty to forty hours, evidently from impeded respiration.

The importance, therefore, of these movements of the glottis in respiration becomes very evident. They are, in fact, part and parcel of the general respiratory movements, and are necessary to a due performance of the function. It has been found, moreover, that the motor filaments concerned in this action are not derived, like those of the voice, from a single source. While the vocal movements of the larynx are arrested, as mentioned above, by division of the spinal accessory alone, those of respiration still go on; and in order to put a stop to the latter, either the pneumogastrics themselves must be divided, or all five of the motor nerves from which their accessory filaments are derived. This fact has been noticed by Longet as showing that nature multiplies the safeguards of a function in proportion to its importance; for while the spinal accessory, or any other one of the above-mentioned nerves, might be affected by local accident or disease, it would be very improbable that any single injury should paralyze simultaneously the spinal accessory, the facial, the hypoglossal, and the first and second cervicals. The respiratory movements of the larynx are consequently much more thoroughly protected than those which are merely concerned in the formation of the voice.

Lungs.—The influence of the pneumogastric upon the function of the lungs is exceedingly important. The nerve acts here, as in most other organs to which it is distributed, in a double or mixed capacity; but it is principally as the sensitive nerve of the lungs that it has thus far received attention. It is this nerve which conveys from the lungs to the medulla oblongata that peculiar impression known as the *demand for breath*, which excites by reflex action the diaphragm and intercostal muscles, and keeps up the play of the respiratory movements. As we have already shown, this action is an involuntary one, and will even take place when consciousness is entirely suspended. It may indeed be arrested for a time by an effort of the will; but the impression conveyed to the medulla soon becomes so strong, and the stimulus to inspiration so urgent, that they can no longer be resisted, and the muscles contract in spite of our attempts to restrain them.

A very remarkable effect is accordingly produced on respiration

by simultaneous division of both pneumogastric nerves. This experiment is best performed on adult dogs, which may be etherized, and the nerves exposed while the animal is in a condition of insensibility, avoiding, in this way, the disturbance of respiration, which would follow if the dissection were performed while the animal was conscious and sensible to pain. After the effects of the etherization have entirely passed off, and respiration and circulation have both returned to a quiescent condition, the two nerves, which have been previously exposed and secured by a loose ligature, may be instantaneously divided, and the effects of the operation readily appreciated.

Immediately after the division of the nerves, when performed in the above manner, the respiration is hurried and difficult, owing to the sudden paralysis of the larynx and partial closure of the glottis by the vocal chords, as already described. This condition, however, is of short continuance. In a few moments, the difficulty of breathing and the general agitation subside, the animal becomes perfectly quiet, and the only remaining visible effect of the operation is *a diminished frequency in the movements of respiration.* This diminution is frequently strongly marked from the first, the number of respirations falling at once to ten or fifteen per minute, and becoming, in an hour or two, still farther reduced. The respirations are performed easily and quietly; and the animal, if left undisturbed, remains usually crouched in a corner, without giving any special signs of discomfort. If he be aroused and compelled to move about, the frequency of the respiration is temporarily augmented; but as soon as he is again quiet, it returns to its former standard. By the second or third day, the number of respirations is often reduced to five, four, or even three per minute; when this is the case, the animal usually appears very sluggish, and is roused with difficulty from his inactive condition. At this time the respiration is not only diminished in frequency, but is also performed in a peculiar manner. The movement of inspiration is slow, easy, and silent, occupying several seconds in its accomplishment; expiration, on the contrary, is sudden and audible, and is accompanied by a well marked expulsive effort, which has the appearance of being, to a certain extent, voluntary in character. The intercostal spaces also sink inward during the lifting of the ribs; and the whole movement of respiration has an appearance of insufficiency, as if the lungs were not thoroughly filled with air. This insufficiency of respira-

tion is undoubtedly owing to a peculiar alteration in the pulmonary texture, which has by this time already commenced.

Death takes place at a period varying from one to six days after the operation, according to the age and strength of the animal. The only symptoms accompanying it are a steady failure of the respiration, with increased sluggishness and indisposition to be aroused. There are no convulsions, nor any evidences of pain. After death the lungs are found in a peculiar state of solidification, which is almost exclusively a consequence of this operation, and which is entirely different from ordinary inflammatory hepatization. They are not swollen, but rather smaller than natural. They are of a dark purple color, leathery and resisting to the feel, destitute of crepitation, and infiltrated with blood. Pieces of the lung cut out sink in water. The pleural surfaces, at the same time, are bright and polished, and their cavity contains no effusion or exudation. The lungs, in a word, are simply engorged with blood and empty of air; their tissue having undergone no other alteration.

These changes are not generally uniform over both lungs. The organs are usually mottled on their exterior; the variations in color corresponding with the different degrees of alteration exhibited by different parts.

The explanation usually adopted of the above consequences following division of the pneumogastrics is as follows: The nerves being divided, the impression which originates in the lungs from the accumulation of carbonic acid, and which is destined to excite the respiratory movements by reflex action, can no longer be transmitted to the medulla oblongata. The natural stimulus to respiration being wanting, it is, accordingly, less perfectly performed. The respiratory movements diminish in frequency, and, growing continually slower and slower, finally cease altogether, and death is the result.

The above explanation, however, is not altogether sufficient. It accounts very well for the diminished frequency of respiration, but not for its partial continuance. For if the pneumogastric nerves be really the channel through which the stimulus to respiration is conveyed to the medulla, the difficulty is not to understand why respiration should be retarded after division of these nerves, but why it should continue at all. In point of fact, the respiratory movements, though diminished in frequency, continue often for some days after this operation. This cannot be owing to force of habit, or to any remains of nervous influence, as has been some-

times suggested, since, when the medulla itself is destroyed, respiration, as we know, stops instantaneously, and no attempt at movement is made after the action of the nervous centre is suspended.

It is evident, therefore, that the pneumogastric nerve, though the chief agent by which the respiratory stimulus is conveyed to the medulla, is not the only one. The lungs are undoubtedly the organs which are most sensitive to an accumulation of carbonic acid, and an imperfect arterialization of the blood; and the sensation which results from such an accumulation is accordingly first felt in them. There is reason to believe, however, that all the vascular organs are more or less capable of originating this impression, and that all the sensitive nerves are capable, to some extent, of transmitting it. Although the first disagreeable sensation, on holding the breath, makes itself felt in the lungs, yet, if we persist in suspending the respiration, we soon become conscious that the feeling of discomfort spreads to other parts; and at last, when the accumulation of carbonic acid and the impurity of the blood have become excessive, all parts of the body suffer alike, and are pervaded by a general feeling of derangement and distress. It is easy, therefore, to understand why respiration should be retarded, after section of the pneumogastrics, since the chief source of the stimulus to respiration is cut off; but the movements still go on, though more slowly than before, because the other sensitive nerves, which continue to act, are also capable, in an imperfect manner, of conveying the same impression.

The immediate cause of death, after this operation, is no doubt the altered condition of the lungs. These organs are evidently very imperfectly filled with air, for some time previous to death; and their condition, as shown in *post-mortem* examination, is evidently incompatible with a due performance of the respiratory function. It is not at all certain, however, that these alterations in the pulmonary tissue are directly dependent on division of the pneumogastric nerves. It must be recollected that when the section of the pneumogastrics is performed in the middle of the neck, the filaments of the inferior laryngeal nerves are also divided, and the narrowing of the glottis, produced by their paralysis, must necessarily interfere with the free admission of air into the chest. This difficulty, either alone or combined with the diminished frequency of respiration, must have a very considerable effect in impeding the pulmonary circulation, and bringing the lungs into such a condition as unfits them for maintaining life.

In order to ascertain the comparative influence upon the lungs of division of the inferior laryngeals and that of the other filaments of the pneumogastrics, we have resorted to the following experiment.

Two pups were taken, belonging to the same litter and of the same size and vigor, about two weeks old. In one of them (No. 1) the pneumogastrics were divided in the middle of the neck; and in the other (No. 2) a section was made at the same time of the inferior laryngeals, the trunk of the pneumogastrics being left untouched. For the first few seconds after the operation, there was but little difference in the condition of the two animals. There was the same obstruction of the breath (owing to closure of the glottis), the same gasping and *sucking* inspiration, and the same frothing at the mouth. Very soon, however, in pup No. 1, the respiratory movements became quiescent, and at the same time much reduced in frequency, falling to ten, eight, and five respirations per minute, as usual after section of the pneumogastrics; while in No. 2 the respiration continued frequent as well as laborious, and the general signs of agitation and discomfort were kept up for one or two hours The animal, however, after that time became exhausted, cool, and partially insensible, like the other. They both died, between thirty and forty hours after the operation. On *post-mortem* inspection it was found that the peculiar congestion and solidification of the lungs, considered as characteristic of division of the pneumogastrics, existed to a similar extent in each instance; and the only appreciable difference between the two bodies was that in No. 1 the blood was coagulated, and the abdominal organs natural, while in No. 2 the blood was fluid and the abdominal organs congested. We are led, accordingly, to the following conclusions with regard to the effect produced by division of this nerve.

1. After section of the pneumogastrics, death takes place by a peculiar congestion of the lungs.
2. This congestion is not directly produced by division of the nerves, but is caused by the imperfect admission of air into the chest.

In adult dogs, the closure of the glottis from paralysis of the laryngeal muscles is less complete than in pups; but it is still sufficient to exert a very decided influence on respiration, and to take an active part in the production of the subsequent morbid phenomena.

We therefore regard the death which takes place after division

of both pneumogastric nerves, as produced in the following manner:—

The glottis is first narrowed by paralysis of the laryngeal muscles, and an imperfect supply of air is consequently admitted, by each inspiration, into the trachea. Next, the stimulus to respiration being very much diminished, the respiratory movements take place less frequently than usual. From these two causes combined, the blood is imperfectly arterialized. But the usual consequence of such a condition, viz., an increased rapidity of the respiratory movements, does not follow. The imperfect arterialization of the blood does not excite the respiratory muscles to increased activity as it would do in health, owing to the division of the pneumogastrics. At the same time, the accumulation of carbonic acid in the blood and in the tissues begins to exert a narcotic effect, diminishing the sensibility of the nervous centres, and tending to retard still more the movements of respiration. Thus all these causes react upon and aggravate each other; because the connection, naturally existing between imperfectly arterialized blood and the stimulus to respiration, is now destroyed. The narcotism and pulmonary engorgement, therefore, continue to increase, until the lungs are so seriously altered and engorged that they are no longer capable of transmitting the blood, and circulation and respiration come to an end at the same time.

It must be remembered, also, that the pneumogastric nerve has other important distributions, beside those to the larynx and the lungs; and the effect produced by its division upon these other organs has no doubt a certain share in producing the results which follow. Bearing in mind the very extensive distribution of the pneumogastric nerve and the complicated character of its functions, we may conclude that after section of this nerve death takes place from a combination of various causes; the most active of which is a peculiar engorgement of the lungs and imperfect performance of the respiratory function.

Stomach, and Digestive Function.—After division of the pneumogastric nerves, the sensations of hunger and thirst remain, and the secretion of gastric juice continues. Nevertheless the digestive function is disturbed in various ways, though not altogether abolished. The appetite is more or less diminished, as it would be after any serious operation, but it remains sufficiently active to show that its existence is not directly dependent on the integrity of the pneumogastric nerve. Digestion, however, very seldom takes

place, to any considerable extent, owing to the following circumstances: The animal is frequently seen to take food and drink with considerable avidity; but in a few moments afterward the food and drink are suddenly rejected by a peculiar kind of regurgitation. This regurgitation does not resemble the act of vomiting, but the substances swallowed are again discharged so easily and instantaneously as to lead to the belief that they had never passed into the stomach. Such, indeed, is actually the case, as any one may convince himself by watching the process, which is often repeated by the animal at short intervals. The food and drink, taken voluntarily, pass down into the œsophagus, but owing to the paralysis of the muscular fibres of this canal, are not conveyed into the stomach. They accumulate consequently in the lower and middle part of the œsophagus; and in a few moments are rejected by a sudden antistaltic action of the parts, excited, apparently, through the influence of the great sympathetic.

The muscular coat of the stomach is also paralyzed to a considerable extent by section of this nerve. Longet has shown, by introducing food artificially into the stomach, that gastric juice may be secreted and the food be actually digested and disappear, when introduced in small quantity. But when introduced in large quantity, it remains undigested, and is found after death, with the exterior of the mass softened and permeated by gastric juice, while the central portions are unaltered, and do not even seem to have come in contact with the digestive fluid. This is undoubtedly owing both to the diminished sensibility of the mucous membrane of the stomach, and to the paralysis of its muscular fibres. The peristaltic action of the organ is very important in digestion, in order to bring successive portions of the food in contact with its mucous membrane, and to carry away such as are already softened or as are not capable of being digested in the stomach. This constant movement and agitation of the food is probably also one great stimulus to the continued secretion of the gastric juice. The digestive fluid will therefore be deficient in quantity after division of the pneumogastric nerve, at the same time that the peristaltic movements of the stomach are suspended. Under these circumstances, the secretion of gastric juice may be sufficient to permeate and digest small quantities of food, while a larger mass may resist its action, and remain undigested. The effect produced by division of these nerves on the digestive, as on the respiratory organs, is therefore of a complicated character, and results from the combined

action of several different causes, which influence and modify each other.

The effect produced upon the *liver* by section of the pneumogastrics, as well as the influence usually exerted by these nerves upon the hepatic functions, has been so little studied that nothing definite has been ascertained in regard to it. We shall therefore pass over this portion of the subject in silence.

Spinal Accessory.—This nerve originates, by many filaments, from the side of the medulla oblongata, immediately below the level of the pneumogastric, and also from the lateral column of the spinal cord, between the anterior and posterior roots of the upper five or six cervical nerves. The nerve has, accordingly, two sets of root-fibres, viz., the *spinal* roots, or those originating from the lateral portion of the spinal cord; and the *medullary* roots, or those originating from the medulla oblongata. The fibres of spinal origin pass upward, uniting into a slender rounded filament, which enters the cavity of the cranium by the foramen magnum, and is then joined by the fibres which originate from the medulla oblongata. The spinal accessory nerve, thus constituted, passes out from the cavity of the skull by the posterior foramen lacerum, in company with the glosso-pharyngeal and pneumogastric nerves. Immediately afterward it divides into two principal branches: First, the *internal* or *anastomotic* branch, which joins the pneumogastric nerve, and becomes mingled with its fibres; and, secondly, the *external* or *muscular* branch, which passes downward and outward, and is distributed to the sterno-mastoid and trapezius muscles. The internal or anastomotic branch, as has been well shown by Bernard,[1] is composed exclusively of the medullary roots of the nerve, while the external or muscular branch consists altogether of the fibres originating from the spinal cord.

The spinal accessory is essentially a motor nerve. It has been found, both by Bernard and Longet, to be insensible at its origin, like the anterior roots of the spinal nerves; but if irritated after its exit from the skull, it gives signs of sensibility. This sensibility it acquires from the filaments of inosculation which it receives from the anterior branches of the first, second, and third cervical nerves. Though its external branch, accordingly, is exclusively distributed to muscles, as we have already seen, this branch contains some sensitive fibres, which have the same destination. The reason for this

[1] Recherches Expérimentales sur les Fonctions du Nerf Spinal. Paris, 1851

anatomical fact, viz., that motor nerves are supplied during their course with sensitive fibres, becomes evident when we reflect that the muscles themselves possess a certain degree of sensibility, though less acute than that which belongs to the skin. The sensibility of the muscles is undoubtedly essential to the perfect performance of their function; and as the motor nerves are incapable, by themselves, of transmitting sensitive impressions, they are joined, soon after their origin, by other filaments which communicate to them this necessary power.

The most important result which has been obtained by experiment upon the spinal accessory nerve, is that its internal or anastomotic branch is *directly connected with the vocal movements of the glottis.* It has been found by Bischoff, by Longet, and by Bernard, that if the spinal accessory nerves on both sides, or their branches of inosculation with the pneumogastric, be divided or lacerated, the pneumogastric nerves themselves being left entire, the voice is instantly lost, and the animal becomes incapable of making a vocal sound. We have also found this result to follow, in the cat, after the spinal accessory nerves have been torn out by their roots, through the jugular foramen. The animal, after this operation, can no longer make an audible sound. At the same time the respiratory movements of the glottis go on undisturbed, and most of the other animal functions remain unaffected.

The fibres of communication, therefore, derived from the spinal accessory, pass to the pneumogastric nerve and become entangled with its other filaments, so that they can no longer be traced by anatomical dissection. They pass downward, however, and become a part of the motor fibres of the inferior laryngeal or recurrent branches of the pneumogastric; being finally distributed to the muscles of the larynx, which they supply with those nervous influences which are required for the formation of the voice.

The special function of the external or muscular branch of the spinal accessory is not so fully understood. This branch, as we have seen, is distributed to the sterno-mastoid and trapezius muscles. But these muscles also receive filaments from the cervical spinal nerves; and, accordingly, they still retain the power of motion, to a certain degree, after the external branches of the spinal accessory have been divided on both sides.

The spinal accessory is, accordingly, a nerve of very peculiar distribution. For it partly supplies motor fibres to the pneumogastric nerve, and is partly distributed to two muscles, both of

which also receive motor nerves from another source. Sir Charles Bell, noticing the close connection between this nerve and the pneumogastric, regarded the two as associated also in their function, as nerves of respiration. He considered, therefore, the external branch of the spinal accessory as destined to assist in the movements of respiration, when these movements become unusually laborious, by bringing into play the sterno-mastoid and trapezius muscles, in aid of the action of the intercostals. He therefore called this nerve the "superior respiratory nerve."

But the most satisfactory explanation of this peculiarity is that proposed by M. Bernard. According to this explanation, whenever a muscle, or set of muscles, derive their nervous influence from two different sources, this is not for the purpose of assisting them in the performance of the same function, but of enabling them to perform *two different functions*. We have seen this already exemplified in the muscles of the larynx. For these muscles perform certain movements of respiration for which they receive indirectly filaments from the facial, hypoglossal, and cervical nerves. But they also perform the movements necessary to the formation of the voice, the nervous stimulus for which is derived altogether from the spinal accessory.

The internal branch of the spinal accessory, accordingly, excites, in the parts to which it is distributed a function which is incompatible with respiration. For the movements of respiration cannot go on while the voice is sounded; and a necessary preliminary to the production of a vocal sound, is the temporary stoppage of respiration. The movements of respiration, therefore, and the movements of the voice alternate with each other, but are never simultaneous; so that the internal branch of the spinal accessory is antagonistic to the motor fibres of the larynx derived from other nerves.

It is thought by M. Bernard, that the fibres of the external branch of the spinal accessory have also a function which is antagonistic to respiration. For respiration is naturally suspended in all steady and prolonged muscular efforts. In these efforts, such as those of straining, lifting, and the like, the movements of respiration cease, the spinal column is made rigid by the contraction of its muscles, and the head and neck are placed in a fixed position, principally by the contraction of the sterno-mastoid and trapezius muscles. The function of the spinal accessory, in both its branches, is therefore regarded as destined to excite movements which are

incompatible with those of respiration; and which accordingly come into play only when the ordinary movements of respiration have been temporarily suspended.

HYPOGLOSSAL.—The hypoglossal nerve originates from a collection of gray matter, in the medulla oblongata, which is termed the 'hypoglossal nucleus,'[1] and which is a continuation of the anterior horn of gray matter of the spinal cord. Its fibres emerge from the lower portion of the medulla, just outside the anterior pyramids, and passing through the anterior condyloid foramen, are finally distributed to the muscles of the tongue. Irritation of the nerve in any part of its course produces convulsive twitching in this organ. Its section paralyzes completely the movements of the tongue without affecting directly the sensibility of its mucous membrane. This nerve, accordingly, is the motor nerve of the tongue. If irritated at its origin, the hypoglossal nerve, according to the experiments of Longet, is entirely insensible; but if the irritation be applied in the middle of its course, signs of pain are immediately manifested. Its sensibility, like that of the facial, is consequently derived from its inosculation with other sensitive nerves, after its emergence from the skull.

[1] Dr. John Dean. Gray Substance of the Medulla, &c., p. 13.

CHAPTER VI.

THE SPECIAL SENSES.

General and Special Sensibility.—We have already seen that there exists, in the general integument, a power of sensation, by which we are made acquainted with surrounding objects and some of their most important physical qualities. By this power we feel the sensations of heat and cold, and are enabled to distinguish between hard and soft substances, rough bodies and smooth, solids and liquids. This kind of power is termed *General Sensibility*, because it resides in the general integument, and because by its aid we obtain information with regard to the simplest and most material properties of external objects.

The general sensibility, thus existing in the integument, is an endowment of the sensitive nerves derived from the cerebro-spinal system. These nerves ramify in the substance of the skin, and by subsequent inosculation form a minute plexus in the superficial portions of the tissue of the corium. From this plexus, the ultimate filaments, reduced to an exceedingly minute size, pass upward into the conical papillæ with which the free surface of the corium is covered. In the papillæ the nervous filaments terminate, sometimes by loops returning upon themselves, and sometimes apparently by free extremities. The papillæ are also supplied with looped capillary bloodvessels, and are capable of receiving an abundant vascular injection.

These papillæ appear to be the most essential organs of general sensation, since the sensibility of the skin is most acute where they are most abundant and most highly developed, as, for example, on the palm of the hand and the tips of the fingers.

The best method of measuring accurately the sensibility of different regions is that adopted by Professors Weber and Valentin. They applied the rounded points of a pair of compasses to the integument of different parts, and found that if they were held very near together they could no longer be distinguished as sepa-

rate points, but the two sensations were confounded into one. The distance, however, at which the two points failed to be distinguished from each other, was much shorter for some parts of the body than for others. Prof. Valentin's measurements,[1] which are the most varied and complete, give the following as the limits of distinct perception in various parts:—

	Paris Line.
At the tip of tongue	.483
" palmar surface of tips of fingers	.723
" " " of second phalanges	1.558
" " " of first phalanges	1.650
" dorsum of tongue	2.500
" dorsal surface of fingers	3.900
" cheek	4.541
" back of hand	6.966
" skin of throat	8.292
" dorsum of foot	12.525
" skin over sternum	15.875
" middle of back	24.208

This method cannot, of course, give the absolute measure of the *acuteness* of sensibility in the different regions, since the two points might be less easily distinguished from each other in any one region, and yet the absolute amount of sensation produced might be as great as in the surrounding parts; still it is undoubtedly a very accurate measure of the *delicacy* of tactile sensation, by which we are enabled to distinguish slight inequalities in the surface of solid bodies. We find, furthermore, that certain parts of the body are particularly well adapted to exercise the function of general sensation, not only on account of the acute sensibility of their integument, but also owing to their peculiar formation. Thus, in man, the hands are especially well formed in this respect, owing to the articulation and mobility of the fingers, by which they may be adapted to the surface of solid bodies, and brought successively in contact with all their irregularities and depressions. The hands are therefore more especially used as organs of touch, and we are thus enabled to obtain by their aid the most delicate and precise information as to the texture, consistency, and configuration, of foreign bodies.

But the hands are not the exclusive organs of touch, even in the human subject, and in some of the lower animals, the same func-

[1] In Todd's Cyclopædia of Anatomy and Physiology, vol. iv., article on Touch, by Dr. Carpenter.

tion is fully performed by various other parts of the body. Thus in the cat and in the seal, the long bristles seated upon the lips are used for this purpose, each bristle being connected at its base with a highly developed nervous papilla: in some of the monkeys the extremity of the prehensile tail, and in the elephant the end of the nose, which is developed into a flexible and sensitive proboscis, is employed as an organ of touch. This function, therefore, may be performed by either one part of the body or another, provided the accessory organs be developed in a favorable manner.

About the head and face, the sensibility of the skin is dependent mainly upon branches of the fifth pair. In the neck, trunk, and extremities it is due to the sensitive fibres of the cervical, dorsal, and lumbar spinal nerves. It exists also, to a considerable extent, in the mucous membranes of the mouth and nose, and of the passages leading from them to the interior of the body. In these situations, it depends upon the sensitive filaments of certain of the cranial nerves, viz., the fifth pair, the glosso-pharyngeal, and the pneumogastric. The sensibility of the mucous membranes is most acute in those parts supplied by branches of the fifth pair, viz., the conjunctiva, anterior part of the nares, inside of the lips and cheeks, and the anterior two-thirds of the tongue. At the base of the tongue and in the fauces, where the mucous membrane is supplied by filaments of the glosso-pharyngeal nerve, the general sensibility is less perfect; and finally it diminishes rapidly from the upper part of the œsophagus and the glottis toward the stomach and the lungs. Thus, we can appreciate the temperature and consistency of a foreign substance very readily in the mouth and fauces, but these qualities are less distinctly perceived in the œsophagus, and not at all in the stomach, unless the foreign body happen to be excessively hot or cold, or unusually hard and angular in shape. The general sensibility, which is resident in the skin and in a certain portion of the mucous membranes, diminishes in degree from without inward, and disappears altogether in those organs which are not supplied with nerves from the cerebro-spinal system.

It is particularly to be observed, however, that while the general sensibility of the skin, and of the mucous membranes above mentioned, varies in acuteness in different parts of the body, it is *everywhere the same in kind.* The tactile sensations, produced by the contact of a foreign body, are of precisely the same nature whether they be felt by the tips of the fingers, the dorsal or palmar surfaces of the hands, the lips, cheeks, or any other part of the integument.

The only difference in the sensibility of these parts lies in the degree of its development.

But there are certain other sensations which are different in kind from those perceived by the general integument, and which, owing to their peculiar and special character, are termed *special sensations*. Such are, for example, the sensation of light, the sensation of sound, the sensation of savor, and the sensation of odors. The special sensibility which enables us to feel the impressions derived from these sources is not distributed over the body, like ordinary sensibility, but is localized in distinct organs, each of which is so constituted as to receive the special sensation peculiar to it, and no other.

Thus we have, beside the general sensibility of the skin and mucous membranes, certain peculiar faculties or *special senses*, as they are called, which enable us to derive information from external objects, which we could not possibly obtain by any other means. Thus light, however intense, produces no perceptible sensation when allowed to fall upon the skin, but only when admitted to the eye. The sensation of sound is perceptible only by the ear, and that of odors only by the olfactory membrane. These different sensations, therefore, are not merely exaggerations of ordinary sensibility, but are each distinct and peculiar in their nature, and are in relation with distinct properties of external objects.

In examining the organs of special sense, we shall find that they each consist—First, of a nerve, endowed with the special sensibility required for the exercise of its peculiar function; and, Secondly, of certain accessory parts, forming an apparatus more or less complicated, which is intended to assist in its performance and render it more delicate and complete. We shall take up the consideration of the special senses in the following order. First, the sense of Taste; second, that of Smell; third, that of Sight; and fourth, that of Hearing.

TASTE.—We begin the study of the special senses with that of Taste, because this sense is less peculiar than any of the others, and differs less, both in its nature and its conditions, from the ordinary sensibility of the skin. In the first place, the organ of taste is no other than a portion of the mucous membrane, beset with vascular and nervous papillæ, similar to those of the general integument.

Secondly, it gives us impressions of such substances only as are actually in contact with sensitive surfaces, and can establish no communication with objects at a distance. Thirdly, the surfaces which exercise the sense of taste are also endowed with general sensibility; and Fourthly, there is no one special and distinct nerve of taste, but this property resides in portions of two different nerves, viz., the fifth pair and the glosso-pharyngeal; nerves which also supply general sensibility to the mouth and surrounding parts.

The sense of taste is localized in the mucous membrane of the tongue, the soft palate, and the fauces. The tongue, which is more particularly the seat of this sense, is a flattened, leaf-like, muscular organ, attached to the inner surface of the symphysis of the lower jaw in front, and to the os hyoides behind. It has a vertical sheet or lamina of fibrous tissue in the median line, which serves as a framework, and is provided with an abundance of longitudinal transverse and radiating muscular fibres, by which it can be elongated, retracted, and moved about in every direction.

The mucous membrane of the fauces and posterior third of the tongue, like that lining the cavity of the mouth, is covered with minute vascular papillæ, similar to those of the skin, which are, however, imbedded and concealed in the smooth layer of epithelium forming the surface of the organ. But about the junction of its posterior and middle thirds, there is, upon the dorsum of the tongue, a double row of rounded eminences, arranged in a V-shaped figure, running forward and outward, on each side, from the situation of the foramen cæcum; and, from this point forward, the upper surface of the organ is everywhere covered with an abundance of thickly-set, highly developed papillæ, projecting from its surface, and readily visible to the naked eye.

These lingual papillæ are naturally divided into three different sets or kinds. First, the *filiform papillæ*, which are the most numerous, and which cover most uniformly the upper surface of the organ. They are long and slender, and are covered with a somewhat horny epithelium, usually prolonged at their free extremity into a filamentous tuft. At the edges of the tongue these papillæ are often united into parallel ranges or ridges of the mucous membrane. Secondly, the *fungiform papillæ*. These are thicker and larger than the others, of a rounded club-shaped figure, and covered with soft, permeable epithelium. They are most abundant at the tip of the tongue, but may be seen elsewhere on the surface of the organ, scattered among the filiform papillæ. Thirdly, the *circum-*

vallate papillæ. These are the rounded eminences which form the V-shaped figure near the situation of the foramen cæcum. They are eight or ten in number. Each one of them is surrounded by a circular wall, or circumvallation, of mucous membrane, which gives to them their distinguishing appellation. The circumvallation, as well as the central eminence, has a structure similar to that of the fungiform papillæ.

The sensitive nerves of the tongue, as we have already seen, are two in number, viz., the lingual branch of the fifth pair, and the lingual portion of the glosso-pharyngeal. The lingual branch of the fifth pair enters the tongue at the anterior border of the hyo-glossus muscle, and its fibres then run through the muscular tissue of the organ, from below upward and from behind forward, without any ultimate distribution, until they reach the mucous membrane. The nervous filaments then penetrate into the lingual papillæ, where they finally terminate. The exact mode of their termination is not positively known. According to Kölliker, they sometimes seem to end in loops, and sometimes by free extremities.

The lingual portion of the glosso-pharyngeal nerve passes into the tongue below the posterior border of the hyo-glossus muscle. It then divides into various branches, which pass through the muscular tissue, and are finally distributed to the mucous membrane of the base and sides of the organ.

Fig. 164.

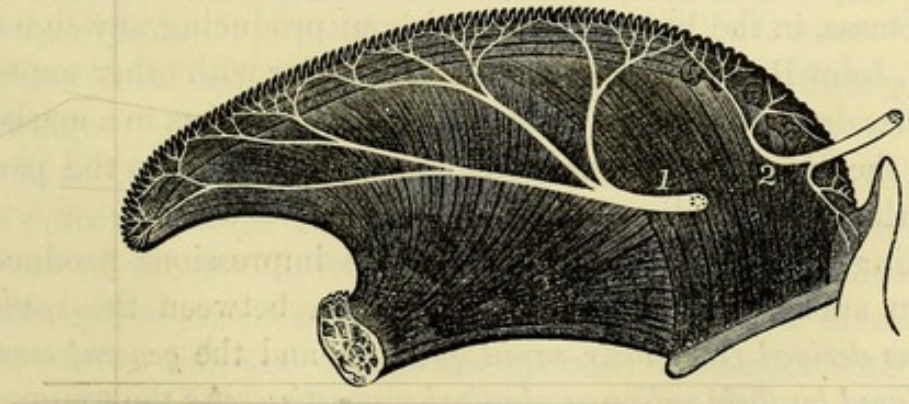


Diagram of Tongue, with its sensitive nerves and papillæ.—1. Lingual branch of fifth pair 2. Glosso-pharyngeal nerve.

The mucous membrane of the base of the tongue, of its edges, and its under surface near the tip, as well as the mucous membrane of the mouth and fauces generally, is also supplied with mucous follicles, which furnish a viscid secretion by which the free surface of the parts is lubricated.

Finally, the muscles of the tongue, it will be remembered, are animated exclusively by the filaments of the hypoglossal nerve.

The *exact seat* of the sense of taste has been determined by placing in contact with different parts of the mucous membrane a small sponge, moistened with a solution of some sweet or bitter substance. The experiments of Vernière, Longet and others have shown that the sense of taste resides in the whole superior surface, the point and edges of the tongue, the soft palate, fauces, and part of the pharynx. The base, tip, and edges of the tongue seem to possess the most acute sensibility to savors, the middle portion of its dorsum less of this sensibility, and its inferior surfaces little or none. Now as the whole anterior part of the organ is supplied by the lingual branch of the fifth pair alone, and the whole of its posterior portion by the glosso-pharyngeal, it follows that the sense of taste, in these different parts, is derived from these two different nerves.

Furthermore, the tongue is supplied, *at the same time and by the same nerves, with general sensibility and with the special sensibility of taste.* The general sensibility of the anterior portion of the tongue, and that of the branch of the fifth pair with which it is supplied, are sufficiently well known. Section of the fifth pair destroys the sensibility of this part of the tongue as well as that of the rest of the face. Longet has found that after the lingual branch of this nerve has been divided, the mucous membrane of the anterior two-thirds of the tongue may be cauterized with a hot iron or with caustic potassa, in the living animal, without producing any sign of pain. Dr. John Reid, on the other hand, together with other experimenters, has determined that ordinary sensibility exists in a marked degree in the glosso-pharyngeal, and is supplied by it to the parts to which this nerve is distributed.

Accordingly we must distinguish, in the impressions produced by foreign substances taken into the mouth, between the *special impressions derived from their sapid qualities,* and the *general sensations produced by their ordinary physical properties.* As the tongue is exceedingly sensitive to ordinary impressions, and as the same body is often capable of exciting both the tactile and gustatory functions, these two properties are sometimes liable to be confounded with each other by careless observation. The truly sapid qualities, however, the only ones, properly speaking, which we perceive by the sense of taste, are such savors as we designate by the term *sweet, bitter, salt, sour, alkaline,* and the like. But there are many

other properties, belonging to various articles of food, which belong really to the class of ordinary physical qualities and are appreciated by the ordinary sensibility of the tongue, though we usually speak of them as being perceived by the taste. Thus a *starchy, viscid, watery,* or *oleaginous* taste is merely a certain variety of consistency in the substance tasted, which may exist either alone or in connection with real savors, but which is exclusively perceived by means of the general sensibility. So also with a *pungent* or *burning* taste, such as that of red pepper or any other irritating powder. The quality of *piquancy* in the preparation of artificial kinds of food is always communicated to them by the addition of some such irritating substance. The *styptic* taste seems to be a combination of an ordinary irritant or astringent effect with a peculiar taste, which we always associate with the former quality in astringent substances.

There is also sometimes a liability to confound the real taste of certain substances with their odorous properties, or *flavors.* Thus in most aromatic articles of food, such as tea and coffee, and in various kinds of wine, a great part of what we call the taste is in reality due to the aroma, or smell which reaches the nares during the act of swallowing. Even in many solid kinds of food, such as freshly cooked meats, the odor produces a very important part of their effect on the senses. We can easily convince ourselves of this by holding the nose while swallowing such substances, or by recollecting how much a common catarrh interferes with our perception of their taste.

The most important conditions of the sense of taste are the following:—

In the first place, the sapid substance, in order that its taste may be perceived, must be brought in contact with the mucous membrane of the mouth *in a state of solution.* So long as it remains solid, however marked a savor it may possess, it gives no other impression than that of any foreign body in contact with the sensitive surfaces. But if it be applied in a liquid form, it is then spread over the surface of the mucous membrane, and its taste is immediately perceived. Thus it is only the liquid and soluble portions of our food which are tasted, such as the animal and vegetable juices and the soluble salts. Saline substances which are insoluble, such as calomel or carbonate of lead, when applied to the tongue, produce no gustatory sensation whatever.

The mechanism of the sense of taste is, therefore, in all proba-

bility, a direct and simple one. The sapid substances in solution penetrate the lingual papillæ by endosmosis, and, coming in actual contact with the terminal nervous filaments, excite their sensibility by uniting with their substance. We have already seen that the rapidity with which endosmosis will take place under certain conditions is sufficiently great to account for the almost instantaneous perception of the taste of sapid substances when introduced into the mouth.

It is on this account that a free secretion of the salivary fluids is so essential to the full performance of the gustatory function. If the mouth be dry and parched, our food seems to have lost its taste; but when the saliva is freely secreted, it is readily mixed with the food in mastication, and assists in the solution of its sapid ingredients; and the fluids of the mouth, thus impregnated with the savory substances, are absorbed by the mucous membrane, and excite the gustatory nerves. An important part, also, is taken in this process by the movements of the tongue; for by these movements the food is carried from one part of the mouth to another, pressed against the hard palate, the gums, and the cheeks, its solution assisted, and the penetration of the fluids into the substance of the papillæ more rapidly accomplished. If a little powdered sugar, or some vegetable extract be simply placed upon the dorsum of the tongue, but little effect is produced; but as soon as it is pressed by the tongue against the roof of the mouth, as naturally happens in eating or drinking, its taste is immediately perceived. This effect is easily explained; since we know how readily movement over a free surface, combined with slight friction, will facilitate the imbibition of liquid substances. The nervous papillæ of the tongue may therefore be regarded as the essential organs of the sense of taste, and the lingual muscles as its accessory organs.

The full effect of sapid substances is not obtained until they are actually swallowed. During the preliminary process of mastication a sufficient degree of impression is produced to enable us to perceive the presence of any disagreeable or injurious ingredient in the food, and to get rid of it, if we desire. But it is only when the food is carried backward into the fauces and pharynx, and is compressed by the constrictor muscles of these parts, that we obtain a complete perception of its sapid qualities. For at that time the food is spread out by the compression of the muscles, and brought at once in contact with the entire extent of the mucous membrane possessing gustative sensibility. Then, it is no longer under the control of the

will, and is carried by the reflex actions of the pharynx and œsophagus downward to the stomach.

The impressions of taste made upon the tongue *remain for a certain time afterward.* When a very sweet or very bitter substance is taken into the mouth, we retain the taste of its sapid qualities for several seconds after it has been ejected or swallowed. Consequently, if several different savors be presented to the tongue in rapid succession, we soon become unable to distinguish them, and they produce only a confused impression, made up of the union of various different sensations; for the taste of the first, remaining in the mouth, is mingled with that of the second, the taste of these two with that of the third, and so on, until so many savors become confounded together that we are no longer able to recognize either of them. Thus it is notoriously impossible to recognize two or three different kinds of wine with the eyes closed, if they be repeatedly tasted in quick succession.

If the substance first tasted have a particularly marked savor, its taste will preponderate over that of the others, and perhaps prevent our recognizing them at all. This effect is still more readily produced by substances which excite the general sensibility of the tongue, such as acrid or stimulating powders. In the same manner as a painful sensation, excited in the skin, prevents the nerves, for the time, from perceiving delicate tactile impressions, so any pungent or irritating substance, which excites unduly the general sensibility of the tongue, blunts for a time its special sensibility of taste. This effect is produced, however, in the greatest degree, by substances which are at the same time sapid, pungent and aromatic, like sweetmeats flavored with peppermint. Advantage is sometimes taken of this in the administration of disagreeable medicines. By first taking into the mouth some highly flavored and pungent substance, nauseous drugs may be swallowed immediately afterward with but little perception of their disagreeable qualities.

A very singular fact, in connection with the sense of taste, is that *it is sometimes affected in a marked degree by paralysis of the facial nerve.* No less than six cases of this kind, occurring in the human subject, have been collected by M. Bernard, and we have also met with a similar instance in which the peculiar phenomena were well marked. M. Bernard has furthermore seen a similar effect upon the taste produced in animals by division of the facial nerve within the cranium. The result of these experiments and observations is as follows: When the facial nerve is divided or seriously injured

by organic disease, before its emergence from the stylo-mastoid foramen, not only is there a paralysis of the superficial muscles of the face, but the sense of taste is diminished on the corresponding side of the tongue. If the tongue be protruded, and salt, citric acid or sulphate of quinine be placed upon its surface on the two sides of the median line, the taste of these substances is perceived on the affected side more slowly and obscurely than on the other. It is not, therefore, a destruction, but only a diminution of the sense of taste, which follows paralysis of the facial in these instances. At the same time the general tactile sensibility of the tongue is unaltered, retaining its natural acuteness on both sides of the tongue.

The exact mechanism of this peculiar influence of the facial nerve upon the sense of taste is not perfectly understood. It may be considered as certain, however, that it is derived through the medium of that branch of the facial nerve known as the *chorda tympani*. This filament leaves the facial at the intumescentia gangliformis, in the interior of the aqueduct of Fallopius, enters the cavity of the tympanum, passes across the membrane of the tympanum, and then, emerging from the cranium, runs downward and forward and joins the lingual branch of the fifth pair. It then accompanies this nerve as far as the posterior extremity of the submaxillary gland. Here it divides into two portions; one of which passes to the submaxillary ganglion, and, through it, to the substance of the submaxillary gland, while the other continues onward, still in connection with the lingual branch of the fifth pair, and, in company with the filaments of this nerve, is distributed to the tongue.

The chorda tympani thus forms the only anatomical connection between the facial nerve and the anterior part of the tongue. When the facial, accordingly, is divided or injured after its emergence from the stylo-mastoid foramen, no effect is produced upon the sense of taste; but when it is injured during its course through the aqueduct of Fallopius, and before it has given off the chorda tympani, this nerve suffers at the same time, and the sense of taste is diminished in activity, as above described. It is probable that this effect is produced in an indirect way, by a diminution in the activity of secretion in the lingual follicles, or by some alteration in the vascularity of the parts.

SMELL.—The main peculiarity of the sense of smell consists in the fact that it gives us intelligence of the physical character of bodies in a *gaseous* or *vaporous* condition. Thus we are enabled to

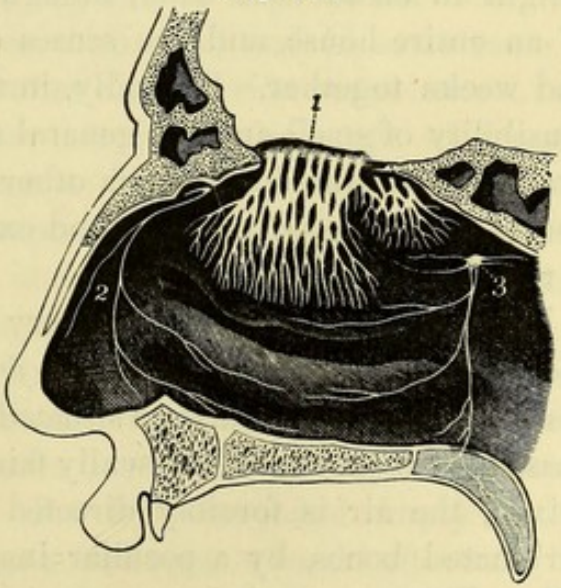
perceive the existence of an odorous substance at a distance, and when it is altogether concealed from sight. The minute quantity of volatile material emanating from it, and thus pervading the atmosphere, comes in contact with the mucous membrane of the nose, and produces a peculiar and special sensation.

The apparatus of this sense consists, first, of the olfactory membrane, supplied by the filaments of the olfactory nerve, as its special organ; and secondly, of the nasal passages, with the turbinated bones and the muscles of the anterior and posterior nares, as its accessory organs. At the upper part of the nasal fossæ, the mucous membrane is very thick, soft, spongy and vascular, and is supplied with mucous follicles which exude a secretion, by which its surface is protected and kept in a moist and sensitive condition.

It is only this portion of the mucous membrane of the nares which is supplied by filaments of the olfactory nerve, and which is capable of receiving the impressions of smell; it is therefore called the *Olfactory* membrane. Elsewhere, the nasal passages are lined with a mucous membrane which is less vascular and spongy in structure, and which is called the *Schneiderian* membrane.

The filaments derived from the olfactory ganglia, and which penetrate through the cribriform plate of the ethmoid bone, are distributed to the mucous membrane of the superior and middle turbinated bones, and to that of the upper part of the septum nasi. The exact mode in which these filaments terminate in the olfactory membrane has not been definitely ascertained. They are of a soft consistency and gray color, and, after dividing and ramifying freely in the membrane, appear to become lost in its substance. It is these nerves which exercise the special function of smell. They are, to all appearance, incapable of receiving ordinary impressions, and must be regarded as entirely peculiar in their

Fig. 165.



DISTRIBUTION OF NERVES IN THE NASAL PASSAGES.—1. Olfactory ganglion, with its nerves 2. Nasal branch of fifth pair. 3. Spheno-palatine ganglion.

nature and endowments. The nasal passages, however, are supplied with other nerves beside the olfactory. The nasal branch of the ophthalmic division of the fifth pair, after entering the anterior part of the cavity of the nares, just in advance of the cribriform plate of the ethmoid bone, is distributed to the mucous membrane of the inferior turbinated bone and the inferior meatus. Thus the organ of smell is provided with sensitive nerves from two different sources, viz., at its upper part, with the olfactory nerves proper, derived from the olfactory ganglion (Fig. 165, 1), which are nerves of special sensation; and secondly, at its lower part, with the nasal branch of the fifth pair (2), a nerve of general sensation. Beside which, the spheno-palatine ganglion of the great sympathetic (3) sends filaments to the mucous membrane of the whole posterior part of the nasal passages, and to the levator palati and azygos uvulæ muscles. Finally, the muscles of the anterior nares are supplied by filaments of the facial nerve.

The conditions of the sense of smell are much more special in their nature than those of taste. For, in the first place, this sense is excited, not by actual contact with the foreign body, but only with its vaporous emanations; and the quantity of these emanations, sufficient to excite the smell, is often so minute as to be altogether inappreciable by other means. We cannot measure the loss of weight in an odorous body, though it may affect the atmosphere of an entire house, and the senses of all its inhabitants, for days and weeks together. Secondly, in the olfactory organ, the special sensibility of smell and the general sensibility of the mucous membrane are separated from each other and provided for by different nerves, not mingled together and exercised by the same nerves, as is the case in the tongue.

In order to produce an olfactory impression, the emanations of the odorous body must be *drawn freely through the nasal passages.* As the sense of smell, also, is situated only in the upper part of these passages, whenever an unusually faint or delicate odor is to be perceived, the air is forcibly directed upward, toward the superior turbinated bones, by a peculiar inspiratory movement of the nostrils. This movement is very marked in many of the lower animals. As the odoriferous vapors arrive in the upper part of the nasal passages, they are undoubtedly dissolved in the secretions of the olfactory membrane, and thus brought into relation with its nerves. Inflammatory disorders, therefore, interfere with the sense of smell, both by checking or altering the secretions of the part, and by

producing an unnatural tumefaction of the mucous membrane, which prevents the free passage of the air through the nasal fossæ.

As in the case of the tongue, also, we must distinguish here between the perception of *true odors*, and the excitement of the general sensibility of the Schneiderian mucous membrane by *irritating substances*. Some of the true odors are similar in their nature to impressions perceived by the sense of taste. Thus we have sweet and sour smells, though none corresponding to the alkaline or the bitter tastes. Most of the odors, however, are of a very peculiar nature and are difficult to describe; but they are always distinct from the simply irritating properties which may belong to vapors as well as to liquids. Thus, pure alcohol has little or no odor, and is only irritating to the mucous membrane; while the odor of wines, of cologne water, &c., is communicated to them by the presence of other ingredients of a vegetable origin. In the same way, pure acetic acid is simply irritating; while vinegar has a peculiar odor in addition, derived from its vegetable impurities. Ammonia, also, is an irritating vapor, but contains in itself no odoriferous principle.

The sensations of smell, like those of taste, *remain for a certain time* after they have been produced, and modify in this way other less strongly marked odors which are presented afterward. As a general thing, the longer we are exposed to a particular odor, the longer its effect upon our senses continues; and in some cases it may be perceived many hours after the odoriferous substance has been removed. Odors, however, are particularly apt to remain after the removal or destruction of the source from which they were derived, owing to their vaporous character, and the facility with which they are entangled and retained by porous substances such as plastered walls, woollen carpets, and hangings, and woollen clothes. It is supposed to be in this way that the odor of a post-mortem examination will sometimes remain so as to be perceptible for several hours or even an entire day afterward. But this alone does not fully explain the fact. For if it depended simply on the retention of the odor by porous substances, it would afterward be perceived constantly, until it gradually and continuously wore off; while in point of fact, the physician who has made an autopsy of this kind does not afterward perceive its odor constantly, but only *occasionally*, and by sudden and temporary fits.

The explanation is probably this. As the odor remains constantly by us, we soon become insensible to its presence, as in the

case of all other continuous and unvarying impressions. Our attention is only called to it when we meet suddenly with another and familiar odor. This second odor, we find, does not produce its usual impression, because it is mingled with and modified by the other, which is more persistent and powerful. Thus we are again made aware of the former one, to which we had become insensible by reason of its constant presence.

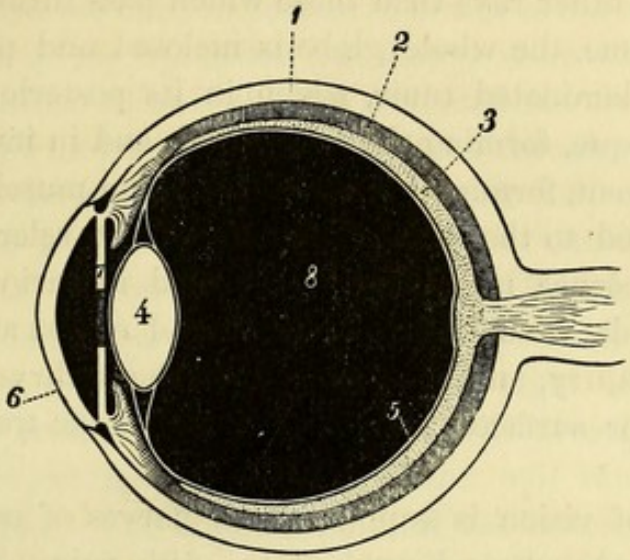
The sense of smell is comparatively feeble in the human species, but is excessively acute in some of the lower animals. Thus, the dog will not only distinguish different kinds of game in the forest by this sense, and follow them by their tracks, but will readily distinguish particular individuals by their odor, and will recognize articles of dress belonging to them by the minute quantity of odoriferous vapors adhering to their substance.

SIGHT.—The sight undoubtedly occupies the first rank in the list of special nervous endowments. It is the most peculiar in its operation, and the most immaterial in its nature, of all the senses, and it is through it that we receive the most varied and valuable impressions. The physical agent, also, to which the organ of sight is adapted, and by which its sensibility is excited, is more subtle and peculiar than any of those which act upon our other senses. For the senses of touch, taste, and smell require, for their exercise, the actual *contact* of a foreign body, either in a solid, liquid, or aeriform condition; and even the hearing depends upon the mechanical vibrations of the atmosphere, or some other sonorous medium. But the eye does not need to be in contact with the luminous body. It will receive the impressions of light with perfect distinctness, even when they are transmitted from an immeasurable distance, as in the case of the fixed stars; and the light itself is not only immaterial in its nature, so far as we can ascertain, but is also capable of being transmitted through space without the intervention of any material conducting medium, yet discoverable.

Finally, the apparatus of vision is more complicated in its structure than that of any other of the special senses. This apparatus consists, first, of the retina, as a special sensitive nervous membrane; and secondly, of the vitreous body, crystalline lens, choroid, sclerotic, iris and cornea, together with the muscles moving the eyeball and eyelids, lachrymal gland, &c., as accessory organs. The arrangement of the parts, constituting the globe of the eye, is shown in the following figure. (Fig. 166.)

The filaments of the optic nerve, after running forward and penetrating the posterior part of the eyeball, spread out into the substance of the *retina* (3), thus forming a delicate and vascular nerv-

Fig. 166.



Vertical Section of the EYEBALL.—1. Sclerotic. 2 Choroid. 3. Retina. 4. Lens. 5 Hyaloid membrane. 6. Cornea. 7. Iris. 8. Vitreous body.

ous expansion, in the form of a spheroidal bag or sac, with a wide opening in front, where the retina terminates at the posterior margin of the ciliary body. This expansion of the retina is the essential nervous apparatus of the eye. It is endowed with the special sensibility which renders it capable of receiving luminous impressions; and, so far as we have been able to ascertain, it is incapable of perceiving any other. On the outside, the retina is covered by the *choroid coat* (2), a vascular membrane, which is rendered opaque by the presence of an abundant layer of blackish-brown pigment-cells, and which thus absorbs the light which has once passed through the retina, and prevents its being reflected in such a way as to confuse and dazzle the sight. Inside the retina is the *vitreous body*, a transparent spheroidal mass of a gelatinous consistency, which is surrounded and retained in position by a thin, structureless membrane, called the hyaloid membrance (5), lying immediately in contact with the internal surface of the retina. The *lens* (4) is placed in front of the vitreous body, in the central axis of the eyeball, enveloped in its capsule, which is continuous with the hyaloid membrane. Just at the edge of the lens, the hyaloid membrane divides into two laminæ, which separate from each other, leaving between them a triangular canal, the *canal of Petit*, which can be seen in the above figure. In front of the lens is the *iris* (7), a nearly

vertical muscular curtain, formed of radiating and concentric fibres, pierced at its centre with a circular opening, the *pupil*, through which the light is admitted, and covered on its posterior surface with a continuation of the choroidal pigment, which excludes the passage of any other rays than those which pass through the pupil. At the same time, the whole globe is inclosed and protected by a thick, fibrous, laminated tunic, which in its posterior and middle portions is opaque, forming the *sclerotic* (1), and in its anterior portion is transparent, forming the *cornea* (6). The muscles of the eyeball are attached to the external surface of the sclerotic in such a way that the cornea may be readily turned in various directions; while the eyelids, which may be opened and closed at will, protect the eye from injury, and, with the aid of the lachrymal secretion, keep its anterior surfaces moist, and preserve the transparency of the cornea.

The organ of vision is supplied with nerves of ordinary sensibility by the ophthalmic branch of the fifth pair. The filaments of this nerve which terminate about the eye are distributed mostly to the conjunctiva, lachrymal gland, and skin of the eyelids; while a very few of them run forward in company with the ciliary nerves proper, and are distributed to the ciliary circle and iris. All these parts, therefore, but more particularly the conjunctiva and skin of the eyelids, possess ordinary sensibility, which appears to be totally wanting in the deeper parts of the eye. The ophthalmic ganglion gives off the ciliary nerves, which are distributed to the iris and ciliary muscle. Finally, the muscles moving the eyeball and eyelids are supplied with motor nerves from the third, fourth, sixth and seventh pairs.

Of all the properties and functions belonging to the different structures of the eyeball, the most peculiar and characteristic is the special sensibility of the retina. This sensibility is such that the retina appreciates both the intensity and the quality of the light—that is to say, its color and the different shades which this color may present. On account of the form, also, in which the retina is constructed, viz., that of a spheroidal membranous bag, with an opening in front, it becomes capable of appreciating the *direction* from which the rays of light have come, and, of course, the situation of the luminous body and of its different parts. For the rays which enter through the pupil from below can reach the retina only at its upper part, while those which come in from above, can reach it only at its lower part; so that in both instances the rays strike the

sensitive surface perpendicularly, and thus convey the impression of their direction from above or below.

But beside the sensibility of the retina, the perfection and value of the sense of sight depend very much on the arrangement of the accessory organs, the most important of which is the crystalline lens.

The function of the crystalline lens is to produce distinct perception of form and outline. For if the eye consisted merely of a sensitive retina, covered with transparent integument, though the impressions of light would be received by such a retina they could not give any idea of the form of particular objects, but could only produce the sensation of a confused luminosity. This condition is illustrated in Fig. 167, where the arrow, *a*, *b*, represents the luminous object, and the vertical dotted line, at the right of the diagram, represents the retina. Rays, of course, will diverge from every point of the object in every direction, and will thus reach every part of the retina. The different parts of the retina, consequently, 1, 2, 3, 4, will each receive rays coming both from the point of the arrow, *a*, and from its butt, *b*. There will therefore be no distinction, upon the retina, between the different parts of the object, and no

Fig. 167.

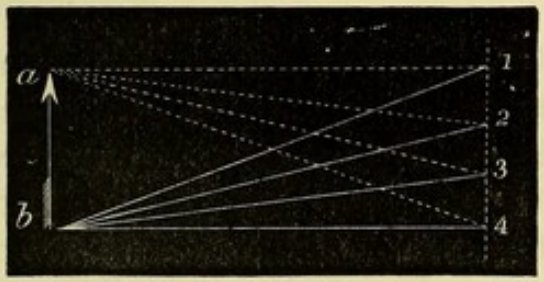
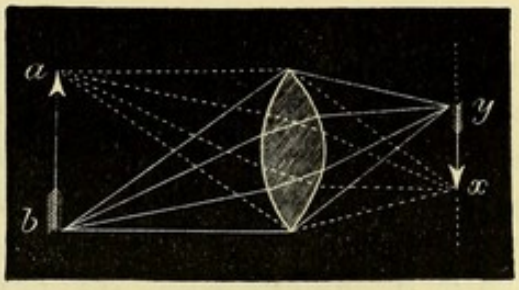


Fig. 168.



definite perception of its outline. But if, between the object and the retina, there be inserted a double convex refracting lens, with the proper curvatures and density, as in Fig. 168, the effect will be different. For then all the rays emanating from *a* will be concentrated at *x*, and all those emanating from *b* will be concentrated at *y*. Thus the retina will receive the impression of the point of the arrow separate from that of the butt; and all parts of the object, in like manner, will be distinctly and accurately perceived.

This convergence of the rays of light is accomplished to a certain extent by the other transparent and refracting parts of the eyeball; but the lens is the most important of all in this respect, owing to its superior density and the double convexity of its figure. The distinctness of vision, therefore, depends upon the action of the

lens in converging all the rays of light, emanating from a given point, to an accurate focus, *at the surface of the retina.* To accomplish this, the density of the lens, the curvature of its surfaces, and its distance from the retina, must all be accurately adapted to each other. For if the lens were too convex, and its refractive power excessive, or its distance from the retina too great, the rays would converge to a focus too soon, and would not reach the retina until after they had crossed each other and become partially dispersed, as in Fig. 169. The visual impression, therefore, coming from any particular point in the object, would not be concentrated and distinct, but diffused and dim, from being dispersed more or less over the retina, and interfering with the impressions coming from other parts. On the other hand, if the lens were either too flat, or placed

Fig. 169.

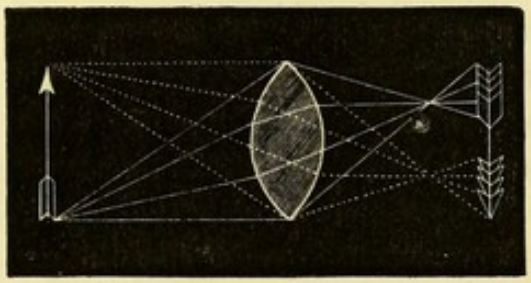
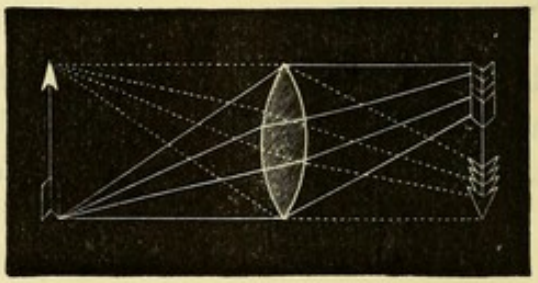


Fig. 170.



too near the retina, as in Fig. 170, the rays would fail to come together at all, and would strike the retina separately, producing a confused image, as before. In both these cases, the immediate cause of the confusion of sight is the same, viz., that the rays coming from the same point of the object strike the retina at different points; but in the first instance, this is because the rays have actually converged, and then crossed; in the second, it is because they have only approached each other, but have never converged to a focus.

Another important particular in regard to the action of the lens is the *accommodation of the eye to distinct vision at different distances.* It is evident that the same arrangement of refractive parts, in the eye, will not produce distinct vision when the distance of the object from the eye is changed. If this arrangement be such that the object is seen distinctly at a certain distance, and the object be then removed to a remoter point, the image will become confused; for the rays will then converge to a focus at a point in front of the retina; since, being less divergent when they strike the lens, the same amount of refraction will bring them together sooner than before. On the other hand, if the object be moved to a point nearer

the eye, the rays, becoming more divergent as they strike the lens, will converge less rapidly to a focus, and vision will again become indistinct.

This may easily be seen by the aid of a very simple experiment. If two needles be placed upright, at different distances from the eye, one for example at eight and the other at eighteen inches, but nearly in the same linear range, and if then, closing one eye, we look at them alternately with the other, we shall find that we cannot see both distinctly at the same time. For when we look at the one nearer the eye, so as to perceive its form distinctly, the image of the more remote one becomes confused; and when we see the more remote object in perfection, that which is nearer loses its sharpness of outline. This shows, in the first place, that the same condition of the eye will not allow us to see two objects at different distances with distinctness at the same time; and secondly that, on looking from one object to the other, there is a *change* of some kind in the focus of the eye, by which it is adapted to different distances. Indeed we are conscious of a certain effort at the time when the point of vision is transferred from one object to the other, by which the eye is adapted to the new distance; and this alteration is not quite instantaneous, but requires a certain interval of time for its completion.

The precise manner in which this accommodation is effected has given rise to much discussion. It evidently might be accomplished, either, 1st, by a change in the curvature of the cornea, or 2d, by a change in the curvature of the lens, or 3d, by an antero-posterior movement of the lens, by which its distance from the retina might be increased or diminished, or 4th, by a change in the figure of the entire eyeball, by which its longitudinal axis might be elongated or shortened. All these causes have in turn been supposed to be active in producing the requisite effect.

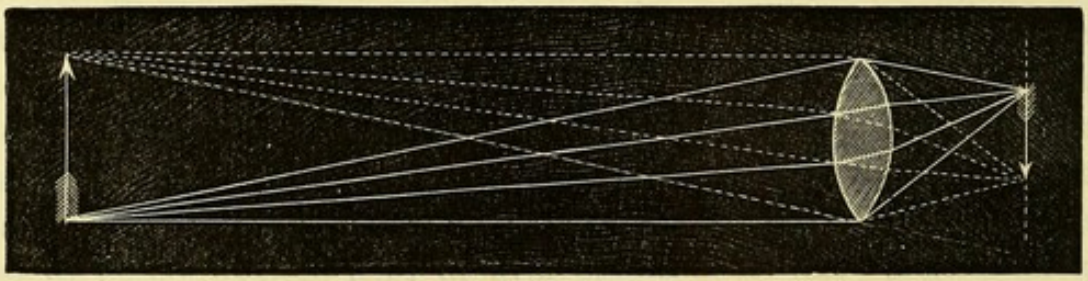
The facts now known in regard to the matter are as follows:—

I. In the first place it is certain that accommodation of the eye for distant objects is a *passive* condition,—that for near objects an *active* one. When we look at distant images, the eye is comparatively at rest. It is when we fix the sight upon near objects that we are conscious of an active change in the eye, which requires a certain exertion on our part; and this exertion is the more marked, as the objects which we examine are more closely situated. Continued application of the eye to near objects may even produce a perceptible fatigue, which gives place to a sense of repose on again

directing our sight to the distance. Our sensations, also, in vision of near objects, give the impression that this active accommodation of the eye is accomplished, in some way, by *muscular* effort.

II. In the second place, it is now rendered sufficiently certain, from the investigations of Donders[1] and others, that the active accommodation of the eye, for vision of near objects, is accomplished by an increased *convexity of the crystalline lens.* If the eye be accommodated for vision of a distant object, and a candle be then held near the front of the eye, and a little on one side, an observer will see three reflected images of its flame in the eyeball, viz., one reflection from the anterior surface of the cornea, one from the anterior surface of the lens, and one from the posterior surface of the lens. Now, if the patient change his sight from the distant to a near object, accurate measurements will show that the reflection on the cornea remains unaltered, but that the reflected image on the anterior surface of the lens diminishes in size and approximates to that on the cornea. Both these changes indicate that, in accommodation for near objects, *the anterior surface of the lens becomes more convex and approaches the cornea.* The image on the posterior surface of the lens at the same time diminishes slightly in size, but does not alter its position, showing that this surface of the lens, also, becomes a little more convex, but does not move either forward or

Fig. 171.



Vision for Distant Objects.

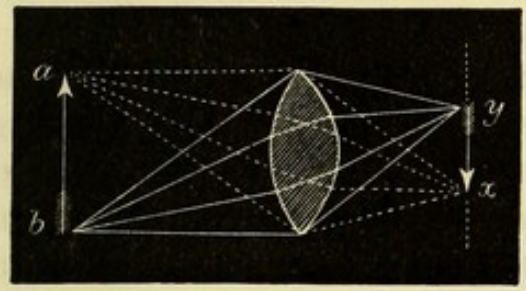
backward. The unaltered appearance of the reflection on the cornea shows that this part of the eye does not change its convexity.

We can now see how these alterations produce the required changes in accommodation. When the eye is accommodated for distant vision, the lens assumes the form which is normal to it, when in repose and unaffected by external agencies. Its curvatures are then such that rays coming from distant points, and having consequently but a slight divergence, are brought to a focus behind the lens, exactly at the sensitive surface of the retina. (Fig. 171.)

[1] Accommodation and Refraction of the Eye. Sydenham Ed., London, 1864, p. 10.

If, with the eye in this condition, the sight be turned toward a near object, its image is imperfectly perceived; since the lens, which was sufficiently convex for distant objects, is still too flat for the widely divergent rays of near objects, and the image upon the retina is accordingly diffused and indistinct, as in Fig. 170. But by the change of form above described, the lens, in accommodating the eye to near vision, becomes more convex, especially on its anterior surface; and, its refractive power being thus increased, it becomes capable of bringing the divergent rays to a focus at the retina, and the object is distinctly perceived, as in Fig. 172.

Fig. 172.



VISION FOR NEAR OBJECTS.

It will also be seen that if, with the eye thus accommodated, the sight be directed again to remote objects, they in their turn will appear indistinct; since the strongly convex lens is too highly refractive for rays coming from a distance, and the image will be diffused, as in Fig. 169. To produce distinct vision at a distance, the lens must return to its original form, as in Fig. 171.

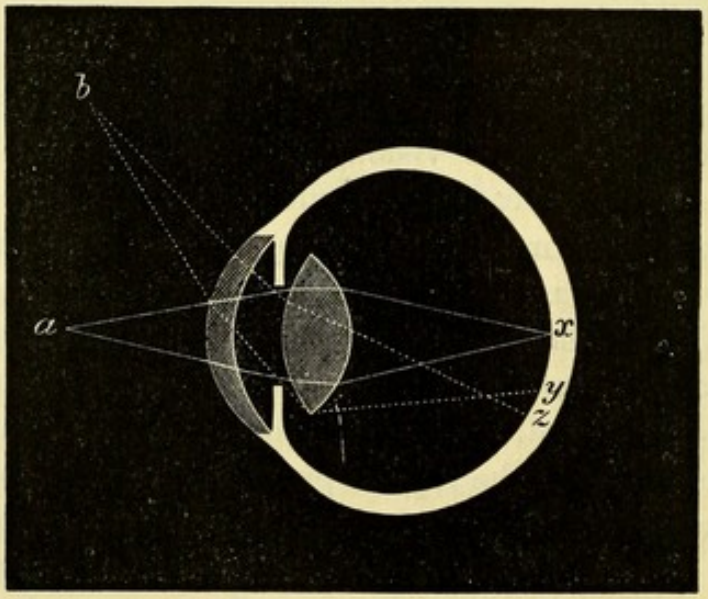
It is supposed that the alteration of the form of the lens, in these changes, is due to a circular compression of its edges, by some or all of the fibres of the ciliary muscle. It is this active compression which increases its convexity in vision of near objects. When this pressure ceases, the lens resumes its former shape, by the passive elasticity of its tissue, and becomes again adapted for distant vision.

A little examination shows, also, that the amount of accommodation, necessary to distinct vision, varies very much for different distances. A much greater accommodating power is required for near distances than for remote; since the difference in divergence between rays, entering the pupil from a distance of one inch and from that of six inches, is much greater than the difference between six inches and a yard, or even distances which are immeasurably remote. Indeed, for all distances beyond a certain limit, the difference in divergence of the rays is practically imperceptible, and no sensible change in accommodation is required for objects beyond that limit. It is for near distances, then, that we find the necessary changes of accommodation most marked, and these changes become greater and more difficult, the nearer to the eye the object is situ-

ated, until at last a limit is reached beyond which they become impossible. The eye accordingly cannot be made to see distinctly at very short distances. For all ordinary eyes, accommodation fails and vision becomes imperfect, when the object is placed at a distance of less than six inches from the eye. But from that point outward, the healthy eye can adapt itself to any distance at which light is perceptible, even to the immeasurable distances of the fixed stars.

Circle of Vision.—Since the opening of the pupil will admit rays of light coming from various directions, there is in front of the eye a circle, or space, within which luminous objects are perceived, and beyond which nothing can be seen, because the rays, coming from the side or from behind, cannot enter the pupil. This space, within which external objects can be perceived, is called the "circle of vision." But, for short distances, there is only a single point, in the centre of the circle of vision, at which objects can be seen *distinctly*. Thus, if we place ourselves in front of a row of vertical stakes or palisades, we can see those directly in front of the eye with perfect distinctness, but those at a little distance on each side are only perceived in a confused and uncertain manner. On looking at the middle of a printed page, in the direct range of vision, we see the distinct outlines of the letters; while at successive distances from this point, the eye remaining fixed, we can distinguish first only the separate letters with confused outlines, then only the words, and lastly only the lines and spaces.

Fig. 173.



This is because rays of light coming into the eye very obliquely, in a lateral or vertical direction, are not brought to their proper focus. Thus, in Fig. 173, the rays diverging from the point *a*, directly in

front of the eye, fall upon the lens in such a way that they are all brought together at *x*, at the surface of the retina; but those coming from *b* fall upon the lens so obliquely that, for rays having an equal divergence with those coming from *a*, there is more difference in their angles of incidence, and of course more difference in the amount of their refraction. They are consequently brought together more rapidly, and on reaching the retina are dispersed over the space *y*, *z*.

The perfection of the eye, as a visual apparatus, is very much increased by the action of the *iris*. This organ, as we have already mentioned, is a nearly vertical muscular curtain, placed in front of the lens, attached by its external margin to the junction of the cornea and sclerotic, and pierced about its centre by the circular opening of the pupil. It consists, according to most anatomists, of two sets of muscular fibres—viz., the circular and the radiating. The circular fibres, which are much the most abundant, are arranged in concentric lines about the inner edge of the iris, near the pupil; the others are said to radiate in a scattered manner, from its central parts to its outer margin. The action of these two sets of fibres is to contract and enlarge the orifice of the pupil. The circular fibres, in contracting, draw together the edges of the pupil, and so diminish its opening; and when these are relaxed, the radiating fibres come into play, and by drawing apart the edges of the orifice, enlarge the pupillary opening. The action of the circular fibres, at the same time, is much the most marked and important of the two. For when the whole muscular apparatus of the eye is paralyzed by the action of belladonna, or by the division of the third pair of nerves, or in the general relaxation of the muscular system at the moment of death, the pupil is invariably dilated, probably by the passive elasticity of its tissues.

During life, however, these different conditions of the pupil correspond with the different degrees of light to which the eye is exposed. In a strong light, the pupil contracts and shuts out the superfluous rays; in a feeble light, it dilates, in order to collect into the eye all the light which can be received from the object. This contractile and expansive movement of the pupil is a *reflex action*. It is not produced by the direct impression of the light upon the iris itself, but upon the retina; since, if the retina be affected with complete amaurosis, or if the light be entirely shut out from it by an opacity of the lens, no such effect is produced, though the iris itself be exposed to the direct glare of day. From the retina the impression is transmitted, through the optic nerve, to the

optic tubercles and the brain, thence reflected outward by the oculo-motorius nerve to the ophthalmic ganglion, and so through the ciliary nerves to the iris.

The pupil is subject, however, to various other nervous influences beside the impressions of light received by the retina. Thus in poisoning by opium, it is contracted; in coma from compression of the brain, it is dilated; in natural sleep it is contracted, and the eye-ball rolled upward and inward. In various mental conditions, the pupil is also enlarged or diminished, and thus modifies the expression of the eye; and in viewing remote objects, it is generally enlarged, while, in looking at near objects, it is comparatively contracted. But still, the most constant and important function belonging to the iris is the admission or exclusion of the rays, according to the intensity of the light.

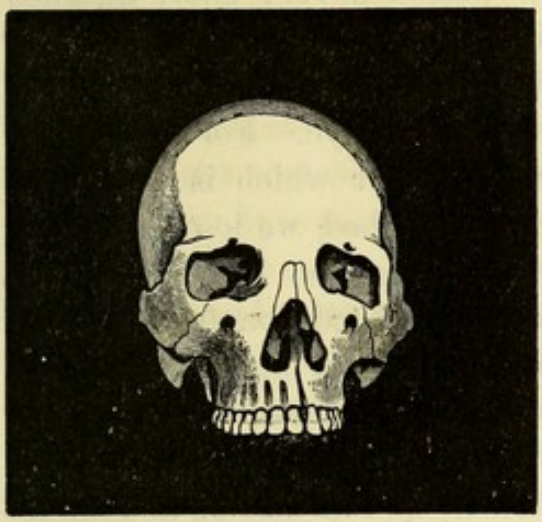
Our impressions of *distance* and *solidity*, in viewing external objects, are produced mainly by the *combined action of the two eyes*. For, as the eyes are seated a certain distance apart from each other in the head, when they are both directed toward the same object, their axes meet at the point of sight, and form a certain angle with each other; and this angle varies with the distance of the object. Thus, when the object is within a short distance, the axes of the two eyes will necessarily be very convergent, and the angle which they form with each other a large one; but for remote objects, the visual axes will become more nearly parallel, and their angle consequently smaller. It is on this account that we can always distinguish whether any person at a short distance is looking *at us*, or at some other object in our direction; since we instinctively appreciate, from the appearance of the eyes, whether their visual axes meet at the level of our own face.

In looking at a landscape, accordingly, we do not see the whole of it distinctly at the same moment, but only those parts to which out attention is immediately directed. This is because, in the first place, the *focus* of distinct vision varies, in each eye, for different distances, as we have seen in a former paragraph, and secondly, because both eyes can only be directed together, at one time, to objects at a certain distance. Thus, when we see the foreground or the middle ground distinctly, the distance is vague and uncertain, and when we direct our eyes more particularly to the horizon, objects in the foreground become indistinct. In this way we appreciate the difference in distance between the various portions of the landscape as a whole. In the case of particular objects, we are

assisted also by the alteration in their individual characters; for distance produces a diminution, both in apparent size and in intensity of color.

The combined action of the two eyes is also very valuable, for near objects, in giving us an idea of *solidity* or *projection*. For within a certain distance, the visual axes when directed together

Fig. 174.



As seen by the Left Eye.

Fig. 175.

As seen by the Right Eye.

at a solid object, are so convergent that the two eyes do not receive the same image. As in Figs. 174 and 175, which represent a skull as seen by the two eyes, when placed exactly in front of the observer at the distance of eighteen inches or two feet, the right eye will see the object partly on one side, and the left eye partly on the other. And by the union or combination of these two images by the visual organs, the impression of solidity is produced.

By the employment of double pictures, so drawn as to represent the appearances presented to the two eyes by the same object, and so arranged that each shall be seen only by the corresponding eye, a deceptive resemblance may be produced to the actual projection of solid objects. This is accomplished in the contrivance known as the *Stereoscope*. Thus, if two pictures similar to those in Figs. 174 and 175 be so placed that one shall be seen only with the right eye and the other only with the left, the combination of the two figures will take place as if they came from the real object, and all the natural projections will come out in relief.

But this effect is produced only in the case of objects situated within a moderately short distance. For very remote objects, we lose the impression of solidity, since the difference in the images on the two eyes becomes so slight as to be inappreciable, and we see

only a plane expanse of surface, with sharp outlines and various shades of color, but no actual projections or depressions.

The sensibility of the retina is such that it cannot distinguish luminous points which are received upon its surface *at a very minute distance from each other.* In this particular, the sensibility of the retina resembles that of the skin, since we have already found that the integument cannot distinguish the impressions made by the points of two needles placed a very short distance apart. The delicacy of this discriminating power, in the retina, is immeasurably superior to that of the skin; and yet it has its limits, even in the nervous expansion of the eye. For if we look at an object which is excessively minute, or which is so remote that its apparent size is very much diminished, we lose the power of distinguishing its different parts, and can no longer perceive its real outline. This is a very different condition from that in which the confusion of vision arises from defect of focusing in the eye, as, for example, in long or short-sightedness, or where the object is placed too near the eye or too much on one side. For when the difficulty depends simply on its minute size or its remoteness, the rays coming from the top of the object and those coming from the bottom, are all brought to their proper focus at distinct points on the retina—*only these points are too near each other for the retina to distinguish them apart.* Consequently we can no longer appreciate the form of the object.

For the same reason, when we mix together minute grains of a different hue, we produce an intermediate color. If yellow and blue be mingled in this way, we no longer perceive the separate blue and yellow grains, but only a uniform tinge of green; and white and black granules, mixed together, produce, at a short distance, the appearance of a continuous shade of gray.

Impressions, once produced upon the retina, remain for a short time afterward. Usually these impressions are so evanescent after the removal of their immediate cause, and are so soon followed by others which are more vivid, that we do not notice their existence. They may very readily be demonstrated, however, by swinging rapidly in a circle before the eyes, in a dark room, a stick lighted at one end. As soon as the motion has attained a certain degree of velocity, the impression produced on the retina, when the lighted end of the stick arrives at any particular spot, remains until it has completed its revolution and has again reached the same point; so that the effect thus produced upon the eye is that of a continu-

ous circle of light. The same fact has been illustrated by the optical contrivance, known as the *Thaumatrope*, in which successive pictures of similar figures in different positions are made to revolve rapidly before the eye, and thus to produce the apparent effect of a single figure in rapid motion;—since the eye fails to perceive the intervals between the different pictures.

The sense of vision, therefore, through the impressions of light, gives us ideas of form, size, color, position, distance, and movement. But these ideas may also be excited by impressions derived from an *internal* source, as well as those produced by rays coming from without. And it is one of the most striking peculiarities of the sense of sight that these ideal or internal impressions which are excited in it by various causes, *are much more vivid and powerful than those of any other of the senses.* Thus, in a dream, we often see external objects, with all their visible peculiarities of light, color form, &c., nearly or quite as distinctly as when we are awake; but the imaginary impressions of *sound*, in this condition, are always comparatively faint, and those of taste, smell, and touch, almost entirely imperceptible. Even in a reverie, in the waking condition, when the absorption of the mind in its own thoughts is complete, and we are withdrawn altogether from outward influences, we see objects which have no present existence as if they were actually before us. It is this sense also which becomes most easily and thoroughly excited in certain nervous disorders; as, for example, in delirium tremens, where the patient often sees passing before his eyes extensive and magnificent landscapes, crowds of human faces and figures, and series of towns and cities, which seem to be depicted upon the imagination with a force and distinctness, much superior to that of other delirious impressions. Since the sense of sight, therefore, depends less directly than the other senses upon the actual contact of material objects, it is also more easily thrown into activity when withdrawn from their influence.

HEARING.—The sense of hearing depends upon the vibrations excited in the atmosphere by sonorous bodies, which are themselves first thrown into vibration by various causes, and which then communicate similar undulations to the surrounding air. These sonorous vibrations are of such a character that they cannot be directly appreciated by ordinary sensibility, but the result of numerous and well-directed physical experiments on this subject leaves no doubt whatever of their existence; and when such vibrations are commu-

nicated to the auditory apparatus, they produce in it the sensation of *sound.*

In the case of the aquatic animals, which pass their entire existence beneath the surface of the water, the water itself, which is capable of vibrating in the same way, communicates the sonorous impressions to the organ of hearing; but in terrestrial animals, and particularly in man, it is the atmosphere which always serves as the medium of transmission.

The auditory apparatus, in man and in the quadrupeds, consists, first, of a somewhat expanded and trumpet-shaped mouth, or *external ear*, destined to receive and collect the sonorous impulses coming from various quarters. This external ear is constructed of a cartilaginous framework, covered with integument, loosely attached to the bones of the head, and more or less movable by means of various muscles, which by their contraction turn its expanded orifice in different directions. In man, the movements of the external ear are almost always inappreciable, though the muscles may be easily demonstrated; but in many of the lower animals these movements are exceedingly varied and extensive, and play a very important part in the working of the auditory apparatus.

At the bottom of the external ear, its orifice is prolonged into a tube or canal, the *external auditory meatus*, partly cartilaginous and partly bony, which penetrates the lateral part of the temporal bone in a nearly horizontal and transverse direction. In the human subject, this canal is a little over one inch in length, and is lined by a continuation of the external integument. The integument toward its outer portion is beset with small hairs, and provided with ceruminous glands which supply a secretion of a waxy or resinous consistency. By these means the passage is protected from the accidental ingress of various foreign bodies.

Secondly, at the bottom of the external meatus the auditory passage is closed by a thin fibrous membrane, stretched across its cavity, called the *membrana tympani.* Upon this membrane are received the sonorous vibrations which have been collected by the external ear and conducted inward by the external auditory meatus. Behind the membrana tympani is the cavity of the *middle ear*, or the cavity of the tympanum. This cavity communicates posteriorly with the mastoid cells, and anteriorly with the pharynx, by a narrow passage, lined with ciliated epithelium, and running downward, forward and inward, called the *Eustachian tube.* A chain of small bones, the malleus, incus, and stapes, is stretched across the cavity of the

tympanum, and forms a communication between the membrana tympani on the outside, and the membrane closing the foramen ovale in the petrous portion of the temporal bone. All the vibrations, accordingly, which are received by the membrana tympani, are transmitted by the chain of bones to the membrane of the foramen ovale. The tension of the membranes is regulated by three small muscles, the *tensor tympani*, *laxator tympani*, and *stapedius* muscles, which arise from the bony parts in the neighborhood, and are inserted respectively into the neck and long process of the malleus and the head of the stapes, and which draw these bones forward and backward upon their articulations.

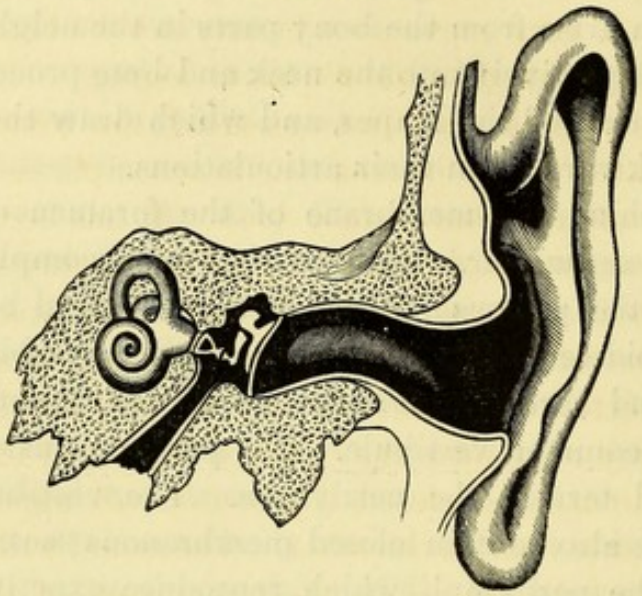
Thirdly, behind the membrane of the foramen ovale lies the *labyrinth*, or *internal ear*. This consists of a complicated cavity, excavated in the petrous portion of the temporal bone, and comprising an ovoid central portion, the *vestibule*, a double spiral canal, the *cochlea*, and three *semicircular canals*, all communicating by means of the common vestibule. All parts of this cavity contain a watery fluid termed the perilymph. The vestibule and semicircular canals also contain closed membranous sacs, suspended in the fluid of the perilymph, which reproduce exactly the form of the bony cavities themselves, and communicate with each other in a similar way. These sacs are filled with another watery fluid, the endolymph; and the terminal filaments of the auditory nerve are distributed upon the membranous sac of the vestibule and upon the ampullæ, or membranous dilatations, at the commencement of the three semicircular canals. The remaining portion of the auditory nerve is distributed upon the septum between the two spiral canals of the cochlea.

Thus, the essential or fundamental portion of the auditory apparatus is evidently the internal ear, a cavity, partly membranous and partly bony, in which is distributed a nerve of special sense, the auditory nerve, capable of appreciating sonorous impressions. The accessory parts, on the other hand, are the chain of bones and the membrane of the tympanum, which communicate the sonorous vibrations directly to the internal ear; and the meatus and external ear, which collect them from the atmosphere. The reception of sonorous impulses is therefore accomplished in a very indirect way. For the sonorous body first communicates its vibrations to the atmosphere. By the atmosphere these vibrations are communicated to the membrana tympani. From the membrana tympani, they are transmitted, through the chain of bones, to the membrane of the

foramen ovale; thence to the perilymph, or fluid of the labyrinthic cavity, and from the perilymph to the membranous parts of the labyrinth and the nerves which are distributed upon them.

The arrangement of the different parts composing the *tympanum* is of the greatest importance for the perfect enjoyment of the sense

Fig. 176.



Human Auditory Apparatus, showing external auditory meatus, tympanum, and labyrinth.

of hearing. For the air on the two sides of the membrane of the tympanum should be in the same condition of elasticity in order to allow of the proper vibration of the membrane; and this equilibrium would be liable to disturbance if the air within the tympanum were completely confined, while that outside is subjected to variations of barometric pressure. By means of the Eustachian tube, however, a communication is established between the cavity of the tympanum and the exterior, and the free vibration of the membrane is thus secured.

The *exact tension of the membrana tympani itself* is also provided for, as we have already observed, by the action of the two muscles inserted into the malleus and the stapes. By the contraction of the internal muscle of the malleus, or *tensor tympani*, the membrane of the tympanum is drawn inward and rendered more tense than usual. The action of the *stapedius* muscle is by some thought to relax the membrana tympani, by others to assist in the tension both of this membrane and that of the foramen ovale, to which the stapes is attached. But there is no doubt that both these muscles, by their combined or alternate action, can regulate the tension

of the tympanic membrane, to an extraordinary degree of nicety, and thus increase the ease and delicacy with which various sounds are distinguished. For if the membrane be so put upon the stretch that its fundamental note shall be the same with that of the sound which is to be heard, it will vibrate more readily in consonance with the undulations of the atmosphere, and the sound will be more distinctly heard. On the contrary, if the membrane be too highly stretched, very grave sounds may not be heard at all, until its tension is diminished to the requisite degree.

Contrary to what is sometimes asserted, the communication of sonorous impulses to the internal ear is accomplished *altogether by means of the tympanum and chain of bones.* It has been thought that sounds were transmitted, in many instances, directly to the internal ear by the medium of the cranial bones. This was inferred from such facts as the following. If a tuning-fork, in vibration, be taken between the teeth, its sound will appear very much louder than if it were simply held near the external ear; and if, while it is so held, one of the ears be closed, the sound will appear very much louder on that side than on the other. The sound will also be heard if the tuning-fork be applied to the upper part of the cranium or the mastoid process, with a similar increase of resonance on closing the ears. Finally our own voices are heard, though the ears be both closed, and the sound is much louder with the ears closed than open.

These are the facts which have led to the belief that, in such instances, the sound was communicated directly through the bones of the head, vibrating in consonance with the sounding body. But a little examination will show that such is not the case. When we hold the end of a vibrating tuning-fork between the teeth, we no longer hear the sound at the vibrating extremity of the instrument or its neighborhood, but *in the mouth and the nasal fossæ.* It is the vibration of the air in these passages which produces the sound; and this vibration is communicated to the cavity of the tympanum, perhaps through the Eustachian tube. The apparent increase of sound, also, on closing the ears, which could not be explained on supposing it to be conducted directly to the internal ear through the bones of the cranium, is due to the same cause. For it can easily be seen, on trying the experiment, either with a tuning-fork held between the teeth, or simply with our own voices, that this apparent increase of sound takes place only when the ears are closed by *gentle* pressure. If the pressure be excessive,

so that the integument is forced inward into the meatus and the air in the meatus subjected to undue compression, the sound no longer appears louder in the corresponding ear, and may even be lost altogether.

The apparent increase of sound, therefore, in such cases, when the ear is gently closed, is due to the fact that the meatus is thus converted into a reverberatory cavity, by which the vibrations of the tympanum are increased in intensity. But if the air in the meatus be too much compressed by forcible closure, the vibrations of the tympanum are then interfered with and the sound is diminished or destroyed.

In all cases, then, it is the sonorous vibrations of the air which produce the sound, and these vibrations are received invariably by the membrane of the tympanum, and thence transmitted to the internal ear by the chain of bones. The cranial bones are incapable of communicating these vibrations to the labyrinth and its contents, except very faintly and imperfectly. For common experience shows that even the loudest and sharpest sounds, coming from without, are almost entirely lost on closing the external ears; and our own respiratory and cardiac sounds, which are so easily heard as soon as the chest is connected with the ear by a flexible stethoscope, are entirely inaudible to us in the usual condition.

The exact function of the different parts of the internal ear is not well understood. It has been thought to be the office of the *semicircular canals* to determine the *direction* from which the sonorous impulses are propagated. This opinion was based upon the curious fact that these canals, always three in number, are placed in such positions as to correspond with the three different directions of vertical, lateral, and longitudinal extension; for one of them is nearly vertical and transverse, another vertical and longitudinal, and the third horizontal in position. The sonorous impulses, therefore, coming in either of these directions, would be received by only one of the semicircular canals (by direct conduction through the bones of the head) perpendicularly to its own plane; and an intermediate direction, it was thought, might be appreciated by the combined effect of the impulse upon two adjacent canals.

Enough has already been said, however, in regard to the communication of sound directly through the bones of the head to the internal ear, to show that this cannot be the mode in which the direction of sound is ascertained. Indeed, when we hear any loud and

well-marked sound coming from a particular region, such as the music of a military band or the whistle of a locomotive, we have only to close the external ears to lose our perception both of the sound and its direction. The direction of sonorous impressions is appreciated in a different way. In the first place, we feel that the sound comes from one side or the other, by its making a more distinct impression on one ear than the opposite; and by inclining the head slightly in various directions, we easily ascertain whether the sound becomes more or less acute, and so judge of its actual source. Many of the lower animals, whose ears are very large and movable, use this method to great extent. A horse, for example, when upon the road, often keeps his ears in constant motion, *feeling*, as it were, in the distance, for the origin of the various sounds which excite his attention.

Beside the above, we are further assisted in our judgment of the direction of sounds by our previous knowledge of the localities, the direction of the wind, and the manner in which the sound is reflected by surrounding objects. When these sources of information fail us, we are often at a loss. It is notoriously difficult, for example, to judge of the place of the chirping of a cricket in a perfectly closed room, or of the direction of a bell heard on the water in a thick fog.

The sense of hearing has a much closer analogy with ordinary sensibility than that of sight. Thus, in the first place, hearing is accomplished by the direct intervention and contact of a material body—the atmosphere; for sonorous impulses cannot be produced in a vacuum, and we hear no sound from a bell rung under an exhausted receiver. Secondly, the nature of the impressions produced by sound is such that we can often describe them by the same terms which are applied to ordinary sensations. Thus, we speak of sounds as sharp and dull, piercing, smooth, or rough; and we feel the impulse of a sudden and violent explosive sound, like that of a *blow* upon the tympanum.

By this sense, therefore, we distinguish the quality, intensity, pitch, duration, and direction of sonorous impulses. The delicacy with which these distinctions are appreciated varies considerably in different individuals; and in different kinds of animals there is reason to believe that the diversity is much greater, some of them being almost insensible to sounds which are readily perceived by others. In man, the number and variety of tones which can usually be discriminated is very great; and this sense, accordingly, in the

complication and finish of its apparatus, and the perfection and delicacy of its action, must be regarded as second only to that of vision

On the Senses in General.—There are several facts connected with the operation of the senses, both general and special, which are common to all of them, and which still remain to be considered. In the first place, an impression of any kind, made upon a sensitive organ, *remains for a time after the removal of its exciting cause.* We have already noticed this in regard to the senses of taste, smell, and sight, but it is equally true of the hearing and the touch. Thus, if the skin be touched with a piece of ice, the acute sensation remains for a few seconds, whether the ice be removed or not. For the higher order of the special senses, the time during which this secondary impression remains is a shorter one. In the case of hearing, however, it has been measured with tolerable approach to accuracy; for it has been found that, if the sonorous undulations follow each other with a greater rapidity than sixteen times per second, they become fused together into a continuous sound, producing upon the ear the impression of a *musical note.* The varying pitch of the note depends upon the rapidity with which the vibrations succeed each other. When the succession of vibrations is very rapid, a high note is the result, and when comparatively slow, a low note is produced; but when the number of impulses falls below sixteen per second, we then perceive the distinct vibrations, and so lose the impression of a continuous note.

All the senses, in the second place, *become accustomed to a continued impression,* so that they no longer perceive its existence. Thus, if a perfectly uniform pressure be exerted upon any part of the body, the compressing substance after a time fails to excite any sensation in the skin, and we remain unconscious of its existence. In order to attract our notice, it is then necessary to increase or diminish the pressure; while, so long as this remains uniform, no effect is perceived. But if, after the skin has thus become accustomed to its presence, the foreign body be suddenly removed, our attention is then immediately excited, and we notice the absence of an impression, in the same way as if it were a positive sensation.

We all know how rapidly we become habituated to odors, whether agreeable or disagreeable in their nature, in the confined air of a close apartment; although, on first entering from without, our attention may have been attracted by them in a very decided manner. A continuous and uniform sound, also, like the steady rumbling of carriages, or the monotonous hissing of boiling water,

becomes after a time inaudible to us; but as soon as the sound ceases, we notice the alteration, and our attention is at once excited. The senses, accordingly, receive their stimulus more from the variation and contrast of external impressions, than from these impressions themselves.

Another important particular, in regard to the senses, is their *capacity for education.* The proofs of this are too common and too apparent to need more than a simple allusion. The touch may be so trained that the blind may read words and sentences by its aid, in raised letters, where an ordinary observer would hardly detect anything more than a barely distinguishable inequality of surface. The educated eye of the artist, or the naturalist, will distinguish variations of color, size, and outline, altogether inappreciable to ordinary vision; and the senses of taste and smell, in those who are in the habit of examining wines and perfumes, acquire a similar superiority of discriminating power.

In these instances, however, it is not probable that the organ of sense itself becomes any more perfect in organization, or more susceptible to sensitive impressions. The increased functional power, developed by cultivation, depends rather upon the greater delicacy of the *perceptive* and *discriminating* faculties. It is a mental and not a physical superiority which gives the painter or the naturalist a greater power of distinguishing colors and outlines, and which enables the physician to detect nice variations of quality in the sounds of the heart or the respiratory murmur of the lungs. The impressions of external objects, therefore, in order to produce their complete effect, must first be received by a sensitive apparatus, which is perfect in organization and functional activity; and, secondly, these impressions must be subjected to the action of an intelligent perception, by which their nature, source and relations are fully appreciated.

That part of the nervous system which we have hitherto studied, viz., the cerebro-spinal system, consists of an apparatus of nerves and ganglia, destined to bring the individual into relation with the external world. By means of the special senses, he is made cognizant of sights, sounds, taste, and odors, by which he is attracted or repelled, and which guide him in the pursuit and choice of food. By the general sensations of touch and the voluntary movements, he is enabled to alter at will his position and location, and to adapt them to the varying conditions under which he may be placed. The great passages of entrance into the body,

and of exit from it, are guarded by the same portion of the nervous system. The introduction of food into the mouth, and its passage through the œsophagus to the stomach, are regulated by the same nervous apparatus; and even the passage of air through the larynx, and its penetration into the lungs, are equally under the guidance of sensitive and motor nerves belonging to the cerebro-spinal system.

It will be observed that the above functions relate altogether either to external phenomena or to the simple introduction into the body of food and air, which are destined to undergo nutritive changes in the interior of the frame.

If we examine, however, the deeper regions of the body, we find located in them a series of internal phenomena, relating only to the substances and materials which have already penetrated into the frame, and which form or are forming a part of its structure. These are the purely vegetative functions, as they are called; or those of growth, nutrition, secretion, excretion, and reproduction. These functions, and the organs to which they belong, are not under the direct influence of the cerebro-spinal nerves, but are regulated by another portion of the nervous system, viz., the "ganglionic system;" or, as it is more commonly called, the "system of the great sympathetic."

CHAPTER VII.

SYSTEM OF THE GREAT SYMPATHETIC.

THE sympathetic system consists of a double chain of nervous ganglia, running from the anterior to the posterior extremity of the body, along the front and sides of the spinal column, and connected with each other by slender longitudinal filaments. Each ganglion is reinforced by motor and sensitive filaments derived from the cerebro-spinal system, and thus the organs under its influence are brought indirectly into communication with external objects and phenomena. The nerves of the great sympathetic are distributed to organs over which the consciousness and the will have no immediate control, as the intestine, kidneys, heart, liver, &c.

Anatomical arrangement of the sympathetic system. — The first sympathetic ganglion in the head is the *ophthalmic ganglion.* It is situated within the orbit of the eye, on the outer aspect of the optic nerve. It communicates by slender filaments with the carotid plexus, which forms the continuation of the sympathetic system from below; and receives a motor root from the oculo-motorius nerve, and a sensitive root from the ophthalmic branch of the fifth pair. Its filaments of distribution, known as the "ciliary nerves," pass forward upon the eyeball, pierce the sclerotic, and finally terminate in the iris.

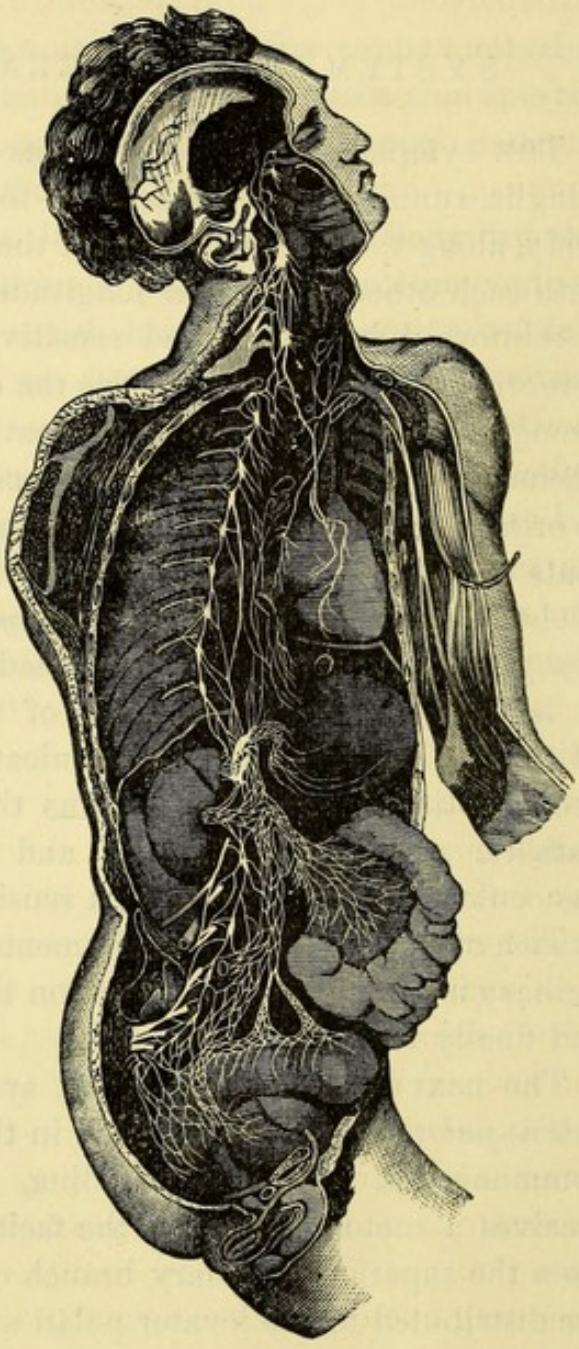
The next division of the great sympathetic in the head is the *spheno-palatine ganglion,* situated in the spheno-maxillary fossa. It communicates, like the preceding, with the carotid plexus, and receives a motor root from the facial nerve, and a sensitive root from the superior maxillary branch of the fifth pair. Its filaments are distributed to the levator palati and azygos uvulæ muscles, and to the mucous membrane about the posterior nares.

The third sympathetic ganglion in the head is the *submaxillary,* situated upon the submaxillary gland. It communicates with the superior cervical ganglion of the sympathetic by filaments which accompany the facial and external carotid arteries. It derives its sensitive filaments from the lingual branch of the fifth pair, and its

motor filaments from the facial nerve, by means of the chorda tympani. Its branches of distribution pass to the sides of the tongue and to the submaxillary and sublingual glands.

The last sympathetic ganglion in the head is the *otic ganglion.* It is situated just beneath the base of the skull, on the inner side of the third division of the fifth pair. It sends filaments of communication to the carotid plexus; and receives a motor root from the facial nerve, and a sensitive root from the inferior maxillary division of the fifth pair. Its branches are sent to the internal muscle of the malleus in the middle ear (tensor tympani), to the circumflexus palati, and to the mucous membrane of the tympanum and Eustachian tube.

Fig. 177.



Course and distribution of the GREAT SYMPATHETIC.

The continuation of the sympathetic nerve in the neck consists of two and sometimes three ganglia, the superior, middle, and inferior. These ganglia communicate with each other, and also with the anterior branches of the cervical spinal nerves. Their filaments follow the course of the carotid artery and its branches, covering them with a network of interlacing fibres, and are finally distributed to the substance of the thyroid gland, and to the walls of the larynx, trachea, pharynx, and œsophagus. By the superior, middle, and inferior cardiac nerves, they also supply sympathetic fibres to the cardiac plexuses and to the substance of the heart.

In the chest, the ganglia of the sympathetic nerve are situated on each side the spinal column, just over the heads of the ribs, with which they accordingly correspond in number. Their communications with the intercostal nerves are double; each sympathetic ganglion receiving two filaments from the intercostal nerve next above it. The filaments originating from the thoracic ganglia are distributed upon the thoracic aorta, and to the lungs and œsophagus.

In the abdomen, the continuation of the sympathetic system consists principally of the aggregation of ganglionic enlargements situated upon the cœliac artery, known as the *semilunar* or *cœliac ganglion.* From this ganglion a multitude of radiating and inosculating branches are sent out, which, from their diverging course and their common origin from a central mass, are termed the "solar plexus." From this, other diverging plexuses originate, which accompany the abdominal aorta and its branches, and are distributed to the stomach, small and large intestine, spleen, pancreas, liver, kidneys, supra-renal capsules, and internal organs of generation.

Beside the above ganglia there are in the abdomen four other pairs, situated in front of the lumbar vertebræ, and having similar connections with those occupying the cavity of the chest. Their filaments join the plexuses radiating from the semilunar ganglion.

In the pelvis, the sympathetic system is continued by four or five pairs of ganglia, situated on the anterior aspect of the sacrum, and terminating, at the lower extremity of the spinal column, in a single ganglion, the "ganglion impar," which is probably to be regarded as a fusion of two separate ganglia.

The entire sympathetic series is in this way composed of numerous small ganglia which are connected throughout, first, with each other; secondly, with the cerebro-spinal system; and thirdly, with the internal viscera of the body.

Physiological properties of the sympathetic nerve. — The properties and functions of the great sympathetic have been less successfully studied than those of the cerebro-spinal system, owing to the anatomical difficulties in the way of reaching and operating upon this nerve for purposes of experiment. The cerebro-spinal axis and its nerves are easily exposed and subjected to examination. It is also easy to isolate particular portions of this system, and to appreciate the disturbances of sensation and motion consequent upon local lesions or irritations. The phenomena, furthermore, which result from experiments upon this part of the nervous apparatus, are promptly produced, are well-marked in character,

and are, as a general rule, readily understood by the experimenter. On the other hand, the principal part of the sympathetic system is situated in the interior of the chest and abdomen; and the mere operation of opening these cavities, so as to reach the ganglionic centres, causes such a disturbance in the functions of vital organs, and such a shock to the system at large, that the results of these experiments have been always more or less confused and unsatisfactory. Furthermore, the connections of the sympathetic ganglia with each other and with the cerebro-spinal axis are so numerous and so scattered, that these ganglia cannot be completely isolated without resorting to an operation still more mutilating and injurious in its character. And finally, the sensible phenomena which are obtained by experimenting on the great sympathetic are, in many cases, slow in making their appearance, and not particularly striking or characteristic in their nature.

Notwithstanding these difficulties, however, some facts have been ascertained with regard to this part of the nervous system, which give us a certain degree of insight into its character and functions.

Influence on movement and sensibility. — The great sympathetic is endowed both with sensibility and the power of exciting motion; but these properties are less active here than in the cerebro-spinal system, and are exercised in a different manner. If we irritate, for example, a sensitive nerve in one of the extremities, or apply the galvanic current to the posterior root of a spinal nerve, the evidences of pain or of reflex action are acute and instantaneous. There is no appreciable interval between the application of the stimulus and the sensations which result from it. On the other hand, experimenters who have operated upon the sympathetic ganglia and nerves of the chest and abdomen find that evidences of sensibility are distinctly manifested here also, but much less acutely, and only after somewhat prolonged application of the irritating cause. These results correspond very closely with what we know of the vital properties of the organs which are supplied either principally or exclusively by the sympathetic; as the liver, intestine, kidneys, &c. These organs are insensible, or nearly so, to ordinary impressions. We are not conscious of the changes and operations going on in them, so long as these changes and operations retain their normal character. But they are still capable of perceiving unusual or excessive irritations, and may even become exceedingly painful when in a state of inflammation.

There is the same peculiar character in the action of the motor

nerves belonging to the sympathetic system. If the facial or hypoglossal, or the anterior root of a spinal nerve be irritated, the convulsive movement which follows is instantaneous, violent, and only momentary in its duration. But if the semilunar ganglion or its nerves be subjected to a similar experiment, no immediate effect is produced. It is only after a few seconds that a slow, vermicular, progressive contraction takes place in the corresponding part of the intestine, which continues for some time after the exciting cause has been removed.

Morbid changes taking place in organs supplied by the sympathetic present a similar peculiarity in the mode of their production. If the body be exposed to cold and dampness, for example, congestion of the kidneys shows itself perhaps on the following day. Inflammation of any of the internal organs is very rarely established within twelve or twenty-four hours after the application of the exciting cause. The internal processes of nutrition, together with their derangements, which are regarded as especially under the control of the great sympathetic, always require a longer time to be influenced by incidental causes, than those which are regulated by the nerves and ganglia of the cerebro-spinal system.

Influence on the special senses. — In the head, the sympathetic has a close and important connection with the exercise of the special senses. This is illustrated more particularly in the case of the eye, by its influence over the alternate expansion and contraction of the pupil. The ophthalmic ganglion sends off a number of ciliary nerves, which are distributed to the iris. It is connected, as we have seen, with the remaining sympathetic ganglia in the head, and receives, beside, a sensitive root from the ophthalmic branch of the fifth pair, and a motor root from the oculo-motorius. The reflex action by which the pupil contracts under a strong light falling upon the retina, and expands under a diminution of light, takes place, accordingly, through this ganglion. The impression conveyed by the optic nerve to the tubercula quadrigemina, and reflected outward by the fibres of the oculo-motorius, is not transmitted directly by the last named nerve to the iris; but passes first to the ophthalmic ganglion, and is thence conveyed to its destination by the ciliary nerves.

The reflex movements of the iris exhibit consequently a somewhat sluggish character, which indicates the intervention of a part of the sympathetic system. The changes in the size of the pupil do not take place instantaneously, with the variation in the amount of light, but always require an appreciable interval of time. If

we pass suddenly from a brilliantly lighted apartment into a dark room, we are unable to distinguish surrounding objects until a certain time has elapsed, and the expansion of the pupil has taken place; and vision even continues to grow more and more distinct for a considerable period afterward, as the expansion of the pupil becomes more complete. Again, if we cover the eyes of another person with the hand or a folded cloth, and then suddenly expose them to the light, we shall find that the pupil, which is at first dilated, contracts somewhat rapidly to a certain extent, and afterward continues to diminish in size during several seconds, until the proper equilibrium is fairly established. Furthermore, if we pass suddenly from a dark room into the bright sunshine, we are immediately conscious of a painful sensation in the eye, which lasts for a considerable time; and which results from the inability of the pupil to contract with sufficient rapidity to shut out the excessive amount of light. All such exposures should be made gradually, so that the movements of the iris may keep pace with the varying quantity of stimulus, and so protect the eye from injurious impressions.

The reflex movements of the iris, however, though accomplished through the medium of the ophthalmic ganglion, derive their original stimulus, through the motor root of this ganglion, from the oculo-motorius nerve. For it has been found that if the oculo-motorius nerve be divided between the brain and the eyeball, the pupil becomes immediately dilated, and will no longer contract under the influence of light. The motive power originally derived from the brain is, therefore, in the case of the iris, modified by passing through one of the sympathetic ganglia before it reaches its final destination.

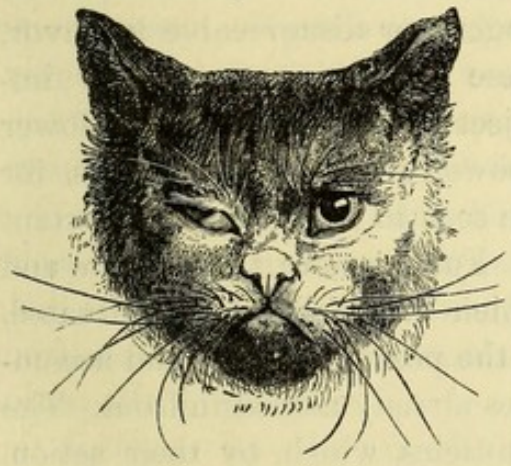
An extremely interesting fact in this connection is the following. Of the three organs of special sense in the head, viz., the eye, the nose, and the ear, each one is provided with two sets of muscles, superficial and deep, which together regulate the quantity of stimulus admitted to the organ, and the mode in which it is received. The superficial set of these muscles is animated by branches of the facial nerve; the deep-seated or internal set, by filaments from a sympathetic ganglion.

Thus, the front of the eyeball is protected by the orbicularis and levator palpebræ superioris muscles, which open or close the eyelids at will, and allow a larger or smaller quantity of light to reach the cornea. These muscles are supplied by the oculo-motorius and

facial nerves, and are for the most part voluntary in their action. The iris, on the other hand, is a more deeply-seated muscular curtain, which regulates the quantity of light admitted through the pupil. Its muscular fibres are supplied, as we have seen, by filaments from the ophthalmic ganglion, and their movements are involuntary in character.

Division of the sympathetic nerve in the middle of the neck has accordingly a very singular and instantaneous effect on the muscular apparatus of the eye. Within a very few seconds after the above operation has been performed upon the cat, the pupil of the corresponding eye becomes strongly contracted, and remains in that condition. At the same time the third eyelid, or "nictitating membrane," with which these animals are provided, is drawn partially over the cornea, and the upper and lower eyelids also approximate very considerably to each other; so that all the apertures guarding the eyeball are very perceptibly narrowed, and the expression of the face on that side is altered in a corresponding degree. This effect upon the pupil has been explained by supposing the circular fibres of the iris, or the constrictors of the pupil, to be animated exclusively by nervous filaments derived from the oculo-motorius; and the radiating fibres, or the dilators, to be supplied by the sympathetic. Accordingly, while division of the oculo-motorius would produce dilatation of the pupil, by paralysis of the circular fibres only, division of the sympathetic would be followed by exclusive paralysis of the dilators, and a permanent contraction of the pupil would consequently take place. The above explanation, however, is not entirely satisfactory; since, in the first place, division of the oculo-motorius, as the experiments of Bernard have shown,[1] does not by itself produce complete dilatation of the pupil; and, secondly, after division of the sympathetic nerve in the cat, as we have already shown, not only is the pupil

Fig. 178.



Cat, after section of the right sympathetic.

[1] Leçons sur la Physiologie et la Pathologie du Système Nerveux, Paris, 1858, vol. ii. p. 203.

contracted, but both the upper and lower eyelids and the nictitating membrane are also drawn partially over the cornea, and assist in excluding the light. The last-named effect cannot be owing to any direct paralysis, from division of the fibres of the sympathetic. It is more probable that the section of this nerve operates simply by exaggerating for a time the sensibility of the retina, owing to the vascular congestion of the parts; and that the partial closure of the eyelids and pupil is a secondary consequence of that condition.

In the olfactory apparatus, the anterior or superficial set of muscles are the compressors and elevators of the alæ nasi, which are animated by filaments of the facial nerve. By their action, odoriferous vapors, when faint and delicate in their character, are snuffed up and directed into the upper part of the nasal passages, where they come in contact with the most sensitive portions of the olfactory membrane; or, if too pungent or disagreeable in flavor, are excluded from entrance. These muscles are not very important or active in the human subject; but in many of the lower animals with a more active and powerful sense of smell, as, for example, the carnivora, they may be seen to play a very important part in the mechanism of olfaction. Furthermore, the levators and depressors of the velum palati, which are more deeply situated, serve to open or close the orifice of the posterior nares, and accomplish a similar office with the muscles already named in front. The levator palati and azygos uvulæ muscles, which, by their action, tend to close the posterior nares, are supplied by filaments from the spheno-palatine ganglion, and are involuntary in their character.

The ear has two similar sets of muscles, similarly supplied. The first, or superficial set, are those moving the external ear, viz., the anterior, superior, and posterior auriculares. Like the muscles of the anterior nares, they are comparatively inactive in man, but in many of the lower animals are well developed and important. In the horse, the deer, the sheep, &c., they turn the ear in various directions so as to catch more distinctly faint and distant sounds, or to exclude those which are harsh and disagreeable. These muscles are supplied by filaments of the facial nerve, and are voluntary in their action.

The deep-seated set are the muscles of the middle ear. In order to understand their action, we must recollect that sounds are transmitted from the external to the middle ear through the membrane of the tympanum, which vibrates, like the head of a drum, on receiving sonorous impulses from without.

The membrane of the tympanum, accordingly, which is an elastic sheet, stretched across the passage to the internal ear, may be made more or less sensitive to sonorous impressions by varying its condition of tension or relaxation. This condition is regulated, as we have already seen, by the combined action of the two muscles of the middle ear, viz., the tensor tympani and the stapedius. The first named muscle, the action of which is perfectly well understood, is supplied with nervous filaments from the otic ganglion of the sympathetic. By its contraction, the handle of the malleus is drawn inward, bringing the membrana tympani with it, and putting this membrane upon the stretch. On the relaxation of the muscle, the chain of bones returns to its ordinary position, by the elasticity of the neighboring parts, and the previous condition of the tympanic membrane is restored. This action, so far as we can judge, is purely involuntary. But the stapedius muscle is separately supplied by a minute branch of the facial nerve. It is probable that this arrangement enables us to make also a certain degree of voluntary exertion, in listening intently for faint or distant sounds.

In all these instances, the reflex action taking place in the deeper seated muscles, originates from a sensation which is conveyed inward to the cerebro-spinal centres, and is then transmitted outward to its final destination through the medium of one of the sympathetic ganglia.

Influence on the circulation. — Perhaps the most important fact concerning the sympathetic is that of its influence over the vascularity and nutrition of the parts supplied by it. In the first place, the division of the sympathetic produces immediately a *vascular congestion in the corresponding parts.* If the sympathetic be divided, in the rabbit, in the middle of the neck, a vascular congestion of all parts of the head, on the corresponding side, immediately follows. This congestion is most distinctly evident in the thin and transparent ears; and within a few minutes after the operation, the difference in their appearance on the two sides is strongly pronounced. All the vessels of the ear on the affected side become turgid with blood; and many which were before imperceptible, become distinctly visible. This effect of the division of the sympathetic, which was first pointed out by Bernard, we have often verified. It lasts for a considerable time and we have even seen it very distinct at the end of three weeks. It remains for a longer time when a portion of the nerve has been cut out, or the cervical ganglion extirpated, than when its filaments

have been simply divided by a transverse section. It finally disappears when the separated filaments have been re-united and their functional activity restored.

The vascular congestion thus produced by division of the sympathetic nerve is accompanied by three important phenomena, all intimately connected with each other.

First, the quantity of blood circulating in the part is increased, and the rapidity of its movement accelerated. The bloodvessels are not in a state of passive congestion, due to an obstruction to the return of the venous blood. On the contrary, all the vessels of the part are simultaneously dilated, a larger quantity of blood passes through the capillaries in a given time, and returns by the veins in greater abundance than before.

Secondly, there is a remarkable elevation of temperature in the affected part. This elevation of temperature is very perceptible to the touch in the ear of the rabbit and even in the integument of the corresponding side of the head. Measured by the thermometer, it has been found by Bernard to reach, in some cases, 8° or 9° F. It is evidently due to the increased quantity of blood circulating in the vessels of the part; since the blood coming from the interior and warmer parts of the body supplies the ear with more heat in proportion to the greater abundance and rapidity with which it traverses the vascular tissues.

Thirdly, the color of the venous blood in the affected part becomes brighter and more ruddy. This effect is also due to the increased rapidity of the circulation. As the arterial blood is deprived of its oxygen and darkened in color by the changes of nutrition which usually take place in the tissues, if the rapidity of the circulation be suddenly increased, a certain proportion of the blood escapes deoxidation, and its change in color, from arterial to venous, is incomplete. The blood accordingly, under these circumstances, returns by the veins of the affected part in greater abundance, of a higher temperature, and of a more ruddy color, than on the uninjured side of the body.

Now it is found that, when a vascular congestion of the part has been thus produced by division of the sympathetic, if that portion of the divided nerve which remains in connection with the tissues be irritated by electricity, all the above effects rapidly disappear; the bloodvessels of the ear and corresponding side of the head contract to their previous diameter, the quantity of blood circulating through the tissues is diminished, the temperature of the parts is reduced

in a corresponding degree, and the blood in the veins returns to its ordinary dark color. The variations in the rapidity of the circulation dependent on the condition of the sympathetic nerve are shown by Bernard[1] in the following experiment. In a living rabbit the upper part of one ear is cut off with a pair of very sharp scissors, so that the blood may escape in jets from the divided ends of the small arteries. The force and height of the arterial jets having been observed, the sympathetic nerve is then divided in the middle of the neck on the corresponding side. Immediately the blood escapes from the wounded ear in greater abundance, and the arterial jets rise to double or even triple their former height. The galvanic current is then applied to the divided extremity of the sympathetic, above the point of section, when the streams of blood escaping from the wound gradually diminish and disappear; but recommence and again increase in intensity so soon as the galvanization of the nerve is suspended.

The same author has shown that a similar influence is exerted by the sympathetic nerve upon the circulation in the limbs.[2] If the lumbar nerves of one side be divided, in the dog, within the cavity of the spinal canal, a paralysis of motion and sensibility is produced in the corresponding limb, but there is no change in its vascularity or temperature; while if the lumbar portion of the sympathetic be divided or excised, without disturbing the spinal nerves, all the signs of increased temperature and activity of the circulation are at once manifested in the limb below, without any loss of motion or sensibility. Exsection of the first thoracic ganglion of the sympathetic produces similar effects in the anterior extremity; and these effects are diminished or suspended by electrical irritation applied to the upper end of the divided nerve.

Division of the sympathetic nerve, accordingly, produces a dilatation of the vessels and consequent increased rapidity of the circulation, and causes the blood to retain its red color even in the veins; while galvanization of the same nerve produces contraction of the vessels, diminishes the quantity of the circulating fluid, and causes the change in color of the blood, from arterial to venous.

The same thing takes place in the glandular organs. If the submaxillary or parotid gland be exposed in the living animal,[3] so

[1] Journal de la Physiologie. July, 1862, p. 397.

[2] Journal de la Physiologie, loc. cit.

[3] Bernard. Leçons sur les Liquides de l'Organisme. Paris, 1859, vol. i. p. 230, et seq.

long as the gland is in its ordinary condition it will be seen that the blood passing through it is converted from arterial to venous, and returns dark colored by the veins. But if the filament of the sympathetic nerve which accompanies the external carotid artery be divided, the quantity of blood flowing through the gland is at once increased, and at the same time appears of a red color in the veins. The same changes occur when the gland is excited to secretion by stimulating the organs of taste.

An antagonism appears to exist, in the regulation of the circulation in the vascular organs, between the sympathetic nerve and the motor filaments derived from the cerebro-spinal system. For if the branch of the chorda tympani which penetrates the submaxillary gland be galvanized, it produces an excitement of the glandular secretion,[2] increased activity of the circulation, and a red color of the blood in the veins. The division of this nerve is followed by a contrary result. The effects produced, therefore, by galvanization of the chorda tympani are those produced by division of the sympathetic; and the effects produced by galvanizing the sympathetic are those which follow division of the chorda tympani.

The vascularity of the parts, accordingly, as well as the functional activity of the vascular organs, are under the control of the nervous system. The filaments of the sympathetic nerve, as we have seen, accompany everywhere the bloodvessels, enveloping the arterial branches with an abundant plexus, and following them to their minutest ramifications. These sympathetic fibres appear to act by causing a contraction in the organic muscular fibres of the small arteries, and thus to regulate the resistance of these vessels, and the passage of the blood through them. When the sympathetic nerve is excited, the vessels are contracted, the blood passes through them but slowly, and is fully converted, during its passage, into venous blood. When the influence of this nerve is diminished or suspended, the vessels are dilated, the circulation is increased, and the blood, passing through the vessels with greater rapidity, does not suffer the nutritive changes which result in the alteration of its color from arterial to venous.

Influence on reflex actions. — The influence of the sympathetic nerve and the consequences of its division upon the thoracic and abdominal viscera have been only very imperfectly investigated by experimental methods. It undoubtedly serves as a medium of reflex action between the sensitive and motor

[1] Bernard. Op. cit., vol. i. p. 312.

portions of the digestive, excretory, and generative apparatuses; and it is certain that it also takes part in reflex actions in which the cerebro-spinal system is at the same time interested. There are accordingly three different kinds of reflex action, taking place wholly or partially through the sympathetic system, which may be observed to occur in the living body.

1st. *Reflex actions taking place from the internal organs, through the sympathetic and cerebro-spinal systems, to the voluntary muscles and sensitive surfaces.*—The convulsions of young children are often owing to the irritation of undigested food in the intestinal canal. Attacks of indigestion are also known to produce temporary amaurosis, double vision, strabismus, and even hemiplegia. Nausea, and a diminished or capricious appetite, are often prominent symptoms of early pregnancy, induced by the peculiar condition of the uterine mucous membrane.

2d. *Reflex actions taking place from the sensitive surfaces, through the cerebro-spinal and sympathetic systems, to the involuntary muscles and secreting organs.*—Imprudent exposure of the integument to cold and wet, will often bring on a diarrhœa. Mental and moral impressions, conveyed through the special senses, will affect the motions of the heart, and disturb the processes of digestion and secretion. Terror, or an absorbing interest of any kind, will produce a dilatation of the pupil, and communicate in this way a peculiarly wild and unusual expression to the eye. Disagreeable sights or odors, or even unpleasant occurrences, are capable of hastening or arresting the menstrual discharge, or of inducing premature delivery.

3d. *Reflex actions taking place, through the sympathetic system, from one part of the internal organs to another.*—The contact of food with the mucous membrane of the small intestine excites a peristaltic movement in the muscular coat. The mutual action of the digestive, urinary and internal generative organs upon each other takes place through the medium of the sympathetic ganglia and their nerves. The variations of the capillary circulation in different abdominal viscera, corresponding with the state of activity or repose of their associated organs, are to be referred to a similar nervous influence. These phenomena are not accompanied by any consciousness on the part of the individual, nor by any apparent intervention of the cerebro-spinal system.

SECTION III.

REPRODUCTION.

CHAPTER I.

ON THE NATURE OF REPRODUCTION, AND THE ORIGIN OF PLANTS AND ANIMALS.

THE process of reproduction is the most characteristic, and in many respects the most interesting, of all the phenomena presented by organized bodies. It includes the whole history of the changes taking place in the organs and functions of the individual at successive periods of life, as well as the production, growth, and development of the new germs which make their appearance by generation.

For all organized bodies pass through certain well-defined epochs or phases of development, by which their structure and functions undergo successive alterations. We have already seen that the living animal or plant is distinguished from inanimate substances by the incessant changes of nutrition and growth which take place in its tissues. The muscles and the mucous membranes, the osseous and cartilaginous tissues, the secreting and circulatory organs, all incessantly absorb oxygen and nutritious material from without, and assimilate their molecules; while new substances, produced by a retrogressive alteration and decomposition, are at the same time excreted and discharged. These nutritive changes correspond in rapidity with the activity of the other vital phenomena; since the production of these phenomena, and the very existence of the vital functions, depend upon the regular and normal continuance of the nutritive process. Thus the organs and tissues, which are always the seat of this double change of renovation and decay,

retain nevertheless their original constitution, and continue to be capable of exhibiting the vital phenomena.

The above changes, however, are not in reality the only ones which take place. For although the structure of the body and the composition of its constituent parts appear to be maintained in an unaltered condition, by the nutritive process, from one moment to another, or from day to day, yet a comparative examination of them at greater intervals of time will show that this is not precisely the case; but that the changes of nutrition are, in point of fact, progressive as well as momentary. The composition and properties of the skeleton, for example, are not the same at the age of twenty-five that they were at fifteen. At the later period it contains more calcareous and less organic matter than before; and its solidity is accordingly increased, while its elasticity is diminished. Even the *anatomy* of the bones alters in an equally gradual manner; the medullary cavities enlarging with the progress of growth, and the cancellated tissue becoming more open and spongy in texture. We have already noticed the difference in the quantity of oxygen and carbonic acid inspired and exhaled at different ages. The muscles, also, if examined after the lapse of some years, are found to be less irritable than formerly, owing to a slow but steady and permanent deviation in their intimate constitution.

The vital properties of the organs, therefore, change with their varying structure; and a time comes at last when they are perceptibly less capable of performing their original functions than before. This alteration, being dependent on the varying activity of the nutritive process, continues necessarily to increase. The very exercise of the vital powers is inseparably connected with the subsequent alteration of the organs employed in them; and the functions of life, therefore, instead of remaining indefinitely the same, pass through a series of successive changes, which finally terminate in their complete cessation.

The history of a living animal or plant is, therefore, a history of successive epochs or phases of existence, in each of which the structure and functions of the body differ more or less from those in every other. Every living being has a definite term of life, through which it passes by the operation of an invariable law, and which, at some regularly appointed time, comes to an end. The plant germinates, grows, blossoms, bears fruit, withers, and decays. The animal is born, nourished, and brought to maturity, after which he retrogrades and dies. The very commencement of existence, by

leading through its successive intermediate stages, conducts at last necessarily to its own termination.

But while individual organisms are thus constantly perishing and disappearing from the stage, the particular kind, or *species*, remains in existence, apparently without any important change in the cha racter or appearance of the organized forms belonging to it. The horse and the ox, the oak and the pine, the different kinds of wild and domesticated animals, even the different races of man himself, have remained without any essential alteration ever since the earliest historical epochs. Yet during this period innumerable individuals, belonging to each species or race, must have lived through their natural term and successively passed out of existence. A *species* may therefore be regarded as a type or class of organized beings, in which the particular forms or structures composing it die off constantly and disappear, but which nevertheless repeats itself from year to year, and maintains its ranks constantly full by the regular accession of new individuals. This process, by which new organisms make their appearance, to take the place of those which are destroyed, is known as the process of *reproduction* or *generation*. Let us now see in what manner it is accomplished.

It has always been known that, as a general rule in the process of generation, the young animals or plants are produced directly from the bodies of the elder. The relation between the two is that of parents and progeny; and the new organisms, thus generated, become in turn the parents of others which succeed them. For this reason, wherever such plants or animals exist, they indicate the previous existence of others belonging to the same species; and if by any accident the whole species should be destroyed in any particular locality, no new individuals could be produced there, unless by the previous importation of others of the same kind.

The commonest observation shows this to be true in regard to those animals and plants with whose history we are most familiarly acquainted. An opinion, however, has sometimes been maintained that there are exceptions to this rule; and that living beings may, under certain circumstances, be produced from inanimate substances, withont any similar plants or animals having preceded them; presenting, accordingly, the singular phenomenon of a progeny without parents. Such a production of organized bodies is known by the name of *spontaneous generation*. It is believed by the majority of physiologists at the present day that no such spontaneous generation ever takes place; but that plants and animals are always

derived, by direct reproduction, from previously existing parents of the same species. As this, however, is a question of some importance, and one which has been frequently discussed in works on physiology, we shall proceed to pass in review the facts which have been adduced in favor of the occurrence of spontaneous generation, as well as those which would lead to its disproval and rejection.

It is evident, in the first place, that many apparent instances of spontaneous generation are found to be of a very different character as soon as they are subjected to a critical examination. Thus grasshoppers and beetles, earthworms and crayfish, the swarms of minute insects that fill the air over the surface of stagnant pools, and even frogs, moles, and lizards, have been supposed in former times to be generated directly from the earth or the atmosphere; and it was only by investigating carefully the natural history of these animals that they were ascertained to be produced in the ordinary manner by generation from parents, and were found to continue the reproduction of their species in the same way. A still more striking instance is furnished by the production of maggots in putrefying meat, vegetables, flour paste, fermenting dung, &c. If a piece of meat be exposed, for example, and allowed to undergo the process of putrefaction, at the end of a few days it will be found to contain a multitude of living maggots which feed upon the decomposing flesh. Now these maggots are always produced under the same conditions of warmth, moisture and exposure, and at the same stage of the putrefactive process. They are never to be found in fresh meat, nor, in fact, in any other situation than the one just mentioned. They appear, consequently, without any similar individuals having existed in the same locality; and considering the regularity of their appearance under the given conditions, and their absence elsewhere, it has been believed that they were spontaneously generated, under the influence of warmth, moisture, and the atmosphere, from the decaying organic substances.

A little examination, however, discovers a very simple solution of the foregoing difficulty. On watching the exposed animal or vegetable substances during the earlier periods of their decomposition, it is found that certain species of flies, attracted by the odor of the decaying material, hover round it and deposit their eggs upon its surface or in its interior. These eggs, hatched by the warmth to which they are exposed, produce the maggots; which are simply the young of the winged insects, and which after a time become transformed, by the natural progress of development, into

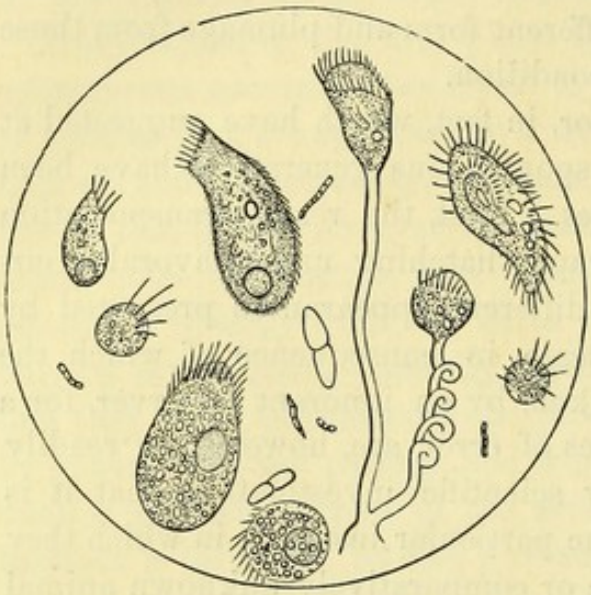
perfect insects similar to their parents. The difficulty of accounting for the presence of the maggots by generation, therefore, depended simply on the difference in appearance between them and their parents. This difference, however, is merely a temporary one, corresponding with the difference in age, and disappears when the development of the animal is complete; just as the young chicken, when recently hatched, has a different form and plumage from those which it presents in the adult condition.

Nearly all the causes of error, in fact, which have suggested at various times the doctrine of spontaneous generation, have been derived from these two sources. First, the ready transportation of eggs or germs, and their rapid hatching under favorable circumstances; and secondly, the different appearances presented by the same animal at different ages, in consequence of which the youthful animal may be mistaken, by an ignorant observer, for a different species. These sources of error are, however, so readily detected, as a general rule, by scientific investigation, that it is hardly necessary to point out the particular instances in which they exist. In fact, whenever a rare or comparatively unknown animal or plant has been at any time supposed to be produced by spontaneous generation, it has only been necessary, for the most part, to investigate thoroughly its habits and functions, to discover its secret methods of propagation, and to show that they correspond, in all essential particulars, with the ordinary laws of reproduction. The limits, therefore, within which the doctrine of spontaneous generation can be applied, have been narrowed in precisely the same degree that the study of natural history and comparative physiology has advanced. At present, indeed, there remain but two classes of phenomena which are ever supposed to lend any support to the above doctrine; viz., the existence and production, 1st, of infusorial animalcules, and 2d, of animal and vegetable parasites. We shall now proceed to examine these two parts of the subject in succession.

Infusorial Animalcules.—If water, holding in solution organic substances, be exposed to the contact of the atmosphere at ordinary temperatures, it is found after a short time to be filled with swarms of minute living organisms, which are visible only by the microscope. The forms of these microscopic animalcules are exceedingly varied; owing either to the great number of species in existence, or to their rapid alteration during the successive pe-

riods of their growth. Ehrenberg has described more than 300 different varieties of them. They are generally provided with cilia attached to the exterior of their bodies, and are, for the most part, in constant and rapid motion in the fluid which they inhabit.

Fig. 179.



Different kinds of INFUSORIA.

Owing to their presence in animal and vegetable watery infusions, they have received the name of "infusoria," or "infusorial animalcules."

Now these infusoria are always produced under the conditions which we have described above. The animal or vegetable substance used for the infusion may be previously baked or boiled, so as to destroy all living germs which it might accidentally contain; the water in which it is infused may be carefully distilled, and thus freed from all similar contamination; and yet the infusorial animalcules will make their appearance at the usual time and in the usual abundance. It is only requisite that the infusion be exposed to a moderately elevated temperature, and to the access of atmospheric air; conditions which are equally necessary for maintaining the life of all animal and vegetable organisms, whatever be the source from which they are derived. Under the above circumstances, therefore, either the animalcules must have been produced by spontaneous generation in the watery infusion, or their germs must have been introduced into it through the medium of the atmosphere. No such introduction has ever been directly demonstrated, nor have even any eggs or germs belonging to the infusoria ever been detected.

Nevertheless, there is every probability that the infusoria are produced from germs, and not by spontaneous generation. Since the infusoria themselves are microscopic in size, it is not surprising that their eggs, which must be smaller still, should have escaped observation. We know, too, that in many instances the minute germs of animals or plants may be wafted about in a dry state by the atmosphere, until, by accidentally coming in contact with warmth and moisture, they become developed and bring forth living organ-

isms. The eggs of the infusoria, accordingly, may be easily raised and held suspended in the atmosphere, under the form of minute dust-like particles, ready to germinate and become developed whenever they are caught by the surface of a stagnant pool, or of any artificially prepared infusion. In point of fact, the atmosphere does really contain an abundance of such dust-like particles, even when it appears to be most transparent and free from impurities. This may be readily demonstrated by admitting a single beam of sunshine into a darkened apartment, when the shining particles suspended in the atmosphere become immediately visible in the track of the sunbeam. Again, if a perfectly clean and polished mirror be placed with its face upward in a securely closed room, and left undisturbed for several days, its surface at the end of that time will be found to be dimmed by the settling upon it of minute dust, deposited from the atmosphere. There is no reason, therefore, for disbelieving that the air may always contain a sufficient number of organic germs for the production of infusorial animalcules.

A certain degree of doubt, however, still remains respecting the origin of some kinds of infusoria, owing to the fact that they will make their appearance, under some circumstances, in organic infusions which have been subjected to a boiling temperature and afterward kept in hermetically closed vessels. The most recent and perhaps the most satisfactory experiments of this kind are those of Prof. Jeffries Wyman,[1] who operated with infusions of both animal and vegetable substances. He boiled these infusions under the ordinary pressure of the atmosphere, that is, at a temperature of 212° F., for periods varying from fifteen minutes to two hours, in glass vessels so arranged that the atmospheric air could only gain access to their interior through tubes filled with red-hot iron wire. Any germs passing into the solution with the atmosphere would undoubtedly, therefore, be destroyed by contact with the heated iron. Nevertheless, he found, after some days, that living infusoria had made their appearance in the solutions. In other instances he placed the fresh solutions in hermetically sealed glass vessels, which were then submerged, for from five to fifteen minutes, in boiling water under a pressure of two to five atmospheres, that is, at a temperature of 250° to 307° F.

In none of these experiments did the infusoria appear as soon as

[1] American Journal of Science and Arts. Second Series, vol. 34, p. 79.

in similar infusions exposed to the air; and although simple boiling for a short time does not prevent the subsequent appearance of living organisms, yet a prolonged boiling at the ordinary temperature, or a short boiling at unusually high temperatures, does so prevent it. According to Prof. Wyman, the appearance of infusorial life is absolutely prevented by exposure of the organic solution to ordinary boiling for five hours, or to boiling for fifteen minutes under a pressure of five atmospheres.

The only difficulty, therefore, in supposing the infusoria which appear in these cases to be produced from previously existing germs, is that we must attribute to these germs the power of withstanding, for a certain time, a temperature at and above that of boiling water. This is not an impossible supposition, for two reasons. First, because this power is limited, as we have seen, even for these infusoria; which do not appear in a solution which has once been boiled for a long time, or at a very high temperature, even though it be kept afterward at the ordinary temperature of the air. Secondly, because we know already that certain species of plants and animals will easily withstand an elevated temperature which is fatal to others. The amphibious reptiles, for example, are easily killed by being confined in water at 100° F., which is the natural temperature of the warm-blooded animals. Because the temperature of boiling water, therefore, is fatal to the germs of many kinds of animals, we cannot be sure that it is necessarily fatal to those of all. Dr. S. Weir Mitchell[1] has even found that vibriones, the infusoria which most frequently appear in boiled organic solutions, will also grow and thrive in the venom of the rattlesnake, when beginning to putrefy, and when it is still a deadly poison to all the higher animals.

It is therefore probable that the infusoria of organic solutions are produced from germs which have the power of withstanding, to a certain degree, the action of a high temperature.

Animal and Vegetable Parasites.—This very remarkable group of organized bodies is distinguished by the fact that they live either upon the surface or in the interior of other animal or vegetable organisms. Thus, the *mistletoe* fixes itself on the branches

[1] Researches on the Venom of the Rattlesnake Smithsonian Contributions to Knowledge. Washington, 1861, pp. 32. 53.

of aged trees; the *Oidium albicans* vegetates upon the mucous surfaces of the mouth and pharynx; the *Botrytis Bassiana* attacks the body of the silkworm, and plants itself in its tissues; while many species of *trematoid worms* live attached to the gills of fish and of water-lizards.

These parasites are usually nourished by the fluids of the animal whose body they inhabit. Each particular species of parasite is found to inhabit the body of a particular species of animal, and is not found elsewhere. They are met with, moreover, as a general rule, only in particular organs, or even in particular parts of a single organ. Thus the Tricocephalus dispar is found only in the cæcum; the Strongylus gigas in the kidney; the Distoma hepaticum in the biliary passages. The Distoma variegatum is found only in the lungs of the green frog, the Distoma cylindraceum in those of the brown. The Tænia solium is found in the intestine of the human subject in certain parts of Europe, while the Bothriocephalus latus occurs exclusively in others. It appears, therefore, as if some local combination of conditions were necessary to the production of these parasites; and they have been supposed, accordingly, to originate by spontaneous generation in the localities where they are exclusively known to exist.

A little consideration will show, however, that the above conditions are not, properly speaking, necessary or sufficient for the *production*, but only for the *development* of these parasites. All the parasites mentioned above reproduce their species by generation. They have male and female organs, and produce fertile eggs, often in great abundance. The eggs contained in a single female Ascaris are to be counted by thousands; and in a tapeworm, it is said, even by millions. Now these eggs, in order that they may be hatched and produce new individuals, require certain special conditions which are favorable for their development; in the same manner as the seeds of plants require, for their germination and growth, a certain kind of soil and a certain supply of warmth and moisture. It is accordingly no more surprising that the Oxyuris vermicularis should inhabit the rectum, and the Ascaris lumbricoides the ileum, than that the Lobelia inflata should grow only in dry pastures, and the Lobelia cardinalis by the side of running brooks. The lichens flourish on the exposed surfaces of rocks and stone walls; while the fungi vegetate in darkness and moisture, on the decaying trunks of dead trees. Yet no one imagines these vegetables to be spontaneously generated from the soil which they inhabit. The truth

is simply this, that if the animal or vegetable germ be deposited in a locality which affords the requisite conditions for its development, it becomes developed; otherwise not. Each female Ascaris produces, as we have said, many thousands of ova. Now, though the chances are very great against any particular one of these ova being accidentally transported into the intestinal canal of another individual, it is easy to see that there are many causes in operation by which *some* of them might be so transported. By far the greater number undoubtedly perish, from not meeting with the conditions necessary for their development. One in a thousand, or perhaps one in a million, is accidentally introduced into the body of another individual, and consequently becomes developed there into a perfect Ascaris.

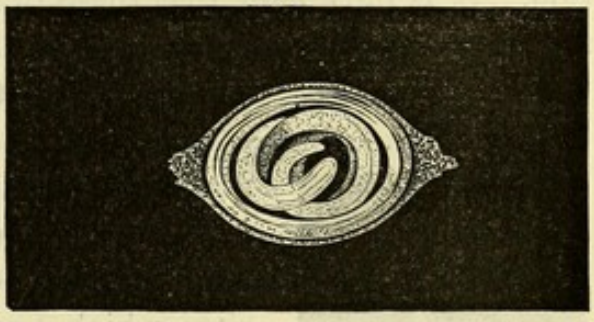
The circumstance, therefore, that particular parasites are confined to particular localities, presents no greater difficulty as to their mode of reproduction, than the same fact regarding other animal and vegetable organisms.

Neither is there any difficulty in accounting for the introduction of parasitic germs into the interior of the body. The air and the food offer a ready means of entrance into the respiratory and digestive passages; and, a parasite once introduced into the intestine, there is no difficulty in accounting for its presence in any of the ducts leading from or opening into the alimentary canal. Some parasites are known to insinuate themselves directly underneath the surface of the skin; as the Pulex penetrans or "chiggo" of South America, and the Ixodes Americanus or "tick." Others, like the Œstrus bovis, penetrate the integument for the purpose of depositing their eggs in the subcutaneous areolar tissue. Some may even gain an entrance into the bloodvessels, and circulate in this way all over the body. Thus the Filaria rubella is found alive in the bloodvessels of the frog, the Distoma hæmatobium in those of the human subject, and a species of Spiroptera in those of the dog. It is easy to see, therefore, how, by such means, parasitic germs may be conveyed to any part of the body; and may even be deposited, by accidental arrest of the circulation, in the substance of the solid organs.

The most serious difficulty, however, in the way of accounting for the production of parasitic organisms, was that presented by the existence of a class known as the *encysted* or *sexless* entozoa. These parasites for the most part occupy the interior of the solid organs and tissues, into which they could not have gained access by the

mucous canals. Thus the Cœnurus cerebralis is found imbedded in the substance of the brain, the Trichina spiralis in the voluntary muscles, and the Cysticercus cellulosæ in the areolar tissue of various parts of the body. They are also distinguished from all other parasites by two peculiar characters. First, they are enclosed in a distinct cyst, with which they have no organic connection and from which they may be readily separated; and secondly, their generative organs are either imperfectly developed or altogether wanting. The *Trichina spiralis*, for example, (Fig. 180,) is enclosed in an ovoid cyst, composed of an organic material deposited in concentric layers; the whole enveloped in a membranous or tubular prolongation tapering from the two extremities. The worm lies loose in the central cavity of the cyst, coiled up in a spiral form.

Fig. 180.



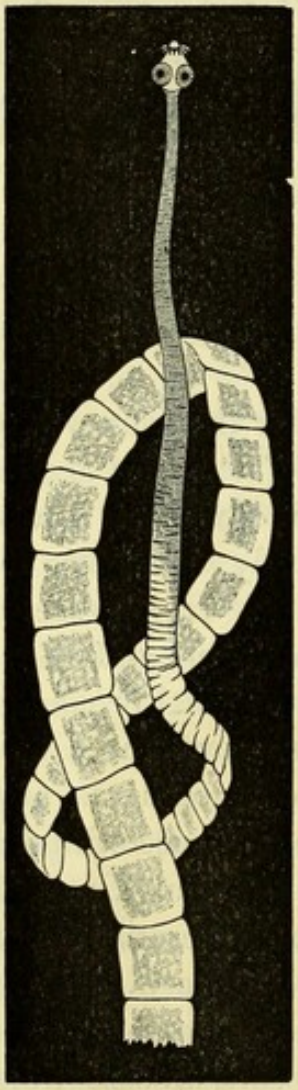
TRICHINA SPIRALIS: from muscles of thigh of human subject. Magnified 40 diameters.

Now we have seen that it is easy to account for the conveyance of these or any other parasites into the interior of vascular organs and tissues; the eggs from which they are produced being transported by the bloodvessels to any part of the body, and there retained by a local arrest of the capillary circulation. In the case of the encysted entozoa, however, we have a much greater difficulty; since many of these parasites are entirely without sexual organs or generative apparatus of any sort, nor have they ever been discovered in the act of producing eggs, or of developing in any manner a progeny similar to themselves. It appears, accordingly, difficult to understand how animals, which are without a sexual apparatus, should have been produced by sexual generation. As it is certain that they can have no progeny, it would seem equally evident that they must have been produced without a parentage.

This difficulty, however, serious as it at first appears, is susceptible of a very simple explanation. The case is in many respects analogous to that of the maggots, hatched from the eggs of flies in putrefying meat. These maggots are also without sexual organs; for they are still imperfectly developed, and in a kind of embryonic condition. It is only after their metamorphosis into perfect insects, that generative organs are developed and a distinction between the

sexes manifests itself. This is, indeed, more or less the case with all animals and with all vegetables. The blossom, which is the sexual apparatus of the plant, does not appear, as a general rule, until the growth of the vegetable has continued for a certain time, and it has acquired a certain age and strength. Even in the human subject the sexual organs, though present at birth, are still very imperfectly developed as to size, and altogether inactive in function. It is only later that these organs acquire their full growth, and the sexual characters become complete. In very many of the lower animals the sexual organs are entirely absent at birth, and appear only at a later period of development.

Fig. 181.



TÆNIA.

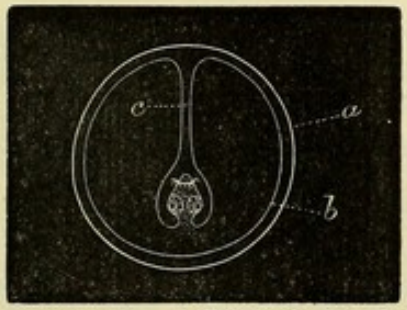
Now the encysted or sexless entozoa are simply the undeveloped young of other parasites which propagate by sexual generation; the membrane in which they are inclosed being either an embryonic envelope, or else an adventitious cyst formed round the parasitic embryo. These embryos have come, in the natural course of their migrations, into a situation which is not suitable for their complete development. Their development is accordingly arrested at that point; and the parasite never reaches the adult condition, until removed from the situation in which it has been placed, and transported to another locality.

The above explanation has been demonstrated to be the true one, more particularly with regard to the Tænia, or tapeworm, and several varieties of Cysticercus. The *Tænia* (Fig. 181) is a parasite of which different species are found in the intestine of the human subject, the dog, cat, fox, and other of the lower animals. Its upper extremity, termed the "head," consists of a nearly globular mass, presenting upon its lateral surfaces a set of four muscular disks, or "suckers," and terminating anteriorly in a conical projection which is provided with a crown of curved processes or hooks, by which the parasite attaches itself to the intestinal mucous membrane. To this "head" succeeds a slender ribbon-shaped neck, which is at first smooth, but

which soon becomes transversely wrinkled, and afterward divided into distinct rectangular pieces or "articulations." These articulations multiply by a process of successive growth or budding, from the wrinkled portion of the neck; and are constantly removed farther and farther from their point of origin by new ones formed behind them. As they gradually descend, by the process of growth, farther down the body of the tapeworm, they become larger and begin to exhibit a sexual apparatus, developed in their interior. In each fully formed articulation there are contained both male and female organs of generation; and the mature eggs, which are produced in great numbers, are thrown off together with the articulation itself from the lower extremity of the tapeworm. Since the articulations are successively produced, as we have mentioned above, by budding from the neck and the back part of the head, the parasite cannot be effectually dislodged by taking away any portion of the body, however large; since it is subsequently reproduced from the head, and continues its growth as before. But if the head itself be removed from the intestine, no further reproduction of the articulations can take place.

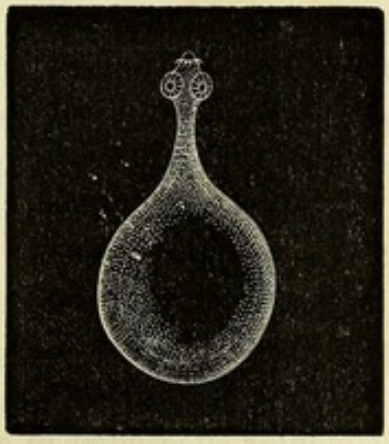
The *Cysticercus* is an encysted parasite, different varieties of which are found in the liver, the peritoneum, and the meshes of the areolar tissue in various parts of the body. It consists (Fig. 182) first, of a globular sac, or cyst (*a*), which is not adherent to the tissues of the organ in which the parasite is found, but may be easily sepa

Fig. 182.



CYSTICERCUS.—*a*. External cyst. *b* Internal sac, containing fluid. c. Narrow canal, formed by involution of walls of sac, at the bottom of which is the head of the tænia.

Fig. 183.



CYSTICERCUS, unfolded.

rated from them. In its interior is found another sac (*b*), lying loose in the cavity of the former, and filled with a serous fluid. This second sac presents, at one point upon its surface, a puckered depression, leading into a long, narrow canal (*c*). This canal, which is formed by an involution of the walls of the second sac, presents

at its bottom a small globular mass, like the head of the Tænia, provided with suckers and hooks, and supported upon a short slender neck. If the outer investing sac be removed, the narrow canal just described may be everted by careful manipulation, and the parasite will then appear as in Fig. 183, with the head and neck resembling those of a Tænia, but terminating behind in a dropsical sac-like swelling, instead of the chain of articulations which are characteristic of the fully formed tapeworm.

Now it has been shown, by the experiments of Küchenmeister, Siebold, and others, that the Cysticercus is only the imperfectly developed embryo, or young, of the Tænia. When the mature articulation of the tapeworm is thrown off, as already mentioned, from its posterior extremity, the eggs which it incloses have already passed through a certain period of development, so that each one contains an imperfectly formed embryo. The articulation, containing the eggs and embryos, is then taken, with the food, into the stomach of another animal; the substance of the articulation, together with the external covering of the eggs, is destroyed by digestion, and the embryos are thus set free. They then penetrate through the walls of the stomach, into the neighboring organs or the areolar tissue, and becoming encysted in these situations, are there developed into cysticerci, as represented in Fig. 182. Afterward, the tissues in which they are contained being devoured by a third animal, the cysticercus passes into the intestine, fixes itself to the mucous membrane, and, by a process of budding, produces the long tape-like series of articulations, by which it is finally converted into the full-grown Tænia.

Prof. Siebold found the head of the Cysticercus fasciolaris, met with in the liver of rats and mice, presenting so close a resemblance to the Tænia crassicollis, inhabiting the intestine of the cat, that he was led to believe the two parasites to be identical. This identity was, in fact, proved by the experiments of Küchenmeister; and Siebold afterward demonstrated[1] the same relation to exist between the Cysticercus pisiformis, found in the peritoneum of rabbits, and the Tænia serrata, from the intestine of the dog. This experimenter succeeded in administering to dogs a quantity of the cysticerci, fresh from the body of the rabbit, mixed with milk; and on killing the dogs, at various periods after the meal, from three hours to eight weeks, he found the cysticerci in various stages of

[1] In Buffalo Medical Journal, Feb. 1853; also in Siebold on Tape and Cystic Worms, Sydenham translation: London, 1857, p. 59.

development in the intestine, and finally converted into the full grown Tænia, with complete articulations and mature eggs.

Dr. Küchenmeister[1] has also performed the same experiment, with success, on the human subject. A number of cysticerci were administered to a criminal, at different periods before his execution, varying from 12 to 72 hours; and upon post-mortem examination of the body, no less than ten young tæniæ were found in the intestine, four of which could be distinctly recognized as specimens of Tænia solium.

On the other hand, both Leuckart and Küchenmeister[2] have shown that the eggs of Tænia solium, introduced into the body of the pig, will give rise to the development of Cysticercus cellulosæ; thus demonstrating that the two kinds of parasites are identical in their nature, and differ only in the manner and degree of their development.

Finally, it is now known, principally from the investigations of Leuckart,[3] that Trichina spiralis is reproduced, in a similar manner, by the process of generation. This parasite is found, as above described, in an encysted and sexless condition, in the muscular tissue of the human subject, and also in that of the pig. When the flesh of the pig, infested with such parasites, is taken, either raw or imperfectly cooked, into the stomach, the cysts are digested, and the worm, set free from its confinement, rapidly increases in size in the intestine, and acquires fully developed sexual organs; — so that the females, after the first week, produce an abundance of living young. These imperfect or embryonic worms penetrate the mucous membrane of the intestine, in great numbers, and find their way into the muscular tissue, where they become encysted; and there remain without further development, until again transferred into the stomach of a living animal.

There remains, accordingly, no good reason for believing that even the encysted parasites are produced by spontaneous generation. Whatever obscurity may hang round the origin or reproduction of this class of animals, the direct investigations of the physiologist always tend to show that they do not, in reality, form any exception to the general law in this respect; and the most probable opinion, from the facts at present within our knowledge, is that *organized beings, animal and vegetable, wherever they may be found, are always the progeny of previously existing parents.*

[1] On Animal and Vegetable Parasites, Sydenham translation: London, 1857, p 115.

[2] Op. cit., p. 120.

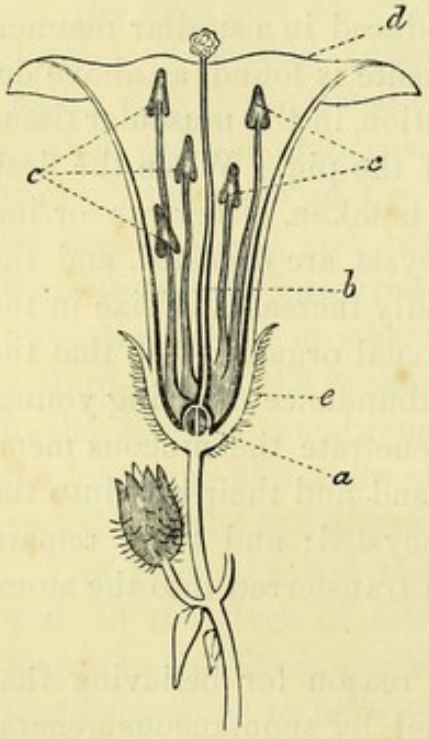
[3] Untersuchungen über Trichina spiralis. Leipzig, 1860.

CHAPTER II.

ON SEXUAL GENERATION, AND THE MODE OF ITS ACCOMPLISHMENT.

THE function of generation is performed by means of two sets of organs, each of which gives origin to a peculiar product, capable of uniting with the other so as to produce a new individual. These two sets of organs, belonging to the two different sexes, are called the male and female organs of generation. The female organs produce a globular body called the *germ*, or *egg*, which is capable of being developed into the body of the young animal or plant; the male organs produce a substance which is necessary to fecundate the germ, and enable it to go through with its natural growth and development.

Fig. 184.



BLOSSOM OF CONVOLVULUS PURPUREUS. (Morning glory.)—*a*. Germ. *b*. Pistil. *c. c.* Stamens, with anthers. *d*. Corolla. *e*. Calyx.

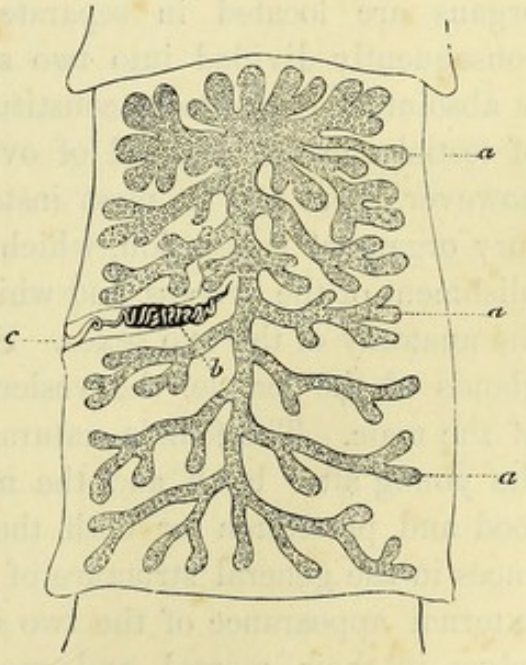
Such are the only essential and universal characters of the organs of generation. These organs, however, exhibit various additions and modifications in different classes of organized beings, while they show throughout the same fundamental and essential characters.

In the flowering plants, for example, the blossom, which is the generative apparatus (Fig. 184), consists first of a female organ containing the germ (*a*), situated usually upon the highest part of the leaf-bearing stalk. This is surmounted by a nearly straight column, termed the pistil (*b*), dilated at its summit into a globular expansion, and occupying the centre of the flower. Around it are arranged several slender filaments, or stamens, bearing upon their extremities the male organs, or anthers (*c, c*). The

whole is surrounded by a circle or crown of delicate and brilliantly colored leaves, termed the corolla (*d*), which is frequently provided with a smaller sheath of green leaves outside, called the calyx (*e*). The anthers, when arrived at maturity, discharge a fine organic dust, called the pollen, the granules of which are caught upon the extremity of the pistil, and then penetrate downward through its tissues, until they reach its lower extremity and come in contact with the germ. The germ thus fecundated, the process of generation is accomplished. The pistil, anthers, and corolla wither and fall off, while the germ increases rapidly in size, and changes in form and texture, until it ripens into the mature fruit or seed. It is then ready to be separated from the parent stem; and, if placed in the proper soil, will germinate and at last produce a new plant similar to the old.

In the above instance, the male and female organs are both situated upon the same flower; as in the lily, the violet, the convolvulus, &c. In other cases, there are separate male and female flowers upon the same plant, of which the male flowers produce only the pollen, the female, the germ and fruit. In others still, the male and female flowers are situated upon different plants, which otherwise resemble each other, as in the willow, poplar, and hemp.

Fig. 185.



Single Articulation of Tænia Crassicollis, from small intestine of cat.—*a*, *a*, *a*. Ovary filled with eggs. *b*. Testicle. *c*. Genital orifice.

In animals, the female organs of generation are called *ovaries*, since it is in them that the egg, or "ovum," is produced. The male organs are the *testicles*, which give origin to the fecundating product, or "seminal fluid," by which the egg is fertilized. We have already mentioned above that in the articulations of the tapeworm the ovaries and testicles are developed together. (Fig. 185.) The ovary (*a*, *a*, *a*) is a series of branching follicles terminating in rounded extremities, and communicating with each other by a central canal. The testicle (*b*) is a narrow, convoluted tube, very much folded

upon itself, which opens by an external orifice (c) upon the lateral border of the articulation, about midway between its two extremities. The spermatic fluid produced in the testicle is introduced into the female generative passage, which opens at the same spot, and, penetrating deeply into the interior, comes in contact with the eggs, which are thereby fecundated and rendered fertile. The fertile eggs are afterward set free by the rupture or decay of the articulation, and a vast number of young are produced by their development.

In snails, also, and in some other of the lower animals, the ovaries and testicles are both present in the same individual; so that these animals are sometimes said to be "hermaphrodite," or of double sex. In reality, however, it appears that the male and female organs do not come to maturity at the same time; but the ovaries are first developed and perform their function, after which the testicles come into activity in their turn. The same individual, therefore, is not both male and female at any one time; but is first female and afterward male, exercising the two generative functions at different ages.

In all the higher animals, however, the two sets of generative organs are located in separate individuals; and the species is consequently divided into two sexes, male and female. All that is absolutely requisite to constitute the two sexes is the existence of testicles in the one, and of ovaries in the other. Beside these, however, there are, in most instances, certain secondary or accessory organs of generation, which assist more or less in the accomplishment of the process, and which occasion a greater difference in the anatomy of the two sexes. Such are the uterus and mammary glands of the female, the vesiculæ seminales and prostate gland of the male. The female naturally having the immediate care of the young after birth, and the male being occupied in providing food and protection for both, there are also corresponding differences in the general structure of the body, which affect the whole external appearance of the two sexes, and which even show themselves in their mental and moral, as well as in their physical characteristics. In some cases this difference is so excessive that the male and female would never be recognized as belonging to the same species, unless they were seen in company with each other. Not to mention some extreme instances of this among insects and other invertebrate animals, it will be sufficient to refer to the well-known examples of the cock and the hen, the lion and lioness, the

buck and the doe. In the human species, also, the distinction between the sexes shows itself in the mental constitution, the disposition, habits, and pursuits, as well as in the general conformation of the body, and the peculiarities of external appearance.

We shall now study more fully the character of the male and female organs of generation, together with their products, and the manner in which these are discharged from the body, and brought into relation with each other.

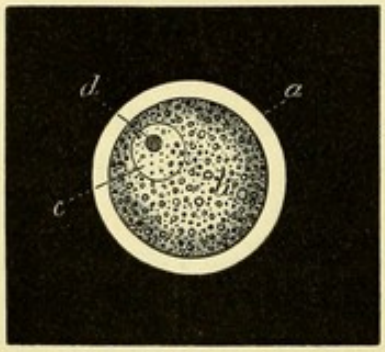
CHAPTER III.

ON THE EGG, AND THE FEMALE ORGANS OF GENERATION.

THE egg is a globular body which varies considerably in size in different classes of animals, according to the peculiar conditions under which its development is to take place. In the frog it measures $\frac{1}{12}$ of an inch in diameter, in the lamprey $\frac{1}{25}$, in quadrupeds and in the human species $\frac{1}{120}$. It consists, first, of a membranous external sac or envelope, the *vitelline membrane;* and secondly, of a spherical mass inclosed in its interior, called the *vitellus.*

The *vitelline membrane* in birds and reptiles is very thin, measuring often not more than $\frac{1}{1500}$ of an inch in thickness, and is at the same time of a somewhat fibrous texture. In man and the higher animals, on the contrary, it is perfectly smooth, structureless and transparent, and is about $\frac{1}{1500}$ of an inch in thickness. Notwithstanding its delicate and transparent appearance, it has a considerable degree of resistance and elasticity. The egg of the human subject, for example, may be perceptibly flattened out under the microscope by pressing with the point of a needle upon the slip of glass which covers it; but it still remains unbroken, and when the pressure is removed, readily resumes its globular form. When the egg is somewhat flattened under the microscope in this way, by pressure of the glass slip, the apparent thickness of the vitelline membrane is increased, and it then appears (Fig. 186) as a rather wide, colorless, and pellucid border or zone, surrounding the granular and opaque vitellus. Owing to this appearance, it has sometimes received the name of the "zona pellucida." The name of

Fig. 186.

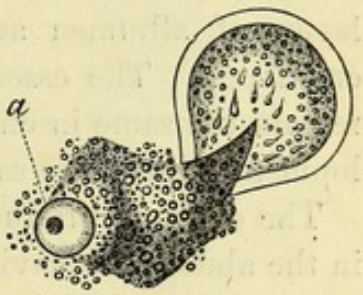


HUMAN OVUM, magnified 85 diameters. *a.* Vitelline membrane. *b.* Vitellus. *c.* Germinative vesicle. *d.* Germinative spot.

vitelline membrane, however, is the one more generally adopted, and is also the more appropriate of the two.

The *vitellus* (*b*) is a globular, semi-solid mass, contained within the vitelline membrane. It consists of a colorless albuminoid substance, with an abundance of minute molecules and oleaginous granules scattered through it. These minute oleaginous masses give to the vitellus a partially opaque and granular aspect under the microscope. Imbedded in the vitellus, usually near its surface and almost immediately beneath the vitelline membrane, there is a clear, colorless, transparent vesicle (*c*) of a rounded form, known as the *germinative vesicle*. In the egg of the human subject and of the quadrupeds, this vesicle measures $\frac{1}{300}$ to $\frac{1}{300}$ of an inch in diameter. It presents upon its surface a dark spot, like a nucleus (*d*), which is known by the name of the *germinative spot*. The germinative vesicle, with its nucleus-like spot, is often partially concealed by the granules of the vitellus by which it is surrounded, but it may always be discovered by careful examination.

Fig. 187.



HUMAN OVUM, ruptured by pressure; showing the vitellus partially expelled, the germinative vesicle at *a*, and the smooth fracture of the vitelline membrane.

If the egg be ruptured by excessive pressure under the microscope, the vitellus is seen to have a gelatinous consistency. It is gradually expelled from the vitelline cavity, but still retains the granules and oil globules entangled in its substance. (Fig. 187.) The edges of the fractured vitelline membrane, under these circumstances, present a smooth and nearly straight outline, without any appearance of laceration or of a fibrous structure. The membrane is, to all appearance, perfectly homogeneous.

The most essential constituent of the egg is the vitellus. It is from the vitellus that the body of the embryo will afterward be formed, and the organs of the new individual developed. The vitelline membrane is merely a protective inclosure, intended to secure the vitellus from injury, and enable it to retain its figure during the early periods of development.

The egg, as above described, consists therefore of a simple vitellus of minute size, and a vitelline membrane inclosing it. It is such an egg which is found in the human subject, the quadrupeds, most aquatic reptiles, very many fish, and some invertebrate animals. In nearly all those species, in fact, where the fecundated

eggs are deposited and hatched in the water, as well as those in which they are retained in the body of the female until the development of the young is completed, such an egg as above described is sufficient for the formation of the embryo; since during its development it can absorb freely, either from the water in which it floats, or from the mucous membrane of the female generative organs, the requisite supply of nutritious fluids. But in birds and in the terrestrial reptiles, such as lizards, tortoises, &c., where the eggs are expelled from the body of the female at an early period, and incubated on land, there is no external source of nutrition, to provide for the support of the young animal during its development. In these instances accordingly the vitellus, or "yolk," as it is called, is of very large size; and the bulk of the egg is still further increased by the addition, within the female generative passages, of layers of albumen and various external fibrous and calcareous envelopes. The essential constituents of the egg, however, still remain the same in character, and the process of embryonic development follows the same general laws as in other cases.

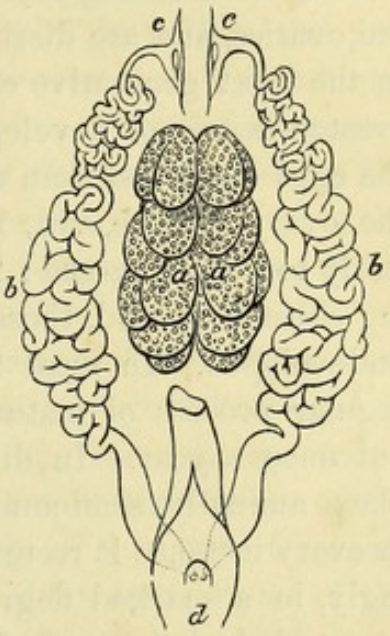
The eggs are produced in the interior of certain organs, situated in the abdominal cavity, called the *ovaries*. These organs consist of a number of globular sacs, or follicles, known as the "Graafian follicles," each one of which contains a single egg. The follicles are connected with each other by a quantity of vascular areolar tissue, which binds them together into a well-defined and consistent mass, covered upon its exterior by a layer of peritoneum. The egg has sometimes been spoken of as a "product," or even as a "secretion" of the ovary. Nothing can be more inappropriate, however, than to compare the egg with a secretion, or to regard the ovary as in any respect resembling a glandular organ. The egg is simply an organized body, growing in the ovary like a tooth in its follicle, and forming a constituent part of the body of the female. It is destined to be finally separated from its attachments and thrown off; but until that time, it is, properly speaking, a part of the ovarian texture, and is nourished like any other portion of the female organism.

The ovaries, accordingly, since they are directly concerned in the production of the eggs, are to be regarded as the essential parts of the female generative apparatus. Beside them, however, there are usually present certain other organs, which play a secondary or accessory part in the process of generation. The most important of these accessory organs are two symmetrical tubes, or

oviducts, which are destined to receive the eggs at their internal extremity and convey them to the external generative orifice. The mucous membrane lining the oviducts is also intended to supply certain secretions during the passage of the egg, which are requisite either to complete its structure, or to provide for the nutrition of the embryo.

In the frog, for example, the oviduct commences at the upper part of the abdomen, by a rather wide orifice, which communicates directly with the peritoneal cavity. It soon after contracts to a narrow tube, and pursues a zigzag course down the side of the abdomen (Fig. 188), folded upon itself in convolutions, like the small intestine, until it opens, near its fellow of the opposite side, into the "cloaca" or lower part of the intestinal canal. The oviducts present the same general characters with those described above, in nearly all species of reptiles and birds; though there are some modifications, in particular instances, which do not require any special notice.

Fig. 188.



Female Generative Organs of Frog.—*a, a.* Ovaries. *b, b.* Oviducts. *c, c.* Their internal orifices. *d.* Cloaca, showing external orifices of oviducts.

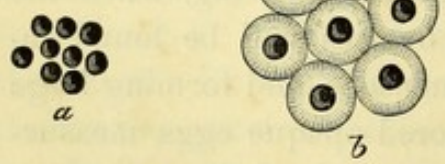
The ovaries, as well as the eggs which they contain, undergo at particular seasons a periodical development or increase in growth. If we examine the female frog in the latter part of summer or the fall, we shall find the ovaries presenting the appearance of small clusters of minute and nearly colorless eggs, the smaller of which are perfectly transparent and not over $\frac{1}{140}$ of an inch in diameter. But in the early spring, when the season of reproduction approaches, the ovaries will be found increased to four or five times their former size, and forming large lobulated masses, crowded with dark-colored opaque eggs, measuring $\frac{1}{12}$ of an inch in diameter. At the approach of the generative season, in all the lower animals, a certain number of the eggs, which were previously in an imperfect and inactive condition, begin to increase in size and become somewhat altered in structure. The vitellus more especially, which was before colorless and transparent, becomes granular in texture as well as increased in volume; and assumes at the same time, in many species of animals, a black,

brown, yellow, or orange color. In the human subject, however, the change consists only in an increase of size and granulation, without any remarkable alteration of color.

The eggs, as they ripen in this way, becoming enlarged and changed in texture, gradually distend the Graafian follicles and project from the surface of the ovary. At last, when fully ripe, they are discharged by a rupture of the walls of the follicles, and, passing into the oviducts, are conveyed by them to the external generative orifice, and there expelled. In this way, as successive seasons come round, successive crops of eggs enlarge, ripen, leave the ovaries, and are discharged. Those which are to be expelled at the next generative epoch may always be recognized by their greater degree of development; and in this way, in many animals, the eggs of no less than three different crops may be recongized in the ovary at once, viz., 1st, those which are perfectly mature and ready to be discharged; 2d, those which are to ripen in the following season; and 3d, those which are as yet altogether inactive and undeveloped. In most fish and reptiles, as well as in birds, this regular process of maturation and discharge of eggs takes place but once a year. In different species of quadrupeds it may take place annually, semi-annually, bi-monthly, or even monthly; but in every instance it recurs at regular intervals, and exhibits accordingly, in a marked degree, the periodic character which we have seen to belong to most of the other vital phenomena.

Action of the Oviducts and Female Generative Passages.—In frogs and lizards, the ripening and discharge of the eggs take place, as above mentioned in the early spring. At the time of leaving the ovary, the eggs consist simply of the dark-colored and granular vitellus, inclosed in the vitelline membrane. They are then received by the inner extremity of the oviducts, and carried downward by the peristaltic movement of these canals, aided by the more powerful contraction of the abdominal muscles. During the passage of the eggs, moreover, the mucous membrane of the oviduct secretes a colorless, viscid, albuminoid substance, which is deposited in successive layers round each egg, forming a thick and tenacious coating or envelope. (Fig. 189.) When the eggs are finally discharged, this albuminoid matter

Fig. 189.



MATURE FROGS' EGGS.—*a*. While still in the ovary. *b*. After passing through the oviduct.

absorbs the water in which the spawn is deposited, and swells up into a transparent gelatinous mass, in which the eggs are separately imbedded. This substance supplies, by its subsequent liquefaction and absorption, a certain amount of nutritious material, during the development and early growth of the embryo.

In the terrestrial reptiles and in birds, the oviducts perform a still more important secretory function. In the common fowl, the ovary consists, as in the frog, of a large number of follicles, loosely connected by areolar tissue, in which the eggs can be seen in different stages of development. (Fig. 190, *a*.) As the egg which is approaching maturity enlarges, it distends the cavity of its follicle, and projects farther from the general surface of the ovary; so that it hangs at last into the peritoneal cavity, retained only by the attenuated wall of the follicle, and a slender pedicle through which run the bloodvessels by which its circulation is supplied. A rupture of the follicle then occurs, at its most prominent part, and the egg is discharged from the lacerated opening.

At the time of its leaving the ovary, the egg of the fowl consists of a large, globular, orange-colored vitellus, or "yolk," inclosed in a thin and transparent vitelline membrane. Immediately underneath the vitelline membrane, at one point upon the surface of the vitellus, is a round white spot, consisting of a layer of minute granules, termed the "cicatricula." It is in the central part of the cicatricula that the germinative vesicle is found imbedded, at an early stage of the development of the egg. At the time of its discharge from the ovary, the germinative vesicle has usually disappeared; but the cicatricula is still a very striking and important part of the vitellus, as it is from this spot that the body of the chick begins afterward to be developed.

At the same time that the egg protrudes from the surface of the ovary, it projects into the inner orifice of the oviduct; so that, when discharged from its follicle, it is immediately embraced by the upper or fringed extremity of this tube, and commences its passage downward. In the fowl, the muscular coat of the oviduct is highly developed, and its peristaltic contractions gently urge the egg from above downward, precisely as the œsophagus or the intestines transport the food in a similar direction. While passing through the first two or three inches of the oviduct (*c*, *d*), where the mucous membrane is smooth and transparent, the yolk merely absorbs a certain quantity of fluid, so as to become more flexible and yielding in consistency. It then passes into a second division of the generative

canal, in which the mucous membrane is thick and glandular in texture, and is also thrown into numerous longitudinal folds, which project into the cavity of the oviduct. This portion of the oviduct (*d*, *e*), extends over about nine inches of its entire length. In its upper part, the mucous membrane secretes a viscid material, by which the yolk is encased, and which soon consolidates into a gelatinous, membranous deposit; thus forming a second homogeneous layer, outside the vitelline membrane.

Now the peristaltic movements of this part of the oviduct are such as to give a rotary, as well as a progressive motion to the egg; and the two extremities of the membranous layer described above become, accordingly, twisted in opposite directions into two fine cords, which run backward and forward from the opposite poles of the egg. These cords are termed the "chalazæ," and the membrane with which they are connected, the "chalaziferous membrane."

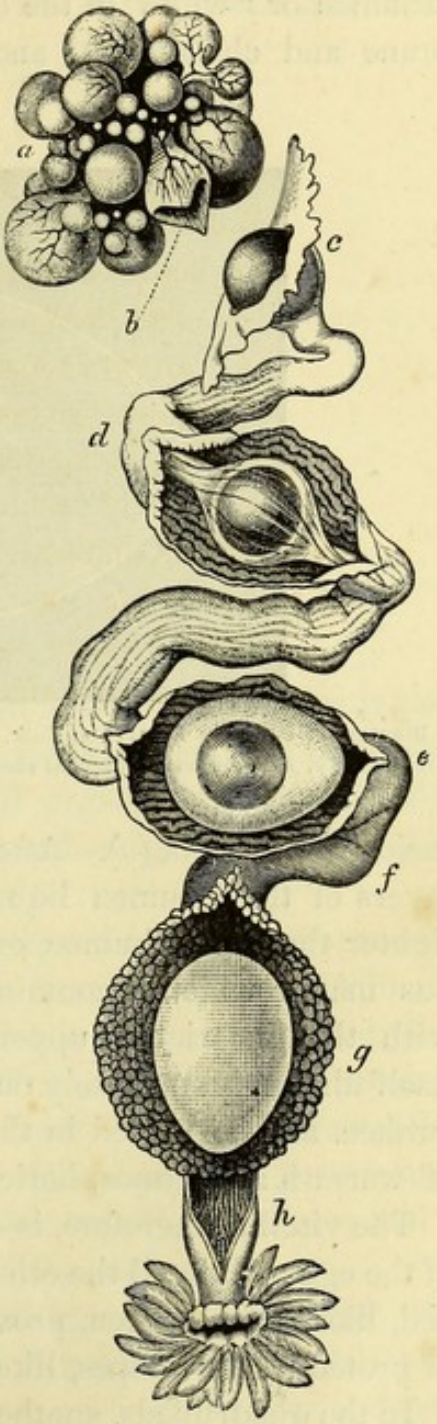
Throughout the remainder of the second division of the oviduct, the mucous membrane exudes an abundant, gelatinous, albuminoid substance, which is deposited in successive layers round the yolk, inclosing at the same time the chalaziferous membrane and the chalazæ. This substance, which forms the so-called albumen, or "white of egg," is semi-solid in consistency, nearly transparent, and of a faint amber color. It is deposited in greater abundance in front of the advancing egg than behind it, and forms accordingly a pointed or conical projection in front, while behind, its outline is rounded off, parallel with the spherical surface of the yolk. In this way, the egg acquires, when covered with its albumen, an ovoid form, of which one end is round, the other pointed; the pointed extremity being always directed downward, as the egg descends along the oviduct.

In the third division of the oviduct (*f*), which is about three and a half inches in length, the mucous membrane is arranged in longitudinal folds, which are narrower and more closely packed than in the preceding portion. The material secreted in this part, and deposited upon the egg, condenses into a firm fibrous covering, composed of three different layers which closely embrace the surface of the albuminous mass, forming a tough, flexible, semi-opaque envelope for the whole. These layers are known as the external, middle, and internal fibrous membranes of the egg.

Finally the egg passes into the fourth division of the oviduct (*g*), which is wider than the rest of the canal, but only a little over two inches in length. Here the mucous membrane, which is arranged

in abundant, projecting, leaf-like villosities, exudes a fluid very rich in calcareous salts. The most external of the three membranes just described is permeated by this fluid, and very soon the calcareous matter begins to crystallize in the interstices of its fibres. This deposit of calcareous matter goes on, growing constantly thicker and more condensed, until the entire external membrane is converted into a white, opaque, brittle, calcareous shell, which incloses the remaining portions and protects them from external injury. The egg is then driven outward by the contraction of the muscular coat through a narrow portion of the oviduct (*h*), and, gradually dilating the passages by its conical extremity, is finally discharged from the external orifice.

Fig. 190.



The egg of the fowl, after it has been discharged from the body, consists, accordingly, of various parts; some of which, as the yolk and the vitelline membrane, entered into its original formation, while the remainder have been deposited round it during its passage through the oviduct. On examining such an egg (Fig. 191), we find externally the calcareous shell (*h*), while immediately beneath it are situated the middle and internal fibrous shell-membranes (*e*, *f*).

Soon after the expulsion of the egg there is a partial evaporation of its watery ingredients, which are replaced by air penetrating through the pores

FEMALE GENERATIVE ORGANS OF FOWL.—*a*. Ovary. *b*. Graafian follicle, from which the egg has just been discharged. *c*. Yolk, entering upper extremity of oviduct. *d*, *e*. Second division of oviduct, in which chalaziferous membrane, chalazæ, and albumen are formed. *f*. Third portion, in which the fibrous shell membranes are produced. *g*. Fourth portion laid open, showing egg completely formed, with calcareous shell. *h*. Narrow canal through which the egg is discharged.

of the shell at its rounded extremity. The air thus introduced accumulates between the middle and internal fibrous membranes at this spot, separating them from each other, and forming a cavity or air-chamber (*g*), which is always found between the two fibrous membranes at the rounded end of the egg. Next we come to the albumen or "white" of the egg (*d*); next to the chalaziferous membrane and chalazæ (*c*); and finally to the vitelline membrane (*b*)

Fig. 191.

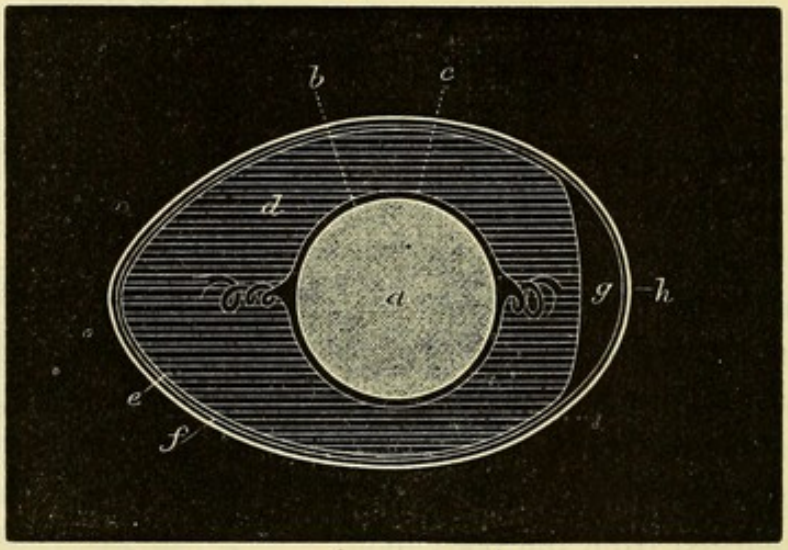


Diagram of Fowl's Egg.—*a*. Yolk. *b*. Vitelline membrane. *c*. Chalaziferous membrane *d*. Albumen. *e*, *f*. Middle and internal shell membranes. *g*. Air-chamber. *h*. Calcareous shell.

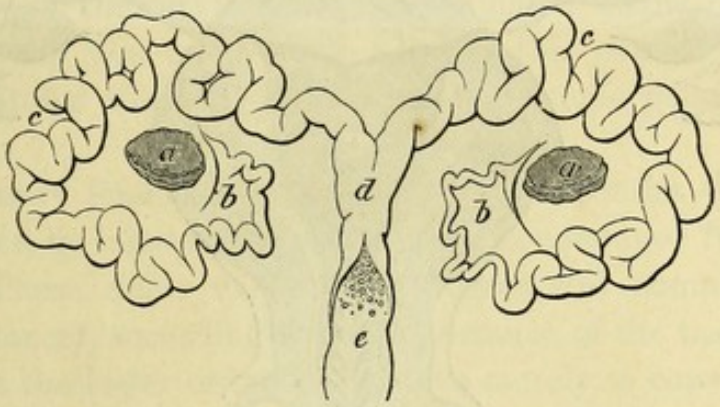
inclosing the yolk (*a*). After the expulsion of the egg, the external layers of the albumen liquefy; and the vitellus, being specifically lighter than the albumen, owing to the large proportion of oleaginous matter which it contains, rises toward the surface of the egg, with the cicatricula uppermost. This part, therefore, presents itself almost immediately on breaking open the egg upon its lateral surface, and is placed in the most favorable position for the action of warmth and atmospheric air in the development of the chick.

The vitellus, therefore, is still the essential and constituent portion of the egg; while all the other parts consist either of nutritious material, like the albumen, provided for the support of the embryo, or of protective envelopes, like the shell and the fibrous membranes.

In the quadrupeds, another and still more important modification of the oviducts takes place. In these animals, the egg, which is originally very minute in size, is destined to be retained within the generative passages of the female during the development of the embryo. While the upper part of the oviduct, therefore, is quite narrow, and intended merely to transmit the egg from the ovary,

and to supply it with a little albuminous secretion, its lower portions are very much increased in size, and are lined, moreover, with a mucous membrane, so constructed as to provide for the protection and nourishment of the embryo, during the entire period of gestation. The upper and narrower portions of the oviduct are known as the "Fallopian tubes" (Fig. 192); while the lower and more

Fig. 192.



Uterus and Ovaries of the Sow.—*a*, *a*. Ovaries. *b*, *b*. Fallopian tubes. *c*, *c*. Horns of uterus. *d*. Body of uterus. *e*. Vagina.

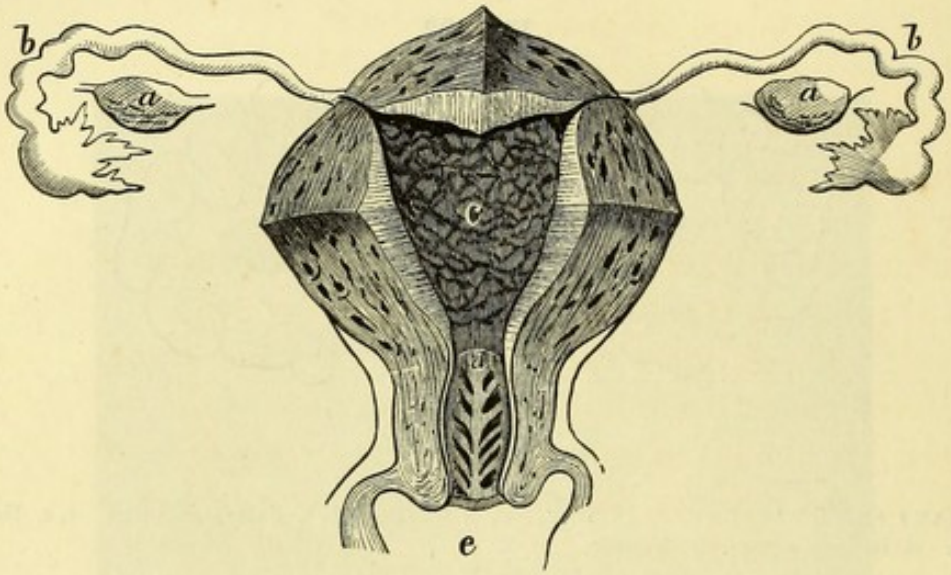
highly developed portions constitute the uterus. These lower portions unite with each other upon the median line near their inferior termination, so as to form a central organ, termed the "body" of the uterus; while the remaining ununited parts are known as its "cornua" or "horns."

In the human subject, the female generative apparatus presents the following peculiarities. The ovaries consist of Graafian follicles, which are imbedded in a somewhat dense areolar tissue, supplied with an abundance of bloodvessels. The entire mass is covered with a thick, opaque, yellowish white layer of fibrous tissue called the "albugineous tunic." Over the whole is a layer of peritoneum, which is reflected upon the vessels which supply the ovary, and is continuous with the broad ligaments of the uterus.

The oviducts commence by a wide expansion, provided with fringed edges, called the "fimbriated extremity of the Fallopian tube." The Fallopian tubes themselves are very narrow and convoluted, and terminate on each side in the upper part of the body of the uterus. In the human subject, the body of the uterus is so much developed at the expense of the cornua, that the latter hardly appear to have an existence; and in fact no trace of them is visible externally. But on opening the body of the uterus its cavity is

seen to be nearly triangular in shape, its two superior angles running out on each side to join the lower extremities of the Fallopian tubes. This portion evidently consists of the cornua, which have been consolidated with the body of the uterus, and enveloped in its thickened layer of muscular fibres.

Fig. 193.



GENERATIVE ORGANS OF HUMAN FEMALE.—*a*, *a*. Ovaries. *b*, *b*. Fallopian tubes. *c*. Body of uterus. *d*. Cervix. *e*. Vagina.

The cavity of the body of the uterus terminates below by a constricted portion termed the os internum, by which it is separated from the cavity of the cervix. These two cavities are not only different from each other in shape, but differ also in the structure of their mucous membrane and the functions which it is destined to perform.

The mucous membrane of the body of the uterus in its usual condition is smooth and rosy in color, and closely adherent to the subjacent muscular tissue. It consists of minute tubular follicles somewhat similar to those of the gastric mucous membrane, ranged side by side, and opening by distinct orifices upon its free surface. The secretion of these follicles is destined for the nutrition of the embryo during the earlier periods of its formation.

The internal surface of the neck of the uterus, on the other hand, is raised in prominent ridges which are arranged usually in two lateral sets, diverging from a central longitudinal ridge; presenting the appearance known as the "arbor vitæ uterina." The follicles of this part of the uterine mucous membrane are different in structure from those of the foregoing. They are of a globular or sac-

like form, and secrete a very firm, adhesive, transparent mucus, which is destined to block up the cavity of the cervix during gestation, and guard against the accidental displacement of the egg. Some of these follicles are frequently distended with their secretion, and project, as small, hard, rounded eminences, from the surface of the mucous membrane. In this condition they are sometimes designated by the name of "ovula Nabothi," owing to their having been formerly mistaken for eggs, or ovules.

The cavity of the cervix uteri is terminated below by a second constriction, the "os externum." Below this comes the vagina, which constitutes the last division of the female generative passages.

The accessory female organs of generation consist therefore of ducts or tubes, by means of which the egg is conveyed from within outward. These ducts vary in the degree and complication of their development, according to the importance of the task assigned to them. In the lower orders, they serve merely to convey the egg rapidly to the exterior, and to supply it more or less abundantly with an albuminous secretion. In the higher classes and in the human subject, they are adapted to the more important function of retaining the egg during the period of gestation, and of providing during the same time for the nourishment of the young embryo.

CHAPTER IV.

ON THE SPERMATIC FLUID, AND THE MALE ORGANS OF GENERATION.

THE mature egg is not by itself capable of being developed into the embryo. If simply discharged from the ovary and carried through the oviducts toward the exterior, it soon dies and is decomposed, like any other portion of the body separated from its natural connections. It is only when fecundated by the spermatic fluid of the male, that it is stimulated to continued development, and becomes capable of a more complete organization.

The product of the male generative organs consists of a colorless, somewhat viscid, and albuminous fluid, containing an innumerable quantity of minute filamentous bodies, termed *spermatozoa.* The name spermatozoa has been given to these bodies, on account of their exhibiting under the microscope a very active and continuous movement, bearing some resemblance to that of certain animalcules.

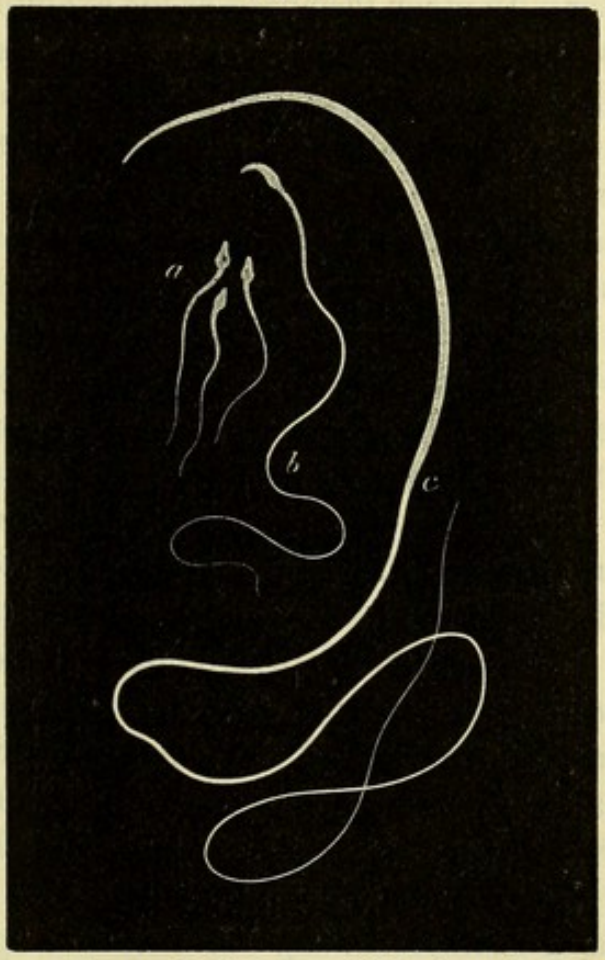
Anatomical characters of the spermatozoa.—The spermatozoa of the human subject (Fig. 194, *a*) are about $\frac{1}{600}$ of an inch in length, according to the measurements of Kölliker. Their anterior extremity presents a somewhat flattened, triangular-shaped enlargement, termed the "head." The head constitutes about one-tenth part the entire length of the spermatozoon. The remaining portion is a very slender filamentous prolongation, termed the "tail," which tapers gradually backward, becoming so exceedingly delicate towards its extremity, that it is difficult to be seen except when in motion. There is no further organization or internal structure to be detected in any part of the spermatozoon; and the whole appears to consist, so far as can be seen by the microscope, of a completely homogeneous, tolerably firm, albuminoid substance. The terms head and tail, therefore, as justly remarked by Bergmann and Leuckart,[1] are not used, when describing the different parts of the spermatozoon, in the same sense as that in which they would be applied to the corre-

[1] Vergleichende Physiologie. Stuttgart, 1852.

sponding parts of an animal, but simply for the sake of convenience; just as one might speak of the head of an arrow, or the tail of a comet.

In the lower animals, the spermatozoa have usually the same general form as in the human subject; that is, they are slender filamentous bodies, with the anterior extremity more or less enlarged. In the rabbit they have a head which is roundish and flattened in shape, somewhat resembling the globules of the blood. In the rat (Fig. 194, *b*) they are much larger than in man, measuring nearly $\frac{1}{125}$ of an inch in length. The head is conical in shape,

Fig. 194.



SPERMATOZOA.—*a*. Human. *b*. Of Rat. *c*. Of Menobranchus. Magnified 480 times.

about one-twentieth the whole length of the filament, and often slightly curved at its anterior extremity. In the frog and in reptiles generally, the spermatozoa are longer than in quadrupeds. In the Menobranchus, or great American water-lizard, they are of very unusual size (Fig. 194, *c*), measuring not less than $\frac{1}{44}$ of an inch in length, about one-third of which is occupied by the head, or enlarged portion of the filament.

The most remarkable peculiarity of the spermatozoa is their

very singular and active movement, to which we have already alluded. If a drop of fresh seminal fluid be placed under the microscope, the numberless minute filaments with which it is crowded are seen to be in a state of incessant and agitated motion. This movement of the spermatozoa, in many species of animals, strongly resembles that of the tadpole; particularly when, as in the human subject, the rabbit, &c., the spermatozoa consist of a short and well defined head, followed by a long and slender tail. Here the tail-like filament keeps up a constant lateral or vibratory movement, by which the spermatozoon is driven from place to place in the spermatic fluid, just as the fish or the tadpole is propelled through the water. In other instances, as for example in the water-lizard, and in some parasitic animals, the spermatozoa have a continuous writhing or spiral-like movement, which presents a very peculiar and elegant appearance when large numbers of them are viewed together.

It is the existence of this movement which first suggested the name of spermatozoa to designate the animated filaments of the spermatic fluid; and which has led some writers to attribute to them an independent animal nature. This is, however, a very erroneous mode of regarding them; since they cannot properly be considered as animals, notwithstanding the active character of their movement, and the striking resemblance which it sometimes presents to a voluntary act. The spermatozoa are organic forms, which are produced in the testicles, and constitute a part of their tissue; just as the eggs, which are produced in the ovaries, naturally form a part of the texture of these organs. Like the egg, also, the spermatozoon is destined to be discharged from the organ where it grew, and to retain, for a certain length of time afterward, its vital properties. One of the most peculiar of these properties is its power of keeping in constant motion; which does not, however, mark it as a distinct animal, but only distinguishes it as a peculiar structure belonging to the parent organism. The motion of a spermatozoon is precisely analogous to that of a ciliated epithelium cell. The movement of the latter will continue for some hours after it has been separated from its mucous membrane, provided its texture be not injured, nor the process of decomposition allowed to commence. In the same manner, the movement of the spermatozoa is a characteristic property belonging to them, which continues for a certain time, even after they have been separated from the rest of the body.

In order to preserve their vitality, the spermatozoa must be kept at the ordinary temperature of the body, and preserved from the contact of the air or other unnatural fluids. In this way, they may be kept without difficulty many hours for purposes of examination. But if the fluid in which they are kept be allowed to dry, or if it be diluted by the addition of water, in the case of birds and quadrupeds, or if it be subjected to extremes of heat or cold, the motion ceases, and the spermatozoa themselves soon begin to disintegrate.

The spermatozoa are produced in certain glandular-looking organs, the *testicles*, which are characteristic of the male, as the ovaries are characteristic of the female. In man and all the higher animals, the testicles are solid, ovoid-shaped bodies, composed principally of numerous long, narrow, and convoluted tubes, the "seminiferous tubes," somewhat similar in their general anatomical characters to the tubuli uriniferi of the kidneys. These tubes lie for the most part closely in contact with each other, so that nothing intervenes between them except capillary bloodvessels and a little areolar tissue. They commence, by blind, rounded extremities, near the external surface of the testicle, and pursue an intricately convoluted course toward its central and posterior part. They are not strongly adherent to each other, but may be readily unravelled by manipulation, and separated from each other.

The formation of the spermatozoa, as it takes place in the substance of the testicle, has been fully investigated by Kölliker. According to his observations, as the age of puberty approaches, beside the ordinary pavement epithelium lining the seminiferous tubes, other cells or vesicles of larger size make their appearance in these tubes, each containing from one to fifteen or twenty nuclei, with nucleoli. It is in the interior of these vesicles that the spermatozoa are formed; their number corresponding usually with that of the nuclei just mentioned. They are at first developed in bundles of ten to twenty, held together by the thin membranous substance which surrounds them, but are afterward set free by the liquefaction of the vesicle, and then fill nearly the entire cavity of the seminiferous ducts, mingled only with a very minute quantity of transparent fluid.

In the seminiferous tubes themselves, the spermatozoa are always inclosed in the interior of their parent vesicles; they are liberated, and mingled promiscuously together, only after entering the rete testis and the head of the epididymis.

Beside the testicles, which are, as above stated, the primary and essential parts of the male generative apparatus, there are certain secondary or accessory organs, by means of which the spermatic fluid is conveyed to the exterior, and mingled with various secretions which assist in the accomplishment of its functions.

As the sperm leaves the testicle, it consists, as above mentioned, almost entirely of the spermatozoa, crowded together in an opaque, white, semi-fluid mass, which fills up the vasa efferentia, and completely distends their cavities. It then enters the single duct which forms the body and lower extremity of the epididymis, following the long and tortuous course of this tube, until it reaches the vas deferens; through which it is still conveyed onward to the point where this canal opens into the urethra. Throughout this course, it is mingled with a glairy, mucus-like fluid, secreted by the walls of the epididymis and vas deferens, in which the spermatozoa are enveloped. The mixture is then deposited in the vesiculæ seminales, where it accumulates, as fresh quantities are produced in the testicle and conveyed downward by the spermatic duct. It is probable that a second secretion is supplied also by the internal surface of the vesiculæ seminales, and that the sperm, while retained in their cavities, is not only stored up for subsequent use, but is at the same time modified in its properties by the admixture of another fluid.

At the time when the evacuation of the sperm takes place, it is driven out from the seminal vesicles by the muscular contraction of the surrounding parts, and meets in the urethra with the secretions of the prostate gland, the glands of Cowper, and the mucous follicles opening into the urethral passage. All these organs are at that time excited to an unusual activity of secretion, and pour out their different fluids in great abundance.

Necessary conditions of fecundation by the spermatic fluid.—There are several conditions which are essential to the successful accomplishment of the act of fecundation.

First, the spermatozoa must be present and in a state of active vitality. We have shown already that the sperm, at the moment of its discharge from the urethra, is an exceedingly mixed fluid, consisting of the spermatozoa derived from the testicles, together with the secretions of the epididymis and vas deferens, the prostate, Cowper's glands, and the mucous follicles of the urethra. Of all these ingredients, it is the spermatozoa

which constitute the essential part of the seminal fluid. They are the true fecundating element of the sperm, while all the others are secondary in importance, and perform only accessory functions.

Spallanzani found that if frog's semen be passed through a succession of filters, so as to separate the spermatozoa from the liquid portions, the filtered fluid is destitute of any fecundating properties; while the spermatozoa remaining entangled in the filter, if mixed with a sufficient quantity of fluid of the requisite density for dilution, may still be successfully used for the impregnation of eggs. It is well known, also, that animals or men from whom both testicles have been removed, are incapable of impregnating the female or her eggs, notwithstanding that all the other generative organs may remain uninjured. The spermatic fluid, furthermore, must be in a fresh condition, so that the spermatozoa themselves retain their anatomical characters and their active movement. The experiments of Spallanzani,[1] on artificial impregnation in the cold-blooded animals, have shown that, if the above conditions be preserved, the spermatic fluid, removed from the seminal ducts of the male, is capable of successfully fecundating the eggs of the female. But if it be allowed to remain too long exposed to the atmosphere, or to an unnatural temperature, it loses its impregnating power and becomes inert. So long as the spermatozoa continue in active motion, they are usually found to retain their physiological properties; the cessation of this movement, on the other hand, being a sign that their vitality is exhausted, and that they are no longer capable of impregnating the egg.

Secondly, both eggs and spermatozoa must have arrived at a certain degree of development before fecundation can take place. Previous to this time the immature eggs are incapable of impregnation, and the imperfectly developed spermatozoa have not yet acquired their fecundating power. This necessary process of growth takes place within the generative organs; and when it is complete, both the spermatozoa of the male and the eggs of the female are ready to be discharged, and are in a condition to exert upon each other the necessary mutual influence.

The fecundating power, however, of the spermatozoa, when fully developed, is exceedingly active. Spallanzani found that three grains of the spermatic fluid of the frog, diffused in water, was sufficient for the impregnation of several thousands of eggs. The process also seems to be accomplished almost instantaneously, since the

[1] Expériences pour servir à l'histoire de la génération. Geneva, 1786.

eggs which had been allowed to remain in the fecundating mixture for only a single second were successfully impregnated and became afterward hatched at the end of the usual period.

Thirdly, in order to accomplish fecundation, the spermatozoa must come into actual contact with the egg or its immediate envelopes. Spallanzani first demonstrated this fact by attaching some mature eggs to the concave surface of a watch-glass, which he then placed, in an inverted position, over a second watch-glass containing fresh spermatic fluid. The eggs, which were allowed to remain in this way for several hours exposed to the vapor of the spermatic fluid, but without touching its surface, were afterward found to have failed of impregnation; while others, which were actually moistened with a portion of the same sperm, became developed into living tadpoles.

There is even reason to believe that the spermatozoa, at the time of impregnation, actually penetrate into the interior of the egg, and thus come into contact with the substance of the vitellus. Spermatozoa have been seen in the interior of the egg, by Martin Barry, Newport, and Bischoff, in the frog and the rabbit, and by other observers in various invertebrate animals. The substance of the spermatozoon, thus introduced into the egg, undoubtedly becomes liquefied and united with the substance of the vitellus; so that the fecundated egg is a combination of materials derived from both the male and female organisms.

Periodical development of the spermatic fluid. — In most of the lower orders of animals there is a periodical development of the testicles in the male, corresponding in time with that of the ovaries in the female. As the ovaries enlarge and the eggs ripen in the one sex, so in the other the testicles increase in size, as the season of reproduction approaches, and become turgid with spermatozoa. The accessory organs of generation, at the same time, share the unusual activity of the testicles, and become increased in vascularity and ready to perform their part in the reproductive function.

In the fish, for example, where the testicles occupy the same position in the abdomen as the ovaries in the opposite sex, these bodies enlarge, become distended with their contents, and project into the peritoneal cavity. Each of the two sexes is then at the same time under the influence of a corresponding excitement. The unusual development of the generative organs reacts upon the entire system, and produces a state of peculiar activity and excitability.

known as the condition of "erethism." The female, distended with eggs, feels the impulse which leads to their expulsion; while the male, bearing the weight of the enlarged testicles and the accumulation of newly-developed spermatozoa, is impelled by a similar sensation to the discharge of the spermatic fluid. The two sexes, accordingly, are led by instinct at this season to frequent the same situations. The female deposits her eggs in some spot favorable to the protection and development of the young; after which the male, apparently attracted and stimulated by the sight of the new-laid eggs, discharges the spermatic fluid upon them, and their impregnation is accomplished.

In such instances as the above, where the male and female generative products are discharged separately by the two sexes, the subsequent contact of the eggs with the spermatic fluid would seem to be altogether dependent on the occurrence of fortuitous circumstances, and their impregnation, therefore, often liable to fail. In point of fact, however, the simultaneous functional excitement of the two sexes and the operation of corresponding instincts, leading them to ascend the same rivers and to frequent the same spots, provide with sufficient certainty for the impregnation of the eggs. In these animals, also, the number of eggs produced by the female is very large, the ovaries being often so distended as to fill nearly the whole of the abdominal cavity; so that, although many of the eggs may be accidentally lost, a sufficient number will still be impregnated and developed, to provide for the continuation of the species.

In other instances, an actual contact takes place between the sexes at the time of reproduction. In the frog, for example, the male fastens himself upon the back of the female by the anterior extremities, which seem to retain their hold by a kind of spasmodic contraction. This continues for one or two days, during which time the mature eggs, which have been discharged from the ovary, are passing downward through the oviducts. At last they are expelled from the anus, while at the same time the seminal fluid of the male is discharged upon them, and impregnation takes place.

In the higher classes of animals, however, and in man, where the egg is to be retained in the body of the female parent during its development, the spermatic fluid is introduced into the female generative passages by sexual congress, and meets the egg at or soon after its discharge from the ovary. The same correspondence, however, between the periods of sexual excitement in the male and

female, is visible in many of these animals, as well as in fish and reptiles. This is the case in most species which produce young but once a year, and at a fixed period, as the deer and the wild hog. In other species, on the contrary, such as the dog, as well as the rabbit, the guinea pig, &c., where several broods of young are produced during the year, or where, as in the human subject, the generative epochs of the female recur at short intervals, so that the particular period of impregnation is comparatively indefinite, the generative apparatus of the male is almost constantly in a state of full development; and is excited to action at particular periods, apparently by some influence derived from the condition of the female.

In the quadrupeds, accordingly, and in the human species, the contact of the sperm with the egg and the fecundation of the latter take place in the generative passages of the female; either in the uterus, the Fallopian tubes, or even upon the surface of the ovary; in each of which situations the spermatozoa have been found, after the accomplishment of sexual intercourse.

CHAPTER V.

ON PERIODICAL OVULATION, AND THE FUNCTION OF MENSTRUATIO

I. PERIODICAL OVULATION.

We have already spoken in general terms of the periodical ripening of the eggs and their discharge from the generative organs of the female. This function is known by the name of "ovulation," and may be considered as the primary and most important act in the process of reproduction. We shall, therefore, enter more fully into the consideration of certain particulars in regard to it, by which its nature and conditions may be more clearly understood.

1st. *Eggs exist originally in the ovaries of all animals, as part of their natural structure.* In describing the ovaries of fish and reptiles we have said that they consist of nothing more than Graafian vesicles, each vesicle containing an egg, and united with the others by loose areolar tissue and a peritoneal investment. In the higher animals and in the human subject, the essential constitution of the ovary is the same; only its fibrous tissue is more abundant, so that the texture of the entire organ is more dense, and its figure more compact. In all classes, however, without exception, the interior of each Graafian vesicle is occupied by an egg; and it is from this egg that the young offspring is afterward produced.

The process of reproduction was formerly regarded as essentially different in the oviparous and the viviparous animals. In the oviparous classes, such as most fish, and all reptiles and birds, the young animal was well known to be formed from an egg produced by the female; while in the viviparous animals, or those which bring forth their young alive, such as the quadrupeds and the human species, the embryo was supposed to originate in the body of the female, by some altogether peculiar and mysterious process, in consequence of sexual intercourse. As soon, however, as the microscope began to be used in the examination of the tissues,

the ovaries of quadrupeds were also found to contain eggs. These eggs had previously escaped observation on account of their simple structure and minute size; but they were nevertheless found to possess all the most essential characters belonging to the larger eggs of the oviparous animals.

The true difference in the process of reproduction, between the two classes, is therefore merely an apparent, not a fundamental one. In fish, reptiles, and birds, the egg is discharged by the female before or immediately after impregnation, and the embryo is subsequently developed and hatched externally. In the quadrupeds and the human species, on the other hand, the egg is retained within the body of the female until the embryo is developed; when the membranes are ruptured and the young expelled at the same time. In all classes, however, viviparous as well as oviparous, the young is produced equally from an egg; and in all classes the egg, sometimes larger and sometimes smaller, but always consisting essentially of a vitellus and a vitelline membrane, is contained originally in the interior of an ovarian follicle.

The egg is accordingly, as we have already intimated, an integral part of the ovarian tissue. It may be found there long before the generative function is established, and during the earliest periods of life. It may be found without difficulty in the newly born female infant, and may even be detected in the fœtus before birth. Its growth and nutrition, also, are provided for in the same manner with that of other portions of the bodily structure.

2d. *These eggs become more fully developed at a certain age, when the generative function is about to be established.* During the early periods of life, the ovaries and their contents, like many other organs, are imperfectly developed. They exist, but they are as yet inactive, and incapable of performing any function. In the young chick, for example, the ovary is of small size; and the eggs, instead of presenting the voluminous, yellow, opaque vitellus which they afterward exhibit, are minute, transparent, and colorless. In the young quadrupeds, and in the human female during infancy and childhood, the ovaries are equally inactive. They are small, friable, and of a nearly homogeneous appearance to the naked eye; presenting none of the enlarged follicles, filled with transparent fluid, which are afterward so readily distinguished. At this time, accordingly, the female is incapable of bearing young, because the ovaries are inactive, and the eggs which they contain immature.

At a certain period, however, which varies in the time of its

occurrence for different species of animals, the sexual apparatus begins to enter upon a state of activity. The ovaries increase in size, and their circulation becomes more active. The eggs, also, instead of remaining quiescent, take on a rapid growth, and the structure of the vitellus is completed by the abundant deposit of oleaginous granules in its interior. Arrived at this state, the eggs are ready for impregnation, and the female becomes capable of bearing young. She is then said to have arrived at the state of "puberty," or that condition in which the generative organs are fully developed. This condition is accompanied by a visible alteration in the system at large, which indicates the complete development of the entire organism. In many birds, for example, the plumage assumes at this period more varied and brilliant colors; and in the common fowl the comb, or "crest," enlarges and becomes red and vascular. In the American deer (Cervus virginianus), the coat, which during the first year is mottled with white, becomes in the second year of a uniform tawny or reddish tinge. In nearly all species, the limbs become more compact and the body more rounded; and the whole external appearance is so altered, as to indicate that the animal has arrived at the period of puberty, and is capable of reproduction.

3d. *Successive crops of eggs, in the adult female, ripen and are discharged independently of sexual intercourse.* It was formerly supposed, as we have mentioned above, that in the viviparous animals the germ was formed in the body of the female only as a consequence of sexual intercourse. Even after the important fact became known that eggs exist originally in the ovaries of these animals, and are only fecundated by the influence of the spermatic fluid, the opinion still prevailed that the occurrence of sexual intercourse was the cause of their being discharged from the ovary, and that the rupture of a Graafian vesicle in this organ was a certain indication that coitus had taken place.

This opinion, however, was altogether unfounded. We already know that in fish and reptiles the mature eggs not only leave the ovary, but are actually discharged from the body of the female while still unimpregnated, and only subsequently come in contact with the spermatic fluid. In fowls, also, it is a matter of common observation that the hen will continue to lay fully-formed eggs, if well supplied with nourishment, without the presence of the cock; only these eggs, being unimpregnated, are incapable of producing

chicks. In oviparous animals, therefore, the discharge of the egg, as well as its formation, is independent of sexual intercourse.

Continued observation shows this to be the case, also, in the viviparous quadrupeds. The researches of Bischoff, Pouchet, and Coste have demonstated that in the sheep, the pig, the bitch, the rabbit, &c., if the female be carefully kept from the male until after the period of puberty is established, and then killed, examination of the ovaries will show that Graafian vesicles have matured, ruptured, and discharged their eggs, in the same manner as though sexual intercourse had taken place. Sometimes the vesicles are found distended and prominent upon the surface of the ovary; sometimes recently ruptured and collapsed; and sometimes in various stages of cicatrization and atrophy. Bischoff,[1] in several instances of this kind, actually found the unimpregnated eggs in the oviduct, on their way to the cavity of the uterus. In those animals in which the ripening of the eggs takes place at short intervals, as, for example, the sheep, the pig, and the cow, it is very rare to examine the ovaries in any instance where traces of a more or less recent rupture of the Graafian follicles are not distinctly visible.

One of the most important facts, derived from the examination of such cases as the above, is that the ovarian eggs become developed and are discharged in successive crops, which follow each other regularly at periodical intervals. If we examine the ovary of the fowl, for example (Fig. 190), we see at a glance how the eggs grow and ripen, one after the other, like fruit upon a vine. In this instance, the process of evolution is very rapid; and it is easy to distinguish, at the same time, eggs which are almost microscopic in size, colorless, and transparent; those which are larger, firmer, somewhat opaline, and yellowish in hue; and finally those which are fully developed, opaque, of a deep orange color, and just ready to leave the ovary.

It will be observed that in this instance the difference between the undeveloped and the mature eggs consists principally in the size of the vitellus, which is furthermore, for reasons previously given (Chap. III.), very much larger than in the quadrupeds. It is also seen that it is the increased size of the vitellus alone, by which the ovarian follicle is distended and ruptured, and the egg finally discharged.

[1] Mémoire sur la chute périodique de l'œuf, &c., Annales des Sciences Naturelles, Août—Septembre, 1844.

In the human species and the quadrupeds, on the other hand, the microscopic egg never becomes large enough to distend the follicle by its own size. The rupture of the follicle and the liberation of the egg are accordingly provided for, in these instances, by a totally different mechanism.

In the earlier periods of life, in man and the higher animals, the egg is contained in a Graafian follicle which closely embraces its exterior, and is consequently hardly larger than the egg itself. As puberty approaches, those follicles which are situated near the free surface of the ovary become enlarged by the accumulation of a colorless serous fluid in their cavity. We then find that the ovary, when cut open, shows a considerable number of globular, transparent vesicles, readily perceptible by the eye, the smaller of which are deep seated, but which increase in size as they approach the free surface of the organ. These vesicles are the Graafian follicles, which, in consequence of the advancing maturity of the eggs contained in them, gradually enlarge as the period of generation approaches.

The Graafian follicle at this time consists of a closed globular sac or vesicle, the external wall of which, though quite translucent has a fibrous texture under the microscope and is well supplied with bloodvessels. This fibrous and vascular wall is distinguished by the name of the "membrane of the vesicle." It is not very firm in texture, and if roughly handled is easily ruptured.

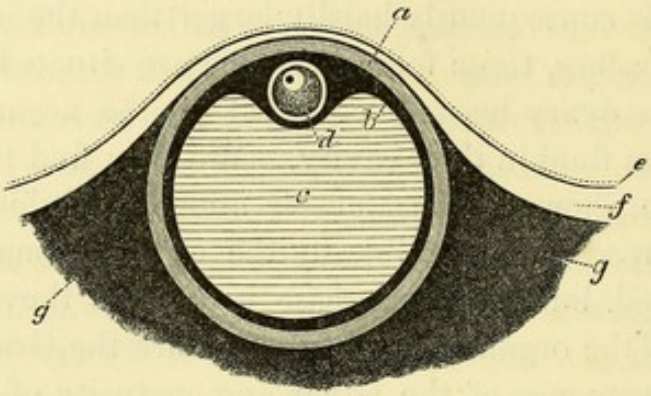
The membrane of the vesicle is lined throughout by a thin layer of minute granular cells, which form for it a kind of epithelium, similar to the epithelium of the pleura, pericardium, and other serous membranes. This layer is termed the *membrana granulosa.* It adheres but slightly to the membrane of the vesicle, and may easily be detached by careless manipulation before the vesicle is opened, being then mingled, in the form of light flakes and shreds, with the serous fluid contained in the vesicle.

At the most superficial part of the Graafian follicle, or that which is nearest the surface of the ovary, the membrana granulosa is thicker than elsewhere. Its cells are here accumulated, in a kind of mound or "heap," which has received the name of the *cumulus proligerus.* It is sometimes called the *discus proligerus,* because the thickened mass, when viewed from above, has a somewhat circular or disk-like form. In the centre of this thickened portion of the membrana granulosa the egg is imbedded. It is

accordingly always situated at the most superficial portion of the follicle. and advances in this way toward the surface of the ovary.

As the period approaches at which the egg is destined to be discharged, the Graafian follicle becomes more vascular, and enlarges by an increased exudation of serum into its cavity. It then begins

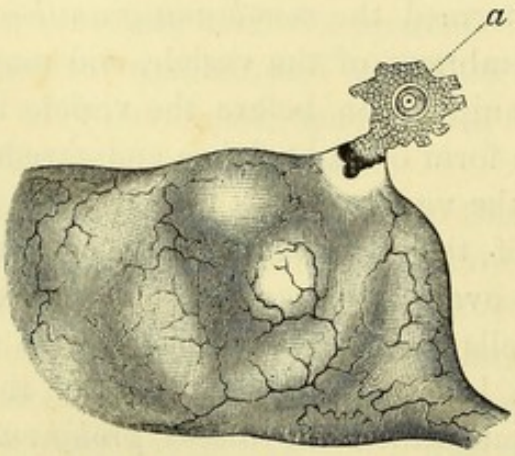
Fig. 195.



GRAAFIAN FOLLICLE, near the period of rupture —*a*. Membrane of the vesicle. *b*. Membrana granulosa. *c*. Cavity of follicle. *d*. Egg. *e*. Peritoneum. *f*. Tunica albuginea. *g*, *g*. Tissue of the ovary.

to project from the surface of the ovary, still covered by the albugineous tunic and the peritoneum. (Fig. 195.) The constant accumulation of fluid, however, in the follicle, exerts such a steady and increasing pressure from within outward, that the albugineous tunic and the peritoneum successively yield before it; until the Graafian follicle protrudes from the ovary as a tense, rounded, translucent vesicle, in which the sense of fluctuation can be readily perceived on applying the fingers to its surface. Finally, the process of effusion and distension still going on, the wall of the vesicle yields at its most prominent portion, the contained fluid is driven out with a gush, by the reaction and elasticity of the neighboring ovarian tissues, carrying with it the egg, still entangled in the cells of the proligerous disk.

Fig. 196.



OVARY WITH GRAAFIAN FOLLICLE RUPTURED: at *a*, egg just discharged with a portion of membrana granulosa.

The rupture of the Graafian vesicle is accompanied, in some instances, by an abundant hemor-

rhage, which takes place from the internal surface of the congested follicle, and by which its cavity is filled with blood. This occurs in the human subject and in the pig, and to a certain extent, also, in other of the lower animals. Sometimes, as in the cow, where no hemorrhage takes place, the Graafian vesicle when ruptured simply collapses; after which a slight exudation, more or less tinged with blood, is poured out during the course of a few hours.

Notwithstanding, however, these slight variations, the expulsion of the egg takes place, in the higher animals, always in the manner above described, viz., by the accumulation of serous fluid in the cavity of the Graafian follicle, by which its walls are gradually distended and finally ruptured.

This process takes place in one or more Graafian follicles at a time, according to the number of young which the animal produces at a birth. In the bitch and the sow, where each litter consists of from six to twenty young ones, a similar number of eggs ripen and are discharged at each period. In the mare, in the cow, and in the human female, where there is usually but one fœtus at a birth, the eggs are matured singly, and the Graafian vesicles ruptured, one after another, at successive periods of ovulation.

4th. *The ripening and discharge of the egg are accompanied by a peculiar condition of the entire system, known as the "rutting" condition, or "œstruation."* The peculiar congestion and functional activity of the ovaries at each period of ovulation, act by sympathy upon the other generative organs and produce in them a greater or less degree of excitement, according to the particular species of animal. Almost always there is a certain amount of congestion of the entire generative apparatus; Fallopian tubes, uterus, vagina, and external organs. The secretions of the vagina and neighboring parts are more particularly affected, being usually increased in quantity and at the same time altered in quality. In the bitch, the vaginal mucous membrane becomes red and tumefied, and pours out an abundant secretion which is often more or less tinged with blood. The secretions acquire also at this time a peculiar odor, which appears to attract the male, and to excite in him the sexual impulse. An unusual tumefaction and redness of the vagina and vulva are also very perceptible in the rabbit; and in some species of apes it has been observed that these periods are accompanied not only by a bloody discharge from the vulva, but also by an engorgement and infiltration of the neighboring parts, extending even

to the skin of the buttocks, the thighs, and the under part of the tail.[1]

The system at large is also visibly affected by the process going on in the ovary. In the cow, for example, the approach of an œstrual period is marked by an unusual restlessness and agitation, easily recognized by an ordinary observer. The animal partially loses her appetite. She frequently stops browsing, looks about uneasily, perhaps runs from one side of the field to the other, and then recommences feeding, to be disturbed again in a similar manner after a short interval. Her motions are rapid and nervous, and her hide often rough and disordered; and the whole aspect of the animal indicates the presence of some unusual excitement. After this condition is fully established, the vaginal secretions show themselves in unusual abundance, and so continue for one or two days; after which the symptoms, both local and general, subside spontaneously, and the animal returns to her usual condition.

It is a remarkable fact, in this connection, that the female of these animals will allow the approaches of the male only during and immediately after the œstrual period; that is, just when the egg is recently discharged, and ready for impregnation. At other times, when sexual intercourse would be necessarily fruitless, the instinct of the animal leads her to avoid it; and the concourse of the sexes is accordingly made to correspond in time with the maturity of the egg and its aptitude for fecundation.

II. MENSTRUATION.

In the human female, the return of the period of ovulation is marked by a peculiar group of phenomena which are known as *menstruation*, and which are of sufficient importance to be described by themselves.

During infancy and childhood the sexual system, as we have mentioned above, is inactive. No discharge of eggs takes place from the ovaries, and no external phenomena show themselves, connected with the reproductive function.

At the age of fourteen or fifteen years, however, a change begins to manifest itself. The limbs become rounder, the breasts increase in size, and the entire aspect undergoes a peculiar alteration, which indicates the approaching condition of maturity. At the same time a discharge of blood takes place from the generative passages,

[1] Pouchet, Théorie positive de l'ovulation, &c. Paris, 1847, p. 230.

accompanied by some disturbance of the general system, and the female is then known to have arrived at the period of puberty.

Afterward, the bloody discharge just spoken of returns at regular intervals of four weeks; and, on account of this recurrence corresponding with the passage of successive lunar months, its phenomena are designated by the name of the "menses" or the "menstrual periods." The menses return with regularity, from the time of their first appearance, until the age of about forty-five years. During this period, the female is capable of bearing children, and sexual intercourse is liable to be followed by pregnancy. After the forty-fifth year, the periods first become irregular, and then cease altogether; and their final disappearance is an indication that the woman is no longer fertile, and that pregnancy cannot again take place.

Even during the period above referred to, from the age of fifteen to forty-five, the regularity and completeness of the menstrual periods indicate to a great extent the aptitude of individual females for impregnation. It is well known that all those causes of ill health which derange menstruation are apt at the same time to interfere with pregnancy; so that women whose menses are habitually regular and natural are much more likely to become pregnant, after sexual intercourse, than those in whom the periods are absent or irregular.

If pregnancy happen to take place, however, at any time during the child-bearing period, the menses are suspended during the continuance of gestation, and usually remain absent, after delivery, as long as the woman continues to nurse her child. They then recommence, and subsequently continue to appear as before.

The menstrual discharge consists of an abundant secretion of mucus mingled with blood. When the expected period is about to come on, the female is affected with a certain degree of discomfort and lassitude, a sense of weight in the pelvis, and more or less disinclination to society. These symptoms are in some instances slightly pronounced, in others more troublesome. An unusual discharge of vaginal mucus then begins to take place, which soon becomes yellowish or rusty brown in color, from the admixture of a certain proportion of blood; and by the second or third day the discharge has the appearance of nearly pure blood. The unpleasant sensations which were at first manifest then usually subside; and the discharge, after continuing for a certain period, begins to grow more scanty. Its color changes from a pure red to a brownish or

rusty tinge, until it finally disappears altogether, and the female returns to her ordinary condition.

The menstrual epochs of the human female correspond with the periods of œstruation in the lower animals. Their general resemblance to these periods is too evident to require demonstration. Like them, they are absent in the immature female; and begin to take place only at the period of puberty, when the aptitude for impregnation commences. Like them, they recur during the child-bearing period at regular intervals; and are liable to the same interruption by pregnancy and lactation. Finally, their disappearance corresponds with the cessation of fertility.

The periods of œstruation, furthermore, in many of the lower animals, are accompanied, as we have already seen, with an unusual discharge from the generative passages; and this discharge is frequently more or less tinged with blood. In the human female the bloody discharge is more abundant than in other instances, but it is evidently a phenomenon differing only in degree from that which shows itself in many species of animals.

The most complete evidence, however, that the period of menstruation is in reality that of ovulation, is derived from the results of direct observation. A sufficient number of instances have now been observed to show that at the menstrual epoch a Graafian vesicle becomes enlarged, ruptures, and discharges its egg. Cruikshank[1] noticed such a case so long ago as 1797. Negrier[2] relates two instances, communicated to him by Dr. Ollivier d'Angers, in which, after sudden death during menstruation, a bloody and ruptured Graafian vesicle was found in the ovary. Bischoff[3] speaks of four similar cases in his own observation, in three of which the vesicle was just ruptured, and in the fourth distended, prominent, and ready to burst. Coste[4] has met with several of the same kind. Dr. Michel[5] found a vesicle ruptured and filled with blood in a woman who was executed for murder while the menses were present. We have also[6] met with the same appearances in a case of death from acute disease, on the second day of menstruation.

[1] London Philosophical Transactions, 1797, p. 135.

[2] Recherches sur les Ovaires, Paris, 1840, p. 78.

[3] Annales des Sciences Naturelles, August, 1844.

[4] Histoire du Developpement des Corps Organisés, Paris, 1847, vol. i. p. 221.

[5] Am. Journ. Med. Sci., July, 1848.

[6] Corpus Luteum of Menstruation and Pregnancy, in Transactions of American Medical Association, Philadelphia, 1851.

The process of ovulation, accordingly, in the human female, accompanies and forms a part of that of menstruation. As the menstrual period comes on, a congestion takes place in nearly the whole of the generative apparatus; in the Fallopian tubes and the uterus, as well as in the ovaries and their contents. One of the Graafian follicles is more especially the seat of an unusual vascular excitement. It becomes distended by the fluid which accumulates in its cavity, projects from the surface of the ovary, and is finally ruptured in the same manner as we have already described this process taking place in the lower animals.

It is not quite certain at what particular period of the menstrual flow the rupture of the vesicle and discharge of the egg take place. It is the opinion of Bischoff, Pouchet, and Raciborski, that the regular time for this rupture and discharge is not at the commencement, but towards the termination of the period. Coste[1] has ascertained, from his observations, that the vesicle ruptures sometimes in the early part of the menstrual epoch, and sometimes later. So far as we can learn, therefore, the precise period of the discharge of the egg is not invariable. Like the menses themselves, it may apparently take place a little earlier, or a little later, according to various accidental circumstances; but it always occurs at some time in connection with the menstrual flow, and constitutes the most essential and important part of the catamenial process.

The egg, when discharged from the ovary, enters the fimbriated extremity of the Fallopian tube, and commences its passage toward the uterus. The mechanism by which it finds its way into and through the Fallopian tube is different, in the quadrupeds and the human species, and in birds and reptiles. In the latter, the bulk of the egg or mass of eggs discharged is so great as to fill entirely the wide extremity of the oviduct, and they are afterward conveyed downward by the peristaltic action of the muscular coat of this canal. In the higher classes, on the contrary, the egg is microscopic in size, and would be liable to be lost, were there not some further provision for its safety. The wide extremity of the Fallopian tube, accordingly, which is here directed toward the ovary, is lined with ciliated epithelium; and the movement of the cilia, which is directed from the ovary toward the uterus, produces a kind of converging stream, or vortex, by which the egg is necessarily drawn toward the narrow portion of the tube, and subsequently conducted to the cavity of the uterus.

[1] Loc cit.

Accidental causes, however, sometimes disturb this regular course or passage of the egg. The egg may be arrested, for example, at the surface of the ovary, and so fail to enter the tube at all. If fecundated in this situation, it will then give rise to "ovarian pregnancy." It may escape from the fimbriated extremity into the peritoneal cavity, and form attachments to some one of the neighboring organs, causing "abdominal pregnancy;" or finally, it may stop at any part of the Fallopian tube, and so give origin to "tubal pregnancy."

The egg, immediately upon its discharge from the ovary, is ready for impregnation. If sexual intercourse happen to take place about that time, the egg and the spermatic fluid meet in some part of the female generative passages, and fecundation is accomplished. It appears from various observations of Bischoff, Coste, and others, that this contact may take place between the egg and the sperm, either in the uterus or any part of the Fallopian tubes, or even upon the surface of the ovary. If, on the other hand, coitus do not take place, the egg passes down to the uterus unimpregnated, loses its vitality after a short time, and is finally carried away with the uterine secretions.

It is easily understood, therefore, why sexual intercourse should be more liable to be followed by pregnancy when it occurs about the menstrual epoch than at other times. This fact, which was long since established as a matter of observation by practical obstetricians, depends simply upon the coincidence in time between menstruation and the discharge of the egg. Before its discharge, the egg is immature, and unprepared for impregnation; and after the menstrual period has passed, it gradually loses its freshness and vitality. The exact length of time, however, preceding and following the menses, during which impregnation is still possible, has not been ascertained. The spermatic fluid, on the one hand, retains its vitality for an unknown period after coition, and the egg for an unknown period after its discharge. Both these occurrences may, therefore, either precede or follow each other within certain limits, and impregnation be still possible; but the precise extent of these limits is still uncertain, and is probably more or less variable in different individuals.

The above facts indicate also the true explanation of certain exceptional cases, which have sometimes been observed, in which fertility exists without menstruation. Various authors (Churchill, Reid, Velpeau, &c.) have related instances of fruitful women in whom

the menses were very scanty and irregular, or even entirely absent. The menstrual flow is, in fact, only the external sign and accompaniment of a more important process taking place within. It is habitually scanty in some individuals, and abundant in others. Such variations depend upon the condition of vascular activity of the system at large, or of the uterine organs in particular; and though the bloody discharge is usually an index of the general aptitude of these organs for successful impregnation, it is not an absolute or necessary requisite. Provided a mature egg be discharged from the ovary at the appointed period, menstruation properly speaking exists, and pregnancy is possible.

The blood which escapes during the menstrual flow is supplied by the uterine mucous membrane. If the cavity of the uterus be examined after death during menstruation, its internal surface is seen to be smeared with a thickish bloody fluid, which may be traced through the uterine cervix and into the vagina. The Fallopian tubes themselves are sometimes found excessively congested, and filled with a similar bloody discharge. The menstrual blood has also been seen to exude from the uterine orifice in cases of procidentia uteri, as well as in the natural condition by examination with the vaginal speculum. It is discharged by a kind of capillary hemorrhage, similar to that which takes place from the lungs in cases of hæmoptysis, only less sudden and violent. The blood does not form any visible coagulum, owing to its being gradually exuded from many minute points, and mingled with a large quantity of mucus. When poured out, however, more rapidly or in larger quantity than usual, as in cases of menorrhagia, the menstrual blood coagulates in the same manner as if derived from any other source. The hemorrhage which supplies it comes from the whole extent of the mucous membrane of the body of the uterus, and is, at the same time, the consequence and the natural termination of the periodical congestion of the parts.

CHAPTER VI.

ON THE CORPUS LUTEUM OF MENSTRUATION AND PREGNANCY.

After the rupture of the Graafian follicle at the menstrual period, a bloody cavity is left in the ovary, which is subsequently obliterated by a kind of granulating process, somewhat similar in character to the healing of an abscess. For the Graafian follicle is intended simply for the formation and growth of the egg. After the egg therefore has arrived at maturity and has been discharged, the Graafian follicle has no longer any function to perform. It then only remains for it to pass through a process of obliteration and atrophy, as an organ which has become useless and obsolete. While undergoing this process, the Graafian follicle is at one time converted into a peculiar, solid, globular body, which is called the *corpus luteum;* a name given to it on account of the yellow color which it acquires at a certain period of its formation.

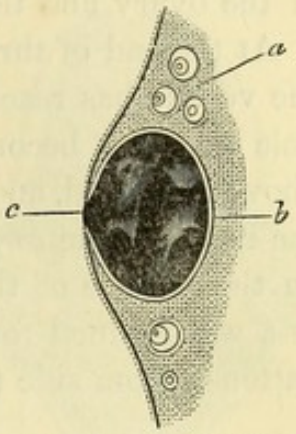
We shall proceed to describe the corpus luteum in the human species; first, as it follows the ordinary course of development after menstruation; and secondly, as it is modified in its growth and appearance during the existence of pregnancy.

I. CORPUS LUTEUM OF MENSTRUATION.

We have already described, in the preceding chapter, the manner in which a Graafian follicle, at each menstrual epoch, swells, protrudes from the surface of the ovary, and at last ruptures and discharges its egg. At the moment of rupture, or immediately after it, an abundant hemorrhage takes place in the human subject from the vessels of the follicle, by which its cavity is filled with blood. This blood coagulates soon after its exudation, as it would do if extravasated in any other part of the body, and the coagulum is retained in the interior of the Graafian follicle.

The opening by which the egg makes its escape is usually not an extensive laceration, but a minute rounded perforation, often not more than half a line in diameter. A small probe, introduced through this opening, passes directly into the cavity of the follicle. If the Graafian follicle be opened at this time by a longitudinal incision (Fig. 197), it will be seen to form a globular cavity, one-half to three-quarters of an inch in diameter, containing a soft, recent, dark-colored coagulum. This coagulum has no organic connection with the walls of the follicle, but lies loose in its cavity and may be easily turned out with the handle of a knife. There is sometimes a slight mechanical adhesion of the clot to the edges of the lacerated opening, just as the coagulum in a recently ligatured artery is entangled by the divided edges of the internal and middle coats; but there is no continuity of substance between them, and the clot may be everywhere readily separated by careful manipulation. The membrane of the vesicle presents at this time a smooth, transparent, and vascular internal surface, without any alteration of color, consistency, or texture.

Fig. 197.



GRAAFIAN FOLLICLE recently ruptured during menstruation, and filled with a bloody coagulum; shown in longitudinal section.—*a*. Tissue of the ovary. *b*. Membrane of the vesicle. *c*. Point of rupture.

An important change, however, soon begins to take place, both in the central coagulum and in the membrane of the vesicle.

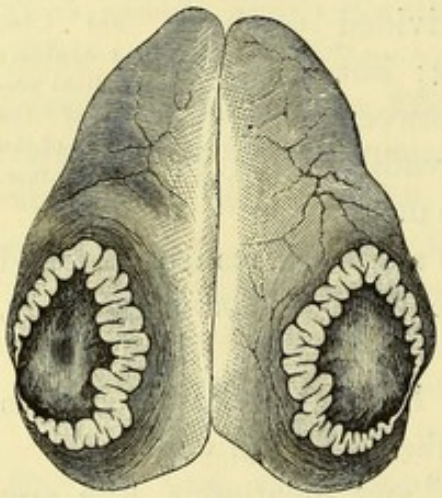
The clot, which is at first large, soft, and gelatinous, like any other mass of coagulated blood, begins to contract; and the serum separates from the coagulum proper. The serum, as fast as it separates from the coagulum, is absorbed by the neighboring parts; and the clot, accordingly, grows every day smaller and denser than before. At the same time the coloring matter of the blood undergoes the changes which usually take place in it after extravasation, and is partially reabsorbed together with the serum. This second change is somewhat less rapid than the former, but still a diminution of color is very perceptible in the clot, at the expiration of two weeks.

The membrane of the vesicle during this time is beginning to undergo a process of hypertrophy or development, by which it becomes thickened and convoluted, and tends partially to fill up

the cavity of the follicle. This hypertrophy and convolution of the membrane just named commences and proceeds most rapidly at the deeper part of the follicle, directly opposite the situation of the superficial rupture. From this point the membrane gradually becomes thinner and less convoluted as it approaches the surface of the ovary and the edges of the ruptured orifice.

At the end of three weeks, this hypertrophy of the membrane of the vesicle has reached its maximum. The ruptured Graafian follicle has now become so completely solidified by the new growth above described, and by the condensation of its clot, that it receives the name of the *corpus luteum*. It forms a perceptible prominence on the surface of the ovary, and may be felt between the fingers as a well-defined rounded tumor, which is nearly always somewhat flattened from side to side. It measures about three-quarters of an inch in length and half an inch in depth. On its surface may be seen a minute cicatrix of the peritoneum, occupying the spot of the original rupture.

Fig. 198.



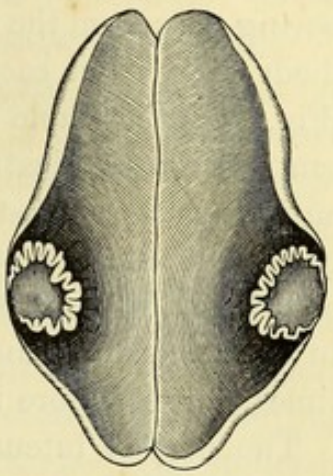
OVARY cut open, showing corpus luteum divided longitudinally; three weeks after menstruation. From a girl dead of hæmoptysis.

On cutting it open at this time (Fig. 198), the corpus luteum is seen to consist, as above described, of a central coagulum and a convoluted wall. The coagulum is semi-transparent, of a gray or light greenish color, more or less mottled with red. The convoluted wall is about one-eighth of an inch thick at its deepest part, and of an indefinite yellowish or rosy hue, not very different in tinge from the rest of the ovarian tissue. The convoluted wall and the contained clot lie simply in contact with each other, as at first, without any intervening membrane or other organic connection; and they may still be readily separated from each other by the handle of a knife or the flattened end of a probe. The corpus luteum at this time may also be stripped out, or enucleated entire, from the ovarian tissue, just as might have been done with the Graafian follicle previously to its rupture. When enucleated in this way, the corpus luteum presents itself under the form of a solid globular or flattened tumor, with convolutions upon it somewhat similar in appearance to those of the brain, and covered with the remains of

the areolar tissue, by which it was previously connected with the substance of the ovary.

After the third week from the close of menstruation, the corpus luteum passes into a retrograde condition. It diminishes perceptibly in size, and the central coagulum continues to be absorbed and loses still farther its coloring matter. The whole body undergoes a process of partial atrophy; and at the end of the fourth week it is not more than three-eighths of an inch in its longest diameter. (Fig. 199.) The external cicatrix may still usually be seen, as well as the point where the central coagulum comes in contact with the peritoneum. There is still no organic connection between the central coagulum and the convoluted wall; but the partial condensation of the clot and the continued folding of the wall prevent the separation of the two being so easily accomplished as before, though it may still be effected by careful management. The entire corpus luteum may also still be extracted from its bed in the ovarian tissue.

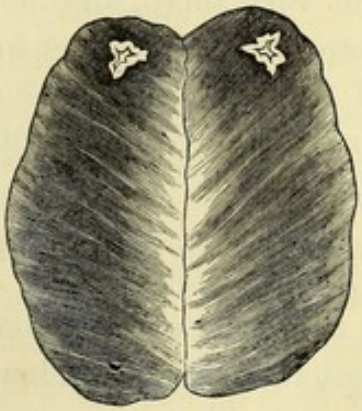
Fig. 199.



Ovary, showing corpus luteum four weeks after menstruation, from a woman dead of apoplexy.

The color of the convoluted wall, during the early part of this retrograde stage, instead of fading, like that of the fibrinous coagulum, becomes more strongly marked. From having a dull yellowish or rosy hue, as at first, it gradually assumes a brighter and more decided yellow. This change of color in the convoluted wall is produced in consequence of a kind of fatty degeneration which takes place in its texture; a large quantity of oil-globules being deposited in it at this time, as may be readily recognized under the microscope. At the end of the fourth week, this alteration in hue is complete; and the outer wall of the corpus luteum is then of a clear chrome-yellow color, by which it is readily distinguished from all the neighboring tissues.

Fig. 200.



Ovary, showing corpus luteum, nine weeks after menstruation; from a girl dead of tubercular meningitis.

After this period, the process of atrophy and degeneration goes on rapidly. The clot becomes constantly

more dense and shrivelled, and is soon converted into a minute, stellate, white, or reddish-white cicatrix. The yellow wall becomes softer and more friable, as is the case with all tissues undergoing fatty degeneration, and shows less distinctly the marking of its convolutions. At the same time its surfaces become confounded with the central coagulum on the one hand, and with the neighboring tissues on the other, so that it is no longer possible to separate them fairly from each other. At the end of eight or nine weeks (Fig. 200) the whole body is reduced to the condition of an insignificant, yellowish, cicatrix-like spot, measuring less than a quarter of an inch in its longest diameter, in which the original texture of the corpus luteum can be recognized only by the peculiar folding and coloring of its constituent parts. Subsequently its atrophy goes on in a less active manner, and a period of seven or eight months sometimes elapses before its final and complete disappearance.

The corpus luteum, accordingly, is a formation which results from the filling up and obliteration of a ruptured Graafian follicle. Under ordinary conditions, a corpus luteum is produced at every menstrual period; and notwithstanding the rapidity with which it retrogrades and becomes atrophied, a new one is always formed before its predecessor has completely disappeared.

When, therefore, we examine the ovaries of a healthy female, in whom the menses have recurred with regularity for some time previous to death, several corpora lutea will be met with, in different stages of formation and atrophy. Thus we have found, under such circumstances, four, five, six, and even eight corpora lutea in the ovaries at the same time, perfectly distinguishable by their texture, but very small, and most of them evidently in a state of advanced retrogression. They finally disappear altogether, and the number of those present in the ovary, therefore, no longer corresponds with that of the Graafian follicles which have been ruptured.

II. CORPUS LUTEUM OF PREGNANCY.

Since the process above described takes place at every menstrual period, it is independent of impregnation and even of sexual intercourse. The mere presence of a corpus luteum, therefore, is no indication that pregnancy has existed, but only that a Graafian follicle has been ruptured and its contents discharged. We find, nevertheless, that when pregnancy takes place, the appearance of the corpus luteum becomes so much altered as to be readily dis-

tinguished from that which simply follows the ordinary menstrual process. It is proper, therefore, to speak of two kinds of corpora lutea; one belonging to menstruation, the other to pregnancy.

The difference between these two kinds of corpora lutea is not an essential or fundamental difference; since they both originate in the same way, and are composed of the same structures. It is, properly speaking, only a difference in the degree and rapidity of their development. For while the corpus luteum of menstruation passes rapidly through its different stages, and is very soon reduced to a condition of atrophy, that of pregnancy continues its development for a long time, attains a larger size and firmer organization, and disappears finally only at a much later period.

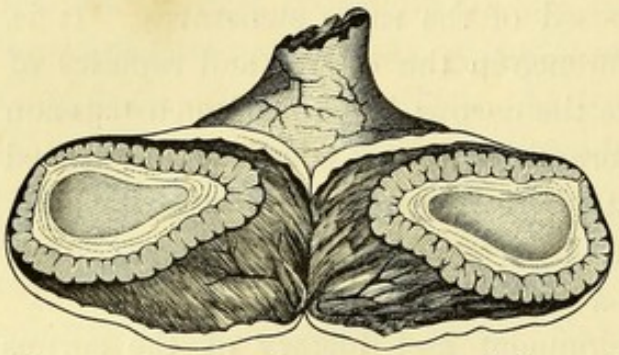
This variation in the development and history of the corpus luteum depends upon the unusually active condition of the pregnant uterus. This organ exerts a powerful sympathetic action, during pregnancy, upon many other parts of the system. The stomach becomes irritable, the appetite is capricious, and even the mental faculties and the moral disposition are frequently more or less affected. The ovaries, however, feel the disturbing influence of gestation more certainly and decidedly than the other organs, since they are more closely connected with the uterus in the ordinary performance of their function. The moment that pregnancy takes place, the process of menstruation is arrested. No more eggs come to maturity, and no more Graafian follicles are ruptured, during the whole period of gestation. It is not at all singular, therefore, that the growth of the corpus luteum should also be modified, by an influence which affects so profoundly the system at large, as well as the ovaries in particular.

During the first three weeks of its formation, the growth of the corpus luteum is the same in the impregnated as in the unimpregnated condition. After that time, however, a difference becomes manifest. Instead of commencing a retrograde course during the fourth week, the corpus luteum of pregnancy continues its development. The external wall grows thicker, and its convolutions more abundant. Its color alters in the same way as previously described, and becomes a bright yellow by the deposit of fatty matter in microscopic globules and granules.

By the end of the second month, the whole corpus luteum has increased in size to such an extent as to measure seven-eighths of an inch in length by half an inch in depth. (Fig. 201.) The central coagulum has by this time become almost entirely decolorized, so as

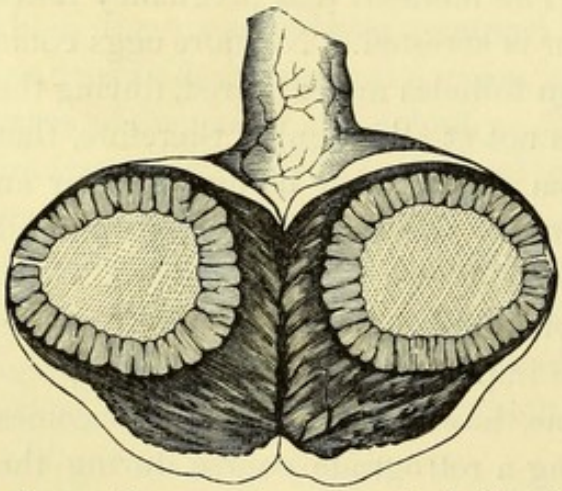
to present the appearance of a purely fibrinous deposit. Sometimes we find that a part of the serum, during its separation from the clot, has accumulated in the centre of the mass, as in Fig. 201, forming a little cavity containing a few drops of clear fluid and inclosed by a whitish, fibrinous layer, the remains of the solid portion of the clot. It is this fibrinous layer which has sometimes been mistaken for a distinct organized membrane, lining the internal surface of the convoluted wall, and which has thus led to the belief that the yellow matter of the corpus luteum is normally deposited outside the membrane of the Graafian follicle. Such, however, is not its real structure. The convoluted wall of the corpus luteum *is* the membrane of the follicle itself, partially altered by hypertrophy, as may be readily seen by examination in the earlier stages of its growth; and the fibrinous layer, situated internally, is the original bloody coagulum, decolorized and condensed by continued absorption. The existence of a central cavity containing serous fluid, is merely an occasional, not a constant phenomenon. More frequently, the fibrinous clot is solid throughout, the serum being gradually absorbed, as it separates spontaneously from the coagulum.

Fig. 201.



CORPUS LUTEUM of pregnancy, at end of second month; from a woman dead from induced abortion.

Fig. 202.



CORPUS LUTEUM of pregnancy, at end of fourth month, from a woman dead by poison.

During the third and fourth months, the enlargement of the corpus luteum continues; so that at the end of that time it may measure seven-eighths of an inch in length by three-quarters of an inch in depth. (Fig. 202.) The convoluted wall is still thicker and more highly developed than before, having a thickness, at its deepest part, of three-sixteenths of an inch. Its color, however, has already begun to fade, and is now of a dull yellow, instead of the bright, clear tinge which it previously ex-

hibited. The central coagulum, perfectly colorless and fibrinous in appearance, is often so much flattened by the lateral compression of its mass, that it has hardly a line in thickness. The other relations of the different parts of the corpus luteum remain the same.

The corpus luteum has now attained its maximum of development, and remains without any very perceptible alteration during the fifth and sixth months. It then begins to retrograde, diminishing constantly in size during the seventh and eighth months. Its external wall fades still more perceptibly in color, becoming of a faint yellowish white, not unlike that which it presented at the end of the third week. Its texture is thick, soft, and elastic, and it is still strongly convoluted. An abundance of fine red vessels can be seen penetrating from the exterior into the interstices of its convolutions. The central coagulum is reduced by this time to the condition of a whitish, radiated cicatrix.

Fig. 203.

CORPUS LUTEUM of pregnancy, at term; from a woman dead in delivery from rupture of the uterus.

The atrophy of the organ continues during the ninth month. At the termination of pregnancy, it is reduced to the size of half an inch in length and three-eighths of an inch in depth. (Fig. 203.) It is then of a faint indefinite hue, but little contrasted with the remaining tissues of the ovary. The central cicatrix has become very small, and appears only as a thin whitish lamina, with radiating processes which run in between the interstices of the convolutions. The whole mass, however, is still quite firm and resisting to the touch, and is readily distinguishable, both from its size and texture, as a prominent feature in the ovarian tissue, and a reliable indication of pregnancy. The convoluted structure of its external wall is very perceptible, and the point of rupture, with its external peritoneal cicatrix, distinctly visible.

After delivery, the corpus luteum retrogrades rapidly. At the end of eight or nine weeks, it has become so much altered that its color is no longer distinguishable, and only faint traces of its convoluted structure are to be discovered by close examination. These traces may remain, however, for a long time afterward, more or less

concealed in the ovarian tissue. We have distinguished them so late as nine and a half months after delivery. They finally disappear entirely, together with the external cicatrix which previously marked their situation.

During the existence of gestation, the process of menstruation being suspended, no new follicles are ruptured, and no new corpora lutea are produced; and as the old ones, formed before the period of conception, gradually fade and disappear, the corpus luteum which marks the occurrence of pregnancy after a short time exists alone in the ovary, and is not accompanied by any others of older date. In twin pregnancies, we of course find two corpora lutea in the ovaries; but these are precisely similar to each other, and, being evidently of the same date, will not give rise to any confusion. Where there is but a single fœtus in the uterus, and the ovaries contain two corpora lutea of similar appearance, one of them belongs to an embryo which has been blighted by some accident in the early part of pregnancy. The remains of the blighted embryo may often be discovered, in such cases, in some part of the Fallopian tubes, where it has been arrested in its descent toward the uterus.

After the process of lactation comes to an end, the ovaries again resume their ordinary function. The Graafian follicles mature and rupture in succession, as before, and new corpora lutea follow each other in alternate development and disappearance.

We find, then, that the corpus luteum of menstruation differs from that of pregnancy in the extent of its development and the duration of its existence. While the former passes through all the important phases of its growth and decline in the period of two months, the latter lasts from nine to ten months, and presents, during a great portion of the time, a larger size and a more solid organization. It will be observed that, even with the corpus luteum of pregnancy, the bright yellow color, which is so important a characteristic, is only temporary in its duration; not making its appearance till about the end of the fourth week, and again disappearing after the sixth month.

The following table contains, in a brief form, the characters of the corpus luteum, as belonging to the two different conditions of menstruation and pregnancy, corresponding with different periods of its development.

	Corpus Luteum of Menstruation.	Corpus Luteum of Pregnancy.
At the end of three weeks	Three-quarters of an inch in diameter; central clot reddish; convoluted wall pale.	
One month	Smaller; convoluted wall bright yellow; clot still reddish.	Larger; convoluted wall bright yellow; clot still reddish.
Two months	Reduced to the condition of an insignificant cicatrix.	Seven-eighths of an inch in diameter; convoluted wall bright yellow; clot perfectly decolorized.
Six months	Absent.	Still as large as at end of second month; clot fibrinous; convoluted wall paler.
Nine months	Absent.	One-half an inch in diameter; central clot converted into a radiating cicatrix; the external wall tolerably thick and convoluted, but without any bright yellow color.

CHAPTER VII.

ON THE DEVELOPMENT OF THE IMPREGNATED EGG—SEGMENTATION OF THE VITELLUS—BLASTODERMIC MEMBRANE—FORMATION OF ORGANS IN THE FROG.

We have seen, in the foregoing chapters, how the egg, produced in the ovarian follicle, becomes gradually developed and ripened, until it is ready to be discharged. The egg, accordingly, passes through several successive stages of formation, even while still contained within the ovary; and its vitellus becomes gradually completed, by the formation of albuminous material and the deposit of molecular granulations. The last change which the egg undergoes, in this situation, and that which marks its complete maturity, is the disappearance of the germinative vesicle. This vesicle, which is, in general, a prominent feature of the ovarian egg, disappears but a short time previous to its discharge, or even just at the period of its leaving the Graafian follicle.

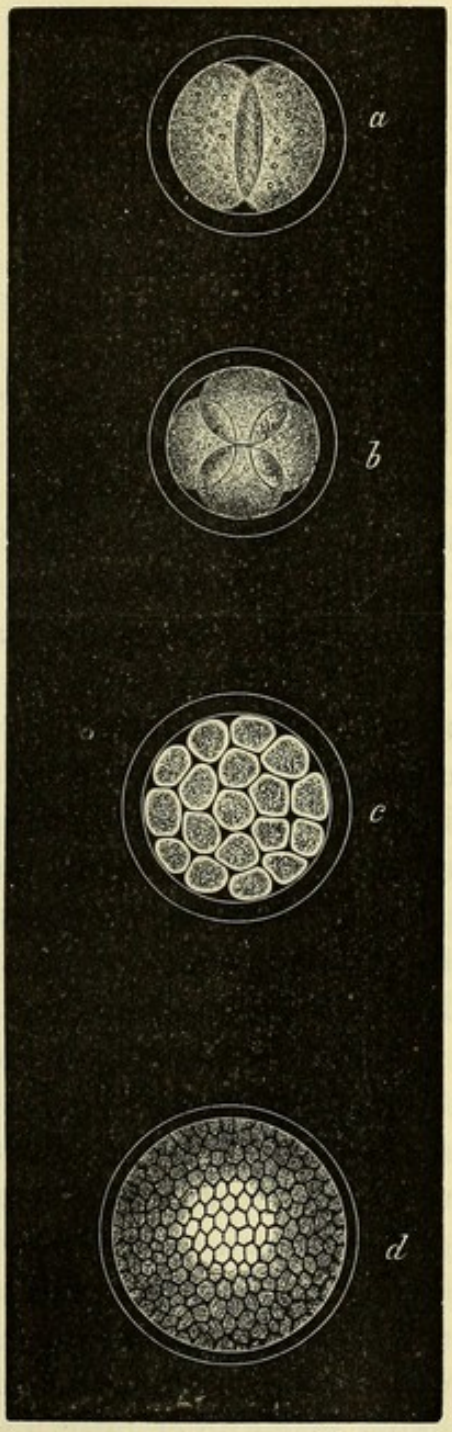
The egg, therefore, consisting simply of the mature vitellus and the vitelline membrane, comes in contact, after leaving the ovary, and while passing through the Fallopian tube, with the spermatic fluid, and is thereby fecundated. By the influence of fecundation, a new stimulus is imparted to its growth; and while the vitality of the unimpregnated germ, arrived at this point, would have reached its termination, the fecundated egg, on the contrary, starts upon a new and more extensive course of development, by which it is finally converted into the body of the young animal.

The egg, in the first place, as it passes down the Fallopian tube, becomes covered with an albuminous secretion. In the birds, as we have seen, this secretion is very abundant, and is deposited in successive layers around the vitellus. In the reptiles, it is also poured out in considerable quantity, and serves for the nourishment of the egg during its early growth. In quadrupeds, the albuminous matter is supplied in the same way, though in smaller quantity, by the

mucous membrane of the Fallopian tubes, and envelopes the egg in a layer of nutritious material.

A very remarkable change now takes place in the impregnated egg, which is known as the spontaneous division, or *segmentation*, of the vitellus. A furrow first shows itself, running round the globular mass of the vitellus in a vertical direction, which gradually deepens until it has divided the vitellus into two separate halves or hemispheres. (Fig. 204, *a*.) Almost at the same time another furrow, running at right angles with the first, penetrates also the substance of the vitellus and cuts it in a transverse direction. The vitellus is thus divided into four equal portions (Fig. 204, *b*), the edges and angles of which are rounded off, and which are still contained in the cavity of the vitelline membrane. The spaces between them and the internal surface of the vitelline membrane are occupied by a transparent fluid.

Fig. 204.



SEGMENTATION OF THE VITELLUS

The process thus commenced goes on by a successive formation of furrows and sections, in various directions. The four vitelline segments already produced are thus subdivided into sixteen, the sixteen into sixty-four, and so on; until the whole vitellus is converted into a mulberry-shaped mass, composed of minute, nearly spherical bodies, which are called the "vitelline spheres." (Fig. 204, *c*.) These vitelline spheres have a somewhat firmer consistency than the original substance of the vitellus; and this consistency appears to increase, as they successively multiply in numbers and diminish in size. At last they have become so abundant as to be closely crowded together, compressed into polygonal forms, and flattened

against the internal surface of the vitelline membrane. (Fig 204, *d*.) They have by this time been converted into true animal cells; and these cells, adhering to each other by their adjacent edges, form a continuous organized membrane, which is termed the *Blastodermic membrane.*

During the formation of this membrane, moreover, the egg, while passing through the Fallopian tubes into the uterus, has increased in size. The albuminous matter with which it was enveloped has liquefied; and, being absorbed by endosmosis through the vitelline membrane, has furnished the materials for the more solid and extensive growth of the newly-formed structures. It may also be seen that a large quantity of this fluid has accumulated in the central cavity of the egg, inclosed accordingly by the blastodermic membrane, with the original vitelline membrane still forming an external envelope round the whole.

The next change which takes place consists in the division or splitting of the blastodermic membrane into two layers, which are known as the *external* and *internal layers of the blastodermic membrane.* They are both still composed exclusively of cells; but those of the external layer are usually smaller and more compact, while those of the internal are rather larger and looser in texture. The egg then presents the appearance of a globular sac, the walls of which consist of three concentric layers, lying in contact with and inclosing each other, viz., 1st, the structureless vitelline membrane on the outside; 2d, the external layer of the blastodermic membrane, composed of cells; and 3d, the internal layer of the blastodermic membrane, also composed of cells. The cavity of the egg is occupied by a transparent fluid, as above mentioned.

This entire process of the segmentation of the vitellus and the formation of the blastodermic membrane is one of the most remarkable and important of all the changes which take place during the development of the egg. It is by this process that the simple globular mass of the vitellus, composed of an albuminous matter and oily granules, is converted into an organized structure. For the blastodermic membrane, though consisting only of cells nearly uniform in size and shape, is nevertheless a truly organized membrane, made up of fully formed anatomical elements. It is, moreover, the first sign of distinct organization which makes its appearance in the egg; and as soon as it is completed, the body of the new fœtus is formed. The blastodermic membrane is, in fact, the body of the fœtus. It is at this time, it is true, exceedingly simple

in texture; but we shall see hereafter that all the future organs of the body, however varied and complicated in structure, arise out of it, by modification and development of its different parts.

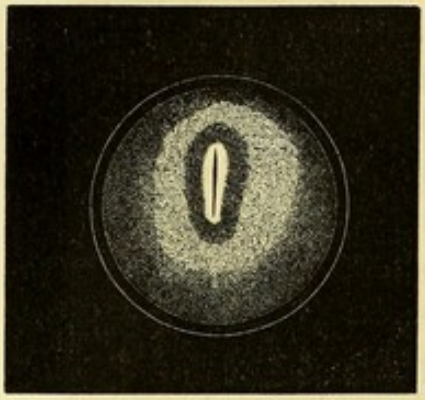
The segmentation of the vitellus, moreover, and the formation of the blastodermic membrane, take place in essentially the same manner in all classes of animals. It is always in this way that the egg commences its development, whether it be destined to form afterward a fish or a reptile, a bird, a quadruped, or a man. The peculiarities belonging to different species show themselves afterward, by variations in the manner and extent of the development of different parts. In the higher animals and in the human subject the development of the egg becomes an exceedingly complicated process, owing to the formation of various accessory organs, which are made requisite by the peculiar conditions under which the development of the embryo takes place. It is, in fact, impossible to describe or understand properly the complex embryology of the quadrupeds, and more particularly that of the human subject, without first tracing the development of those species in which the process is more simple. We shall commence our description, therefore, with the development of the egg of the frog, which is for many reasons particularly appropriate for our purpose.

The egg of the frog, when discharged from the body of the female and fecundated by the spermatic fluid of the male, is deposited in the water, enveloped in a soft elastic cushion of albuminous substance. It is therefore in a situation where it is freely exposed to the light, the air, and the moderate warmth of the sun's rays, and where it can absorb directly an abundance of moisture and appropriate nutritious material. We find accordingly that under these circumstances the development of the egg is distinguished by a character of great simplicity; since *the whole of the vitellus is directly converted into the body of the embryo.* There are no accessory organs required, and consequently no complications of the formative process.

The two layers of the blastodermic membrane, above described, represent together the commencement of all the organs of the fœtus. They are intended, however, for the production of two different systems; and the entire process of their development may be expressed as follows: *The external layer of the blastodermic membrane produces the spinal column and all the organs of animal life; while the internal layer produces the intestinal canal, and all the organs of vegetative life.*

The first sign of advancing organization in the external layer of the blastodermic membrane shows itself in a thickening and condensation of its structure. This thickened portion has the form of an elongated oval-shaped spot, termed the "embryonic spot" (Fig. 205), the wide edges of which are somewhat more opaque than the rest of the blastodermic membrane. Inclosed within these opaque edges is a narrower colorless and transparent space, the "area pellucida," and in its centre is a delicate line, or furrow, running longitudinally from front to rear, which is called the "primitive trace."

Fig. 205.



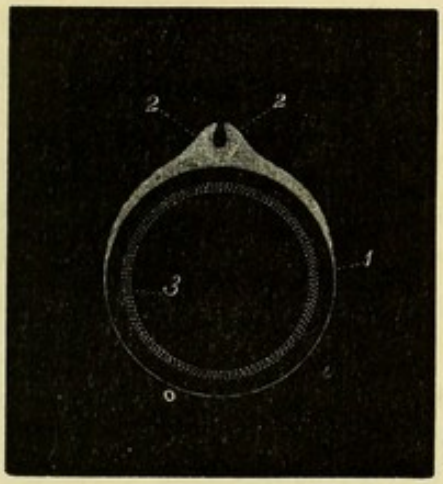
IMPREGNATED EGG, with commencement of formation of embryo: showing embryonic spot, area pellucida, and primitive trace.

On each side of the primitive trace, in the area pellucida, the substance of the blastodermic membrane rises up in such a manner as to form two nearly parallel vertical plates or ridges, which approach each other over the dorsal aspect of the fœtus and are therefore called the "dorsal plates." They at last meet on the median line, so as to inclose the furrow above described and convert it into a canal. This afterward becomes the spinal canal, and in its cavity is formed the spinal cord, by a deposit of nervous matter upon its internal surface. At the anterior extremity of this canal, its cavity is large and rounded, to accommodate the brain and medulla oblongata; at its posterior extremity it is narrow and pointed, and contains the extremity of the spinal cord.

In a transverse section of the egg at this stage (Fig. 206), the dorsal plates may be seen approaching each other above, on each side of the primitive furrow or "trace." At a more advanced period (Fig. 207) they may be seen fairly united with each other, so as to inclose the cavity of the spinal canal. At the same time, the edges of the thickened portion of the blastodermic membrane grow outward and downward, so as to spread out more and more over the lateral portions of the vitelline mass. These are called the "abdominal plates;" and as they increase in extent they tend to unite with each other below and inclose the abdominal cavity, just as the dorsal plates unite above, and inclose the spinal canal. At last the abdominal plates actually do unite with each other on the median line (at 1, Fig. 207), embracing of course the whole internal layer of the blastodermic membrane (5), which incloses in

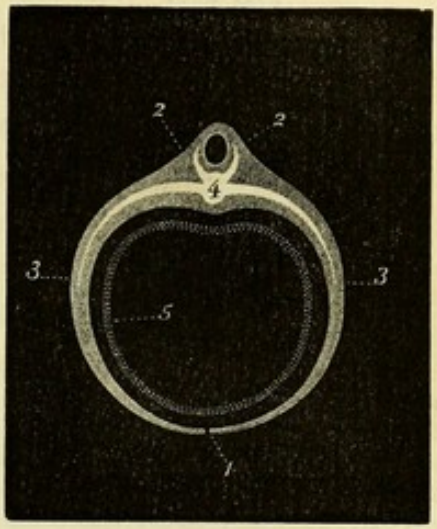
its turn the remains of the original vitellus and the albuminous fluid which has accumulated in its cavity.

Fig. 206.



Transverse section of Egg in an early stage of development.—1. External layer of blastodermic membrane. 2, 2. Dorsal plates. 3. Internal layer of blastodermic membrane.

Fig. 207.



Impregnated Egg, at a somewhat more advanced period.—1. Umbilicus, or point of union between abdominal plates. 2, 2. Dorsal plates united with each other on the median line and inclosing the spinal canal. 3, 3. Abdominal plates. 4. Section of spinal column, with laminæ and ribs. 5. Internal layer of blastodermic membrane.

During this time, there is formed, in the thickness of the external blastodermic layer, immediately beneath the spinal canal, a longitudinal cartilaginous cord, called the "chorda dorsalis." Around the chorda dorsalis are afterward developed the bodies of the vertebræ (Fig. 207, 4), forming the chain of the vertebral column; and the oblique processes of the vertebræ run upward from this point into the dorsal plates; while the transverse processes, and ribs, run outward and downward in the abdominal plates, to encircle more or less completely the corresponding portion of the body.

If we now examine the egg in longitudinal section, while this process is going on, the thickened portion of the external blastodermic layer may be seen in profile, as at 1, Fig. 208. The anterior portion (2), which will form the head, is thicker than the posterior (3), which will form the tail of the young animal. As the whole mass grows rapidly, both in the anterior and the posterior direction, the head becomes very thick and voluminous, while the tail also begins to project backward, and the whole egg assumes a distinctly elongated form. (Fig. 209.) The abdominal plates at the same time

meet upon its under surface, and the point at which they finally unite forms the abdominal cicatrix or *umbilicus*. The internal blastodermic layer is seen, of course, in the longitudinal section of the

Fig. 208.

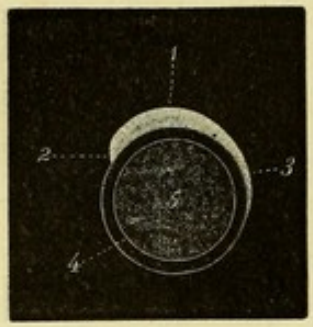
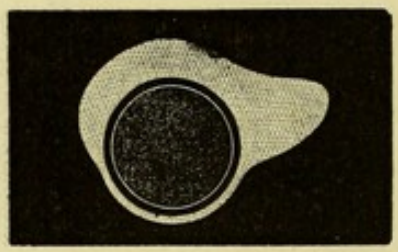


Diagram of FROG'S EGG, in an early stage of development; longitudinal section.—1. Thickened portion of external blastodermic layer, forming body of fœtus. 2. Anterior extremity of fœtus. 3. Posterior extremity. 4. Internal layer of blastodermic membrane. 5. Cavity of vitellus.

Fig. 209.

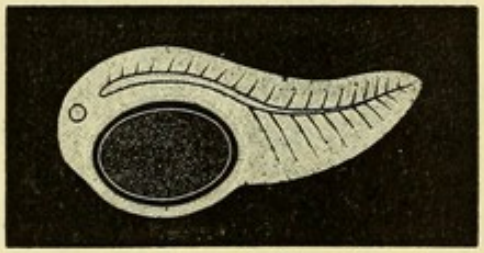


EGG OF FROG, in process of development.

egg, as well as in the transverse, embraced by the abdominal plates, and inclosing, as before, the remains of the vitellus.

As the development of the above parts goes on (Fig. 210), the head becomes still larger, and soon shows traces of the formation

Fig. 210.



EGG OF FROG, farther advanced.

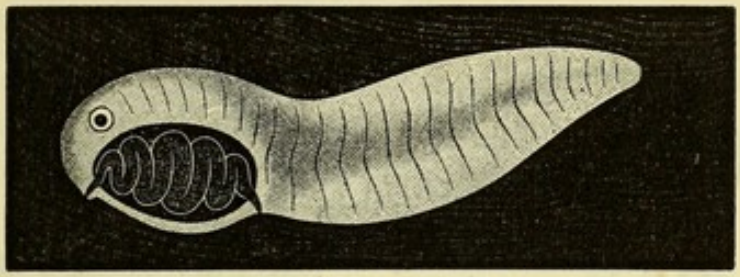
of organs of special sense. The tail also increases in size, and projects farther from the posterior extremity of the embryo. The spinal cord runs in a longitudinal direction from front to rear, and its anterior extremity enlarges, so as to form the brain and medulla oblongata. In the mean time, the internal blastodermic layer, which is subsequently to be converted into the intestinal canal, has been shut in by the abdominal walls, and still forms a perfectly closed sac, of a slightly elongated figure, without either inlet or outlet. Afterward, the mouth is formed by a process of atrophy and perforation, which takes place through both external and internal layers,

at the anterior extremity, while a similar perforation, at the posterior extremity, results in the formation of the anus.

All these parts, however, are as yet imperfect; and, being merely in the course of formation, are incapable of performing any active function.

By a continuation of the same process, the different portions of the external blastodermic layer are further developed, so as to result in the complete formation of the various parts of the skeleton, the integument, the organs of special sense, and the voluntary muscles and nerves. The tail at the same time acquires sufficient size and strength to be capable of acting as an organ of locomotion. (Fig. 211.) The intestinal canal, which has been formed from

Fig. 211.



TADPOLE fully developed.

the internal blastodermic layer, is at first a short, wide, and nearly straight tube, running directly from the mouth to the anus. It soon, however, begins to grow faster than the abdominal cavity which incloses it, becoming longer and narrower, and is at the same time thrown into numerous convolutions. It thus presents a larger internal surface for the performance of the digestive process.

Arrived at this period, the young tadpole ruptures the vitelline membrane, by which he has heretofore been inclosed, and leaves the cavity of the egg. He at first fastens himself upon the remains of the albuminous matter deposited round the egg, and feeds upon it for a short period. He soon, however, acquires sufficient strength and activity to swim about freely in search of other food, propelling himself by means of his large, membranous, and muscular tail. The alimentary canal increases very rapidly in length and becomes spirally coiled up in the abdominal cavity, so as to attain a length from seven to eight times greater than that of the entire body.

After a time, a change takes place in the external form of the young animal. The posterior extremities or limbs begin to show

themselves, by budding or sprouting from the sides of the body just at the base of the tail. (Fig. 212.) The anterior extremities also grow at this time, but are at first concealed underneath the integu ment. They afterward, however, become liberated, and show themselves externally. At first both the fore and hind legs are very small, imperfect in structure, and altogether useless for purposes of locomotion. They soon, however, increase in size and strength; and while they keep pace with the increasing development of the whole body, the tail on the contrary ceases to grow, and becomes shrivelled and atrophied. The limbs, in fact, are destined finally to replace the tail as organs of locomotion; and a time at last arrives (Fig. 213) when the tail has altogether disappeared, while

Fig. 212.

TADPOLE, with limbs beginning to be formed.

Fig. 213.

Perfect FROG.

the legs have become fully developed, muscular and powerful. Then the animal, which was before confined to an aquatic mode of life, becomes capable of living also upon land, and a transformation is thus effected from the tadpole into the perfect frog.

During the same time, other changes of an equally important character have taken place in the internal organs. The tadpole at first breathes by gills; but these organs subsequently become atrophied and disappear, being finally replaced by well developed lungs. The structure of the mouth, also, of the integument, and of the circulatory system, is altered to correspond with the varying conditions and wants of the growing animal; and all these changes taking place, in part successively and in part simultaneously, bring the animal at last to a state of complete formation.

The process of development may then be briefly recapitulated as follows:—

1. The blastodermic membrane, produced by the segmentation of the vitellus, consists of two cellular layers, viz., an external and an internal blastodermic layer.

2. The external layer of the blastodermic membrane incloses by its dorsal plates the cerebro-spinal canal, and by its abdominal plates the abdominal or visceral cavity.

3. The internal layer of the blastodermic membrane forms the intestinal canal, which becomes lengthened and convoluted, and communicates with the exterior by a mouth and anus of secondary formation.

4. Finally the cerebro-spinal axis and its nerves, the skeleton the organs of special sense, the integument, and the muscles, are developed from the external blastodermic layer; while the anterior and posterior extremities are formed from the same layer by a process of sprouting, or continuous growth.

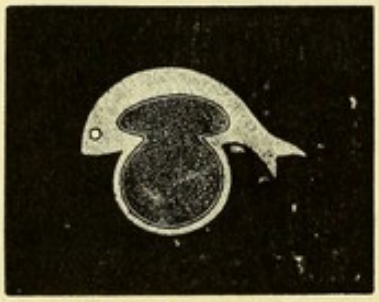
CHAPTER VIII.

THE UMBILICAL VESICLE.

In the frog, as we have seen, the abdominal plates, closing together in front and underneath the body of the animal, shut in directly the whole of the vitellus, and join each other upon the median line, at the umbilicus. The whole remains of the vitellus are then inclosed in the abdomen of the animal, and in the intestinal sac formed by the internal blastodermic layer.

In many instances, however, as, for example, in several kinds of fish, and in all the birds and quadrupeds, the abdominal plates do not immediately embrace the whole of the vitelline mass, but tend to close together about its middle; so that the vitellus is constricted, in this way, and divided into two portions: one internal, and one external. (Fig. 214.) As the process of development proceeds, the body of the fœtus increases in size, out of proportion to the vitelline sac, and the constriction just mentioned becomes at the same time more strongly marked; so that the separation between the internal and external portions of the vitelline sac is nearly complete. (Fig. 215.) The internal layer of the blastodermic membrane is by the same means divided into two portions, one of which forms the intestinal canal, while the other, remaining outside, forms a sac-like appendage to the abdomen, which is known by the name of the *umbilical vesicle.*

Fig. 214.

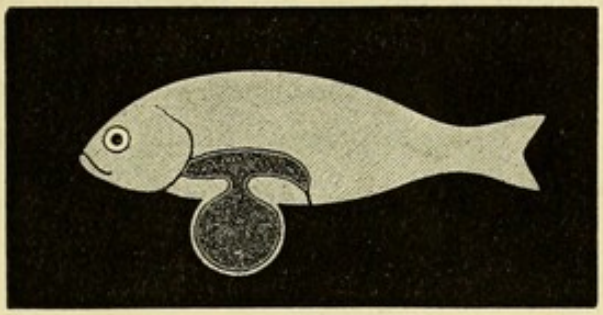


Egg of Fish, showing formation of umbilical vesicle.

The umbilical vesicle is accordingly lined by a portion of the internal blastodermic layer, continuous with the mucous membrane of the intestinal canal; while it is covered on the outside by a portion of the external blastodermic layer, continuous with the integument of the abdomen.

After the young animal leaves the egg, the umbilical vesicle in some species becomes withered and atrophied by the absorption of its contents; while in others, the abdominal walls gradually

Fig. 215.

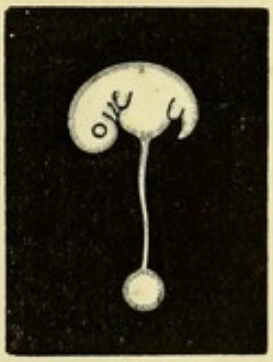


Young Fish with umbilical vesicle.

extend over it, and crowd it back into the abdomen; the nutritious matter which it contained passing from the cavity of the vesicle into that of the intestine by the narrow passage or canal which remains open between them.

In the human subject, however, as well as in the quadrupeds, the umbilical vesicle becomes more completely separated from the abdomen than in the cases just mentioned. There is at first a wide communication between the cavity of the umbilical vesicle and that of the intestine; and this communication, as in other instances, becomes gradually narrowed by the increasing constriction of the abdominal walls. Here, however, the constriction proceeds so far that the opposite surfaces of the canal come in contact with each other, and adhere; so that the narrow passage previously existing, between the cavity of the intestine and that of the umbilical vesicle, is obliterated, and the vesicle is then connected with the abdomen only by an impervious cord. This cord afterward elongates, and becomes converted into a slender, thread-like pedicle (Fig. 216), passing out from the abdomen of the fœtus, and connected by its farther extremity with the umbilical vesicle, which is filled with a transparent, colorless fluid. The umbilical vesicle is very distinctly visible in the human fœtus so late as the end of the third month. After that period it diminishes in size, and is gradually lost in the advancing development of the neighboring parts.

Fig. 216.



Human Embryo, with umbilical vesicle; about the fifth week.

In the formation of the umbilical vesicle, we have the first varia

tion from the simple plan of development described in the preceding chapter. Here, the whole of the vitellus is not directly converted into the body of the embryo; but while a part of it is taken, as usual, into the abdominal cavity, and used immediately for the purposes of nutrition, a part is left outside the abdomen, in the umbilical vesicle, a kind of secondary organ or appendage of the fœtus. The contents of the umbilical vesicle, however, are afterward absorbed, and so appropriated, finally, to the nourishment of the newly-formed tissues.

CHAPTER IX.

AMNION AND ALLANTOIS.—DEVELOPMENT OF THE CHICK.

We shall now proceed to the description of two other accessory organs, which are formed, during the development of the fecundated egg, in all the higher classes of animals. These are the *amnion* and the *allantois;* two organs which are always found in company with each other, since the object of the first is to provide for the formation of the second. The amnion is formed from the external layer of the blastodermic membrane, the allantois from the internal layer.

In the frog and in fish, as we have seen, the egg is abundantly supplied with moisture, air, and nourishment, by the water with which it is surrounded. It can absorb directly all the gaseous and liquid substances, which it requires for the purposes of nutrition and growth. The absorption of oxygen, the exhalation of carbonic acid, and the imbibition of albuminous and other liquids, can all take place without difficulty through the simple membranes of the egg; particularly as the time required for the formation of the embryo is very short, and as a great part of the process of development remains to be accomplished after the young animal leaves the egg.

But in birds and quadrupeds, the time required for the development of the fœtus is longer. The young animal also acquires a much more perfect organization during the time that it remains inclosed within the egg; and the processes of absorption and exhalation necessary for its growth, being increased in activity to a corresponding degree, require a special organ for their accomplishment. This special organ, destined to bring the blood of the fœtus into relation with the atmosphere and external sources of nutrition, is the *allantois.*

In the frog and the fish, the internal blastodermic layer, forming the intestinal mucous membrane, is inclosed everywhere, as above described, by the external layer, forming the integument; and

consequently it can nowhere come in contact with the investing membrane of the egg. But in the higher animals, the internal blastodermic layer, which is the seat of the greatest vascularity, and which is destined to produce the allantois, is made to come in contact with the external membrane of the egg for purposes of exhalation and absorption; and this can only be accomplished by opening a passage for it through the external germinative layer. This is done in the following manner, by the formation of the *amnion.*

Soon after the body of the fœtus has begun to be formed by the thickening of the external layer of the blastodermic membrane, a double fold of this external layer rises up on all sides about the edges of the newly-formed embryo; so that the body of the fœtus appears as if sunk in a kind of depression, and surrounded with a membranous ridge or embankment, as in Fig. 217. The embryo (*c*) is here seen in profile, with the double membranous folds, above mentioned, rising up just in advance of the head, and behind the posterior extremity. It must be understood, of course, that the same thing takes place on the two sides of the fœtus, by the formation of lateral folds simultaneously with the appearance of those in front and behind. As it is these folds which are destined to form the amnion, they are called the "amniotic folds."

Fig. 217.

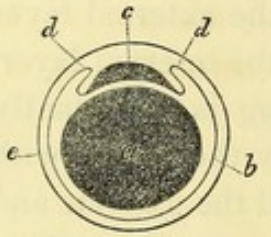


Diagram of FECUNDATED EGG; showing formation of amnion.—*a*. Vitellus. *b*. External layer of blastodermic membrane. *c*. Body of embryo. *d*, *d*. Amniotic folds. *e*. Vitelline membrane.

The amniotic folds continue to grow, and extend themselves, forward, backward, and laterally, until they approach each other at a point over the back of the fœtus (Fig. 218), which is termed the "amniotic umbilicus." Their opposite edges afterward actually come in contact with each other at this point, and adhere together, so as to shut in a space or cavity (Fig. 218, *b*) between their inner surface and the body of the fœtus. This space, which is filled with a clear fluid, is called the amniotic cavity. At the same time, the intestinal canal has begun to be formed, and the umbilical vesicle has been partially separated from it, by the constriction of the abdominal walls on the under surface of the body.

There now appears a prolongation or diverticulum (Fig. 218, *c*) growing out from the posterior portion of the intestinal canal, and following the course of the amniotic fold which has preceded it: occupying, as it gradually enlarges and protrudes, the space left

vacant by the rising up of the amniotic fold. This diverticulum is the commencement of the allantois. It is an elongated membranous sac, continuous with the posterior portion of the intestine, and containing bloodvessels derived from those of the intestinal circulation. The cavity of the allantois is also continuous with the cavity of the intestine.

Fig. 218.

FECUNDATED EGG, farther advanced.—*a*. Umbilical vesicle. *b* Amniotic cavity. *c*. Allantois.

After the amniotic folds have approached and touched each other, as already described, over the back of the fœtus, at the amniotic umbilicus, the adjacent surfaces, thus brought in contact, fuse together, so that the cavities of the two folds, coming respectively from front and rear, are separated only by a single membranous partition (Fig. 219, *c*) running from the inner to the outer lamina of the amniotic folds. This partition itself soon after atrophies and disappears; and the inner and outer laminæ become consequently separated from each other. The inner lamina (Fig. 219, *a*) which remains continuous with the integument of the fœtus, inclosing the body of the embryo in a distinct cavity, is called the *amnion* (Fig. 220, *b*), and its cavity is known as the amniotic cavity. The outer lamina of the amniotic fold, on the other hand (Fig. 219, *b*), recedes farther and farther from the inner, until it comes in contact with the original vitelline membrane, still covering the exterior of the egg; and by continued growth and expansion it at last fuses with the vitelline membrane and unites with its substance, so that the two membranes form but one. This membrane, formed by the fusion and consolidation of two others, constitutes then the external investing membrane of the egg.

Fig. 219.

FECUNDATED EGG, with allantois nearly complete.—*a*. Inner lamina of amniotic fold. *b*. Outer lamina of ditto. *c*. Point where the amniotic folds come in contact. The allantois is seen penetrating between the inner and outer laminæ of the amniotic folds.

The allantois, during all this time, is increasing in size and vascularity. Following the course of the amniotic folds as before, it insinuates itself between them, and of course soon comes in contact with the external investing membrane just described. It then begins to expand laterally in every direction, enveloping more and more the body of the fœtus, and bringing its vessels into contact with the external membrane of the egg.

By a continuation of the above process, the allantois at last grows to such an extent as to envelope completely the body of the embryo, together with the amnion; its two extremities coming in contact with each other and fusing together over the back of the fœtus, just as the amniotic folds had previously done. (Fig. 220.) It lines, therefore, the whole internal surface of the investing membrane with a flattened, vascular sac, the vessels of which come from the interior of the body of the fœtus, and which still communicates with the cavity of the intestinal canal.

Fig. 220.

FECUNDATED EGG, with allantois fully formed.—*a*. Umbilical vesicle. *b*. Amnion. *c*. Allantois.

It is evident, from the above description, that there is a close connection between the formation of the amnion and that of the allantois. For it is only in this manner that the allantois, which is an extension of the internal layer of the blastodermic membrane, can come to be situated outside the fœtus and the amnion, and be brought into relation with external surrounding media. The two laminæ of the amniotic folds, in fact, by separating from each other as above described, open a passage for the allantois, and allow it to come in contact with the external membrane of the egg.

In order to explain more fully the physiological action of the allantois, we shall now proceed to describe the process of development, as it takes place in the egg of the fowl.

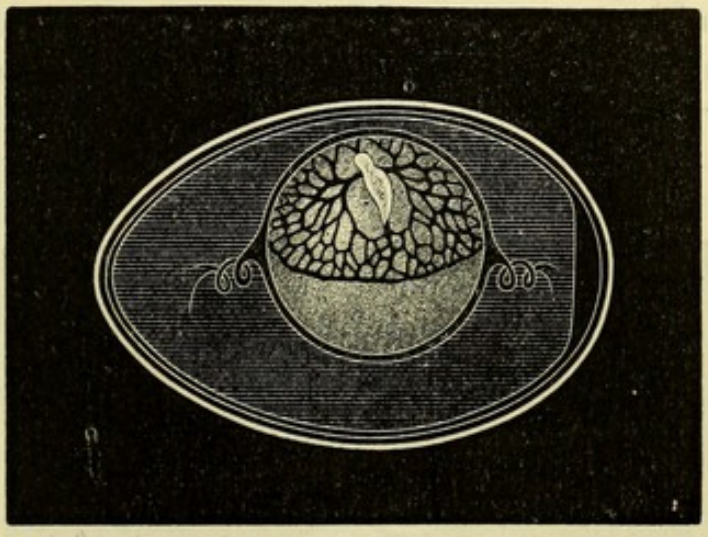
In order that the embryo may be properly developed in any case, it is essential that it be freely supplied with air, warmth, moisture, and nourishment. The egg of the fowl contains already, when discharged from the generative passages, a sufficient quantity of moisture and albuminous material. The necessary warmth is supplied by the body of the parent during incubation; while the atmospheric gases can pass and repass through the porous egg-shell, and by endosmosis through the fibrous membranes which line its cavity.

When the egg is first laid, the vitellus, or yolk, is enveloped in a thick layer of semi-solid albumen. On the commencement of incubation, a liquefaction takes place in the albumen immediately above that part of the vitellus which is occupied by the cicatricula; so that the vitellus rises or floats upward toward the surface, by virtue of its specific gravity, and the cicatricula comes to be

placed almost immediately underneath the lining membrane of the egg-shell. As the cicatricula is the spot from which the process of embryonic development commences, the body of the young fœtus is by this arrangement placed in the most favorable position for the reception of warmth and other necessary external influences through the egg-shell. The liquefied albumen is also absorbed by the vitelline membrane, and the vitellus thus becomes larger, softer, and more diffluent than before the commencement of incubation.

As soon as the circulatory apparatus of the embryo has been fairly formed, two minute arteries are seen to run out from its lateral edges and spread into the neighboring parts of the blastodermic membrane, breaking up into inosculating branches, and covering the adjacent portions of the vitellus with a plexus of capillary bloodvessels. The space occupied in the blastodermic membrane, on the surface of the vitellus, by these vessels, is called the *area vasculosa.* (Fig. 221.) It is of a nearly circular shape,

Fig. 221.



Egg of Fowl during early periods of incubation; showing the body of the embryo, and the area vasculosa partially covering the surface of the vitellus.

and is limited, on its outer edge, by a terminal vein or sinus, called the "sinus terminalis." The blood is returned to the body of the fœtus by two veins which penetrate beneath its edges, one near the head and one near the tail.

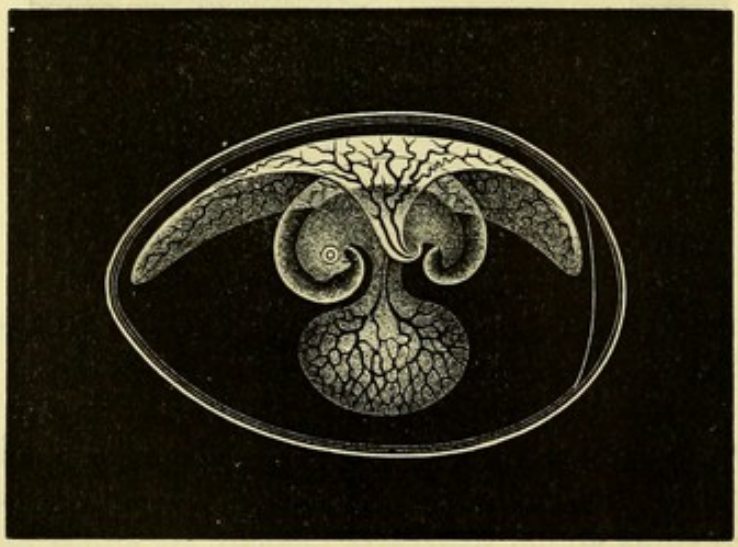
The area vasculosa tends to increase in extent, as the development of the fœtus proceeds and its circulation becomes more active. It soon covers the upper half, or hemisphere, of the vitellus, and the terminal sinus then runs like an equator round the middle of the vitelline sphere. As the growth of the vascular plexus con-

tinues, it passes this point, and embraces more and more of the inferior, as well as of the superior hemisphere, the vessels converging toward its under surface, until at last nearly the whole of the vitellus is covered with a network of inosculating capillaries.

The function of the vessels of the area vasculosa is to absorb nourishment from the cavity of the vitelline sac. As the albumen liquefies during the process of incubation, it passes by endosmosis, more and more abundantly, into the vitelline cavity; the whole vitellus growing constantly larger and more fluid in consistency. The blood of the fœtus, then circulating in the vessels of the area vasculosa, absorbs freely the oleagino-albuminous matters of the vitellus, and, carrying them back to the fœtus by the returning veins, supplies the newly-formed tissues and organs with abundance of appropriate nourishment.

During this period the amnion and the allantois have been also in process of formation. At first the body of the fœtus lies upon its abdomen, as in the cases previously described; but, as it increases in size, it alters its position so as to lie more upon its side. The allantois then, emerging from the posterior portion of the abdominal cavity, turns directly upward over the body of the fœtus, and comes immediately in contact with the shell membrane. (Fig. 222.) It

Fig. 222.



Egg of Fowl at a more advanced period of development. The body of the fœtus is enveloped by the amnion, and has the umbilical vesicle hanging from its under surface; while the vascular allantois is seen turning upward and spreading out over the internal surface of the shell-membrane.

then spreads out rapidly, extending toward the extremities and down the sides of the egg, enveloping more and more completely

the fœtus and the vitelline sac, and taking the place of the albumen which has been liquefied and absorbed.

It will also be seen, by reference to the figure, that the umbilical vesicle is at the same time formed by the separation of part of the vitellus from the abdomen of the chick; and the vessels of the area vasculosa, which were at first distributed over the vitellus, now ramify, of course, upon the surface of the umbilical vesicle.

At last the allantois, by its continued growth, envelopes nearly the whole of the remaining contents of the egg; so that toward the later periods of incubation, at whatever point we break open the egg, we find the internal surface of the shell-membrane lined with a vascular membranous expansion, supplied by arteries which emerge from the abdomen of the fœtus.

It is easy to see, accordingly, with what readiness the absorption and exhalation of gases may take place by means of the allantois. The air penetrates from the exterior through the minute pores of the calcareous shell, and then acts upon the blood in the vessels of the allantois very much in the same manner that the air in the minute bronchial tubes and air-vesicles of the lungs acts upon the blood in the pulmonary capillaries. Examination of the egg, furthermore, at various periods of incubation, shows that changes take place in it which are entirely analogous to those of respiration.

The egg, in the first place, during its development, loses water by exhalation. This exhalation is not a simple effect of evaporation, but is the result of the nutritive changes going on in the interior of the egg; since it does not take place, except in a comparatively slight degree, in unimpregnated eggs, or in those which are not incubated, though they may be freely exposed to the air. The exhalation of fluid is also essential to the processes of development, for it has often been found, in hatching eggs by artificial warmth, that if the air of the chamber in which they are inclosed become unduly charged with moisture, so as to retard or prevent further exhalation, the eggs readily become spoiled, and the development of the embryo is arrested. The loss of weight during natural incubation, principally due to the exhalation of water, has been found by Baudrimont and St. Ange[1] to be over 15 per cent. of the entire weight of the egg.

Secondly, the egg absorbs oxygen and exhales carbonic acid. The two observers mentioned above, ascertained that during eigh-

[1] Du Développement du Fœtus. Paris, 1850, p. 143.

teen days' incubation, the egg absorbs nearly 2 per cent. of its weight of oxygen, while the quantity of carbonic acid exhaled from the sixteenth to the nineteenth day of incubation amounts to no less than 3 grains in the twenty-four hours.[1] It is curious to observe, also, that in the egg during incubation, as well as in the adult animal, more oxygen is absorbed than is returned by exhalation under the form of carbonic acid.

It is evident, therefore, that a true respiration takes place, by means of the allantois, through the membranes of the shell.

The allantois, however, is not simply an organ of respiration; it takes part also in the absorption of nutritious matter. As the process of development advances, the skeleton of the young chick, at first entirely cartilaginous, begins to ossify. The calcareous matter, necessary for this ossification, is, in all probability, derived from the shell. The shell is certainly lighter and more fragile toward the end of incubation than at first; and, at the same time, the calcareous ingredients of the bones increase in quantity. The lime-salts, requisite for the process of ossification, are apparently absorbed from the shell by the vessels of the allantois, and by them transferred to the skeleton of the growing chick; so that, in the same proportion that the former becomes weaker, the latter grows stronger. This diminution in density of the shell is connected not only with the development of the skeleton, but also with the final escape of the chick from the egg. This deliverance is accomplished mostly by the movements of the chick itself, which become, at a certain period, sufficiently vigorous to break out an opening in the attenuated and weakened egg-shell. The first fracture is generally accomplished by a stroke from the end of the bill; and it is precisely at this point that the solidification of the skeleton is most advanced. The egg-shell itself, therefore, which at first only serves for the protection of the imperfectly-formed embryo, afterward furnishes the materials which are used to accomplish its own demolition, and at the same time to effect the escape of the fully developed fœtus.

Toward the latter periods of incubation, the allantois becomes more and more adherent to the internal surface of the shell-membrane. At last, when the chick, arrived at the full period of development, escapes from its confinement, the allantoic vessels are torn off at the umbilicus; and the allantois itself, cast off as a use-

[1] Op. cit., pp. 138 and 149.

less and effete organ, is left behind in the cavity of the abandoned egg-shell. The allantois is, therefore, strictly speaking, a fœtal organ. Developed as an accessory structure from a portion of the intestinal canal, it is exceedingly active and important during the middle and latter periods of incubation; but when the chick is completely formed, and has become capable of carrying on an independent existence, both the amnion and the allantois are detached and thrown off as obsolete structures, their place being afterward supplied by other organs belonging to the adult condition.

CHAPTER X.

DEVELOPMENT OF THE EGG IN THE HUMAN SPECIES.—FORMATION OF THE CHORION.

We have already described, in a preceding chapter, the manner in which the outer lamina of the amniotic fold becomes adherent to the adjacent surface of the vitelline membrane, so as to form with it but a single layer; and in which these two membranes, thus fused and united with each other, form at that time the single external investing membrane of the egg. The allantois, in its turn, afterward comes in contact with the investing membrane, and lies immediately beneath it, as a double vascular membranous sac. In the egg of the human subject the development of the membranes, though carried on essentially upon the same plan with that which we have already described, undergoes, in addition, some further modifications, which we shall now proceed to explain.

The first of these peculiarities is that the allantois, after spreading out upon the inner surface of the external investing membrane, adheres to, and fuses with it, just as the outer lamina of the amniotic fold has previously fused with the vitelline membrane. At the same time, the two layers belonging to the allantois itself also come in contact and fuse together; so that the cavity of the allantois is obliterated, and instead of forming a membranous sac containing fluid, this organ is *converted into a simple vascular membrane.* (Fig. 223.) This membrane, moreover, being, after a time, thoroughly fused and united with the two which have preceded it, takes the place which was previously

Fig. 223.

Human Ovum, about the end of the first month; showing formation of chorion.—1. Umbilical vesicle. 2. Amnion. 3. Chorion.

occupied by them. It is then termed the *chorion*, and thus becomes the sole external investing membrane of the egg.

We find, therefore, that the chorion, that is, the external coat or investment of the egg, is formed successively by three distinct membranes, as follows: first, the original vitelline membrane; secondly, the outer lamina of the amniotic fold; and, thirdly, the allantois; the last predominating over the two former by the rapidity of its growth, and absorbing them into its substance, so that they become finally completely incorporated with its texture.

It is easy to see, also, how, in consequence of the above process, the body of the fœtus, in the human egg, becomes inclosed in two distinct membranes, viz., the amnion, which is internal and continuous with the fœtal integument, and the chorion, which is external and supplied with vessels from the cavity of the abdomen. The umbilical vesicle is, of course, situated between the two; and the rest of the space between the chorion and the amnion is occupied by a semi-fluid gelatinous material, somewhat similar in appearance to that of the vitreous body of the eye.

The obliteration of the cavity of the allantois takes place very early in the human subject, and, in fact, keeps pace almost entirely with the progress of its growth; so that this organ never presents, in the human egg, the appearance of a hollow sac, filled with fluid, but rather that of a flattened vascular membrane, enveloping the body of the fœtus, and forming the external membrane of the egg. Notwithstanding this difference, however, the chorion of the human subject, in respect to its mode of formation, is the same thing with the allantois of the lower animals; its chief peculiarity consisting in the fact that its opposite surfaces are adherent to each other, instead of remaining separate and inclosing a cavity filled with fluid.

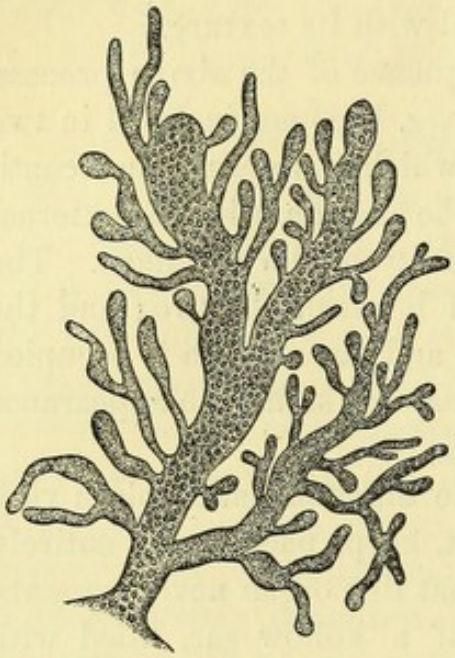
The next peculiarity of the human chorion is, that *it becomes shaggy*. Even while the egg is still very small, and has but recently found its way into the uterine cavity, its exterior is already seen to be covered with little transparent prominences, like so many villi (Fig. 223), which increase the extent of its surface, and assist in the absorption of fluids from without. The villi are at this time quite simple in form, and altogether homogeneous in structure.

As the egg increases in size, the villi rapidly elongate, and become divided and ramified by the repeated budding and sprouting of lateral offshoots from every part. After this process of growth

has gone on for some time, the external surface of the chorion presents a uniformly velvety or shaggy appearance, owing to its being covered everywhere with these tufted and compound villosities.

The villosities themselves, when examined by the microscope, have an exceedingly well-marked and characteristic appearance. (Fig. 224.) They originate from the surface of the chorion by a somewhat narrow stem, and divide into a multitude of secondary and tertiary branches, of varying size and figure; some of them slender and filamentous, others club-shaped, many of them irregularly swollen at various points. All of them terminate by rounded extremities, giving to the whole tuft a certain resemblance to some varieties of sea-weed. The larger trunks and branches of the villosity are seen to contain numerous minute nuclei, imbedded in a nearly homogeneous, or finely granular substratum. The smaller ones appear, under a low magnifying power, simply granular in texture.

Fig. 224.



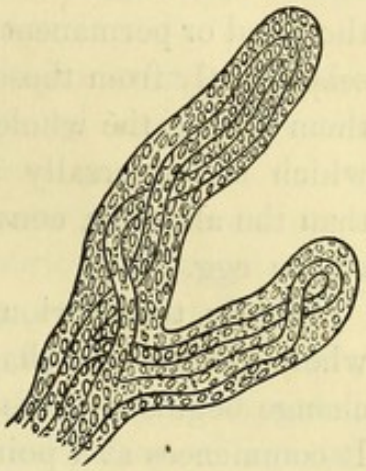
Compound villosity of HUMAN CHORION, ramified extremity. From a three months' fœtus. Magnified 30 diameters.

These villi are altogether peculiar in appearance, and quite unlike any other structure which may be met with in the body. Whenever we find, in the uterus, any portion of a membrane having villosities like these, we may be sure that pregnancy has existed; for such villosities can only belong to the chorion, and the chorion itself is a part of the fœtus. It is developed, as we have seen, as an outgrowth from the intestinal canal, and can only exist, accordingly, as a portion of the fecundated egg. The presence of portions of a shaggy chorion is therefore as satisfactory proof of the existence of pregnancy, as if he had found the body of the fœtus itself.

While the villosities which we have just described are in process of formation, the allantois itself has completed its growth, and has become converted into a permanent chorion. The bloodvessels coming from the allantoic arteries accordingly ramify over the chorion, and supply it with a tolerably abundant vascular network. The growth of the fœtus, moreover, at this time, has reached such a state of activity, that it requires to be supplied with nourishment

by vascular absorption instead of the slow process of imbibition which has heretofore taken place through the comparatively incomplete and structureless villi of the chorion. The capillary vessels, accordingly, with which the chorion is supplied, begin to penetrate into the substance of its villosities. They enter the base or stem of each villosity, and, following every division of its compound ramifications, finally reach its rounded extremities. Here they turn upon themselves in loops (Fig. 225), like the vessels in the papillæ of the skin, and retrace their course, to unite finally with the venous trunks of the chorion.

Fig. 225.



Extremity of VILLOSITY OF CHORION, more highly magnified; showing the arrangement of bloodvessels in its interior.

The villi of the chorion are, therefore, very analogous in structure to those of the intestine; and their power of absorption, as in other similar instances, corresponds with the abundance of their ramifications, and the extent of their vascularity.

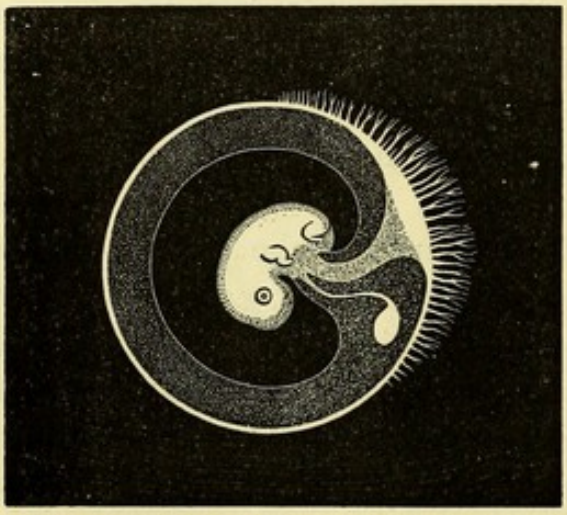
It must be remembered, also, that these vessels all come from the abdomen of the fœtus; and that whatever substances are taken up by them are transported directly to the interior of the embryo, and used for the nourishment of its tissues. The chorion, therefore, as soon as its villi and bloodvessels are completely developed, becomes an exceedingly active organ in the nutrition of the fœtus; and constitutes, in fact, the only means by which new material can be introduced from without.

The existence of this general vascularity of the chorion affords also, as Coste was the first to point out, a striking indication that this membrane is in reality identical with the allantois of the lower animals. If the reader will turn back to the illustrations of the formation of the amnion and allantois (Chap. IX.), he will see that the first chorion or investing membrane is formed exclusively by the vitelline membrane, which is never vascular and cannot become so by itself, since it has no direct connection with the fœtus. The second chorion is formed by the union of the vitelline membrane with the outer lamina of the amniotic fold. Both laminæ of the amniotic fold are at first vascular, since they are portions of the external blastodermic layer, and derive their vessels from the integument of the fœtus. But after the outer lamina has become

completely separated from the inner, by the disappearance of the partition which for a time connected the two with each other (Fig. 219, *c*), this source of vascular supply is cut off; and the second chorion cannot, therefore, remain vascular after that period. But the third or permanent chorion, that is, the allantois, derives its vessels directly from those of the fœtus, and retains its connection with them during the whole period of gestation. A chorion, therefore, which is universally and permanently vascular, can be no other than the allantois, converted into an external investing membrane of the egg.

Thirdly, the chorion, which is at one time, as we have seen, everywhere villous and shaggy, *becomes afterward partially bald.* This change begins to take place about the end of the second month. It commences at a point opposite the situation of the fœtus and the insertion of the fœtal vessels. The villosities of this region cease growing; and as the entire egg continues to enlarge, the villosities at the point indicated fail to keep pace with its growth, and with the progressive expansion of the chorion. They accordingly become at this part thinner and more scattered, leaving the surface of the chorion comparatively smooth and bald. This baldness increases in extent and becomes more and more complete, spreading and advancing over the adjacent portions of the chorion, until at least two-thirds of its surface have become nearly or quite destitute of villosities.

Fig. 226.



HUMAN OVUM at end of third month; showing placental portion of the chorion fully formed.

At the opposite point of the surface of the egg, however, that portion, namely, which corresponds with the insertion of the fœtal vessels, the villosities, instead of becoming atrophied, continue to grow; and this portion of the chorion becomes even more shaggy and thickly set than before. The consequence is that the chorion afterward presents a very different appearance at different portions of its surface. (Fig. 226.) The greater part of it is smooth; but a certain portion, constituting about one-third of the whole, is covered with a soft and spongy mass of long, thickly-set, compound villosities. It is this thickened

and shaggy portion, which is afterward concerned in the formation of the *placenta;* while the remaining smooth portion continues to be known under the name of the chorion. The placental portion of the chorion becomes distinctly limited and separated from the remainder by about the end of the third month.

The vascularity of the chorion keeps pace, in its different parts respectively, with the atrophy and development of its villosities. As the villosities shrivel and disappear over a part of its extent, the looped capillary vessels, which they at first contained, disappear also; so that the smooth portion of the chorion shows afterward only a few straggling vessels running over its surface, and does not contain any abundant capillary plexus. In the thickened portion, on the other hand, the vessels lengthen and ramify to an extent corresponding with that of the villosities in which they are situated. The allantoic arteries, coming from the abdomen of the fœtus, enter the villi, and penetrate through their whole extent; forming, at the placental portion of the chorion, a mass of tufted and ramified vascular loops, while over the rest of the membrane they are merely distributed as a few single and scattered vessels.

The chorion, accordingly, is the external investing membrane of the egg, produced by the consolidation and transformation of the allantois. The placenta, furthermore, so far as it has now been described, is evidently a part of the chorion; that part, namely which is thickened, shaggy, and vascular, while the remainder is comparatively thin, smooth, and membranous.

CHAPTER XI.

DEVELOPMENT OF UTERINE MUCOUS MEMBRANE.—FORMATION OF THE DECIDUA.

In fish, reptiles, and birds, the egg is either provided with a supply of nutritious material contained within its membranes, or it is so placed, after its discharge from the body of the parent, that it can absorb these materials from without. Thus, in the egg of the bird, the young embryo is supported upon the albuminous matter deposited around the vitellus; while in the frog and fish, moisture, oxygen, saline substances, &c., are freely imbibed from the water in which the egg is placed.

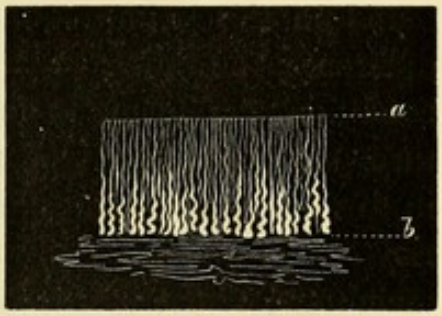
But in the quadrupeds, as well as in the human species, the egg is of minute size, and the quantity of nutritious matter which it contains is sufficient to last only for a very short time. Moreover, the development of the fœtus takes place altogether within the body of the female, and no supply, therefore, can be obtained directly from the external media. In these instances, accordingly, the mucous membrane of the uterus, which is found to be unusually developed and increased in functional activity during the period of gestation, becomes a source of nutrition for the fecundated egg. The uterine mucous membrane, thus developed and hypertrophied, is known by the name of the *Decidua*.

It has received this name because, as we shall hereafter see, it becomes exfoliated and thrown off, at the same time that the egg itself is finally discharged.

The mucous membrane of the body of the uterus, in the unimpregnated condition, is quite thin and delicate, and presents a smooth and slightly vascular internal surface. There is, moreover, no layer of submucous cellular tissue between it and the muscular substance of the uterus; so that the mucous membrane cannot here, as in most other organs, be easily dissected up and separated from the subjacent parts. The structure of the mucous membrane itself, however, is sufficiently well marked and readily distinguishable

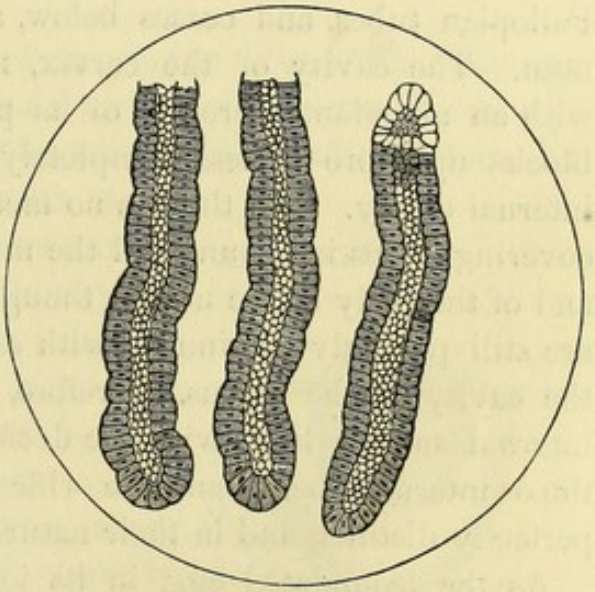
from that of other parts. It consists, throughout, of minute tubular follicles, ranged side by side, and running perpendicularly to the free surface of the mucous membrane. (Fig. 227.) Near this free surface, they are nearly straight; but toward the deeper surface of the mucous membrane, where they terminate in blind extremities, they become more or less wavy or spiral in their course. The tubules are about $\frac{1}{150}$ of an inch in diameter, and are lined throughout with columnar epithelium. (Fig. 228.) They occupy the entire thickness of the uterine mucous membrane, their closed extremities resting upon the subjacent muscular tissue, while their mouths open into the cavity of the uterus. A few fine bloodvessels penetrate the mucous membrane from below, and, running upward between the tubules, encircle their superficial extremities with a capillary network. There is no areolar tissue in the uterine mucous membrane, but only a small quantity of spindle-shaped fibroplastic fibres, scattered between the tubules.

Fig. 227.



Uterine Mucous Membrane, as seen in vertical section.—*a*. Free surface. *b*. Attached surface.

Fig. 228.



Uterine Tubules, from mucous membrane of unimpregnated human uterus.

As the fecundated egg is about to descend into the cavity of the uterus, the mucous membrane, above described, takes on an increased activity of growth and an unusual development. It becomes tumefied and vascular; and, as it increases in thickness, it projects, in rounded eminences or convolutions, into the uterine cavity. (Fig. 229.) In this process, the tubules of the uterus increase in length, and also become wider; so that their open mouths may be readily seen by the naked eye upon the uterine surface, as numerous minute perforations. The bloodvessels of the mucous membrane also enlarge and multiply, and inosculate freely with

each other; so that the vascular network encircling the tubules becomes more extensive and abundant.

The internal surface of the uterus, accordingly, after this process has been for some time going on, presents a thick, rich, soft, vascular, and velvety lining, quite different from that which is to be found in the unimpregnated condition. In consequence of this difference, the lining membrane of the uterus, in the impregnated condition, was formerly supposed to be an entirely new product, thrown out by exudation from the uterine surface, and analogous, in this respect, to the inflammatory exudations of croup and pleurisy. It is now known, however, to be no other than the mucous membrane of the uterus itself, thickened and hypertrophied to an extraordinary degree, but still retaining all its natural connections and its original anatomical structure.

The hypertrophied mucous membrane, above described, constitutes the *Decidua vera*. Its formation is confined altogether to the body of the uterus, the mucous membrane of the cervix taking no part in the process, but retaining its original appearance. The decidua vera, therefore, commences above, at the orifices of the Fallopian tubes, and ceases below, at the situation of the os internum. The cavity of the cervix, meanwhile, begins to be filled with an abundant secretion of its peculiarly viscid mucus, which blocks up, more or less completely, its passage, and protects the internal cavity. But there is no membranous partition at this time covering the os internum, and the mucous membranes of the cervix and of the body of the uterus, though very different in appearance, are still perfectly continuous with each other. When we cut open the cavity of the uterus, therefore, in this condition, we find its internal surface lined with the decidua vera, with the opening of the os internum below and the orifices of the Fallopian tubes above, perfectly distinct, and in their natural positions. (Fig. 229.)

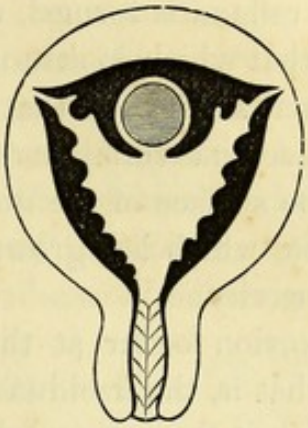
As the fecundated egg, in its journey from above downward, passes the lower orifice of the Fallopian tube, it insinuates itself between the opposite surfaces of the uterine mucous membrane, and becomes soon afterward lodged in one of the furrows or depressions between the projecting convolutions of the decidua. (Fig. 229.) It is at this situation that an adhesion subsequently takes place between the external membranes of the egg, on the one hand, and the uterine decidua on the other. Now, at the point where the egg becomes fixed and entangled, as above stated, a still more rapid development than before takes place in the uterine

mucous membrane. Its projecting folds begin to grow up around the egg in such a manner as to partially inclose it in a kind of circumvallation of the decidua, and to shut it off, more or less com-

Fig. 229.

IMPREGNATED UTERUS; showing formation of decidua. The decidua is represented in black; and the egg is seen, at the fundus of the uterus, engaged between two of its projecting convolutions.

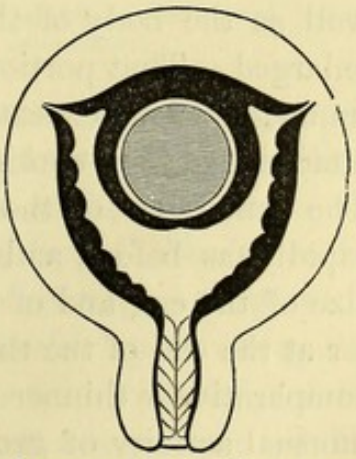
Fig. 230.



IMPREGNATED UTERUS, with projecting folds of decidua growing up around the egg. The narrow opening where the edges of the folds approach each other, is seen over the most prominent portion of the egg.

pletely, from the general cavity of the uterus. (Fig. 230.) The egg is thus soon contained in a special cavity of its own, which still communicates for a time with the general cavity of the uterus by a small opening, situated over its most prominent portion, which is known as the "decidual umbilicus." As the above process of growth goes on, this opening becomes narrower and narrower, while the projecting folds of decidua approach each other over the surface of the egg. At last these folds actually touch each other and unite, forming a kind of cicatrix which remains for a certain time, to mark the situation of the original opening.

Fig. 231.



IMPREGNATED UTERUS;—showing egg completely inclosed by decidua reflexa.

When the development of the uterus and its contents has reached this point (Fig. 231), it will be seen that the egg is completely inclosed in a distinct cavity of its own; being everywhere covered with a decidual layer of new formation, which has thus gradually enveloped it, and by which it is concealed from view when the uterine cavity is laid open. This

newly-formed layer of decidua, enveloping, as above described, the projecting portion of the egg, is called the *Decidua reflexa;* because it is reflected over the egg, by a continuous growth from the general surface of the uterine mucous membrane. The orifices of the uterine tubules, accordingly, in consequence of the manner in which the decidua reflexa is formed, will be seen not only on its external surface, or that which looks toward the cavity of the uterus, but also on its internal surface, or that which looks toward the egg.

The decidua vera, therefore, is the original mucous membrane lining the surface of the uterus; while the decidua reflexa is a new formation, which has grown up round the egg and inclosed it in a distinct cavity.

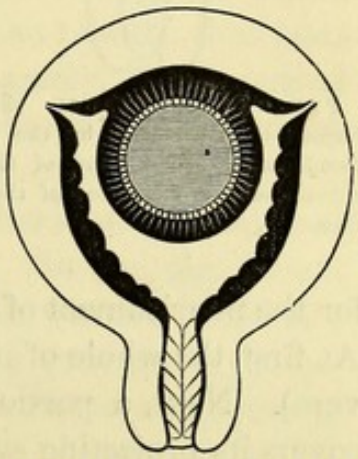
If abortion occur at this time, the mucous membrane of the uterus, that is, the decidua vera, is thrown off, and of course brings away with it the egg and decidua reflexa. On examining the mass discharged in such an abortion, the egg will accordingly be found imbedded in the substance of the decidual membrane. One side of this membrane, where it has been torn away from its attachment to the uterine walls, is ragged and shaggy; the other side, corresponding to the cavity of the uterus, is smooth or gently convoluted, and presents very distinctly the orifices of the uterine tubules; while the egg itself can only be extracted by cutting through the decidual membrane, either from one side or the other, and opening in this way the special cavity in which it has been inclosed.

During the formation of the decidua reflexa, the entire egg, as well as the body of the uterus which contains it, has considerably enlarged. That portion of the uterine mucous membrane situated immediately underneath the egg, and to which the egg first became attached, has also continued to increase in thickness and vascularity. The remainder of the decidua vera, however, ceases to grow as rapidly as before, and no longer keeps pace with the increasing size of the egg and of the uterus. It is still very thick and vascular at the end of the third month; but after that period it becomes comparatively thinner and less glandular in appearance, while the unusual activity of growth and development is concentrated in the egg, and in that portion of the uterine mucous membrane which is in immediate contact with it.

Let us now see in what manner the egg becomes attached to the decidual membrane, so as to derive from it the requisite supply of nutritious material. It must be recollected that, while the above changes have been taking place in the walls of the uterus, the

formation of the embryo in the egg, and the development of the amnion and chorion have been going on simultaneously. Soon after the entrance of the egg into the uterine cavity, its external investing membrane becomes covered with projecting filaments, or villosities, as previously described. (Chap. X.) These villosities, which are at first, as we have seen, solid and non-vascular, insinuate themselves, as they grow, into the uterine tubules, or between the folds of the decidual surface with which the egg is in contact, penetrating in this way into little cavities or follicles of the uterine mucous membrane, formed either from the cavities of the tubules themselves, or by the adjacent surfaces of minute projecting folds. When the formation of the decidua reflexa is accomplished, the chorion has already become uniformly shaggy; and its villosities, spreading in all directions from its external surface, penetrate everywhere into the follicles above described, both of the decidua vera underneath it and the contiguous surface of the decidua reflexa with which it is covered. (Fig. 232.) In this way the egg becomes entangled with the decidua, and cannot then be readily separated from it, without rupturing some of the filaments which have grown from its surface, and have been received into the cavity of the follicles. The nutritious fluids, exuded from the soft and glandular textures of the decidua, are now readily imbibed by the villosities of the chorion; and a more rapid supply of nourishment is thus provided, corresponding in abundance with the increased and increasing size of the egg.

Fig. 232.



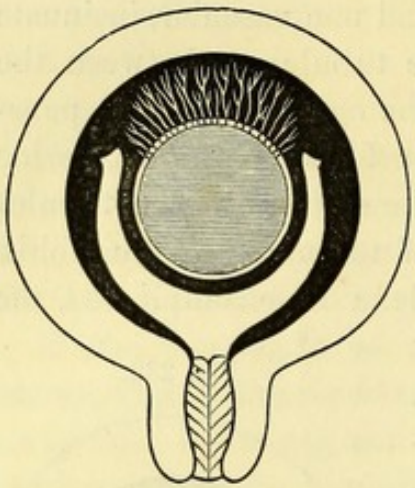
IMPREGNATED UTERUS; showing connection between villosities of chorion and decidual membranes.

Very soon, however, a still greater activity of absorption becomes necessary; and, as we have seen in a preceding chapter, the external membrane of the egg becomes vascular by the formation of the allantoic bloodvessels, which emerge from the body of the fœtus, to ramify in the chorion, and penetrate everywhere into the villosities with which it is covered. Each villosity, then, as it lies imbedded in its uterine follicle, contains a vascular loop through which the fœtal blood circulates, increasing the rapidity with which absorption and exhalation take place.

Subsequently, furthermore, these vascular tufts, which are at first uniformly abundant throughout the whole extent of the chorion,

disappear over a portion of its surface, while they at the same time become concentrated and still further developed at a particular spot, the situation of the future placenta. (Fig. 233.) This is the spot at which the egg is in contact with the decidua vera. Here, therefore, both the decidual membrane and the tufts of the chorion continue to increase in thickness and vascularity; while elsewhere, over the prominent portion of the egg, the chorion not only becomes bare of villosities, and comparatively destitute of vessels, but the decidua reflexa, which is in contact with it, also loses its activity of growth, and becomes expanded into a thin layer, nearly destitute of vessels, and without any remaining trace of tubules or follicles.

Fig. 233.



PREGNANT UTERUS; showing formation of placenta, by the united development of a portion of the decidua and the villosities of the chorion.

The uterine mucous membrane is therefore developed, during the process of gestation, in such a way as to provide for the nourishment of the fœtus in the different stages of its growth. At first, the whole of it is uniformly increased in thickness (decidua vera). Next, a portion of it grows upward around the egg, and covers its projecting surface (decidua reflexa). Afterward, both the decidua reflexa and the greater part of the decidua vera diminish in the activity of their growth, and lose their importance as a means of nourishment for the egg; while that part which is in contact with the vascular tufts of the chorion continues to grow, becoming exceedingly developed, and taking an active part in the formation of the placenta.

In the following chapter, we shall examine more particularly the structure and development of the placenta itself, and of those parts which are immediately connected with it.

CHAPTER XII.

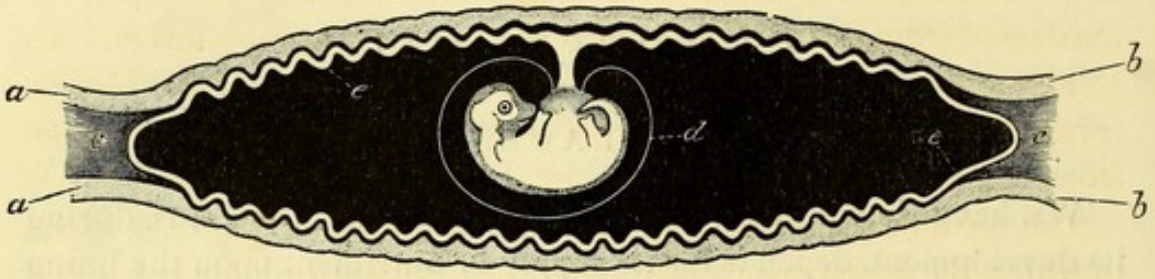
THE PLACENTA.

We have shown in the preceding chapters that the fœtus, during its development, depends for its supply of nutriment upon the lining membrane of the maternal uterus; and that the nutriment, so supplied, is absorbed by the bloodvessels of the chorion, and transported in this way into the circulation of the fœtus. In all instances, accordingly, in which the development of the fœtus takes place within the body of the parent, it is provided for by the relation thus established between two sets of membranes; namely, the maternal membranes which supply nourishment, and the fœtal membranes which absorb it.

In some species of animals, the connection between the maternal and fœtal membranes is exceedingly simple. In the pig, for example, the uterine mucous membrane is everywhere uniformly vascular; its only peculiarity consisting in the presence of numerous transverse folds, which project from its surface, analogous to the valvulæ conniventes of the small intestine. The external investing membrane of the egg, which is the allantois, is also smooth and uniformly vascular like the other. No special development of tissue or of vessels occurs at any part of these membranes, and no direct adhesion takes place between them; but the vascular allantois or chorion of the fœtus is everywhere closely applied to the vascular mucous membrane of the maternal uterus, each of the two contiguous surfaces following the undulations presented by the other. (Fig. 234.) By this arrangement, transudation and absorption take place from the bloodvessels of the mother to those of the fœtus, in sufficient quantity to provide for the nutrition of the latter. When parturition takes place, accordingly, in these animals, a very moderate contraction of the uterus is sufficient to expel its contents. The egg, displaced from its original position, slides easily forward over the surface of the uterine mucous membrane, and is at last discharged without any hemorrhage or laceration of connecting parts. In other instances, however, the development of the fœtus requires a more elaborate arrangement of the vascular membranes.

In the cow, for example, the external membrane of the egg, beside being everywhere supplied with branching vessels, presents upon

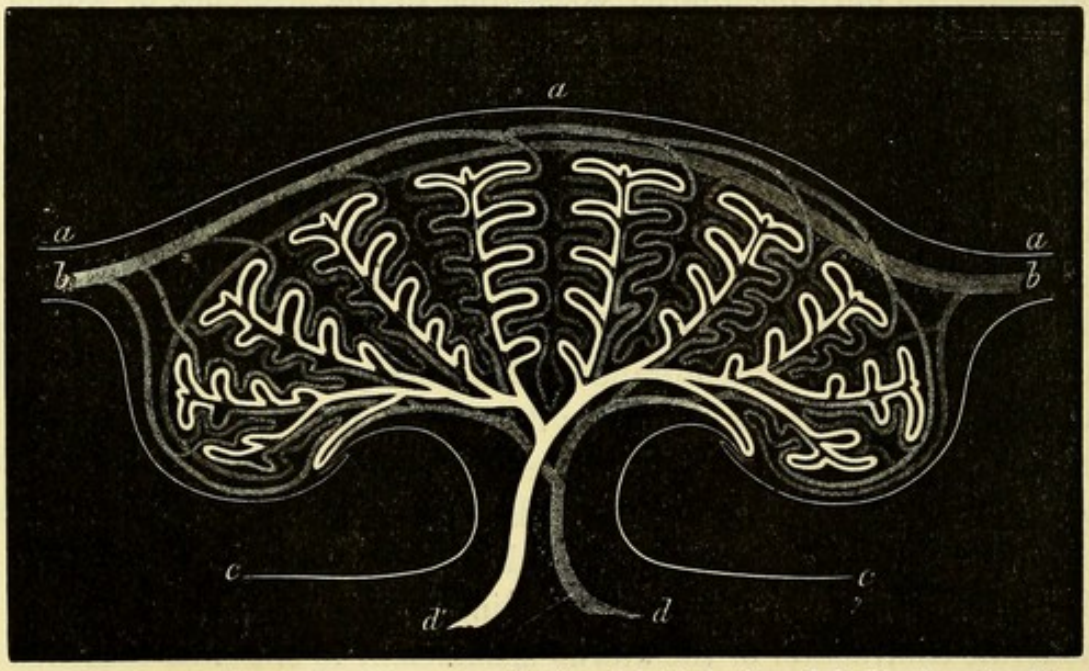
Fig. 234.



Fœtal Pig, with its membranes, contained in cavity of uterus.—*a*, *a*, *b*, *b*. Walls of uterus. *c*, *c*. Cavity of uterus. *d*. Amnion. *e*, *e*. Allantois.

various points of its surface no less than from seventy to eighty oval spots, at each of which the vessels of the chorion are developed into abundant tufted prominences, hanging from its exterior in thick, velvety, vascular masses. At each point of the uterine mucous membrane, corresponding with one of these tufted masses, the maternal bloodvessels are developed in a similar manner, projecting into the uterine cavity as a flattened rounded mass or cake; which, with that part of the fœtal chorion which is adherent to it, is known by the

Fig. 235.



Cotyledon of Cow's Uterus.—*a*, *a*. Surface of fœtal chorion. *b*, *b*. Bloodvessels of fœtal chorion. *d*, *d*. Bloodvessels of uterine mucous membrane. *c*, *c*. Surface of uterine mucous membrane

name of the *Cotyledon*. Each cotyledon forms, therefore, a little placenta. (Fig. 235.) In its substance the tufted vascular loops coming from the uterine mucous membrane (*d*, *d*) are entangled

with those coming from the membranes of the fœtus (*b*, *b*). There is no absolute adhesion between the two sets of vessels, but only an interlacement of their ramified extremities; and, with a little care in manipulation, the fœtal portion of the cotyledon may be extricated from the maternal portion, without lacerating either. In consequence, however, of this intricate interlacement of the vessels, transudation of fluids will evidently take place with great readiness, from one system to the other.

The form of placenta, therefore, met with in these animals, is one in which the bloodvessels of the fœtal chorion are simply entangled with those of the uterine mucous membrane. In the human subject, the structure of the placenta is a little more complicated, though the main principles of its formation are the same as in the above instances.

From what has been said in the foregoing chapters, it appears that in the human subject, as well as in the lower animals, the placenta is formed partly by the vascular tufts of the chorion, and partly by the thickened mucous membrane of the uterus in which they are entangled. During the third month, those portions of the chorion and decidua which are destined to undergo this transformation become more or less distinctly limited in their form and dimensions; and a thickened vascular mass, partly maternal and partly fœtal in its origin, shows itself at the spot where the placenta is afterward to be developed. This mass is constituted in the following manner.

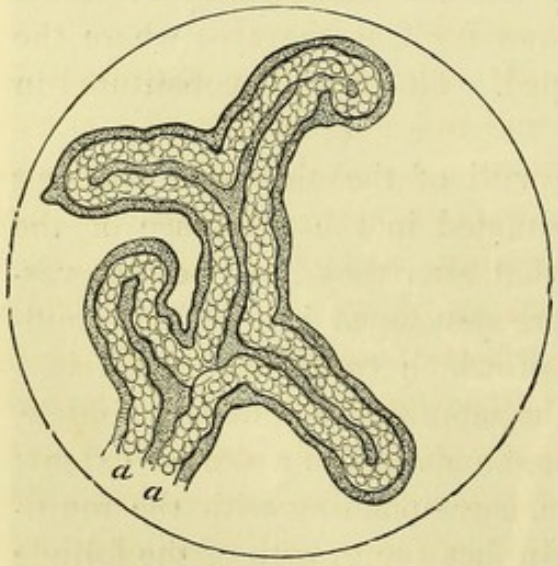
It will be recollected that the villi of the chorion, when first formed, penetrate into follicles situated in the substance of the uterine mucous membrane; and that after they have become vascular, they rapidly elongate and are developed into tufted ramifications of bloodvessels, each one of which turns upon itself in a loop at the end of the villus. At the same time the uterine follicle, into which the villus has penetrated, enlarges to a similar extent; sending out branching diverticula, corresponding with the multiplied ramifications of the villus. In fact, the growth of the follicle and that of the villus go on simultaneously, and keep pace with each other; the latter constantly advancing as the cavity of the former enlarges.

But it is not only the uterine follicles which increase in size and in complication of structure at this period. The capillary bloodvessels, which lie between them and ramify over their exterior, also become unusually developed. They enlarge and inosculate freely with each other; so that every uterine follicle is soon covered

with an abundant network of dilated capillaries, derived from the bloodvessels of the original decidua. At this time, therefore, each vascular loop of the fœtal chorion is covered, first, with a layer forming the wall of the villus. This is in contact with the lining membrane of a uterine follicle, and outside of this again are the capillary vessels of the uterine mucous membrane; so that two distinct membranes intervene between the walls of the fœtal capillaries on the one hand and those of the maternal capillaries on the other, and all transudation must take place through the substance of these two membranes.

As the formation of the placenta goes on, the anatomical arrangement of the fœtal vessel remains the same. They continue to form vascular loops, penetrating deeply into the decidual membrane; only they become constantly more elongated, and their ramifications more abundant and tortuous. The maternal capillaries, however, situated on the outside of the uterine follicles, become considerably altered in their anatomical relations. They enlarge excessively; and, by encroaching constantly upon the little islets or spaces between them, fuse successively with each other; and, losing gradually in this way the characters of a capillary network, become dilated into wide sinuses, which communicate freely with the enlarged vessels in the muscular walls of the uterus. As the original capillary plexus occupied the entire thickness of the hypertrophied decidua, the vascular sinuses, into which it is thus converted, are equally extensive. They commence at the inferior surface of the placenta, where it is in contact with the muscular walls of the uterus, and extend through its whole thickness, quite up to the surface of the fœtal chorion.

Fig. 236.

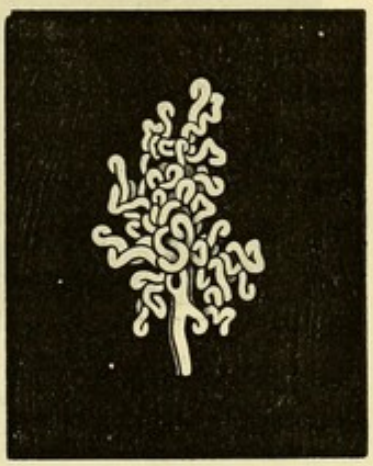


Extremity of FŒTAL TUFT, from human placenta at term, in its recent condition. *a*, *a*. Capillary bloodvessels. Magnified 135 diameters.

As the maternal sinuses grow upward, the vascular tufts of the chorion grow downward, and extend also through the entire thickness of the placenta. At this period, the development of the bloodvessels, both in the fœtal and maternal portions of the placenta, is so excessive that all the other tissues, which originally co-existed

with them, become retrograde and disappear almost altogether. If a villus from the fœtal portion of the placenta be examined at this time by transparency, in the fresh condition (Fig. 236) it will be seen that its bloodvessels are covered only with a layer of homogeneous, or finely granular material, $\frac{1}{350}$ of an inch in thickness, in which are imbedded small oval-shaped nuclei, similar to those seen at an earlier period in the villosities of the chorion. The villosities of the chorion are now, therefore, hardly anything more than ramified and tortuous vascular loops; the remaining substance of the villi having been atrophied and absorbed in the excessive growth of the bloodvessels, the abundance and development of which can be readily shown by injection from the umbilical arteries. (Fig. 237.) The uterine follicles have at the same time lost all trace of their original structure, and have become mere vascular sinuses, into which the tufted fœtal bloodvessels are received, as the villosities of the chorion were at first received into the uterine follicles.

Fig. 237.



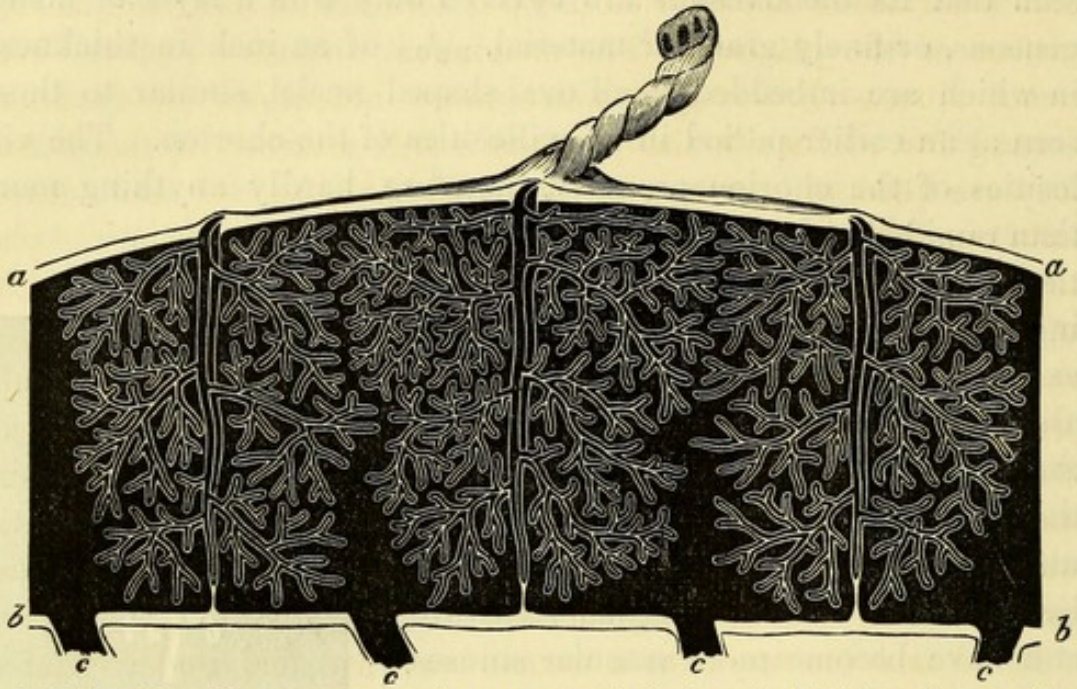
Extremity of FŒTAL TUFT of human placenta; from an injected specimen. Magnified 40 diameters.

Finally, the walls of the fœtal bloodvessels having come into close contact with the walls of the maternal sinuses, the two become adherent and fuse together; so that a time at last arrives, when we can no longer separate the fœtal vessels, in the substance of the placenta, from the maternal sinuses, without lacerating either the one or the other, owing to the secondary adhesion which has taken place between them.

The placenta, therefore, when perfectly formed, has the structure which is shown in the accompanying diagram (Fig. 238), representing a vertical section of the organ through its entire thickness. At *a*, *a*, is seen the chorion, receiving the umbilical vessels from the body of the fœtus through the umbilical cord, and sending out its compound and ramified vascular tufts into the substance of the placenta. At *b*, *b*, is the attached surface of the decidua, or uterine mucous membrane; and at *c*, *c*, *c*, *c*, are the orifices of uterine vessels which penetrate it from below. These vessels enter the placenta in an extremely oblique direction, though they are represented in the diagram, for the sake of distinctness, as nearly perpendicular. When they have once penetrated, however, the lower portion of

the decidua, they immediately dilate into the placental sinuses (represented, in the diagram, in black), which extend through the

Fig. 238.



Vertical section of PLACENTA, showing arrangement of maternal and fœtal vessels. *a, a.* Chorion. *b, b.* Decidua. *c, c, c, c.* Orifices of uterine sinuses.

whole thickness of the organ, closely embracing all the ramifications of the fœtal tufts. It will be seen, therefore, that the placenta, arrived at this stage of completion, is composed essentially of nothing but bloodvessels. No other tissues enter into its structure; for all those which it originally contained have disappeared, excepting the bloodvessels of the fœtus, entangled with and adherent to the bloodvessels of the mother.

There is, however, no direct communication between the fœtal and maternal vessels. The blood of the fœtus is always separated from the blood of the mother by a membrane which has resulted from the successive union and fusion of four different membranes, viz., first, the membrane of the fœtal villus; secondly, that of the uterine follicle; thirdly, the wall of the fœtal bloodvessel; and, fourthly, the wall of the uterine sinus. The single membrane, however, into which these four finally coalesce, is extremely thin, as we have seen, and of enormous extent, owing to the extremely abundant branching and subdivision of the fœtal tufts. These tufts, accordingly, in which the blood of the fœtus circulates, are bathed everywhere, in the placental sinuses, with the blood of the mother; and the processes of endosmosis and exosmosis, of exhalation and absorption, go on between the two with the greatest possible activity.

It is very easy to demonstrate the arrangement of the fœtal tufts in the human placenta. They can be readily seen by the naked eye, and may be easily traced from their attachment at the under surface of the chorion to their termination near the uterine surface of the placenta. The anatomical disposition of the placental sinuses, however, is much more difficult of examination. During life, and while the placenta is still attached to the uterus, they are filled, of course, with the blood of the mother, and occupy fully one-half the entire mass of the placenta. But when the placenta is detached, the maternal vessels belonging to it are torn off at their necks (Fig. 238, *c*, *c*, *c*, *c*), and the sinuses, being then emptied of blood by the compression to which the placenta is subjected, are apparently obliterated; and the fœtal tufts, falling together and lying in contact with each other, appear to constitute the whole of the placental mass. The existence of the placental sinuses, however, and their true extent, may be satisfactorily demonstrated in the following manner.

If we take the uterus of a woman who has died undelivered at the full term or thereabout, and open it in such a way as to avoid wounding the placenta, this organ will be seen remaining attached to the uterine surface, with all its vascular connections complete. Let the fœtus be now removed by dividing the umbilical cord, and the uterus, with the placenta attached, placed under water, with its internal surface uppermost. If the end of a blowpipe be now introduced into one of the divided vessels of the uterine walls, and air forced in by gentle insufflation, we can easily inflate, first, the venous sinuses of the uterus itself, and next, the deeper portions of the placenta; and lastly, the bubbles of air insinuate themselves everywhere between the fœtal tufts, and appear in the most superficial portions of the placenta, immediately underneath the transparent chorion (*a*, *a*, Fig. 238); thus showing that the placental sinuses, which freely communicate with the uterine vessels, really occupy the entire thickness of the placenta, and are equally extensive with the tufts of the chorion. We have verified this fact in the above manner, on six different occasions, and in the presence of Prof. C. R. Gilman, Prof. Geo. T. Elliot, Prof. Henry B. Sands, Prof. T. G. Thomas, Dr. T. C. Finnell, and various other medical gentlemen of New York.

If the placenta be now detached and examined separately, it will be found to present upon its uterine surface a number of openings which are extremely oblique in their position, and which are

accordingly bounded on one side by a very thin, projecting, crescentic edge. These are the orifices of the uterine vessels, passing into the placenta and torn off at their necks, as above described; and by carefully following them with the probe and scissors, they are found to lead at once into extensive empty cavities (the placental sinuses), situated between the fœtal tufts. We have already shown that these cavities are filled during life with the maternal blood; and there is every reason to believe that before delivery, and while the circulation is going on, the placenta is at least twice as large as after it has been detached and expelled from the uterus.

The placenta, accordingly, is a double organ, formed partly by the chorion and partly by the decidua; and consisting of maternal and fœtal bloodvessels, inextricably entangled and united with each other.

The part which this organ takes in the development of the fœtus is an exceedingly important one. From the date of its formation, at about the beginning of the fourth month, it constitutes the only channel through which nourishment is conveyed from the mother to the fœtus. The nutritious materials, which circulate in abundance in the blood of the maternal sinuses, pass through the intervening membrane by endosmosis, and enter the blood of the fœtus. The healthy or injurious regimen, to which the mother is subjected, will accordingly exert an almost immediate influence upon the child. Even medicinal substances, taken by the mother and absorbed into her circulation, may readily transude through the placental vessels; and they have been known in this way to exert a specific effect upon the fœtal organization.

The placenta is, furthermore, an organ of exhalation as well as of absorption. The excrementitious substances, produced in the circulation of the fœtus, are undoubtedly in great measure disposed of by transudation through the walls of the placental vessels, to be afterward discharged by the excretory organs of the mother. The system of the mother may therefore be affected in this manner by influences derived from the fœtus. It has been remarked more than once, in the lower animals, that when the female has two successive litters of young by different males, the young of the second litter will sometimes bear marks resembling those of the first male. In these instances, the peculiar influence which produces the external mark must have been transmitted by the first male directly to the fœtus, from the fœtus to the mother, and from the mother to the fœtus of the second litter.

It is also through the placental circulation that those disturbing effects are produced upon the nutrition of the fœtus, which result from sudden shocks or injuries inflicted upon the mother. There is now little room for doubt that various deformities and deficiencies of the fœtus, conformably to the popular belief, do really originate, in certain cases, from nervous impressions, such as disgust, fear or anger, experienced by the mother. The mode in which these effects may be produced is readily understood from what has been said above of the anatomy and functions of the placenta. We know very well how easily nervous impressions will disturb the circulation in the brain, the face, the lungs, &c.; and the uterine circulation is quite as readily influenced by similar causes, as physicians see every day in cases of amenorrhœa, menorrhagia, &c. If a nervous shock may excite premature contraction in the muscular fibres of the pregnant uterus and produce abortion, as not unfrequently happens, it is certainly capable of disturbing the course of the circulation through the same organ. But the fœtal circulation is dependent, to a great extent, on the maternal. Since the two sets of vessels are so closely entwined in the placenta, and since the fœtal blood has here much the same relation to the maternal, that the blood in the pulmonary capillaries has to the air in the air-vesicles, it will be liable to derangement from similar causes. If the circulation of air through the pulmonary tubes be suspended, that of the blood through the general capillaries is disturbed also. In the same way, whatever arrests or disturbs the circulation through the vessels of the maternal uterus must necessarily be liable to interfere with that in the fœtal capillaries forming part of the placenta. And lastly, as the nutrition of the fœtus is provided for wholly by the placenta, it will of course suffer immediately from any such disturbance of the placental circulation. These effects may be manifested either in the general atrophy and death of the fœtus; or, if the disturbing cause be slight, in the atrophy or imperfect development of particular parts; just as, in the adult, a morbid cause operating through the entire system, may be first or even exclusively manifested in some particular organ, which is more sensitive to its influence than other parts.

The placenta must accordingly be regarded as an organ which performs, during intra-uterine life, offices similar to those of the lungs and the intestine after birth. It absorbs nourishment, renovates the blood, and discharges by exhalation various excrementitious matters, which originate in the processes of fœtal nutrition.

CHAPTER XIII.

DISCHARGE OF THE OVUM, AND RETROGRADE DEVELOPMENT (INVOLUTION) OF THE UTERUS.

During the growth of the ovum and the formation of the placental structures, the muscular substance of the uterus also increases in thickness, while the whole organ enlarges, in order to accommodate the growing fœtus and its appendages. The relative positions of the amnion and chorion, furthermore, undergo a change during the latter periods of gestation, and the umbilical cord becomes developed, at the same time, in the following manner.

In the earlier periods of fœtal life, the umbilical cord consists simply of that portion of the allantois lying next the abdomen. It is then very short, and contains the umbilical vessels running in a nearly straight course, and parallel with each other, from the abdomen of the fœtus to the external portions of the chorion. At this time the amnion closely invests the body of the fœtus, so that the size of its cavity is but little larger than that of the fœtus. (Fig. 239.) The space between the amnion and the chorion is then occupied by an amorphous gelatinous material, in which lies imbedded the umbilical vesicle.

Fig. 239.

Human Ovum about the end of the first month.—1. Umbilical vesicle. 2. Amnion. 3. Chorion.

Afterward, however, the amnion enlarges faster than the chorion, and encroaches upon the layer of gelatinous matter situated between the two (Fig. 240), at the same time that an albuminous fluid, the "amniotic fluid," is exuded into its cavity, in constantly increasing quantity. Subsequently, the gelatinous layer, above described, altogether disappears, and the amnion, at about the begin-

ning of the fifth month, comes in contact with the internal surface of the chorion. Finally, toward the end of gestation, the contact becomes so close between these two membranes that they are partially adherent to each other, and it requires a little care to separate them without laceration.

Fig. 240.

HUMAN OVUM at end of third month; showing enlargement of amnion.

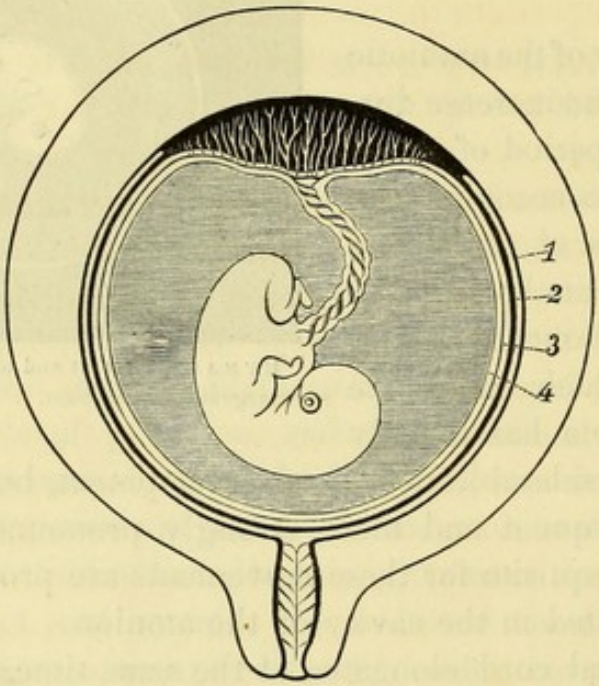
The quantity of the amniotic fluid continues to increase during the latter period of gestation in order to accommodate the movements of the fœtus. These movements begin to be perceptible about the fifth month, at which time the muscular system has already attained a considerable degree of development, but become afterward more frequent and more strongly pronounced. The space and freedom requisite for these movements are provided for by the fluid accumulated in the cavity of the amnion.

The umbilical cord elongates, at the same time, in proportion to the increasing size of the amniotic cavity. During its growth, it becomes spirally twisted from right to left, the two umbilical arteries winding round the vein in the same direction. The gelatinous matter, as already described as existing between the amnion and chorion, while it disappears elsewhere, accumulates in the cord in considerable quantity, covering the vessels with a thick, elastic envelope, which protects them from injury and prevents their being accidentally compressed or obliterated. The whole is covered by a portion of the amnion, which is connected at one extremity with the integument of the abdomen, and invests the whole of the cord with a continuous sheath, like the finger of a glove. (Fig. 241.)

The cord also contains, for a certain period, the pedicle or stem of the umbilical vesicle. The situation of this vesicle, it will be recollected, is always between the chorion and the amnion. Its pedicle gradually elongates with the growth of the umbilical cord: and the vesicle itself, which generally disappears soon after the third month, sometimes remains as late as the fifth, sixth, or seventh. According to Prof. Mayer, of Bonn, it may even be found, by careful search, at the termination of pregnancy. When discovered in

the middle and latter periods of gestation, it presents itself as a small, flattened, and shrivelled vesicle, situated underneath the amnion, at a variable distance from the insertion of the umbilical cord. A minute bloodvessel is often seen running to it from the cord, and ramifying upon its surface.

Fig. 241.



Gravid Human Uterus and Contents, showing the relations of the cord, placenta, membranes, &c., about the end of the seventh month.—1. Decidua vera. 2. Decidua reflexa. 3. Chorion. 4. Amnion.

The decidua reflexa, during the latter months of pregnancy, is constantly distended and pushed back by the increasing size of the egg; so that it is finally pressed closely against the opposite surface of the decidua vera, which still lines the greater part of the uterine cavity. By the end of the seventh month, the opposite surfaces of the decidua vera and reflexa are in complete contact with each other, though still distinct and capable of being separated without difficulty. After that time, they fuse together and become confounded with each other; the two at last forming only a single, thin, friable, semi-opaque layer, in which no trace of their original glandular structure can be discovered.

This is the condition of things at the termination of pregnancy. Then, the time having arrived for parturition to take place, the hypertrophied muscular walls of the uterus contract forcibly upon its contents, and the egg is discharged, together with the whole of the decidual uterine mucous membrane.

In the human subject, as well as in most quadrupeds, the membranes of the egg are usually ruptured during the process of parturition; and the fœtus escapes first, the placenta and the rest of the appendages following a few moments afterward. Occasionally, however, even in the human subject, the egg is discharged entire, and the fœtus liberated afterward by the laceration of the membranes. In each case, however, the mode of separation and expulsion is in all particulars the same.

The process of parturition, therefore, consists essentially in a separation of the decidual membrane, which, on being discharged, brings away the ovum with it. The greater part of the decidua vera, having fallen into a state of atrophy during the latter months of pregnancy, is by this time nearly destitute of vessels, and separates, accordingly, without any perceptible hemorrhage. That portion, however, which enters into the formation of the placenta, is, on the contrary, excessively vascular; and when the placenta is separated, and its maternal vessels torn off at their necks, as before mentioned, a gush of blood takes place, which accompanies or immediately follows the birth of the fœtus. This hemorrhage, which occurs as a natural phenomenon at the time of parturition, does not come from the uterine vessels proper. It consists of the blood which was contained in the placental sinuses, and which is expelled from them owing to the compression of the placenta by the walls of the uterus. Since the whole amount of blood thus lost was previously employed in the placental circulation, and since the placenta itself is thrown off at the same time, no unpleasant effect is produced upon the mother by such a hemorrhage, because the natural proportion of blood in the rest of the maternal system remains the same. Uterine hemorrhage at the time of parturition, therefore, becomes injurious only when it continues after complete separation of the placenta; in which case it is supplied by the mouths of the uterine vessels themselves, left open by failure of the uterine contractions. These vessels are usually instantly closed, after separation of the placenta, by the contraction of the muscular fibres of the uterus. They pass, as we have already mentioned, in an exceedingly oblique direction, from the uterine surface to the placenta; and the muscular fibres, which cross them transversely above and below, necessarily constrict them, and effectually close their orifices, immediately on being thrown into a state of contraction

Another very remarkable phenomenon, connected with pregnancy and parturition is the appearance in the uterus of a new

mucous membrane, growing underneath the old, and ready to take the place of the latter after its discharge.

If the internal surface of the body of the uterus be examined immediately after parturition, it will be seen that at the spot where the placenta was attached, every trace of mucous membrane has disappeared. The muscular fibres of the uterus are here perfectly exposed and bare; while the mouths of the ruptured uterine sinuses are also visible, with their thin, ragged edges hanging into the cavity of the uterus, and their orifices plugged with more or less abundant bloody coagula.

Over the rest of the uterine surface, the decidua vera has also disappeared. Here, however, notwithstanding the loss of the original mucous membrane, the muscular fibres are not perfectly bare, but are covered with a thin, semi-transparent film, of a whitish color and soft consistency. This film is an imperfect mucous membrane of new formation, which begins to be produced, underneath the old decidua vera, as early as the beginning of the eighth month. We have seen this new mucous membrane very distinctly in the uterus of a woman who died undelivered at the above period. The old mucous membrane, or decidua vera, is at this time somewhat opaque, and of a slightly yellowish color, owing to a partial fatty degeneration which it undergoes in the latter months of pregnancy. It is easily raised and separated from the subjacent parts, owing to the atrophy of its vascular connections; and the new mucous membrane, situated beneath it, is readily distinguished by its fresh color, and healthy, transparent aspect.

The mucous membrane of the cervix uteri, which takes no part in the formation of the decidua, is not thrown off in parturition, but remains in its natural position; and after delivery it may be seen to terminate at the os internum by an uneven, lacerated edge, where it was formerly continuous with the decidua vera.

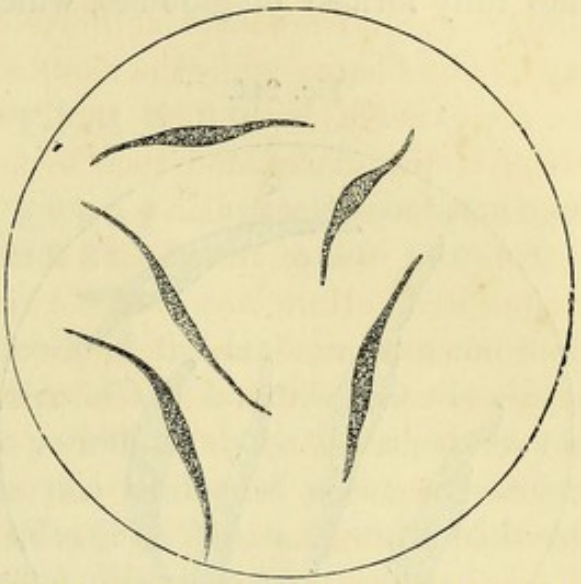
Subsequently, a regeneration of the mucous membrane takes place over the whole extent of the body of the uterus. The mucous membrane of new formation, which is already in existence at the time of delivery, becomes thickened and vascular; and glandular tubules are gradually developed in its substance. At the end of two months after delivery, according to Heschl[1] and Longet,[2] it has entirely regained the natural structure of the uterine mucous mem-

[1] Zeitschrift der K. K. Gesellschaft der Aerzte, in Wien, 1852.

[2] Traité de Physiologie. De la Génération, p. 173.

brane. It unites at the os interum, by a linear cicatrix, with the mucous membrane of the cervix, and the traces of its laceration at this spot afterward cease to be visible At the point, however, where the placenta was attached, the regeneration of the mucous membrane is less rapid; and a cicatrix-like spot is often visible at this situation for several months after delivery.

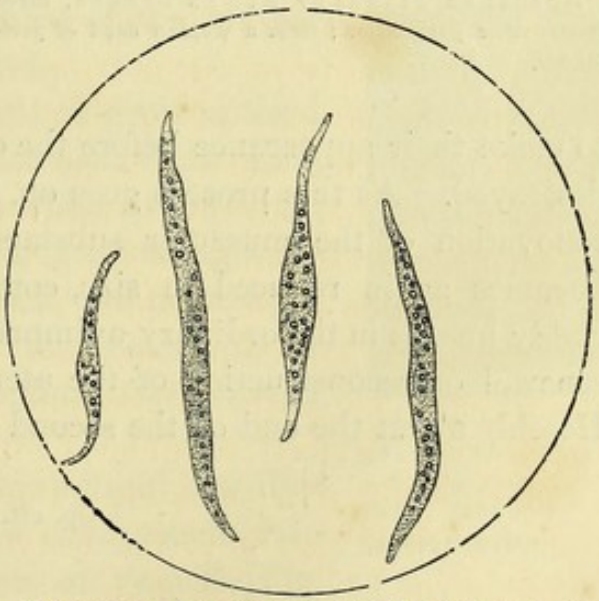
Fig. 242.



Muscular Fibres of Unimpregnated Uterus; from a woman aged 40, dead of phthisis pulmonalis.

The only further change which remains to be described in this connection, is the fatty degeneration and reconstruction of the muscular substance of the uterus. This process, which is sometimes known as the "involution" of the uterus, takes place in the following manner. The muscular fibres of the unimpregnated uterus are pale, flattened, spindle-shaped bodies (Fig. 242) nearly homogeneous in structure or very faintly granular, and measuring from $\frac{1}{500}$ to $\frac{1}{250}$ of an inch in length, by $\frac{1}{10000}$ to $\frac{1}{6000}$ of an inch in width. During gestation these fibres increase very considerably in size. Their texture becomes much more distinctly granular, and their outlines more strongly marked. An oval nucleus also shows itself in the central part of each fibre.

Fig. 243.



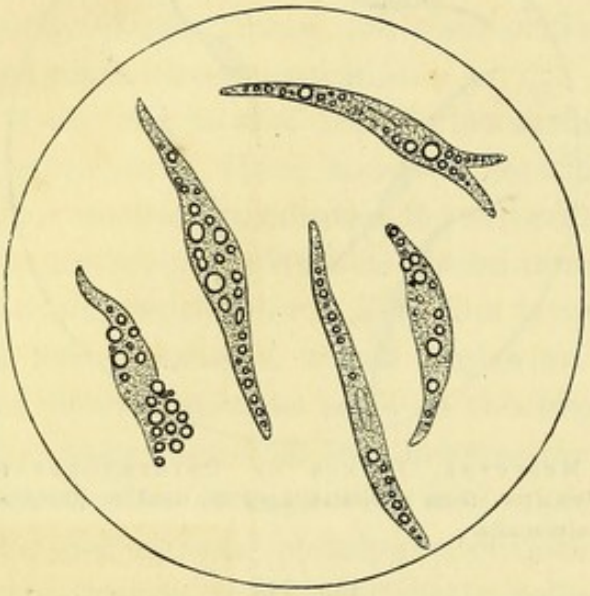
Muscular Fibres of Human Uterus, ten days after parturition; from a woman dead of puerperal fever.

The entire walls of the uterus, at the time of delivery, are composed of such muscular fibres, arranged in circular, oblique, and longitudinal bundles.

About the end of the first week after delivery, these fibres begin

to undergo a fatty degeneration. (Fig. 243.) Their granules become larger and more prominent, and very soon assume the appearance of molecules of fat, deposited in the substance of the fibre. The fatty deposit, thus commenced, increases in abundance, and the molecules continue to enlarge until they become converted into fully formed oil-globules, which fill the interior of the fibre more or less completely, and mask, to a certain extent, its anatomical characters. (Fig. 244.) The universal fatty degeneration, thus induced, gives to the uterus a softer consistency, and a pale yellowish color which is characteristic of it at this period. The muscular fibres which have become altered by the fatty deposit are afterward gradually absorbed and disappear; their place being subsequently taken by other fibres of new formation, which already begin to make their appearance before the old ones have been completely destroyed. As this process goes on, it results finally in a complete renovation of the muscular substance of the uterus. The organ becomes again reduced in size, compact in tissue, and of a pale ruddy hue, as in the ordinary unimpregnated condition. This entire renewal or reconstruction of the uterus is completed, according to Heschl,[1] about the end of the second month after delivery.

Fig. 244.



Muscular Fibres of Human Uterus, three weeks after parturition; from a woman dead of peritonitis.

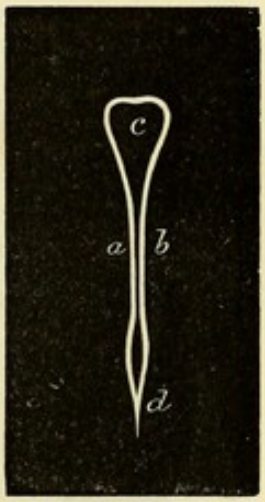
[1] Op. cit.

CHAPTER XIV.

DEVELOPMENT OF THE EMBRYO—NERVOUS SYSTEM. ORGANS OF SENSE, SKELETON, AND LIMBS.

THE first trace of a spinal cord in the embryo consists of the double longitudinal fold or ridge of the blastodermic membrane, which shows itself at an early period, as above described, on each side the median furrow. The two laminæ of which this is composed, on the right and left sides (Fig. 245, *a*, *b*), unite with each other in front, forming a rounded dilatation (*c*), the cephalic extremity, and behind at *d*, forming a pointed or caudal extremity. Near the posterior extremity, there is a smaller dilatation, which marks the future situation of the lumbar enlargement of the spinal cord.

Fig. 245.



Formation of CEREBRO-SPINAL AXIS.—*a*, *b*. Spinal cord. *c*. Cephalic extremity. *d*. Caudal extremity

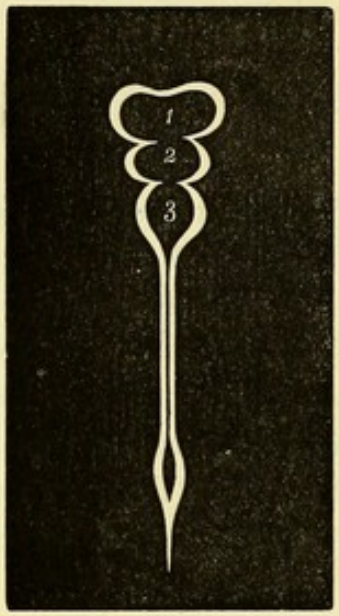
As the laminæ above described grow upward and backward, they unite with each other upon the median line, so that the whole is converted into a hollow cylindrical cord, terminating anteriorly by a bulbous enlargement, and posteriorly by a pointed enlargement; the central cavity which it contains running continuously through it, from front to rear.

The next change which shows itself is a division of the anterior bulbous enlargement into three secondary compartments or vesicles (Fig. 246), which are partially separated from each other by transverse constrictions. These vesicles are known as the *three cerebral vesicles*, from which all the different parts of the encephalon are afterward to be developed. The first, or most anterior cerebral vesicle is destined to form the hemispheres; the second, or middle, the tubercula quadrigemina; and the third, or posterior, the medulla oblongata. All three vesicles are at this time hollow, and their

cavities communicate freely with each other, through the intervening constrictions.

Very soon the anterior and the posterior cerebral vesicles suffer a further division; the middle one remaining undivided. The anterior vesicle thus separates into two portions, of which the first, or larger, constitutes the hemispheres, while the second, or smaller, becomes the optic thalami. The third vesicle also separates into two portions, of which the anterior becomes the cerebellum, and the posterior the medulla oblongata.

Fig. 246.



Formation of the CEREBRO-SPINAL AXIS.—1. Vesicle of the hemispheres. 2. Vesicle of the tubercula quadrigemina. 3. Vesicle of the medulla oblongata.

There are, therefore, at this time five cerebral vesicles, all of whose cavities communicate with each other and with the central cavity of the spinal cord. The entire cerebro-spinal axis, at the same time, becomes very strongly curved in an anterior direction, corresponding with the anterior curvature of the body of the embryo (Fig. 247); so that the middle vesicle, or that of the tubercula quadrigemina, occupies a prominent angle at the upper part of the encephalon, while the hemispheres and the medulla oblongata are situated below it, anteriorly and posteriorly.

At first, it will be observed, the relative size of the various parts of the encephalon is very different from that which they afterward attain in the adult condition. The hemispheres, for example, are hardly larger than the tubercula quadrigemina; and the cerebellum is very much inferior in size to the medulla oblongata. Soon afterward, the relative position and size of the parts begin to alter. The hemispheres and tubercula quadrigemina grow faster than the posterior portions of the encephalon; and the cerebellum becomes doubled backward over the medulla oblongata. (Fig. 248.) Subsequently, the hemispheres rapidly enlarge, growing upward and backward, so as to cover in and conceal both the optic thalami and the tubercula quadrigemina (Fig. 249); the cerebellum tending in the same way to grow backward, and projecting farther

Fig. 247.

FŒTAL PIG, five-eighths of an inch long, showing brain and spinal cord.—1. Hemispheres. 2. Tubercula quadrigemina. 3. Cerebellum. 4. Medulla oblongata.

and farther over the medulla oblongata. The subsequent history of the development of the encephalon is little more than a con-

Fig. 248.

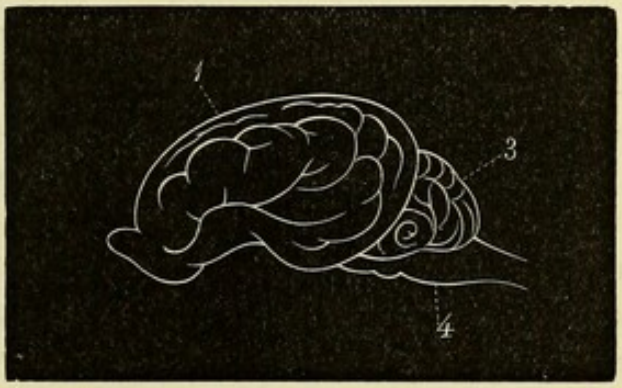
Fœtal Pig, one and a quarter inch long.—1. Hemispheres. 2. Tubercula quadrigemina. 3. Cerebellum. 4. Medulla oblongata.

Fig 249.

Head of Fœtal Pig, three and a half inches long.—1. Hemispheres. 3. Cerebellum. 4. Medulla oblongata.

tinuation of the same process; the relative dimensions of the parts constantly changing, so that the hemispheres become, in the adult condition (Fig. 250), the largest of all the divisions of the ence-

Fig. 250



Brain of Adult Pig.—1. Hemispheres. 3. Cerebellum. 4. Medulla oblongata.

phalon, while the cerebellum is next in size, and covers entirely the upper portion of the medulla oblongata. The surfaces, also, of the hemispheres and cerebellum, which were at first smooth, become afterward convoluted; increasing, in this way, still farther the extent of their nervous matter. In the human fœtus, these convolutions begin to appear about the beginning of the fifth month (Longet), and grow constantly deeper and more abundant during the remainder of fœtal life.

The lateral portions of the brain growing at the same time more rapidly than that which is situated on the median line, they soon project on each side outward and upward; and by folding over

against each other in the median line, form the right and left hemispheres, separated from each other by the *longitudinal fissure*. A similar process of growth taking place in the spinal cord results in the formation of the two lateral columns and the anterior and posterior median fissures of the cord. Elsewhere the median fissure is less complete, as, for example, between the two lateral halves of the cerebellum, the two optic thalami and corpora striata, and the two tubercula quadrigemina; but it exists everywhere, and marks more or less distinctly the division between the two sides of the nervous centres, produced by the excessive growth of their lateral portions. In this way the whole cerebro-spinal axis is converted into a double organ, equally developed upon the right and left sides, and partially divided by a longitudinal median fissure.

Organs of Special Sense.—The eyes are formed by a diverticulum which grows out on each side from the first cerebral vesicle. This diverticulum is at first hollow, its cavity communicating with that of the hemisphere. Afterward, the passage between the two is filled up with a deposit of nervous matter, and becomes the *optic nerve*. The globular portion of the diverticulum, which is converted into the globe of the eye, has a very thin layer of nervous matter deposited upon its internal surface, which becomes the *retina;* the rest of its cavity being occupied by a gelatinous semi-fluid substance, the *vitreous body*. The crystalline lens is formed in a distinct follicle, which is an offshoot of the integument, and becomes partially imbedded in the anterior portion of the globe of the eye. The cornea also is originally a part of the integument, and remains partially opaque until a very late period of development. Its tissue clears up, however, and becomes perfectly transparent, shortly before birth.

The iris is a muscular septum which is formed in front of the crystalline lens, separating the anterior and posterior chambers of the aqueous humor. Its central opening, which afterward becomes the pupil, is at first closed by a vascular membrane, the *pupillary membrane*, passing directly across the axis of the eye. The vessels of this membrane, which are derived from those of the iris, subsequently become atrophied. They disappear first from its centre, and afterward recede gradually toward its circumference; returning always upon themselves in loops, the convexities of which are directed toward the centre of the membrane. The pupillary membrane itself finally becomes atrophied and destroyed, following in this retrograde process the direction of its receding bloodvessels, viz., from

the centre toward the circumference. It has completely disappeared by the end of the seventh month. (Cruveilhier.)

The eyelids are formed by folds of the integument, which gradually project from above and below the situation of the eyeball. They grow so rapidly during the second and third months that their free margins come in contact and adhere together, so that they cannot be separated at that time without some degree of violence. They remain adherent from this period until the seventh month (Guy), when their margins separate and they become perfectly free and movable. In the carnivorous animals, however (dogs and cats), the eyelids do not separate from each other until eight or ten days after birth.

The internal ear is formed in a somewhat similar manner with the eyeball, by an offshoot from the third cerebral vesicle; the passage between them filling up by a deposit of white substance, which becomes the auditory nerve. The tympanum and auditory meatus are both offshoots from the external integument.

Skeleton.—At a very early period of development there appears, as we have already described (Chap. VII.), immediately beneath the cerebro-spinal axis, a cylindrical cord, of a soft, cartilaginous consistency, termed the *chorda dorsalis*. It consists of a fibrous sheath containing a mass of simple cells, closely packed together and united by adhesive material. This cord is not intended to be a permanent part of the skeleton, but is merely a temporary organ destined to disappear as development proceeds.

Immediately around the chorda dorsalis there are deposited soon afterward a number of cartilaginous plates, which encircle it in a series of rings, corresponding in number with the bodies of the future vertebræ. These rings increase in thickness from without inward, encroaching upon the substance of the chorda dorsalis, and finally taking its place altogether. The thickened rings, which have been filled up in this way and solidified by cartilaginous deposit, become the bodies of the vertebræ; while their transverse and articulating processes, with the laminæ and spinous processes, are formed by subsequent outgrowths from the bodies in various directions.

When the union of the dorsal plates upon the median line fails to take place, the spinal canal remains open at that situation, and presents the malformation known as *spina bifida*. This malformation may consist simply in a fissure of the spinal canal, more or less extensive, in which case it may often be cured, or may even close spontaneously; or it may be complicated with an imperfect deve

lopment or complete absence of the spinal cord at the same spot, when it is accompanied of course by paralysis of the lower extremities, and almost necessarily results in early death.

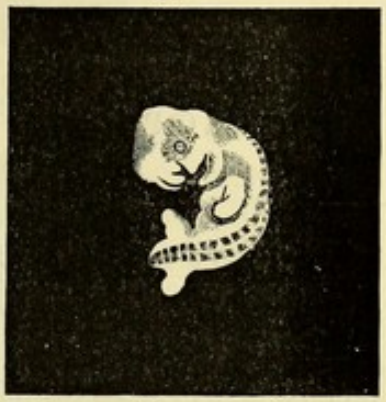
The entire skeleton is at first cartilaginous. The first points of ossification show themselves about the beginning of the second month, almost simultaneously in the clavicle and the upper and lower jaw. Then come in the following order, the long bones of the extremities, the bodies and processes of the vertebræ, the bones of the head, the ribs, pelvis, scapula, metacarpus and metatarsus, and the phalanges of the fingers and toes. The bones of the carpus, however, are all cartilaginous at birth, and do not begin to ossify until a year afterward. The calcaneum and astragalus begin to ossify, according to Cruveilhier, during the latter periods of fœtal life, but the remainder of the tarsus is cartilaginous at birth. The lower extremity of the femur begins to ossify, according to the same author, during the latter half of the ninth month. The pisiform bone of the carpus is said to commence its ossification later than any other bone in the skeleton, viz., at from twelve to fifteen years after birth. Nearly all the bones ossify from several distinct points; the ossification spreading as the cartilage itself increases in size, and the various bony pieces, thus produced, uniting with each other at a later period, usually some time after birth.

The limbs appear by a kind of budding process, as offshoots of the external layer of the blastodermic membrane. They are at first mere rounded elevations, without any separation between the fingers and toes, or any distinction between the different articulations. Subsequently the free extremity of each limb becomes divided into the phalanges of the fingers or toes; and afterward the articulations of the wrist and ankle, knee and elbow, shoulder and hip, appear successively from below upward.

The posterior extremities, in the human subject, are less rapid in their development than the anterior. Throughout the term of fœtal life, indeed, the anterior parts of the body are generally more voluminous than the posterior. The younger the embryo, the larger are the head and upper parts in proportion to the rest of the body. The lower limbs and the pelvis, more particularly, are very slightly developed in the early periods of growth, as compared with the spinal column, to which they are attached. The inferior extremity of the spinal column, formed by the sacrum and coccyx, projects at this time considerably beyond the pelvis, forming a tail, like that of the lower animals, which is curled forward toward the

abdomen, and terminates in a pointed extremity. The entire lower half of the body, with the spinal column and appendages, is also strongly twisted, from left to right; so that the pelvis is not only curled forward, but also faces at right angles to the direction of the head and upper part of the body. Subsequently the spinal column becomes straighter and loses its twisted form. At the same time the pelvis and the muscular parts seated upon it grow so much faster than the sacrum and coccyx, that the latter become concealed under the adjoining soft parts, and the rudimentary tail accordingly disappears.

Fig. 251.



HUMAN EMBRYO, about one month old. Showing the large size of the head and upper parts of the body; — the twisted form of the spinal column; — the rudimentary condition of the upper and lower extremities; — and the rudimentary tail at the end of the spinal column.

The *integument* of the embryo is at first thin, vascular, and exceedingly transparent. It afterward becomes thicker, more opaque, and whitish in color; even at birth, however, it is considerably more vascular than in the adult condition, and the ruddy color of its abundant capillary vessels very strongly marked. The hairs begin to appear about the middle of intra-uterine life; showing themselves first upon the eyebrows, and afterward upon the scalp, trunk and extremities. The nails are in process of formation from the third to the fifth month; and, according to Kölliker, are still covered with a layer of epidermis until after the latter period. The sebaceous matter of the cutaneous glandules accumulates upon the skin after the sixth month, and forms a whitish, semi-solid, oleaginous layer, termed the *vernix caseosa*, which is most abundant in the flexures of the joints, between the folds of the integument, behind the ears and upon the scalp.

CHAPTER XV.

DEVELOPMENT OF THE ALIMENTARY CANAL AND ITS APPENDAGES.

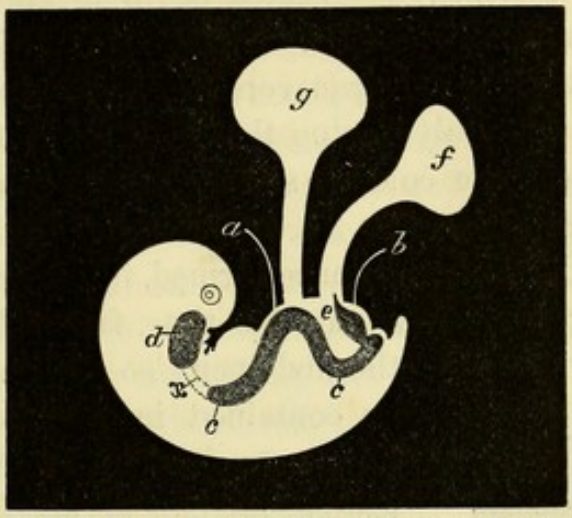
We have already seen, in a preceding chapter, that the intestinal canal is formed by the internal layer of the blastodermic membrane, which curves forward on each side, and is thus converted into a nearly straight cylindrical tube, terminating at each extremity in a rounded cul-de-sac, and inclosed by the external layer of the blastodermic membrane. The abdominal walls, however, do not unite with each other upon the median line until long after the formation of the intestinal canal; so that, during a certain period, the abdomen of the embryo is widely open in front, presenting a long oval excavation, in which the nearly straight, intestinal tube is to be seen, running from its anterior to its posterior extremity.

The formation of the stomach takes place in the following manner: The alimentary canal, originally straight, soon presents two lateral curvatures at the upper part of the abdomen; the first to the left, the second to the right. The first of these curvatures becomes expanded into a wide sac, projecting laterally from the median line into the left hypochondrium, forming the great pouch of the stomach. The second curvature, directed to the right, marks the boundary between the stomach and the duodenum; and the tube at that point becoming constricted and furnished with a circular layer of muscular fibres, is converted into the pylorus. Immediately below the pylorus, the duodenum again turns to the left; and these curvatures, increasing in number and complexity, form the convolutions of the small intestine. The large intestine forms a spiral curvature; ascending on the right side, then crossing over to the left as the transverse colon, and again descending on the left side, to terminate by the sigmoid flexure in the rectum.

The curvatures of the intestinal canal take place, however, in an antero-posterior, as well as in a lateral direction, and may be best studied in a profile view, as in Fig. 252. The abdominal walls are

here still imperfectly closed, leaving a wide opening at *a*, *b*, where the integument of the fœtus becomes continuous with the commencement of the amniotic membrane. The intestine makes at

Fig. 252.



Formation of ALIMENTARY CANAL.—*a*, *b*. Commencement of amnion. *c*, *c* Intestine. *d*. Pharynx. *e*. Urinary bladder. *f* Allantois. *g*. Umbilical vesicle. *x*. Dotted line, showing the place of formation of the œsophagus.

first a single angular turn forward, and opposite the most prominent portion of this angle is to be seen the obliterated duct, which forms the stem of the umbilical vesicle. (*g*.) A short distance below this point the intestine subsequently enlarges in its calibre, and the situation of this enlargement marks the commencement of the colon. The two portions of the intestine, after this period, become widely different from each other. The upper portion, which is the small intestine, grows mostly in the direction of its length, and becomes a very long, narrow, and convoluted tube; while the lower portion, which is the large intestine, increases rapidly in diameter, but elongates less than the former.

At the point of junction of the small and large intestines, a lateral bulging or diverticulum of the latter shows itself, and increases in extent, until the ileum seems at last to be inserted obliquely into the side of the colon. This diverticulum of the colon is at first uniformly tapering or conical in shape; but afterward that portion which forms its free extremity, becomes narrow and elongated, and is slightly twisted upon itself in a spiral direction, forming the appendix vermiformis; while the remaining portion, which is continuous with the intestine, becomes exceedingly enlarged, and forms the caput coli.

The caput coli and the appendix are at first situated near the

umbilicus; but between the fourth and fifth months (Cruveilhier) their position is altered, and they then become fixed in the right iliac region. During the first six months, the internal surface of the small intestine is smooth. At the seventh month, according to Cruveilhier, the valvulæ conniventes begin to appear, after which they increase in size till birth. The division of the colon into sacculi by longitudinal and transverse bands, is also an appearance which presents itself only during the last half of fœtal life. Previous to that time, the colon is smooth and cylindrical in figure, like the small intestine.

After the small intestine is once formed, it increases very rapidly in length. It grows, indeed, at this time, faster than the walls of the abdomen; so that it can no longer be contained in the abdominal cavity, but protrudes, under the form of an intestinal loop, or hernia, from the umbilical opening. (Fig. 253.) In the human embryo, this protrusion of the intestine can be readily seen during the latter part of the second month. At a subsequent period, however, the walls of the abdomen grow more rapidly than the intestine. They accordingly gradually envelop the hernial protrusion, and at last inclose it again in the cavity of the abdomen.

Fig. 253.

FŒTAL PIG, showing loop of intestine, forming umbilical hernia; from a specimen in the author's possession. From the convexity of the loop a thin filament is seen passing to the umbilical vesicle, which is here flattened into a leaf-like form.

Owing to an imperfect development of the abdominal walls, and an imperfect closure of the umbilicus, this intestinal protrusion, which is normal during the early stages of fœtal life, sometimes remains at birth, and we then have a *congenital umbilical hernia.* As the parts at that time, however, have a natural tendency to cicatrize and unite with each other, simple pressure is generally effectual, in such cases, in retaining the hernia within the abdomen, and in producing at last a complete cure.

Urinary Bladder, Urethra, &c.—It will be recollected that very soon after the formation of the intestine, a vascular outgrowth takes place from its posterior portion, which gradually protrudes from the open walls of the abdomen in front, until it comes in contact with the external investing membrane of the egg, and forms, by its continued growth and expansion, the *allantois.* (Fig. 252, *f.*) It is at

first, as we have shown above, a hollow sac, but, as it spreads out over the surface of the investing membrane of the egg, its two opposite walls adhere to each other, so that its cavity is obliterated at this situation, and it is thus converted into a single vascular membrane, the *chorion*. This obliteration of the cavity of the allantois commences at its external portion, and gradually extends inward toward the point of its emergence from the abdomen. The hollow tube, or duct, which connects the cavity of the allantois with the posterior part of the intestine, is accordingly converted, as the process of obliteration proceeds, into a solid, rounded cord. This cord is termed the *urachus*.

After the walls of the abdomen have come in contact, and united with each other at the umbilicus, that portion of the above duct which is left outside the abdominal cavity, forms a part of the umbilical cord, and remains connected with the umbilical arteries and vein. That portion, on the contrary, which is included in the abdomen, does not close completely, but remains as a pointed fusiform sac, terminating near the umbilicus in the solid cord of the urachus, and still communicating at its base with the lower extremity of the intestinal canal. This fusiform sac (Fig. 252, *e*), becomes the *urinary bladder;* and in the fœtus at term, the bladder is still conical in form, its pointed extremity being attached, by means of the urachus, to the internal surface of the abdominal walls at the situation of the umbilicus. Afterward, the bladder loses this conical form, and its fundus in the adult becomes rounded and bulging.

The urinary bladder, as it appears from the above description, at first communicates freely with the intestinal cavity. The intestine, in fact, terminates, at this time, in a wide passage, or *cloaca*, at its lower extremity, which serves as a common outlet for the urinary and intestinal passages. Subsequently, however, a horizontal partition makes its appearance just above the point of junction between the bladder and rectum, and grows downward and forward in such a manner as to divide the above-mentioned cloaca into two parallel and unequal passages. The anterior or smaller of these passages becomes the urethra, the posterior or larger becomes the rectum; and the lower edge of the septum between them becomes finally united with the skin, forming, at its most superficial part, a tolerably wide band of integument, the *perineum*, which intervenes between the anus and the external portion of the urethra.

The *contents of the intestine*, which accumulate during fœtal life, vary in different parts of the alimentary canal. In the small intes-

tine they are semifluid or gelatinous in consistency, of a light yellowish or grayish-white color in the duodenum, becoming yellow reddish-brown and greenish-brown below. In the large intestine they are of a dark greenish hue, and pasty in consistency; and the contents of this portion of the alimentary canal have received the name of *meconium*, from their resemblance to inspissated poppy-juice. The meconium contains a large quantity of fat, as well as various insoluble substances, probably the residue of epithelial and mucous accumulations. It does not contain, however, any trace of the biliary substances (tauro-cholates and glyko-cholates) when carefully examined by Pettenkofer's test; and cannot therefore properly be regarded, as is sometimes incorrectly asserted, as resulting from the accumulation of bile. In the contents of the small intestine, on the contrary, traces of bile may be found, according to Lehmann,[1] so early as between the fifth and sixth months. We have also found distinct traces of bile in the small intestine at birth, but it is even then in extremely small quantity, and is sometimes altogether absent.

The meconium, therefore, and the intestinal contents generally, are not composed principally, or even to any appreciable extent, of the secretions of the liver. They appear rather to be produced by the mucous membrane of the intestine itself. Even their yellowish and greenish color does not depend on the presence of bile, since the yellow color first shows itself, in very young fœtuses, about the middle of the small intestine, and not at its upper extremity. The material which accumulates afterward appears to extend from this point upward and downward, gradually filling the intestine, and becoming, in the ileum and large intestine, darker and more pasty as gestation advances.

It is a singular fact, perhaps of some importance in this connection, that the amniotic fluid, during the latter half of fœtal life, finds its way, in greater or less abundance, into the stomach, and through that into the intestinal canal. Small cheesy-looking masses may sometimes be found at birth in the fluid contained in the stomach, which are seen on microscopic examination to be no other than portions of the vernix caseosa exfoliated from the skin into the amniotic cavity, and afterward swallowed. According to Köl-liker,[2] the soft downy hairs of the fœtus, exfoliated from the skin,

[1] Physiological Chemistry, Philadelphia edition, vol. i. p. 532.

[2] Gewebelehre. Leipzig, 1852, p. 139.

are often swallowed in the same way, and may be found in the meconium.

The *gastric juice* is not secreted before birth; the contents of the stomach being generally in small quantity, clear, nearly colorless, and neutral or alkaline in reaction.

The *liver* is developed at a very early period. Its size in proportion to that of the entire body is, in fact, very much greater in the early months than at birth or in the adult condition. In the fœtal pig we have found the relative size of the liver greatest within the first month, when it amounts to very nearly 12 per cent. of the entire weight of the body. Afterward, as it grows less rapidly than other parts, its relative weight diminishes successively to 10 per cent. and 6 per cent.; and is reduced before birth to 3 or 4 per cent. In the human subject, also, the weight of the liver at birth is between 3 and 4 per cent. of that of the entire body.

The secretion of *bile* takes place, as we have intimated above, during fœtal life, in a very scanty manner. We have found it, in minute quantity, in the gall-bladder, as well as in the small intestine at birth; but it does not probably take any active part in the nutritive or other functions of the fœtus before that period.

The *glycogenic function* of the liver commences during fœtal life, and at birth the tissue of the organ is abundantly saccharine. It is remarkable, however, that in the early periods of gestation sugar is produced in the fœtus from other sources than the liver. In very young fœtuses of the pig, for example, both the allantoic and amniotic fluids are saccharine, a considerable time before any sugar makes its appearance in the tissue of the liver. Even the urine, in half-grown fœtal pigs, contains an appreciable quantity of sugar, and the young animal is therefore, at this period, in a diabetic condition. This sugar, however, disappears from the urine before birth, and also from the amniotic fluid, as has been ascertained by M. Bernard;[1] while the liver begins to produce a saccharine substance, and to exercise the glycogenic function, which it continues after birth.

Development of the Pharynx, Œsophagus, &c.—We have already seen that the intestinal canal consists at first of a cylindrical tube terminated at each extremity of the abdominal cavity by a rounded cul-de-sac (Fig. 252, *c*, *c*); and that the openings of the mouth and anus are subsequently formed by perforations which take place through the integument and the intervening tissues, and so estab-

[1] Leçons de Physiologie Expérimentale, Paris, 1855, p. 398

lish a communication with the intestinal tube. The formation of the anterior perforation, and its appendages, takes place in the following manner:—

After the early development of the intestinal tube in the mode above described, the head increases in size out of all proportion to the remainder of the fœtus, projecting as a large rounded mass from the anterior extremity of the body, and containing the brain and the organs of special sense. This portion soon bends over toward the abdomen, in consequence of the increasing curvature of the whole body which takes place at this time. In the interior of this cephalic mass there is now formed a large cavity (Fig. 252, *d*), by the melting down and liquefaction of a portion of its substance. This cavity is the *pharynx*. It corresponds by its anterior extremity to the future situation of the mouth; and by its posterior portion to the upper end of the intestinal canal, the future situation of the stomach. It is still, however, closed on all sides, and does not as yet communicate either with the exterior or with the cavity of the stomach. There is, accordingly, at this time, no thorax whatever; but the stomach lies at the upper extremity of the abdomen, immediately beneath the lower extremity of the pharynx, from which it is separated by a wall of intervening tissue.

Subsequently, a perforation takes place between the adjacent extremities of the pharynx and stomach, by a short narrow tube, the situation of which is marked by the dotted lines *x*, in Fig. 241. This tube afterward lengthens by the rapid growth of that portion of the body in which it is contained, and becomes the *œsophagus*. Neither the pharynx nor œsophagus, therefore, are, properly speaking, parts of the intestinal canal, formed from the internal layer of the blastodermic membrane; but are, on the contrary, formations of the external layer, from which the entire cephalic mass is produced. The lining membrane of the pharynx and œsophagus is to be regarded, also, for the same reason, as rather a continuation of the integument than of the intestinal mucous membrane; and even in the adult, the thick, whitish, and opaque pavement epithelium of the œsophagus may be seen to terminate abruptly, by a well-defined line of demarkation, at the cardiac orifice of the stomach: beyond which, throughout the remainder of the alimentary canal. the epithelium is of the columnar variety, and easily distinguishable by its soft, ruddy, and transparent appearance.

As the œsophagus lengthens, the lungs are developed on each side of it by a protrusion from the pharynx which extends and

becomes repeatedly subdivided, forming the bronchial tubes and their ramifications. At first, the lungs project into the upper part of the abdominal cavity; for there is still no distinction between the chest and abdomen. Afterward, a horizontal partition begins to form on each side, at the level of the base of the lungs, which gradually closes together at a central point, so as to form the diaphragm, and finally shuts off altogether the cavity of the chest from that of the abdomen. Before the closure of the diaphragm, thus formed, is complete, a circular opening exists on each side the median line, by which the peritoneal and pleural cavities communicate with each other. In some instances the development of the diaphragm is arrested at this point, either on one side or the other, and the opening accordingly remains permanent. The abdominal organs then partially protrude into the cavity of the chest on that side, forming *congenital diaphragmatic hernia.* The lung on the affected side also usually remains in a state of imperfect development. Diaphragmatic hernia of this character is more frequently found upon the left side than upon the right. It may sometimes continue until adult life without causing any serious inconvenience.

The *heart* is formed, at a very early period, directly in front of the situation of the œsophagus. Its size soon becomes very large in proportion to the rest of the body; so that it protrudes beyond the level of the thoracic parietes, covered only by the pericardium. Subsequently, the walls of the thorax, becoming more rapidly developed, grow over it and inclose it. In certain instances, however, they fail to do so, and the heart then remains partially or completely uncovered, in front of the chest, presenting the condition known as *ectopia cordis.* This malformation is necessarily fatal.

Development of the Face.—While the lower extremity of the pharynx communicates with the cavity of the stomach, as above described, its upper extremity also becomes perforated in a similar manner, and establishes a communication with the exterior. This perforation is at first wide and gaping. It afterward becomes divided into the mouth and nasal passages; and the different parts of the face are formed round it in the following manner:—

From the sides of the cephalic mass five buds or processes shoot out, and grow toward each other, so as to approach the centre of the oral orifice above mentioned. (Fig. 254.) One of them grows directly downward from the frontal region and is called the frontal or intermaxillary process because it afterward contains in

its lower extremity the intermaxillary bones, in which the incisor teeth of the upper jaw are inserted. The next process originates from the side of the opening, and, advancing toward the median line, forms, with its fellow of the opposite side, the superior maxilla. The processes of the remaining pair also grow from the side, and form, by their subsequent union upon the median line, the inferior maxilla. The inferior maxillary bone is finally consolidated, in man, into a single piece, but remains permanently divided, in the lower animals, by a suture upon the median line.

Fig. 254.

HUMAN EMBRYO, about one month old: showing the growth of the frontal process downward, and that of the superior and inferior maxillary processes from the side; also the lateral situation of the eye. From a specimen in the author's possession.

As the frontal process grows from above downward, it becomes double at its lower extremity, and at the same time two offshoots show themselves upon its sides which curl round and enclose two circular orifices, the opening of the anterior nares; the offshoots themselves becoming the alæ nasi. (Fig. 255.) The mouth at this period is very widely open, owing to the imperfect development of the upper and lower jaw, and the incomplete formation of the lips and cheeks.

Fig. 255.

HEAD OF HUMAN EMBRYO at about the sixth week. From a specimen in the author's possession.

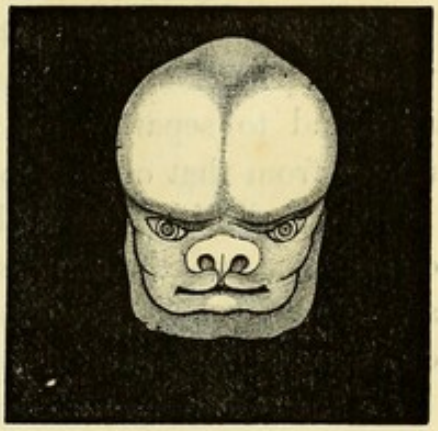
The processes of the superior maxilla continue their growth, but less rapidly than those of the inferior; so that the two sides of the lower jaw are already consolidated with each other, while those of the upper jaw are still separate.

As the processes of the superior maxilla continue to enlarge, they also tend to unite with each other on the median line, but are prevented from doing so by the intermaxillary processes which grow down between them. They then unite with the intermaxillary processes, which have at the same time united with each other, and the upper jaw and lip are thus completed. (Fig. 256.) The external edge of the ala nasi also adheres to the superior maxillary process and unites with it, leaving only a curved crease

or furrow, as a sort of cicatrix, to mark the line of union between them.

Sometimes the superior maxillary and the intermaxillary processes fail to unite with each other; and we then have the malformation known as *hare-lip*. The fissure of hare-lip, consequently, as a general rule, is not situated exactly in the median line, but a little to one side of it, on the external edge of the intermaxillary process. Occasionally, the same deficiency exists on both sides, producing "double hare-lip;" in which case, if the fissures extend through the bony structures, the central piece of the superior maxilla, which is detached from the remainder, contains the four upper incisor teeth, and corresponds with the intermaxillary bone of the lower animals. In some rare instances the fissure of hare-lip is situated in the median line, the two intermaxillary bones never having united with each other. A case of this kind has been observed by Prof. Jeffries Wyman.[1]

Fig. 256.



HEAD OF HUMAN EMBRYO, about the end of the second month.—From a specimen in the author's possession.

The eyes at an early period are situated laterally, each on one side of the head. (Fig. 254.) As development proceeds, they come to be situated farther forward (Fig. 255), their axes being divergent and directed obliquely forward and outward. At a later period still they are placed on the anterior plane of the face (Fig. 256), and have their axes nearly parallel and looking directly forward. This change in the situation of the eyes is effected by the more rapid growth of the posterior and lateral parts of the head, which enlarge in such a manner as to alter the relative position of the parts seated in front of them.

The palate is formed by a septum between the mouth and nares, which arises on each side as a horizontal plate or offshoot from the superior maxilla. These two plates afterward unite with each other upon the median line, forming a complete partition between the oral and nasal cavities. The right and left nasal passages are also separated from each other by a vertical plate (vomer), which grows from above downward and fuses with the palatal plates be-

[1] Transactions Boston Society for Medical Improvement, March 9th, 1863.

low. *Fissure of the palate* is caused by a deficiency, more or less complete, of one of the horizontal maxillary plates. It is accordingly situated a little on one side of the median line, and is frequently associated with hare-lip and fissure of the upper jaw. The fissures of the palate and of the lip are very often continuous with each other.

The anterior and posterior pillars of the fauces are incomplete vertical partitions, which grow from the sides of the oral cavity, and tend to separate, by a slight constriction, the cavity of the mouth from that of the pharynx.

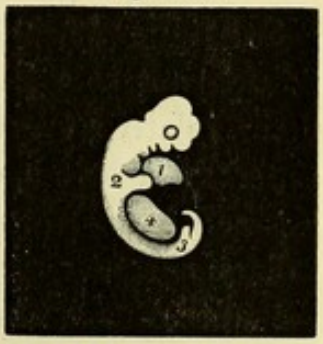
When all the above changes are accomplished, the pharynx, œsophagus, mouth, nares, and fauces, with their various projections and divisions, have been successively formed; and the development of the upper part of the alimentary canal is then complete.

CHAPTER XVI.

DEVELOPMENT OF THE KIDNEYS, WOLFFIAN BODIES, AND INTERNAL ORGANS OF GENERATION.

THE first trace of a urinary apparatus in the embryo, consists of two long, fusiform bodies, which make their appearance in the abdomen at a very early period, situated on each side the spinal column. These are known by the name of the *Wolffian bodies.* They are fully formed in the human subject, toward the end of the first month (Coste), at which time they are the largest organs in the cavity of the abdomen, extending from just below the heart, nearly to the posterior extremity of the body. In the fœtal pig, when a little over half an inch in length (Fig. 257), the Wolffian bodies are rounded and kidney-shaped, and occupy a very large part of the abdominal cavity. Their importance may be estimated from the fact that their weight at this time is equal to a little over $\frac{1}{3}\frac{1}{2}$ of that of the entire body—a proportion which is seven or eight times as large as that of the kidneys in the adult condition. There are, indeed, at this period only three organs perceptible in the abdomen, viz., the liver, which has begun to be formed at the upper part of the abdominal cavity; the intestine, which is already somewhat convoluted, and occupies its central portion; and the Wolffian bodies, which project on each side the spinal column.

Fig. 257.



FŒTAL PIG, ⅝ of an inch long; from a specimen in the author's possession. 1. Heart. 2. Anterior extremity. 3. Posterior extremity. 4. Wolffian body. The abdominal walls have been cut away, in order to show the position of the Wolffian bodies.

The Wolffian bodies, in their intimate structure, closely resemble the adult kidney. They consist of secreting tubules, lined with epithelium, which run from the outer toward the inner edge of the organ, terminating at their free ex-

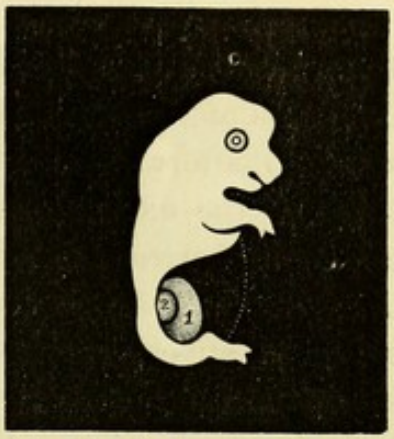
tremities in small rounded dilatations. Into each of these dilated extremities is received a globular coil of capillary bloodvessels, or *glomerulus*, similar to that of the adult kidney. The tubules of the Wolffian body all empty into a common excretory duct, which leaves the organ at its lower extremity, and communicates afterward with the lower part of the intestinal canal, just at the point where the diverticulum of the allantois is given off, and where the urinary bladder is afterward to be situated. The principal, if not the only distinction in minute structure, between the Wolffian bodies and the true kidneys, consists in the size of the tubules and of their glomeruli; these elements being considerably larger in the Wolffian body than in the kidney. In the fœtal pig, for example, when about an inch and a half in length, the diameter of the tubules of the Wolffian body is $\frac{1}{200}$ of an inch, while in the kidney of the same fœtus, the diameter of the tubules is only $\frac{1}{725}$ of an inch. The glomeruli in the Wolffian bodies measure $\frac{1}{45}$ of an inch in diameter, while those of the kidney measure only $\frac{1}{180}$ of an inch. The Wolffian bodies are therefore urinary organs, so far as regards their anatomical structure, and are sometimes known, accordingly, by the name of the "false kidneys." There is little doubt that they perform, at this early period, a function analogous to that of the kidneys, and separate from the blood of the embryo an excrementitious fluid which is discharged by the ducts of the organ into the cavity of the allantois.

Subsequently, the Wolffian bodies increase for a time in size, though not so rapidly as the rest of the body; and consequently their relative magnitude diminishes. Still later, they begin to suffer an absolute diminution or atrophy, and become gradually less and less perceptible. In the human subject, they are hardly to be detected after the end of the second month (Longet), and in the quadrupeds also they completely disappear long before birth. They are consequently fœtal organs, destined to play an important part during a certain stage of development, but to become afterward atrophied and absorbed, as the physiological condition of the fœtus alters. During the period, however, of their retrogression and atrophy, other organs appear in their neighborhood, which become afterward permanently developed. These are, first, the kidneys, and secondly, the internal organs of generation.

The *kidneys* are formed just behind the Wolffian bodies, and are at first entirely concealed by them in a front view, the kidneys being at this time not more than a fourth or a fifth part the size of

the Wolffian bodies. (Fig. 258.) As the kidneys, however, subsequently enlarge, while the Wolffian bodies diminish, the proportion existing between the two organs is reversed; and the Wolffian bodies at last come to be mere small rounded or ovoid masses, situated on the anterior surface of the kidneys. (Figs. 259 and 260.) The kidneys, during this period, grow more rapidly in an upward than in a downward direction, so that the Wolffian bodies come to be situated near their inferior extremity, and seem to have performed a sliding movement from above downward, over their anterior surface. This apparent sliding movement, or descent of the Wolffian bodies, is owing to the rapid growth of the kidneys in an upward direction, as we have already explained.

Fig. 258.



FŒTAL PIG, one and a half inches long. From a specimen in the author's possession.—1. Wolffian body. 2. Kidney.

The kidneys, during the succeeding periods of fœtal life, become in their turn very largely developed in proportion to the rest of the organs; attaining a size, in the fœtal pig, equal to $\frac{1}{14}$ (in weight) of the entire body. This proportion, however, diminishes again very considerably before birth, owing to the increased development of other parts. In the human fœtus at birth, the weight of the two kidneys taken together is $\frac{1}{166}$ that of the entire body.

Fig. 259.

INTERNAL ORGANS OF GENERATION, &c.; in a fœtal pig three inches long. From a specimen in the author's possession.—1, 1. Kidneys. 2, 2. Wolffian bodies. 3, 3. Internal organs of generation; testicles or ovaries. 4. Urinary bladder turned over in front. 5. Intestine.

Internal Organs of Generation. — About the same time that the kidneys are formed behind the Wolffian bodies, two oval-shaped organs make their appearance in front, on the inner side of the Wolffian bodies and between them and the spinal column. These bodies are the internal organs of generation; viz., the testicles in the male, and the ovaries in the female. At first they occupy precisely the same situation and present precisely the same appearance, whether the fœtus is afterward to belong to the male or the female sex. (Fig. 259.)

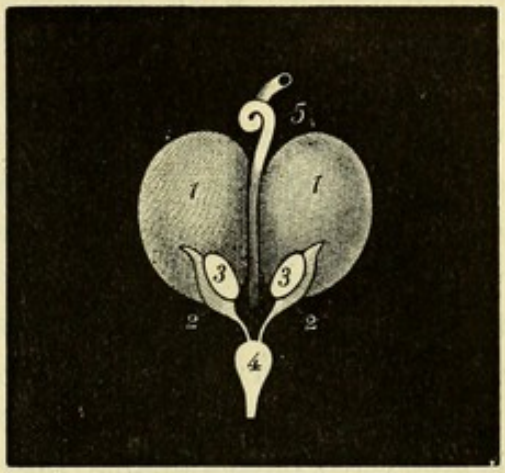
A short distance above the internal organs of generation there commences, on each side, a narrow tube or duct, which runs from above downward along the anterior border of the Wolffian body, immediately in front of and parallel with the excretory duct of this organ. The two tubes, right and left, then approach each other below; and, joining upon the median line, empty, together with the ducts of the Wolffian bodies, into the base of the allantois, or what will afterward be the base of the urinary bladder. These tubes serve as the excretory ducts of the internal organs of generation; and will afterward become the *vasa deferentia* in the male, and the *Fallopian tubes* in the female. According to Coste, the vasa deferentia at an early period are disconnected with the testicles; and originate, like the Fallopian tubes, by free extremities, presenting each an open orifice. It is only afterward, according to the same author, that the vasa deferentia become adherent to the testicles, and a communication is established between them and the tubuli seminiferi. In the female, the Fallopian tubes remain permanently disconnected with the ovaries, except by the edge of the fimbriated extremity; which in many of the lower animals becomes closely adherent to the ovary, and envelopes it more or less completely.

Male Organs of Generation; Descent of the Testicles.—In the male fœtus there now commences a movement of translation, or change of place, in the internal organs of generation, which is known as the "descent of the testicles." In consequence of this movement, the above organs, which are at first placed near the middle of the abdomen, and directly in front of the kidneys, come at last to be situated in the scrotum, altogether outside and below the abdominal cavity. They also become inclosed in a distinct serous sac of their own, the tunica vaginalis testis. This apparent movement of the testicles is accomplished in the same manner as that of the Wolffian bodies, above mentioned, viz., by a disproportionate growth of the middle and upper portions of the abdomen and of the organs situated above the testicles, so that the relative position of these organs becomes altered. The descent of the testicles is accompanied by certain other alterations in the organs themselves and their appendages, which take place in the following manner.

By the upward enlargement of the kidneys, both the Wolffian bodies and the testicles are soon found to be situated near the lower extremity of these organs. (Fig. 260.) At the same time, a slender rounded cord (not represented in the figure) passes from the lower extremity of each testicle in an outward and downward

direction, crossing the corresponding vas deferens a short distance above its union with its fellow of the opposite side. Below this point, the cord spoken of continues to run obliquely outward and downward; and, passing through the abdominal walls at the situation of the inguinal canal, is inserted into the subcutaneous tissue near the symphysis pubis. The lower part of this cord becomes the *gubernaculum testis;* and muscular fibres are soon developed in its substance which may be easily detected, even in the human fœtus, during the latter half of gestation. At the period of birth, however, or soon afterward, these muscular fibres disappear and can no longer be recognized.

Fig. 260.



INTERNAL ORGANS OF GENERATION, &c., in a fœtal pig nearly four inches long. From a specimen in the author's possession.—1, 1. Kidneys. 2, 2. Wolffian bodies. 3, 3. Testicles. 4. Urinary bladder. 5. Intestine.

All that portion of the excretory tube of the testicle which is situated outside the crossing of the gubernaculum, is destined to become afterward convoluted, and converted into the *epididymis.* That portion which is situated inside the same point remains comparatively straight, but becomes considerably elongated, and is finally known as the *vas deferens.*

As the testicles descend still farther in the abdomen, they continue to grow, while the Wolffian bodies, on the contrary, diminish rapidly in size, until the latter become much smaller than the testicles; and at last, when the testicles have arrived at the internal inguinal ring, the Wolffian bodies have altogether disappeared, or at least have become so much altered that their characters are no longer recognizable. In the human fœtus, the testicles arrive at the internal inguinal ring, about the termination of the sixth month (Wilson).

During the succeeding month, a protrusion of the peritoneum takes place through the inguinal canal, in advance of the testicle; while the last named organ still continues its descent. As it then passes downward into the scrotum, certain muscular fibres are given off from the lower border of the internal oblique muscle of the abdomen, growing downward with the testicle, in such a manner as to form a series of loops upon it, and upon the elongating spermatic cord. These loops constitute afterward the *cremaster muscle.*

At last, the testicles descend fairly to the bottom of the scrotum, the gubernaculum constantly shortening, and the vas deferens elongating as it proceeds. The convoluted portion of the efferent duct, viz., the epididymis, then remains closely attached to the body of the testicle; while the vas deferens passes upward, in a reverse direction, enters the abdomen through the inguinal canal, again bends downward, and joins its fellow of the opposite side; after which they both open into the prostatic portion of the urethra by distinct orifices, situated on each side the median line. At the same time, two diverticula arise from the median portion of the vasa deferentia, and, elongating in a backward direction, underneath the base of the bladder, become developed into two compound sacculated reservoirs—the *vesiculæ seminales*.

The left testicle is a little later in its descent than the right, but it afterward passes farther into the scrotum, and, in the adult condition, usually hangs a little lower than its fellow of the opposite side.

After the testicle has fairly passed into the scrotum, the serous pouch, which preceded its descent, remains for a time in communication with the peritoneal cavity. In many of the lower animals, as, for example, the rabbit, this condition is permanent; and the testicle, even in the adult animal, may be alternately drawn downward into the scrotum, or retracted into the abdomen, by the action of the gubernaculum and the cremaster muscle. But in the human fœtus, the two opposite surfaces of the peritoneal pouch, covering the testicle, approach each other at the inguinal canal, forming at that point a constriction or neck, which partly shuts off the testicle from the cavity of the abdomen. By a continuation of this process, the serous surfaces come actually in contact with each other, and, adhering together at this situation (Fig. 261, 4), form a kind of cicatrix, or umbilicus, by the complete closure and consolidation of which the cavity of the tunica vaginalis (2) is finally shut off altogether from the general cavity of the peritoneum (3). The tunica vaginalis testis is, therefore, originally a part of the peritoneum, from which it is subsequently separated by the process just described.

Fig. 261.

Formation of TUNICA VAGINALIS TESTIS.—1. Testicle nearly at the bottom of the scrotum. 2 Cavity of tunica vaginalis. 3. Cavity of peritoneum. 4. Obliterated neck of peritoneal sac.

The separation of the tunica vaginalis from the peritoneum is usually completed in the human subject before birth. But sometimes it fails to take place at the proper time, and the intestine is then apt to protrude into the scrotum, in front of the spermatic cord, giving rise, in this way, to a *congenital inguinal hernia.* (Fig. 262.) The parts implicated, however, in this malformation, have still, as in the case of congenital umbilical hernia, a tendency to unite with each other and obliterate the unnatural opening; and if the intestine be retained by pressure in the cavity of the abdomen, cicatrization usually takes place at the inguinal canal, and a cure is effected.

Fig. 262.

Congenital Inguinal Hernia.—1. Testicle. 2, 2, 2. Intestine.

The descent of the testicle, above described, is not accomplished by the forcible traction of the muscular fibres of the gubernaculum, as has been described by certain writers, but by a simple process of growth taking place in different parts, in different directions, at successive periods of fœtal life. The gubernaculum, accordingly, has no proper function as a muscular organ, in the human subject, but is merely the anatomical vestige, or analogue, of a corresponding muscle in certain of the lower animals, where it has really an important function to perform. For in them, as we have already mentioned, both the gubernaculum and the cremaster remain fully developed in the adult condition, and are then employed to elevate and depress the testicle, by the alternate contraction of their muscular fibres.

Female Organs of Generation.—At an early period, as we have mentioned above, the ovaries have the same external appearance, and occupy the same position in the abdomen, as the testicles in the opposite sex. The descent of the ovaries also takes place, to a great extent, in the same manner with the descent of the testicles. When, in the early part of this descent, they have reached the level of the lower edge of the kidneys, a cord, analogous to the gubernaculum, may be seen proceeding from their lower extremity, crossing the efferent duct on each side, and passing downward, to be attached to the subcutaneous tissues at the situation of the inguinal ring. That part of the duct situated outside the crossing of this cord, becomes afterward convoluted, and is converted into the *Fallopian*

tube; while that point which is inside the same point, becomes converted into the *uterus.* The upper portion of the cord itself becomes the *ligament of the ovary;* its lower portion, the *round ligament of the uterus.*

As the ovaries continue their descent, they pass below and behind the Fallopian tubes, which necessarily perform at the same time a movement of rotation, from before backward and from above downward; the whole, together with the ligaments of the ovaries and the round ligaments, being enveloped in double folds of peritoneum, which enlarge with the growth of the parts themselves, and constitute finally the *broad ligaments of the uterus.*

It will be seen from what has been said above, that the situation occupied by the Wolffian bodies in the female is always the space between the ovaries and the Fallopian tubes; for the Wolffian bodies accompany the ovaries in their descent, just as, in the male, they accompany the testicles. As these bodies now become gradually atrophied, their glandular structure disappears altogether; but their bloodvessels, in many instances, remain as a convoluted vascular plexus, occupying the situation above mentioned. The Wolffian bodies may therefore be said, in these instances, to undergo a kind of vascular degeneration. This peculiar degeneration is quite evident in the Wolffian bodies of the fœtal pig, some time before the organs have entirely lost their original form. In the cow, a collection of convoluted bloodvessels may be seen, even in the adult condition, near the edge of the ovary, and between the two folds of peritoneum forming the broad ligament. These are undoubtedly vestiges of the Wolffian bodies, which have undergone the vascular degeneration above described.

While the above changes are taking place in the adjacent organs, the two lateral halves of the uterus fuse with each other more and more upon the median line, and become covered with an excessively developed layer of muscular fibres. In the lower animals, the uterus remains divided at its upper portion, running out into two long conical tubes or cornua (Fig. 192), presenting the form known as the *uterus bicornis.* In the human subject, however, the fusion of the two lateral halves of the organ is nearly complete; so that the uterus presents externally a rounded, but somewhat flattened and triangular figure (Fig. 193), with the ligaments of the ovary and the round ligaments passing off from its superior angles. But, internally, the cavity of the organ still presents a strongly marked triangular form, the vestige of its original division.

Occasionally the human uterus, even in the adult condition, remains divided into two lateral portions by a vertical septum, which runs from the middle of its fundus downward toward the os internum. This septum may even be accompanied by a partial external division of the organ, corresponding with it in direction and producing the malformation known as "uterus bicornis," or "double uterus."

The os internum and os externum are produced by partial constrictions of the original generative passage; and the anatomical distinctions between the body of the uterus, the cervix and the vagina, are produced by the different development of the mucous membrane and muscular tunic in its corresponding portions. During fœtal life, however, the neck of the uterus grows much faster than its body; so that, at the period of birth, the entire organ is very far from presenting the form which it exhibits in the adult condition. In the human fœtus at term, the cervix uteri constitutes nearly two-thirds of the entire length of the organ; while the body forms but little over one-third. The cervix, at this time, is also much larger in diameter than the body; so that the whole organ presents a tapering form from below upward. The arbor vitæ uterina of the cervix is at birth very fully developed, and the mucous membrane of the body is also thrown into three or four folds which radiate upward from the os internum. The cavity of the cervix is filled with a transparent semi-solid mucus.

The position of the uterus at birth is also different from that which it assumes in adult life; nearly the entire length of the organ being above the level of the symphysis pubis, and its inferior extremity passing below that point only by about a quarter of an inch. It is also slightly anteflexed at the junction of the body and cervix. After birth, the uterus, together with its appendages, continues to descend; until, at the period of puberty, its fundus is situated just below the level of the symphysis pubis.

The *ovaries* at birth are narrow and elongated in form. They contain at this time an abundance of eggs; each inclosed in a Graafian follicle, and averaging $\frac{1}{125}$ of an inch in diameter. The vitellus, however, is imperfectly formed in most of them, and in some is hardly to be distinguished. The Graafian follicle at this period envelops each egg closely, there being no fluid between its internal surface and the exterior of the egg, but only the thin layer of cells forming the "membrana granulosa." Inside this

layer is to be seen the germinative vesicle, with the germinative spot, surrounded by a faintly granular vitellus, more or less abundant in different parts. Some of the Graafian follicles containing eggs are as large as $\frac{1}{150}$ of an inch; others as small as $\frac{1}{1055}$. In the very smallest, the cells of the membrana granulosa appear to fill entirely the cavity of the follicle, and no vitellus or germinative vesicle is to be seen.

CHAPTER XVII.

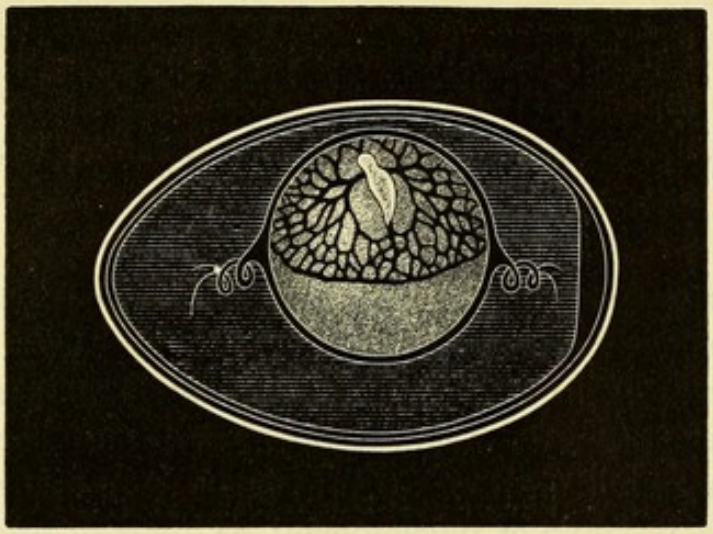
DEVELOPMENT OF THE CIRCULATORY APPARATUS.

THERE are three distinct forms or phases of development assumed by the circulatory system during different periods of life. These different forms of the circulation are intimately connected with the manner in which nutrition and respiration, or the renovation of the blood, are accomplished at different epochs; and they follow each other in the progress of development, as different organs are employed in turn to accomplish the above functions. The first form is that of the *vitelline circulation*, which exists at a period when the vitellus, or the umbilical vesicle, is the sole source of nutrition for the fœtus. The second is the *placental circulation*, which lasts through the greater part of fœtal life, and is characterized by the existence of the placenta; and the third is the complete or *adult circulation*, in which the renovation and nutrition of the blood are provided for by the lungs and the intestinal canal.

First, or Vitelline Circulation.—It has already been shown, in a previous chapter, that when the body of the embryo has begun to be formed in the centre of the blastodermic membrane, a number of bloodvessels shoot out from its sides, and ramify over the remainder of the vitelline sac, forming, by their inosculation, an abundant vascular plexus. The area occupied by this plexus in the blastodermic membrane around the fœtus is, as we have seen, the "area vasculosa." In the egg of the fowl (Fig. 263), the plexus is limited, on its external border, by a terminal vein or sinus—the "sinus terminalis;" and the blood of the embryo, after circulating through the capillaries of the plexus, returns by several venous branches, the two largest of which enter the body near its anterior and posterior extremities. The area vasculosa is, accordingly, a vascular appendage to the circulatory apparatus of the embryo, spread out over the surface of the vitellus for the purpose of absorbing from it the nutritious material requisite for the growth of the

newly-formed tissues. In the egg of the fish (Fig. 264), the principal vein is seen passing up in front underneath the head; while the arteries emerge all along the lateral edges of the body. The entire

Fig. 263.



Egg of Fowl in process of development, showing area vasculosa, with vitelline circulation, terminal sinus, &c.

vitellus, in this way, becomes covered with an abundant vascular network, connected with the internal circulation of the fœtus by arteries and veins.

Very soon, as the embryo and the entire egg increase in size, there are two arteries and two veins which become larger than the others, and which subsequently do the whole work of conveying the blood of the fœtus to and from the area vasculosa. These two arteries emerge from the lateral edges of the fœtus, on the right and left sides; while the two veins re-enter at about the same point, and nearly parallel with them. These four vessels are then termed the *omphalo-mesenteric arteries and veins*.

Fig. 264.

Egg of Fish (Jarrabacca), showing vitelline circulation.

The arrangement of the circulatory apparatus in the interior of the body of the fœtus, at this time, is as follows: The heart is situated at the median line, just beneath the head and in front of the œsophagus. It receives at its lower extremity the trunks of the two omphalo-mesenteric veins, and at its upper extremity divides into two vessels, which, arching over backward, attain the anterior surface of the vertebral column, and then run from above downward along the spine, quite to the posterior

extremity of the fœtus. These arteries are called the *vertebral arteries*, on account of their course and situation, running parallel with the vertebral column. They give off, throughout their course, many small lateral branches, which supply the body of the fœtus, and also two larger branches—the omphalo-mesenteric arteries—which pass out, as above described, into the area vasculosa. The two vertebral arteries remain separate in the upper part of the body, but soon fuse with each other a little below the level of the heart; so that, below this point, there remains afterward but one large artery, the abdominal aorta, running from above downward along the median line, giving off the omphalo-mesenteric arteries to the area vasculosa, and supplying smaller branches to the body, the walls of the intestine, and the other organs of the fœtus.

The above description shows the origin and formation of the first or vitelline circulation. A change, however, now begins to take place, by which the vitellus is superseded, as an organ of nutrition, by the placenta, which takes its place; and the second or *placental* circulation becomes established in the following manner:—

Second Circulation.—After the umbilical vesicle has been formed by the process already described, a part of the vitellus remains included in it, while the rest is retained in the abdomen and inclosed in the intestinal canal. As these two organs (umbilical vesicle and intestine) are originally parts of the same vitelline sac, they remain supplied by the same vascular system, viz: the omphalo-mesenteric vessels. Those which remain within the abdomen of the fœtus supply the mesentery and intestine; but the larger trunks pass outward, and ramify upon the walls of the umbilical vesicle. (Fig. 265.) At first, there are, as we have mentioned above, two omphalo-mesenteric arteries emerging from the body, and two omphalo-mesenteric veins returning to it; but soon afterward, the two arteries are replaced by a common trunk, while a similar change takes place in the two veins. Subsequently, therefore, there remains but a single artery and a

Fig. 265.

Diagram of YOUNG EMBRYO AND ITS VESSELS, showing circulation of umbilical vesicle, and also that of allantois, beginning to be formed.

single vein, connecting the internal and external portions of the vitelline circulation.

The vessels belonging to this system are therefore called the omphalo-mesenteric vessels, because a part of them (omphalic vessels) pass outward, by the umbilicus, or "omphalos," to the umbilical vesicle, while the remainder (mesenteric vessels) ramify upon the mesentery and the intestine.

At first, the circulation of the umbilical vesicle is more important than that of the intestine; and the omphalic artery and vein appear accordingly as large trunks, of which the mesenteric vessels are simply small branches. (Fig. 265.) Afterward, however, the intestine rapidly enlarges, while the umbilical vesicle diminishes, and the proportions existing between the two sets of vessels are therefore reversed. (Fig. 266.) The mesenteric vessels then

Fig. 266.

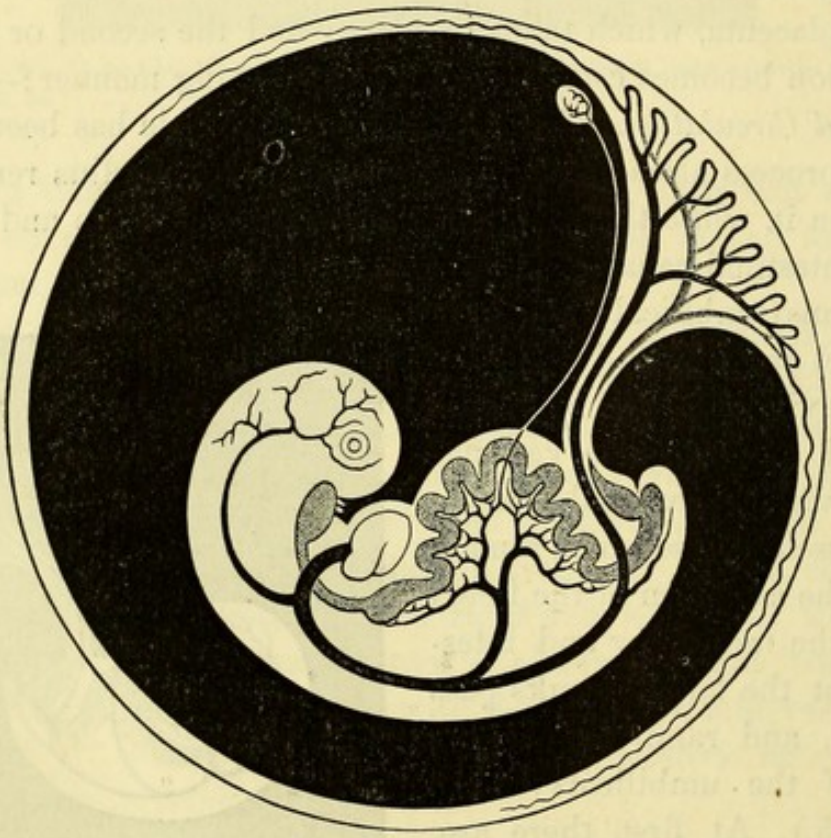


Diagram of EMBRYO AND ITS VESSELS; showing the second circulation. The pharynx, œsophagus, and intestinal canal, have become further developed, and the mesenteric arteries have enlarged, while the umbilical vesicle and its vascular branches are very much reduced in size. The large umbilical arteries are seen passing out to the placenta.

come to be the principal trunks, while the omphalic vessels are simply minute branches, running out along the slender cord of the umbilical vesicle, and ramifying in a few scanty twigs upon its surface.

In the mean time, the allantois is formed by a protrusion from the lower extremity of the intestine, which, carrying with it two arteries and two veins, passes out by the anterior opening of the body, and comes in contact with the external membrane of the egg. The arteries of the allantois, which are termed the *umbilical arteries,* are supplied by branches of the abdominal aorta; the umbilical veins, on the other hand, join the mesenteric veins, and empty with them into the venous extremity of the heart. As the umbilical vesicle diminishes, the allantois enlarges; and the latter soon becomes converted, in the human subject, into a vascular chorion, a part of which is devoted to the formation of the placenta. (Fig. 266.) As the placenta soon becomes the only source of nutrition for the fœtus, its vessels are at the same time very much increased in size, and preponderate over all the other parts of the circulatory system. During the early periods of the formation of the placenta, there are, as we have stated above, two umbilical arteries and two umbilical veins. But subsequently one of the veins disappears, and the whole of the blood is returned to the body of the fœtus by the other, which becomes enlarged in proportion. For a long time previous to birth, therefore, there are in the umbilical cord two umbilical arteries, and but a single umbilical vein.

Such is the second, or placental circulation. It is exchanged, at the period of birth, for the third or *adult* circulation, in which the blood which had previously circulated through the placenta, is diverted to the lungs and the intestine. These are the organs upon which the whole system afterward depends for the nourishment and renovation of the blood.

During the occurrence of the above changes, certain other alterations take place in the arterial and venous systems, which will now require to be described by themselves.

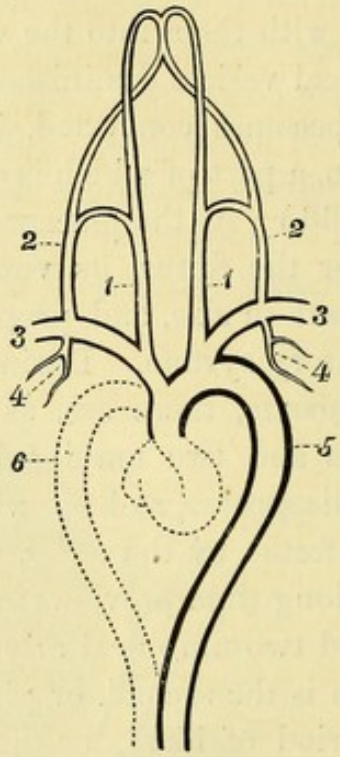
Development of the Arterial System.—At an early period of development, as we have shown above, the principal arteries pass off from the anterior extremity of the heart in two arches, which curve backward on each side, from the front of the body toward the vertebral column, after which they again become longitudinal in direction, and receive the name of "vertebral arteries." Very soon these arches divide successively into two, three, four, and five secondary arches, placed one above the other, along the sides of the neck. (Fig. 267.) These are termed the *cervical arches.* In the fish, these cervical arches remain permanent, and give off from their convex borders the branchial arteries, in the form of vascular tufts,

to the gills on each side of the neck; but in the human subject and the quadrupeds, the branchial tufts are never developed, and the cervical arches, as well as the trunks with which they are connected, become modified by the progress of development in the following manner:—

Fig. 267.

Early condition of ARTERIAL SYSTEM: showing the heart (1), with its two ascending arterial trunks, giving off on each side five cervical arches, which terminate in the vertebral arteries (2, 2). The vertebral arteries unite below the heart to form the aorta (3).

Fig. 268.



Adult condition of ARTERIAL SYSTEM.—1, 1. Carotids. 2, 2. Vertebrals. 3, 3. Right and left subclavians. 4, 4. Right and left superior intercostals. 5. Left aortic arch, which remains permanent. 6. Right aortic arch, which disappears.

The two ascending arterial trunks on the anterior part of the neck, from which the cervical arches are given off, become converted into the carotids. (Fig. 268, 1, 1.) The fifth, or uppermost cervical arch, remains at the base of the brain as the inosculation, through the circle of Willis, between the internal carotids and the basilar artery, which is produced by the union of the two vertebrals. The next, or fourth cervical arch, may be recognized in an inosculation which is said to be very constant between the superior thyroid arteries, branches of the carotids, and the inferior thyroids, which come from the subclavians at nearly the same point from which the vertebrals are given off. The next, or third cervical arch, remains on each side, as the subclavian artery (3, 3). This vessel,

though at first a mere branch of communication between the carotid and the vertebral, has now increased in size to such an extent that it has become the principal trunk, from which the vertebral itself is given off as a small branch. Immediately below this point of intersection, also, the vertebral artery diminishes very much in relative size, loses its connection with the abdominal aorta, and supplies only the first two intercostal spaces, under the name of the superior intercostal artery (4, 4). The second cervical arch becomes altered in a very different manner on the two opposite sides. On the left side, it becomes enormously enlarged, so as to give off, as secondary branches, all the other arterial trunks which have been described, and is converted in this manner into the *arch of the aorta* (5). On the right side, however, the corresponding arch (6) becomes smaller and smaller, and at last altogether disappears; so that, finally, we have only a single aortic arch, projecting to the left of the median line, and continuous with the thoracic and abdominal aorta.

The first cervical arch remains during fœtal life upon the left side, as the "ductus arteriosus," presently to be described. In the adult condition, however, it has disappeared equally upon the right and left sides. In this way the permanent condition of the arterial circulation is gradually established in the upper part of the body.

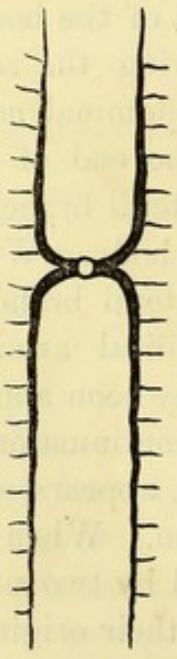
Corresponding changes take place, however, during the same time, in the lower part of the body. Here the abdominal aorta runs undivided, upon the median line, quite to the end of the spinal column; giving off on each side successive lateral branches, which supply the intestine and the parietes of the body. When the allantois begins to be developed, two of these lateral branches accompany it, and become, consequently, the umbilical arteries. These two vessels increase so rapidly in size, that they soon appear as divisions of the aortic trunk; while the original continuation of this trunk, running to the end of the spinal column, appears only as a small branch given off at the point of bifurcation. When the lower limbs begin to be developed, they are supplied by two small branches, given off from the umbilical arteries near their origin.

Up to this time the pelvis and posterior extremities are but slightly developed. Subsequently, however, they grow more rapidly, in proportion to the rest of the body, and the arteries which supply them increase in a corresponding manner. That portion of the umbilical arteries, lying between the bifurcation of the aorta and the origin of the branches going to the lower ex-

tremities, becomes the common iliacs, which in their turn afterward divide into the umbilical arteries proper, and the femorals. Subsequently, by the continued growth of the pelvis and lower extremities, the relative size of their vessels is still further increased; and at last the arterial system in this part of the body assumes the arrangement which belongs to the latter periods of gestation. The aorta divides, as before, into the two common iliacs. These also divide into the external iliacs, supplying the lower extremities, and the internal iliacs, supplying the pelvis; and this division is so placed that the umbilical or hypogastric arteries arise from the internal iliacs, of which they now appear to be secondary branches.

After the birth of the fœtus, and the separation of the placenta, the hypogastric arteries become partially atrophied, and are converted, in the adult condition, into solid, rounded cords, running upward toward the umbilicus. Their lower portion, however, remains pervious, and gives off arteries supplying the urinary bladder. The obliterated hypogastric arteries, therefore, the remnants of the original umbilical or allantoic arteries, run upward from the internal iliacs along the sides of the urinary bladder, which is the remnant of the original allantois itself. The terminal continuation of the original abdominal aorta, is the arteria sacra media, which, in the adult, runs downward on the anterior surface of the sacrum, supplying branches to the rectum and the anterior sacral nerves.

Fig. 269.



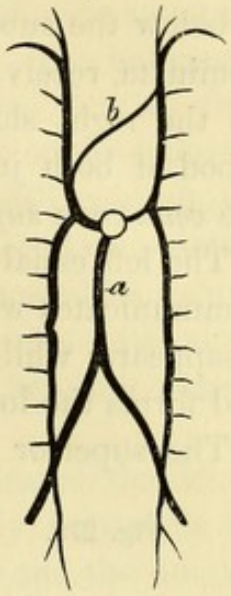
Early condition of Venous System; showing the vertebral veins emptying into the heart by two lateral trunks, the "canals of Cuvier."

Development of the Venous System.—According to the observations of M. Coste, the venous system at first presents the same simplicity and symmetry with the arterial. The principal veins of the body consist of two long venous trunks, the *vertebral veins* (Fig. 269), which run along the sides of the spinal column, parallel with the vertebral arteries. They receive in succession all the intercostal veins, and empty into the heart by two lateral trunks of equal size, the *canals of Cuvier*. When the inferior extremities become developed, their two veins, returning from below, join the vertebral veins near the posterior portion of the body; and, crossing them, afterward unite with each other, thus

constituting another vein of new formation (Fig. 270, *a*), which runs upward a little to the right of the median line, and empties by itself into the lower extremity of the heart. The two branches, by means of which the veins of the lower extremities thus unite, become afterward, by enlargement, the common iliac veins; while the single trunk (*a*) resulting from their union becomes the *vena cava inferior*. Subsequently, the vena cava inferior becomes very much larger than the vertebral veins; and its two branches of bifurcation are afterward represented by the two iliacs.

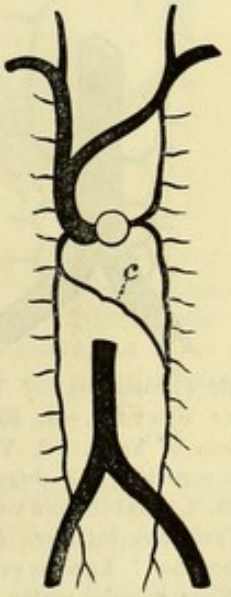
Above the level of the heart, the vertebral and intercostal veins retain their relative size until the development of the superior extremities has commenced. Then two of the intercostal veins increase in diameter (Fig. 270), and become converted into the right and left subclavians; while those portions of the vertebral veins situated above the subclavians become the right and left jugulars. Just below the junction of the jugulars with the subclavians, a small branch of communication now appears between the two vertebrals (Fig. 270, *b*), passing over from left to right, and emptying into the right vertebral vein a little above the level of the heart; so that a part of the blood coming from the left side of the head, and the left upper extremity, still passes down the left vertebral vein to the heart upon its own side, while a part crosses over by the communicating branch (*b*), and is finally conveyed to the heart by the right descending vertebral. Soon afterward, this branch of communication enlarges so rapidly that it preponderates altogether over the left superior vertebral vein, from which it originated (Fig. 271), and, serving then to convey all the blood coming from the left side of the head and left upper extremity over to the right side above the heart, it becomes the left *vena innominata*.

Fig. 270.



VENOUS SYSTEM farther advanced, showing formation of iliac and subclavian veins.—*a*. Vein of new formation, which becomes the inferior vena cava. *b*. Transverse branch of new formation, which afterward becomes the left vena innominata.

Fig. 271.



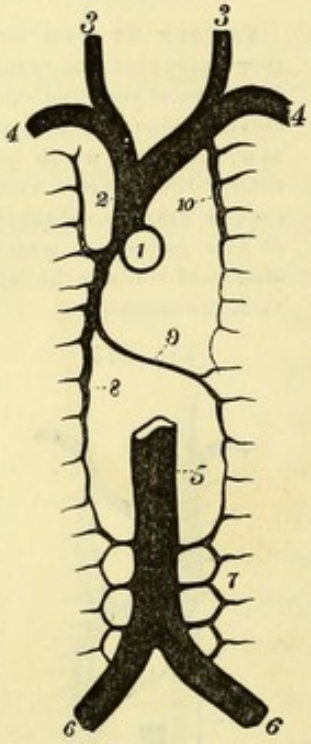
Further development of the VENOUS SYSTEM.—The vertebral veins are much diminished in size, and the canal of Cuvier, on the left side, is gradually disappearing. *c*. Transverse branch of new formation, which is to become the vena azygos minor.

On the left side, that portion of the superior vertebral vein, which is below the subclavian, remains as a small branch of the vena innominata, receiving the six or seven upper intercostal veins; while on the right side it becomes excessively enlarged, receiving the blood of both jugulars and both subclavians, and is converted into the *vena cava superior.*

The left canal of Cuvier, by which the left vertebral vein at first communicates with the heart, subsequently becomes atrophied and disappears; while on the right side it becomes excessively enlarged, and forms the lower extremity of the vena cava superior.

The superior and inferior venæ cavæ, accordingly, do not correspond with each other so far as regards their mode of origin, and are not to be regarded as analogous veins. For the superior vena cava is one of the original vertebral veins; while the inferior vena cava is a totally distinct vein, of new formation, resulting from the union of the two lateral trunks coming from the inferior extremities.

Fig. 272.



Adult condition of VENOUS SYSTEM.—1. Right auricle of heart. 2. Vena cava superior. 3, 3. Jugular veins. 4, 4. Subclavian veins. 5. Vena cava inferior. 6, 6. Iliac veins. 7. Lumbar veins. 8. Vena azygos major. 9. Vena azygos minor. 10. Superior intercostal vein.

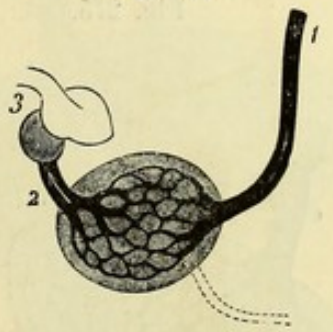
The remainder of the vertebral veins finally assume the condition shown in Fig. 272, which is the complete or adult form of the venous circulation. At the lower part of the abdomen, the vertebral veins send inward small transverse branches, which communicate with the vena cava inferior, between the points at which they receive the intercostal veins. These branches of communication, by increasing in size, become the *lumbar veins* (7), which, in the adult condition, communicate with each other by arched branches, a short distance to the side of the vena cava. Above the level of the lumbar arches, the vertebral veins retain their original direction. That upon the right side still receives all the right intercostal veins, and becomes the *vena azygos major* (8). It also receives a small branch of communication from its fellow of the left side (Fig. 271, *c*), and this branch soon enlarges to such an extent as to bring over to the vena azygos major all the blood of the five or six lower intercostal veins of the left side, becoming, in this way, the *vena azygos minor* (9). The six or seven

upper intercostal veins on the left side still empty, as before, into their own vertebral vein (10), which, joining the left vena innominata above, is known as the *superior intercostal vein.* The left canal of Cuvier has by this time entirely disappeared; so that all the venous blood now enters the heart by the superior or the inferior vena cava. But the original vertebral veins are still continuous throughout, though very much diminished in size at certain points; since both the greater and lesser azygous veins inosculate below with the superior lumbar veins, and the superior intercostal vein also inosculates below with the lesser azygous, just before it passes over to the right side.

There are still two parts of the circulatory apparatus, the development of which presents peculiarities sufficiently important to be described separately. These are, first, the liver and the ductus venosus, and secondly, the heart, with the ductus arteriosus.

Development of the Hepatic Circulation and the Ductus Venosus.— The liver appears at a very early period in the upper part of the abdomen, as a mass of glandular and vascular tissue, which is developed around the upper portion of the omphalo-mesenteric vein, just below its termination in the heart. (Fig. 273.) As soon as the organ has attained a considerable size, the omphalo-mesenteric vein (1) breaks up in its interior into a capillary plexus, the vessels of which unite again into venous trunks, and so convey the blood finally to the heart. The omphalo-mesenteric vein below the liver then becomes the *portal vein;* while above the liver, and between that organ and the heart, it receives the name of the *hepatic vein* (2). The liver, accordingly, is at this time supplied with blood entirely by the portal vein, coming from the umbilical vesicle and the intestine; and all the blood derived from this source must pass through the hepatic circulation before reaching the venous extremity of the heart.

Fig. 273.

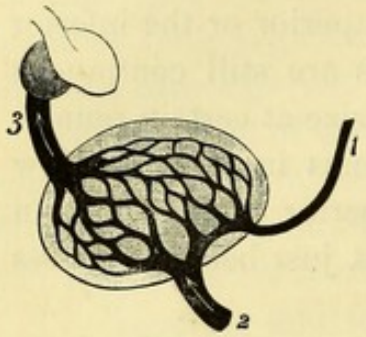


Early form of HEPATIC CIRCULATION. 1. Omphalo-mesenteric vein. 2. Hepatic vein. 3. Heart. The dotted line shows the situation of the future umbilical vein.

But soon afterward the allantois makes its appearance, and becomes rapidly developed into the placenta; and the umbilical vein coming from it joins the omphalo-mesenteric vein in the substance of the liver, and takes part in the formation of the hepatic capillary plexus. As the umbilical vesicle, however, becomes atrophied, and

the intestine also remains inactive, while the placenta increases in size and in functional importance, a time soon arrives when the liver receives more blood by the umbilical vein than by the portal vein. (Fig. 274.) The umbilical vein then passes into the liver at the longitudinal fissure, and supplies the left lobe entirely with its own branches. To the right it sends off a large branch of communication, which opens into the portal vein, and partially supplies the right lobe with umbilical blood. The liver is thus supplied with blood from two different sources, the most abundant of which is the umbilical vein; and all the blood entering the liver circulates, as before, through its capillary vessels.

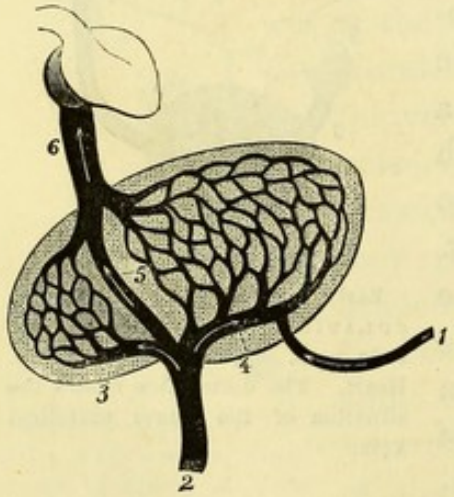
Fig. 274.



HEPATIC CIRCULATION farther advanced.—1. Portal vein. 2. Umbilical vein. 3. Hepatic vein.

But we have already seen that the liver is much larger, in proportion to the entire body, at an early period of fœtal life than in the later months. In the fœtal pig, when very young, it amounts to nearly twelve per cent. of the weight of the whole body; but before birth it diminishes to seven, six, and even three or four per cent. For some time, therefore, previous to birth, there is much more blood returned from the placenta than is required for the capillary circulation of the liver. Accordingly, a vascular duct or canal is formed in its interior, by which a portion of the placental blood is carried directly through the organ, and conveyed to the heart without having passed through the hepatic capillaries. This duct is called the *Ductus venosus*.

Fig. 275.



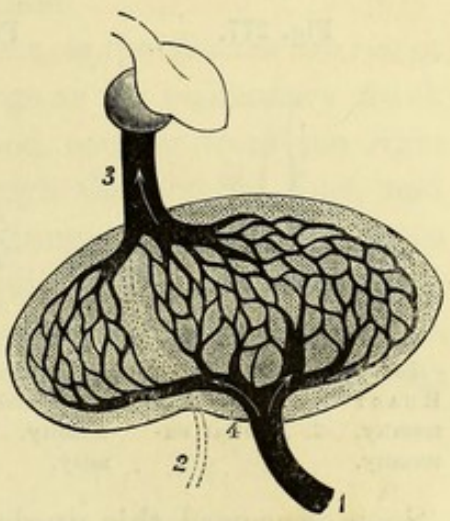
HEPATIC CIRCULATION during latter part of fœtal life.—1. Portal vein. 2. Umbilical vein. 3. Left branch of umbilical vein. 4. Right branch of umbilical vein. 5. Ductus venosus. 6. Hepatic vein.

The ductus venosus is formed by a gradual dilatation of one of the hepatic capillaries at (5) (Fig. 275), which, enlarging excessively, becomes at last converted into a wide canal, or branch of communication, passing directly from the umbilical vein below to the hepatic vein above. The circulation through the liver, thus established, is

as follows: A certain quantity of venous blood still enters through the portal vein (1), and circulates in a part of the capillary system of the right lobe. The umbilical vein (2), bringing a much larger quantity of blood, enters the liver also, a little to the left, and the blood which it contains divides into three principal streams. One of them passes through the left branch (3) into the capillaries of the left lobe; another turns off through the right branch (4), and, joining the blood of the portal vein, circulates through the capillaries of the right lobe; while the third passes directly onward through the venous duct (5), and reaches the hepatic vein without having passed through any part of the capillary plexus.

This condition of the hepatic circulation continues until birth. At that time, two important changes take place. First, the placental circulation is altogether cut off; and secondly, a much larger quantity of blood than before begins to circulate through the lungs and the intestine. The superabundance of blood, previously coming from the placenta, is now diverted into the lungs; while the intestinal canal, entering upon the active performance of its functions, becomes the sole source of supply for the hepatic venous blood. The following changes, therefore, take place at birth in the vessels of the liver. (Fig. 276.) First, the umbilical vein shrivels and becomes converted into a solid rounded cord (2). This cord may be seen, in the adult condition, running from the internal surface of the abdominal walls, at the umbilicus, to the longitudinal fissure of the liver. It is then known under the name of the *round ligament*. Secondly, the ductus venosus also becomes obliterated, and converted into a fibrous cord. Thirdly, the blood entering the liver by the portal vein (1), passes off by its right branch, as before, to the right lobe. But in the branch (4), the course of the blood is reversed. This was formerly the right branch of the umbilical vein, its blood passing in a direction from left to right. It now becomes the left branch of the portal vein; and its blood passes

Fig. 276.



Adult form of HEPATIC CIRCULATION.—1. Portal vein. 2. Obliterated umbilical vein, forming the round ligament; the continuation of the dotted lines through the liver shows the situation of the obliterated ductus venosus. 3. Hepatic vein. 4. Left branch of portal vein.

from right to left, to be distributed to the capillaries of the left lobe.

According to Dr. Guy, the umbilical vein is completely closed at the end of the fifth day after birth.

Development of the Heart, and the Ductus Arteriosus.—When the embryonic circulation is first established, the heart is a simple tubular sac (Fig. 277), receiving the veins at its lower extremity, and giving off the arterial trunks at its upper extremity. By the progress of its growth, it soon becomes twisted upon itself; so that the entrance of the veins, and the exit of the arteries, come to be placed more nearly upon the same horizontal level (Fig. 278); but the entrance of the veins (1) is behind and a little below, while the exit of the arteries (2) is in front and a little above. The heart is, at this time, a simple twisted tube; and the blood passes through it in a single continuous stream, turning upon itself at the point of curvature, and passing directly out by the arterial orifice.

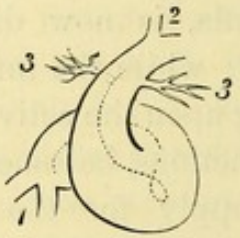
Fig. 277.

Earliest form of FŒTAL HEART.—1. Venous extremity. 2. Arterial extremity.

Fig. 278.

FŒTAL HEART, twisted upon itself.—1. Venous extremity. 2. Arterial extremity.

Fig. 279.



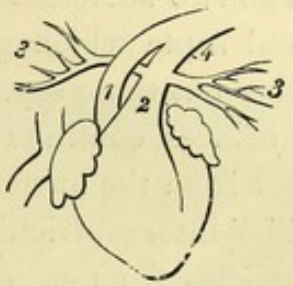
FŒTAL HEART, divided into right and left cavities.—1. Venous extremity. 2. Arterial extremity. 3, 3. Pulmonary branches.

Soon afterward, this single cardiac tube is divided into two parallel tubes, right and left, by a longitudinal partition, which grows from the inner surface of its walls and follows the twisted course of the organ itself. (Fig. 279.) This partition, which is indicated in the figure by a dotted line, extends a short distance into the commencement of the primitive arterial trunk, dividing it into two lateral halves, one of which is in communication with the right side of the heart, the other with the left.

About the same time, the pulmonary branches (3, 3) are given off from each side of the arterial trunk near its origin; and the longitudinal partition, above spoken of, is so placed that both these branches fall upon one side of it, and are both, consequently, given off from that division of the artery which is connected with the right side of the heart.

Very soon a superficial line of demarcation, or furrow shows itself upon the external surface of the heart, corresponding in situation with the internal septum; while at the root of the arterial trunk this furrow becomes much deeper, and finally the two lateral portions of the vessel are separated from each other altogether, in the immediate neighborhood of the heart, joining again, however, a short distance beyond the origin of the pulmonary branches. (Fig. 280.) It then becomes evident that the left lateral division of the arterial trunk is the commencement of the aorta (1); while its right lateral division is the trunk of the pulmonary artery (2), giving off the right and left pulmonary branches (3,3), at a short distance from its origin. That portion of the pulmonary trunk (4) which is beyond the origin of the pulmonary branches, and which communicates freely with the aorta, is the *Ductus arteriosus*.

Fig. 280.



FŒTAL HEART still farther developed.—1 Aorta. 2. Pulmonary artery. 3, 3. Pulmonary branches. 4. Ductus arteriosus.

The ductus arteriosus is at first as large as the pulmonary trunk itself; and nearly the whole of the blood, coming from the right ventricle, passes directly onward through the arterial duct, and enters the aorta without going to the lungs. But as the lungs gradually become developed, they require a larger quantity of blood for their nutrition, and the pulmonary branches increase in proportion to the pulmonary trunk and the ductus arteriosus. At the termination of fœtal life, in the human subject, the ductus arteriosus is about as large as either one of the pulmonary branches; and a very considerable portion of the blood, therefore, coming from the right ventricle still passes onward to the aorta without being distributed to the lungs.

Fig. 281.

HEART OF INFANT, showing disappearance of arterial duct after birth.—1. Aorta. 2 Pulmonary artery. 3. 3. Pulmonary branches. 4. Ductus arteriosus becoming obliterated

But at the period of birth, the lungs enter upon the active performance of the function of respiration, and immediately require a much larger supply of blood. The right and left pulmonary branches then enlarge, so as to become the two principal divisions of the pulmonary trunk. (Fig. 281.) The ductus arteriosus at the

same time becomes contracted and shrivelled to such an extent that its cavity is obliterated; and it is finally converted into an impervious, rounded cord, which remains until adult life, running from the point of bifurcation of the pulmonary artery to the under side of the arch of the aorta. The obliteration of the arterial duct is complete, at latest, by the tenth week after birth. (Guy.)

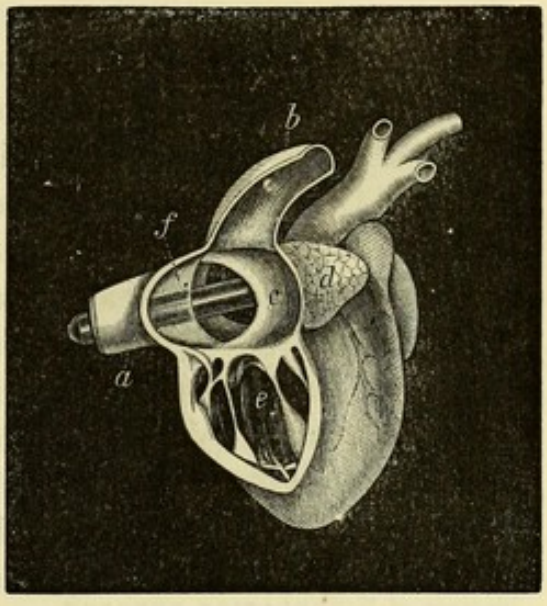
The two auricles are separated from the two ventricles by horizontal septa which grow from the internal surface of the cardiac walls; but these septa remaining incomplete, the auriculo-ventricular orifices continue pervious, and allow the free passage of the blood from the auricles to the ventricles.

The interventricular septum, or that which separates the two ventricles from each other, is completed at a very early date; but the interauricular septum, or that which is situated between the two auricles, remains incomplete for a long time, being perforated by an oval-shaped opening, the *foramen ovale*, allowing, at this situation, a free passage from the right to the left side of the heart. The existence of the foramen ovale and of the ductus arteriosus gives rise to a peculiar crossing of the streams of blood in passing through the heart, which is characteristic of fœtal life, and which may be described as follows:—

It will be found upon examination that the two venæ cavæ, superior and inferior, do not open into the auricular sac on the same plane or in the same direction; for while the superior vena cava is situated anteriorly, and is directed downward and forward, the inferior is situated quite posteriorly, and passes into the auricle in a direction from right to left, and transversely to the axis of the heart. A nearly vertical curtain or valve at the same time hangs downward behind the orifice of the superior vena cava and in front of the orifice of the inferior. This curtain is formed by the lower edge of the septum of the auricles, which, as we have before stated, is incomplete at this age, and which terminates inferiorly and toward the right in a crescentic border, leaving at that part an oval opening, the foramen ovale. The stream of blood, coming from the superior vena cava, falls accordingly in front of this curtain, and passes directly downward, through the auriculo ventricular orifice, into the right ventricle. But the inferior vena cava, being situated farther back and directed transversely, opens, properly speaking, not into the right auricle, but into the left; for its stream of blood, falling behind the curtain above mentioned, passes across, through the foramen ovale, directly into the cavity of

the left auricle. This direction of the current of blood, coming from the inferior vena cava, is further secured by a peculiar membranous valve, which exists at this period, termed the *Eustachian valve.* This valve, which is very thin and transparent (Fig. 282, *f*), is attached to the anterior border of the orifice of the inferior vena cava, and terminates by a crescentic edge, directed toward the left; the valve, in this way, standing as an incomplete membranous partition between the cavity of the inferior vena cava and that of the right auricle. A bougie, accordingly, placed in the inferior vena cava, as shown in Fig. 282, lies naturally quite behind the Eustachian valve, and passes directly through the foramen ovale, into the left auricle.

Fig. 282.



HEART OF HUMAN FŒTUS, at the end of the sixth month; from a specimen in the author's possession.—*a.* Inferior vena cava. *b.* Superior vena cava. *c.* Cavity of right auricle, laid open from the front. *d.* Appendix auricularis. *e.* Cavity of right ventricle, also laid open. *f.* Eustachian valve. The bougie, which is placed in the inferior vena cava, can be seen passing behind the Eustachian valve, just below the point indicated by *f*, then crossing behind the cavity of the right auricle, and passing through the foramen ovale, to the left side of the heart.

The two streams of blood, therefore, coming from the superior and inferior venæ cavæ, cross each other upon entering the heart. This crossing of the streams does not take place, however, as it is sometimes described, in the cavity of the right auricle; but, owing to the peculiar position and direction of the two veins at this period, with regard to the septum of the auricles, the stream coming from the superior vena cava enters the right auricle exclusively, while that from the inferior passes almost directly into the left auricle.

It will also be seen, by examining the positions of the aorta, pulmonary artery, and ductus arteriosus, at this time, that the arteria innominata, together with the left carotid and left subclavian, are given off from the arch of the aorta, before its junction with the ductus arteriosus, and this arrangement causes the blood of the two venæ cavæ, not only to enter the heart in different directions, but also to be distributed, after leaving the ventricles, to different parts of the body. (Fig. 283.) For the blood of the superior vena cava

passes through the right auricle downward into the right ventricle, thence through the pulmonary artery and ductus arteriosus, into the thoracic aorta, while the blood of the inferior vena cava, entering the left auricle, passes into the left ventricle, thence into the arch of the aorta, and is distributed to the head and upper extremities, before reaching the situation of the arterial duct. The two streams, therefore, in passing through the heart, cross each other both behind and in front. The venous blood, returning from the head and upper extremities by the superior vena cava, passes through the abdominal aorta and the umbilical arteries, to the lower part of the body, and to the placenta; while that returning from the placenta, by the inferior vena cava, is distributed to the head and upper extremities, through the vessels given off from the arch of the aorta.

Fig 283.

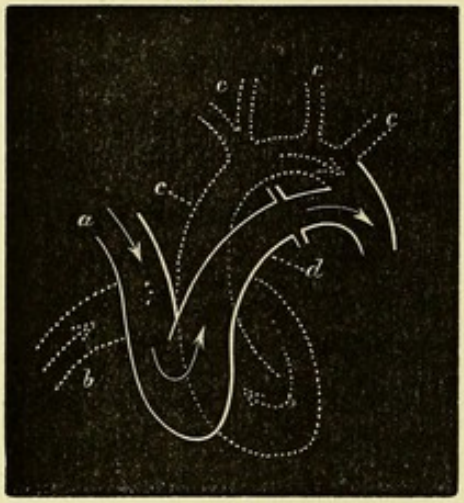


Diagram of CIRCULATION THROUGH THE FŒTAL HEART.—*a*. Superior vena cava. *b*. Inferior vena cava. *c*, *c*, *c*, *c*. Arch of aorta and its branches. *d*. Pulmonary artery.

This division of the streams of blood, during a certain period of fœtal life, is so complete that Dr. John Reid,[1] on injecting the inferior vena cava with red, and the superior with yellow, in a seven months' human fœtus, found that the red had passed through the foramen ovale into the left auricle and ventricle and arch of the aorta, and had filled the vessels of the head and upper extremities; while the yellow had passed into the right ventricle, pulmonary artery, ductus arteriosus, and thoracic aorta, with only a slight admixture of red at the posterior part of the right auricle. All the branches of the thoracic and abdominal aorta were filled with yellow, while the whole of the red had passed to the upper part of the body.

We have repeated the above experiment several times on the fœtal pig, when about one-half and three-quarters grown, first taking the precaution to wash out the heart and large vessels with a watery injection, immediately after the removal of the fœtus from the body of the parent, and before the blood had been allowed to coagulate. The injections used were blue for the superior vena cava,

[1] Edinburgh Medical and Surgical Journal, vol. xliii. 1835.

and yellow for the inferior. The two syringes were managed, at the same time, by the right and left hands: their nozzles being firmly held in place by the fingers of an assistant. When the points of the syringes were introduced into the veins, at equal distances from the heart, and the two injections made with equal force and rapidity, it was found that the admixture of the colors which took place was so slight, that at least nineteen-twentieths of the yellow injection had passed into the left auricle, and nineteen-twentieths of the blue into the right. The pulmonary artery and ductus arteriosus contained a similar proportion of blue, and the arch of the aorta of yellow. In the thoracic and abdominal aorta, however, contrary to what was found by Dr. Reid, there was always an admixture of the two colors, generally in about equal proportions. This discrepancy may be owing to the smaller size of the head and upper extremities, in the pig, as compared with those of the human subject, which would prevent their receiving all the blood coming from the left ventricle; or to some differences in the manipulation of these experiments, in which it is not always easy to imitate exactly the force and rapidity of the different currents of blood in the living fœtus. The above results, however, are such as to leave no doubt of the principal fact, viz., that up to an advanced stage of fœtal life, by far the greater portion of the blood coming from the inferior vena cava passes through the foramen ovale, into the left side of the heart; while by far the greater portion of that coming from the head and upper extremities passes into the right side of the heart, and thence outward by the pulmonary trunk and ductus arteriosus. Toward the latter periods of gestation, this division of the venous currents becomes less complete, owing to the three following causes:—

First, the lungs increasing in size, the two pulmonary arteries, as well as the pulmonary veins, enlarge in proportion; and a greater quantity of the blood, therefore, coming from the right ventricle, instead of going onward through the ductus arteriosus, passes to the lungs, and returning thence by the pulmonary veins to the left auricle and ventricle, joins the stream passing out by the arch of the aorta.

Secondly, the Eustachian valve diminishes in size. This valve, which is very large and distinct at the end of the sixth month (Fig. 282), subsequently becomes atrophied to such an extent that, at the end of gestation, it has altogether disappeared, or is at least reduced to the condition of a very narrow, almost imperceptible

membranous ridge, which can exert no influence on the direction of the current of blood passing by it. Thus, the cavity of the inferior vena cava, at its upper extremity, ceases to be separated from that of the right auricle; and a passage of blood from one to the other may, therefore, more readily take place.

Thirdly, the foramen ovale becomes partially closed by a valve which passes across its orifice from behind forward. This valve, which begins to be formed at a very early period, is called the *valve of the foramen ovale.* It consists of a thin, fibrous sheet, which grows from the posterior surface of the auricular cavity, just to the left of the foramen ovale, and projects into the left auricle, its free edge presenting a thin crescentic border, and being attached, by its two extremities, to the auricular septum upon the left side. This valve does not at first interfere at all with the flow of blood from right to left, since its edge hangs freely and loosely into the cavity of the left auricle. It only opposes, therefore, during the early periods, any accidental regurgitation from left to right.

But as gestation advances, while the walls of the heart continue to enlarge, and its cavities to expand in every direction, the fibrous bundles, forming the valve, do not elongate in proportion. The valve, accordingly, becomes drawn downward more and more toward the foramen ovale. It thus comes in contact with the edges of the interauricular septum, and unites with its substance; the adhesion taking place first at the lower and posterior portion, and proceeding gradually upward and forward, so as to make the passage, from the right auricle to the left, more and more oblique in direction.

At the same time, an alteration takes place in the position of the inferior vena cava. This vessel, which at first looked transversely toward the foramen ovale, becomes directed more obliquely forward; so that, the Eustachian valve having mostly disappeared, a part of the blood of the inferior vena cava enters the right auricle, while the remainder still passes through the equally oblique opening of the foramen ovale.

At the period of birth a change takes place, by which the foramen ovale is completely occluded, and all the blood coming through the inferior vena cava is turned into the right auricle.

This change depends upon the commencement of respiration. A much larger quantity of blood than before is then sent to the lungs, and of course returns from them to the left auricle. The left auricle, being then completely filled with the pulmonary blood,

no longer admits a free access from the right auricle through the foramen ovale; and the valve of the foramen, pressed backward more closely against the edges of the septum, becomes after a time adherent throughout, and obliterates the opening altogether. The cutting off of the placental circulation diminishes at the same time the quantity of blood arriving at the heart by the inferior vena cava. It is evident, indeed, that the same quantity of blood which previously returned from the placenta by the inferior cava, on the right side of the auricular septum, now returns from the lungs, by the pulmonary veins upon the left side of the same septum; and it is owing to all these circumstances combined, that while before birth a portion of the blood always passed from the right auricle to the left through the foramen ovale, no such passage takes place after birth, since the pressure is then equal on both sides of the auricular septum.

The fœtal circulation, represented in Fig. 283, is then replaced by the adult circulation, represented in Fig. 284.

Fig. 284.

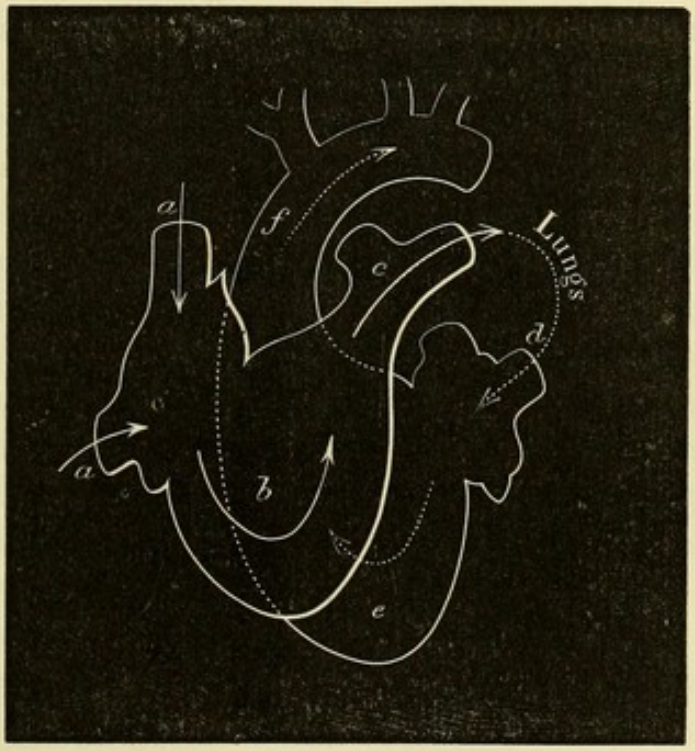


Diagram of ADULT CIRCULATION THROUGH THE HEART.—*a*, *a*. Superior and inferior venæ cavæ. *b*. Right ventricle. *c*. Pulmonary artery, dividing into right and left branches. *d*. Pulmonary vein. *e*. Left ventricle. *f*. Aorta.

That portion of the septum of the auricles, originally occupied by the foramen ovale, is accordingly constituted, in the adult condition, by the valve of the foramen ovale, which has become adhe-

rent to the edges of the septum. The auricular septum in the adult heart is, therefore, thinner at this spot than elsewhere; and presents, on the side of the right auricle, an oval depression, termed the *fossa ovalis*, which indicates the site of the original foramen ovale. The fossa ovalis is surrounded by a slightly raised ring, the *annulus ovalis*, representing the curvilinear edge of the original auricular septum.

The foramen ovale is sometimes completely obliterated within a few days after birth. It often, however, remains partially pervious for several weeks or months. We have a specimen, taken from a child of one year and nine months, in which the opening is still very distinct; and it is not unfrequent to find a small aperture existing even in adult life. In these instances, however, although the adhesion and solidification of the auricular septum may not be complete, yet no disturbance of the circulation results, and no admixture of blood takes place between the right and left sides of the heart; since the passage through the auricular septum is always very oblique in its direction, and its valvular arrangement prevents any regurgitation from left to right, while the complete filling of the left auricle with pulmonary blood, as above mentioned, equally opposes any passage from right to left.

CHAPTER XVIII.

DEVELOPMENT OF THE BODY AFTER BIRTH.

THE newly-born infant is still very far from having arrived at a state of complete development. The changes through which it has passed during intra-uterine life are not more marked than those which are to follow during the periods of infancy, childhood, and adolescence. The anatomy of the organs, both internal and external, their physiological functions, and even the morbid derangements to which they are subject, continue to undergo gradual and progressive alterations, throughout the entire course of subsequent life. The history of development extends, properly speaking, from the earliest organization of the embryonic tissues to the complete formation of the adult body. The period of birth, accordingly, marks only a single epoch in a constant series of changes, some of which have preceded, while many others are to follow.

The weight of the newly-born infant is between six and seven pounds. The middle point of the body is nearly at the umbilicus, the head and upper extremities being still very large, in proportion to the lower extremities and pelvis. The abdomen is larger and the chest smaller, in proportion, than in the adult. The lower extremities are curved inward, as in the fœtal condition, so that the soles of the feet look obliquely toward each other, instead of being directed horizontally downward, as at a subsequent period. Both upper and lower extremities are habitually curled upward and forward over the chest and abdomen, and all the joints are constantly in a semi-flexed position.

The process of respiration is very imperfectly performed for some time after birth. The expansion of the pulmonary vesicles, and the changes in the circulatory apparatus described in the preceding chapter, far from being sudden and instantaneous, are always more or less gradual in their character, and require an interval of several days for their completion. Respiration, indeed

seems to be accomplished, during this period, to a considerable extent through the skin, which is remarkably soft, vascular, and ruddy in color. The animal heat is also less actively generated than in the adult, and requires to be sustained by careful protection, and by contact with the body of the mother. The young infant sleeps during the greater part of the time; and even when awake there are but few manifestations of intelligence or perception. The special senses of sight and hearing are dull and inexcitable, though their organs are perfectly formed; and even consciousness seems present only to a very limited extent. Voluntary motion and sensation are nearly absent; and the almost constant irregular movements of the limbs, observable at this time, are evidently of a reflex or automatic character. Nearly all the nervous phenomena, indeed, presented by the newly-born infant, are of a similar nature. The motions of its hands and feet, the act of suckling, and even its cries and the contortions of its face, are reflex in their origin, and do not indicate the existence of any active volition, or any distinct perception of external objects. There is at first but little nervous connection established with the external world, and the system is as yet almost exclusively occupied with the functions of nutrition and respiration.

This preponderance of the simple reflex actions in the nervous system of the infant, is observable even in the diseases to which it is peculiarly subject for some years after birth. It is at this age that convulsions from indigestion are of most frequent occurrence, and even temporary strabismus and paralysis, resulting from the same cause. It is well known to physicians, moreover, that the effect of various drugs upon the infant is very different from that which they exert upon the adult. Opium, for example, is very much more active, in proportion to the dose, in the infant than in the adult. Mercury, on the other hand, produces salivation with greater difficulty in the former than in the latter. Blisters excite more constitutional irritation in the young than in the old subject; and antimony, when given to children, is proverbially uncertain and dangerous in its operation.

The difference in the anatomy of the newly-born infant, and that of the adult, may be represented, to a certain extent, by the following list, which gives the relative weight of the most important internal organs at the period of birth and that of adult age; the weight of the entire body being reckoned, in each case, as 1000. The relative weight of the adult organs has been calculated from

the estimates of Cruveilheir, Solly, Wilson, &c.: that of the organs in the fœtus at term from our own observations.

			Fœtus at Term.	Adult.
Weight of the entire body			1000.00	1000.00
"	"	encephalon	148.00	23.00
"	"	liver	37.00	29.00
"	"	heart	7.77	4.17
"	"	kidneys	6.00	4.00
"	"	renal capsules	1.63	0.13
"	"	thyroid gland	0.60	0.51
"	"	thymus gland	3.00	0.00

It will be observed that most of the internal organs diminish in relative size after birth, owing principally to the increased development of the osseous and muscular systems, both of which are in a very imperfect condition throughout intra-uterine life, but which come into activity during childhood and youth.

Within the first day after birth the remains of the umbilical cord begin to wither, and become completely desiccated by about the third day. A superficial ulceration then takes place about the point of its attachment, and it is separated and thrown off within the first week. After the separation of the cord, the umbilicus becomes completely cicatrized by the tenth or twelfth day after birth. (Guy.)

An exfoliation and renovation of the cuticle also take place over the whole body soon after birth. According to Kölliker, the eyelashes, and probably all the hairs of the body and head are thrown off and replaced by new ones within the first year.

The teeth in the newly-born infant are but partially developed, and are still inclosed in their follicles, and concealed beneath the gums. They are twenty in number, viz., two incisors, one canine, and two molars, on each side of each jaw. At birth there is a thin layer of dentine and enamel covering their upper surfaces, but the body of the tooth and its fangs are formed subsequently by progressive elongation and ossification of the tooth-pulp. The fully-formed teeth emerge from the gums in the following order The central incisors in the seventh month after birth; the lateral incisors in the eighth month; the anterior molars at the end of the first year; the canines at a year and a half; and the second molars at two years (Kölliker). The eruption of the teeth in the lower jaw generally precedes by a short time that of the corresponding teeth in the upper.

During the seventh year a change begins to take place by which

the first set of teeth are thrown off and replaced by a second or permanent set, differing in number, size, and shape from those which preceded. The anterior permanent molar first shows itself just behind the posterior temporary molar, on each side. This happens at about six and a half years after birth. At the end of the seventh year the middle incisors are thrown off and replaced by corresponding permanent teeth, of larger size. At the eighth year a similar exchange takes place in the lateral incisors. In the ninth and tenth years, the anterior and second molars are replaced by the anterior and second permanent bicuspids. In the twelfth year, the canine teeth are changed. In the thirteenth year, the second permanent molars show themselves; and from the seventeenth to the twenty-first year, the third molars, or "wisdom teeth," emerge from the gums, at the posterior extremities of the dental arch. (Wilson.) The jaw, therefore, in the adult condition, contains three teeth on each side more than in childhood, making in all thirty-two permanent teeth; viz., on each side, above and below, two incisors, one canine, two bicuspids, and three permanent molars.

The entire generative apparatus, which is still altogether inactive at birth, begins to enter upon a condition of functional activity from the fifteenth to the twentieth year. The entire configuration of the body alters in a striking manner at this period, and the distinction between the sexes becomes more complete and well marked. The beard is developed in the male; and in the female the breasts assume the size and form characteristic of the condition of puberty. The voice, which is shrill and sharp in infancy and childhood, becomes deeper in tone, and the countenance assumes a more sedate and serious expression. After this period, the muscular system increases still further in size and strength, and the consolidation of the skeleton also continues; the bony union of its various parts not being entirely accomplished until the twenty-fifth or thirtieth year. Finally, all the different organs of the body arrive at the adult condition, and the entire process of development is then complete.

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