A manual of veterinary physiology / by F. Smith.

Contributors

Smith, Frederick, 1857-1929.
Royal College of Physicians of Edinburgh

Publication/Creation

London : Bailliere Tindall, 1895.

Persistent URL

https://wellcomecollection.org/works/f5jbrke8

Provider

Royal College of Physicians Edinburgh

License and attribution

This material has been provided by This material has been provided by the Royal College of Physicians of Edinburgh. The original may be consulted at the Royal College of Physicians of Edinburgh. where the originals may be consulted.
This work has been identified as being free of known restrictions under copyright law, including all related and neighbouring rights and is being made available under the Creative Commons, Public Domain Mark.

You can copy, modify, distribute and perform the work, even for commercial purposes, without asking permission.

wellcome collection

Wellcome Collection
183 Euston Road
London NW1 2BE UK
T +44 (0)20 7611 8722
E library@wellcomecollection.org
https://wellcomecollection.org

R.C.P. EDINBURGH LIBRARY
R26586P0236



15/-

2 4.10

A MANUAL OF VETERINARY PHYSIOLOGY.

A MANUAL

OF

VETERINARY PHYSIOLOGY.

BY

VETERINARY-CAPTAIN F. SMITH, F.R.C.V.S.,

ARMY VETERINARY DEPARTMENT,

EXAMINER IN PHYSIOLOGY ROYAL COLLEGE OF VETERINARY SURGEONS,

FELLOW OF THE INSTITUTE OF CHEMISTRY,

AUTHOR OF 'A MANUAL OF VETERINARY HYGIENE,' ETC.

SECOND EDITION—REWRITTEN.





LONDON:
BAILLIÈRE, TINDALL AND COX,
20 & 21, KING WILLIAM STREET, STRAND.
NEW YORK: W. R. JENKINS.
1895.

[*All rights reserved.*]

TO

MICHAEL FOSTER, M.A., M.D., LL.D., F.R.S.,

Professor of Physiology in the University of Cambridge,

THIS ATTEMPT TO DEAL WITH A BRANCH OF PHYSIOLOGY

IS DEDICATED,

IN ACKNOWLEDGMENT OF THE

ENCOURAGEMENT AND ASSISTANCE HE HAS GIVEN

THE AUTHOR

IN PROSECUTING THE STUDY OF VETERINARY PHYSIOLOGY.

PREFACE TO THE SECOND EDITION.

I GREATLY regret the considerable delay which has occurred in the production of this edition, but it has been unavoidable; the work has been rewritten in order to admit of its scope being enlarged, and this has taken longer than I anticipated.

In the revision of the sheets I have received great assistance from Professors M'Kendrick, Halliburton, Haycraft, Sherrington, and Dr. Waller. Professor Sherrington revised the whole of the Nervous System and supplied Figure 58. Professor Mettam, of the Royal Veterinary College, Edinburgh, kindly wrote the chapter dealing with the Development of the Ovum, while to Professor Macqueen, of the London Veterinary College, I am indebted for many useful suggestions and valuable criticism.

To all these gentlemen I offer my cordial thanks; their corrections, suggestions, and criticisms have been of the greatest help, and cannot fail to enhance the value of the book.

As in the first edition, I have avoided dealing with

histology, excepting where such was necessary to the clear understanding of the subject under consideration.

After due deliberation, I determined not to introduce for the present the metrical system of weights and measures.

The number of illustrations has been doubled, and for electrotypes of blocks I am indebted to Professor Foster, of Cambridge; Professor M'Kendrick, of Glasgow; Professor Hamilton, of Aberdeen; and Dr. Waller, of London.

The rewriting of this edition has unfortunately necessitated an increase in the size of the book.

WOOLWICH,
September, 1895.

PREFACE TO THE FIRST EDITION.

My object throughout this manual has been to condense the information as much as possible, for which purpose I have omitted all special reference to the physiology of the dog, and have not touched upon the histology of the tissues, or methods of physiological inquiry.

The reasons for these omissions are obvious: special canine physiology is of subordinate interest to the profession, and our information about this animal is so complete, that when required no difficulty is experienced in obtaining it from human text-books. The histology of the tissues is already before the profession, and methods of physiological inquiry are only needed for laboratory work, for which purpose this book is not intended.

In the description of the physiology of the various organs and tissues the horse is necessarily taken as the type, but the ox, sheep, and pig are dealt with wherever their special physiology requires it.

It was my original intention to publish nothing until I had gone over the field of equine physiology, but I found after several years of work, that the information I had collected was a mere drop in the ocean, for inquiries of this

kind are necessarily slow, and as there appeared no reasonable prospect of covering within the space of one life the ground I had mapped out, I was advised that only good could result from placing on record what little we know of veterinary physiology.

I have, therefore, ventured, I know well how imperfectly, to state the broad facts of the science, so as to render them of use to the student and practitioner. The work does not pretend to be anything more than a stepping-stone to the study of physiology; for those requiring more detailed information, reference must be made to the various text-books of human and comparative physiology which are available.

Incomplete as the work is, it would have been still more so but for the assistance I have received from my friend Dr. Sheridan Lea, F.R.S., of Caius College, Cambridge, who, at great personal inconvenience, has kindly read and revised nearly all the sheets as they passed through the press. In saying this, and expressing to him my very great indebtedness, I in no way wish to shift the responsibility for error or inaccuracy which may exist, but I feel that whatever merit the book possesses is entirely due to him.

I have to thank Professor Michael Foster, F.R.S., for the loan of many of the woodcuts which illustrate this manual, and elsewhere I have acknowledged how much I owe to his encouragement.

To my friend and colleague, Assistant-Professor Butler, A.V.D., my best thanks are due for assistance in revising

the proofs, and in the preparation of the index; to Mr. W. Hunting, F.R.C.V.S., for suggestions on the chapter dealing with Locomotion; and to Professor M'Fadyean for the loan of two woodcuts illustrating the chapter on the Foot.

To facilitate the study of locomotion, I have had the plates so arranged as to face as nearly as possible the letterpress describing the movements.

I have laid under contribution Colin's invaluable 'Traité de Physiologie comparée des Animaux'; Ellenberger's 'Physiologie der Haussäugethiere'; Foster's, M'Kendrick's, and Landois and Stirling's Text-books of Physiology; Gamgee's translation of 'Hermann's Physiology'; the same author's 'Physiological Chemistry of the Animal Body'; Halliburton's 'Text-book of Chemical Physiology and Pathology'; Bunge's 'Physiological and Pathological Chemistry'; Meade Smith's 'Physiology of the Domestic Animals,' and others mentioned in the text. With reference to Dr. Meade Smith's work, I regret to find that on page 105 I have inadvertently given the title as 'A Text-book of Comparative Physiology.'

I have endeavoured to acknowledge all sources of information, though it is possible that in drawing from such a wide area I may have omitted in places to do so.

Army Veterinary School, Aldershot,
August, 1892.

CONTENTS.

CHAPTER I.

THE BLOOD.

PAGE

Functions of the blood—Physical characters, colour, reaction, odour, taste, specific gravity—Composition of the blood—The liquor sanguinis—Difference between serum and plasma—Proteids of serum—Their varieties and proportions in different animals—Red blood corpuscles—Proportion found—Their shape and structure—Composition of the red cells—The number of red cells—Circumstances which influence the number—Cause of the blood being opaque—How this can be removed—Death of the red cells—How their hæmoglobin is utilised—Reproduction of red cells—Red cells of the embryo—Hæmoglobin—Its affinity for oxygen—Its state of oxidation and reduction—Composition of hæmoglobin—Its crystalline state—Total amount in the body—Proportion found in the blood of different animals—Spectrum of hæmoglobin—Compounds formed by hæmoglobin—Methæmoglobin, its characters and spectrum—Carbonic oxide hæmoglobin—Its stability—The colour it imparts to blood—Its spectrum—Nitric oxide hæmoglobin—Decomposition of hæmoglobin—Hæmatin—Its appearance and composition—Its spectrum—Hæmin—Character of its crystals—How obtained—Hæmochromogen Hæmatoporphyrin—Hæmatoidin—Where obtained in the body—Its identity with bilirubin—Connection between hæmatin and bile pigments—The white corpuscles—Proportion in which they are found—Structure—Amœboid movements—Diapedesis—Composition of the white cells—Origin of the white cells—How the white cells are used up—Function of the white cells—The substance yielded by their death—Blood-plates—Coagulation—The process described—The buffy coat—Time occupied in coagulation—The clot—Whipping blood—Fibrin, its appearance and

PAGE

character—Its proportion in blood—The fibrin ferment—Its origin—Calcium necessary for its production—Theories of coagulation—Nucleo-albumins, their share in clotting—Circumstances influencing coagulation within the vessels—diseased vessels, addition of certain salts, injection of peptone, tissue fibrinogen, fibrin ferment—Circumstances influencing coagulation outside the vessels—exposure to air, low temperature, high temperature, neutral salts, oil—Blood extractives, urea, sugar, fat, etc.—Difference between arterial and venous blood—Cause of the colour of venous blood—The salts of the blood—Their distribution—Use of the salts—Temperature of the blood—Quantity of blood in the body—Distribution of the blood—Blood gases—Their proportion in arterial and venous blood—Chemical composition of the blood - - - - - 1-24

CHAPTER II.

THE HEART.

Use of the heart—Anatomical arrangement—Course of the circulation—Position of the heart in the chest—The heart muscle, its structure—The cells of Purkinje—The arrangement of the muscular fibres—Valves of the heart, their use—Function of the papillæ and moderator bands—The sigmoid valves—The cardiac cycle; auricular systole, ventricular systole, the pause; the diastole of the heart—Changes in the shape of the heart during the cycle—Action of the valves during the cycle—Their shape under pressure; position in the blood stream, and manner in which they are closed—The cardiac sounds—Cause of the first sound, cause of the second sound—Intra-cardiac pressure during systole and diastole—The blood pressure in the two ventricles—The cardiograph—Capacity of the chambers of the heart—The amount of blood pumped out at each contraction—The work of the heart—How calculated—The right heart does less work than the left—Weight of the blood pumped out at each systole—The time occupied by the entire mass of blood passing through the heart—Blood pressure—Nervous mechanism of the heart—Heart apparently insensitive—Origin and structure of the vagus—Its function on the heart—Origin and structure of the cardiac sympathetic—Effect of stimulating the vagus; effect of dividing it—Effect of dividing the sympathetic—Effect of vagus stimulation on blood pressure—Effect of blood gases on the cardiac centre in the medulla—Reflex cardiac inhibition, methods by which it may be excited—Effect of expiration on cardiac inhibition—How this may be abolished

PAGE

—Influence of atropine on vagus inhibition—Effect of muscarin — Vagus influence always in operation —The trophic nerve of the heart—The sympathetic excites katabolism—The depressor nerve—Its function and the manner in which it acts—Its effect on the blood pressure—Nature of a cardiac contraction—Heart contraction differs from that of ordinary red muscle—Heart muscle compared with skeletal and visceral muscle—Effect of weak and strong stimulation on heart muscle—The refractory period in heart muscle—Cardiac ganglia—They are not local mechanisms—Their probable function—Gaskell's view of the cause of a cardiac contraction — The nutrition of the heart muscle — The factors which help the heart to variously modify the beat—Action of drugs on the heart - - - 25-48

CHAPTER III.

THE BLOODVESSELS.

The arteries—Their structure—Value of the elastic coat—Contractility of arteries—Use of the muscular coat—The capillaries—Their structure and function—Size of capillaries varies—The veins—Their structure—They possess great power of expansion—Valves in veins—Mechanics of the circulation—Influence of pumping fluid through a rigid tube ; through an elastic tube ; through an elastic tube with obstructed outlet—Explanation of the continuous stream —The peripheral resistance—How it is varied—Influence of high and low peripheral resistance on pressure within the vessels—Mean pressure—How it is maintained and varied—Blood pressure, definition of—How it is maintained and varied—Where it is highest and lowest—Where it is negative—The measured pressure in the carotid of the horse and dog—Influence of respiration on blood pressure —Blood pressure in the capillaries and veins — How a negative pressure is produced, and its value—Influence of bleeding on blood pressure—Amount of blood which may be abstracted—Influence of adding fluid to the circulation with an intact and divided spinal cord—The circulation in living tissues—Changes in inflammation—Influence of the vessel wall—The pulse—Its cause—Why it dies out at the arterioles—The pulse wave—Its length and velocity—Pulse wave and blood velocity are not the same—Sphygmograms —Origin of the dicrotic wave—Influence on this by destroying the aortic valves—Pulse tension—Its definition—Sphygmograms of high and low tension—Pulse rate in animals—Influence on of age and height—Blood velocity, where it is greatest and least—Velocity is due to the width of bed—Where the bed is the widest—Cause of the blood flow—

PAGE

Velocity in the carotid and jugular—Influence of systole and diastole on velocity—Where the velocity is greatest—Effect of peripheral resistance on velocity—Circulation time—Aids to the circulation—Influence of the nervous system on the circulation — Vascular tone — Vaso-motor nerves—All vessels do not possess dilator nerves—Parts where no vaso-motor nerves have been found—Effect on blood pressure of dividing constrictor nerves—The vaso-constrictor centre—No dilator centre known—Seat of the vaso-motor centre—Centre affected by the character of the blood—Its influence on blood pressure—Stimulation of vaso-motor centre does not necessarily lead to vascular constriction—Traube-Hering curves ; how produced—The origin and distribution of the vaso-constrictor nerves—Origin and course of the dilator fibres—Chorda and nervi erigentes are good examples of dilator nerves—Effect on the vessels of the heart and neck on dividing the sympathetic—What the experiment demonstrates—The effect on blood pressure of stimulating the depressor nerve—Explanation of the effect—Pressor effects—How they may be demonstrated—Parallelism between vaso-constrictor nerves and cardiac sympathetic, vaso-dilator nerves and cardiac branches of the vagus—Peculiarities in the circulation—Function of Circle of Willis and Rete Mirabile—Venous arrangement of the brain—Pulsations in exposed brain are of respiratory origin—Value of the cerebral fluid - 49-74

CHAPTER IV.

THE VASCULAR GLANDS.

Their function—Influence of the spleen on blood destruction and formation—The spleen as a vascular reservoir—Movements of the spleen ; cause of—Compensation for spleen destruction — Use of the thymus—Use of the thyroid—Effect of removal—Some animals suffer more than others—Supposed use of the renal capsules—Effect of removal in dogs—Animal extracts - - - - 75-77

CHAPTER V.

RESPIRATION.

Value of an air-tight thorax—Effect of admitting air—The act of inspiration—The increase in the size of the chest which follows it—Movements of the diaphragm—Motion is greater in some parts of it than in others—Displacement of abdominal viscera during inspiration—Liver pressure—Shape of the diaphragm during expiration and inspiration—Expiration, cause of—The supplemental factors—Move-

PAGE

ments of the abdominal wall—The fœtal lung—Absence of negative pressure—Rapid thoracic development after birth —The muscles of respiration — Intra-thoracic pressure during respiration—The number of respirations—Effect of muscular work on respirations—Ratio of heart-beats to respiration—Effect of inspiration and expiration on the circulation — Respiratory undulations in blood-pressure tracings explained—Pulse frequency during inspiration and expiration—The nostrils and glottis—Warming of incoming air—Nasal respiration alone possible in some animals—The false nostril—Movements of the nostrils during inspiration and expiration—Cause of the nasal expiratory movement—General features of the nasal chambers—Object of a narrow but deep passage—Movements of the glottis during inspiration and expiration—Movements of the larynx during inspiration—The facial sinuses ; their use—Air enters them during expiration - - - - - - 78-86

Respiratory changes in the air and blood—Composition of atmospheric air—Watery vapour—Less air returns from lungs than enters them ; how explained — Respiratory quotient — Hydrogen and marsh gas in expired air — Absorption of gases by fluids—Law of Dalton and Henry —Partial pressure of a gas—Passage of oxygen into the blood—Forms a compound with hæmoglobin—Oxyhæmoglobin does not obey the law of Dalton and Henry —Respiratory change in the tissues—Oxygen pressure *nil*—Arterial blood in the tissues supplies oxygen ; venous blood takes up carbonic acid—Fate of the oxygen in the tissues—An attempt to study this question by enquiring into the respiration of muscle—Apparently the oxygen is stored up, but not in a free state—From this stored up oxygen carbonic acid is formed—Why the CO_2 in the tissues passes into the blood—The substance in blood which carries the CO_2—How the CO_2 passes from the blood into the alveoli of the lungs—Breathing and rebreathing the same air, effect on the oxygen—Percentage of oxygen in which animals can live — Inhalation of oxygen — Apnœa, how produced—Dyspnœa, how produced—Asphyxia, its stages - - 86-94

Nervous mechanism of respiration—The centre is double—It receives impulses from the periphery—These impulses may be of very opposite nature—From the centre impulses are issued to the lungs—The centre is also automatic—The vagus conveys impulses to the medulla—The bulk of such impulses are probably stimulating—Effect of dividing the vagi —Effect of stimulating the upper cut end—The vagi may contain respiratory fibres of opposite character—Inspiratory portion of centre in medulla more active than expiratory

PAGE

portion—Self-adjusting mechanism—The evidence of such a mechanism—Afferent channels through which respirations are decreased or increased in frequency—Effect on respiration of dividing the superior laryngeal nerve—Respiratory centre affected by the character of the circulating blood—Suggested action of sarcolactic acid on respiratory centre—Evidence that increased respirations may be due to something formed in the muscles—Breathlessness may also be due to the heart—The efferent channels from the respiratory centre are viâ the phrenic nerve and spinal cord—Effect on respiration of dividing the spinal cord—Effect of dividing the phrenic nerves—Respiration requires the co-operation of other nerves not wholly respiratory—Effect of dividing the 7th cranial nerve - - - 94-100

Amount of air required—Capacity of the lungs—Average inspiration—The lungs cannot be emptied of air—Influence of work on amount of air required—Respiratory exchange of the horse during repose—The loss of oxygen and gain of carbonic acid in the expired air—Influence of work on the respiratory exchange — Influence of diet — Respiratory exchange of other animals - - - - 100-102

The larynx—Its uses—Movements of the larynx—Muscles of the larynx, respiratory and phonatory—Movements of the glottis during inspiration and expiration—Closure of the larynx, how effected—Nervous mechanism of the larynx, sensory source, motor source—Motor supply to the crico-thyroid ; origin of the motor fibres to this muscle in the horse—Recurrent laryngeal supplies abductor and adductor muscles—Effect of powerful stimulation of the divided recurrent—Effect of weak stimulation—Effect of stimulation under ether—Peculiarities observed in laryngeal paralysis—Effect on vocal cord of hemiplegia of larynx—Cause of the noise in roaring—Effect of section of the superior laryngeal nerve (Exner's experiment)—Suggested explanation of results—Cause of the voice, its pitch and quality—Action of the crico-thyroid muscle—Shape of the glottis in a high and low note—Use of the ventricles of the larynx—Character of the voice in different animals—Indications furnished by the voice—Central innervation of the larynx—Neighing, braying, bellowing, bleating, etc.—Yawning, sneezing—coughing, hiccough - - - - 103-110

CHAPTER VI.

DIGESTION.

Prehension of food—Method in different animals—Movements of the incisors of ruminants—The molar teeth—How the

PAGE

rough surface is produced--Growth of the teeth—Oblique tables of the molars ; how produced—Movements of the tongue—Differences in the tongue of the horse and ox—Nerve supply to the tongue, sensory, motor, and special sense—Drinking, lapping, and sucking, how produced—Mastication ; movements of the temporo-maxillary articulation—Use of the cartilaginous disc—Unilateral mastication in the horse—Difference in the width of the jaws in consequence—Explanation of sharp teeth—Length of time occupied in mastication—The muscles of mastication—Nerve supply of masticatory muscles—Deglutition, stages of—Use of the soft palate—How the larynx is protected—Effect of excising the epiglottis—Position of epiglottis—Effect of diverting the salivary flow on swallowing—Structure of the œsophagus in different animals—Nerve supply of swallowing—Inhibitory nerve of deglutition—Peristaltic nature of œsophageal wave - - - 111-119

The saliva—Classification of salivary glands—Amount of secretion—Influence of food on the amount—Physical and chemical characters of saliva—Microscopical appearance of saliva—Percentage of organic and mineral matter—Presence of mucin—Ptyalin—Salts of saliva—Gases—Physical properties of the three salivas—Secretion unilateral in the horse—Secretion during rumination and fasting—Effect of the sight of food on secretion—Use of saliva—Starch, its structure—Action of saliva on starch—Various changes from starch to sugar—Circumstances which modify the action—Difference between the starch produced by boiling acid and that formed by saliva—Saliva of herbivora probably non-amylolitic—Secretion of saliva—Nerve supply to the submaxillary gland—Function of the chorda—Function of the sympathetic—Effect on secretion of dividing the chorda and stimulating the mouth—Effect on the gland of stimulating the chorda—Character of the saliva produced—Sympathetic stimulation, effect on the gland—Character of the saliva—Evidence that blood pressure does not produce the secretion—Paralytic secretion—Explanation of the experiments—Changes occurring in the cells during secretion—Serous gland during rest and activity—Mucous gland during rest and activity - - - - 119-129

Stomach digestion—General considerations—Stomach digestion in the horse—Stomach rarely empty—Circumstances which regulate the passage of food through it—Most favourable distension for digestion—Rate at which the chyme passes out—Capacity of stomach—Peculiarities of the mucous membrane—The area over which the gastric juice is secreted—The secretion of mucin—Duodenal trap ;

PAGE

its function—The chief physiological points in the stomach of the horse—The digestion of hay—Amount of saliva hay absorbs—Appearance of the contents of stomach, colour and odour—No churning motion present—Compression present—Duration of hay digestion—Factors which regulate the rate—Digestion of oats—Time occupied—Appearance of the contents of the stomach—Arrangement of food in stomach—Influence of mixed diet on rate of output—Circumstances which disturb regular arrangement of food—Appearance of food acted upon by gastric juice—Reaction of stomach contents—Nature of the stomach acid—Gastric glands—Region of pyloric and fundus glands—Cells of the fundus and pyloric glands during rest and activity—The stomach mucin—Composition of gastric juice—Characters of the juice—Pepsin—Seat of its secretion—Function of pepsin—Acid necessary—Destruction of pepsin—Rennin—Its function—General action of gastric juice—Peptones, their characteristics—Amylolysis in the stomach—How induced—Cellulose digestion, how brought about—The various periods of stomach digestion—Stomach digestion in ruminants—Arrangement of rumen—Character of contents—Churning movement—Use of rumen—Percentage of cellulose digested—Other substances digested—Rumen never empty—Reticulum, character of contents—Function—Its power of contraction—Effect of excision on rumination—Omasum, character of contents—Function—Abomasum, function—Stomach digestion in pig—Peculiarity of pig's stomach—Digestive acid—Various stages of digestion—Stomach digestion in dog—Digestion slow—Absorption from the stomach—Percentage of proximate principles digested—No absorption from the stomach of the horse—No absorption from the first three reservoirs of ruminants—Active absorption from the stomach of pig and dog—Self-digestion of the stomach—Gases of the stomach 130-159

Vomiting—Reasons for the horse not vomiting—Vomiting in the horse a sign of ruptured stomach—The physiological features in vomiting—Rumination—The œsophageal groove—Its function—Experiments performed on it—Physiology of rumination—Conditions necessary for rumination—Salivary secretion during rumination—Nervous centre for rumination—Effect on rumination of dividing phrenics, vagus, and spinal cord—The movements of the stomach—No churning movement in the horse—The nervous mechanism of the stomach—Effect of section of the vagus—Central representation - - - - - 159-166

Intestinal digestion in the horse—The succus entericus—Its source and composition—Amount secreted—Function of

PAGE

the succus—Digestive value supposed to vary—Reaction of the intestinal contents—Physical characters of chyme—Function of the ileum—The chyme travels to and fro—Rapidity of digestion in the small intestines—The time. water takes to traverse them—The digestive juices poured into the bowel—Large intestines—Digestion in them important to solipeds—Large compared with the small intestines—The cæcum, its size, shape, inlet, and outlet—Character of the contents—Function of the cæcum—The length of time occupied by the food in reaching the cæcum —Digestion of cellulose and other matters—How the material is assisted to escape from the cæcum—The colon, peculiarity in its arrangement and calibre—Character and reaction of the ingesta in its different portions—Movements of large intestines—The function of the colon—Importance of the digestion of cellulose—Use of cellulose —Single colon, character of its contents—Rectum, reaction of the fæces—Absorption from the large intestines—Intestinal digestion in ruminants—Its subordinate position —Length of time it lasts—Intestinal digestion in the pig and dog—Statistics of the intestinal canal - - - 167-179

Nervous mechanism of the intestinal canal—Function of the vagus—Function of the sympathetic—The longitudinal and circular muscle have each a distinct source of supply—The normal stimulus to peristalsis—Effect of exercise and nervous excitement—Influence of nervous system on the secretion of intestinal fluid—Putrefactive processes in the intestinal canal—The causes of intestinal fermentation—Infusoria in the intestines—Gases in the intestines, their composition—The fæces, their nature and composition in different animals—Influence of food on the character of the fæces—Colour and reaction of fæces—Substances found in the fæces—Composition of the mineral matter of the fæces —Amount of fæces produced—Influence of the time of day —Number of evacuations—Odour of fæces—The act of defæcation—Meconium - - - - - 179-189

CHAPTER VII.

THE LIVER AND PANCREAS.

Source of the blood supplied to the liver—Bile, its colour, reaction, taste—Appearance of bile—Why that from gall-bladder is viscid—Composition of bile—Analysis of bile in different animals — Bile pigments — Vary in different animals—Solubility of the pigments—Gmelin's test—Source of the bile pigments—Composition of gall-stones—Bilirubin found elsewhere—Seat of bile pigment production—The

PAGE

bile salts—Where they are formed—Vary in different animals—Character of the salts—Influence of diet on cholalic acid—Difference between glyco- and tauro-cholic acid—Source of glycin—Pettenkofer's bile acid test—Origin of bile acids—Source of taurin—Source of cholalic acid—Bile pressure—Channel of bile absorption from liver—Secretion of bile constant—Its maximum in the dog—How the gall-bladder is filled and emptied—Amount of bile secreted in different animals—Character of food influences secretion—Use of bile—Its action on chyme, on fats, on free fatty acids—Its value in absorption—Supposed action on starch—On intestinal contents—Fate of the bile - 190-198

Glycogen, its characters — Difference between animal and vegetable starch—Proportion of sugar in blood—Source of glycogen—How it is liberated from the liver—Difference in the nature of the sugar reaching the liver and that leaving it—Amount of glycogen which can be stored in liver—Other seats of glycogen storing—The value of glycogen in nutrition — Use of glycogen — Sources of glycogen — Evidence that proteid can furnish sugar — Glycogen diminishes after death—Explanation of this, and how it can be prevented—Effect of arsenic on glycogen production, and of glycerine on glycogen conversion—Glucose destroying ferment in blood—Effect of removing pancreas—Evidences of this ferment—Diabetic puncture—Explanation of—Effect of division of splanchnics on diabetic puncture—Kaufmann's views on Bernard's puncture—Further uses of the liver ; the production of urea, etc., protects system against certain nitrogenous poisons - - - 198-204

The pancreas—Character of the fluid—Great variation in the organic solids—What these consist of—Use of the secretion—Its action on proteids, fat, and carbo-hydrates—The ferments which bring this about—Comparisons between peptic and pancreatic digestion—Action of the juice on starch—Form of sugar produced—Action on fats—Fat emulsion — Its value — Fat-splitting — Soap formation — Changes in the cells of the resting and active gland—Amount of secretion—Secretion continuous—Period of maximum secretion in ruminants—Maximum secretion in dogs — Pancreatic diabetes — Diabetes after excision of pancreas — Explanation of the phenomenon — Pancreas grafting—Influence of nervous system on secretion - 204-210

CHAPTER VIII.

ABSORPTION.

Lymph, its origin and function—Lymph spaces, capillaries, and vessels—Destination of lymph vessels—Appearance of

PAGE

their contents—Nature of the serous cavities—The intestinal villi, their structure, difference in herbivora and carnivora—The solitary follicles, their structure—Lymphatic glands, their structure—Lymph, colour, reaction, nature—Lymph clotting—Lymph gases and extractives—Lymph cells—Where the lymph obtains them—Source of the lymph cells—Lymph compared with blood—Quantity of lymph in body—Lymph formation, the physical and vital theories—Lymphagogues, their classification—Œdema, its causes—Movement of lymph in the vessels—Movement in thoracic duct—Pressure in thoracic duct—Velocity of lymph flow - - - - - - 211-225

Chyle, its distinction from lymph—Percentage of fat it contains—Reaction and colour—Movement of chyle - - 225-227

Absorption from the respiratory passages—From cellular tissue—From conjunctiva—From surface of skin—From a wound—From pleural and peritoneal cavities—Intestinal absorption, its rapidity—Paths of absorption, lacteals and blood-vessels—Absorption of fat by bowels—How the fat gains the lacteal—Fat embolism—How this is prevented in fat absorption—Absorption of sugar—Absorption of proteids—No peptone in portal vein, explanation of the fact - 228-235

CHAPTER IX.

THE SKIN.

Function of skin — Value of hairy covering — Amount of hair—Growth of hair, how regulated—Pigment in hair—Value of clipping—Erection of hair—Nerve supply to the hair—Sweat, seat of formation — Only certain animals sweat generally, several sweat locally—Two kinds of sweat—Probable amount of insensible sweat—Reaction, colour, odour, etc., of sweat—Composition of sweat—Proteids in sweat—Nervous influence in sweating, evidence—Evidence that blood supply is not essential — Effect of high temperature on sweating—Death sweating—Influence of pilocarpine on sweating — Action of drugs before and after dividing nerves to the sweat glands—Breaking out into sweats—The sweat nerve supply—Division of cervical sympathetic, effect in horse — Effect on muzzle of ox — Changes in the cells of active sweat glands—Amount of sweat—Amount of vapour passing from lungs and skin during rest and work — Certain parts of the body sweat more readily than others—Sebum, its source—Peculiarity of its secretion—Function of sebum—Dandruff, its composition—Nature of the skin fat—Amount in sheep—Colour-

PAGE

ing matter of dandruff—Respiratory function of skin—Varnishing the skin - - - - - 236-246

CHAPTER X.

THE URINE.

Vascular arrangements of the kidney—Swelling of kidney—Structure of Malpighian tuft—Peculiarity of its efferent vessels—Structure of Bowman's capsule—Tortuous arrangement of uriniferous tubes—Supposed use of this—Epithelial cells of the tubes, their special features in different parts—Secretion of urine depends on the blood-pressure, evidence — Profuse secretion may occur when blood-pressure is low, evidence—Dilatation of kidney without increase of general blood-pressure, how produced—Region of tubes where active secretion occurs—Region of kidney where urea, sugar, peptone, and salts are separated, and water secreted—Some substances are formed in the kidney—Amount of blood passing through the kidney - - 247-255

Composition of the urine—The organic constituents—The salts—Urea, its source from proteid—Its seat of formation—No urea in muscle, explanation—Other sources of urea—Daily amount of urea—Influence of diet—Percentage found in urine—Uric acid, its source — Production influenced by diet—Presence in herbivora—Seat of formation—Hippuric acid, food a source—Seat of formation—Combinations of hippuric acid—Amount of hippuric secreted—Influence of diet—Benzoic, its origin in the system—Its amount—Creatinin—Sulphuric acid, its two forms in the urine—Origin of sulphates—Ethereal sulphates, their source—Difference between carnivora and herbivora—Indican—Oxalic acid—Colouring matter—Seat of formation—Inorganic substances—Differ in various animals—Calcium, its combinations and source — Magnesium — Potassium—Sodium—Chlorine—Phosphoric acid—Importance of phosphoric acid in carnivora—Explanation of small amount in urine of herbivora—Ammonia—Reaction of urine—Source of alkalinity—Cause of acidity - - - - 255-267

Urine of horse, quantity, physical characters, total solids—Urine of rest and work—Urine of ox, quantity, influence of diet—Urine of calves—Urine of sheep, general features—Urine of pig, general features—Urine of dog—Great variation owing to diet, its general characters—Glycuronic acid—The discharge of urine — Structure of bladder — Nerve supply of bladder—Micturition centre—Micturition—Process in different animals - - - - 267-275

CHAPTER XI.

NUTRITION.

PAGE

Composition of the body—Proportion in various animals—Income, source of—Expenditure, chaunels of—Metabolism—Katabolism may occur through nerve channels, examples—Nitrogenous food — Effect on excretion of urea—Nitrogenous equilibrium—Conditions under which equilibrium experiment possible—Purely nitrogenous diet deficient in carbon—Proteid can furnish fat—Explanation of this—Circulating and tissue albumin — Metabolism of proteid leads to urea—Non-nitrogenous food cannot support life—Proteid-sparing action of fat—Explanation of the sparing action—Destruction of fat by proteid—Formation of fat in the body ; evidence that proteid food may supply it—Fat is not deposited in the form received—Explanation of the respiratory quotient of herbivora — Inorganic food, its function — Distribution of body salts — Potassium and sodium salts—Starvation—Effect on the urine of herbivora —Elimination of nitrogen during starvation—Excretion of CO_2 and absorption of O during starvation—Influence of water in prolonging life—Herbivora withstand starvation badly—Length of time horses, dogs, and sheep will live without food—Loss in weight of various organs during starvation—Cause of body waste—Internal and external work—Non-nitrogenous tissues supply heat and work—Urea no measure of muscular work—Explanation why proteid required as food—Energy yielded by food—Heat units and energy—Muscles are economical machines—Amount of food required—Subsistence diet for horse—Amount of elements it contains—Subsistence diet for ox and sheep—Working diet—Amount depends upon the pace —Fattening diet—Amount of food required by oxen, sheep, and pigs—Digestibility of food—Factors on which this depends—Influence of work on digestibility—Digestive coefficients in various animals - - - - 276-296

CHAPTER XII.

ANIMAL HEAT.

Definition of warm and cold blooded animals—Source of body heat—Seat of heat production—Influence of exercise—Glandular activity—Loss of heat, how brought about—Effect of heat and cold on body temperature—Explanation of the results—A high temperature not necessarily due to increased production of heat—Influence of season on meta-

PAGE

bolism—Clipping, effect on body temperature—Surface cooling the result of clipping—Evaporation from the lungs and mouth a source of heat loss—Influence of feeding and drinking on temperature—Shivering—Other causes affecting body temperature—Nervous mechanism of heat production—Thermotaxic mechanism—How this may be suspended experimentally—Central heat centres—Effect of fever—Amount of heat produced in different animals—Normal body temperature of animals—Circumstances which influence it—Temperature topography—Hybernation—Post-mortem temperature - - - - 297-307

CHAPTER XIII.

THE MUSCULAR SYSTEM.

Different muscular movements compared—Structure of muscle—Cause of the striation; Englemann's view; Haycraft's theory—Characteristics of striped muscle—Muscle, wave of contraction—Differences in red and pale muscle—Heart muscle—Chemical composition of muscle—Muscle plasma—Myosin, its origin—Glycogen and extractives in muscle—Gases in muscle—Gaseous exchange during contraction—Blood supply during contraction—Reaction of resting and active muscle—Heidenhain's views respecting heat and work produced in a muscle—Nerve supply of muscle, its function—Excitability of muscle—Muscle currents—A muscle curve—Changes occurring during the latent period—Influence of fatigue on latent period—Influence of successive contractions on muscle curve—Curve of tetanus—Contraction-remainder—Elastic after-effect—Effect of heat and cold on muscular contraction—Muscle fatigue, its cause—Effect of fatigue on muscle curve—Restoration of fatigued muscle—Exhaustion of motor end-plate—Influence of resistance to contraction—Relaxation of muscle—Electrical stimulation of red and pale muscle compared—The cause of a muscular contraction—Probable nature of 'inogen'—The oxygen of muscle—Changes, physical, chemical, and microscopical, occurring during a muscular contraction—Elasticity in muscle—Definition of elasticity—Advantage of muscles being elastic—Muscular tone—Muscle fatigue—Cause of the soreness—Condition—Several factors essential to its production—Rigor mortis, changes in the muscles, chemical and physical—Circumstances determining the rapidity of rigor mortis - - - - - - - 308-325

CHAPTER XIV.

THE NERVOUS SYSTEM.

PAGE

Classification of nerves—Afferent impressions are of various kinds—Efferent impressions vary—Structure of nerves—The essential feature in nerve structure—Ganglia—Nerve-cells, varieties of—Blood and lymphatic supply to nerves——Excitability of nerves—Electric currents in nerves—Electrotonus, definition of—Explanation of—Nature of nervous impulses, 'avalanche' theory—Conductivity of nerves — Velocity of nerve impulses — Degeneration of nerves, cause of—Changes occurring in a degenerated nerve—Nerve suturing—Trophic nerves—Nerve terminations - - - - - - - 326-336

Spinal cord, arrangement of—The white ramus, function of—Structure of the grey and white matter—Nerve cells of cord—Clarke's column—Distribution of nerves entering and leaving the cord—Function of the two roots—Function of spinal ganglion—Wallerian degeneration—Tracts in the cord descending and ascending—The great motor path—Termination of the tracts in the medulla—Afferent and efferent paths in the cord—Function of the superior and lateral columns—Path taken by voluntary motor impulses—Reflex action, definition of—Conditions necessary for—Characteristic reflexes in divided cord of dog—In cord of higher animals reflexes not complex—Reflex acts in locomotion—Examples of different kinds of reflex acts—Reflex time—Tendon reflexes—Co-ordinate movements—Automatic action, examples—Centres in cord - - 337-359

Medulla oblongata, how formed—Centres in—Function of medulla—Function of Pons—Crura cerebri—Basal ganglia, function of—Cerebellum, function of—Effect of injury to—Effect of total removal—How it influences locomotion - 359-365

Cerebrum, its convolutions—Moral sense in animals—Intelligence, reason, affection, courage, cowardice, physical suffering, memory, childishness—Reason and instinct—Complex reflex acts highly developed in newly-born animals — Effect of removing cerebral hemispheres—Frog experiment—Motor and sensory areas—Effect of removing parts of the cerebrum—Circulation—The brain—Coverings of the brain—Cerebral fluid—Movements of the brain - 365-376

The cranial nerves, third and fourth pair—Fifth pair, its division, function of each—Ganglia of the fifth—Bell's experiment on the horse—Explanation of the phenomenon—Sixth pair—Seventh pair, function—Effect of dividing the seventh—Eighth pair—Ninth pair, the special nerve of

PAGE

taste—Tenth pair, its distribution and arrangement—Its laryngeal branches—Cardiac branches—Branches for abdominal viscera—Effect of dividing the vagi on respiration and digestion—Eleventh and twelfth pair, effect of division - - - - - - - - 377-386

Sympathetic system—Peculiar character of nerve fibres—Ganglia—Function of ganglia—Changes in medullated nerves by passing through ganglia—Action of nicotin on nerve cells—Classification of sympathetic ganglia—Course of white and grey rami—The various fibres in the cervical sympathetic—Effect of dividing cervical sympathetic, vascular and nutritive changes—Effect of stimulating abdominal splanchnics—Effect of section—Function of these nerves—Extirpation of solar and mesenteric plexuses—Functions of the sympathetic - - - - 386-389

CHAPTER XV.

THE SENSES.

Sight—General arrangement of orbit and eye—Second cranial nerve, its decussation—The humours—Sclerotic and cornea—Shape of cornea—Structure of lens—Its elasticity—The iris—Structure and pigment—Muscle of iris—Nerve supply of iris—The pupil—Its direction in different animals—Corpora nigra, their function—Ligamentum pectinatum—Choroid, its structure—Tapetum lucidum, its structure and use—Ciliary muscle, its function; action of atropine on—The retina, arrangement and structure—Visual axis—Ophthalmoscopic appearance of fundus—Accommodation, its object—Mechanism of accommodation—Nature of emmetropia, myopia, and hypermetropia—Astigmatism—Katoptric phenomena—Movements of the eyeball—How affected by moving the head—Muscles of the eyeball—Nerve supply of muscles—How torsion of the globe is produced—Nerve supply of eyelids—Monocular and binocular vision in different animals—Explanation of binocular vision—Cartilago nictitans—The tears—Eyelashes - - 390-411

Physiological optics—The refractive media of the eye—The schematic eye—The reduced eye—Cardinal points of the eye—Passage of light through lenses; parallel rays, divergent rays, divergent rays beyond the focus, divergent rays within the focus—Formation of retinal image—The visual angle—Size of retinal image—Spherical aberration—Chromatic aberration - - - - - 411-419

PAGE

Smell, arrangement of nasal cavities—Olfactory nerves, their distribution, structure, and endings—Odours—Sense of smell in animals—Organ of Jacobson - - - 419-422

Taste, classification of tastes—Papillæ of tongue—Structure of taste-buds—Their number—Nerves of taste—Sensory and motor nerves of tongue—Sweet and bitter taste areas—Flavour - - - - - - - 422-424

Touch, temperature, and painful sensations—Touch organs—Temperature sensations—Pain, different kinds of—Muscle sense, its value—Thirst—Hunger - - - 424-427

Hearing—Nature of sound—Simple and compound sounds—Quality of sound—External ear—Its movements and their indications—Middle ear—Tympanum—Internal ear—The labyrinth, bony and membranous—Movements of tympanum and small bones—Arrangement of cochlea—Organ of Corti—Its nerve terminations—Auditory sensations, how they are transmitted from the external ear to the organ of Corti—Function of vestibule and semicircular canals—The guttural pouches - - - - - - 427-435

CHAPTER XVI.

THE LOCOMOTOR APPARATUS.

The lever—Examples in the body—Weight of the limbs—Co-operative antagonism, its use—Function of the fore and hind legs—Joints, their structure—Hock joint—Function of astragalus—Object of outward movement of stifle—Automatic flexion—Use of flexor metatarsi—Nature of the movement between tibia and astragalus—How over-flexion is prevented—Nature of the movement between the small bones—Where the greatest pressure occurs in the hock—Value of resting the hind-leg—The stifle—Its function—The patella—Hip joint—Shoulder joint—Elbow joint—Knee joint, movements of the small bones—Depression of the scaphoid—Its use—Cause of 'dishing,' 'brushing,' 'speedy cutting'—Fetlock joint, a yielding articulation—Advantages of this arrangement—Function of the suspensory ligament—Effect of dividing it—Effect of dividing the flexors—Function of check ligaments—Use of flexor and extensor tendons in leg—Use of the fascia of the arm and thigh—Centre of gravity—Distribution of the weight on the limbs—Effect of depressing or elevating the head—Distribution of the man's weight on the back—Why fore-legs suffer more than hind—Structure and function of the limbs in relation to lameness—Nature of the strains to which the limb is exposed—A comparison of how these

strains affect the fore and hind leg—Nature of the anti-concussion mechanisms in the limbs—How they are provided by the bones, muscles, and tendons—Influence of fatigue on bones and tendons—How sprains occur—The lessons learned from fracture of the pastern—The compression to which the suffraginis and corona are exposed—The act of standing—Lying down—Rising—The walk—The trot—Cause of stumbling—The amble—The canter—The gallop—How the foot and limbs come to the ground in all fast paces—Jumping—Rearing, kicking, etc.—The normal daily work of horses—Velocity—Weight carried—Draught—Amount of force a horse can exert - 436-465

CHAPTER XVII.

THE FOOT.

General considerations—Bones of the foot—Foot joint, its peculiarities—Use of the navicular bone—Movements between the tendon and navicular bone—How the navicular becomes compressed—Lateral cartilages, their arrangement—Plantar cushion—Corium of foot—Vascular wall—Arrangement of laminæ—Sub-laminal tissue—Microscopical appearance of the laminæ—The secondary laminæ—The wall-secreting substance—The vascular sole—Blood supply to foot—The hoof, general arrangement—The wall—The periople—Length and thickness of wall—Reason of variations in thickness—Origin of the bars—Horny laminæ—Arrangement of the two laminal surfaces—The sole—Shape and thickness—Growth of horn of sole and wall compared—The horn at the junction of wall and sole—The foot-pad—Nature of its horn—Method of wear—Microscopical structure of horn—The horn cells, shape and straining reaction—Effect of alkali on horn—Horn tubes, how formed—Papillated and non-papillated horn secreting surface—Difference between the horn secreted by these—Use of the canal system in horn—Evaporation from the foot—Sweat-glands in foot-pad—Use of moisture in the foot—Distinction between dry and moist horn—Analysis of the horn of the foot—Keratin—Elements found in horn—The wall, how arranged for wear and tear—Two main features provided for in the wall—Its regular growth—The age of the wall—Value of a wall of varying age—How the weight is carried by the foot—Total number of primary and secondary laminæ—Difference between the anterior and posterior laminæ—Relation of the posterior

PAGE

laminæ to the lateral cartilages — Use of the laminæ— Strain to which the laminæ are exposed—Effect of destroying the union between the laminæ—Where the laminæ grow from—Evidence against the vascular secreting the horny laminæ—The gliding movement between the leaves—Use of the bars—Use of the sole—Evidence that it is not a weight-supporter—Use of the foot-pad—Conditions necessary for a healthy foot-pad—Lateral cartilages, their uses—Movements of the cartilages—Anti-concussion mechanisms —Expansion of the foot—Amount of—Other alterations in shape—Advantages of expansion and other movements —Compression of the wall—Descent of pedal bone, its use —Vascular mechanism, how assisted—Pumping action in the foot—Physiological shoeing - - - 466-503

CHAPTER XVIII.

GENERATION AND DEVELOPMENT.

Spermatic fluid, its composition — Spermatozoa — Erection, mechanism of—Ejaculation—Division of the nerves of the penis—Sexual intercourse—Erection of the uterus—Period of puberty—Ovaries—Germinal epithelium—Ovulation—The ovum—Polar bodies—Testicles, their development and formation of spermatozoa—Segmentation of the ovum—Organs developed from the epiblast, from the mesoblast, from the hypoblast—Growth of the embryo—Placentæ—Formation of membranes—Composition of amniotic fluid—Function of fluid—Composition of allantoic fluid—Hippomanes—Union of chorion to uterus—Structure of umbilical cord — Embryonic circulation — Fœtal circulation — Difference in that of ruminant and soliped—Duration of pregnancy—Uterine milk—Parturition - - 504-533

Secretion of milk—Appearance of the alveoli of active and passive gland — Changes in the cells during secretion—Evidence that the milk is a secretion—Composition of milk —Analysis of milk in different animals—Salts of milk compared with the body requirements—Colostrum - 534-538

CHAPTER XIX.

GROWTH, DECAY, AND DEATH.

Growth rapid—Great development of nervous system at birth—Development of the body after birth—Rate of increase in weight—Rate of growth—Dentition in horse, ox, sheep, and pig — Influence of feeding on development — Decay—Death - - - - - - - 539-546

PAGE

APPENDIX.

THE CHEMICAL CONSTITUENTS OF THE BODY.

The elements—Proteids, composition, classification, and tests—Ferments — Pigments — Nitrogenous fats — Amides and amida acids—The urea and uric acid group—The aromatic series—The indigo series—Bile acids—Fats and their components — Carbo-hydrates—The starch group — The sugar group — Tests for sugar — Inorganic constituents of the body - - - - - - - - 547-560

A

MANUAL OF VETERINARY PHYSIOLOGY.

CHAPTER I.

THE BLOOD.

The special functions of the blood are to nourish all the tissues of the body, and thus aid in their growth and repair; to furnish material for the purpose of the body secretions, to supply the organism with oxygen without which life is impossible, and finally to convey from the tissues the products of their activity.

To enable all this to be carried out the blood is constantly in circulation, is rapidly renewed, is instantaneously purified in the lungs, and by means of certain channels it is placed directly in communication with the nourishing fluid absorbed from the intestines by which it is being constantly repaired.

Physical Characters of the Blood.—The colour of blood varies, depending upon whether it is drawn from an artery or a vein; in the former it is of a bright scarlet colour, whilst in the latter it is of a purplish red. The colour of the blood is due to a pigment called hæmoglobin contained in the red corpuscles. This substance is peculiar because it differs from allied proteids in containing iron, and in being crystallisable. The scarlet or purplish colour of the blood depends on the amount of oxygen with which the hæmoglobin is combined.

The reaction of blood is alkaline; as the process of

coagulation occurs this alkalinity diminishes. The alkaline reaction is due to the phosphate and bicarbonate of soda found in the fluid; the decreasing alkalinity observed on standing is probably due to the formation of an acid. The alkalinity of the blood is reduced by muscular work, owing to the production of an acid by the muscles.

The odour of blood is believed to be due to a volatile body of the fatty acid series. The blood of the cat and dog has a peculiar and decidedly disagreeable smell; such is not observed in the blood of the horse and ox, though it is said that the odour of butyric acid can always be obtained from the blood of the latter by heating it with sulphuric acid.

The taste of blood is saltish, due to the amount of sodium chloride contained in the serum.

The specific gravity varies in different animals: in the horse, ox and pig, 1060; sheep, 1050-1058; dog, 1050 (Colin). According to Hoppe-Seyler the specific gravity of the liquor sanguinis of the horse is 1027 to 1028, and the specific gravity of the cells 1105. The considerable difference between the specific gravity of the cells and the liquor sanguinis in the horse, accounts for the rapid manner in which the cells sink in blood drawn from the body, producing during the process of clotting the so-called 'buffy coat.'

The **composition of the blood** of animals will, as might be expected, possess almost absolute uniformity so far as the presence of various substances is concerned; the amount of these substances, however, will vary in animals of different classes. The source from which the blood is taken will also affect its composition, for the blood from an artery does not represent exactly that found in a vein.

Blood contains:

1. Liquor sanguinis or Plasma, containing in solution proteids, extractives, mineral matter and gases.
2. Corpuscles.
   - *α*. Red corpuscles.
   - *β*. White ,,

The **Liquor Sanguinis**, or **Plasma**, forms about 66 per cent.

of the total blood; it is an albuminous fluid possessing a small and variable amount of a yellow colouring matter of a fatty nature. It contains at least three proteids, one of which may by certain processes be shown to be composed of two or three others. The proteids are:

Serum albumin.
Serum globulin.
Fibrinogen.

During the life of the blood the liquor sanguinis is termed the plasma, but after it has been shed from the body and coagulation has occurred, the liquid residue is called serum. **Serum** is, therefore, plasma which is modified as the result of coagulation, and as this latter process is attended by the production of fibrin, we may say that serum is plasma minus the fibrin-forming elements. Perhaps the nearest approach to pure plasma is the fluid found in the pericardium and abdominal cavity.

The fluid poured into the pleural cavity during pleurisy is plasma to start with, but if the fibrin in it becomes thrown down (forming the so-called false membranes), the remaining fluid is converted into serum which is no longer coagulable.

The **Proteids of Serum** are serum albumin and serum globulin, and in addition there is the ferment produced as the result of coagulation; fibrinogen does not occur, having been used up in the process of coagulation. The following table from Halliburton* exhibits these points:

Proteids of the Plasma.	*Proteids of the Serum.*
Fibrinogen.	Serum globulin.
Serum globulin.	Serum albumin.
Serum albumin.	Fibrin ferment.

It has been shown that the proportion in which serum globulin and serum albumin exist in the blood varies in different animals. In the horse and ox the globulins are in excess of the albumins; in man and the rabbit this

* 'A Text-book of Chemical Physiology.'

is reversed; the following table is from Gamgee,* after Hammarsten:

Variety of Serum.	Total Solids in 100 parts.	Total Proteids in 100 parts.	Serum Globulin in 100 parts.	Serum Albumin in 100 parts.	Lecithin, Fats, Salts, etc., in 100 parts.	Serum Globulin to Serum Albumin.
From blood of horse -	8·597	7·257	4·565	2·677	1·340	$\frac{1}{0·591}$
,, ,, ox -	8·965	7·499	4·169	3·329	1·466	$\frac{1}{0·842}$
,, ,, man -	9·207	7·619	3·103	4·561	1·587	$\frac{1}{1·511}$
,, ,, rabbit -	7·525	6·225	1·788	4·436	1·299	$\frac{1}{2·5}$

The table shows that the amount of total proteids is more regular than the different albumins of which they are composed.

Serum globulin (also known as paraglobulin and fibrinoplastic substance) exists in different proportions in the blood of domestic animals; its greatest interest lies perhaps in the part it was supposed to play in the process of coagulation, a part which we have now good reason to believe does not exist.

Fibrinogen is the precursor of fibrin in the blood—a substance we shall have more to say about in dealing with coagulation—it is found in blood plasma, but not in the serum; it also exists in the fluids thrown out into the cavity of the chest, pericardium, etc.

Corpuscles of the Blood.—Blood examined under the microscope is found to consist of an enormous number of bodies termed corpuscles floating in the liquor sanguinis. These corpuscles are found to be both red and white; the former are the most numerous, the latter are the largest.

The **Red Corpuscles** constitute 33 per cent. or one-third of the total blood. Viewed under the microscope, they are found to be biconcave discs, circular in shape, and

* 'Physiological Chemistry.'

possessing no nucleus, though, owing to their shape, certain focussing may produce a dark centre which might be mistaken for a nucleus, but which is really an optical effect.

In all mammals excepting the Camel tribe the red cells are circular; in all vertebrates below mammals the red cells are bi-convex, oval, and nucleated.

The red cells in some animals have a tendency to lie on top of each other in the form of piles of pence; this condition, which is not marked in the blood of the horse, is spoken of as forming rouleaux. The circular shape of the red cell is affected by the amount of fluid in the blood; where this is small, as occurs in many diseases, the corpuscles become covered with spines or projections; when the fluid is in excess the corpuscles swell.

A red blood cell is composed of a stroma, holding in its meshes the red colouring matter. The stroma or framework of the corpuscle consists of an albuminous material allied to the globulins, and a fatty matter termed lecithin; the red colouring matter consists of an albuminous crystalline substance, hæmoglobin, which forms no less than 90 per cent. of the total solid matter of the corpuscle.

The number of corpuscles in the blood is approximately determined either by the method of Gowers or Malassez. The principle on which these are based is the same—a known quantity of blood is diluted with a known bulk of artificial serum and accurately mixed; of this a small drop is placed in a counting-chamber, which is ruled into squares, and examined under the microscope. The blood cells occupying the squares are counted, which can readily be done, and the mean of them taken.

In the horse the mean number of red blood corpuscles per cubic millimetre* is 7,212,500, and in the ox 5,073,000. Taking the amount of blood in the horse at 66 lbs., this gives 204,113,750,000,000 as the approximate number of red cells in the body (Ellenberger).† It is evident that a

* A cube having its edges about one-twenty-fifth of an inch.

† 'Physiologie der Haussäugethiere.'

loss of water from the blood means a larger relative proportion of red cells present, while an excess of water by diluting the blood would show a loss of red cells; thus the number of the red cells is increased by sweating, by the excretion of water from the bowels and kidneys, and by starvation, while they are diminished by pregnancy and copious draughts of water. But apart from these conditions, it is undoubted that an actual increase or decrease in the number of red cells may exist, especially is this marked in some diseases.

Each red cell offers a certain absorbing surface for oxygen, which, if calculated on the total number of corpuscles, is something enormous, being equal for the horse to a square having a side of 180 yards.

The opacity of blood is due to the red cells reflecting light owing to their peculiar shape; if the cells be destroyed either by freezing and thawing the blood alternately, or by the passage through it of electric shocks, or by the addition of certain agents such as chloroform, ether, bile salts, water, etc., the hæmoglobin becomes liberated from the broken-up cell and stains the naturally yellow serum of a red colour. Further, the destruction of the corpuscles leads to the blood becoming transparent or, as it is termed, 'laky.'

The greater part of the red cell is hæmoglobin, a substance possessing a remarkable affinity for oxygen; this it obtains at the lungs and leaves behind it in the tissues. The hæmoglobin of the red cells, therefore, exists in two states, one in which it is charged with oxygen called oxy-hæmoglobin, and the other in which it has lost its oxygen known as reduced hæmoglobin. The process of oxidation and partial reduction is constantly occurring at every revolution of the circulation, with the ultimate result that the red blood disc gets worn out and dies. In this condition it is cast off from the system, being got rid of through the medium of the liver, and also, probably, destroyed in the spleen and elsewhere. When the red cells die their hæmoglobin is set free, and decomposed into an iron

free residue, from which, probably, all the pigments of the body are formed, especially those of the bile.

The production of red cells is a matter of extreme rapidity, as may be witnessed for example after hæmorrhage; the seat of their formation is in the red marrow of bones, where they are formed from certain nucleated cells; these cells are known as hæmatoblasts. All other seats of formation are doubtful, and the idea that the red cell is derived from the white is not now accepted.

In the embryo the red cells for a certain period are nucleated and contain no hæmoglobin, but these are gradually replaced by non-nucleated hæmoglobin-holding corpuscles before birth.

It is interesting to observe that both in the embryo and in the adult the red cells are derived from a nucleated predecessor.

We have mentioned that retained in the pores of the stroma of the red cells is the red colouring substance hæmoglobin, and with this we must now deal.

Hæmoglobin, also known as hæmato-globulin, and hæmato-crystalline, is a most remarkable body; it is a proteid yet it crystallises, whilst its behaviour in the dialyser is not that of a colloid but a crystalloid. It is one of the most complex substances in organic chemistry, containing C, H, O, N, S, and Fe, and its molecule is an enormous one, the molecular weight being quoted at 13,000 to 14,000.

Crystals of hæmoglobin are of a dark-red or bluish colour; they are extremely soluble in water, and are remarkable for being the most important proximate constituent of the body containing iron, the amount being about ·4 per cent.

The total amount of hæmoglobin in a horse's body is about 8·8 lbs., and the amount of iron contained in this is about 257 grains. This calculation is based on the assumption that the amount of blood in the body is 66 lbs.

In the red blood cells hæmoglobin exists in the proportion

of 86 to 94 per cent., whilst in the total blood of the horse it forms 13·15 per cent., in the ox 9·96 per cent., sheep 10·34 per cent., pig 12·7 per cent., and dog 9·77 per cent. (Ellenberger).* The younger the animal the less hæmoglobin; males have more than females, and castrated animals more than entires (G. Müller).†

Hæmoglobin has a remarkable affinity for oxygen, and the laws relating to the absorption of gases by fluids and solids do not apply—as we shall see later when dealing with Respiration—to the absorption of oxygen by hæmoglobin. At standard temperature and pressure 15½ grains of hæmoglobin will absorb ·095 cubic inches of oxygen gas.

We have mentioned that when hæmoglobin is charged with oxygen it is spoken of as oxy-hæmoglobin; when it has discharged its oxygen, which it is capable of doing with considerable facility, it is spoken of as reduced hæmoglobin, or simply as hæmoglobin. These, therefore, are its two conditions of oxidation; as oxy-hæmoglobin it is charged in the capillaries of the lungs, brought back to the heart and distributed all over the body; as partly reduced hæmoglobin it is produced in the tissues, and brought back by the veins to the heart for distribution to the lungs, where it renews its oxidized condition. Hæmoglobin is never completely reduced in the body, excepting in the last stage of asphyxia.

Oxy-hæmoglobin crystallises in some animals, horse, cat, dog, and guinea-pig, with facility; in others, ox, sheep, and pig, with difficulty. The crystals are generally rhombic plates and prisms; but the form differs according to the animal. Reduced hæmoglobin can only be crystallised with great difficulty in an atmosphere free from oxygen.

The two hæmoglobins produce quite distinctive spectra when examined by the spectroscope, by which they may be readily recognised. To put the matter roughly, oxy-hæmoglobin gives two well-marked dark absorption bands or shadows in the green portion of the spectrum, one band being wide, the other narrow; while reduced hæmoglobin

* 'Physiologie der Haussäugethiere.' † *Ibid.*

gives one wide single band in nearly the same position (Fig. 1).

Oxygen and hæmoglobin are so lightly bound together that they are readily separated; oxygen is given off if the blood be placed in a vacuum or boiled, or if it be brought in contact with indifferent gases such as nitrogen and hydrogen; it is the facility with which hæmoglobin parts with its oxygen which enables the tissues to obtain it.

Hæmoglobin forms certain compounds with oxygen, carbonic oxide, and nitric oxide:

With oxygen it forms oxy-hæmoglobin and methæmoglobin.
,, carbonic oxide it forms CO hæmoglobin.
,, nitric oxide ,, NO ,,

Oxy-hæmoglobin we have dealt with; the others, in a

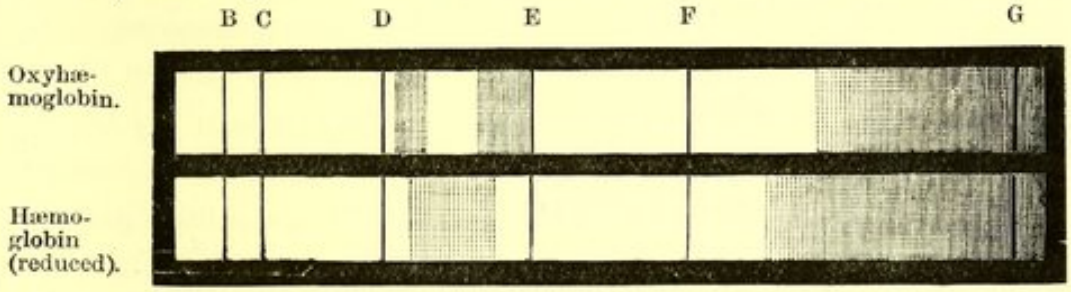


Fig. 1.—Blood Spectra (Waller).

work of this kind, can only receive a short notice at our hands, though the subject is one which is full of interest.

Methæmoglobin is produced by allowing blood to be exposed to the air until it becomes brown in colour and acid in reaction; or it may be prepared by the action of acids or alkalies on oxy-hæmoglobin. This substance parts from its oxygen with difficulty, and gives a three-banded spectrum.

Carbonic Oxide Hæmoglobin. — In this compound the oxygen is displaced by carbonic oxide, which forms a stable compound with the hæmoglobin and is not displaced on breathing oxygen; hence the rapidly fatal results of this form of poisoning. The blood of people who have died from CO poisoning is of a cherry-red colour, and yields the spectrum of CO hæmoglobin—viz., two bands very much like those of oxy-hæmoglobin, but situated nearer to the

violet end of the spectrum. **Nitric oxide hæmoglobin** in many respects resembles CO hæmoglobin.

Hæmoglobin may be decomposed either by boiling or the addition of alkalies, acids, or acid salts; in either case it splits up into a substance containing all the iron of the hæmoglobin known as **hæmatin**, and a proteid substance or substances termed **globin**.

Hæmatin strongly resembles iodine in appearance; it has a metallic lustre, a blue-black colour, is free from crystalline formation, and yields a dark brown powder when pulverised which contains 8·82 per cent. of iron.

Hæmatin is a remarkably stable substance, and the colouring matter presents a distinctive spectrum both in an acid and alkaline solution.

When hæmatin is boiled with glacial acetic acid and common salt it yields **hæmin**, which, microscopically, is found to consist of prismatic crystals, dark, or nearly black in colour. Hoppe-Seyler considers this substance to be hydrochloride of hæmatin. The ready production of hæmin crystals by warming the dried blood with a drop of glacial acetic acid on a slide is used as a microscopical test, but it is said that in the blood of the ox and pig hæmin can only be obtained in very irregular crystalline masses.

There are other derivatives of hæmatin, such as **Hæmochromogen**, which is produced by the action of acids or alkalies on reduced hæmoglobin in the entire absence of oxygen; **Hæmatoporphyrin**, which is obtained by the action of strong sulphuric acid on hæmatin, which thereby loses its iron; hæmatoporphyrin is really hæmatin from which the iron has been removed.

Hæmatoidin is found in old blood-clots and in the ovary; it is an iron-free product of hæmatin, and gives the same reaction with nitric acid as bile pigment, viz., a play of colours; hæmatoidin is, in fact, chemically identical with bilirubin, and the name is only retained as a matter of convenience.

The connection between hæmin, hæmatin, and bile pigments has recently assumed a new light, which though

not absolutely accepted by physiologists (and so must be received with caution) yet facilitates our conception of the production of iron-free bile pigments from iron-containing hæmoglobin. The view is as follows: When hæmin is decomposed by caustic alkali it yields hæmatin; this latter treated with strong sulphuric acid loses its iron, and uniting with oxygen yields hæmatoporphyrin or iron-free hæmatin; this latter is found to be isomeric with bilirubin.*

The **White Corpuscles**, also termed leucocytes, are found in blood, lymph, pus, connective tissue, etc.; they exist in blood in the proportion of 1 in 300 to 1 in 700, the proportion varying according to the vessel from which the blood is examined. In the splenic artery there are very few, in the splenic vein they are exceedingly numerous. Blood which has been removed from the vessels contains but few, for the reason that they are probably broken down during the formation of fibrin.

The white corpuscle is somewhat larger than the red; it consists of a granular-looking protoplasm, within which is a nucleus; the nucleus shows no sign of a nuclear network, which is a distinguishing difference between the white cell and its very close ally the lymph cell.

The granular condition of the corpuscle is due to minute particles of fat, proteid, and probably other substances, which are on their way either to or from the tissues, probably both. These corpuscles possess no cell-wall or envelope.

The white corpuscles are capable of undergoing changes in shape; the movements known as amœboid are exhibited by projections shooting out from the surface and being again retracted; the amœboid movements are destroyed by heat or by shocks from an induction coil.

The white corpuscle has the power of taking up into its interior small particles of colouring matter, bacteria, etc., the value of which will presently be alluded to.

The changes in shape which the white corpuscle is capable of undergoing, assist it materially in its passage through the wall of the vessel into the tissues. The process

* S. Lea.—Foster's 'Text-book of Physiology.'

is termed diapedesis; within moderation it is a perfectly normal phenomenon, though under inflammatory and other disturbing influences it becomes greatly exaggerated.

The white corpuscles contain about 10 per cent. of solids, which consist of serum globulin, serum albumin, and myosin, or its precursor, myosinogen, as myosin probably only occurs after death; this myosin appears to be an intermediate body between globulin and fibrin. Another nitrogenous principle is nuclein, which is largely found in the corpuscle, it is remarkable for being a very stable substance and also for containing phosphorus. Besides these we have the complex fatty body lecithin, cholesterin, glycogen (especially in the horse), and salts, the latter principally phosphates being probably derived from the phosphorus containing compounds.

The origin of the white corpuscles is from the lymphatic system, from which they enter the blood stream through the large lymphatic channels opening into the vena cava at the junction of the two jugular veins. The white corpuscles, as well as the red, are constantly being used up and as constantly replaced. This using up consists in the power they possess of passing through the walls of the vessels into the surrounding tissues, from which they are removed by the lymph channels, and so find their way back to the blood.

No doubt many corpuscles leave the blood the destruction of which we are unable to account for, but it is suggested that by their death they influence the composition of the blood plasma, as in this fluid their component parts must become dissolved after their death.

During the life of the white corpuscle great activity prevails, it is constantly giving up and taking in material which must affect the composition of the plasma. It is known that the white cell possesses the power of digesting certain substances, both solid and liquid; the researches of Metschnikoff have paved the way towards a better understanding of the probable manner in which protection against certain diseases is obtained; he has shown that the white

cells take the bacteria up into their interior and digest them; it is really a fight between bacteria and leucocytes. The protection afforded to the system by the white blood-cells is therefore not the least important of the functions performed by them.

On the death of the blood the white cells yield the so-called fibrin ferment, which produces the clotting of the blood.

A **Third Corpuscle** is described as found in the blood, termed by some **Hæmatoblasts**, and by others **Blood-plates.** The term hæmatoblast is somewhat misleading, as it is probable that the blood-plates take no part in supplying the red corpuscles; their function and nature is unknown, though according to some they take an active part in that obscure process the clotting of the blood. Blood-plates are found in large numbers in the white thrombi formed in vessels, and they may be readily obtained by passing a thread through a bloodvessel, or suspending threads in freshly-drawn blood (Bizzozero). Semmer calls these plates red granular corpuscles; he states that they exhibit amœboid movement, and that they are found in the blood of the horse and other animals.

Coagulation.—We are now brought to a consideration of the subject of blood-clotting, a process by which the naturally fluid blood becomes converted into a solid.

If blood be drawn from the body and left at rest, it will be found within a few minutes to have undergone the process of clotting, the fluid first becomes a jelly and then a firm clot or crassamentum, taking a complete cast of the vessel in which it is placed, and so firm in consistence that the vessel may be inverted without any blood being lost. In a short time, fluid which has been produced by the process of contraction may be seen on the surface of the clot, and in the course of a few hours the clot commences to sink in the now abundant serum which has collected as the result of this process. The blood of the horse is remarkable for the slow rate at which coagulation occurs, and the red cells being specifically heavier than the plasma have time to fall in the fluid before the process is com-

pleted, the result being that the upper solid layer is considerably decolourised, forming the so-called **Buffy coat**, which though considered to be natural to the horse, is indicative in other animals of the presence of an inflammatory process in the system.

We have here closely followed the account given by human physiologists of the coagulation of the blood in the horse, but the appearance described is by no means invariable; coagulation in this animal is often complete in less than five minutes, when, of course, no buffy coat forms, and we are inclined to believe that rapid coagulation and non-buffy coat are the rule rather than the exception; we have repeatedly observed the blood of the horse clot so rapidly as to be almost instantaneous.

The average time occupied in coagulation varies in different animals, but according to Nasse is as follows:

Pig	- - -	½ to 1½	minutes.
Sheep	- - -	½ „ 1½	„
Dog	- - -	1 „ 3	„
Ox	- - -	5 „ 13	„
Horse	- - -	5 „ 13	„

In my experience the extreme time mentioned for the horse is exceptionally long.

If the clot be examined microscopically, it is found to consist of fine fibrils, entangled in which are the blood corpuscles; if the fibrin produced be washed completely free from blood, its appearance is well described by its name.

If instead of allowing the blood to clot spontaneously it be whipped with a rod or bunch of twigs, the fibrin separates rapidly and coats the rod, whilst coagulation in the remaining fluid is absolutely prevented. The power of spontaneous clotting lies then in the production of fibrin.

These changes may be graphically represented thus:

Clotting.

Blood. { Plasma. { Serum. / Fibrin. } Clot.
Blood. { Corpuscles. { Red. / White. / Blood platelets. } Clot.

(Halliburton.)

		When Whipped.	
Blood.	Plasma.	Fibrin.	
		Serum.	
	Corpuscles.	Red.	Defibrinated blood.
		White.	
		Blood tablets.	

Fibrin is a yellowish-white, stringy-looking, bulky mass; it may be dissolved by hydrochloric acid forming acid albumin or syntonin, also by dilute alkalies with the production of alkali albumin. Its general appearance would lead to the belief that it exists in blood in large quantities, it is found, however, to be by weight relatively small: in human blood its proportion is ·2 per cent.; sheep, ·2 to ·3 per cent.; ox, ·3 to ·4 per cent.; horse, ·4 per cent.; pig, ·4 to ·5 per cent.; dog ·2 per cent.

Fibrin is produced by the action of the **fibrin ferment** on fibrinogen, the whole of the latter being used up in the process. The ferment does not exist in living blood, but is produced by the disintegration of the white corpuscles immediately the blood is shed. Schmidt's view that fibrin can only be produced by the action of the fibrin ferment on fibrinogen and serum globulin, is held to be against the weight of evidence, which points to the presence of serum globulin as being unnecessary to coagulation.

The presence of calcium or its salts is necessary for the conversion of fibrinogen into fibrin; in fact the latest view on the matter is that fibrin is a calcium compound of fibrinogen, and that the main action of the ferment is the handing over of calcium to fibrinogen (Halliburton).*

This view is the outcome of the discovery by Arthus and Pagès that blood may be kept liquid by decalcification, such as by mixing it with a ·1 per cent. solution of potassium oxalate.

The **Theories of Coagulation** may be reduced to two in number—viz., Hammarsten's and Wooldridge's.

Hammarsten believes the clotting of blood to be brought

* Goulstonian Lectures, 'The Chemical Physiology of the Animal Cell,' reviewing the work of Green, Arthus, Pagès, and Pekelharing.

about by the action of a ferment on fibrinogen converting it into solid fibrin, the ferment being produced by the white cells and blood platelets.

Wooldridge regarded blood-clotting as independent of a ferment, but resulting from the interaction between two or more fluid fibrinogens, the chemical composition of which should differ sufficiently to permit of interchange occurring between them.*

We cannot pretend to judge between these rival theories, but at the present time the view most generally accepted is Hammarsten's, and as a simple working hypothesis it commends itself. The observations which support it are the following: If a solution of fibrinogen be prepared in a pure condition, it will clot on the addition of the ferment, the fibrinogen by itself being non-coagulable; conversely, if fibrinogen be removed from a fluid the latter will not coagulate even on the addition of the ferment. Certain fluids, serum from the pericardial sac, etc., may be made to coagulate on the addition of a little washed blood clot, which contains the ferment in considerable quantities.

Experiments made by injecting into the vessels of animals the active fibrin ferment, do not lead to coagulation of the blood in the vessels as we might suppose; the ferment is either destroyed, or else fibrinogen is not present; the former is the most likely.

Fibrin Ferment.—The term 'ferment' in connection with fibrin is used more as a convenient expression than as an actual statement of its action. In fact, if Pekelharing's view is correct that the ferment is a calcium carrier (see p. 15), it is probable that the term will in course of time have to be abandoned.

Wooldridge showed that the injection into the circulation of the living animal of watery extracts of certain glands, such as the thymus, testicle, etc., produced instantaneous

* From the introduction by Professor Horsley to 'The Chemistry of the Blood and other Scientific Papers,' by the late L. C. Wooldridge, M.D., D.Sc.

clotting of the blood; he attributed this to the 'tissue fibrinogen' contained in the extract, and regarded the experiment as proving that blood-clotting could be produced without a fibrin ferment.

It would appear that the substances isolated by various observers, and to which such names as fibrino-plastic substance, fibrin ferment, cell globulin, tissue fibrinogen, etc., have been given, are all varieties of one substance which Pekelharing's investigations cause him to class with nucleo-albumin, which in co-operation with calcium compounds brings about coagulation of the blood (Halliburton).*

The similarity between blood-clotting and milk-curdling has been recognised for many years. In the curdling of milk by the addition of rennet the presence of a calcium salt is necessary, for without it none can occur.

Circumstances influencing Coagulation.—It is a matter of common observation, that after death the coagulation of blood in the vessels is a slow process, though by exposure to the air clotting is almost at once produced; it was supposed that the air in some way influenced this, but it has been shown that the action is rather due to the influence on the blood exerted by the wall of the vessel. The jugular vein of a horse has been included between ligatures and excised, yet the blood has remained fluid in it for one or two days, though suspended in such a way as to be left freely exposed to the air; nevertheless on removal from the vein clotting has at once occurred.

While the vein is suspended the corpuscles sink, and it is found that the plasma in the upper layer has considerably lost its power of coagulation, though the blood drawn from the lower stratum clots readily. This is regarded as evidence that the corpuscles take an active part in the production of clotting. Such was the view held by Schmidt, who maintained that the white corpuscles were rapidly dissolved in the plasma, in the horse to the extent of 71·7 per cent., and that the result of this dissolution was serum globulin and the fibrin ferment.

* *Op. cit.*

When bloodvessels are injured during life, or when pathological changes occur in the blood, coagulation in the vessels will take place; this is due to the influence exercised over the blood by the injured vascular wall which acts like a foreign body.

Clotting in dead blood may be retarded or hastened by certain conditions. The blood of a horse received into a vessel so constructed as to expose it to a freezing temperature may be kept fluid for an indefinite period, though coagulation will at once occur when the temperature is allowed to rise. Clotting is delayed by the addition to the blood of the neutral salts of the alkalies and earths, ammonia, and sulphate of magnesia. The addition of acetic acid or a current of carbonic acid entirely prevents it, by precipitating the fibrinogen.

On adding to blood even a weak solution of potassium oxalate, lime oxalate is formed and clotting prevented, as without the lime no fibrin can be produced. Wright has shown that the administration of citric acid to the living animal renders the blood uncoagulable, and this it effects by binding up the lime salts. If peptone be injected into the blood of the dog such blood will not clot, and much the same effect is produced if instead of peptone an extract of the ordinary medicinal leech be used; on the other hand, injection into the living blood of Wooldridge's 'tissue fibrinogen' produces instantaneous clotting. Wright has shown that the addition of lime salts to the blood, or the inhalation of carbonic acid, increases the coagulability of the fluid.

By rapidly heating blood to 133° F., by which means the fibrin-forming substances are precipitated, clotting is prevented; it is also considerably retarded if the blood be exposed to the action of oil in the vessel in which it is collected.

The shape of the collecting vessel has an influence over coagulation, clotting being much slower in a smooth deep vessel than in a rough shallow one.

The **Extractives of the Blood** are fats, cholesterin, lecithin,

creatin, urea, hippuric acid, uric acid, and grape sugar, all in small and varying quantities. Fats occur as neutral fats, olein, stearin, and palmatin; the peculiar fat lecithin occurs only in very small proportions. The amount of fat in the blood during digestion is ·4 to ·6 per cent.; in fasting animals, ·2 per cent.; in dogs fed on a fatty diet it may reach 1·25 per cent. (Landois and Stirling). Schmidt states that there is twice as much fat in the serum of recently fed horses as in the serum of those kept starving. Other extractives as soaps are found to the extent of ·05 to ·1 per cent.; urea, ·02 to ·04 per cent.; sugar, ·1 to ·15 per cent. Bilirubin has been found in the serum of the blood of calves.

The **Difference between Arterial and Venous Blood** is that the former contains more oxygen and less carbonic acid; arterial blood also contains more water, fibrin, extractives, salts, and sugar, fewer blood corpuscles, and less urea; its temperature is, on the average, 1° C. lower.

The dark colour of venous blood is not due to the greater amount of CO_2 it contains, but to the diminution of oxygen in the red blood-cells. The alteration in colour effected by the addition of reagents and gases to blood, is probably due partly to alterations in the shape of the corpuscles themselves, which become more concave on the addition of oxygen and less concave on its removal, and also to the fact that oxy-hæmoglobin is brighter in colour than reduced hæmoglobin.

The **Salts** of the blood are divided between the plasma and the corpuscles, the distribution of these is not the same in all animals; in the horse and pig, for example, sodium only exists in the plasma and none in the corpuscles, whereas in the ox and dog both corpuscles and plasma contain it. Sodium chloride is the most abundant salt of the blood, potassium chloride and sodium carbonate follow, and lastly phosphates of calcium, magnesium and sodium. Iron is found in hæmoglobin but not in the serum. The chief inorganic substances of the cells are potassium and phosphates, whilst sodium and chlorides

are mainly found in the serum. In this connection the following table from Bunge is interesting:

	1,000 *grammes of Corpuscles contain*			1,000 *grammes of Serum contain*		
	K.	Na.	Cl.	K.	Na.	Cl.
Horse -	4·92	0	1·93	·27	4·43	3·75
Ox - -	·747	2·093	1·635	·254	4·351	3·717
Pig - -	5·543	0	1·504	·273	4·272	3·611

The use of the salts is to assist in secretion, repair, and disintegration. The growth of the solid tissues of the body absolutely depends on the inorganic material supplied by the blood. Water free from salts is destructive to protoplasm; no doubt, therefore, one important function of the salts in the blood is to maintain the vitality of the tissues. Sodium chloride is here especially valuable, and its extensive presence in blood (60 per cent. to 90 per cent. of the total amount of ash) corresponds to its importance. As the blood is simply the carrier of the salts, and the only means by which the tissues can obtain them, it by no means follows that all the mineral matter found in it is essential to its own repair and constitution.

The **Temperature of the Blood** in the domestic animals varies from 100° F. to 105° F. The warmest blood in the body being found in the hepatic veins.

The **Quantity of Blood in the Body** can only be estimated approximately; direct bleeding alone does not furnish us with a true result; after all the blood is drained off, the vessels require to be washed out, and the quantity of blood in the water estimated by the colour present; the body has then to be minced and macerated, and the quantity of blood in this estimated by the colour test, comparison being made with a standard solution of blood.

Sussdorf,* quoting recent experiments, puts the propor-

* Ellenberger's 'Physiologie der Haussäugethiere.'

tion which the weight of the blood bears to the body weight as follows:

Horse	-	$\frac{1}{15}$ = 6·6 per cent. of the body weight.
Ox	-	$\frac{1}{13}$ = 7·71 ,, ,, ,,
Sheep	-	$\frac{1}{12}$ = 8·01 ,, ,, ,,
Pig	-	$\frac{1}{22}$ = 4·6 ,, ,, ,,
Dog	-	$\frac{1}{11}$ to $\frac{1}{18}$ = 5·5 to 9·1 per cent. of the body weight.

The same observer gives the amount of blood in the body of the horse at 66 lbs., or nearly 50 pints.

The **Distribution of Blood in the Body**, according to Ranke, is as follows:

About one-fourth in the heart, lungs, large vessels, and veins.
,, ,, liver.
,, ,, skeletal muscles.
,, ,, other organs.

It is probable that in the horse the liver would contain less than one-fourth the bulk of blood, whilst the skeletal muscles would contain more. Under certain conditions the abdominal veins are capable of containing the whole of the blood in the body.

When an organ is active it receives more blood than when in a state of rest, this increase has been variously estimated at from 30 to 50 per cent.

The Gases of Blood.—The blood gases are obtained by introducing the fluid into a Toricellian vacuum, the instrument used to obtain it being a mercury pump. In a vacuum the blood froths up and gives off its gases, which are then collected and analysed.

The gases are oxygen, carbon dioxide, and nitrogen. The proportion of these found depends upon whether the blood be taken from an artery or a vein; in the former the oxygen is much larger than in the latter, and the carbonic acid less. The nitrogen in both cases practically remains the same.

At a pressure of 30 inches of the barometer and a

temperature of 32° F., the following gases are found in 100 volumes of blood:

	Arterial.	*Venous.*
Oxygen - -	20	12
Carbonic acid -	40	45
Nitrogen - -	2	2
	62	59

The exact amount of gas varies, the above can only be taken as mean quantities.

Oxygen exists in arterial blood in the proportion of about 20 per cent., whilst in venous blood the proportion is found to vary within wide limits, depending upon the vessel from which it is taken and the activity of the part.

Carotid artery, O 21 per cent. Renal vein (kidney active), O 17 per cent.
Renal ,, ,, 19 ,, Renal ,, (kidney passive), ,, 6 ,,
(Landois and Stirling.)

In the blood of asphyxia oxygen is nearly absent.

It will be remembered that by far the greater part of the oxygen is in combination with the hæmoglobin of the red blood corpuscles; in fact the proportion of oxygen in the blood bears a relation to the amount of iron contained by the hæmoglobin; it has been determined that 15½ grains of hæmoglobin is capable of absorbing ·095 cubic inches of oxygen. Whatever oxygen the serum of blood contains is simply absorbed, the amount held in solution is therefore small. Oxygen chemically united with hæmoglobin is quite independent of the laws which regulate the absorption of gases (see Respiration).

Besides the vacuum of the air-pump, various chemical substances have the power of deoxidizing the blood-cells: such reducing substances are ammonium sulphide, sulphuretted hydrogen, iron salts, etc. Blood exposed to the air loses oxygen, due to the production of reducing substances formed as the result of decomposition.

The **Carbonic Acid** in arterial blood is about 39 per cent.; in venous blood it varies, depending on the vessel from which the blood is drawn. The CO_2 is principally combined

with the sodium carbonate in the plasma of the blood, only a very small amount being simply absorbed.

The **Nitrogen** in the blood is small in amount, about 2 vols. per cent.; it does not vary in arterial or venous blood, as in both cases it is simply absorbed by the plasma.

Chemical Composition of the Blood.—The following are the analytical tables of the blood of animals furnished by various authors.

HORSE.

100 *parts by weight of blood contain:*

Blood corpuscles	34·418, containing 12·8 per cent. of solids (chiefly hæmoglobin).
Plasma	65·582, containing 10·0 per cent. of solids (chiefly proteids).

(C. SCHMIDT.)

100 *parts of venous blood contain:*

Corpuscles	32·6 per cent.
Plasma	67·4 ,,

The corpuscles contain:

Water	56·5 per cent.
Solid matter	43·5 ,,

The plasma contains:

Water	90·8 per cent.
Solids	9·2 ,,

The solids consist of:

Fibrin	·4 per cent.
Albumin	7·5 ,,
Fats	·1 ,,
Extractives	·4 ,,
Soluble salts	·6 ,,
Insoluble salts	·2 ,,

(HOPPE-SEYLER.)

PERCENTAGE COMPOSITION OF BLOOD.

	Horse. (Hoppe-Seyler.)	*Ox.* (Bunge.)	*Dog.* (Hoppe-Seyler.
Blood corpuscles	33·45	31·87	35·70
Solids	13·03	12·75	15·38
Water	20·42	19·12	20·32
Plasma	66·55	68·13	64·30
Solids	6·50	5·91	5·60
Water	60·05	62·22	58·70

1,000 *parts of Defibrinated blood contain :*

	Horse.	*Ox.*	*Pig.*
Corpuscles - -	531·5	317·7	436·8
Serum - -	468·5	681·3	563·2

(BUNGE.)

Reviewing these analyses, we may say the following represents the average composition of the plasma and corpuscles :

The Plasma.

Water - - -	90 parts per cent.
Proteids - - -	8 or 9 parts.
Fats - - -	·1 ,,
Fibrin - - -	·2 or ·4 ,,
Extractives - - -	·4 ,,
Salts - - -	·8 ,,

The Corpuscles.

Water - -	56 parts.	
Solids - -	43 ,,	consisting of 90 per cent. hæmoglobin, 8 per cent. proteids.
Salts - -	1 ,,	

Taking the blood as a whole the following will approximately represent its composition in every 100 parts :

Water - -	80 parts.		
Solids - -	20 ,,	Hæmoglobin -	10 parts.
		Proteids - -	8 ,,
		Salts - -	2 ,,

CHAPTER II.

THE HEART.

The blood in the body has to be kept in constant motion, so that the tissues which are depending upon it for their vitality may be continuously supplied, and also in order that the impure fluid resulting from these changes, may be rapidly and effectually conveyed to those organs where its purification is carried out.

The heart is the organ which pumps the blood over the body, not only distributing it to the tissues, but forcing it on from these back to the heart again to be prepared for redistribution. It may be described as a hollow muscle divided into two compartments, usually described as right and left, but in quadrupeds really anterior and posterior, each compartment being capable of division into an upper or auricle, and a lower or ventricle. Opening into the auricles are large veins which convey the blood back to the heart; from the ventricles other vessels, arteries, take their origin for the conveyance of blood from the heart; the two cavities are separated by a valvular arrangement.

So far the general arrangement of both right and left sides of the heart is much the same, each having to receive and then to get rid of a certain quantity of blood pumped into it; but the blood pumped into the right heart is very different from that pumped into the left, and with this difference we must for a moment deal.

Into the right heart the whole of the impure or venous blood in the body is brought for the purpose of being

purified in the lungs; into the left heart the arterial or purified blood is brought back from the lungs for distribution over the body. The former is often called the Pulmonic, the latter the Systemic circulation.

Mention has been made of valves in the cavities of the heart; they are found on both sides separating auricle from ventricle, and are known as the right auriculo-ventricular or tricuspid valve, and the left auriculo-ventricular or mitral valve. Besides these, valves are found in the vessels arising from the ventricles, viz., in the pulmonary artery and the aorta; these valves, pulmonary and aortic, are often spoken of as the semi-lunar valves. No valves are found guarding the entrance of the vessels into the auricles.

In order that we may understand the function of the valves, which play such an important part in the physiology of the heart, it is necessary that we should briefly detail the course which the blood takes from the time it enters the right auricle, until it completes the round of the circulation and finds itself at the auricle again.

Course of the Circulation.—The venous blood flows from the whole of the body into the right auricle by means of the anterior and posterior vena cava; it passes from this through the tricuspid valve into the right ventricle; from here it passes to the lungs by means of the pulmonary artery, where, having been exposed to the action of the air and become greatly changed in its composition, it returns to the heart by means of the pulmonary veins, emptying itself into the left auricle. It now passes through the auriculo-ventricular opening into the left ventricle, and from thence into the aorta to be pumped all over the body, to which it is distributed by means of the arteries and capillaries; it is then collected by the veins, and eventually brought back to the heart to undergo afresh its distribution to lungs and body.

The use of the valves is to allow of the transference of blood from auricle to ventricle, and from the ventricles to the aorta and pulmonary artery without any chance of regurgitation.

Position of the Heart.—The heart occupies a position in the middle line of the chest, being enclosed in a sac and suspended from the spine by its aortic vessels. Its base is uppermost, its apex nearly touches the sternum but does not rest on the ribs, and the organ occupies in the horse a position corresponding to the third, fourth, fifth, and sixth ribs; it is between the fifth and sixth ribs, at their sternal insertion, where the impulse of the heart may be felt in the horse. Its other relations are with the diaphragm which is just behind the apex, but with which it has no connection. On its right side is the right lung, and on its left part of the left lung; there is a triangular notch in the left lung of the horse which exposes the left ventricle, and allows it to make its impulse felt against the chest wall. The anterior face of the heart is formed by the right auricle and ventricle, the posterior by the left auricle and ventricle.

Heart Muscle.—The heart though an involuntary muscle, does not conform histologically with the involuntary muscular fibre met with in other parts of the body. The muscle is red in appearance, microscopically its fibres are short, striated, possess no sarcolemma, freely anastomose, and contain a nucleus; the network formed by the fibres of the heart is a most distinctive feature. In some animals, sheep and ox in particular, cells of a peculiar kind are found beneath the endocardium; they are polyhedral in shape, containing protoplasm and a nucleus, and are surrounded by striated fibres; they are called the cells of Purkinje.

The arrangement of the fibres of the heart is peculiar; those of the auricle are quite distinct from the ventricle,* and both are arranged in layers. Two layers have been described in the auricle, transverse and longitudinal, with circular fibres around the entrance of the veins, whilst in the ventricle no less than seven layers have been described. Owing to the peculiar direction in which these fibres run a

* A recent paper published by Kent, *Journal of Physiology*, vol. xiv., makes it probable that the auricles and ventricles are connected by bands of altered muscular tissue.

somewhat spiral arrangement results, but this is not fully accepted.

The heart is lined by the endocardium which is reflected over the valves; this membrane in the left auricle of the horse is naturally of a peculiar grey colour.

Certain fibrous rings are found in the heart where the valves are situated, and to which these obtain a firm attachment. The ring surrounding the aortic opening in the ox has constantly in its substance one or more pieces of bony tissue; this is also common in the horse.

Valves of the Heart.—The auriculo-ventricular valves are made up of fibrous and elastic membrane, in which a small proportion of muscular fibre is found close to the attached border. The mitral or bicuspid valve in the horse consists of one large distinct segment, and several smaller ones united to form a second; the tricuspid consists of three segments, one much larger than the others being placed opposite to that portion of the ventricle leading to the pulmonary artery.

All the valves are held in position by large and small tendinous cords composed of fibrous tissue, which are inserted into musculi papillares found on the internal surface of the ventricle; the cords from one papilla do not all pass to one segment of the valve, but to two or three. The function of the papillæ is to restrain the valves from passing into the auricle during the contraction of the ventricle, and this they accomplish by exerting traction on the cords. Other bands pass from one side of the ventricle to the opposite wall; they are called moderator bands, and their function is to restrain the ventricular wall from undue dilatation.

Both the mitral and tricuspid valves meet in the most perfect apposition when the ventricle contracts, and nothing can escape upwards into the auricle. This may be readily demonstrated in the dead heart by tying the aorta and pulmonary veins, and introducing into the left auricle a tube which admits of a powerful jet of water; the left side of the heart distends and hardens, and at last water forces

its way out of the side of the vessel or hole in the auricle in which the tube is inserted. If the auricle be now opened, the ventricle is found cut off from view by a tense membranous dome, convex towards the auricle, which is the mitral valve in position; not a drop of water will escape from the ventricle, though the heart be turned upside down, and it requires some little force to depress the valves.

The semi-lunar or sigmoid valves, which guard the entrance into the aorta and pulmonary artery, are composed of fibrous and elastic material, and possess at the centre of each segment a small hard body, corpus Arantii, which is particularly marked in the aorta.

Owing to the arrangement of the muscular fibres of the heart, the auricles and ventricles are capable of acting quite independently of each other; the two auricles contract, and then the two ventricles. The contraction of either auricle or ventricle is spoken of as its **systole**, whilst the dilatation is described as its **diastole.** When the two auricles are in a condition of diastole the two ventricles are in a state of systole.

A **Cardiac Revolution**, or **Cardiac Cycle**, is the term used to describe the changes which occur in the heart, during the time which elapses between one contraction or dilatation of the auricle, and the one which immediately succeeds it.

We may take as the most convenient point to start our description, the moment when the blood is entering the auricles from the venæ cavæ and pulmonary veins. This flow of blood into the auricles is brought about by the pressure of blood in the veins, which though comparatively low is yet higher than that in the auricles; further, the flow into the right heart is assisted by gravity, especially the blood in the anterior cava, and likewise by an aspiration produced by a relaxation of the walls of the auricle after the previous contraction.

The auricles being full, a wave of contraction which first appears at the vessels leading into them, passes over the auricles, which by a sudden sharp and brief contraction empty their contents into the ventricles.

The systole of the auricle produces a positive wave in the vessels leading into it, and this wave passing through the anterior cava, shows itself in the jugulars of the horse by a distinct regurgitation at the root of the neck.

The auricular contraction forces the blood into the ventricles, which have been partly filling during the time the auricles were distending, and the final filling of the ventricle by the auricular systole forces up the auriculo-ventricular valves, which in the horse bulge into the auricle under the increasing pressure to which the ventricular contents are exposed. The ventricles by a simple prolonged contraction, produce a peculiar wringing movement due to the spiral arrangement of their muscular fibres; the pressure which now exists in the ventricles is greater than that in the vessels leading from them, and as the auriculo-ventricular valves cannot be thrown open owing to their chordæ tendinæ, the semi-lunar valves are forced open, and the stream of blood passes into the aorta and pulmonary artery.

It is said by Colin, that in the horse the ventricles do not empty themselves at each systole, but that a certain amount of blood is left behind; this does not appear to be the case in all animals.

At the moment the ventricles contract, the heart slightly rotates around its vertical axis from left to right, and the left ventricle hardens and makes its impulse against the chest wall; further, the ventricular systole produces a dull, booming, prolonged sound, which is brought about by the muscular contraction of its walls, and probably by a vibration of the auriculo-ventricular valves, the sound being known as the first sound of the heart.

The blood now rushes into the aorta and pulmonary artery, and the elastic resistance of these arteries being brought into play, the fluid has a tendency to regurgitate towards the ventricles; by this process the semi-lunar valves (which do not lie up against the wall of the vessel, but rather stand out in the stream) are closed, the closure

being accompanied by the second sound of the heart, which is short and sharp.

At the moment the blood in the aorta recedes on the heart the latter shortens itself, the base approaches the apex, the apex remaining immovable. The arterial trunks which during the systole of the ventricles elongate and curve, now at the diastole shrink and shorten, and so bring the base of the heart back to its former place (Chauveau).

It is not until the semi-lunar valves are firmly closed that the ventricles begin to relax; they now do so, and the relaxation of the walls produces a negative pressure, which in the dog has been measured at from 1 to 2 inches of mercury, viz., a pressure below that of the atmosphere. This negative pressure opens the auriculo-ventricular valves, and blood flows in from the auricle, while the auricle and ventricle, neither contracting nor dilating, assume a passive condition during a period known as the **pause.** Throughout the pause blood is flowing into the auricles from the pulmonary veins and venæ cavæ, and into the ventricles from the auricles; towards the close of the pause the auricles contract, and the whole process is repeated.

We have thus the contraction of the auricles, the contraction of the ventricles, and the pause. The periods these occupy have been determined for the horse, by Chauveau and Marey, by means of a cardiac sound. The value of the periods they give us is as follows: auricular systole, two-tenths of a second, ventricular systole, four-tenths, and pause, four-tenths of a second.

We cannot accept the value of these periods as correct, owing to the fact that they cause the horse to have a pulse of 60 to the minute, which is distinctly abnormal.

A complete revolution of the horse's heart occurs, on an average, once in every 1·5 seconds; but the exact value of the various phases which make up this period cannot be stated.

Burdon Sanderson points out that, no matter how fast the heart is beating, the frequency depends not on the

duration of the ventricular systole, but on the length of the pause.

Summary of Events occurring during a Cardiac Cycle.—If we divide these into three periods, and start with the contraction of the auricles, the following is a summary of the changes occurring in the heart :

1*st Period.*—The contraction of the auricles completes the filling of the ventricles.

2*nd Period.*—The ventricles contract, the auriculo-ventricular valves are closed, the aortic and pulmonary valves open, blood is pumped into the aorta and pulmonary artery, the impulse of the heart is made against the wall of the chest, the first sound is produced, the auricles fill with blood, and the whole is followed by a short pause.

3*rd Period.*—The aortic and pulmonary valves close, the auriculo-ventricular valves open, the second sound of the heart is produced, diastole of both auricles and ventricles occurs, followed by a long pause, and blood flows into all the chambers.

Changes in the Shape of the Heart.—During systole the heart becomes narrower from side to side, but increases in width from front to rear ; the observation of Chauveau that it shortens from base to apex is not agreed upon. During diastole the base is elliptical, whilst during systole it is circular.

The rotation of the heart, previously described, is due to the spiral arrangement of its fibres, and it may assist in producing the impulse against the chest wall, which in the horse occurs between the fifth and sixth ribs. Colin insists that in the horse the impulse is not given by the apex, but by the lower half of the wall of the left ventricle, and experiments made on some animals prove that the apex does not leave the chest wall, but that the impulse is due to the hardening of the ventricular wall in contact with the chest wall. This impulse against the chest agrees with the closure of the auriculo-ventricular valves, and the bursting open of the sigmoid valves.

The **Action of the Valves of the Heart** during a cardiac

cycle is peculiar and interesting. We have described how the auriculo-ventricular curtains are floated up as the ventricle fills, and how with increased pressure they come together, being prevented by the chordæ tendinæ, and the muscular pillars to which these are attached, from being carried too far. We may also notice how the reduction in the horizontal diameter of the heart assists the action of these valves; further, experimental inquiry has determined that when the ventricular systole is at its height these valves bulge upwards into the auricles, assuming a concave surface towards the ventricle. This appears to be especially the case in the horse, and the information is obtained by the researches of Chauveau and Colin. The pulmonary valves, and probably the aortic, not only meet at their free border but actually overlap. Chauveau states that he has tried experimentally to hold back one of the pulmonary valves, but the others have applied themselves so closely around the finger that it was impossible to produce a patent opening. In the aorta it is probable that overlapping does not occur to the same extent, and here the corpora Arantii are of value. When the sigmoid valves are not acting they still lie in the blood stream, and not against the wall of the vessel as was at one time supposed; nor do those in the aorta cover the openings of the coronary arteries.

The elastic recoil of the aorta does not exercise its entire pressure upon the valves, for we observe that the diameter of the aorta at its origin is greater than the aortic opening from the ventricle, and so the muscular substance of the heart largely bears the shock of recoil.

It is generally believed that both the aortic and pulmonary valves are closed by the regurgitation of the blood; but Chapman* points out that as the blood is leaving both ventricles, it is streaming through orifices which at that time are mere chinks, owing to the pads of muscle which take their origin from all sides of the mouth of the vessels. Vortices are thus created in the space between the arterial

* *British Medical Journal*, March 10, 1894.

root and the edge of the valves. These vortices tend to press the edges of the valves together, and the valves consequently close the moment the blood actually ceases to stream through the narrow crevice. In this way there is no regurgitation, as the valves are closed before the recoil of the aorta.

If this explanation be correct, the second sound of the heart must be considered as due to the *tension*, and not the closure, of the aortic valves at the time of the aortic recoil.

The **Cardiac Sounds** are really four in number, but as they are in pairs we recognise only two. The first sound is a long booming one, due to the muscle sound of the contracting ventricle, and probably the vibration of the auriculo-ventricular valves. The second sound is due either to the closing of the semi-lunar valves of the aorta and pulmonary artery, or to the tension of the valves at the recoil; it is a short sound, and its source has been clearly proved by hooking back the valves, which causes the sound to cease. The two sounds are reproduced by the words '*lubb dŭpp.*'

Stockman* says that in the horse the sounds of the heart may not be synchronous, giving rise to a re-duplication; this has been considered by continental authorities, who first observed the condition, to be due to changes in the intra-thoracic or cardiac pressure, by which the valves are not closed together.

Intra-Cardiac Pressure.—The internal pressure exercised by the walls of the heart on the blood is ascertained by means of an instrument termed a cardiac sound, first used by Chauveau and Marey. It is a double tube having at its extremity two elastic balls; the air in these is compressed when the cavities contract, and the compression moves a lever placed in connection with a recording surface. The instrument is passed into the right heart through the jugular vein, one ball being in the auricle, the other in the ventricle. Burdon Sanderson states that it causes no inconvenience to the animal, due to the fact that no sentient

* *Journal of Comparative Pathology*, vol. vii.

nerves are supplied to the lining membrane of the blood-vessels or even to the heart.

A tracing obtained from the heart of the horse is shown in Fig. 2; the curves do not indicate the force of the stroke, but only the intra-cardiac pressure. It is seen from the

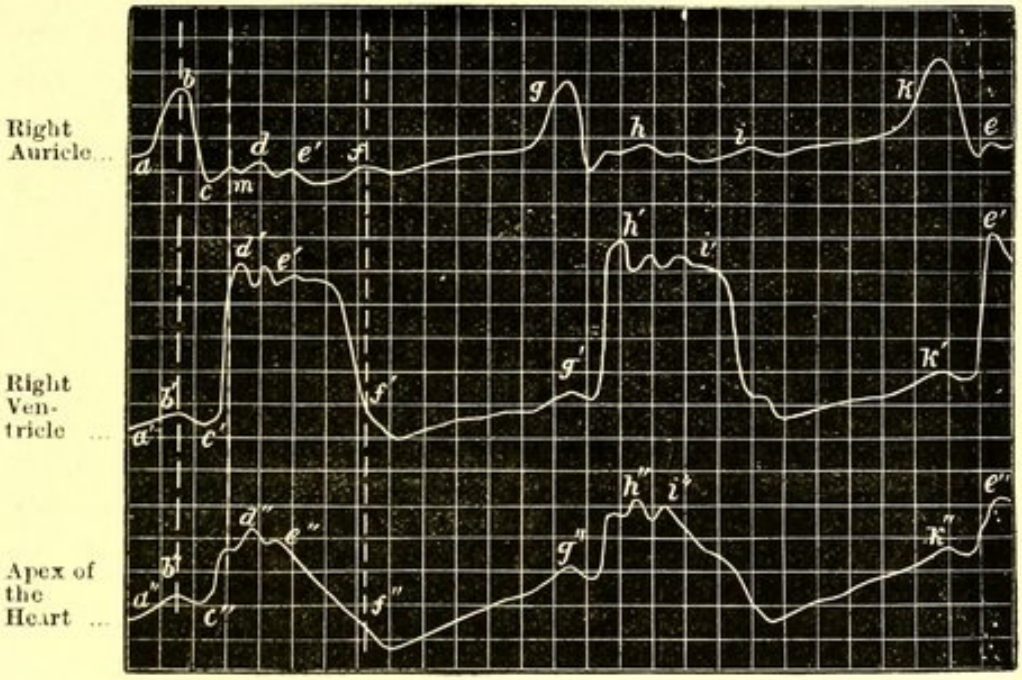


FIG. 2.—SIMULTANEOUS TRACINGS FROM THE INTERIOR OF THE RIGHT HEART OF THE HORSE, AFTER CHAUVEAU AND MAREY (M'KENDRICK).

Each horizontal line equals $\frac{1}{10}$ second, the vertical lines indicate pressure; the vertical dotted lines mark coincident points in the three movements.

The auricular curve is *a*, *b*, *c*, the ventricular curve is *c'*, *d'*, *e'*, *f'*. The auricle contracts sharply, relaxes rapidly, and is followed by the sudden contraction of the ventricle which is maintained with certain oscillations for about three-tenths of a second, and then suddenly relaxes; the pause follows at *f*, *f'*.

The oscillations seen at *d*, *d'*, *d*," and *e'*, *e'*, *e''*, are believed to indicate vibrations of the tricuspid valve.

tracing that the auricles contract first, followed by the ventricles; the former is slower and shorter than the ventricular systole, which is sudden, maintained for some time, and then rapidly falls.

Observations on the intra-cardiac pressure show that it is greatest at the beginning of contraction, and then gradually falls; a negative pressure occurs during the period of

diastole, and is brought about by the relaxation of the walls of the heart during the long pause; this relaxation causes a sucking action which assists in filling the heart with blood.

Though both ventricles deliver the same amount of blood the pressure in each cavity is different. The systolic pressure in the left ventricle of the horse is equal to a column of blood from 9 to 14 feet in height; and in the right ventricle one equal to 1½ feet in height.

In the dog the intra-cardiac pressure has been estimated as follows:

Left ventricle	-	-	7 inches of mercury.
Aorta - - - -	6¼	,,	,,
Right ventricle	-	-	1¾ ,, ,,

In the same animal during diastole a *negative* pressure in the left ventricle of from 1 to 2 inches of mercury has been measured, and in the right ventricle one of ⅝ inch of mercury; in other words, during the time the heart is dilating the pressure recorded within it is below atmospheric pressure.

The Cardiograph.—The impulse of the heart against the chest wall is graphically obtained by means of the cardiograph, of which there are many forms. Their essential construction consists of a button which is pressed upon by each impulse of the heart, and conveys the movement to an elastic air-chamber which transmits it to a recording lever. By this means we get a graphic representation of the heart's impulse.

The cardiograph demonstrates that the aortic valves close slightly before the pulmonary.

Capacity of Heart.—The quantity of blood in the heart can only be ascertained approximately; measuring the capacity of the chambers is no guide. Munk states that the capacity of the ventricle in a horse weighing 880 lbs. is about 1·76 pints, equivalent to 2·35 lbs. of blood; each ventricle contains one-thirtieth of the total blood, so that when both contract one-fifteenth of the total blood is ejected (M'Kendrick).

Colin gives the capacity of the left ventricle of the horse at 1·76 pints, and states that at each systole two-thirds or three-fourths of this quantity are injected into the aorta, viz., 1·172 pints to 1·364 pints; the left ventricle at each contraction, according to this observer, forces into the aorta about one-twenty-fifth of the total blood of the body.

Colin gives the following table of capacities of right and left ventricle:

	Right Ventricle.	*Left Ventricle.*
	Pints.	Pints.
Small horse - -	1·42	1·29
Medium size horse -	1·76	1·23
Big horse - - -	3·34	2·36

This is only a part of the table, the figures of which are found to vary widely. Measuring the capacity of the heart is therefore fallacious, for in the above table each side of the organ should have held the same quantity of blood, inasmuch as it is evident that the amount of blood entering the heart must be equal to the amount leaving it.

Work of the Heart.—This may be calculated if we know the amount of blood being discharged from the heart at each stroke, and the pressure against which it is pumped out. The amount pumped at every systole of the ventricle is liable to great variation, at least such are the results of experiments on the dog.

It is obvious that the right ventricle does less work than the left, for the reason that it has to pump the same volume of blood a much shorter distance; it has been said that the right heart does one quarter the work of the left

If we take the amount of blood pumped at each stroke into the aorta of the horse at about 2·25 lbs. in weight, and the pressure under which it is forced upwards as equivalent to a column of blood 10 feet in height, then the work of the left ventricle at each stroke is equal to 22·5 lbs. raised one foot high, or for 24 hours, allowing the work of the right heart to be one fourth that of the left, 1,539,000 foot pounds. This amounts to about one-thirtieth of a horse

power per diem; Munk places it at one-thirty-sixth of a horse power.

It is obvious that the work done by the heart is increased by body work, the above calculation is for a horse during repose.

If we take the amount of blood expelled by the left ventricle at each stroke as equal to 2·25 lbs., then the entire amount of blood in the body of a horse in a state of repose, passes through the heart in about thirty beats, or in three quarters of a minute. Munk says the entire blood in the body of the horse passes through the heart in five-sixths of a minute, in the ox two-thirds of a minute, and dog one-third of a minute.

The term **Blood Pressure** is frequently used in the physiology of the circulatory system. It is one we shall have to consider in detail when we come to speak of the bloodvessels; but we should clearly understand that the condition is due to the amount of blood pumped into the vessels by the heart, and this amount will depend principally on the rate at which that which is in front of it in the vessels escapes into the veins. If the arterioles are contracted so that the amount passing into the veins is reduced in quantity, then a larger bulk of blood will be between the pump and its outlets, and the blood pressure rises; if, on the other hand, the blood is passing rapidly through its extensive arterioles into the veins the blood pressure falls. When the amount poured into the venous system in any given time, is equivalent to that pumped into the arterial system during the same time (which is the perfectly normal condition), the pressure is described as being constant.

The above facts may be tabulated as follows:

When the heart is more active the blood pressure rises.
„ „ less „ „ „ falls.
When the arterioles contract the blood pressure rises.
„ „ dilate „ „ falls.

The heaviest work the heart performs is in overcoming

the resistance offered by the bloodvessels; only a very small part of the heart's work is expended on producing blood velocity.

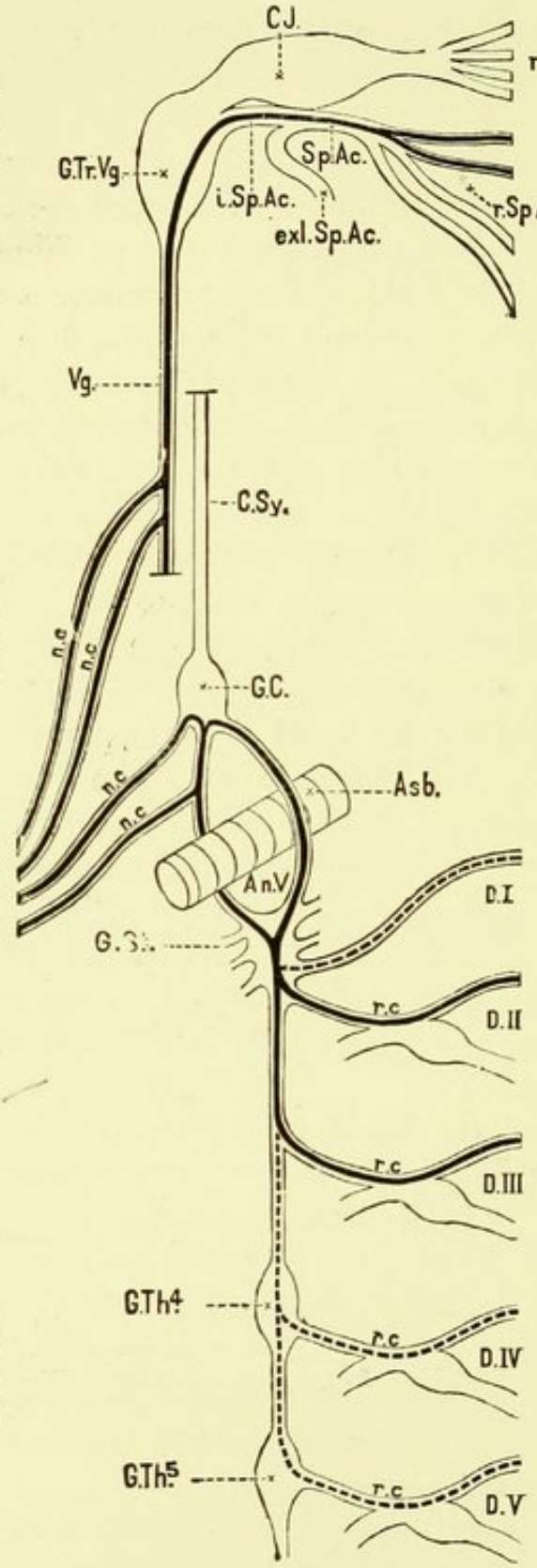
Nervous Mechanism.—The heart is said to possess no sensory nerves; it may be handled, pinched, pricked, or otherwise injured without provoking the least sign of pain on the part of the animal; Colin's experiments in this direction on horses appear most conclusive. Not only is it considered that the external surface is insensible to pain, but the internal surface also; for, as previously noted, the experimental introduction of foreign bodies into the cavities of the heart appears to produce no pain.

Under pathological conditions the results are otherwise; foreign bodies, so common in the heart of the cow, cause great suffering, therefore, there must be sensory nerves, though normally their excitability is probably low.

The nerves supplying the heart are the pneumogastrics and sympathetics. The function of these two nerves is diametrically opposite. Whilst one, the pneumogastric, has a controlling, or, as it is termed, an inhibitory effect over the movements of the heart, the sympathetic has an accelerating or augmenting effect. Histologically the two nerves differ greatly in structure, the pneumogastric being a medullated, whilst the sympathetic is a non-medullated nerve.

The inhibitory fibres found in the vagus are derived from the internal branch of the spinal accessory, which joins the vagus within the skull, and travelling with this nerve, reaches the heart by its cardiac branches. The accelerator nerves arise from the spinal cord, by the inferior roots of the second and third dorsal nerves and probably others; they pass through the sympathetic ganglia, and reach the inferior cervical ganglion, from which they are distributed to the heart. (See Fig. 3.)

If the vagus nerve in the neck be gently excited, the heart's beats are reduced in *force* and *frequency*; if strongly stimulated, the heart stops in diastole. If the nerve be divided the heart beats more rapidly, for now the in-



G.Tr.Vg. Ganglion on the trunk of the vagus; the black line through it is the internal branch of the spinal accessory.

Vg. The vagus nerve.

nc., nc. The cardiac branches of the vagus conveying ; inhibitory fibres to the heart.

G.Th.4 and G.Th.5 Fourth and fifth thoracic ganglia on sympathetic chain.

rSpAc. Inhibitory fibres from spinal accessory entering the vagus.

C.Sy. The cervical sympathetic nerve.

G.C. Inferior cervical ganglion.

Asb. Subclavian artery.

An.V. Annulus of Vieussens.

G.St. Ganglion stellatum.

D.II., D.III. The inferior roots of the second and third spinal nerves, passing by means of r.c the ramus communicans to the ganglion stellatum. These are the augmentor fibres, passing both by the annulus and inferior cervical ganglion to the heart by nc. nc.

The dotted line in certain thoracic nerves, D.I., D.IV., and D.V., indicate that they may contribute augmentor fibres to the sympathetic.

FIG. 3.—DIAGRAMMATIC REPRESENTATION OF THE CARDIAC INHIBITORY AND AUGMENTOR FIBRES IN THE DOG (FOSTER).

The upper portion of the figure are the inhibitory, the lower the augmentor fibres.

hibitory power over the sympathetic is lost, and the latter has it all its own way. When the cut end of the pneumogastric is stimulated we restore to an extent the inhibitory power, and the heart's beats become fewer and more feeble. If the spinal cord and both sympathetics be divided, the inhibitory power over the heart produced by the vagus is intensified owing to the loss of its antagonistic nerve, and the result is that even feeble stimulation of its fibres arrests the action of the heart.

The inhibitory effect of the vagus over the heart is often

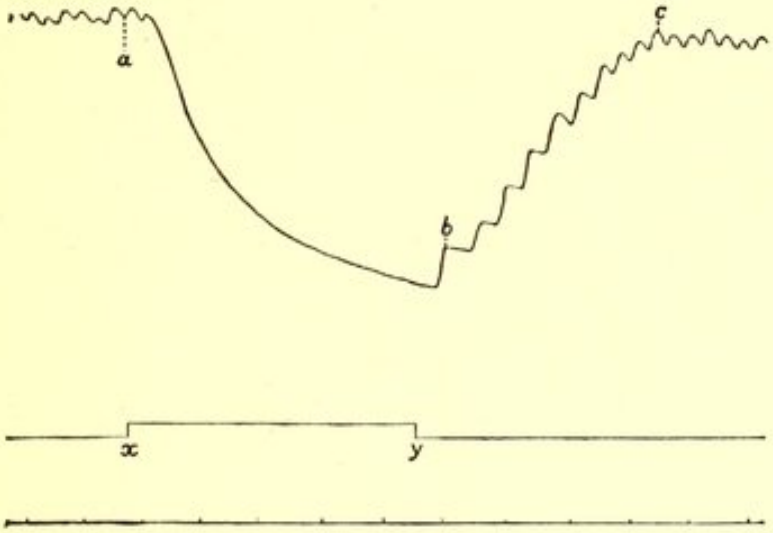


FIG. 4.—TRACING SHOWING THE INFLUENCE OF STIMULATING THE VAGUS NERVE; FALL OF BLOOD PRESSURE DUE TO ARREST OF THE HEART. FROM A RABBIT. (FOSTER.)

x marks on the signal line when the current is thrown into, and *y* shut off from the vagus. The time marker below marks seconds. *a* corresponds in point of time with *x*, the heart does not at once cease to beat; the first beat *b* occurs a short time after shutting off the current. The notches in the tracing are the beats of the heart.

better demonstrated through one nerve (frequently the right) than through its fellow. If the heart be placed in communication with a recording apparatus and the vagus then stimulated, it is observed that the tracing obtained (Fig. 4), shows that the inhibitory effect is not seen immediately, but that at least one beat of the heart may occur after the passage of the current into the nerve; and in the same way the beats of the heart are not immediately established after withdrawing the current. On the with-

drawal of the current a reaction appears to set in, and the heart makes up for lost time by beating more vigorously than before.

If the vagus of an animal be stimulated during the experiment of graphically recording the blood pressure, it is found that almost immediately after the stimulation the blood pressure falls, due to the heart stopping; when the current is shut off the beats of the heart return, and the pressure rises rapidly until the normal condition is obtained. (See Fig. 4.)

In the medulla is found an inhibitory and augmenting centre for the heart in connection with the vagus and sympathetic; these are both differently affected by the gases brought to them by the blood; carbonic acid in large quantities excites the inhibitory centre, whilst oxygen stimulates the augmenting centre. The inhibitory or controlling centre is in the constant exercise of its function throughout the whole life of the animal; this is not the case with the augmenting or accelerating centre.

Cardiac inhibition may be brought about reflexly; striking the exposed intestines of the frog, or crushing its foot, will cause the heart to stop; this shows that impulses are conveyed to the cardio-inhibitory centre in the medulla and transmitted down the vagi. Much the same effect may be produced in the higher animals, as, for instance, the fainting which accompanies a blow on the abdomen, or the emotional fainting of the human subject. In the dog cardiac inhibition is present during expiration, so that in this animal the heart beats slower during expiration than during inspiration, this effect is abolished by section of the vagi.

The inhibitory effect of the vagus may be reflexly excited in other ways; if for example the sciatic, splanchnic, or other nerves be divided and their central end stimulated, an inhibition of the heart may be obtained.

Under the influence of atropine, applied either directly to the heart or injected into the circulation, the inhibitory power of the vagus is lost; small doses of this alkaloid are

quite sufficient to prevent stoppage of the heart's action, even though a powerful current be employed to stimulate the vagus.

The action of atropine is counteracted by muscarin; this alkaloid produces a remarkable slowing of the heart, or even causes it to stop, behaving, in fact, very much like vagus stimulation.

Experiments on strips of the isolated heart have shown that it is probable both these alkaloids act on the actual muscular structure, and that the ganglia found in the wall of the heart take no share in the process; these ganglia cannot, therefore, be regarded as local mechanisms.

The general effect of the vagus, then, is to keep control over the heart, and cardiac inhibition, which is constantly in operation, is an important factor in preventing the too rapid wearing out of the organ.

The sympathetic fibres are the augmentor fibres of the heart, increasing the *force* and *rate* of the beat. This influence only occasionally comes into operation, thereby contrasting strongly with the vagus.

Contrary to what might be imagined, repeated excitation of the vagus, during the period of reaction following the withdrawal of the current, rather increases than decreases the force of the contraction; and, on the other hand, repeated stimulation of the sympathetic is followed in the reactionary period by a weakening of the heart's beats.

According to Gaskell the vagus is the trophic nerve of the heart; it excites processes of repair (anabolism), builds up the muscular tissue, and is, in fact, the nutrient nerve of this organ; the sympathetic, on the other hand, excites processes of decomposition or destruction (katabolism), in just the same way as a motor nerve passing to muscle excites katabolic processes in the muscle elements as the result of work. If we carefully consider this theory in conjunction with what we have previously stated respecting the opposite action of the vagus and sympathetic, we can see that it receives every support.

Besides the various mechanisms for increasing or de-

creasing the work of the heart, we have yet another to which allusion must be made.

All the nerves previously described have come from some part of the central nervous system to the heart, but the nerve we are now dealing with passes from the heart to the central nervous system. Owing to its action on the circulation it is spoken of as the *depressor* nerve. By means of it the central nervous system is made acquainted with the condition of the heart, so that if the latter is labouring heavily, and its muscular structure becoming weakened, impulses pass along the depressor to the vaso-motor centre in the medulla, with the result that the vessels of the abdomen dilate and hold more blood, the peripheral resistance is diminished, and the blood pressure falls considerably. In this way the heart is capable of an amount of self-regulation.

Nature of the Cardiac Contraction.—The contraction of the heart muscle differs from that of ordinary muscle, inasmuch as it is a prolonged contraction and not a tetanus. The contraction of cardiac muscle is eight or ten times longer than the contraction of an ordinary voluntary muscle, and it is impossible to produce tetanus of it by electrical stimulation. If we compare the heart muscle with voluntary muscle, the rhythmic contraction so prominent a feature in the former is only rudimentary in voluntary muscle; whilst the rapidity of contraction of the heart muscle is only rudimentary in pale muscle. From this and other considerations, Gaskell has placed the heart muscle in a position intermediate between plain and striated muscle.

But in addition to these, there are other differences between voluntary and heart muscle. Stimulation of heart muscle, be it weak or strong, leads to a maximum contraction; in skeletal muscle this is not so, a weak stimulation leads to a weak contraction, and a strong stimulation to a strong contraction; but with the heart a weak stimulation will give the largest contraction which the heart at that moment is capable of performing, and no greater contraction can be obtained even with a strong stimulation.

It is evident, therefore, that the magnitude of the contraction of the heart muscle does not depend upon the intensity of the stimulation; if the heart is capable of responding to stimulation it does so to the fullest extent, to use the words of Waller, its motto is 'all or nothing.'

In the stimulation of muscle there is not only a latent period but a *refractory period*, viz., a period during which it is insensible to stimulation; such refractory period in skeletal muscle is very short, whereas in heart muscle it is very long; its existence prevents the heart muscle from being tetanised, for during the refractory period even powerful stimulation is unable to provoke a contraction.

Such are the differences between the contraction of ordinary skeletal muscle and heart muscle; we see that the two things are very distinct and not comparable, and that we must look for some other explanation of the heart beat.

When life is suddenly destroyed in horses by shooting through the head, it is not unusual for the heart to continue beating for a few minutes. Colin divided the spinal cord in a horse and established artificial respiration, fifteen minutes after the operation the heart was beating 42 to the minute, and it did not cease contracting for 50 minutes after the section. In another case the cord and both pneumogastrics and sympathetics were divided; artificial respiration being established the heart beat for 24 minutes. In a third experiment the animal was decapitated and both carotids tied; artificial respiration being established the ventricles contracted for 17 minutes, and the auricles for 34 minutes.

This contraction of the heart even after destruction of the centres presiding over it, is a common phenomenon in the frog, in which the heart will contract rhythmically for some days after removal from the body. Many theories have been advanced to account for this, the chief one being that based on the existence of certain ganglia in the substance of the heart which excite contraction.

In the frog two well-defined ganglia known as Bidder's and Remak's are found. In mammals ganglia are found

in the venæ cavæ and pulmonary veins, also in the wall of the auricles, auriculo-ventricular groove, and in the base of the ventricles; no ganglia are found in the central part of the auricular septum.

Experiments on the frog's heart have shown that the ganglia theory cannot account for the rhythmical beating of the heart, for however tempting the theory may be it will not stand the test of experimental enquiry; the ganglia may be removed and the nerves connecting them divided without interfering with the rhythmical contraction of the heart, and further, parts of the heart like the apex contain no ganglia, and yet may be made to contract rhythmically by distending it with blood.

It has been sought to make the ganglia responsible for the regular sequence of events occurring in the heart, viz., the contraction of the veins leading to the auricles, the contraction of the auricles and lastly the ventricles, but even this is not supported by experiment. It is possible to block the impulses by clamping or compressing the wall of the auricle, and so to divide the single beat into two; this has led to the theory that the tissue connecting veins with auricles and auricles with ventricles possesses a lower conducting power than the muscular substance of the heart, and in this way converts what might be a continuous wave into a broken one.

We have previously mentioned that the ganglia cannot be regarded as local mechanisms either inhibitory or augmenting, and the only functions at present assigned to them possessing any degree of probability are, that they may be concerned in de-medullating the vagus fibres (which up to the heart are medullated, but in the muscle itself have no medulla), further that they may increase the number of the fibres by passing through the cells of the ganglia, and lastly that they may be concerned in the nutrition of the heart itself.

Gaskell does not regard either the cardiac ganglia or the nerves supplying the heart as the cause of the beat of the heart, but rather that this is due to changes taking place

in the muscle itself; and he calls especial attention to the cellular and protoplasmic features of the heart's muscle in support of this statement, likening the contraction of cardiac muscle to the spontaneous movements of undifferentiated primordial protoplasm.

The nutrition of the heart muscle is brought about by the blood supplied to it through the coronary arteries. Roy and Adami have shown that the blood pressure in the coronary arteries is one of the important factors in the force of the cardiac beat; a reduction of pressure in these vessels weakens the contractions of both auricles and ventricles. The force of the heart beat is, therefore, in part automatically regulated by changes in its own arterial pressure.

But besides this, the condition of distension of the cavities is an important factor in the heart's beat; within reasonable limits a full heart contracts more vigorously than one less full, while the presence of a depressor mechanism enables an overfull heart to lower the blood pressure to a point at which it can successfully continue to contract. By a reflex mechanism the blood pressure in the vessels may also regulate the beats of the heart, a high pressure stimulating the cardio-inhibitory centre in the medulla and so slowing the heart through the vagus, or a low blood pressure may increase the force of the heart through the sympathetic system.

Finally, the quality of the blood may influence the heart's beat; chemical substances taken up from various parts of the body such as the muscles, and circulating with the blood, may act on the muscular walls of the organ and variously modify the beat, but the subject is at present little understood.

The Action of Drugs on the Heart.—This has been very carefully studied in the dog, frog, and rabbit. It has been found that *aconitin*, *muscarin*, and *pilocarpine*, slow the heart and then stop it in diastole, very much as the heart behaves to stimulation of a divided vagus. *Atropine* and *nicotine* increase the frequency of the heart's beats, behaving very much as if the vagus were divided, and as it is found that

stimulation of the vagus fails to slow or arrest the rapid beating of an atropinised heart, it is generally considered that the action of this drug is to destroy vagus inhibition. *Physostigmine* increases the energy of the cardiac muscle; *digitalin* first excites the vagus so that the frequency of the heart's beats are reduced, later it excites the cardiac muscle so that the systole of the heart is stronger and prolonged. In medicinal doses the effect of digitalin on the heart is to increase the strength and duration of the beat, and at the same time diminish its frequency; in this way it has been described as a heart tonic. *Neutral Salts of Potash* produced a well-marked action of the heart, causing it to stand still in diastole. *Alcohol*, *Ether*, and *Chloroform*, in medicinal doses cause the heart to beat stronger and more rapidly.

Many other drugs have had their effect on the heart determined, but the above are those of most interest.

CHAPTER III.

THE BLOODVESSELS.

The use of the bloodvessels is to distribute the blood over the body, to bring it in contact with the tissues, and return it to the heart for the absorption of oxygen and purification in the lungs. To accomplish this purpose there are arteries, capillaries, and veins.

The **Arteries** all arise from one common trunk, the aorta, which by the process of dividing and subdividing like the branches of a tree, produces the innumerable large and small vessels known under this name in the body. By this process of division and subdivision, the arterial tree formed is very much larger than the parent trunk, in fact its area has been estimated as several hundred times greater.

The large arteries differ somewhat in construction from the small ones. The microscope shows that while the large vessels are principally elastic the small ones are principally muscular. This latter fact does not preclude the smaller vessels from enjoying the elasticity possessed by the larger ones, for muscular tissue is endowed with what is known as perfect elasticity, a property which also belongs to the large arteries with their elastic coats.

The elastic properties of arteries is an essential feature in their construction, it admits of the vessel stretching both in its width and length, and at the same time ensures its recovery to its original diameter. When we remember the intermittent force exercised by the left ventricle on the

arteries, we have no difficulty in understanding the necessity for this elastic property. The arteries are always full, every contraction of the left ventricle in the horse during rest, throws into them one and a half pints of blood which must be accommodated, and this accommodation is provided for by the distension of their walls. For every one and a half pints of blood entering the root of the arterial tree, an equal amount must pass out at the branches, and the reduction in the diameter of the vessels is brought about by the elastic recoil of the arterial wall.

We shall study presently another use of the elastic arterial wall, when we come to describe the flow of fluid through tubes.

Another essential feature possessed by arteries is their power of contractility. Just as we saw the larger arteries were principally elastic, so are the smaller ones principally contractile. This contractility or power of reducing their diameter is produced by the muscular coat previously spoken of. Though the smaller vessels possess this muscular coat, it by no means follows that they are always contracted; in fact special nerves exist supplying the muscular tissue which controls or regulates the diameter of the vessels, so that the muscular artery may be contracted or relaxed depending upon the set of nerves brought into operation. In this way the smaller muscular vessels act as a tap and regulate the blood supply to a part.

Capillaries.—The minute arteries terminate in the capillaries. It is in these vessels where the interchange between the blood on the one hand and the tissues on the other takes place, and this is rendered easy by the fact that the wall of the capillary consists simply of very thin membrane composed of cells known as endothelial plates, the cells being united at their margin by a cement substance. It is through this wall that the exchange of material with the tissues occurs. The capillary is capable of dilating and so accommodating more blood; this is brought about by the elastic nature of the membrane composing the capillary wall.

The size of the capillaries varies, in places like the lungs they are relatively large, in other parts such as the skin they are very small; further, their size depends upon the amount of blood allowed to pass through them; for instance, the capillaries of the skin during active exercise are much larger than during rest.

If they are observed in the living animal the capillaries may be seen to enclose islands of tissue, these are the areas where the interchange between the blood and tissues occurs.

The **Veins** receive their blood from the capillaries; these vessels are thinner than the arteries, and their walls collapse when empty. Though some variation exists in their structure, yet speaking generally they contain less elastic material than arteries, and while some may possess a muscular coat others have none.

The veins have a distinctly expansile power, yet in comparison with the arteries they cannot be termed elastic. The necessity for this expansile power is evident when it is remembered that the veins are capable of containing the whole of the blood in the body—as we frequently witness at post-mortem examinations—and even the abdominal veins alone are capable of holding the entire blood contained in an animal's system.

The veins as they pass from the capillaries towards the heart become reduced in number and increased in size, and they terminate in the right auricle of the heart by means of two trunks, the united areas of which greatly exceed the aorta.

In the veins are found valves, these are well-marked in the veins of the head, neck, and extremities, the valves look towards the heart and supply a simple and useful means of assisting the blood flow. In certain places like the bones. intestines, foot, and brain, the veins have no valves.

Veins are normally pulseless, but an exception must be made to this statement in the case of the lower extremity of the jugulars, just where they enter the chest. It is quite common in the horse to observe pulsations in these vessels

for an inch or so along the neck, due no doubt to the contraction of the right auricle. It is, however, distinctly abnormal for these venous pulsations to extend a great distance up the neck, for then it indicates insufficient closure of the tricuspid, due to a debilitated state of the system or actual disease of the valve itself, which latter condition is rare in the horse.

Mechanics of the Circulation.—At each systole of the ventricle a certain amount of blood is forced under great pressure into an already full aorta, and imprisoned there by the closure of the aortic valves. The aorta dilates to receive this extra blood, because owing to the friction in the smaller vessels, or as we shall speak of it, peripheral resistance, it is impossible for the amount pumped into the aorta at each systole to pass out at once at the periphery; in this way high blood pressure is produced in the arteries.

The increase in the size of the aorta to accommodate this extra blood commences near the heart, and runs as a wave to the periphery, this wave is the pulse.

The two important points in the circulation which we have now to consider are blood pressure and pulse, and to understand these it is necessary that we should study briefly the laws which govern the flow of fluids through tubes.

If water be pumped through a rigid tube or pipe, at every stroke of the pump as much fluid passes out at one end of the tube as enters it at the other; between the strokes of the pump no fluid issues from the pipe, the jet is only produced at the moment the pump is in action. No more water can enter this rigid tube from the pump end than can leave it at the outlet.

If now water be pumped through a short elastic tube, the outlet of which is in no way obstructed, the current of water through it behaves just as if it were a rigid tube, viz., a stream of water from the outlet during the action of the pump, and nothing more until the next stroke.

An important alteration can now be made to the current through the elastic tube, by offering an obstruction at the outlet to the free passage of the water; the effect of this

obstruction is that the elastic tube expands to accommodate the contents, while a stream pours from the partly obstructed outlet which no longer only corresponds to the stroke of the pump, but a continuous stream issues so long as the pumping is continued. This continuous stream is produced by the elastic recoil of the tube keeping up the pressure which the pump imparted to the fluid, and the reason why the elastic recoil of the tube is now brought into play, is owing to the partly obstructed outlet or, as we have already termed it, the peripheral resistance. If the elastic tube is of sufficient length the same phenomena occur, although there is no obstruction at the outlet.

In elastic tubes, therefore, the recoil of the tube converts an intermittent into a continuous flow, and the distension of the tube which produces the recoil is caused by the peripheral resistance.

The whole mechanics of the circulation can be worked out on a model consisting of a syringe to represent the heart, elastic tubes to represent the bloodvessels, and a few clamps to offer the needful peripheral resistance.

If with such a model, water be forced into the arterial tubes, the clamps being open and the peripheral resistance therefore very small, it is found by means of a manometer that the pressure in the arterial tube rises with the stroke of the syringe, and falls with the free pouring of the contents into the tubes representing the veins. As the peripheral resistance is small the pulsation set up in the fluid readily passes into the veins, and a manometer here will register the same rise and fall as was met with in the arteries.

If, however, the vessels be clamped so as to produce a resistance, the first stroke of the pump causes the arteries to become distended, they then recoil, and while undergoing this they receive another stroke from the pump and become still more distended, once more they recoil on their contents and are once more distended by the action of the pump, and so on. If all this time the arterial manometer be watched, it will be observed that the mercury or water rises with each stroke of the pump, but instead of falling

at once to zero as it did in the unclamped tube, it only has time to fall a short distance before a second stroke of the pump sends it still higher than before, and this is repeated at every stroke of the pump until the water or mercury refuses to go any higher in the tube, only contenting itself with rising to a certain height at each stroke of the pump, and falling to a certain height during the interval between one stroke and another.

In other words, a mean pressure has been established in the tubes representing the arteries, which has been brought about by the clamped tubes or peripheral resistance, the elastic recoil of the tube, and the pumping of the syringe, and so long as these factors remain the same the mean pressure will not vary; if, however, the clamped vessels be released, so as to allow fluid to flow more easily into the tubes representing the veins, at once the manometer shows a fall in the mean pressure owing to the removal of a certain amount of resistance, and by removing this resistance completely the mean pressure falls to zero.

The mean pressure, then, represents the force which is necessary to cause as much fluid to pass through the periphery as is being pumped into the system of tubes by the syringe; if the peripheral resistance is high the pressure is high, and *vice-versâ*.

A careful study of this experiment places us in complete possession of the main facts of the circulation, but even up to this point we have not learned all the lessons it is capable of teaching.

If a manometer be placed on the venous side of the model, it will show a very low pressure at the time when the arterial pressure is high. If the arterial tubes be felt it will be observed that at each stroke of the pump they expand, producing what is known in living tubes as the pulse; this expansion of the tube is greatest nearest to the syringe, dying out entirely at the peripheral resistance, viz., the clamps; but it is evident that if we loosen the clamps, and so reduce the resistance and lower the mean pressure, that pulsatile waves will pass over to the venous

side of the model, and these can again be obliterated by screwing up the clamp. Lastly, our model, if working at mean pressure, will show the effect of injury to the arterial tubes, for if these be pricked a continuous jet of water shoots out, the strength of the jet varying with each stroke of the syringe, whilst an injury to the venous side produces no jet of water but only a 'welling' out.

Practically this embraces our knowledge of the main facts of the circulation, for all that we have found true of elastic tubes, clamps, and syringe, will be found true of heart, bloodvessels, and peripheral resistance.

The heart has to keep the arteries full; the innumerable smaller arteries with their muscular coat represent the peripheral resistance, under the influence of which and the contraction of the left ventricle, the pressure in the arteries rises so high, and the distension so great, as to ensure that as much blood passes through the periphery during the contraction of the heart and the pause, as enters the aorta during the contraction of the left ventricle. The elastic system of arteries ensures that an intermittent is converted into a continuous flow, and so perpetual pressure is kept up on the mass of blood during the heart's pause.

By a contraction of the arterioles the peripheral resistance is increased and the blood pressure raised; by a relaxation of the arterioles the peripheral resistance is reduced and the blood pressure falls. We have stated that a contraction of the arterioles by increasing the resistance raises arterial pressure and as a rule lowers that in the veins; but this is not universally true, for the arterioles by contracting diminish the capacity of the vascular system, and produce the same effect as if more fluid had been poured into the vessels, in this way the venous pressure instead of falling may rise.

Blood Pressure.—From what has been said, it is hardly necessary to define blood pressure as the pressure exercised upon the blood in the elastic vessels by the action of the heart and the peripheral resistance.

The influence of ventricular contraction and peripheral resistance was explained in the chapter on the heart, p. 38 and elsewhere, but we have here to consider other points which have been scarcely touched upon.

In our model of the circulation we described how the mean pressure of the arteries was produced and maintained, and further the use of a high pressure in the arteries; we showed how this pressure might be raised or lowered by tightening or relaxing the clamps on the vessels, and pointed out that the manometer was capable of graphically recording a fall or rise in blood pressure, and that in this instrument, even when a mean arterial pressure was obtained, a

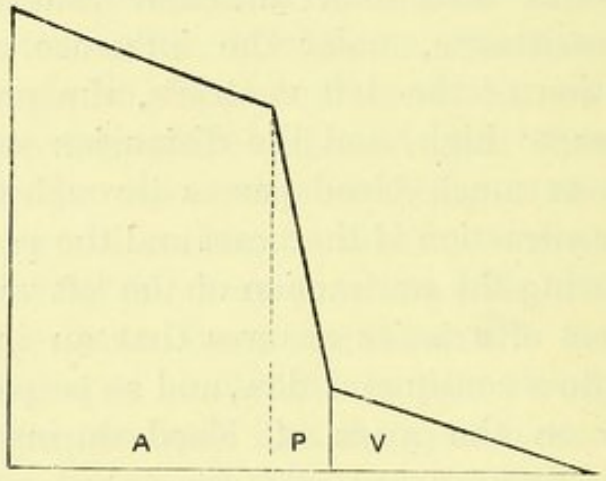


FIG. 5.—DIAGRAM OF BLOOD PRESSURE (FOSTER).

A, Arteries. P, Peripheral Region (minute arteries, capillaries, and veins). V, Veins.

rise and fall agreeing with the systole and diastole of the ventricle occurred.

The mean pressure in the arteries is highest close to the aorta and lowest in the region of the periphery; the fall in pressure from the aorta to the periphery is gradual; in the capillaries the fall in pressure is sudden, and in the veins gradual and very low; in fact, owing to causes to be dealt with under Respiration, a negative pressure may exist in the great veins near the heart. Fig. 5 conveys the fall in blood pressure in a graphic form.

In the carotid of the horse the pressure may be equivalent to $8\frac{1}{2}$ inches to $12\frac{3}{4}$ inches of mercury, or to a column

of blood from $9\frac{1}{4}$ feet to $13\frac{3}{4}$ feet in height; in the dog 4 inches to $6\frac{3}{4}$ inches of mercury, or $4\frac{1}{2}$ feet to $7\frac{1}{4}$ feet of blood, and even in the rabbit a pressure of 3 feet of blood may be obtained.

The arterial pressure varies with each systole of the ventricle, but besides this there are certain undulations obtainable in graphic records of blood pressure which are not due to the heart-beat but are due to respiratory movements. (Fig. 6.) Thus at every inspiration the blood pressure rises and at every expiration it falls; speaking generally this is true, though the tracing (Fig. 7) shows that the pressure does not rise immediately inspiration

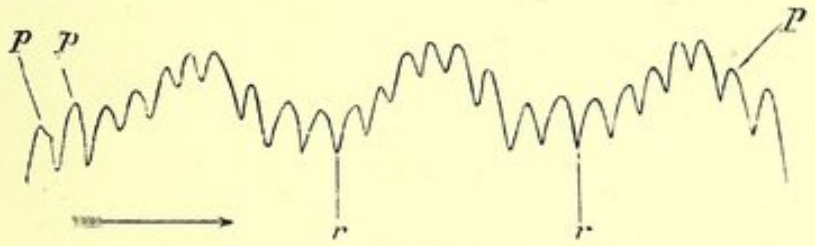


FIG. 6.—TRACING OF ARTERIAL PRESSURE WITH A MERCURY MANOMETER (FOSTER).

The smaller curves *P*, *P* are the pulse curves due to the heart-beat. The space from *r* to *r* embraces a respiratory undulation. The tracing is taken from a dog, and the irregularities visible in it are those frequently met with in this animal.

commences, nor does it fall as soon as expiration begins. The cause of this will be explained under Respiration.

The blood pressure in the capillaries is very difficult to ascertain. Du Bois Reymond calculates it as being one-half that in the large arteries, but it is probable that in many places it is less than this. The capillaries being on the venous side of the peripheral resistance, the pressure in them corresponds with that of the veins.

Blood pressure in the veins is from one-tenth to one-twentieth of that in the corresponding arteries. These results have been obtained on vessels near the heart, the greater distance the veins are from the heart the greater the pressure. McKendrick states that experiment has shown the blood pressure in the facial vein of the sheep to

be 15 inches of blood, in the brachial vein 2 inches, and in the crural vein 5·8 inches of blood.

In the large veins near the heart the pressure is very low, and here the manometer may show even a negative pressure at intervals. This is due to inspiration, which by producing a negative pressure assists the blood to reach the right auricle; it is this negative pressure which in the human subject has rendered operations at the root of the neck dangerous, by aspirating air into the heart should the vessels be wounded.

It is surprising the amount of blood which may be

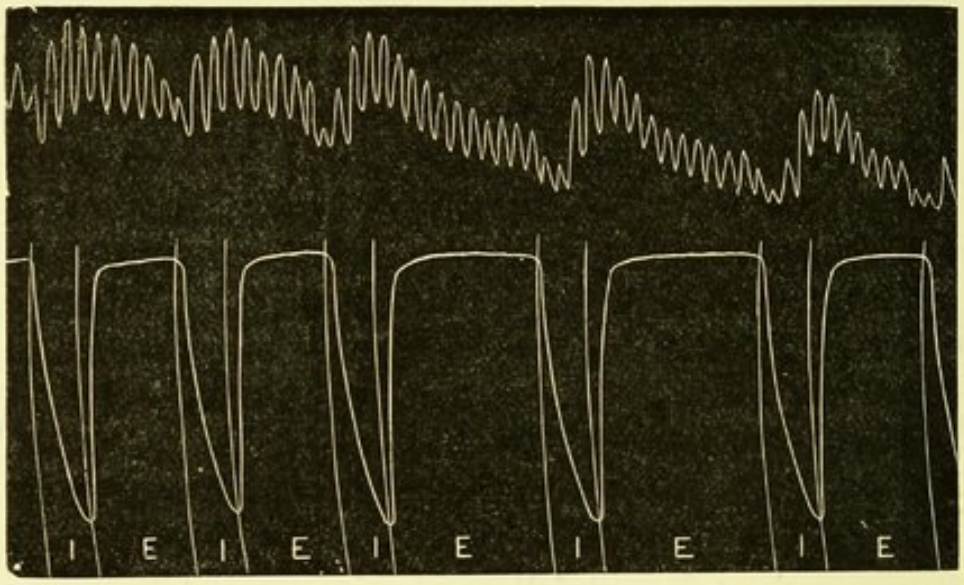


Fig. 7.—Rabbit. Influence of Respiratory Movements upon Arterial Blood Pressure (Waller).

The blood pressure is the upper tracing, the respiratory movement is the lower tracing. I is inspiration, E expiration.

removed from the body without lowering the blood pressure; this is explained by saying that the vessels adjust themselves to the bulk of fluid in circulation, by means of a nervous apparatus to be dealt with presently, and in this way they keep up the blood pressure. Experiment shows that it is not until two-fifths of the blood in the body have been removed that the blood pressure begins to fall; after cessation of the hæmorrhage the pressure again rises unless the loss of blood amounts to 3 per cent. of the body

weight, in which case the low pressure becomes dangerously permanent.

Colin states that horses have lost 55 lbs. of blood in eight days without suffering apparent injury.

On adding a bulk of fluid to the circulation no rise in pressure occurs so long as the nervous mechanism governing the vessels is intact, as the vessels dilate to receive it, but if the cord be divided and a great reduction in pressure thus produced, fluid added to the circulation will raise the pressure to its original amount.

Circulation in the Living Tissues.—The circulation in the living animal may be readily seen in the frog, or in the mesentery of a mammal, and in this way we may learn exactly how the corpuscles behave within the vessels.

In all capillary vessels of small size the corpuscles pass through singly, sometimes revolving in the plasma, traversing some sections very rapidly others very slowly. In the vessels larger than the capillaries, such as the commencement of the small veins, the stream of blood behaves somewhat differently; in these the centre of the vessel is occupied by a column of red cells, whilst between them and the coats of the vessel is a clear layer or zone in which may be seen the white corpuscles strolling lazily along the sides, occasionally stopping, then going forward once more.

This difference in the behaviour of the corpuscles is due to the physical fact that the friction against the sides of the vessel is greater than in the centre; but apart from that, there appears to be an attraction exerted on the white corpuscle by the endothelium, so that it may, as previously pointed out, pass completely through the wall of the vessel into the surrounding tissue.

Especially is this well marked in inflammation, where the slowly moving white corpuscles become attached, as it were, to the lining of the vessel and collect in masses, and with them may also be seen the blood platelets, which under the normal condition of circulation occupy the central zone of the vessel with the red blood cells. The white cells pass completely through the vessel wall in large numbers aided,

as previously pointed out, by their amœboid movements and the spaces existing between the endothelial plates of the vessel. This is known as the migration of white corpuscles.

In inflammation the essential changes taking place are in the wall of the vessel, and the passage of corpuscles through this are not limited solely to the white, but the red may also pass through. That the inflammatory changes are essentially vessel-wall and not blood, is proved by the fact that an artificial corpuscular fluid introduced into the part behaves exactly as the blood behaves. This, and more evidence which might be adduced, all goes to show how essential the wall of the vessel is to the ordinary circulation.

The Pulse.—It is a fact of common observation that the arteries throb or pulsate whilst the veins do not, and we now have to inquire what really produces this pulsation, and why it stops at the arterioles.

When the left ventricle contracts and drives its blood into the aorta, the arteries dilate to accommodate it and then contract owing to their elasticity; each expansion of the arterial wall coincides with a contraction of the ventricle, and so each beat or throb of the pulse agrees with a contraction of the heart.

This intermittent expansion of the arteries gradually becomes less marked at a distance from the aorta, and dies out at the arterioles; it dies out here owing to the frictional resistance it experiences, and this is the normal state of matters. If the arterioles dilate considerably, it may be possible for the 'throb' to pass through not only the arterioles but also the capillaries and appear in the veins; in this way a venous pulse may be produced. An example of this will be given when we come to describe the influence of certain nerves on the vessels of the submaxillary gland of the dog, where dilatation of the arterioles causes a throbbing in the veins.

This intermittent expansion of the arteries, called the pulse, produces a wave in the arterial system, we will speak of it as the pulse-wave; from what we have said it

is evident that the height of this wave is greatest nearest the heart, and falls to nearly zero in the periphery.

The length of the pulse-wave is considerable, viz., about 18 feet in length; in this way the beginning of it is lost in the arterioles before the end of it has left the aorta. Further, the wave travels with considerable velocity, viz., from 15 to 30 feet per second.

At this stage it is necessary to point out that no confusion should exist between the pulse-wave and the velocity of the blood, the two conditions are quite distinct. The pulse-wave runs along the surface of the blood-stream, the blood-current runs within the pulse-wave; the pulse-wave travels at a high rate of speed, the blood-current travels comparatively slowly.

The pulse-wave can be studied by means of the graphic

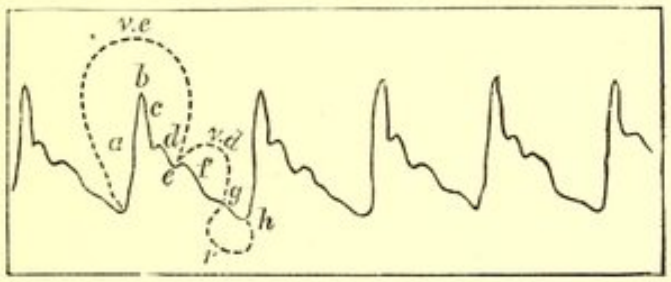


FIG. 8.—NORMAL SPHYGMOGRAM MODIFIED FROM DUDGEON; PRESSURE 2 OZ. (HAMILTON).

method; it is obvious that a lever placed on a pulsating vessel will be moved up and down, and in this way may be made to trace a curve which will represent the passage of the pulse-wave at that particular spot.

A tracing thus obtained simply registers the expansion and recoil of the artery, it will not give a tracing of the pulse-wave itself. Such tracings are called sphygmograms.

The simplest description of a tracing obtained in this way, is that there is a nearly vertical upstroke and an oblique downstroke, the obliquity being broken by two or three waves in the descent. (See Fig. 8.)

The irregularities observed in the downstroke have received several explanations, and the point is far from

settled. *V.E.* represents the events occurring during the systole of the ventricle, *a b c* being the primary or percussion wave, and *d* a curve called the first tidal or predicrotic wave; then follows an angle *e* called the aortic notch, which it is generally agreed is due to the closing of the aortic valves; this is followed by a curve *f* known as the dicrotic wave; it is one of the few curves which appear with any regularity in the tracings, for we may at once say that unless the proper degree of pressure is maintained on the vessel, great irregularity in the sphygmograms will be produced. Some physiologists have even held that certain of the curves or breaks in the downstroke are instrumental errors, and not due to the arterial wave. However this

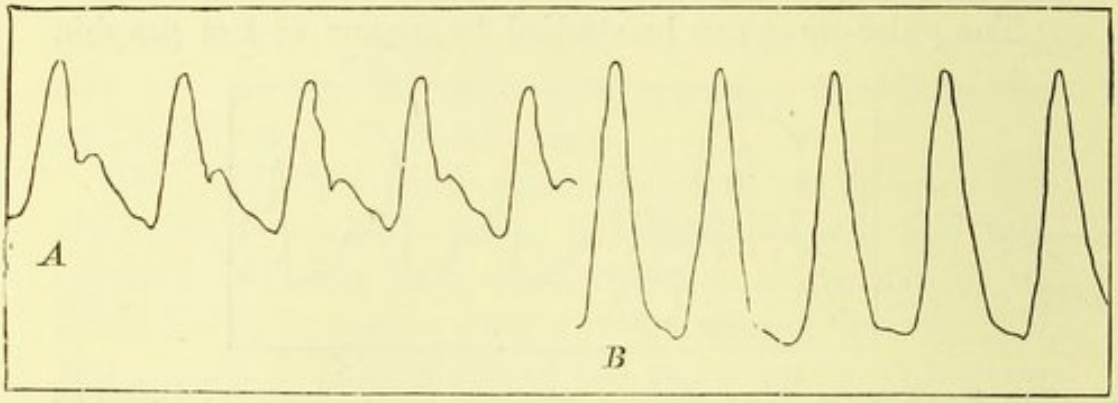


FIG. 9.—TRACING FROM THE FACIAL ARTERY OF THE HORSE (HAMILTON). *A* before, *B* after destruction of the aortic valves.

may be, the dicrotic wave may be accepted as having an undoubted existence, though some difference of opinion is held as to its cause.

In Fig. 8 the small wave *g* is called a second tidal wave, probably both it and *d* are due to oscillations set up by the inertia of the fluid; *c d* marks the events occurring during the ventricular diastole, and *r* the period of rest before the next systole.

The two theories about the origin of the dicrotic-wave are:—1, that it is either a recoil of blood at the root of the aorta, impacted against and reflected from the valves, or, 2, a peripheral wave reflected back through the arteries on the valves, and a second time reflected.

That the dicrotic wave is a reflection from the aortic valves, is shown by the tracing in Fig. 9, taken from the facial artery of the horse, *A* before, and *B* after destruction of the aortic valves. In *B* the dicrotic wave has disappeared.

A well-marked dicrotic pulse gives a double beat of the pulse for each single contraction of the heart.

In connection with pulses the term **tension** has been employed by pathologists; thus pulses of high and of low tension have been described, and an attempt has been made to distinguish between the pathologist's tension and the physiologist's pressure. If tension be defined as the

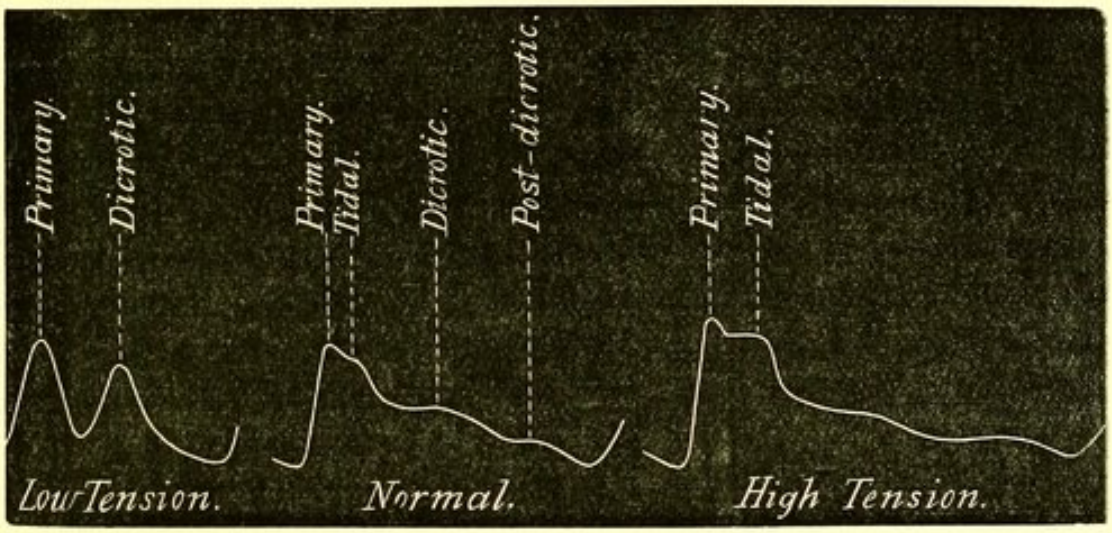


FIG. 10.—SPHYGMOGRAMS OF LOW TENSION, NORMAL, AND HIGH TENSION PULSES (WALLER).

elastic force exerted by the artery on the blood within, it is evident that this force bears some distinct relation to the force distending the artery, viz., the blood pressure; a high blood pressure and high arterial tension describe the same conditions.

In an artery giving a high tension the dicrotic wave is nearly extinguished, the vessels in fact are so full that the recoil wave makes very little impression on the tense arterial wall; when blood pressure is low and the amount of movement in the artery great, the recoil or dicrotic wave is very marked. (Fig. 10.)

The pulse will vary in character depending upon age,

condition, and state of the system ; it also differs according to the animal. Colin gives the following table of pulse-rate in different animals :

Elephant	-	-	25 to 28	beats	per minute.
Camel	-	-	28 ,, 32	,,	,,
Horse	-	-	36 ,, 40	,,	,,
Ox	-	-	45 ,, 50	,,	,,
Sheep	-	-	70 ,, 80	,,	,,
Pig	-	-	70 ,, 80	,,	,,
Dog	-	-	90 ,, 100	,,	,,

The pulse is much quicker in the young animal than in the adult, that of a foal at birth beats 100 to 120 per minute, and of a calf 90 to 130 per minute ; in old age the pulsations become reduced, and the artery much weaker. As a rule, the higher or bigger the animal the lower the pulse rate. The more rapid the pulse, the greater the quantity of blood in circulation.

The **Velocity of the Blood** varies in the arteries, capillaries, and veins, being greatest in the former, least in the capillaries, and rising again in the veins.

The velocity of flow is inversely as the sectional area of the tubes ; the total sectional area of the capillaries is greater than that of the aorta, therefore the velocity is reduced ; from the capillaries to the heart the area becomes smaller and the velocity increases. The velocity of blood-flow is due to the width of the bed formed by the vessels ; as the arterial system expands, the velocity diminishes ; in passing through the capillaries, with their immense network, the velocity is at a minimum ; in passing towards the heart the vessels are reduced in number, hence the bed is smaller and the velocity accordingly increases. The cause of the flow throughout the entire system is the contraction of the left ventricle, and the gradual fall in pressure which occurs from the aorta to the right auricle.

The vascular system has been compared to two cones placed base to base, the apex of one being the left ventricle, of the other the right auricle ; where the bases of the two cones meet is the capillary network. The sectional area of

this has been estimated at 500 times greater than that of the aorta, whilst the passage of blood through it, owing to the width of the bed, is 500 times slower than in the aorta (Volkmann).

According to the same authority, the velocity of blood in the carotid of the horse is from 11·8 inches to 15·75 inches per second; in the metatarsal artery of the horse 2·2 inches per second, and in the jugular vein 8·85 inches per second. A horse which gave a carotid velocity of 12 inches per second gave a jugular velocity of 9 inches per second. Chauveau found in the carotid artery of the horse a velocity of 20·47 inches per second during systole, 8·66 inches per second at the beginning of diastole, and 5·9 inches per second during the pause (M'Kendrick).

The mean velocity in the carotid of the dog is 10½ inches per second, at the end of diastole 8½ inches per second, and at the end of systole 12 inches per second.

The velocity of the blood is therefore increased by each systole of the ventricle, but decreased during diastole, and falls still more during the pause. The flow in the arteries is assisted by expiration, while that in the veins is assisted by inspiration.

The velocity of the blood is greater in the pulmonary than in the systemic capillaries, while the velocity in the venæ cavæ is half of that in the aorta.

Any attempt made to estimate the velocity of the blood by dividing an artery, and measuring the escape of blood from its cut end in a given time, would lead to erroneous conclusions, for the velocity in a closed artery and that in an open one are two different things. In the undivided artery the peripheral resistance reduces the velocity, in the divided artery the peripheral resistance largely disappears and the velocity is five or ten times greater, so that the carotid of a horse does not bleed with a velocity of 16 inches per second but nearer 160 inches per second. Or to put it in a practical way, if the carotid of the horse has a sectional area of ·2 square inches, the amount of blood passing through the unwounded vessel amounts to 2 oz. per second, while

if the same vessel be divided the loss of blood would be nearly 1 pint per second.

The **Duration of the Circulation** depends upon the length of time it takes a red corpuscle to travel from a given point and back to it again. In a horse with a pulse frequency of 42, the complete circuit was performed in 40 seconds (Hering), and is equivalent, according to the latter observer, to about 28 beats of the heart.

In the rabbit with a pulse frequency of 168 per minute, the time occupied in completing the round of the circulation was 10 seconds, or again in 28 heart beats; with the dog 16·7 seconds or in 26·7 heart beats. The blood-cell owing to the diminished velocity spends most of its time in the capillaries of the tissues and lungs.

Aids to the Circulation.—The contraction of the left ventricle is sufficient to drive the blood all over the body, but in the veins this force is assisted by the muscles compressing the vessels, by the presence of valves which prevent regurgitation, (especially in the veins of the limbs where the fluid has to flow against gravity), and, lastly, the circulation is assisted in the larger veins by the process of inspiration and the dilatation of the right auricle, both of which have an aspirating effect on the blood in the larger veins. The sucking action of the left auricle assists also in drawing the blood in the pulmonary veins towards the heart.

Influence of the Nervous System.—An artery may be in the condition of dilatation, contraction, or a something midway between each; it is this midway condition which normally exists in the body and produces that state of vessel spoken of as 'tone.'

The bloodvessels are under the control of a system of nerves known as the **vaso-motor.** It is possible to distinguish certain nerves which produce contraction of arteries, known as **vaso-constrictors**, and of others which dilate the vessels known as **vaso-dilators.** Every vessel does not necessarily possess both a constrictor and a dilator nerve, in fact there are parts of the body like the abdominal

viscera where the dilator-nerves appear to be conspicuous by their absence, and yet the phenomenon of dilatation occurs; this can be explained by supposing that the action of the constrictor fibres is for the time being withheld. In the same way there are parts of the body like the muscles where vaso-constrictor fibres have not been satisfactorily demonstrated, and there are other parts like the brain where no vaso-motor nerves have yet been found.

The vaso-constrictor nerves if in more active operation than that required for the production of ordinary arterial tone, cause by their contraction of the bloodvessels a rise above the normal arterial pressure which may be widely distributed; whereas if the vaso-dilator fibres are in operation, their effect is more essentially of a local nature, inasmuch as their distribution does not cover such a wide area as that of the constrictors.

If, for example, the abdominal splanchnics, which are solely constrictor nerves, be divided the vessels of the abdomen dilate, and the general blood pressure in consequence falls; if the cut end of the nerve be stimulated the vessels contract, a larger amount of blood is sent into the general circulation, there is increased peripheral resistance and the blood pressure rises.

The head centre governing vaso-constrictor action lies in the medulla, with subsidiary centres in the spinal cord, but no special centre is known in connection with the vaso-dilator nerves.

The vaso-motor centre in the medulla is situated in the floor of the fourth ventricle; it is readily affected by the quality and character of the blood circulating through it, for example, an increased venous condition of the blood leads to contraction of the smaller arterioles; this constriction means a considerable opposition to the flow through the arteries, as the result of which the blood pressure is raised. The rise and fall in blood pressure is largely under the control of this centre, through the resistance or otherwise offered to the flow of blood through the periphery. Stimulation of the vaso-motor centre

means a constriction of the smaller vessels, but it is possible for stimulation to bring about the opposite condition, viz., inhibition of the centre, in which case vascular dilatation occurs. There are undulations observable in certain blood pressure tracings, which are not due to the heart nor to the respirations, but to a rhythmical activity of the vaso-motor centre producing a variation in the peripheral resistance. The result is the production of a series of undulations known as Traube-Hering curves (Fig. 11); the

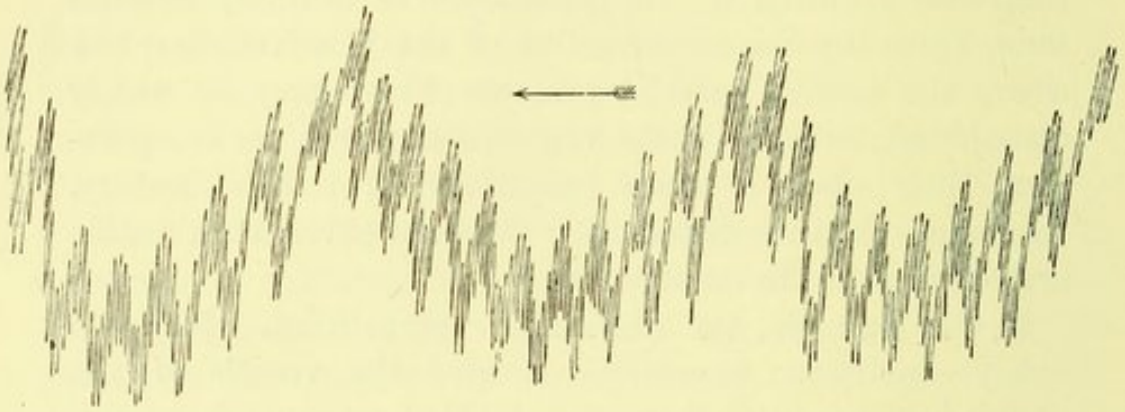


FIG. 11.—BLOOD PRESSURE CURVE OF A RABBIT, RECORDED ON A SLOWLY MOVING SURFACE, TO SHOW TRAUBE-HERING CURVES (FOSTER).

The heart-beats are the closely situated up and down strokes, readily seen by means of a lens. The next curves are those of respiration; the large bold undulations being Traube-Hering curves. In each Traube-Hering curve there are about nine respiratory curves, and in each respiratory curve about nine heart-beats.

rise in the curve being due to contraction, and the fall to relaxation of the arterioles.

This rhythmical activity of the vaso-motor centre, is produced by a deficiency of oxygen in the blood circulating in the medulla; the curves may be obtained by taking a blood pressure tracing in an animal after dividing the vagi —so as to eliminate the cardio-inhibitory centre—and stopping the respirations.

Besides the vaso-motor centre in the brain, and the subsidiary ones in the spinal cord, there is reason to believe that local centres exist, which, so long as they are in connection with the medulla are subordinate to it, but may when separated from it act as centres on their own account;

this latter condition being abnormal, it is probable that the local centres are for the purpose of keeping up a closer touch with those in the cord and medulla, and so maintaining the normal vascular tone.

The course taken by the constrictor and dilator fibres in order to reach the various tissues is markedly different. The **constrictor fibres** in the dog issue from the spinal cord from the second dorsal to the second lumbar spinal nerves, these fibres supply every vessel of the body, where constrictor nerves exist, with constrictor influence; passing out with the inferior or motor root of the spinal cord, they leave this by the white ramus communicans to join the lateral ganglion in the sympathetic chain which is nearest to it. Those fibres intended for the head pass forward through the ganglia, eventually reaching the inferior cervical ganglion, and so gain the cervical sympathetic, and with this enter the head and neck, supplying the skin, glands, and other parts. The arrangement of the fibres intended for the thorax has not been made out, whilst those passing to the abdominal viscera and pelvis reach these parts through the abdominal splanchnics and hypogastric nerves. The fibres intended for the fore leg return to the spinal cord as grey rami from the lateral sympathetic ganglia, and enter the brachial plexus; those for the hind leg by grey rami which reach the sciatic plexus.

In this way the abdominal viscera and the skin of the limbs receives its supply of vaso-constrictor nerves, the muscles receiving, as previously mentioned, hardly any constrictor fibres.

During the passage from the spinal cord to their destination, the constrictor fibres have undergone considerable change; up to the lateral or vertebral ganglia they are very fine medullated nerves, but on passing through the sympathetic ganglia they are found to have lost their medulla, and as non-medullated nerves they eventually reach their destination.

It is in the vertebral ganglia that a recurrent branch or grey ramus is given off, which returning towards the spinal

cord supplies the vessels in the canal, and likewise, as just mentioned, by issuing with the brachial and sacral plexuses supplies the fore and hind limbs.

The origin and course of the **dilator fibres** is different, they appear to arise in various parts of the nervous system, but it is only in the cranial and sacral regions that any exact knowledge of their course has been obtained.

The dilator fibres may arise in the medulla and spinal cord, and so run in cranial or in spinal nerves; if the latter they leave the cord in the inferior roots, and pass to their destination with the ordinary spinal efferent nerve; if the former they run to their destination in company with a cranial nerve. These fibres are distinguishable from the constrictor by the direct instead of roundabout way they take to reach their destination; further, though they are very fine nerves, like the constrictor, they do not lose their medulla until near their termination.

As an example of a dilator nerve running in a cranial, we may take the chorda tympani which is derived from the facial; the effect of stimulating the cut end of this nerve is to dilate in a remarkable manner the vessels of the submaxillary gland. The nervi erigentes, again, are nerves issuing with one or more of the sacral spinal nerves, stimulation of which causes erection of the penis by dilatation of the vessels.

In some nerves both vaso-constrictor and dilator fibres may be mixed up, as for instance in the sciatic and brachial plexus. On section of these the effect of cutting the constrictor nerves is in the first instance the most predominant, viz., the hot, flushed limb; but later the constrictor nerves, owing to their early degeneration, give way to the dilator, for on stimulation the constrictor nerves fail to react whilst the dilator nerves do.

A good illustration of the constrictor fibres of the body, is that demonstrated by dividing the sympathetic in the neck of a rabbit, when owing to the loss of the constrictor influence the vessels dilate, small ones previously unseen come into view, the ear becomes red, and its temperature

rises; to induce the constrictor influences of this nerve it is only necessary to stimulate the upper end, when the vessels contract, the flushed appearance departs, and the temperature falls. This experiment was first performed on the horse, division of the cervical sympathetic being followed by dilatation of the vessels, and sweating of the head and neck.

The effect produced on the bloodvessels of the head and neck by division of the sympathetic, demonstrates that there must constantly be impulses passing along it which maintain the vessels in the normal state of contraction, and the same

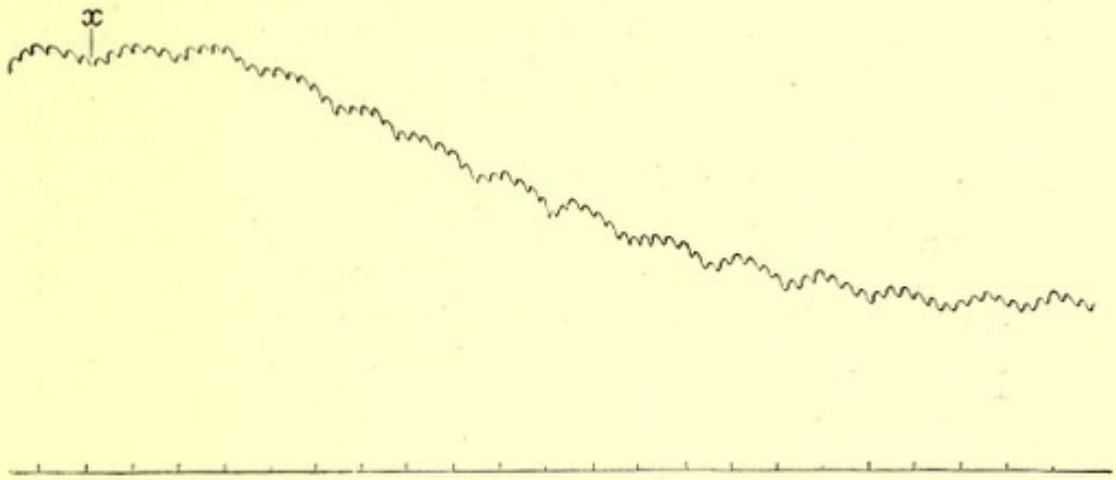


FIG. 12.—TRACING, SHOWING THE EFFECT ON BLOOD-PRESSURE OF STIMULATING THE CENTRAL END OF THE DEPRESSOR NERVE IN THE RABBIT (FOSTER).

The time marker below marks seconds. At *x* an interrupted current is thrown into the nerve, and the blood pressure gradually falls.

is probably true of all vessels; the vaso-dilators do not appear to possess such continued activity.

The tonic state of contraction in which the arterioles of the body are normally found is, as has been pointed out, the explanation of the maintenance of the general blood pressure, the centre for which lies in the medulla; but the tonic constrictor influences sent out by this centre may be modified by impulses passing to it from the periphery. Thus if the **depressor nerve**, which we have already spoken of in dealing with the heart, be divided and the end in connection with the brain stimulated, a steady but considerable fall in blood pressure occurs. (Fig. 12.) This is produced

by the dilatation of the arteries of the abdominal viscera owing to impulses sent out from the medulla, for if the splanchnics, which supply the abdominal viscera, be previously divided no fall in blood pressure occurs.

If under a certain anæsthetic (urari) the central end of the divided sciatic or other nerve be stimulated, an opposite result is obtained, viz., the blood pressure rises, due to the constriction of the arteries of the splanchnic and possibly other areas; such effects are spoken of as **pressor**, but the same nerve which under one anæsthetic will give pressor results, may under another (chloral) yield depressor, from which we draw the conclusion that both pressor and depressor impulses may be transmitted to the medulla along afferent nerves, depending upon the requirements of the system.

As an example of what these requirements are we may mention the regulation of the temperature of the body by either a flow of blood from the skin to the viscera in cold weather, or from the viscera to the skin in hot weather; this however will be dealt with under Animal Heat.

Nothing is known of a vaso-motor nerve supply to veins, though such is considered to exist.

A very close parallelism exists between those nerve fibres which constrict the vessels and those which cause a more forcible contraction of the heart; in both cases they are of the non-medullated variety, in each they excite muscular action, and by so doing increase the wear and tear of the tissues involved. In the same way a close connection exists between those fibres dilating the bloodvessels and those slowing the heart; both are medullated and muscle restraining, and in consequence both excite processes of repair rather than of disintegration.

Peculiarities in the circulation through various tissues occur as the result of their special function; they are observed in the brain, erectile tissues, etc. The great vascularity of the brain necessitates that the blood should pass to it with a degree of uniformity which will ensure the carrying out of its functions. We see this provided for in the frequent arterial anastomoses, for example, the Circle

of Willis and the Rete Mirabile of ruminants, which insures that not only does the blood enter with diminished velocity, but that if a temporary obstruction occurs in one vessel its work is readily performed by the others. The rete mirabile alluded to, which forms the arterial plexus on the base of the brain of ruminants, is considered by some to regulate the flow of blood to the brain while the head is depressed during grazing, and that it accounts for the absence of cerebral hæmorrhage in these animals. It is probable that this may be one of its functions ; but the horse possesses no rete, and his head is depressed during grazing for more hours out of the twenty-four than is the case with ruminants. It has probably, therefore, some other function to perform.

The venous arrangement of the brain is very remarkable ; the walls of the veins are composed of layers of the dura mater, and even portions of the cranial bones may enter into their formation. The veins or sinuses of the brain are large cavities, which from their arrangement are most unlikely to suffer from compression, and from the rigidity of their walls are not capable of bulging as most veins do when obstructed; in this way the return of the venous blood is provided for.

The pulsations observed in the exposed brain are not due to the pulse in the arteries of the brain, but arise from the respiratory movements ; expiration causes the brain to rise by hindering the return of blood, whilst inspiration causes it to fall by facilitating the return of blood.

The cerebral circulation is considerably assisted by the presence of fluid within the ventricles of the brain. This fluid readily passes from ventricle to ventricle, and from ventricle to spinal cord ; in this way, as the external pressure becomes greater the internal becomes less, and so compression of the brain substance is avoided.

The singular arrangement of the venous plexuses of the corpus cavernosum penis, admits of this organ attaining a condition which in the brain every measure is adopted to prevent—viz., a vast increase in size. The enormous size

of the venous plexuses of the penis, their frequent intercommunication, the muscular pressure to which the veins leading from the sinuses are exposed, produce a considerable increase in the volume of the organ under the direction of the vasomotor nervous system.

In some organs the vascular arrangement is peculiar, and probably depends on the function of the part. It is not known why the spermatic artery and plexus of veins should possess such a remarkably tortuous course; probably, in some way or other, it is concerned with the secretion of the glands with which the vessels are connected, but its use is far from clear. On the other hand, tortuous vessels in the walls of hollow viscera, such as the stomach and intestines, perform a very evident function. We have only to think of the size of a collapsed and full stomach in the horse, to recognise the necessity for some arrangement existing to prevent stretching of the vessels or interference with the blood supply.

The vast venous and arterial plexuses of the foot of the horse, are a peculiarity in the circulation which is dealt with in the chapter devoted to the Foot.

CHAPTER IV.

THE VASCULAR GLANDS.

The vascular glands comprise certain so-called ductless or blood glands, of which the spleen is the representative. Their function is obscure; they secrete nothing, but they exercise a certain control over the constitution of the blood and other tissues, though in some cases even this little is unknown respecting them.

The **Spleen** does not appear absolutely essential to life, for it has constantly been removed without causing death. The chief facts in connection with its function which have been ascertained, are those relating to the formation and destruction of blood corpuscles. The blood of the splenic vein contains more white cells than that of the splenic artery, hence it has been inferred that they have been formed in the spleen. The worn-out red cells of the blood appear to undergo disintegration in the spleen, for more iron is obtainable from the spleen than corresponds to the amount of blood it contains, and this is supposed to result from the disintegration of the red cells.

From the intimate connection the spleen has with the stomach, and the fact that it becomes larger after a meal, it has been supposed by some to be concerned in elaborating or storing up the proteid principles of the food.

Clinical experience, especially in the tropics, constantly demonstrates the value of the spleen as a reservoir, especially in those cases where the blood is driven from the surface of the body and thrown on the viscera. After an

attack of continued fever we have known the spleen contain the greater part of the blood in a horse's body, and require two men to lift it out of the abdomen after death.

Roy has shown that the spleen is possessed of rhythmical movements, expanding and contracting at regular intervals ; these movements are brought about through the medium of the muscular fibres of the capsule, and not by means of the blood pressure, of which the circulation in the spleen is found to be independent. The muscular movement is under the control of automatic ganglia situated in the organ itself.

Tizzoni asserts that new splenic structures are formed in the omentum of the horse and dog after destruction of the spleen (Landois). It is certain that when the spleen is destroyed the lymphatic glands and red marrow of bones become, as a compensatory effect, more active in forming red blood cells.

The **Thymus** is especially active during intra-uterine existence, and for a short time after birth. It forms blood corpuscles, and in this way assists the other tissues engaged in this operation, at a time when the greatest activity is required from them—viz., during early life.

The thymus disappears towards puberty; in the horse and ox at about two years old. In hybernating animals it acts as a storehouse for fat.

The **Thyroid** is connected in some way or other with the mucin formed in the body, for removal of this gland gives rise to myxœdema, or mucinoid degeneration of the tissues ; the composition of the blood is also affected by its removal, for there is a reduction in the number of red cells and an increase in the white. Removal of the thyroid leads to a fatal cachexia; the results of the removal depend on the class of animal, carnivora suffer more than herbivora, the horse, calf, sheep, and rabbit, bear the operation well; dogs and cats almost invariably die, though age is an important factor in the matter, the old animal often surviving though with permanently damaged health. The function of this gland, however, is quite obscure, but it is

considerably more active in intra- than in extra-uterine life.

The cachexia which follows removal of the thyroid body is prevented, and even cured, by the administration of thyroid extract either by the digestive canal, or subcutaneously.

The **Renal Capsules** have been supposed to be connected with the removal of worn-out pigment from the body, but their function is involved in mystery. In dogs and other animals, the effect of removing these glands has been the production of profound degeneration in the central nervous system, followed by death. In some animals the removal of the renal capsules is followed by an alteration in the blood, which renders it poisonous to other animals.

It has been found that the juice obtained from the thyroid gland and renal capsules is capable of exercising a marked physiological effect on the nervous system, heart, and bloodvessels, even when administered in minute doses.

It is not known how far these animal extracts represent a material elaborated in the glands for the uses of the body, or poisonous products brought to them to be rendered innocuous. But it appears certain that these small glands are capable in some way or other of directing the metabolism of the body, and maintaining the composition of the blood.

The function of the **Pineal** and **Pituitary bodies**, though classed as blood glands, is absolutely unknown. The pineal has been considered to be the remnant of an ancestral eye.

CHAPTER V.

RESPIRATION.

The lungs occupy the whole cavity of the thorax; during life no space exists between the pulmonary and costal pleura, so that the case is an air-tight one. So long as this air-tight condition is maintained, any movement which tends to increase the size of the case, such as the retreat of the diaphragm and the advance of the ribs, causes a distension of the sacs and the air rushes in; by a reversed process it is pressed out, viz., by a collapse of the chest wall.

If, however, the cavity of the chest be opened to the external atmosphere the lungs collapse owing to their elastic recoil, and the fact that the pressure within and without them is the same; such a condition would lead in the horse to asphyxia, as the pleural cavities communicate, but in those animals where the right and left pleural sacs are distinct, the lung on the wounded side only would collapse.

The process by which the chest is filled with air, known as **Inspiration**, is a purely muscular act; the diaphragm as the chief muscle of inspiration contracts, and thereby recedes; the ribs are drawn forwards and outwards, their posterior edges are everted, and the intercostal space widened; by this means the capacity of the chest is increased and the lungs tend to fill the space thus created, by doing so they rarefy the air already within them, by which means a difference in pressure between the air in the lungs and that outside the body occurs, and air rushes in to restore equilibrium; this inrush is inspiration.

The increase in the size of the chest which occurs during quiet inspiration in the horse is stated by Colin to be as follows: the antero-posterior or longitudinal diameter of the chest is lengthened between four and five inches, whilst the transverse diameter between the eleventh and twelfth ribs is increased by $1\frac{1}{2}$ inches.

Only the last twelve or thirteen pairs of ribs take, under ordinary circumstances, any important share in respiration; this is due to the true ribs being more or less covered by the scapula and its attached muscles. When, however, a difficulty occurs in the breathing, the elbows are turned out which brings other muscles into play as auxiliaries in respiration, and a certain number of the true ribs now assist in increasing the capacity of the chest.

The Movements of the Diaphragm during respiration are of a peculiar kind, as might be imagined from the attachments of the muscle. The diaphragm works to and fro, but not equally over its whole surface, for the central portion is tendinous and moves very little owing to its connection with the posterior vena cava, while the part of the diaphragm below this vessel is so short that its movement is very limited. The chief motion in the diaphragm lies in its upper part, at each inspiration it contracts and recedes carrying back with it the liver, stomach, and spleen; at each expiration it relaxes and advances, carrying with it the viscera which were previously displaced. The diaphragm also advances and recedes at its sides as well as its upper part, and in so doing exerts pressure on the liver, and assists the flow of blood towards the right heart. Obviously the deeper the inspiration the greater the liver pressure.

In ruminants owing to the liver being situated to the right of the central line of the body, it does not experience the same change in shape as that of the horse.

In Fig. 13 the body is supposed to be divided horizontally; the position of the diaphragm and the displacement of the viscera during respiration are clearly seen.

During an expiration the shape of the diaphragm looked at from within the chest is very convex, but during inspira-

tion it becomes considerably flattened, though never entirely flat. Even the pressure of gallons of fluid on the diaphragm, as in hydrothorax of the horse, does not render it flat.

Expiration.—The chest having been filled with air, the next process is its expulsion, and the mechanism here concerned is not fully agreed upon by physiologists. Whilst

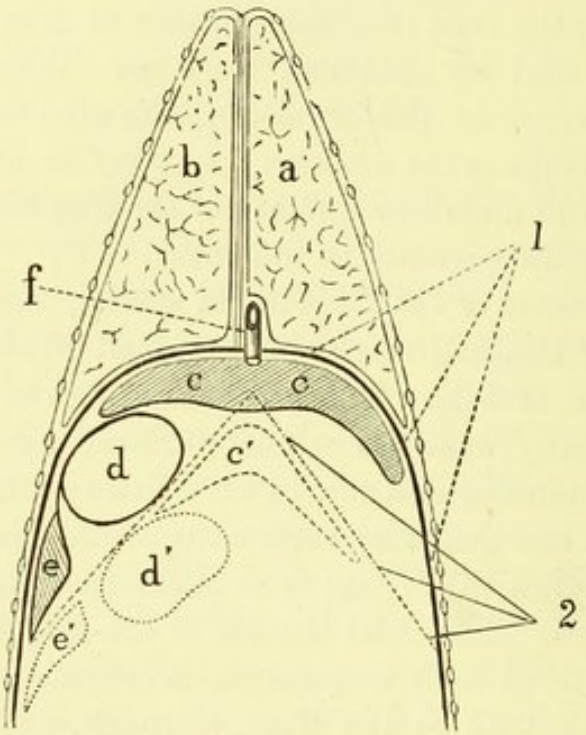


FIG. 13.—HORIZONTAL SECTION OF THE HORSE'S CHEST, LOOKED AT FROM ABOVE, ILLUSTRATING THE MOVEMENTS OF THE DIAPHRAGM. (SUSSDORF.)

a, right lung; *b*, left lung. 1. Position of the diaphragm during deep expiration: *c*, liver during deep expiration; *d*, stomach during deep expiration; *e*, spleen during deep expiration. 2. Position of diaphragm during deep inspiration; *c'*, position of liver; *d'*, of stomach: *e'*, of spleen during deep inspiration; *f*, posterior vena cava as it passes through the diaphragm.

some hold that it is a purely non-muscular act, others contend that certain muscles do share in the process; all are agreed that the elastic reaction of the lung induces it to retract, the effect being to draw the now relaxed diaphragm forward; moreover, the elastic recoil of the cartilages of the false ribs decreases the diameter of the chest and assists the lungs in expelling the air. The compression which

the abdominal contents undergo in inspiration, causes the abdominal muscles to descend; this compression is now relieved, and the process of expiration is further assisted by the contraction of these muscles, by which the viscera are forced forward against the diaphragm.

The **Fœtal Lung** contains no air and therefore sinks in water. The first few inspiratory gasps at birth distend the alveoli, but for some time the conditions found in the adult, viz., the negative pressure in the pleural cavity, and the collapse of the lungs on opening the chest, are not found in the very young animal. Such only occur when the cavity of the thorax is larger than the lung in a state of collapse. Thoracic development in young animals is very rapid, a foal will increase 1½ inches in circumference within the first few hours after birth; when this absolute increase in chest capacity is established, a negative pressure in the pleural cavity is obtained.

Muscles of Respiration.—The action of the muscles of the chest during respiration has been much disputed. The external intercostals doubtless, from the direction taken by their fibres, draw the ribs forward, and by so doing increase the transverse diameter of the chest; in this respect they are regarded as inspiratory muscles. The internal intercostals, the fibres of which run in an opposite direction to the external, draw the ribs backwards and act as muscles of expiration; and speaking generally, we may say that those muscles which draw the ribs forward are inspiratory, whilst those which draw them back are expiratory. The following table shows the inspiratory and expiratory muscles of the chest:

Muscles of Inspiration.	*Muscles of Expiration.*
Diaphragm.	Abdominal muscles.
External intercostals.	Internal intercostals.
Serratus anticus.	Transversalis costarum.
Levatores costarum.	Serratus posticus.
Serratus magnus (during difficult respiration).	Triangularis sterni.
Latissimus dorsi ,, ,,	
Scaleni ,, ,,	

In some animals the ribs do very little work and the diaphragm becomes the chief respiratory muscle. In most quadrupeds the sternum is fixed to the ribs and undergoes little or no movement; even the most powerful respiratory movements in the horse give rise to no sternal movement.

During laboured respiration any muscle which can assist in advancing the ribs directly or indirectly is brought into play. This is well marked in dyspnœa.

After the expiratory act there is a pause before the next inspiration. In the horse during repose the process of expiration is as a rule longer than that of inspiration, though the proportion between the two is not invariable. During work the value of the inspiratory and expiratory acts is about equal.

During inspiration a slight negative pressure exists in the trachea, and during expiration a slight positive pressure. In the pleural cavity a negative pressure exists during both expiration and inspiration, due to the tendency of the elastic lung to collapse; the value of this intra-thoracic pressure has been ascertained for the sheep to be about one-eighth of an inch of mercury, and during dyspnœa three-eighths of an inch. In the dog during inspiration the negative pressure in the pleural sac is one-quarter of an inch of Hg, whilst during expiration one-eighth of an inch has been observed. In the horse one-quarter of an inch of Hg has been registered during a powerful expiration, and $1\frac{1}{8}$ inches during a powerful inspiration. We can recognise this negative pressure post-mortem, by the rush of air produced by the collapse of the lungs when the chest is opened.

The **number of respirations** will vary with the class of animal; as a rule, the larger the animal the slower the respiration:

Horse - - -	8 to 10 per minute.
Ox - - -	12 ,, 15 ,, ,,
Sheep and Goat -	12 ,, 20 ,, ,,
Dog - - -	15 ,, 20 ,, ,,
Pig - - -	10 ,, 15 ,, ,,

Rumination increases the respirations, and muscular

exertion in all animals at once causes them to rise; in experiments on respiration this is most marked; even walking a horse will nearly treble the number of respirations, and unless the fastest pace has been employed the breathing falls immediately the horse stops, though it does not reach the normal for a few minutes.

The ratio of heart-beats to respiration has been placed at 1 : 4 or 1 : 5.

The Effect of Respiration on Circulation.—We have previously alluded to the influence of respiration on the circulation, and the assistance which this renders in aspirating the blood into both sides of the heart, and further we have drawn attention to the assistance which the negative pressure in the chest gives to the diastole of the heart.

The whole of the negative pressure found in the heart (p. 55) is not due to the diastole alone, but to the diastole plus the aspiratory movement, for if the chest be opened a smaller amount of intra-cardiac pressure is registered.

In dealing with blood pressure (p. 57) attention was drawn to certain undulations of respiratory origin. These are produced by the decrease of pressure on the vessels of the thorax during inspiration; this reduction of pressure is small but it produces sufficient suction to sensibly affect the veins opening into the right auricle, the blood pressure in which is very low. By this suction more blood is aspirated at every inspiration into the right auricle, and consequently more blood is ejected from the left ventricle. In this way we have the arterial pressure raised during inspiration or shortly after it, and a fall during expiration or shortly after it. (See Fig. 7, p. 58.)

In examining the blood pressure and respiratory curves of the dog, it is observed that the pulse frequency is increased during inspiration, and reduced during expiration; this reduction is due to the stimulation of the cardio-inhibitory centre, whilst the increase is caused by a suspension of the inhibitory mechanism. (See p. 42.)

In speaking of inspiration raising blood pressure we must not forget the mechanical advantages of a contraction of

the diaphragm compressing the liver and posterior vena cava, and so forcing more blood towards the heart; this no doubt is another cause of the elevated blood pressure during inspiration.

The Nostrils and Glottis.—Before the air reaches the lungs it is warmed by passing through the nasal cavities, so that it enters the trachea at nearly the body temperature. The incoming air also becomes saturated with watery vapour; this saturation likewise occurs in the nasal chambers. In the majority of animals air may pass either through the nose or mouth to enter the trachea, but in the horse owing to the length of the soft palate nasal respiration alone is possible; we therefore find in this animal the nasal chambers with their inlets and outlets well developed.

The opening into the nostrils of the horse is large, funnel-shaped, and capable of considerable dilatation; it is partly cartilaginous, and partly muscular. Immediately inside the nostril is a large blind sac, termed the **false nostril**, and its use appears to be to simply increase the capacity of the nasal opening by allowing considerable and rapid dilatation.

During forced inspiration the nostril expands, especially the outer segment, viz., that part in communication with the false nostril, and the air is rapidly drawn up through the nasal chambers; during expiration the outer segment of the nostril collapses, but the inner segment, composed principally of the cartilaginous ala, dilates. Thus the movement of the outer and upper part of the nostril is principally inspiratory, of the lower and inner part mainly expiratory, producing a peculiar double motion of the nostrils well seen after a gallop or in acute pneumonia.

The dilatation of the inner segment of the nostril is brought about by muscular contraction and by the rush of expired air; striking the cartilaginous wing of the nostril the current is directed outwards at an obtuse angle to its course down the nostrils, as may be well seen on a frosty morning when a horse is respiring rapidly.

The nasal chambers are remarkable for their great depth

and extreme narrowness; the cavities are partly filled by the turbinated bones, which nearly touch the septum on each side, so that a deep but extremely narrow column of air passes through the chambers; the effect of this appears to be to ensure the column of air being raised to the proper temperature.

The nasal chamber is divided into two parts, the lower or respiratory and the upper or olfactory. The latter will be dealt with under the Senses, it comprises the upper portion of the superior turbinated bone, ethmoid cells, and a portion of the middle meatus; the respiratory channel on the other hand lies on the inferior part of the nasal chamber and comprises the inferior meatus, inferior turbinated bone, part of the superior and part of the middle meatus.

The air having been warmed by passing over the septum and turbinated bones enters the glottis, the arytenoid cartilages of which are separated to a greater or less extent to enlarge the opening; in quiet respiration this enlargement of the glottis is not very marked, but during work the cartilages are powerfully drawn upwards and backwards, and the V-shaped glottis fully opened. It is a remarkable fact that the laryngeal opening should be so relatively small, considering the diameter of the trachea and the size of the nasal openings.

During inspiration the larynx and trachea slightly descend while they ascend during expiration. This is particularly well seen in horses during the hurried respirations of disease, producing a well-marked rhythmical movement of the laryngeal region and base of the tongue.

The Facial Sinuses are cavities in the face communicating with the nasal chambers; they are of considerable size, occupying nearly the entire facial region, and they give the needful bulk to the head without adding to its weight; they are lined by a membrane which is continuous with that of the nose. These sinuses are filled with air which enters them through a foramen at the posterior part of the middle meatus; during every act of respiration air is passing in and out of them.

At first sight it would appear that air entered the sinuses during inspiration, but the reverse is the case; it is only during expiration that they are filled, whilst during inspiration air is sucked out. Considering the position of the common inlet to these sinuses, it is difficult to understand why they should fill during expiration, though the advantage of hot instead of cold air entering is self-evident.

Respiratory Changes in the Air and Blood.—We must now consider the changes which the air undergoes on passing into the lungs.

Atmospheric Air contains in 100 Parts:*

	By Volume.	*By Weight.*
Oxygen -	- 20·96	23·015
Nitrogen -	- 79·01	76·985
Carbonic Acid	- ·03	——

The proportion of carbonic acid is small, it is a natural impurity in the air. The atmosphere also contains moisture the amount of which depends upon the temperature; the higher the temperature the greater the amount of water which the air can contain as vapour, and the lower the temperature the less the amount.

Air may be dry or saturated, the latter term implying that it contains as much vapour as it can hold at the observed temperature; it generally contains about one per cent. of moisture, and is spoken of as dry if it contains one-quarter per cent. The air which passes from the lungs is always saturated with moisture.

When air is taken into the lungs it loses a certain proportion of its oxygen and gains a considerable amount of carbonic acid, and perhaps some other gases. More oxygen is abstracted from it than is replaced by carbonic acid, so that if both volumes be reduced to standard barometric pressure and temperature, there is actually less air returned during expiration than entered by inspiration; owing however, to the expansion caused by the warming it undergoes, the expired air is larger in volume than the inspired.

* A new constituent of atmospheric air has recently been described; it has received the name of 'Argon.'

The proportion which the volume of oxygen absorbed bears to the volume of carbonic acid given off is termed the respiratory quotient, and is expressed as $\frac{CO_2}{O}$. The quotient varies with different animals, and probably depends upon the nature of the diet.

In herbivora	the respiratory quotient is			·9	to 1·0
In carnivora	,,	,,	,,	·75 ,,	·8
In omnivora	,,	,,	,,	·87	

(Munk.)

which reads thus, for every 1 part of oxygen absorbed by herbivora there is produced ·9 to 1 part of carbonic acid, and for every 1 part of oxygen absorbed by carnivora ·75 to ·8 parts of CO_2 are produced. In carnivora it will be observed that the amount of CO_2 produced is considerably less than the amount of oxygen absorbed.

We have said that there are other gases returned from the lungs besides CO_2 and O but very little is known about them. According to Reiset, both **hydrogen** and **marsh gas** are given off in the expired air of ruminants, in fact, he places the latter at 183 cubic inches in 24 hours. Both are supposed to be derived from the intestinal canal, being absorbed into the blood by the vessels of the intestinal wall. In our observations on the gases of respiration of horses, it was found, after deducting the oxygen, carbonic acid, and nitrogen, that a balance remained, the nature of which was unfortunately not ascertained, probably it was a mixture of hydrogen and marsh gas, but it did not amount to anything like the quantity found by Reiset.

The nitrogen of the air is returned unabsorbed.

We have previously learned the changes occurring in the blood during its passage through the lungs, we have now to study the way in which the interchange of gases between this fluid and the air is brought about.

The law regulating the absorption of gases by fluids is very clear; every fluid in which a gas is soluble absorbs the same *volume* of gas, no matter what the barometric pressure may be; but as the number of molecules in a gas

depends upon the pressure, it is evident that the *weight* of the absorbed gas rises and falls in proportion to the pressure; this is known as the law of Dalton and Henry.

The volume of gas absorbed by a fluid depends upon the nature of the gas: for instance, 1 volume of water will absorb 1180 volumes of ammonia gas, whilst the same volume of water will only absorb ·00193 volumes of hydrogen. The temperature of the water is also an important factor for the higher the temperature the less the gas absorbed.

If, now, instead of taking a single gas to be absorbed by a fluid we take a mixture of gases, it is found that the volume of each gas forming the mixture is absorbed as perfectly as if it were the only gas present; no more and no less is absorbed whether the gas be by itself or whether it forms only a proportion of the mixed gases present; this is explained by Dalton as resulting from the fact that one gas does not exercise any pressure upon the other gases with which it forms a mixture, and the weight of the gas absorbed depends upon the pressure. The term used by Bunsen to define the pressure exerted by one gas in a mixture of gases is termed the 'partial pressure.' For example, 100 volumes of air contain at freezing-point and standard barometric pressure (30 inches) 21 volumes of oxygen and 79 volumes of nitrogen: what is the partial pressure exercised by each gas in this mixture?

$$\frac{30 \times 21}{100} = 6{\cdot}3$$ inches of mercury, which is the partial pressure of the oxygen.

and

$$\frac{30 \times 79}{100} = 23{\cdot}7$$ inches of mercury, which is the partial pressure of the nitrogen.

The term 'partial pressure' occurs so constantly in the following pages, that the above may make the matter clearer.

If a mixture of gases, say the atmosphere, be exposed over a fluid already containing some of these gases dissolved in it, it is found that if the proportion of gases dissolved in the fluid is less than the proportion in the atmosphere above it, the latter pass into the fluid until the amounts of

gases in the fluid and that in the air above it are equal; but, on the other hand, if the fluid contain more dissolved gas than the atmosphere above it, gas will pass from the fluid to the atmosphere until the amounts both in the fluid and in the atmosphere are equal. This is really a process of diffusion, and is a most important physical law in respiration, as it is the means by which the carbonic acid passes from the blood into the air-cells, and the oxygen from the air-cells into the blood.

If two different gases be placed in a jar, in a short time a complete mixture has occurred, as both gases will pass in opposite directions until a thorough and equal mixture has taken place. This is termed the process of diffusion, and is the chief means by which the air in the deeper part of the lungs mixes with the fresh air introduced by breathing.

Such are the physical laws which it is necessary to understand before the processes involved in respiration can be fully comprehended.

The blood having been robbed of oxygen in the tissues, the hæmoglobin makes its way back to the lungs in a partly reduced condition; here it circulates through the vast capillary system spread over the alveoli of these organs, and is brought as closely as possible into contact with the air in the ultimate air-passages. Between it and the air we have only the membrane of the air-sac and the wall of the capillary, both of which are bathed in fluid; through this wet membrane the oxygen instantaneously passes, being greedily absorbed by the hæmoglobin of the red cells; the gas must, of necessity, first pass into the blood plasma, and from here it is taken up by the red corpuscles.

The oxygen is not simply absorbed by the red cells, but forms with the hæmoglobin a weak chemical compound, for experiment has clearly shown that the union of hæmoglobin with oxygen is largely independent of pressure, and therefore does not obey the law of Dalton and Henry, which it certainly would do if simply absorbed.

We have yet to learn how it is that the oxygen in the air vesicles passes into the capillaries to form this chemical

union with hæmoglobin. Here we have one of the physical laws brought into play which we have previously described. When the venous blood arrives in the lungs it has lost much of its oxygen, the partial pressure of the oxygen is low, whereas the partial pressure of the oxygen in the atmosphere of the air-cells is high; the result of this is that practically instantaneous diffusion occurs through the moist membrane separating the gas and the fluid. The oxygen entering the blood plasma unites at once with hæmoglobin, this latter takes up all or nearly all the oxygen it is capable of holding (an amount which is much greater than if simple absorption of oxygen by hæmoglobin occurred), and distributes it to the tissues through the medium of the arterial circulation.

The tissues are greedy for oxygen, their oxygen pressure is practically *nil*, once more diffusion occurs; the high partial pressure of the oxygen in the arterial blood becomes (through loss of oxygen to the tissues), low partial pressure in venous blood, and the partly reduced hæmoglobin is carried to the lungs, when the process just described is repeated. But the loss of oxygen in the tissues is not the only change the blood undergoes, for not only is its hæmoglobin partly reduced, but as the outcome of tissue activity increased quantities of another gas are added to it. The gas alluded to is carbonic acid; this is largely taken up by the venous blood and conveyed to the lungs, and the method by which it is got rid of will be presently explained.

The fate of the oxygen in the tissues is quite unknown; it is supposed to be stored up in some way or other until required, but in connection with this subject it is necessary that we should glance at the respiration in muscles.

The most remarkable feature in the respiration of muscle (and we select this tissue to elucidate the point we are describing), is that although the working of a muscle cannot occur without oxidation processes taking place, yet no oxygen can be obtained from it; the partial pressure of oxygen in muscles is practically *nil*, they contain no oxygen. Yet oxidation processes ar occurring, and under

such conditions that no free oxygen can reach them, as, for example, when the muscle preparation of a frog is placed in an atmosphere of hydrogen. Such a muscle preparation will go on contracting in this atmosphere of hydrogen and producing carbonic acid, without there being a trace of oxygen either in the atmosphere surrounding it, or in the muscle itself, and this process will continue until the muscle exhausts itself.

The question therefore is, how does the oxygen-free muscle obtain oxygen for the production of CO_2? In other words, what becomes of the oxygen taken to muscles?

Few things in the whole range of physiology are more difficult to understand, oxygen goes to the muscle, it uses oxygen, yet no oxygen is found in it. What is the explanation?

It is supposed that when the oxygen reaches the muscle it is stored up in its substance amongst the muscle molecules, hence it has been termed intra-molecular oxygen; it there forms a complex substance which readily yields carbonic acid and other matters on decomposition, and these pass into the bloodvessels of the muscle and are carried away to be got rid of at the lungs.

It has been suggested that the storing up in the tissues may be closely allied to the storing up of oxygen by hæmoglobin, though with this difference, that the tissue oxygen-holding substance is more stable than the blood oxygen-holding substance. All we do know of the fate of the oxygen is that it eventually assists in producing certain changes in the tissues, which lead to the production of carbonic acid and other substances; but the changes which the oxygen undergoes from the time, to use the words of Foster, it slips from the blood into the muscle substance, to the moment it issues from the tissues united with carbon as carbonic acid, constitute the whole mystery of life.

In the systemic capillaries the partial pressure of the carbonic acid is lower than the partial pressure of this gas in the tissues, the result of which is that it is hurried into the blood by the process of diffusion; but here, as with

oxygen, simple absorption of the gas by the plasma would not be sufficient for the purpose of carrying off the whole of the CO_2 resulting from tissue activity. Now, although there is no compound of CO_2 and hæmoglobin definitely known, still there is a substance in the blood capable of fixing CO_2 until the lungs are reached.

The oxidations taking place in muscle and in every other tissue in the body occur in the substance of the tissue and not in the blood surrounding it. Experiments made to determine whether oxidations occur in the blood have failed, although readily oxidizable substances have been employed for the purpose.

If the serum of blood be exposed to the vacuum of an air-pump, it is found to yield little oxygen but a quantity of CO_2; it yields but little O, because, as we have already learned, this is combined in the red cells, but the fact of its yielding large quantities of CO_2 points to the blood plasma as the chief means by which this substance is carried.

It has been determined experimentally that blood plasma will absorb more CO_2 than the same quantity of water, and it is evident, therefore, that there is something in the plasma which assists in carrying it; this something has been variously stated, but it is generally believed that the sodium carbonate of the blood unites with a portion of the carbonic acid, though other substances may assist. Between the amount absorbed in the plasma, and that held in chemical combination by certain salts of the plasma, the total amount is carried along in the venous blood stream, the partial pressure of the CO_2 in the fluid being high; on arriving at the lungs it circulates through the capillary network spread over the walls of the alveoli, the same wet membrane existing between it and the external air as was described in speaking of the oxygen.

The partial pressure of the CO_2 in the air of the air-sacs being much lower than that of the blood, diffusion occurs between the blood and the air, the CO_2 passing out until equilibrium is established. The air now in the alveoli of

the lungs having lost some of its oxygen, and considerably gained in its carbonic acid—in other words, having the partial pressure of its gases altered—diffusion between the air in the ultimate air-cells and bronchial tubes rapidly occurs until the balance is restored, and the air in the alveoli rendered fit for further blood-reviving processes.

Finally, it is necessary to briefly allude to the manner in which the combined oxygen is liberated in the tissues, and the combined CO_2 liberated in the lungs. This is explained by saying that certain gases have a tendency to leave the substances with which they are united when the pressure upon them becomes reduced, this process is termed 'dissociation'; it liberates the oxygen in the tissues, and assists in liberating the CO_2 in the lungs from the substances with which these are chemically combined, viz., hæmoglobin and carbonate of soda.

When an animal is compelled to breathe the same air over and over again, there is a gradual loss of oxygen and an increase in carbonic acid, and though death will ultimately ensue unless the air be renewed, it is remarkable that before this occurs nearly the whole of the oxygen will have been consumed from the atmosphere; this is further evidence, if any be needed, that the oxygen is not simply absorbed by the blood, and that it does not obey the laws of pressure. Experimental inquiry has proved that animals may live in an atmosphere containing only 14 per cent. of oxygen, but that distress appears at 11 per cent., and rapid asphyxia follows when the oxygen falls to 3 per cent.

By increasing the amount of oxygen in a mixture over and above that contained normally in air, the blood cannot be made to take up much more oxygen than if the normal amount only were present; a pressure of ten atmospheres only causes an increase of 3·4 per cent. absorbed, so that the blood contains 23·4 per cent. of oxygen instead of 20 per cent. The practical application of this fact in the treatment of certain diseases by the inhalation of oxygen is obvious: if we double the amount of oxygen in the air, less than 1 per cent. of the extra addition is absorbed.

Either the small amount of extra oxygen thus absorbed must be very valuable, or we must find some other explanation of the undoubted advantage of oxygen inhalation in some forms of disease.

Apnœa may be produced by distending the lungs several times with air, and holding the breath ; in animals it may be caused during artificial respiration by supplying more air than is actually required at the time. By either of these processes the respiratory centre is controlled by certain impulses passing up the vagus which inhibit inspiration, and the breathing ceases for several seconds, and then gradually starts again.

Dyspnœa is increased and difficult respiration due to an insufficient quantity of oxygen and an excess of carbonic acid in the blood.

If the air supply be entirely cut off, asphyxia and death rapidly ensue. **Asphyxia** has been divided into three stages : In the first stage the attempts at breathing are laboured and painful, deep and frequent, and all the respiratory muscles, including the complemental ones, are brought into play ; convulsions occur, and the blood pressure rises. In the second stage the inspiratory muscles are less active, the expiratory still powerful, and the convulsions cease. In the third stage the animal lies unconscious, occasional violent inspiratory gaspings occur, the mouth open (even in the horse), the pupils dilated, the pulse barely perceptible or absent ; during this stage the blood pressure rapidly falls. Death occurs in from five to six minutes from the commencement of the first stage. Young animals take longer to asphyxiate than adults for the reason that their tissue respiration is much less ; the length of time it takes puppies and kittens to drown is evidence of this, and they may recover even after prolonged immersion.

The Nervous Mechanism governing Respiration is presided over by a centre situated in the medulla close to the deep seated origin of the pneumogastric nerves, and above the vaso-motor centre ; there are also subordinate centres in the spinal cord.

The respiratory centre consists of an inspiratory and an expiratory portion, and further of a right and left half; the two halves under ordinary circumstances work together for one common purpose, yet may be shown to be capable of working independently.

The respiratory centre sends out impulses which pass to the muscles of respiration via the spinal cord, but the nature of these efferent impulses is largely influenced by the character of the impulses conveyed *to* the centre by means of afferent nerves which exist all over the body. Thus some impulses sent up to the medulla may control the breathing or entirely stop it for a few seconds, or they may hasten it or slow it down, or they may quicken the rhythm but decrease the depth, or increase both rhythm and depth; some may stimulate inspiration, some expiration, all depending upon the nature of the impression received in the centre through the afferent nerves in communication with it.

Although afferent nerves keep the centre aware of what is required from it, yet these are not essential to the life of the centre; if every afferent nerve communicating directly or indirectly with the respiratory centre were divided respiration would still go on, for the respiratory centre is capable of originating its own impulses, in other words it is automatic.

It is not possible to say that definite paths convey definite effects to the respiratory centre, for controlling or accelerating impressions may be conveyed by the same path; we do know however that certain channels furnish as a rule impulses of a fairly regular nature to the medulla, and these we must now consider.

The vagus is one of the important afferent channels to the respiratory centre; impressions of different kinds are made upon the terminal fibres of the pulmonary branches of the vagus, and these ascend to the brain and produce different effects. Perhaps the bulk of the impulses are such as stimulate the centre, for if both vagi be divided the respirations become much slower and deeper, whilst if

the cut ends in connection with the brain be stimulated the breathing is increased, and if the stimulation be powerful the respirations may stop in inspiratory tetanus.

These effects on stimulation of the divided vagus are not always obtained, sometimes in fact the reverse is found, viz., the breathing becomes slower instead of quicker, and may even cease altogether, though not with a contracted diaphragm as in the previous experiment, but with a relaxed one.

It is evident, therefore, that the vagus contains two distinct sets of fibres, one set stimulating respiration the other set inhibiting it.

But there are other impressions conveyed up the vagus which are of the greatest importance ; we have previously mentioned that the respiratory centre consists of an inspiratory and an expiratory portion, these both receive through the vagus impulses from the lungs which normally direct their action. It has been supposed that of the two the inspiratory portion is the most active, for the mechanism required to introduce air into the lungs is more complex than that required to drive it out.

If air be driven into the lungs of an animal and the parts thus forcibly distended, an expiratory effort is produced, whilst if air be sucked out of the air passages an inspiratory effort occurs ; if the air be repeatedly sucked out, so as to give no time for an inspiration, the diaphragm may stand still in inspiratory tetanus.

The interpretation of this experiment is that inspiration inflicts on the pulmonary fibres of the vagus an impression which travels to the medulla and produces an expiration, whilst expiration produces an impulse which stimulates inspiration ; in this way the regular discharge of expiratory and inspiratory efforts occurs, and the process is known as the ' self-adjusting mechanism.' The evidence in favour of the existence of such a mechanism, is that if the vagi nerves be divided the above experiment cannot be carried out owing to the loss of the afferent channel.

From the brain impressions may pass to the centre

which may cause an animal to increase its respirations as in sniffing, or to control them entirely as when its head is under water; in the diagram Fig. 14 we have adopted Waller's* symbols to signify an increase or decrease of respiration, and it will be seen that the cortex can supply either plus or minus influences.

Another path to the respiratory centre is that furnished by the nostrils through the medium of the nasal branch of the fifth nerve; through this channel principally minus influences are transmitted, viz., respiration is controlled.

From the skin plus or minus influences may pass to the respiratory centre. A bucket of water dashed against

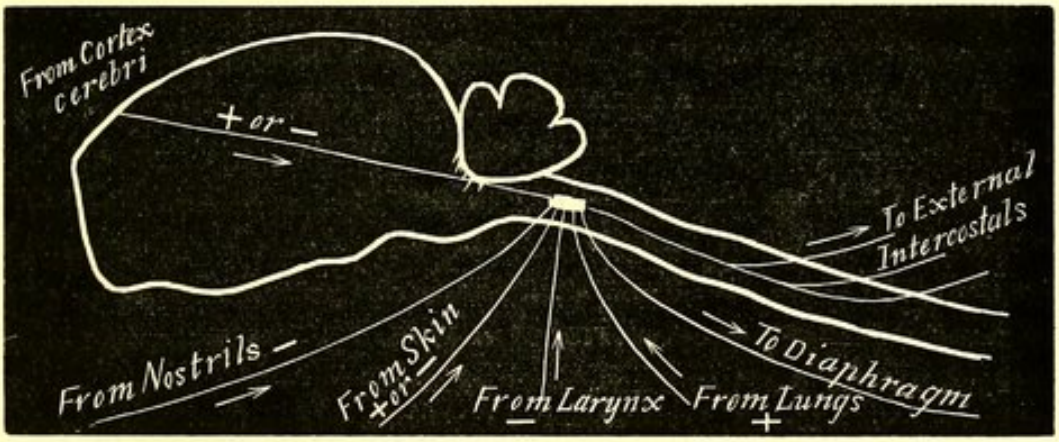


FIG. 14.—DIAGRAM TO ILLUSTRATE THE CHIEF NERVOUS CONNECTIONS OF THE RESPIRATORY CENTRE. AFTER WALLER.

a horse when the breathing is failing in chloroform narcosis will start an inspiration, and painful sensory impressions, as in firing, will greatly increase the respiratory movements.

From the larynx important impressions pass to the respiratory centre through the superior laryngeal nerve. If the nerve be divided and the end in connection with the brain stimulated, respiration is controlled, in fact, if the stimulation be severe the breathing stops in expiration; this would point to the superior laryngeal as stimulating expiration and inhibiting inspiration.

We alluded to the two halves of the respiratory centre; the existence of these can be demonstrated by dividing the

* 'Human Physiology.'

centre longitudinally and cutting the vagus on one side; the respirations on the side on which the nerve is cut will be found to be slower than those on the opposite side of the body. Under ordinary circumstances both halves work in unison.

In addition to the impulses sent to the medulla, the respiratory centre is profoundly affected by the character of the blood circulating through it; blood deficient in oxygen excites respiration, the breathing being rendered deeper and quicker, whereas blood containing a due proportion of oxygen lowers the excitability of the centre and reduces the respirations.

The violent respiratory efforts observed in the second stage of asphyxia are said to be due to the deoxygenated condition of the blood circulating through the medulla. At one time it was supposed that the excess of carbonic acid in the blood stimulated the expiratory centre, whilst a deficiency of oxygen stimulated the inspiratory movement; this view is not generally held at the present day, or only partly believed to be true. Changes in the blood no doubt lead to stimulation of the respiratory centre, but whether these changes are due to the difference in the composition of the blood gases, or to some other substance circulating in the fluid is not known. It has been suggested that sarcolactic acid, which is produced as the result of muscle activity, may increase the respiratory movements, and explain the increased respiratory activity which accompanies work.

Increased respiratory activity produced during work, is to an extent due to a something produced in the muscles, for if the spinal cord be divided in the dog and the hind legs stimulated, panting respirations are produced just as if the animal had been running some distance.

But hurried respirations may be produced through the circulatory system. Trainers have long recognised that an equilibrium must be established between the amount of blood coming to the heart and the amount going to the lungs; if the lungs receive more blood than they can get rid of breathlessness is produced. The gallops by which a

horse or dog are got into a fit state for running and 'staying' simply operate through the circulatory system.

The impulses which leave the respiratory centre find their way to the lungs and thorax by the spinal cord; it is from this portion of the central nervous system that the phrenic nerve supplying the diaphragm, and the nerves supplying the abdominal muscles and chest wall originate.

If, therefore, the spinal cord be divided behind the occiput death results from paralysis of respiration, but such division of the cord does not prevent facial and laryngeal movements occurring, as these parts receive their innervation from a source anterior to the division, viz., from the seventh and tenth cranial nerves. If the cord be divided behind the origin of the phrenics there is paralysis of the abdominal and intercostal muscles, but the action of the diaphragm is rendered stronger, while expiration is carried out by the elastic recoil of the lungs and chest wall.

If one phrenic nerve be divided one half the diaphragm is paralysed; if both be divided the entire diaphragm is paralysed and eventually undergoes fatty degeneration.

The effect of dividing the phrenics is to throw extra work upon the muscles of the chest walls, as inspiration can only now be carried out by increasing the width of the chest.

Sussdorf* states that division of the phrenic nerves in the horse leads to difficulty in breathing, increased heart's action, and collection of fæces in the rectum; in about twenty-four hours these symptoms pass away, and if the animal be worked no appreciable difficulty in breathing is observed.

The perfect carrying out of the respiratory processes can only be accomplished by the assistance of other nerves in addition to those connected with the medulla or spinal cord; the respiratory wave must pass from the nostrils in a perfectly regular order to the abdominal muscles, and from the latter back to the nostrils; this requires the most perfect co-ordination in order that the movement may be harmonious and rhythmical. Colin has shown that if the

* Ellenberger, *Op. cit.*

seventh pair of nerves be divided in the horse and the animal worked asphyxia is produced, as through this nerve the nostrils are opened, and if paralysed the parts become loose and flaccid and are drawn inwards during inspiration.

The tenth pair of nerves require to be in sound working order, not only to act as efficient channels from the lungs, but also as the motor nerves of the larynx by which the needful bulk of air is admitted.

The Amount of Air Required.—Numerous respiration experiments have been made on all animals, to determine the amount of air they require and the gases of respiration. The horse is of all others the one to which perhaps the greatest practical interest attaches to this subject, though a knowledge of it in connection with other animals is of value.

The lungs of a horse will contain about 1½ cubic feet of air; during ordinary repose he draws into them between 80 and 90 cubic feet of air in the hour, though considerable variation may be found even in the same animal.

An average inspiration in the horse during repose amounts to about 250 cubic inches, and this is known as the tidal air. Speaking roughly it is only one-tenth of what the lungs can contain; the remaining nine-tenths are made up of complemental, reserve, and residual air, but the amount of these cannot be stated with any accuracy. The most powerful expiratory effort is unable to remove from the lungs all the air they contain.

The great variations which have been observed in the amount of air taken in by the same animals under apparently identical conditions, cannot be adequately explained; the slightest disturbing influence alters both the rhythm and depth of the respirations.

Under the influence of work the amount of air required is greater, and as a rule the faster the pace the more air needed; but many disturbing factors occur which render experiments on this subject very contradictory, and productive of the greatest variation. During severe work, such as a

gallop, a horse is taking air into his lungs to the extent of 850 cubic feet per hour at least, and probably more; the respirations from being 9 to 10 per minute during repose, may now be anything between 70 and 100 per minute. In such paces as the canter, trot and walk, the amount of air used is correspondingly less; immediately the pace is reduced or the horse stopped the respirations at once fall, and the amount of air inspired becomes correspondingly reduced. This is one of the great difficulties attending respiration experiments on horses under natural conditions.

Respiratory Exchange.—The air passing from the lungs contains more carbonic acid and less oxygen than that which entered; the amount of this profit and loss will vary with the pace, for the heavier the work the more CO_2 produced and the more oxygen required, but owing to the fact that a larger volume of air is passing to the lungs, the percentage amount of oxygen lost and carbonic acid gained may fall below that observed in a state of repose.

A horse in a state of repose, according to Zuntz and Lehmann, produces 3 cubic feet of CO_2 per hour, and absorbs nearly $3\frac{1}{2}$ cubic feet of oxygen; the expired air is found to have lost 4 per cent. of its oxygen and gained $3\frac{1}{2}$ per cent. of CO_2. This is very much more than we found, but it agrees pretty closely with the observations made on other animals and on man. It may be noted that even in animals which, from their small size or other causes, lend themselves to exactitude in experimentation, the most divergent results have been obtained.

There are certain evident factors which considerably influence the amount of CO_2 produced and O_2 absorbed, and of these muscular work and the nature of the diet are the most prominent.

As the result of muscular activity the production of CO_2 is increased; in the same way the amount of oxygen absorbed is greater, but experiment has failed to prove a definite relationship between the amount of oxygen absorbed and the amount of work produced.

A diet rich in starch increases the amount of CO_2 pro-

duced, whilst fats have not such a marked effect in this direction.

The respiratory quotient (p. 87) approaches unity in animals fed on a diet rich in carbo-hydrates, viz., there is very nearly as much CO_2 given off as O_2 absorbed; this is not the case with animals living on a flesh diet, where the respiratory quotient may fall as low as ·7.

The following table gives the amount of air respired and the gases of respiration for several animals; it is an old table by Boussingault, but is the only one of its kind in existence. Recent observations on the horse, which we have previously quoted, give about half the values to those assigned by Boussingault.

	Body Weight.	Amount of Air inspired in 24 hours.	Amount of Oxygen consumed in 24 hours.	Amount of Carbonic Acid produced in 24 hours.
		Cubic feet.	Cubic feet.	Cubic feet.
Horse ...	990 lbs.	3373	150	151·0
Cow	990 ,,	2782	122	122·3
Ass	330 ,,	1112	50	50·4
Pig	165 ,,	1216	54·7	55·1
Sheep ...	99 ,,	720	32·4	22·6
Dog	44 ,,	298	14·0	10·3

THE LARYNX.

The larynx serves a twofold purpose, viz., respiration and phonation; in animals the former holds the most important position, the voice-producing function being of a very subordinate character.

The larynx may be described as a cartilaginous case placed at the summit of the trachea, the opening into it being capable of increasing or decreasing in size, and so

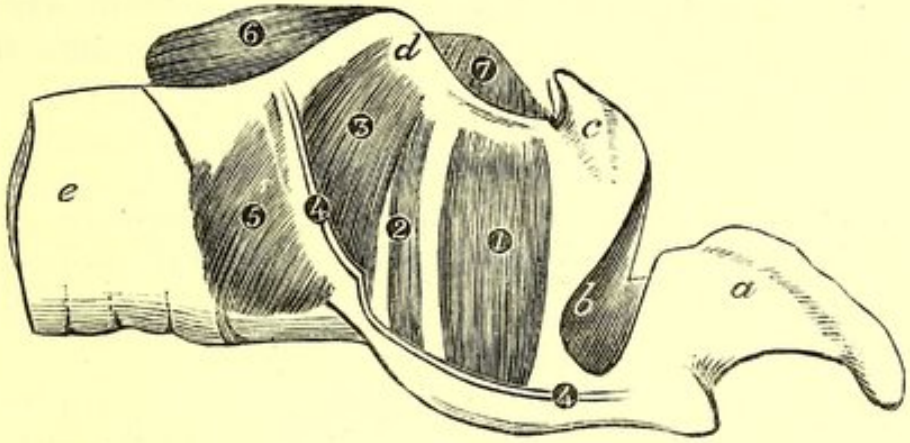


FIG. 15.—THE POSITION OF THE MUSCLES OF THE LARYNX IN THE HORSE.

a, Epiglottis; *b*, glottal opening; *c*, portion of the arytenoid cartilage; *d*, position of the joint formed between the cricoid and arytenoid cartilages; *e*, the trachea.

The wing of the thyroid cartilage has been removed so as to expose the constrictor muscles; 4, 4 represents the cut edge of the thyroid cartilage.

1 and 2, Thyro-arytenoideus: 1 anterior, 2 posterior fasciculus. The space between these two muscles indicates the position of the ventricle of the larynx. 3, Crico-arytenoideus lateralis. 5, Crico-thyroid muscle. 6, Crico-arytenoideus posticus. 7, Arytenoideus muscle.

allowing a larger or smaller amount of air to enter the lungs. Within the larynx are two elastic cords arranged V shaped, the function of which is connected solely with the production of sound.

Both the respiratory and vocal functions require that the several parts of the larynx should move, viz., that the mouth of the organ should be widened or narrowed, or

that the cords should be approximated, drawn apart, tightened or slackened. These movements are brought about by certain groups of muscles, those which approximate the walls of the opening being known as the adductors, whilst those which enlarge it are known as the abductors.

The **Muscles of the Larynx** may therefore be divided into those of respiration and phonation (Fig. 15). As the most important feature in respiration is the opening or dilating of the larynx, the term respiratory muscle might be confined to the dilator of the larynx, while the constrictors would represent the vocal muscles; but the constrictors are not entirely without a respiratory function, as, for example, in coughing, so that in the following table they are included under this head.

Respiratory Muscles.

Dilator or abductor,	*Crico-arytenoideus posticus.*
Constrictors or adductors of the larynx,	*Crico-arytenoideus lateralis, Arytenoideus, and Thyro-arytenoideus.*

The crico-arytenoideus lateralis and posticus are direct antagonists; the lateralis depresses the arytenoid cartilages and closes the entrance into the glottis, the posticus swings the arytenoids upwards and outwards and enlarges the glottis.

Phonatory Muscles.

Muscle which relaxes the vocal cords,	*Thyro-arytenoideus*, anterior and especially posterior fasciculus.
Muscle which renders the cords tense,	*Crico-thyroid.*
Muscles which bring the cords together,	The respiratory adductors.
Muscle which moves the cords apart,	The respiratory abductor.

The entrance to the larynx is formed by the two arytenoid cartilages, the epiglottis and the ary-epiglottic folds; beyond these is the glottis proper, viz., the V-shaped opening formed by the vocal cords. When the laryngeal opening dilates the vocal cords pass towards the wall of the cavity and render

the V-shaped space wider, when the larynx closes the cords are approximated and the space rendered narrower.

During ordinary respiration there is very little if any alteration in the shape and size of the glottis; but during exertion every inspiratory movement is accompanied by an increase in size, every expiration by a decrease. At each expiration the vocal cords pass towards the centre line, and at each inspiration return to the wall of the larynx.

The closure of the larynx, such as during the act of swallowing, is a powerful movement, and if the finger at this moment be introduced into the cavity and placed between the arytenoids, it experiences considerable pressure. The closure of the larynx is brought about by the depression and approximation of the arytenoid cartilages and the approximation of the vocal cords; in addition, during the act of swallowing the base of the tongue presses the epiglottis over the arytenoids and renders the part both air and water-tight.

The **Nervous Mechanism of the Larynx** is peculiar, sensation to the mucous lining membrane and motor power to the crico-thyroid muscle is supplied in the majority of animals by the superior laryngeal of the vagus, this nerve containing both sensory and motor fibres. In the horse the motor fibres running in the superior laryngeal are derived from the first cervical nerve and not from the vagus. All the other muscles both dilator and constrictor are supplied with motor power by the inferior or recurrent laryngeal of the vagus.

It is strange that both adductor and abductor muscles should have the same source of nerve supply, and one naturally asks the question what it is which determines that only the dilators or only the constrictors shall act at any given moment?

No satisfactory explanation of this fact has been offered, all we know is that both constrictor and dilator fibres run in the recurrent and are quite distinct, and that in some animals the different bundles have been experimentally isolated and injured; injury to the dilator fibres producing

abductor paralysis, and injury to the fibres going to the muscles which close the larynx producing adductor paralysis.

If the recurrent be cut and the peripheral end stimulated the glottis almost invariably is found to close, in other words the adductor fibres only appear to be acted upon; if however the stimulation applied be *weak* then the glottis opens, viz., the abductor muscles are affected.

Another curious fact in the history of these recurrent nerves is furnished by pathology. In the disease of horses known as 'roaring' there is paralysis of the left dilator muscle of the larynx, viz., the crico-arytenoideus posticus; the wasting and fatty degeneration of the muscle due to paralysis is very marked, but it is not unusual to find the constrictor muscles almost normal in appearance, or presenting very little sign of disease, and even if pale and wasted the degree of degeneration cannot be compared with that furnished by the dilator muscle.

This is a difficult fact to explain, one would think that as both constrictor and dilator muscles receive the same nerve supply, equal wasting would occur in each.

Again, it is observable when the recurrent has been divided experimentally, that the dilator muscle loses its irritability long before the constrictors, and the same holds good when the nerves are stimulated in *post mortem* experiments on the larynx.

If the recurrent laryngeal nerves be divided under ether, and the peripheral end stimulated, adduction of the larynx is obtained; but if the ether narcosis be pushed to a dangerous extent and the nerves then stimulated the larynx dilates, that is abduction follows.

These and other observations have furnished a law which is of clinical significance, viz., that in *functional* disturbance of the larynx the adductor muscles are first affected, but that in changes accompanied by organic lesions the abductor muscles are the first to suffer.

When one recurrent laryngeal nerve is divided the vocal cord on that side remains immovable and therefore cannot approach its fellow; the healthy cord endeavours to com-

pensate for the weakness of its companion by passing beyond the middle line of the larynx in its attempt to come into contact with it.

The inspiratory distress occasioned in 'roaring' is not brought about, as has been described, by a paralysed vocal cord flapping about, for the elastic nature of the cord and other reasons negative this. The sound is produced by the paralysed left arytenoid being drawn into the glottis at each inspiration, which is the explanation why the noise which accompanies the disease is always inspiratory and never expiratory.

Exner states that section of the superior laryngeal nerve in the horse leads to motor paralysis of the larynx, the muscles suffering acute atrophy, in contrast to the chronic atrophy following section of the inferior laryngeal.*

Bearing in mind the fact that the superior laryngeal in the horse, before being joined by the first cervical, is a purely sensory nerve, it is remarkable that motor paralysis should follow section of it. It is suggested as an explanation of the phenomenon that the superior laryngeal is the trophic or nutritive nerve of the larynx, and that destruction of it leads to loss of nutrition and atrophy.

Phonation.—Voice is produced by the approximation and vibration of the vocal cords, the pitch of the voice being produced by the tension of the cords, whilst the quality is due to the shape of the cord, viz., its thickness or thinness; the position of the resonant chambers such as the mouth, pharynx, posterior nares, and even nasal chambers also affects the quality of the voice.

It is obvious that the chief alterations in the larynx during phonation refer to the vocal cords, these are approximated by the adductor muscles, and separated by the abductor muscles, whilst they are relaxed by the thyro-arytenoideus and tightened by the crico-thyroid. The latter muscle has a peculiar action, it lowers the thyroid cartilage on the cricoid and swings outwards the wing of the thyroid thus rendering the cords tense.

* Waller, 'Human Physiology.'

These changes in the vocal cord produce changes in the shape of the V-shaped glottal opening; in a high note the glottis is reduced to a mere slit, in deeper notes the cords are separated.

If air be forced through the larynx of a dead horse and the tension of the cords altered, a sound remarkably like a neigh may be produced.

The ventricles of the larynx and cavities of the mouth, nose, pharynx, etc., act as resonators being filled with air, they effect the needful alterations in the quality of the voice and assist in giving it its distinctive character; thus the false nostrils furnish the 'snort' of the frightened or 'fresh' horse, the nasal chambers the whinny and neigh of pleasure, the mouth and pharynx the neigh of impatience, loneliness, excitement, etc. We do not consider that the guttural pouches act as resonators, and Colin obtained no alteration in the character of the neigh by opening them.

The voice of each class of animal—horse, ass, ox, sheep, and pig—is so distinctive that we may recognise their presence without seeing them; yet though the larynx in all these animals differs more or less, the difference is not sufficient to offer any explanation why the sounds it emits are so entirely distinct.

The voice of male and female animals differs in intensity. The wild neigh of the stallion is very different from the neigh of the mare, and the bellowing of the bull is distinct from that of the cow. The operation of castration has a remarkable effect on the voice, the neigh of the gelding resembling that of the mare.

In the horse the voice is used during sexual and ordinary excitement, also during fear or especially loneliness, during pain, anger, and as a mark of pleasure. It is not possible to convey in words the difference in the notes produced, but they are easy to recognise. The horse is essentially a sociable animal; when used to be in the company of others he dislikes separation, and shows it by persistent neighing, which is perhaps more noticeable amongst army horses than any others.

The neigh of pleasure is often spoken of as the 'whinny'; the word rather conveys an idea of the sound made. Sounds which can only be described as screams are often evoked during 'horse-play' and temper, or by mares during œstrum. It is not a scream as we know it in the human subject, but no other word conveys an idea of its shrillness.

If a horse cries from pain (which is very rare) as during a surgical operation, the cry is a muffled one and short; it is a groan rather than a cry.

In the cerebral cortex voice is represented in the præcrucial and neighbouring gyrus of the dog, and corresponding regions in other animals. Stimulation of this region leads to *bi-lateral* adduction of the cords; it is curious why stimulation of one side of the brain should lead to movements of both vocal cords.

There is no region of the cortex of the dog which leads to abduction of the cords, though such a region is found in the cat. The cortical centre communicates with a subordinate centre in the medulla situated in the region of the fourth ventricle, and stimulation of certain parts of this centre leads to abduction and in others to adduction of the cords.

Neighing in the horse is produced by an expiration, partly through the nostrils and partly through the mouth; **braying** in the ass is both inspiratory and expiratory, and nostrils and mouth each take a share in it.

In the ox, sheep, and goat, the larynx is very plain, there are only rudimentary vocal cords and no ventricles; the **bellowing** of the ox and **bleating** of the sheep are expiratory efforts through the mouth.

The dog and cat have a larynx something like that of the horse, but the ventricles are shallow; the voice is produced almost entirely through the mouth, though both growling and purring may occur through the nostrils.

It is said that in the horse, sheep, and dog, the voice is produced during expiration, but that in the cat, pig, and ox, it is caused during inspiration.

The ventricles of the larynx are large in the horse and

relatively still larger in the ass and mule; they act as resonators and allow of free vibration of the vocal cords. According to Chauveau both ass and mule have the sub-epiglottic sinus provided with a thin membrane capable of vibrating.

Yawning is a deep slow inspiration followed by a short expiration; the air even in the horse is taken in by the mouth, which is widely opened and the jaws crossed.

Sneezing and **Coughing** are expiratory efforts, the former occurring solely through the nose and being unaccompanied by the peculiar sound attending this act in the human subject; the latter occurring through the mouth, the long palate in the horse being raised for the purpose.

Before coughing can occur the lungs must be filled with air and the glottis closed; a forcible expiration follows, the glottis opens, and the air is expelled through the mouth.

Hiccough is a sudden contraction of the diaphragm, while the air is rushing into the lungs the glottis closes, and the incoming air striking the closed glottis produces the sound.

The condition known as spasm of the diaphragm in the horse is very different from a human hiccough, and it is doubtful how far the cause of the sound in the horse is correctly described.

CHAPTER VI.

DIGESTION.

Prehension of Food.—The methods by which animals convey food to the mouth differ according to the species. In the horse the lips play an important part, for which purpose they are thick, remarkably strong, and endowed with acute sensation; in the ox they serve a subordinate part, being rigid and wanting in mobility; in the sheep the upper lip is cleft in such a manner as to completely divide it into two parts, each possessing independent movement; in the pig the lower lip is pointed and the upper one insignificant.

In manger feeding the horse collects the food with the lips, but in grazing cuts off the grass with the incisor teeth, drawing the lips back in order that they may bite closer to the ground; in the ox the tongue is protruded and curled around the grass, which is thus drawn into the mouth and taken off between the incisor teeth and the dental pad; in the sheep the divided upper lip allows of the incisors and dental pad biting close to the ground, so that animals of the sheep and goat class can live on land where others such as the horse and ox would starve.

In whatever way the food is cut off, it is carried back by the movements of the tongue to the molar teeth, there to undergo a more or less complete grinding.

In the ox and sheep the incisor teeth move freely in their sockets, the object of which is to prevent injury to the dental pad, for which purpose also they are placed very

obliquely in the jaw. In the horse the incisor teeth in early life are very upright but become oblique with age.

The molars in all herbivora are compound teeth; in the horse they are very large especially those in the upper jaw. Being composed of materials of different degrees of hardness they wear with a rough surface, which is very essential to the grinding and crushing they have to inflict on both grasses and grain.

The teeth in herbivora, both incisors and molars, are constantly, though slowly, being pushed out of the sockets which hold them; in this way wear and tear is compensated for, whilst the fang of the tooth becomes correspondingly reduced in length. It is owing to this fact that the incisor teeth alter in shape and direction, and so enable the age to be determined. The tables of the molar teeth are not flat but oblique; this is especially well seen in the horse where the cutting surface is chisel shaped, the upper teeth being longest on the outside, while those of the lower row are longest on the inside (see Fig. 16). This arrangement produces sharp teeth, which are a constant source of trouble and loss of condition in horses.

The movements of the tongue are important, in the ox and dog they are very extensive, the former animal having no difficulty in protruding the tongue and even introducing the tip into the nostrils; it is not a very common habit with horses to protrude the tongue excepting when yawning, but they have considerable power in withdrawing it in the mouth.

A great difference exists between the tongue of the horse and that of the ox; the former is flabby, broad and flat at the end, constricted opposite the frenum, and swells out at the base; it is comparatively smooth on its surface. The tongue of the ox narrows from base to apex the latter being pointed; it is very rough, which may prevent it from losing its hold on the food, protects it from such injury as might be inflicted by coarse grasses, and is also of value to the animal in cleaning its body.

The tongue is supplied with motor power by the hypo-

glossal nerve, and with sensation by the lingual branch of the fifth which supplies the anterior two thirds of the mucous membrane, the posterior third being supplied by the lingual branch of the glosso-pharyngeal; the same nerve also supplies the sense of taste to this part of the organ, while taste for the anterior two thirds is supplied by the chorda tympani of the seventh pair.

The tongue is protruded by the genio-glossus muscle, and retracted by the hyo- and stylo-glossus.

The inside of the mouth of the ox is covered with long papillæ which look backwards; these would appear to be of use in preventing the food from falling out of the mouth. In the horse no such papillæ exist, in fact the lining membrane of the part is remarkably smooth.

The majority of animals have grooves in the palate, they are well marked in the horse, ox, sheep, and even in the dog. Their function is probably connected with assisting the tongue to pass the food back in the mouth.

Drinking is performed by the animal using the tongue as a piston and so pumping up water into the mouth, the lips at the same time being closed all round, excepting a small space in front which is placed under water. Such is the method in both horse and ox; in the former animal the head is extended while drinking, the ears are drawn forward at each swallow and during the interval fall back. The cause of this motion is not clear, but is probably due to the movement of air in the guttural pouches.

Lapping in the dog is performed by curling the tongue in such a way as to convert it into a spoon.

Sucking is produced by the animal creating a vacuum in the mouth by closing the lips, decreasing the size of the tongue in front and increasing it behind, the dorsum being applied to the roof of the mouth. The foal places the tongue beneath the nipple and curls it in from each side, by this means he protects it from the lower incisors and gets a better hold.

Mastication is performed between the molar teeth; the movements which the jaws undergo to admit of this being

carried out depend upon the class of animal. In the dog it is very simple being only a depression and elevation of the jaw; this motion means a simple temporo-maxillary articulation, and such is found to exist in this animal. In the horse and ox the movement is not only up and down, but lateral, and some even say from front to rear. This necessitates a complex joint capable of affording a considerable amount of play, and this is provided by a disc of cartilage being placed between the articulation, which accommodates itself to the varying movements of the joint in the horse, ox, and sheep, and also saves the part from jar. In herbivora therefore we find the cartilage extensively developed, whilst in carnivora it is small and simple.

The character of the movement occurring in the temporo-maxillary articulation of herbivora during mastication is as follows: During rotatory movement, or lateral displacement, one of the articulating heads remains as a fixed point simply turning on its centre, whilst its fellow describes an arc; this is why the movement can only occur on one side at a time (Gamgee). During mastication the contents of the orbital fossæ are observed in the horse to be alternately ascending and descending. This movement is due to the coronoid process of the lower jaw, the fossa being pushed up as it comes forward and depressed as it recedes.

The muscles which bring about this important lateral movement of the jaws, which in the ox owing to the freedom of the articulation may be termed rotatory, are the two pterygoids especially the internal.

The herbivora can only masticate on one side at a time; when this gets tired the process is reversed and the opposite molars take on the crushing. It is surprising the length of time an animal will carry on mastication on one side, even as long as an hour has been observed in the horse by Colin.

Gamgee notices that in the ox the first stroke of the molars is in the opposite direction to the regular action which follows; thus if masticating from right to left the first stroke is made from left to right.

It is important to note that in those animals where a single-sided lateral or rotatory movement in mastication is necessary, the upper jaw is always wider than the lower; this we can understand, for if both were the same width the molar teeth would not meet each other when the jaws were crossed for lateral mastication.

This extra width of the upper over the lower jaw, in conjunction with the peculiarity of mastication, is the explanation why the molar teeth of the horse and other herbivora wear with sharp chisel edges. (See Fig. 16.)

In the horse mastication is slow and as a rule well per-

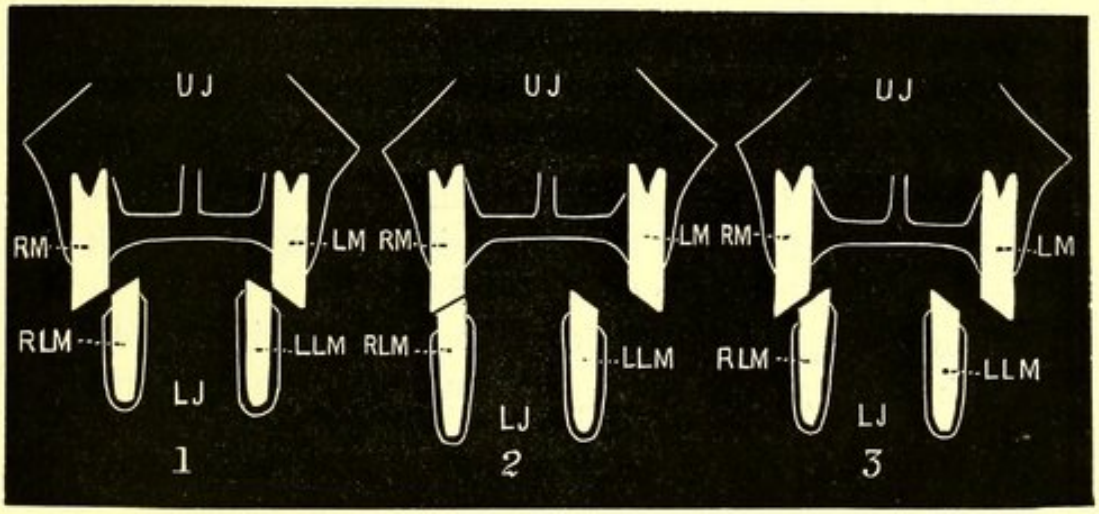


FIG. 16.—SCHEMATIC TRANSVERSE SECTION OF THE UPPER AND LOWER JAWS OF THE HORSE BETWEEN THE THIRD AND FOURTH MOLARS, SHOWING THE POSITION OF THE TABLES OF THE TEETH DURING REST AND MASTICATION.

UJ upper jaw, LJ lower jaw, RM right molar, LM left molar, RLM right lower molar, LLM left lower molar. 1, The position of the teeth during rest, the outside edge of the lower row in apposition with the inside edge of the upper. 2, The jaws fully crossed masticating from right to left; the tables of both upper and lower molars now rest on each other. 3, The position half way through the act of mastication; the outer half of the lower teeth wearing against the inner half of the upper.

formed; it takes from five to ten minutes to eat one pound of corn, and fifteen to twenty minutes to eat one pound of hay.

In the ox mastication is imperfectly performed to start with, but the material is eventually brought back to the mouth by the process of rumination, and undergoes thorough re-mastication.

In the dog mastication is imperfectly performed, after a few hasty snaps of the jaw the material is swallowed.

Opening the mouth is equivalent to depressing the lower jaw, for the upper takes no share in the process. The muscles which open the mouth are comparatively small for very little effort is required, the sterno and stylo maxillaris and digastricus perform this function; on the other hand, the closing of the jaws in mastication is a difficult task, and for this purpose very powerful muscles exist, they are the masseters, temporals and pterygoids. In the dog the temporal muscles are considerably developed, whilst in herbivora the masseters are the largest.

The nerves employed in mastication are the sensory fibres of the fifth which convey to the brain the sensation of food in the mouth, while the motor fibres of the same nerve supply the needful stimulus to all the muscles of mastication excepting the digastricus, which receives its motor supply from the seventh pair.

The process of **Deglutition** is usually described as occurring in three stages. The first stage practically comprises carrying the food back to the base of the tongue and pressing it against the soft palate, it is a simple process and readily understood. In the second stage the act is complex, for the bolus or fluid has to cross the air passage, and must be prevented from falling into the nasal chambers, or finding its way down the trachea : to accomplish this the soft palate is raised and so closes the nasal chambers ; the tongue at the same time is carried backwards whilst the larynx and pharynx are advanced ; this movement causes the base of the tongue to press on the epiglottis and close the larynx, which is further secured by the arytenoid cartilages and vocal cords coming close together. The bolus or fluid can now safely pass towards the pharynx, the former being grasped tightly by the pharyngeal muscles and pressed into the œsophagus. In the third act of swallowing the food is carried down the œsophagus by a continuous wave of contraction, which starts at the pharynx and ends at the stomach.

Chauveau points out that owing to the extreme length of the soft palate in the horse, it passes completely into the pharynx during the second act of deglutition. The length of the soft palate prevents food or water being returned by the mouth once they have entered the pharynx, so that in vomiting, or in cases of sore throat, the food, water, or other material is returned by the nostrils.

The action of the epiglottis in the closure of the glottis has been much discussed, we have described it as being forced over the opening by the base of the tongue and the advancing larynx; but the epiglottis is not essential to swallowing, for an animal can swallow when it has been removed, and even when one of the arytenoid cartilages has been excised. With a finger in the larynx it can easily be demonstrated that the part tightly and forcibly closes during the second stage of swallowing; the vocal cords and arytenoids being brought so close together that the glottis is perfectly air-tight.

Kanthack and Anderson* point out that animals usually swallow with a flexed neck, as in this position the epiglottis is behind the soft palate and in the most favourable place to be applied over the glottis; they show that when the head is extended the epiglottis is in the mouth, viz., anterior to the soft palate. We have found it in this position in the horse, and judging from the fact that in a state of nature the horse and ox swallow with an extended and not with a flexed neck, it is probable that in feeding off the ground the epiglottis is anterior to the soft palate.

During the third stage of deglutition the food can be seen slowly travelling down the channel of the neck; if liquid however be passing the movement is very rapid, for as many as sixty swallows may be made in a minute. Both in eating and drinking the third act of deglutition can occur against gravity; this is due to it being a muscular act.

The whole process of deglutition is considerably assisted by the salivary secretion. When this has been experi-

* *Journal of Physiology*, Nos. 2 and 3, vol. xiv.

mentally diverted swallowing only occurs with difficulty and very slowly.

The œsophagus of the horse is found to differ considerably from that of most other animals. It is composed for the greater part of its length of red voluntary muscle, whilst at and near its termination the previously thin muscular coat becomes very thick and rigid, and the red gives way to pale involuntary muscle; further, the lumen of the tube becomes very narrow. The thick terminal end of the œsophagus of the horse is always closely contracted, so that if cut through close to the stomach no material can escape; this is one explanation why horses vomit with such difficulty. In the ox, sheep, and dog, the tube is composed of red muscle throughout, and owing to its thin distensible walls even bulky material may pass down into the stomach; what the ox and dog can swallow with ease will certainly 'choke' the horse.

The first stage of deglutition is voluntary, but the remaining processes are quite involuntary, and are brought about by the stimulation of a centre in the medulla known as the swallowing centre. By means of afferent nerves supplied by branches of the fifth and the superior laryngeal, the centre is made acquainted with the fact that food exists in the fauces; a reflex act is now set up in the centre and conveyed to the muscles of the part by efferent nerves, furnished by the pharyngeal plexus (composed of the vagus and glosso-pharyngeal) to the constrictor muscles of the pharynx, the hypo-glossal to the tongue, and the recurrent laryngeal to the muscles which close the glottis.

The glosso-pharyngeal is the inhibitory nerve of deglutition; if the central end be stimulated it is impossible to produce the act of swallowing.

Swallowing may be induced without the presence of food in the fauces, touching the rim of the glottis will produce it, as will also pouring fluids into the trachea, or even touching the interior of the trachea as low as the bronchi.

The swallowing centre presides also over the œsophagus, and the wave from the pharynx to the stomach is produced

by impulses sent out from this centre through the vagus; this wave is apparently of a peristaltic nature, and is not arrested either by ligaturing or dividing the œsophagus, though section of the œsophageal nerves prevents it. It is not uncommon in watching a bolus pass down the neck of a horse to see it suddenly come to a standstill, and then slowly pass on again after probably an attempt to ascend. This is generally due to absence of saliva. In rumination and in vomiting the wave runs upwards from the stomach to the pharynx.

The Saliva.

During the process of mastication the food becomes mixed in the mouth with a fluid known as saliva, the secretion of which occurs in three distinct pairs of glands. The method by which it is formed is important to understand, as much the same process occurs in other secretory glands which we have not the same opportunity of watching during activity.

Classification of Salivary Glands.—The three glands which secrete saliva are the parotid, submaxillary, and sublingual; and these are divided into two systems, anterior and posterior. The former comprises the submaxillary and sublingual, the latter the parotid. The two systems are further divided into (1) mucous and (2) serous or albuminous glands, the submaxillary and sublingual being types of the first, the parotid the type of the last.

The salivary glands in the herbivora are of considerable size, the anterior system being well developed in the ox, whilst in the horse it is rudimentary. According to Colin, there is no connection between the weight of the glands and the amount of fluid they secrete; the parotid in all cases secretes more than the others; in the horse it is four times heavier than the submaxillary but it secretes twenty-four times as much saliva; in the ox the parotid is not so

large as the submaxillary, but its secretion is four or five times greater.

Amount of Secretion.—Colin places the daily secretion of saliva in the horse at 84 lbs., and in the ox at 112 lbs., though the amount will depend on the dryness of the food consumed; thus hay absorbs more than four times its weight of saliva, oats rather more than their own weight, and green fodder half its own weight.

Physical and Chemical Characters. — Mixed saliva is an opalescent or slightly-turbid fluid which readily froths; on standing exposed to the air it throws down a deposit of carbonate of lime due to the loss of its carbonic acid; in reaction it is alkaline, and its specific gravity is 1005 in the horse, and 1010 in the ox. Saliva examined microscopically is found to consist of granules, epithelial cells, bacteria, and salivary corpuscles.

About ·6 per cent. of the saliva consists of mineral matter, and ·2 per cent., more or less, of organic matter; the latter consists of mucin (which gives saliva its well-known viscidity and ropiness), and proteid bodies of the serum albumin and globulin class. We make no mention of ptyalin, a substance of which we shall shortly speak, as it is doubtful if it exists in the herbivora, and under any circumstances its amount has not been determined.

Lassaigne gives the following analysis of the mixed saliva of the horse and ox:

	Horse.	*Ox.*
Water	992·00	990·74
Mucin and albumin	2·00	·44
Alkaline carbonates	1·08	3·38
,, chlorides	4·92	2·85
,, phosphates and phosphate of lime (traces)	—	2·59

Lehmann gives the following analysis of horse saliva from the parotid:

Water	990·00
Solids	10·00
Mucin and epithelium Soluble organic matter	4·00
Salts	6·00

The salts of saliva are principally carbonate of lime, alkaline chlorides, and phosphates of lime and magnesia. A substance known as sulphocyanide of potassium has been found in minute quantities in the saliva of the human subject, but is absent from that of the horse.

The gases of the saliva are principally carbonic acid, with traces of oxygen and nitrogen; there is no fluid in the body which contains so much CO_2 as saliva.

The three salivas have different physical properties:— Parotid saliva is watery, clear, and free from mucin, but contains a small quantity of proteid; submaxillary saliva is clear, viscid, contains formed elements, and, in those animals the saliva of which is amylolytic, it possesses ptyalin; sublingual is more viscid than submaxillary saliva, and contains more formed elements and salts.

Colin has observed certain peculiarities in the salivary secretion of herbivora which deserve careful attention. He has discovered that the secretion from the parotids is unilateral; the gland on that side of the mouth on which the animal is masticating secretes two or three times as much as its fellow; the submaxillary and sublingual glands, on the other hand, secrete equally, no matter on which side mastication is being performed. Further, the parotids secrete during rumination the unilateral secretion still being maintained, whilst the submaxillary and sublingual glands are during this process in a state of rest. In a fasting horse the parotids are quiet whilst in the ox they are active, and observations tend to show that in both animals during fasting the mouth is kept moist by secretions from the sublingual, palatine, labial and molar glands. The glands of the mouth are extensively developed in the horse, particularly the palatine and some large ones close to the epiglottis; their secretion is extremely viscid.

Neither the sight of food nor the introduction into the mouth of sapid substances, produce any effect over the salivary secretion from the parotid of the horse; sapid substances, however, stimulate submaxillary secretion.

The **use of the saliva** in herbivora is for the purpose of

perfecting mastication and lubricating the anterior digestive tract, of stimulating the nerves of taste, and in ruminants assisting in rumination; according to our observations on the horse, saliva has no chemical action on the starch of food. So intimately, however, is salivary secretion associated with starch conversion, that it is not possible to pass over without further notice the action produced on starch in man, and according to some observers in horses and cattle, by the presence of ptyalin in the saliva.

The **starch** found in plants exists in the form of granules possessing a shape peculiar to the species, these granules are enveloped in a tough envelope of cellulose; before the starch can be reached the cellulose must be traversed. For this reason some animals like man cannot digest raw starch, but by cooking, boiling for instance, the starch is liberated and free to be acted upon. Raw starch can be digested by the herbivora, which probably explains some of the peculiarities in the nature of their salivary secretion.

If boiled starch be mixed with filtered human saliva and kept at a temperature of 95° F., in a short time the characteristic reaction of a blue colour with iodine disappears, and a reddish colour is formed on the addition of this reagent, indicating the presence of a substance known as **erythrodextrin.** At this time the fluid which before was sugar-free, now contains distinct evidence of its presence; by continuing the action of the saliva it is shortly found that the red colour on the addition of iodine has disappeared, and the fluid now contains a considerable proportion of sugar. Analysis shows that for the amount of starch employed the full amount of sugar has not been obtained; in other words, there is a second substance present in addition to sugar, produced as the result of the action of the saliva, and this is described as **achroodextrin.** The sugar formed from starch by the action of saliva is not grape-sugar but maltose; glucose (dextrose or grape-sugar) only being found in small quantities if at all.

This action of the saliva on starch is described as the **Amylolytic** action, it is due to the presence of **Ptyalin** which

acts the part of a ferment; the process is destroyed by a high or low temperature, retarded by a slightly acid or alkaline medium, and destroyed by free hydrochloric acid.

If starch be boiled with a dilute acid conversion into sugar occurs; the difference between the action on starch of boiling acid and of saliva is that the latter can only produce maltose whereas the acid produces dextrose.

The view we hold as to the non-amylolytic action of saliva in herbivora is not supported by other observers; Ellenberger* distinctly states that both the parotid and sub-maxillary secretions of the horse and ox can convert starch into sugar, but in the case of the horse it is only the saliva first secreted by the glands after a rest which possesses this property; as secretion proceeds the power is nearly, though not entirely, lost. Ellenberger's observations are so reliable that we are bound to accept as a fact that at some period of digestion horse saliva may possess feeble amylolytic properties; this observer places the saliva of the domestic animals in the following order for starch conversion, viz., the pig, dog, sheep, horse, and ox. In the pig and in man all the salivary glands are starch converting, the submaxillary being more active than the parotid; in the rabbit the submaxillary has no action while the parotid is energetic; in the cat, dog, horse, sheep, and ox the action is very feeble or entirely absent.

Meade Smith† states that the saliva of the horse will convert crushed raw starch into sugar in fifteen minutes, and that the process will continue in the stomach (where the early acidity, according to Ellenberger, is due to lactic and not hydrochloric acid); he further adds that horse saliva will convert cane into grape-sugar; in ruminants he believes starch conversion takes place both in the mouth and rumen.

Though we do not accept these views, we shall shortly endeavour to show how starch is converted into sugar in the horse's stomach.

* 'Physiologie der Haussäugethiere.'

† 'Physiology of the Domestic Animals'

Secretion of Saliva.—The mechanism concerned in the secretion of saliva deserves careful attention, for the reason that it throws considerable light on other secretory processes. The subject has been worked out by so many competent observers that the leading points are beyond all doubt; the submaxillary gland of the dog has afforded the desired information, and we have reason to believe that the same process holds good for the parotid and other glands, both of this animal and herbivora.

The chief point in the secretion of saliva is that it is controlled by the nervous system, and is independent of the blood pressure in the gland. Afferent nerves, viz., the gustatory division of the fifth and the glosso-pharyngeal, convey from the mouth to the medulla a certain sensation, which by means of an efferent nerve is conveyed to the gland and secretion results. The efferent nerve of the submaxillary gland of the dog is supplied by the **chorda tympani**, a small branch given off by the seventh cranial nerve, which enters the gland at its hilum and supplies the vessels with dilator and the cells with secretory fibres; how the nerve terminates in the gland is unknown. The second nerve supplying the submaxillary gland is a branch of the sympathetic, which spreads out and invests with constrictor fibres the walls of the artery supplying the part (Fig. 17).

Thus the chorda tympani supplies the gland with secretory fibres and the walls of the vessels with dilator fibres, while the sympathetic supplies the vessels with constrictor fibres, and only a few secretory fibres.

If the tongue or the lingual branch of the fifth or glosso-pharyngeal nerves be stimulated secretion of saliva results; if the sympathetic nerve be divided and the tongue then stimulated secretion follows, but if the chorda tympani be previously divided no secretion follows on stimulation of the tongue, lingual, or glosso-pharyngeal nerves.

If the chorda be stimulated the vessels dilate, the gland becomes red, the blood flowing from the veins is arterial in tint, and the veins pulsate; in addition to this, there is an

abundant secretion of watery saliva poor in solids. When the sympathetic is stimulated, exactly the reverse is obtained, the vessels contract, only a small quantity of

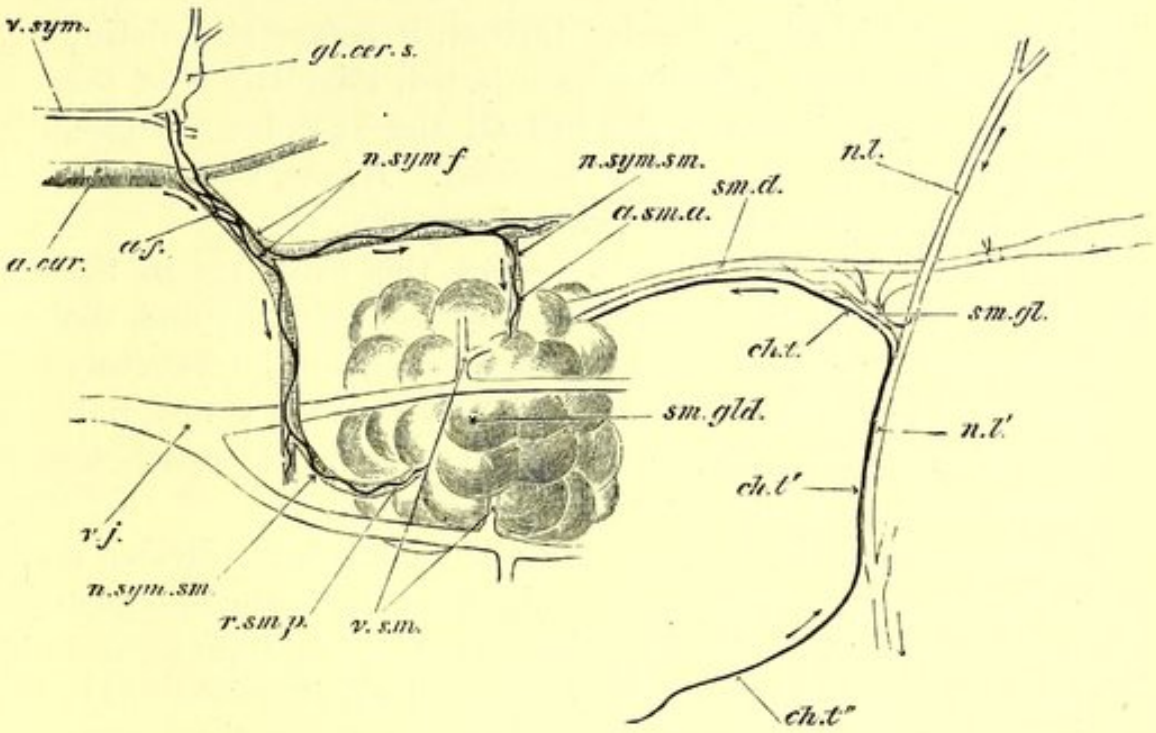


FIG. 17.—DIAGRAMMATIC REPRESENTATION OF THE SUBMAXILLARY GLAND OF THE DOG WITH ITS NERVES AND BLOODVESSELS (FOSTER).

(The dissection has been made with the animal on its back, and is very diagrammatic.)

The submaxillary gland (*sm.gld.*) occupies the centre of the figure, the bloodvessels supplying it derived from the carotid artery *a.car.* are seen on the left, whilst the duct from the gland *sm.d.*, in which a canula is inserted, is on the right of the figure.

The chorda tympani nerve *ch.t''.*, running in company with the lingual branch of the fifth *n.l'.*, is seen to the right and below; after running together the two nerves separate, the chorda tympani *ch.t.* running along the submaxillary duct to the gland. Close to where the two nerves separate is the submaxillary ganglion *sm.gl.*

The sympathetic nerve supply is shown in the figure to the left and above, the fibres being derived from the superior cervical ganglion *gl.cer.s.* and coursing along the bloodvessels to enter the gland.

The bloodvessels leading from the gland fall into the jugular vein *v.j.*

The arrows indicate the direction of the nervous impulses during the reflex act, ascending to the brain by the lingual and descending by the chorda.

extremely viscid saliva flows which is rich in solids, the blood in the veins becomes very dark in colour, and the blood-stream slows.

That the increased flow of blood to the gland produced by irritating the chorda is not the essential cause of the secretion, is proved by the fact that the pressure of the saliva in the duct of the gland is higher than the blood pressure within the vessels; further, if before stimulating the chorda some atropine be injected, stimulation of the nerve still produces to the full all the vascular changes, but not a trace of saliva is secreted. Hence, secretion is not due merely to increased blood pressure.

This atropine experiment proves the existence in the chorda of two sets of nerves, viz., of the secretory and the vaso-dilator; owing to the action of atropine the secretory nerves are paralysed, whilst the vaso-dilators are not. Atropine has no effect on the action of the sympathetic nerve on the submaxillary gland.

Twenty-four hours after the chorda has been divided a watery secretion occurs, not only from the side operated upon but also from the opposite one; this has been termed paralytic secretion, and it diminishes about the eighth day.

Though the effect of the nerves on the submaxillary gland is universally accepted, great difference of opinion exists as to how they act. Heidenhain's view is that a gland is supplied with a trophic or nutritive nerve which excites chemical changes in the protoplasm, and a secretory nerve which separates the manufactured products. The cranial nerves are chiefly secretory, whilst the sympathetic are trophic, hence stimulation of the chorda gives a watery saliva poor in solids, whilst stimulation of the sympathetic gives a scanty saliva rich in solids.

Langley considers that this view is not tenable, and that it is more reasonable to believe that there is only one kind of nerve fibre engaged in secretion, which, being mixed with nerves having opposite actions on the bloodvessels, produces the difference in the results observed.

During secretion the temperature of the gland is said to rise, and the blood in the veins is believed to be warmer than the blood in the arteries, but recent observations have not supported these statements.

The method by which secretion in the parotid gland is carried out differs in no essential respect from that of the submaxillary. The nerves supplying the parotid are the glosso-pharyngeal (the action of which corresponds to the chorda of the submaxillary) and the sympathetic. With the glosso-pharyngeal are dilator fibres, and with the sympathetic constrictor fibres for the bloodvessels, while both trunks contain secretory nerves.

The **changes occurring in the cells** of the salivary glands during secretion depend upon the nature of the gland. We will therefore describe separately, from Langley's observations, the changes in the cells of a serous gland such as the parotid, and in that of a mucous gland of which the submaxillary is a type. In the cells of both glands certain differences are distinguished depending upon whether the

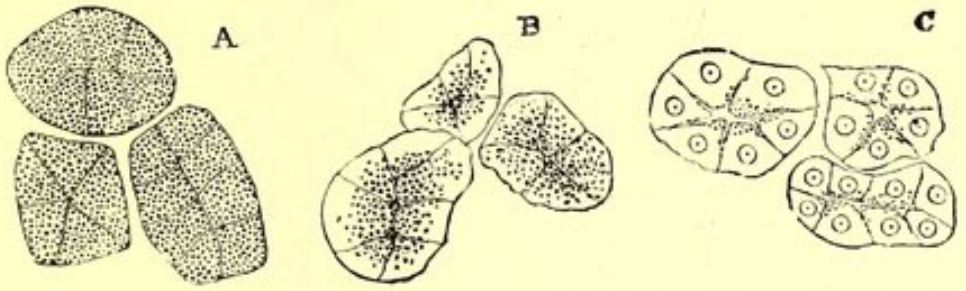


FIG. 18.—CHANGES IN THE CELLS OF THE LIVING PAROTID (SEROUS GLAND) DURING SECRETION.

A, at rest; B, in the first stage of secretion; C, after prolonged secretion (Foster, after Langley).

gland is at rest or whether it is active, viz., whether the cells are charged or whether they are rapidly getting rid of the material which has been formed. In connection with this point, we must remember that differences in the cells may be observed which are more accidental than real, and depend upon the methods which have been employed in demonstrating them; discordant results are not, however, obtained when by suitable means the gland-cells in the living animal are examined during rest and activity.

During the stage of rest in a living serous gland, the cells are found to be filled with a quantity of granular material, and the outline of each individual cell is indistinct; the lumen of the gland is also occluded, and no nucleus can be

observed in the cells; in other words, the gland is charged with its secretory products (Fig. 18, A). During activity the cells get rid of their granular material, which gradually passes towards the centre of the acinus or lumen, leaving each cell with a clear outer edge, whilst that edge next the lumen is still granular (Fig. 18, B). In an exhausted condition the cells are smaller and remarkably clear, only a few granules being left in them on the inner edge, whilst the lumen is now distinct and large, and the nuclei are clearly seen occupying a central position (Fig. 18, C).

If a mucous gland at rest be examined under like conditions, the cells are found filled with granules much larger

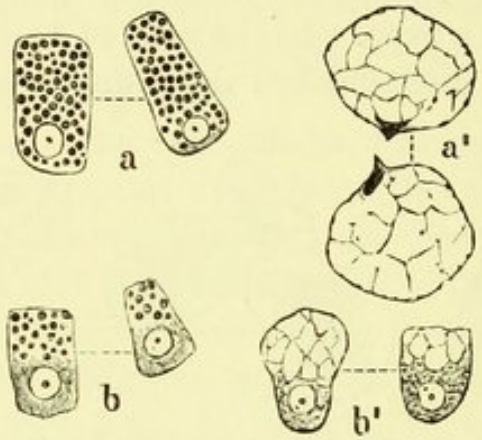


FIG. 19.—CELLS FROM MUCOUS GLAND (SUB-MAXILLARY GLAND OF THE DOG). (FOSTER.)

a, from loaded gland; b, from discharged gland; a′, b′, treated with dilute acid; a′, from loaded; b′, from discharged gland.

than those of a serous gland, and a nucleus is seen occupying one edge of the cell (Fig. 19, a). During activity the granules are passed into the lumen of the gland, but they do not leave behind them in the cells the same clear space seen in the serous cell (Fig. 19, b). If the cells while in an active condition be acted upon by water or dilute acetic acid, the granules swell up and become transparent owing to the mucin they contain, and a delicate network is seen to invade the cell (Fig. 19, a′). A similar appearance is produced in the exhausted cell (Fig. 19, b′), excepting that less transparent mucin is seen and more granular substance, whilst the nucleus of the exhausted irrigated gland is seen

passing towards the centre of the cell instead of remaining towards the outer wall.

Though we have spoken of these granules as mucin, it is probable that in the gland they are not really mucin, but the mother substance of mucin, viz., mucigen, and that during the act of secretion they are converted into mucin.

In hardened and stained sections of the gland the serous variety is recognised by the cells being very granular, and they and the acini are small, whilst in the mucous gland the cells are clear, and they and the acini are large.

In hardened specimens of mucous glands, towards the outer edge in some of the acini, cells may be found shaped like half-moons or crescents, they are not loaded with mucin since they stain with carmine which stains mucin with difficulty. These crescents of Gianuzzi are not found in hardened preparations of serous glands.

The outcome of these changes proves that the organic elements found in the salivary secretion are manufactured by the cells in the glands, whilst the inorganic constituents are probably the result of the transudation through the cells, of the lymph which reaches them through the lymph passages, though experiments made by Langley and Fletcher,* go to prove that even water and salts are the result of an act of cell secretion and not of mere transudation.

* Phil. Trans., 1889, vol. clxxx., B., p. 109. Quoted by Halliburton.

Stomach Digestion.

The first important digestive change occurring in the food of the lower animals takes place in the stomach, and we are not surprised to find that the size and shape of this organ varies with the class of animal. We would expect to meet with a simple stomach in the dog and a complex arrangement in vegetable feeders. It does seem remarkable that any animal should possess a laboratory capable of converting grass, hay, and grain into muscle and fat, and it is evident that the conversion of vegetable into animal tissues must be a more complex process than converting animal into animal matters.

But it is curious to observe that a complex stomach for a vegetable feeder is by no means a necessity, the stomach of the ruminant and the simple stomach of the horse could not be in greater contrast, whilst the resulting laboratory processes are practically identical.

So far as vegetable food is concerned, it does not matter whether the solution and absorption of its readily soluble matters comes before maceration, or whether maceration precedes the extraction of the readily soluble substances.

If maceration comes first, as in ruminants, bulky gastric compartments are provided for the purpose, and the subsequent intestinal canal is small. If the simple stomach comes first, bulky intestines for the purpose of maceration follow; in both cases ample provision is made for the maceration necessary for the solution of the cell wall and fibrous portion of plants.

The dog with its simple stomach and simple intestines offers no difficulty. Advantage has been taken of the fact that a process somewhat like stomach digestion takes place in the intestines, to remove the stomach of the dog experimentally, and it has been shown that it is not an absolute necessity for this animal.

For simplicity in construction the stomach of the dog occupies one end of the scale, for complexity the gastric reservoirs of the ox occupy the other, whilst between the two comes the stomach of the omnivorous pig, partaking of some of the characters of the carnivora and ruminant and belonging to neither.

Stomach Digestion in the Horse.—The subject of stomach digestion in the horse has been worked out by means of feeding experiments, as it has been found impossible to establish a gastric fistula in this animal owing to the distance the stomach lies from the abdominal wall; pure gastric juice has, therefore, probably never been obtained from the horse.

It is to Colin, Ellenberger, and Hofmeister that we owe nearly all we know about the physical and chemical changes occurring in the stomach, these observers having experimented with different foods on a large number of animals which were destroyed at certain intervals. Working on the same lines, we have for years carried on, as opportunity occurred, observations of a similar nature; in this way a large number of facts have been obtained, only a summary of which can be embodied in this chapter.

The first peculiarity to be noticed in soliped digestion is that the stomach is rarely empty; it is only when horses have purposely been deprived of nutriment for not less than twenty-four hours that an empty stomach can be obtained. On the other hand, feeding experiments show that very shortly after food arrives in the stomach it commences to pass out, and the difficulty thus presented to the observer in reconciling these opposite facts is at first sight considerable.

It is perfectly true that food does pass out early, it is equally true that it is long retained; these opposite conditions are the result of the periods of digestion. When food enters an empty stomach it passes towards the pylorus, where it meets with a fluid of an alkaline or neutral reaction which has come from the mouth. As more food is consumed an acid fluid is secreted in the stomach, and

material commences to pass out at the pylorus into the bowel, the amount passing out not equalling at present the amount passing in; thus the stomach becomes gradually distended, and when two-thirds full, which is the condition in which the most active digestion occurs, the amount passing out will, if more food be taken, equal the amount being swallowed, so that we have a stream of partly peptonized chyme streaming out of the right extremity, while a corresponding bulk of ingesta is entering the inert left sac. In fact, the stomach may pass out during feeding two or three times the bulk of food remaining in it when the 'feed' is finished. Let us suppose now that by this time the 'feed' is finished; at once the passage of chyme into the duodenum ceases, or becomes so slowed down that only small quantities of food pass out, and so gradually does this occur that it will be many hours before the stomach is really empty, though had the process continued as it commenced, it would not have contained anything at the end of an hour.

This condition of stomach digestion in the horse may be variously modified depending on the nature of the food, the quantity given, the form in which it is given, the order in which one food follows another, and whether water be given before or after feeding. All these are points requiring our attention, but before giving it we must briefly look at the stomach itself.

The mean capacity of a horse's stomach is, according to Colin, from 25 to 30 pints, or from ·5 to ·63 of a cubic foot; these figures were obtained from a very large number of observations, and give the extreme size of the organ when distended; the viscus is under the best conditions for digestion when it contains about 17½ pints, or is distended to two-thirds of its capacity.

The mucous membrane of the stomach of the horse is peculiar; one portion of it, practically half, is a continuation of the membrane of the œsophagus, this ends abruptly and is succeeded by the villous coat which extends to the pylorus. It is in this latter coat that a true digestive juice

is secreted though not from the entire surface, for on examining the villous membrane it is found to differ greatly in appearance, the fundus being channelled, furrowed, and velvety, whilst the pyloric portion is smooth. It is in the fundus only where true gastric juice, viz., pepsin and acid, is secreted, in the smooth pyloric mucous membrane only pepsin is formed; the area of the fundus-secreting surface is about one square foot. Fig. 20 shows the relative position of the various parts of the mucous membrane of the stomach of the horse; the drawing accurately indicates the shape of

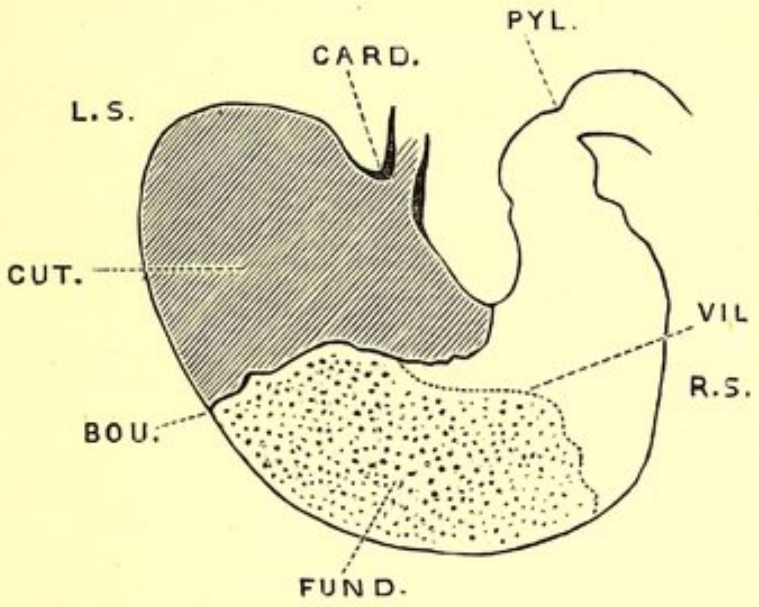


FIG. 20.—LONGITUDINAL SECTION OF THE STOMACH OF THE HORSE.
CARD., cardia; PYL., pylorus; L.S., left sac; R.S., right sac; CUT., cuticular coat; VIL., villous coat; BOU., boundary line between the cuticular and villous portions; FUND., fundus of the stomach: the dotted surface indicates the area for the secretion of gastric juice.

the stomach, the position of the inlet and outlet, and the direction and position of the various areas.

A very remarkable amount of mucin is secreted by the villous sac of the stomach, which forms over the surface of the viscus a thick gelatinous firmly adherent coating like white of egg, which cannot be washed away even by a powerful jet of water.

The pyloric orifice of the stomach is usually large and open, the cardiac is tightly closed; there is a distinct

pyloric ring, behind this the duodenum is dilated, and the gut comports itself in such a singular manner (which has a very important bearing on the pathology of the organ) that mention must be made of it here. From the pylorus the duodenum curves down and then up again, forming a letter U; so much does this remind one of a well-known form of trap used in drainage, that we have described it as the syphon trap of the duodenum (Fig. 21). The use of this trap appears to be to regulate the passage of material from the stomach into the intestines; we have shown that its presence in all probability influences rupture of the stomach,

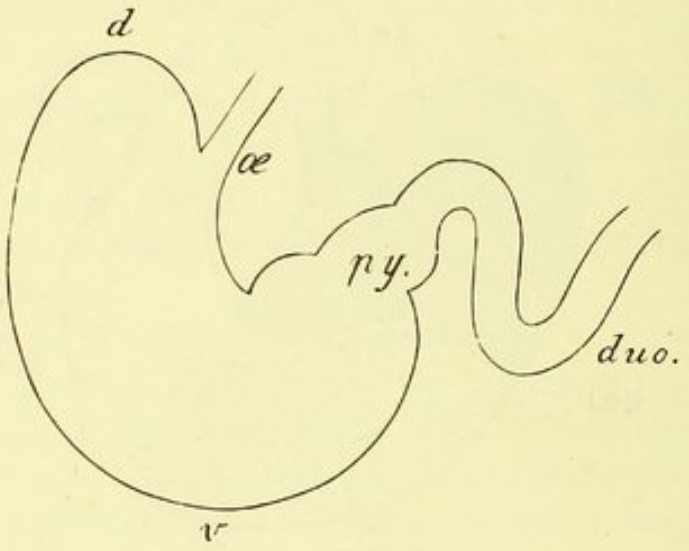


FIG. 21.—LONGITUDINAL SECTION OF THE STOMACH OF THE HORSE, SHOWING THE SYPHON TRAP OF THE DUODENUM.

œ, œsophagus; *py.*, pylorus; *d*, left sac; *v*, fundus; *duo.*, duodenum.

for the more distended the large bowels become, the greater the pressure exercised on the duodenum, and in cases of severe tympany the passage from the stomach to the intestines is completely cut off. Should fermentation still continue in the stomach, the material can neither escape forward into the œsophagus, nor backward into the bowel, and the coats of the viscus may be completely lacerated under the intense strain.

The physiological points of interest in the structure of the horse's stomach are: 1, its small size; 2, not being in

contact with the abdominal wall, but resting on the colon; 3, the outlet and inlet being situated close together; 4, the contracted cardia; 5, only a portion of its surface being capable of secreting a digestive fluid; 6, the remarkable differences in its mucous membrane.

We must now consider the digestion in the stomach of the two chief foods employed for horses, viz., hay and oats.

Digestion of Hay.—Hay, as we have shown, mixes in the mouth with four times its bulk of saliva, and after a very perfect grinding passes into the stomach. If the stomach be empty it passes at once to the pyloric region, as the viscus gradually fills, the gastric juice begins to act, and, as before described, chyme commences to pass into the intestines probably in a very imperfectly elaborated form. Assuming the animal to have finished eating the hay, we now find the output into the intestine becomes small and slow; the gastric juice has an opportunity of acting more thoroughly upon the ingesta, which turns yellow on that surface in contact with the villous-wall; the compression of the stomach on the contents causes them to become distinctly moulded into a mass the shape of the viscus. Owing to gravity there is more fluid towards the pylorus than elsewhere, and for the same reason the greater curvature in all probability is fuller than the lesser. The material in the stomach is perfectly comminuted, resembles firm, green and yellow fæces, and the smell is peculiar, like sour tobacco. The yellowness is due to the gastric juice, and is consequently more marked towards the pylorus; the portion coloured green is the part as yet unacted upon by the juice.

The entire surface of the stomach and its contents are now acid, excepting at the cardia where it may occasionally be alkaline from swallowed saliva; the acidity is greater at the fundus than at the cardia. This general acidity shows that a diffusion of the gastric juice must have been going on. There is no evidence of any churning motion, the cake-like condition into which the hay is compressed, in

spite of its four equivalents of saliva, is due to the compression of the material by the stomach walls.

The duration of stomach digestion of hay is variable, but I quote one or two of Colin's experiments. A horse received 5½ lbs. of hay which he took two hours to eat; at the end of that time he was destroyed, and the stomach contained 2·2 lbs.; thus in two hours he had digested 3·3 lbs. Another horse received 5½ lbs. hay, and was destroyed three hours from the time of commencing to feed; in the stomach were found 1·54 lbs.; in three hours this horse had digested 3·96 lbs.; in the third hour (during which time he was not feeding), judging from the first experiment, he had digested only ·66 lbs., whereas the previous rate of digestion for the first two hours was at the rate of 1·65 lbs. per hour.

To return to our previous statement, when the animal is no longer feeding the rate of digestion at once becomes reduced, and it is probable that several hours must elapse, assuming no further food be given, before the stomach completely empties itself. This period may be fifteen, eighteen, twenty-four or even thirty-six hours.

We starved a horse for twenty-four hours, and at 6 a.m. gave him 6 lbs. of dried grass; he was destroyed at 3 p.m., and the stomach still contained 2½ lbs.; in nine hours, therefore, only 3½ lbs. had been digested. In another observation carried out under similar conditions, only 1 lb. had been digested in four hours and three-quarters. Of 4 lbs. hay given only 1 lb. 11 ozs. were digested in six hours; of 3½ lbs. hay, 2¼ lbs. were digested in five and a half hours, and of 4 lbs. hay, 2 lbs. 12 ozs. were digested in five hours.

Colin's elaborate researches furnish us with very complete data on the question of hay digestion in the horse. He fed fourteen horses on hay, and destroyed two of them at regular intervals; each animal received 5·5 lbs. of hay, and digestion was counted from the time they were fed. Here are the results:

AMOUNT OF HAY GIVEN 5·5 LBS.

				lbs.		*lbs.*
After 2 hours,				the first horse had digested	3·37 ; the second,	3·08
,,	3	,,	,,	,,	3·83 ,,	4·24
,,	4	,,	,,	,,	4·04 ,,	3·56
,,	5	,,	,,	,,	4·32 ,,	5·03
,,	6	,,	,,	,,	4·10 ,,	4·55
,,	7	,,	,,	,,	4·01 ,,	4·35
,,	8	,,	,,	,,	4·87 ,,	4·44

We observe that the rate of digestion during the first two hours is rapid and it then falls off, so that even at the end of eight hours there is still something left in the stomach. The second horse in the five hours' observation had very nearly digested the whole of the ration, but this is an exception.

There is no doubt that it is extremely difficult to get the stomach to empty itself; we fed a horse on dried grass and destroyed it eighteen hours later, there was still a small quantity of food in the stomach; in another case the stomach, after fifteen hours, was found empty; in a third case a horse was given grass twice at intervals of twenty-four hours. He was destroyed eighteen hours after eating his last feed, and a handful of grass was still found in the stomach.

Digestion of Oats.—We have now to consider the digestion of oats, and here we observe the same fact noted under hay, viz., that the stomach commences to pass its contents into the intestine during feeding, and that this considerably slackens when no more food is entering the viscus. Colin fed six horses on 5·5 lbs. of oats each, and destroyed them at certain intervals.

				lbs.		*lbs.*
After 2 hours,				one horse had digested	2·7 ; a second,	2·5
,,	4	,,	,,	,,	3·1 ,,	3·4
,,	6	,,	,,	,,	3·5 ,,	3·0

We have observed in a horse which had received 2 lbs. of oats, and was destroyed twenty hours later, that the stomach had not completely emptied itself; in another experiment

four hours after feeding on 1 lb. of oats, 6 ozs. were recovered from the stomach.

A horse received *lbs. oats.*	And was destroyed in *hours.*	Amount digested *lbs. ozs.*
4	4	2 3
3	4½	1 11¼
4	4	2 4
3	3¾	2 2½
3	4	—
4	4	1 13½
3	6½	2 6½
4	4	3 0
4	4	0 12

The last horse is included to illustrate a point of some little importance in the feeding of animals; for eighteen months this horse had never tasted corn, having been fed on a patent food; a sudden change in diet is the explanation why it only digested 12 ozs. of oats in four hours. It will be observed that the fifth horse in this series digested nothing, even at the end of four hours; we can only account for this by the animal being in a strange place where the feeding experiment was carried out, and being of a very nervous disposition.

Arrangement of Food in the Stomach. — An interesting practical and physiological study is the effect of feeding horses on different foods in succession. When hay is given first and oats afterwards, the hay is found close to the greater curvature and pylorus, and the oats in the lesser curvature and cardia; no mixing has occurred, both foods are perfectly distinct, and a sharp line of demarcation exists between them (Fig. 22, I.). During digestion a mixing of these foods occurs at the pylorus but nowhere else. No matter what compression the contents have undergone as the result of gastric contractions, the foods always remain distinct. The presence of the oats, however, causes the hay to pass out more rapidly than it would have done had it been given alone; Colin observed that half the hay, but only one-fourth or one-sixth of the oats,

would, under these conditions, pass into the intestine in two hours. Ellenberger has shown that when hay and

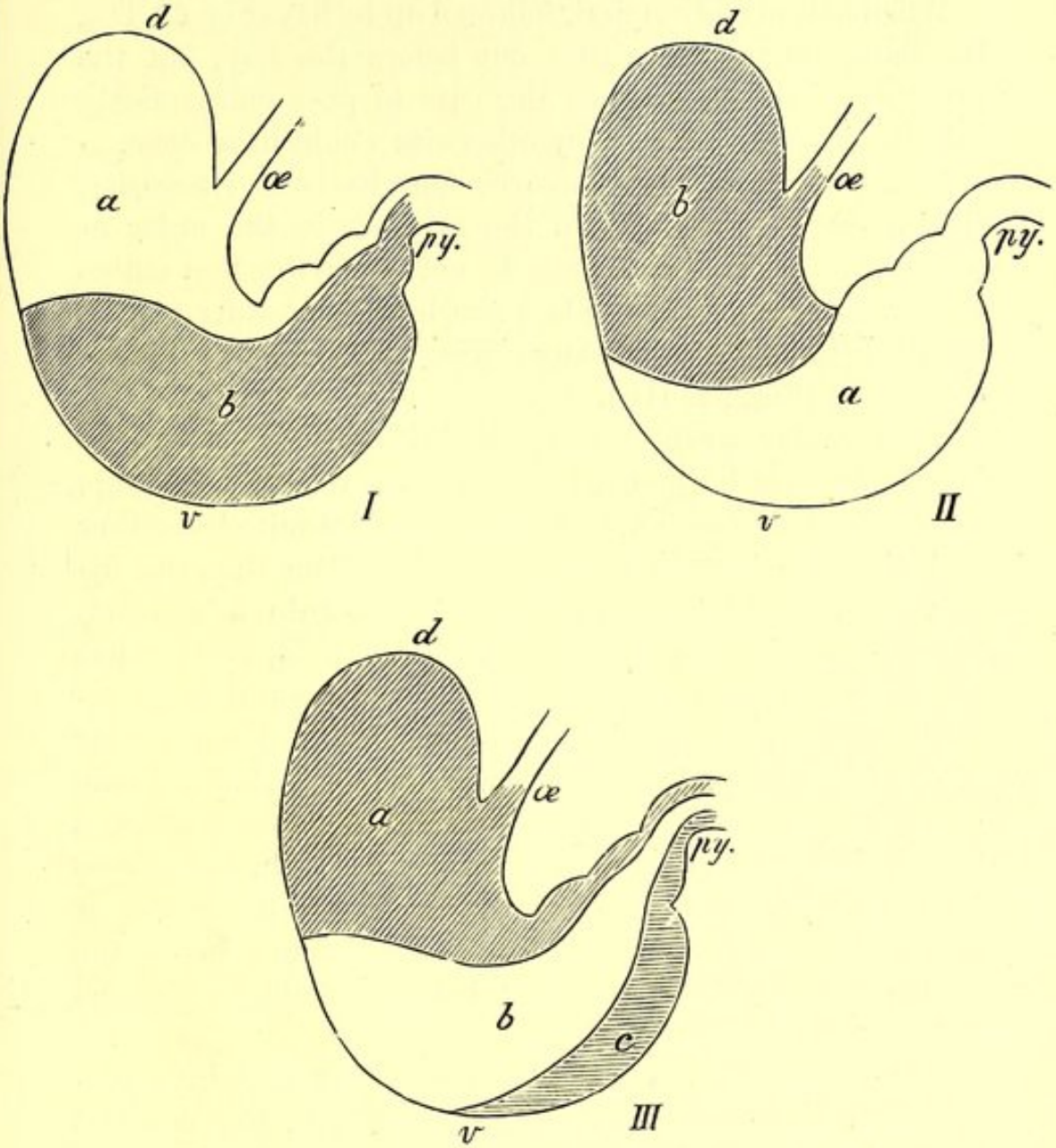


FIG. 22.—LONGITUDINAL SECTION OF THE HORSE'S STOMACH, SHOWING THE ARRANGEMENT OF THE FOOD ACCORDING TO THE ORDER IN WHICH IT WAS RECEIVED (ELLENBERGER).

In each case *œ.* is the œsophagus, *py.*, pylorus; *d*, the left sac; *v*, the fundus. *I.* Hay first, followed by oats: *b*, the hay; *a*, the oats; the latter are passing along the lesser curvature and escaping with the hay at the pylorus. *II.* Oats first, followed by hay: *a*, the oats; *b*, the hay. *III.* The order of three successive feeds: *c*, the first feed; *b*, the second; *a*, the third.

oats are given in this order, a portion of the oats may pass out into the bowel by the lesser curvature without

entering either the left sac or fundus of the stomach (see Fig. 22, I.).

When oats are given first, followed up by hay (Fig. 22, II.), the oats commence to pass out before the hay, but the presence of the hay causes the oats to pass more quickly into the intestines than they otherwise would have done.

If a horse be fed on three or four foods in succession they arrange themselves in the stomach in the order in which they arrived, viz., they do not mix; the first enters the greater curvature, the last the lesser curvature, and it is only at the pylorus that any mixing occurs under ordinary conditions (Fig. 22, III.).

This regular arrangement of the different foods in layers is only disturbed when a horse is watered after feeding; under these circumstances the contents are mixed together and digestion thereby impeded. Apart from this, the influx of a considerable quantity of fluid into a stomach already containing as much as it should hold, means that material is washed out of it into the small and large intestines, and this may set up irritation and colic. By watering a horse after feeding more than half the food may at once be washed out of the stomach. The water which a horse drinks does not remain in the stomach, but passes immediately into the small intestines, and in the course of a few minutes finds its way into the cæcum; hence the golden rule of experience that horses should be watered first and fed afterwards.

We may summarise these facts by saying that in a succession of foods the first taken passes out first; that does not mean to say that the whole of it passes out before any portion of the succeeding food enters the bowel, for we have shown that after a time at the pylorus they mix and pass out together; but the actual influence of giving a food first is to cause it to pass out first.

The practical deduction is that when foods are given in succession, the least albuminous should be given first; this appears to distinctly reverse the English practice of giving oats first and hay afterwards, but perhaps only apparently

so, for experiment shows that the longer digestion is prolonged, the more oats and the less hay pass out, so that some hay (under ordinary circumstances a fair quantity) is always left in the stomach until the commencement of the next meal; the presence of this hay from the previous feed may prevent the corn of the succeeding feed from passing out too early. Ellenberger says in order that horses may obtain the fullest possible nutriment from their oats, hay should be given first *and then water*, this carries some of the hay into the bowel and after a time the oats are to be given; the hay now passes into the bowel and the oats remain in the stomach. This will hardly accord with our English views of feeding and watering.

The **appearance of the food in the stomach** depends upon the period of digestion; we have previously drawn attention to the fact that an hour or two after hay has been taken the material is found in a finely chopped condition, firm, one may almost say dry in places, though towards the pylorus it is liquid. This hay contains between four and five parts of saliva; it is yellow in colour where the gastric juice has attacked it, but of rather a greenish tint elsewhere, and it has a peculiar odour. Several hours after feeding the stomach is found to contain a variable quantity of watery fluid discoloured by the hay which is left behind, part of which may be found floating on the fluid. At other times, when the stomach is empty, the fluid is viscid, contains numerous air bubbles, and is of an amber or yellow tint; this particular fluid is no doubt saliva and mucin, with possibly a little bile.

When oats alone have been given the contents of the stomach are found liquid, the fluid being creamy in consistency and colour; the oats are swollen, soft, and their interior exposed; towards the end of digestion the creamy fluid is replaced by the frothy yellow one. With both hay and oats, and also other foods, there is a peculiar sour-milk-like smell from the contents of the stomach, more marked with bran and oats than with hay, which latter, as previously mentioned, smells like sour tobacco.

The **reaction of the contents of the stomach** is strongly acid; this acid reaction may be obtained on the cuticular as well as the villous portion of the viscus, and is very persistent; the cuticular membrane even after prolonged washing gives an acid reaction. The acidity is derived entirely from the juice secreted by the villous membrane of the fundus.

Our observations on this subject do not agree with those of Ellenberger, who says that during the first hour of digestion the stomach may be alkaline; acidity, he states, then commences in the fundus and extends to the cardia, though for some time the proportion of fundus acidity is three or four times greater than that of the cardia; in the course of five or six hours the proportion of acid throughout the stomach is equal.

When the stomach is empty, as after a few days' starvation, its reaction is neutral or alkaline. We have observed extreme alkalinity towards the pylorus under these conditions, due no doubt to the regurgitation of bile and pancreatic fluid.

The Stomach Acids.—It is not necessary here to enter into a long discussion on the nature of the gastric acids; both in the horse and man a considerable amount has been written to prove that the acidity depends upon lactic or hydrochloric acids, and it is possible that both these views may be reconciled.

Ellenberger and Hofmeister are of opinion that immediately after a meal lactic acid predominates in the horse's stomach, to be replaced by hydrochloric at about four or five hours from the commencement of feeding. These observers found that the nature of the acid depended upon the region of the stomach, the period of digestion, and the nature of the food; oats induced an outpouring of hydrochloric acid, whilst hay favoured the organic acids, as may be seen in the following table:

	Total Acid.	*Hydrochloric Acid.*	*Lactic Acid.*
On a diet of chopped straw and oats	·045%	·0163%	·0287%
On a diet of oats	·110%	·049%	·061%
On a diet of hay	·182%	·002%	·179%

The following are Ellenberger's views on the nature of the stomach acids: In the contents of the stomach, hydrochloric, lactic, butyric and acetic acids may be found, the two latter in insignificant quantities only. In flesh feeders HCl predominates, 2·5 per 1,000, and lactic is found, in small quantities, ·07 per 1,000. In vegetable feeders lactic acid at first predominates, and later HCl is present in small quantities; lactic acid exists throughout the whole stomach, but predominates in the right and left sacs, whilst hydrochloric acid principally exists in the fundus region. Lactic is the first digestive acid employed, but towards the end of digestion hydrochloric exists throughout the whole stomach. The amount of lactic acid found in the stomach of the horse during the first hours of digestion is considerable, amounting to $1\frac{3}{4}$ ozs. or even as much as $3\frac{1}{2}$ ozs.

Having gone carefully into the question of the presence of hydrochloric and organic acids in the stomach contents, we can only say that, no matter at what period of digestion observations have been made, we have only two or three times succeeded in finding hydrochloric acid in the stomach of the horse, and are convinced that lactic is the chief, if not the sole, digestive acid in this animal.

The **Secretion of Gastric Juice** is accomplished in certain glands, known as the gastric. In man these are divided into cardiac and pyloric, each having not only a different structure but a separate function. In the horse cardiac glands are impossible owing to the presence of the cuticular coat; but it has been shown that the villous coat contains glands corresponding to cardiac, which are principally situated in the greater curvature, at the fundus of the stomach, and extending over a limited area, described elsewhere as not larger than 1 square foot (Fig. 20).

The two kinds of gland employed in the production of gastric juice are both found in the villous coat, the one in the fundus, the other in the pyloric portion, though Ellenberger states that he has found fundus glands in the pyloric region. They are simple or divided tubes lying side by side, and opening generally in groups on the surface of

the mucous membrane by means of a shallow depression in the coat; these depressions can readily be seen studded over the tunic of the fundus, giving it a rough appearance owing to the elevation of the mucous membrane between the openings of the glands; in the pyloric region the membrane is as smooth as that found in the intestine. Each gland consists of a body, neck, and mouth, and is lined

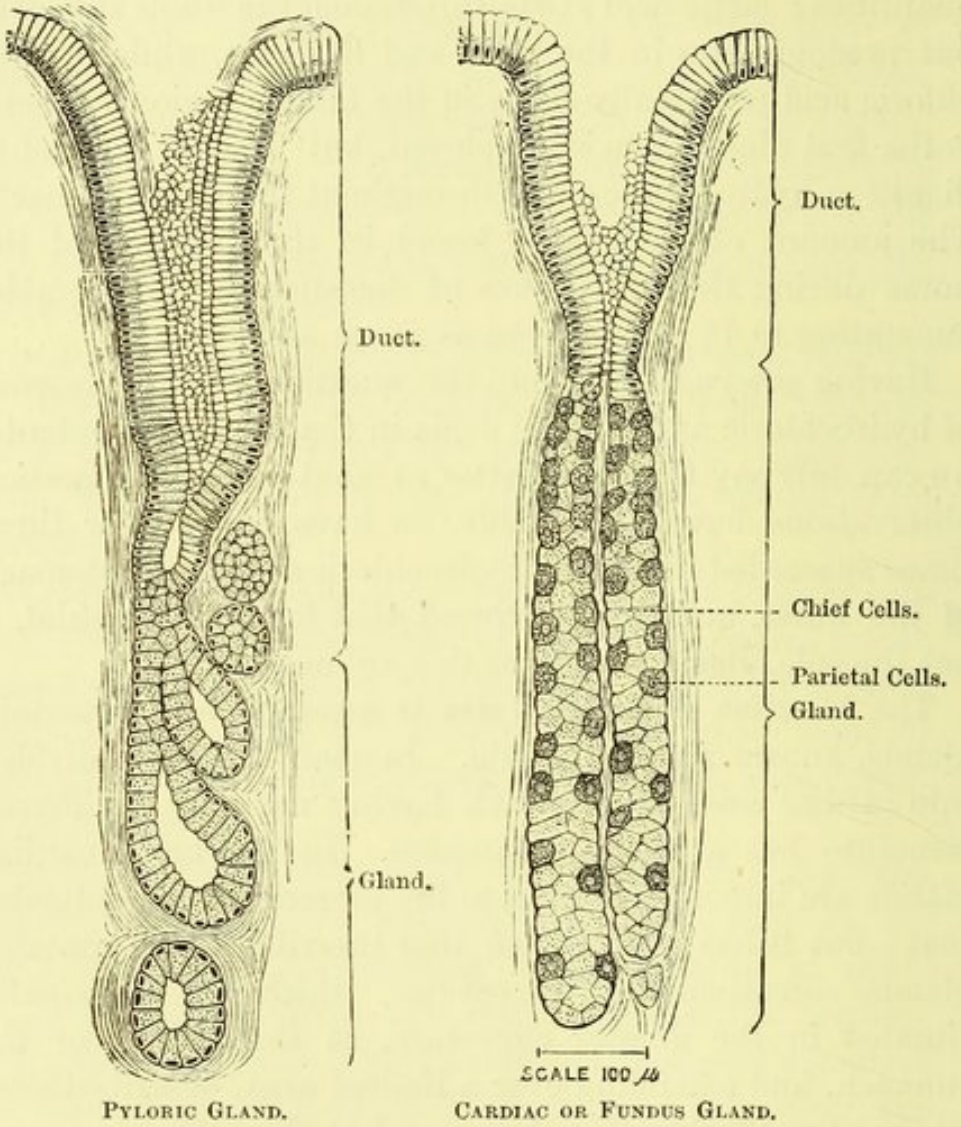


Fig. 23.—The Gastric Glands after Heidenhain (Waller).

with cells; it is in respect of the cellular contents that the pyloric and fundus glands differ.

The cells of the **fundus gland** (Fig. 23) are small, polyhedral, granular, and nucleated, these line the lumen of the gland and are called the *principal*, *central* or *chief cells*;

scattered amongst the principal cells, but existing in larger numbers at the neck of the gland than at its base, are found certain large cells (oval, granular, and nucleated), which from their position relative to the lumen of the gland are called *parietal*, *marginal*, or *border* cells. These cells are distinctive of the fundus glands, and they stain readily with aniline blue.

The **pyloric gland** (Fig. 23) has below its neck but one variety of cell—viz., the cylindrical—containing a nucleus at its attached edge. The duct is lined above the neck by the ordinary epithelium of the stomach, and the same remark applies to the fundus glands; it is from this epithelium that the mucus is secreted.

The difference in the structure of the follicular glands of the stomach depends upon their function; the important distinction between the fundus gland with its principal and parietal cells, and the pyloric gland with only its principal cells, is that the former secretes both the pepsin and acid of the gastric juice, the acid being separated from the blood by the parietal cells, whilst the pepsin only is formed by the principal cells; the pyloric glands, on the contrary, only secrete pepsin and no acid.

We have previously mentioned that the cells of the salivary glands undergo certain changes in appearance the result of rest and activity; the same remark applies to the gastric follicles; these changes have been worked out by Heidenhain and Langley. The former found that the large marginal cells of the fundus glands during activity—viz., digestion—bulged from the side of the gland and encroached on the lumen, and also became much larger than ordinary; while the principal cells of the gland were found as the result of digestive activity to become very granular. During hunger the chief cells of the fundus glands were found to be clear and large, the parietal cells small. The pyloric cells during activity become more granular, and the nuclei leave the base of the cell and work towards the centre of it.

No doubt the appearance presented by the secretory cells depends upon the method by which they are prepared for

examination; Langley has, therefore, by another method of inquiry given an opposite description of the active and passive cells of the gastric glands. He found that in the active state the granules decreased in number, the cells becoming clear, and being capable of differentiation into a clear outer and a granular inner zone, just as we have seen in the parotid gland; during rest the entire cell became granular. The parietal cells during digestion were found to increase in size but did not characteristically lose their granules.

Mucin is secreted in certain mucous glands found in the deep layers of the villous membrane, especially in the region of the fundus; the epithelial cells lining the excretory ducts of the gastric glands also take part in the process. The amount of mucin formed in the stomach of the horse is remarkable, it adheres to the villous coat like unboiled white of egg, and cannot be washed away even by a powerful jet of water.

The amount secreted is unknown but must be considerable; less is formed during hunger than during activity, and there is less in ruminants than in horses.

The **Gastric Juice** of the horse has not been obtained pure; experiments made by Tiedemann and Gmelin of introducing foreign bodies into the stomachs of horses did not lead to a pure secretion, owing to the amount of saliva swallowed. The following table, constructed by C. Schmidt, represents the composition of this juice in man, the dog, and sheep:

	Man.	*Dog.*	*Sheep.*
Water	994·40	973·06	986·14
Organic matter	3·19	17·13	4·05
Sodium chlor.	1·46	2·50	4·37
Calcium ,,	·06	·26	·11
Hydrochloric acid	3·19	17·13	4·05
Potassium chlor.	·55	1·12	1·52
Ammonium ,,		·47	·47
Calcium phosph.	·125	1·73	1·18
Magnesium ,,		·23	·57
Ferric ,,		·08	·33

Gastric juice is acid in reaction, clear when filtered, slightly yellow in the horse, brownish in the sheep, with a specific gravity of 1010. A remarkable peculiarity of the gastric juice of flesh feeders is the power it possesses of resisting putrefaction; this is not the case with the horse. Examined by the polariscope, gastric juice turns the ray of polarized light to the left. The effect of reagents on the secretion shows that acids produce no precipitate, whilst alkalies do, and that alcohol produces a heavy precipitate, which is in part due to the ferments found in the fluid. The amount of salts present is about 7 or 8 per cent.

The acidity of the gastric juice we have before spoken of, it only remains to speak of the ferments—viz., pepsin and rennin.

Pepsin is a body allied to proteids, and can by appropriate methods be obtained in the form of a yellowish powder soluble in water and insoluble in alcohol; it does not give all the tests characteristic of the proteid group of bodies. The ferment is secreted in the principal cells of the fundus and pyloric glands, but exists in them not in the form of pepsin, but as its immediate precursor pepsinogen. There is no pepsin secreted by the cuticular or left sac of the stomach of the horse, and Ellenberger considers that even the pyloric region contains no ferment during the first hour of digestion.

It is found that if pepsin be obtained in a pure condition it produces no action on food. It is essential to its function that it should be associated with an acid, which the majority of observers regard as hydrochloric; in this condition it readily acts on proteids converting them into peptones; this function is spoken of as peptonizing.

Pepsin may be destroyed by heat; it loses its activity at 134° to 136° F., though in the dried state it may be raised to 212° F. without being destroyed. It best manifests its activity at a temperature of 104° F.

Pepsin is described as a ferment, inasmuch as besides splitting up the proteid substances of food, one of its leading characteristics is that a very small amount of it is

capable of performing a considerable amount of work. It is probable that so long as it is acting in an acid medium it is not appreciably used up.

The **Rennin** or milk-curdling ferment is also formed in the same cells as pepsin. It is destroyed at a lower temperature than pepsin, and by means of magnesium carbonate the two ferments may be separated.

The action of rennin is to clot the casein of milk; this process is used in the manufacture of cheese, an infusion of the mucous membrane of the stomach being sufficient to set up this action in the milk. The ferment acts without the presence of an acid, but it is essential in order that the rennin may clot casein that calcium phosphate should be present.

In the fourth stomach of the calf and sheep this ferment may be readily found, and it has been said to exist in the stomach of the horse.

A third or **lactic acid ferment** has been described as existing in the gastric juice, which has the power of converting milk-sugar into lactic acid. Dilute caustic soda, which will destroy both pepsin and rennin, has no effect on this ferment.

We have no knowledge of the nerves governing the secretion of gastric juice.

The **action of the gastric juice** is directed solely against the proteid principles of the food; there are other changes, no doubt, besides peptonizing occurring in the stomach, but these are independent of the gastric juice, and are perhaps, in some cases, inhibited by it.

Gastric juice converts albumins into **Peptones**; this change occurs whether an animal or vegetable proteid be given. The conversion is not a direct one, as between albumins and peptones occur the intermediate products albumoses. It is well known that albumins cannot pass through an animal membrane, whereas the distinctive character of peptones is their power of dialysing, which doubtless enables them to pass readily into the absorbent vessels of the intestines.

The amount of peptone at first produced is small; especially is this the case early in digestion, for, as we shall presently show, according to Ellenberger peptic digestion is the second stage of stomach digestion in the horse. The amount of peptone in the stomach is stated by the same observer to be smaller in the left half of the stomach than in the right; according to our experience peptone disappears as soon as it is formed, for we have never succeeded in finding any in the stomach of the horse.

Peptones are obtained in two forms, one remaining stable and undergoing no further change, whilst the other, under the influence of one of the ferments of the pancreatic juice (trypsin), is split up into leucin and tyrosin, two amido-acids which will engage our attention later on.

All peptones which yield leucin and tyrosin as further products are termed **hemi-peptones**, whilst those which do not are called **anti-peptones.**

This remarkable difference indicates that the proteid molecule may consist of two parts, an anti- and hemi-portion, yielding respectively anti-albumose and anti-peptone, and hemi-albumose and hemi-peptone.

Much confusion has occurred through the difference in the nomenclature adopted by various observers in describing these different products. The one most generally employed is that of Kuhne's, given above, and here tabulated:

Albumin.

Hemi-albumin.	Anti-albumin.
Hemi-albumose.	Anti-albumose.
Hemi-peptone.	Anti-peptone.

Amylolytic Changes.—We have referred to other changes occurring in the stomach independently of peptonizing. There can be no doubt that starch is converted into sugar; all the sugar we have found in the stomach could not have been converted in the mouth, considering the feeble or

negative action of the horse's saliva. Assuming, however, that the saliva assists, we know from the researches of Ellenberger and Hofmeister that it can convert starch into sugar even in the presence of 2 per cent. lactic acid; whilst it ceases in the presence of ·5 per cent. hydrochloric acid. The whole of the starch is not converted in the stomach, for some may be distinctly found in the early part of the small intestines.

Ellenberger and Hofmeister are of opinion that starch conversion in the stomach of the horse occurs not only through the saliva swallowed, *but by the development of ferments from the food;* they found that oats could yield a starch-converting ferment active at the body temperature but destroyed by boiling; they have further stated that starch-converting ferments may in the horse be derived from the air swallowed with the food.

This theory of the food providing its own starch converting enzyme may, at any rate provisionally, be accepted. We have obtained distinct evidence that oats contain an enzyme capable of acting on starch in the presence of lactic acid.

Should this explanation be correct it helps us out of many difficulties, it explains why boiled foods are distinctly improper for horses (amongst other reasons the destruction of the enzyme), and it is additional evidence, if any were needed, of the reason why oats are so universally adopted as food for horses.

Starch when attacked in the stomach by a diastatic ferment is first converted into soluble starch, then into dextrin, and lastly into sugar (maltose); part of the starch may be converted into lactic acid by lactic fermentation.

Fats are not acted upon in the stomach, though the envelope surrounding the fat globule is digested, and the fat set free.

Milk is curdled in the stomach of the young animal by means of rennin; the casein thus produced is converted into peptones in the ordinary manner.

Cellulose fermentation is considered by Tappeiner to

occur in the left sac of the stomach, and when marsh-gas has been found in this organ, it results from cellulose decomposition. Ellenberger lays no stress on these results, but Brown* has shown that the destruction of the cell-wall of oats and barley occurs in the stomach, where it is dissolved by a cyto-hydrolytic ferment *pre-existent in the grain;* the changes occur with extraordinary rapidity in the stomach of the horse. The researches of this observer on a cellulose-dissolving ferment are of the greatest interest to the veterinary physiologist, and of considerable practical importance.

The Various Periods of Stomach Digestion.—From what has been previously said, it will be seen that digestion in the stomach of the horse may be divided into certain periods, the existence of which has been determined by Ellenberger and Hofmeister, whose views are here given:

First period: this lasts but a short time, during which starch is converted into sugar, accompanied by lactic fermentation.

Second period: during this starch is principally converted into sugar in the left sac, and a small quantity of proteid is converted into peptone in the fundus; the acids present are lactic in the left, and a little hydrochloric in the right sac.

Third period: one of mixed digestion, both starch and proteid conversion occurs, the former in the pylorus, the latter in both fundus and pylorus; the acid present is principally hydrochloric.

Fourth period: this consists of pure proteid digestion; no starch conversion can occur owing to the universal presence of hydrochloric acid.

The above periods are given solely on the weight of Ellenberger and Hofmeister's authority.

It is impossible to state definitely the length of these various periods, for so much depends upon the presence of fresh flood in the stomach, but it is believed that the 1st

* 'On the Search for a Cellulose-dissolving Enzyme,' H. J. Brown, F.R.S., *Journal of the Chemical Society*, 1892, p. 352.

and 2nd periods last from two to three hours, whilst the 3rd and 4th periods last four hours and upwards. Where the interval between the meals is considerable, the periods extend over several hours; and in all cases they run into one another.

The above observers fix the period at which digestion is at its height as follows:

After a moderate feed digestion is at its height in 3 or 4 hours.
„ full „ „ „ „ 6 to 8 „
„ an immoderate „ „ delayed still longer.

Stomach Digestion in Ruminants.—The **Rumen**, or first gastric reservoir, is a viscus of enormous proportions capable in the ox of holding 60 gallons; it is divided into certain sacs by means of very thick muscular pillars, and the whole lined by a well developed mucous membrane in part covered by leaf-like papillæ. The mucous membrane, it is said, contains some small glands which are not considered to provide any digestive secretion.

The rumen is in connection with the reticulum, and by means of the œsophageal groove with the omasum. All solid food on first coming from the mouth is received in the rumen, and judging from the contents of the compartment much of the fluid which is swallowed must also find its way into it, though it has been proved by the experiments of Flourens that fluid may find its way into all four stomachs at one and the same time. We know that the digestive changes occurring in this organ are intimately connected with the amount of fluid it contains, and further that rumination is impossible unless a large proportion of water exists in this cavity. The fluid found in the rumen is not all derived from the fluid drunk nor the amount existing in the food, but much of it is saliva of which the ox secretes enormous quantities.

The contents of the rumen are alkaline, which is probably owing to the saliva; in appearance they resemble food which has been coarsely ground. This mass is slowly

and deliberately, not energetically, revolved within the stomach, the material at the posterior part being gradually forced upwards and forwards and so a complete mixing occurs. This churning movement must largely be brought about by the extremely powerful muscular pillars which are so arranged as to separate the organ into various compartments. The process of fermentation may also assist to mix the contents. It is due to the churning movement that the 'hair balls' found in the rumen of cattle are formed.

The essential function of the rumen is to retain the food

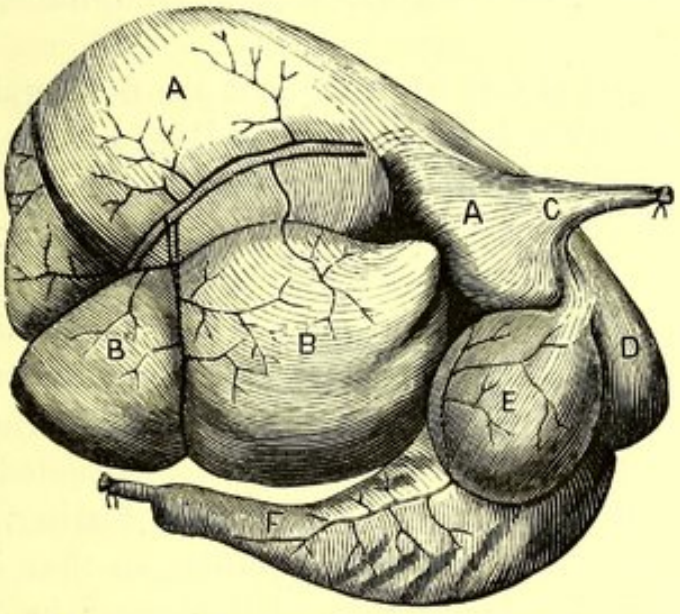


FIG. 24.—THE GASTRIC COMPARTMENTS AND TRUE STOMACH OF RUMINANTS IN THEIR NORMAL POSITION (COLIN).

C, The œsophagus; A, A, B, B, the rumen; D, the reticulum; E, the omasum; F, the abomasum.

for rumination, macerate all fibrous substances, and fit them for cellulose digestion, which here goes on probably under the influence of ferments contained in the food itself; the amount of cellulose thus converted has been estimated at between 60 and 70 per cent. Ellenberger is of opinion that in addition to the functions named other digestive changes occur; he says that carbo-hydrates are digested through enzymes contained in the food, and in this way starch and cane sugar are converted into maltose; proteids are also slowly converted into peptones, not through any true peptic

ferment but by some enzyme provided by the food. The result of the decomposition of cellulose is the production of a considerable quantity of gas.

The rumen never empties itself, even after prolonged starvation it contains food. In young ruminants digestion principally occurs in the fourth stomach, the others being rudimentary; when the young animal is placed on solid food it is remarkable how soon the other compartments develop, and the process of re-mastication is established.

The **Reticulum** or second gastric reservoir is a small one; its interior is arranged like a honeycomb, in the cells of which foreign bodies such as stones, sand, nails, etc., may be found.

The contents of this compartment are fluid and alkaline, the fluid is derived from that swallowed, and from the rumen; the alkaline reaction is due to the saliva, for so far as we know the mucous membrane possesses no secretory activity.

The fluid which is found here is of use in rumination, and is forced into the œsophagus by a contraction of the walls of the viscus; in order that fluid may be contained in this compartment the openings out of it are situated considerably above the base of the organ, and further, the compartment is situated below the rumen, so that it receives the overflow of fluid from it. Ellenberger is of opinion that the reticulum regulates the passage of food from the first to the third compartment, and from the rumen into the œsophagus. In transferring the contents of the rumen *viâ* the reticulum to the omasum, the reticulum contracts and forces the material into the open œsophageal groove. That the reticulum is capable of energetic contraction is specially noted by Colin, whose observations on the physiology of the stomach in ruminants, were mainly carried on by means of a window cut in the abdominal wall.

Flourens showed that the reticulum was not essential to rumination, for he excised it in a sheep and rumination was not interfered with.

The **Omasum**, or third compartment, is peculiar; its

physiology has been elaborately worked out by Ellenberger. This authority says that it possesses no secreting power, that its function is to compress and triturate the food which it crushes between its powerful muscular leaves, and rasps the ingesta down by means of its papillæ. The contents of this sac are always dry, due to the fluid portion being squeezed off and flowing into the fourth stomach by the action of gravity, and the pressure exercised by the viscus.

The food may find its way into the omasum, either directly from the œsophagus after re-mastication, or from the second or first compartments. It is probable that the former is its chief source of supply, the omasum being carried towards the opening of the œsophagus by a contraction of the pillars of the œsophageal groove, by which means communication with the rumen and reticulum is cut off.

Normally the omasum possesses no reaction, if found acid it is due to regurgitation from the true stomach. The omasum has a separate source of nerve supply, irritation of the pneumogastric producing contraction of all the other compartments but this.

The **Abomasum** is the true digestive stomach, and the only compartment secreting gastric juice. In the abomasum proteids are converted into peptones, the region of the cardia being in this respect more active than the pylorus. Ellenberger states that starch is also digested, and that this precedes proteid digestion.

In the fourth stomach of the calf a milk-curdling ferment (rennin) exists, which has already been dealt with.

Stomach Digestion in the Pig has also been worked out by Ellenberger and Hofmeister. The stomach of the pig is peculiar, it is a type between the carnivorous and ruminant, and is divided by the above observers into five distinct regions, which do not all possess the same digestive activity.

The gastric juice of the pig contains for the first hour or two of digestion lactic, and afterwards hydrochloric acid; pepsin is present, and a ferment which converts starch into sugar.

In the pig, according to the above observers, the process of digestion is not the same in all the regions; one may contain hydrochloric acid, another lactic; one may be abundant in sugar, while this substance may be absent elsewhere.

The first stage of digestion is one of starch conversion, the second stage the same only more pronounced; the third stage is one of starch and proteid conversion, both processes occurring at the cardia, but only proteid conversion taking place at the fundus; lactic acid is present in the former and both lactic and hydrochloric acid in the latter. In the fourth stage the starch conversion is nearly complete, hydrochloric acid predominates in all the regions, and proteid conversion is widespread.

Stomach Digestion in the Dog.—A flesh diet requires very little saliva and practically no mastication; but its digestion is slow, in spite of the fact that it is taken in a form closely allied to that in which it is assimilated.

Colin states that it takes a dog twelve hours to digest an amount of meat which it could eat at one meal. The substances most difficult of digestion are tendons and ligaments, but their digestion is improved by boiling; liver and flesh are best given raw as cooking interferes with their digestibility.

The gastric juice of the dog (p. 146) contains pepsin and hydrochloric acid 1·7 per cent., and it has been shown that it is possessed of considerable activity, being in a given time four times more active than that of the sheep. The amount of juice secreted during the day is about one-tenth the body weight.

According to an experiment performed by Czerny a stomach does not appear to be an absolute necessity for the

dog, as it has been completely excised and the animal lived for years. (Bunge.)

Absorption from the Stomach.—The needful changes having occurred in the stomach, and we now refer principally to the stomach of the horse, our next step is to inquire into the proportion of food so altered as to be rendered fit for absorption.

Experiment shows that in the stomach 40 to 50 per cent. of the carbo-hydrates of the food have been converted into sugar; whilst 40 to 70 per cent. of the proteids are converted into peptones. Where food has been long in the stomach, not more than 2 to 10 per cent. of the proteids pass out unacted upon, but under ordinary circumstances we cannot count upon a larger digestion of proteids than 40 per cent.

In ruminants probably the greater part of the food substance is acted upon in the gastric compartments and stomach, leaving comparatively little for the intestines to perform.

In spite of the changes which occur in the stomach, it has been proved by the experiments of Colin that *no absorption occurs from this organ in the horse*. It would be useless to recapitulate all his experiments, they were generally performed with strychnine, and he found, so long as the pylorus was securely tied, no symptoms of poisoning occurred when the alkaloid was introduced into the stomach no matter how long it was left there, but that when the ligature was untied, and the contents of the stomach passed into the intestines, poisoning rapidly followed.

These remarkable results were obtained by him so often, and under such varying conditions, as to leave no doubt as to the accuracy of the observations.

Strychnine experiments are not altogether free from objection, but as matters stand we can only surmise that no absorption of sugar or peptones occurs in the stomach. It is certainly very remarkable what becomes of the peptones;

we have never found any in the stomach contents, no matter at what period of digestion the examination was made, and if they are not absorbed in the stomach they must pass very rapidly into the intestines and enter the vessels at once, as no peptone can be found in the small intestines.

Colin attributes the absence of absorption from the stomach of the horse to the small area of the mucous membrane, which, he says, cannot be secreting gastric juice and absorbing at the same time; in the empty stomach he attributes the non-absorption of poisons to the thick layer of tenacious mucus, which as we have previously mentioned covers the villous stomach of the horse.

In the same way that there is no absorption from the stomach of the horse, Colin's experiments show that there is little or no absorption from the abomasum of ruminants. On the other hand there is active absorption from the stomach of the dog and pig.

Self-digestion of the Stomach.—A question which has for a long time given rise to an energetic discussion, is the reason why the stomach during life does not digest itself, seeing that the action of its secretion is so potent that portions of living material, legs of frogs, ears of rabbits, etc., if introduced into it are readily digested, also that post-mortem digestion of the stomach in some animals is far from rare. No perfectly satisfactory solution of the problem has yet been afforded, the alkalinity of the circulatory blood is not considered to meet the difficulty. In an extensive post-mortem experience amongst horses we have never yet met with post-mortem digestion of the stomach. Whether this be due to the horse's acid being mainly or wholly lactic we cannot say.

The Gases of the Stomach.—The nature of these largely depends upon the food; traces of oxygen, a quantity of carbonic acid, and variable amounts of marsh-gas, sulphuretted hydrogen, hydrogen, and nitrogen are found. The oxygen and nitrogen are derived from the swallowed air, the carbonic acid is derived from the fermentation of

the food, and the action of acids on the saliva, whilst the marsh-gas is obtained by the decomposition of cellulose.

Tappeiner found the following gases in the stomach of a horse fed on hay:

Carbonic acid	75·20	67·73
Oxygen	·23	·00
Hydrogen	14·56	12·66
Nitrogen	9·99	19·54

In cattle fed on hay, the following gases were found by Tappeiner in the rumen:

Carbonic acid and sulphuretted hydrogen	65·27
Hydrogen	·19
Marsh-gas	30·55
Nitrogen	3·99

The gases from the intestines of the horse and rumen of the ox are very commonly inflammable and burn with a pale blue flame. This is due to marsh-gas, which readily ignites on meeting with a due proportion of oxygen.

Vomiting.

Vomiting amongst solipeds and ruminants is rare, but the act is common in the dog and pig.

The reasons given why the horse cannot vomit are various: (1) the thickened and contracted cardiac extremity of the œsophagus; (2) the oblique manner in which this latter enters the gastric walls; (3) the dilated pylorus lying close to the contracted cardia, so that compression of the stomach contents forces them into the duodenum; (4) the cuticular coat thrown into folds over the opening of the cardia; (5) muscular loops encircling the cardia, the contraction of which keep the opening tightly closed; (6) the stomach not being in contact with the abdominal wall.

All these and other reasons have been assigned as the cause of non-vomiting in the horse; yet on turning to

ruminants, which normally do not vomit, we find these conditions reversed; the stomach, gastric compartments, and œsophagus freely communicate; the largest reservoir lies in contact with the abdominal wall, the cardia is freely open, the œsophagus of great size, and, still stranger, the animal has the ability under the control of the will to bring up food from the stomach as a normal condition, and yet no vomiting occurs.

It is evident, therefore, that all these theories are not sufficiently satisfactory to account for the absence of vomiting, and we are bound to suppose that the vomiting centres in the medulla of both horse and ox, are either only rudimentary or very insensitive to ordinary impressions.

Vomition in the horse is no doubt seriously interfered with by the thickened œsophagus and cardia, and the arrangement of the muscular fibres; we do not think the folds of mucous membrane filling up the orifice could offer a serious obstruction to a distended stomach, for we know that even when this membrane is dissected away post-mortem, a stomach will burst rather than allow fluid or air to be forced through the cardia from the pylorus, unless the muscular fibres surrounding it be partly divided.

Vomition in the horse is generally indicative of ruptured stomach, and much has been written as to whether vomiting occurs before or after the rupture. From no inconsiderable experience of these cases, we have arrived at the conclusion that it may occur at either time, and that a horse may vomit though a rent seven or eight inches long exists in the stomach wall.

Dilatation of the cardia and œsophagus is the great inducement for vomiting to occur in the horse, and in every case examined post-mortem where vomiting occurred during life, we have found the cardia so dilated that two or three fingers might be readily introduced into it.

It is perfectly possible for a horse to vomit and recover, (showing that it had not a ruptured stomach), and it is not unusual to have attempts at or actual vomition when the small or large intestines are twisted.

The only case of vomiting we have seen in the horse which resembled the distressing appearance presented by the human subject, was in a case of volvulus of the small bowels; the ingesta gushed in a stream from both nostrils, the horse lying on his chest with the nose extended; moreover, it was the only case we have observed where any sound accompanied the effort. Vomiting in the horse is not as a rule attended by any distressing symptoms; the ingesta dribbles away from one or both nostrils, occasionally an effort is made on the part of the patient, the head being depressed to facilitate expulsion, but more than this is very rarely seen.

Why a horse should vomit more often with a ruptured stomach than a sound one is a fact we cannot explain.

It is important to notice in connection with the subject of vomiting, that agents such as tartar emetic, ipecacuanha, and apomorphia, which excite vomiting by their action on the cerebral centre, have no effect on the horse, nor do horses vomit as the result of sea-sickness, though they suffer extremely from it. The same remarks apply to ruminants.

In those animals where vomiting is a natural process, the three important factors are, the dilatation of the cardia by active contraction of the longitudinal fibres of the œsophagus, pressure on the walls of the stomach by a contraction of the diaphragm and abdominal muscles, and closure of the pylorus.

Rumination.

The physiology of rumination has been principally worked out in France by Flourens and Colin, and our knowledge of this singular process is based entirely on their observations.

Œsophageal Groove.—The œsophagus in ruminants enters and passes through the rumen forming a singular groove or channel known as the œsophageal, which on the left communicates with the first and second compartments, and by an opening on the right and inferiorly, with the third

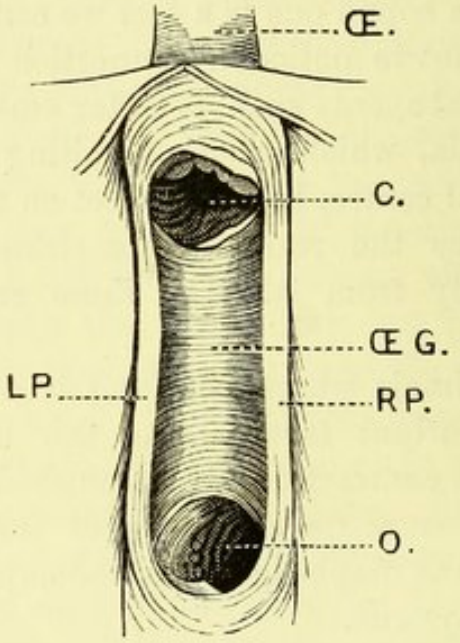


Fig. 25.—Diagram of the Œsophageal Groove. (Carpenter.)
Œ, œsophagus entering the stomach; C, its cardiac opening; RP, right pillar of œsophageal groove; LP, left pillar of the same; O, opening into the omasum; ŒG, œsophageal groove extending from C to O, about 7 inches in length. To the right of the figure is the rumen, to the left the reticulum.

compartment (Figs. 25 and 26). In this way food coming down the œsophagus may enter either of the three first reservoirs, the choice being determined, as we shall presently point out, by the condition in which the food is swallowed.

The œsophageal groove possesses two so-called lips or

pillars, the anterior being formed by the reticulum, the posterior by the rumen. The lips are thin above, and thick below where they overlap ; normally they lie in apposition in such a way as to conceal the groove, but in both Figs. 25 and 26 they are widely separated by being held back. These pillars are composed of involuntary muscular fibres arranged longitudinally and transversely, by which means the groove can be shortened and constricted.

By a contraction of the pillars the omasum may be shut

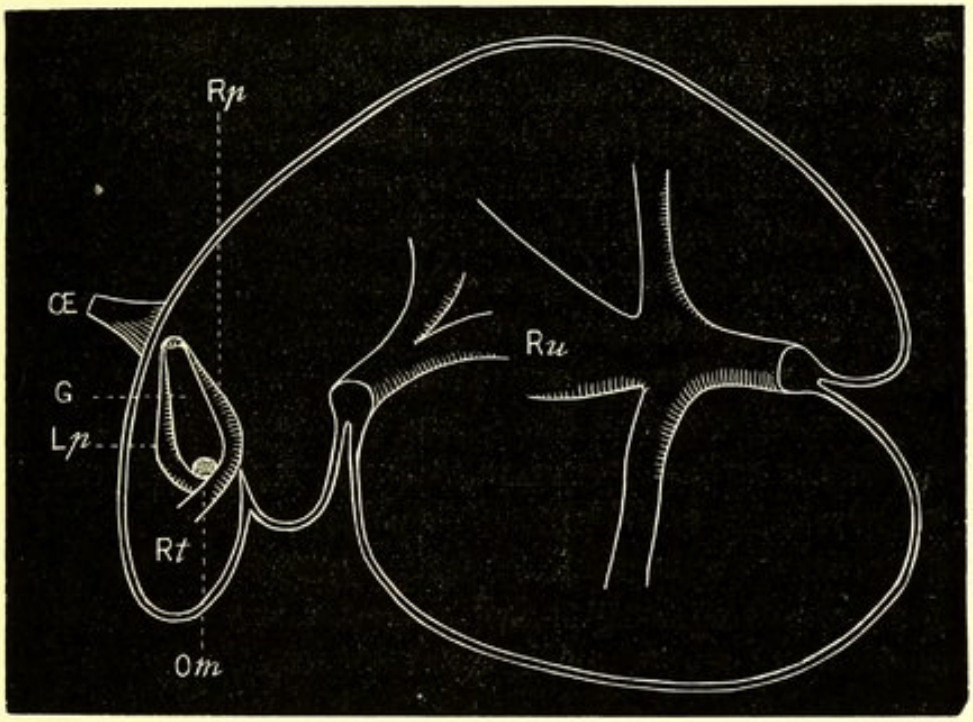


FIG. 26.—LONGITUDINAL SECTION OF THE RUMEN AND RETICULUM TO SHOW THE POSITION OF THE ŒSOPHAGEAL GROOVE IN THE LIVING ANIMAL.

R*u*, rumen, the lettering is placed on the muscular pillars ; R*t*, reticulum : Œ, œsophagus ; R*p*, right pillar, L*p*, left pillar, both held widely apart to show G, the groove ; O*m*, opening leading to the omasum.

off from the first and second compartments, and brought nearly in apposition with the œsophagus ; or by their relaxation the first and second may be made to communicate with the third compartment. When the pillars are relaxed the œsophagus communicates more directly with the rumen and reticulum.

Another function of the groove is said to be to cut off a

pellet of food pressed into it by a contraction of the rumen and reticulum, the pellet or bolus being then passed into the œsophagus for remastication; but Colin has shown that if the lips be stitched together rumination may still occur, so the theory that the bolus is formed between the lips of the canal is not correct according to this observer, and this view is supported by the stomach of the llama which only possesses one pillar and yet is capable of rumination.

Colin's description of the mechanism of rumination is as follows: during the churning movement the food is gently pressed against the lips of the groove, when, by a spasmodic contraction of the diaphragm and abdominal muscles, some of the liquid from the reticulum and some of the solid from the rumen are carried up the œsophagus, which latter by the contraction of its funnel-shaped extremity cuts off the bolus, and by its reversed peristaltic action conveys it to the mouth. In passing under the velum palati the liquid portion is squeezed out and is at once reswallowed, travelling to the third compartment, whilst the solid mass undergoes grinding. After the bolus is re-swallowed it may either pass again to the rumen, or, if in a finely comminuted condition, it passes at once from the œsophagus into the third compartment.

During the process of rumination the parotid glands secrete, but not the submaxillary or sublingual.

The reticulum appears to be only a convenient accessory to rumination, for as previously mentioned Flourens excised it, but this did not interfere with the process of rumination.

Rumination is a reflex nervous act the centre for which probably lies in the medulla; the process can only be performed by means of the united action of the diaphragm, walls of the stomach and abdominal muscles. Hence, if the phrenics be divided rumination is carried out with great difficulty, and only by an extra effort of the abdominal muscles; if the vagi be divided the walls of the stomach are paralysed and the process cannot go on, and if the spinal cord be divided in the mid-dorsal region

the abdominal walls are paralysed and rumination can no longer occur.

The condition of the stomach and its contents also exercise an important influence, rumination can only take place when the organ contains a fair amount of food and a considerable quantity of liquid.

The ascent of the food in the œsophagus can be distinctly seen in the neck, and sounds may be heard on auscultation due to the passage of the bolus with its fluid admixture, and the friction of the rumen against the diaphragm. The amount of each bolus has been estimated by Colin at 3½ to 4 oz.; its formation in the stomach and ascent will occupy about three seconds, and its descent after remastication one and a half seconds; its remastication occupies about fifty seconds. On this data Colin has calculated that at least seven hours out of the twenty-four are required for the process of rumination.

The Movements of the Stomach.—In most animals these are of two kinds, one produced by peristaltic action arising from a contraction of the longitudinal fibres which thereby shorten the stomach, whilst the circular fibres by their contraction reduce the calibre of the viscus; by this combined action the food is forced onwards into the intestine. The second form of movement is difficult to explain, but it is of a rotatory or churning character, by which the contents of the stomach are mixed up or even revolved; this latter movement takes place in the dog and also in cattle, as evidence of which we have the hair balls found in the rumen. In the horse a churning movement is not present, judging from the undoubted fact that the contents of the stomach are never under ordinary circumstances mixed up.

The movements of the stomach are excited by the presence of food, or any irritation applied to the mucous membrane; these movements are rendered more energetic by stimulation of the vagus, but even when all the nerves going to the part are divided the stomach can still contract, which is due to the ganglia contained in its walls.

It is probable that the different muscular layers forming the wall of the stomach have a separate source of nerve supply, so that they can act independently of each other.

The Nervous Mechanism of the Stomach.—Of this there is very little known, so far as experiment can determine there are no nerves governing the secretion of gastric juice, though there is evidence that such a nerve supply exists.

Both pneumogastrics supply the stomach, the nerves here being non-medullated; in addition it obtains sympathetic fibres from the solar plexus, to which the right vagus also sends some fibres (see Fig. 27, p. 178). In the wall of the stomach are found ganglia with which both the vagus and sympathetic communicate.

The vagus may be regarded as the motor nerve of the stomach whilst the sympathetic is inhibitory; irritation of the vagus leads to contraction of the stomach walls, irritation of the sympathetic causes the movements to cease. The vagus supplies the bloodvessels with dilator fibres, whilst the sympathetic supplies them with constrictor fibres.

Section of the vagus in the horse causes paralysis of the stomach, and in other animals if the movements are not abolished they are certainly diminished. The result of stomach paralysis is that nothing passes on to the intestines, so that in the horse even large poisonous doses of strychnia may thus lie inert in the stomach. This experiment demonstrates the uselessness of giving medicine by the mouth in many cases of stomach and intestinal trouble in the horse; the material lies in the stomach owing to paralysis of the organ, and is never absorbed.

In some animals, dog and rabbit, centres have been established in the brain stimulation of which increases or diminishes the activity of the cardiac and pyloric openings; in the corpus striatum is found a region stimulation of which causes the cardia to dilate and the pylorus to contract; in the corpora quadrigemina is found a centre stimulation of which contracts the pylorus.

Intestinal Digestion in the Horse.

Small Intestines.—The chyme which is poured from the stomach into the small intestines meets there with three other digestive fluids, viz., the succus entericus, the bile, and the pancreatic juice.

The **Succus Entericus** is prepared by the glands of the small intestines; in the duodenum the glands of Brunner are found, whilst the follicles of Lieberkühn are met with throughout the whole of the large and small intestines; the latter supply a considerable quantity of intestinal juice, while the secretion from the former is scanty. Brunner's glands, which are very large in the horse, are arranged on the same principle as the gastric glands, while those of Lieberkühn are tubular glands, amongst the lining cylindrical epithelial cells of which numerous mucus-forming goblet cells may be found.

Colin endeavoured to obtain succus entericus by clamping a loop of bowel in the horse, by which means he obtained from 6½ feet of small intestine 2·8 ozs. to 4 ozs. of fluid in half an hour.

We have no satisfactory analysis of intestinal fluid in the horse; it is probable that the methods adopted to obtain it are not completely satisfactory, nor is it likely that, in spite of the precautions taken, it can be obtained free from bile, pancreatic fluid, or gastric juice. Colin states that the juice he obtained was mixed with a little mucus, which he got rid of by filtration; the fluid was then clear, of a slightly yellow colour, saltish taste, alkaline reaction, with a specific gravity of 1010, and its analysis showed it to be composed as follows:

Water	98·10
Albumin	·45
Chloride of sodium, Chloride of potassium, Phosphate and carbonate of soda	1·45

Colin endeavoured to obtain the secretion of Brunner's glands in the horse by ligaturing the common duct and pylorus, and emptying the bowel. In an hour he obtained 2·8 ozs. of viscous thick liquid of saline taste, slightly alkaline reaction, specific gravity 1008, and it was found to give the following analysis:

Water - - - -	98·47
Mucus - - - -	·95
Chloride of sodium Carbonate of soda	·48
Hypophosphate of lime - -	·10

This fluid did not coagulate on heating, nor did it form an emulsion with fatty matter.

The intestinal fluid of the dog is light yellow in colour, opalescent, thin, and contains albumin, ferments, salts, and mucin, the latter especially in the large intestines (Landois).

Use of the Succus Entericus.—According to Ellenberger and Hofmeister, the succus entericus of herbivora contains three ferments; proteids are converted into peptones, starch into sugar, and cane-sugar into grape-sugar, the succus being the only secretion, so far as we are aware, which possesses this power. These results were also previously obtained by Colin, but they do not harmonise with the views of human physiologists, who attribute but a slight action to the intestinal fluid, and consider that its chief function is to change maltose into dextrose.

It is said by Landois that the succus of the dog is the most active, while the juice of the horse, sheep, and ox has no action; this latter can scarcely be correct.

Bunge considers that in the human subject the chief use of the intestinal fluid is to neutralise the acid of the intestinal contents, which it is capable of doing owing to the considerable quantity of carbonate of soda it contains; its further function is to emulsify fats with the surplus soda.

This view will not hold good for the horse, as the contents of the stomach are no doubt neutralised by the pancreatic and biliary secretions immediately or shortly after they leave the stomach; so much is this the case that on the

duodenal side of the pylorus the reaction of previously acid chyme is neutral, and a few inches further back alkaline; this alkaline reaction is at first faint, but becomes more marked as the ileum is approached.

Reaction of the Contents.—Ellenberger describes the small intestines as two-thirds acid, then neutral as far as the ileum where they become alkaline; we have only once found them otherwise than alkaline throughout. He further states that in the fasting horse the contents are alkaline, but that in the digesting animal, whether horse, ox, or sheep, they are acid, the acidity decreasing after passing the common duct, and becoming decidedly alkaline at the posterior portion of the small intestine.

This, as we have said, does not agree with our experience in the horse; it is usual to find the duodenum next the pylorus neutral, and from this point the bowel is faintly alkaline, the reaction increasing in intensity up to the ileum where the contents are always markedly alkaline. We have only once found the small bowels acid in the horse, no matter what diet has been given, or at what period of digestion the examination has been made; a neutral or faintly alkaline reaction in the anterior part of their course, and markedly alkaline in the posterior portion, is doubtless the rule rather than the exception.

Physical Characters of the Chyme.—The chyme having passed into the bowel its appearance at once changes, for the acid albumin is precipitated by the alkaline secretion found there. It is now observed that the material consists of clots floating or suspended in a yellowish fluid, extremely slimy in nature, and resembling in appearance, through its precipitated albumin, nasal mucus suspended in fluid. The proportion of mucin must be considerable judging from the manner in which it pours, and this mucus is probably largely derived from the stomach. Throughout the small intestines the character of the chyme is as follows, viz., a yellow, frothy, precipitated, slimy fluid; the material from the anterior part of the intestinal canal having a peculiar mawkish smell, whilst that from the region of the ileum is

of a distinctly fæcal odour; this latter is due to indol and skatol formed during pancreatic digestion. In the ileum the proportion of fluid material is considerably reduced in amount, and the nature of the ingesta may now be recognised, which was previously almost impossible.

Function of the Ileum.—As the flow of material into the small intestines is controlled by a sphincter, so is the flow out of it; the ileum is a remarkably thick and powerful bowel, it is always found contracted and containing ingesta, which is dry compared with that found in the anterior portion of the intestine. One of the functions of the ileum is to control the passage of material into the cæcum.

Colin describes the chyme in the horse as circulating between the pylorus and ileum, viz., that it is poured backwards and forwards in order to expose it sufficiently to the absorbent surface; this necessitates a reversed peristaltic action. He says that were it not for this the material could not be acted upon and absorbed, as the passage of fluid through the small intestines is so very rapid. One could never have reasoned out that the fluid material of the small intestines was passed to and fro between the stomach and the ileum, exposed, as Colin expresses it, twenty times over to the absorbent surface of the bowels. This observation must have been made as the result of his examination of the living animal.

Experiment shows that water will pass from the stomach to the cæcum in from five to fifteen minutes. By applying the ear over the duodenum as it passes under the last rib on the right side, the water which a horse at that moment is drinking may be heard rushing through the intestines on its way to the cæcum.

One is always struck by the fact that the small intestines are never seen full, in fact, are often practically empty, from which we judge that material passes very rapidly through them. This material is always in a liquid condition excepting at the ileum; the fluid is derived from the secretions poured into and those originating in the bowel, and that

active absorption goes on in the intestines is proved by the difference in the physical characters of the contents.

The rate at which the chyme passes through the small intestines will vary with the nature of the food, and the frequency with which the horse is fed. Ellenberger says it reaches the cæcum six hours after feeding, but has not entirely passed into this bowel for twelve or even twenty hours; we have known it reach the cæcum in four hours.

The remaining digestive fluids which the chyme meets with in the small intestines are the bile and pancreatic juice; the action of these on food is described in the chapter dealing with the liver and pancreas. The little we know about the absorption of chyle, and its elaboration before reaching the blood, are points which must be reserved for the chapter on 'Absorption.'

Large Intestines.—There can be no doubt that in solipeds digestion in the large intestines is a very important process; at least, we judge so from the fact of their enormous development. In many respects they present a considerable contrast to the small intestines; for instance, they are always found filled with ingesta, the contents are more solid, the material lies a considerable time in them, and there are no juices other than the succus entericus poured into the bowel. These are conditions exactly the reverse of those found in the small intestines.

The bowels which are spoken of as the large intestines are the cæcum, double and single colon, and the rectum.

The **Cæcum** has been described by Ellenberger as a second stomach; its enormous capacity, and fantastic shape, have always rendered it an intestine of considerable interest. To our mind its most remarkable feature is that it is a bag the openings into and out of which are both found at the upper part close together; the exit, strange to say, is above the inlet, and the contents have to work against gravity in order to obtain an entry into the next intestine the double colon. The contents of the cæcum are always fluid, sometimes quite watery, occasionally of the colour and consistence of pea-soup, in which condition they are full of gas

bubbles; when watery the fluid is generally brownish in colour, with particles of ingesta floating about in it. The reaction of the contents is always alkaline; all observers are agreed on this point.*

The view we hold of the function of the cæcum, is that it is most admirably arranged as a receptacle for fluids, and though undoubtedly absorption occurs from it, and digestion of cellulose takes place in it, yet we believe its chief function is the storing up of water for the wants of the body and the digestive requirements, as it is absolutely certain that digestion in the horse can only be properly carried out when the contents are kept in a fairly fluid condition. We do not say that the cæcum produces no digestive changes in the food, especially in the face of Ellenberger and Hofmeister's experiments which show that digestion in the cæcum is important, but we consider its digestive function subordinate to its water-holding one.

Ellenberger views the cæcum as a bowel for the digestion of cellulose, where by churning, maceration, and decomposition, this substance is dissolved and rendered fit for absorption, and he likens it to the stomach of ruminants and the crop of birds; he further considers that the cæcum exists owing to the small size of the stomach, and the rapidity with which the contents are sent along the small intestines.

Ellenberger's experiments demonstrated that the entire 'feed' reached the cæcum between 12 and 24 hours after entering the stomach, that it remained 24 hours in the cæcum, and that during this time 10 to 30 per cent. of the cellulose disappeared.

The digestion of cellulose is no doubt a very important matter, especially as we know that the poorer the food the more cellulose digested; but we are not prepared to admit that food remains in the cæcum 24 hours, and believe that cellulose digestion principally, though not entirely, occurs in the colon, and further, that it is not absolutely necessary the material should remain in the cæcum, but it may pass on at once to the colon.

* We once found the cæcum acid.

Our experiments on digestion have shown that ingesta may be in the cæcum 3 to 4 hours after entering the mouth, and we are quite clear on the point that oats may reach even some distance along the colon in 4 hours from the time of being consumed, though this is regarded as exceptionally rapid.

We fed a horse which had never had maize in its life, (and had not tasted oats for two or three years), with, first, 2½ lbs. of maize, and 17 hours later with 4 lbs. of oats. The animal was destroyed 4 hours from the time of commencing to eat the oats. Much maize and a few oats were found in the pelvic flexure of the colon, and a certain proportion of maize and a quantity of oats in the stomach. This bears out what we have said about gastric digestion slowing off (p. 132), and proves how great is the distance food may travel through the bowels in a short time, though in this case its progress was much more rapid than usual.

Colin believes that in the cæcum starch can be converted into sugar, fats emulsified, and that active absorption of assimilable matters occurs.

It is remarkable how the material finds its way against gravity out of the cæcum; the capacious folds in the intestine are likened by Colin to the buckets of the Persian water-wheel, by which means the fluid is handed up and passed on into the colon.

In the absence of experimental evidence, we would hardly like to suggest that food may pass directly from the opening of the ileum into the colon, but we certainly have reason for thinking that this may occur.

The Colon.—The direction taken by the colon of the horse is remarkable; it commences high under the spine on the right side, its origin being very narrow but it immediately becomes of immense size; it descends towards the sternum, and curving to the left side, rests on the ensiform cartilage and inferior abdominal wall. The colon now ascends towards the pelvis, and here makes a curve, the bowel becoming very narrow in calibre; the pelvic flexure having been formed, the intestine retraces its steps towards

where it started from; running on top of the previously described portion it descends towards the diaphragm, gradually getting larger in calibre, and then ascends towards the loin, being here of immense volume—in fact, at its largest diameter; it then suddenly contracts, and forms the single colon. The object of the difference in the volume of the double colon appears to be for the convenience of its accommodation in the abdominal cavity.

The double colon may for the purpose of description be divided into four portions: the ingesta in the first and third descend, in the second and fourth they ascend. It is found that the physical characters of the contents are not the same throughout; in the first colon the food is fairly firm, and the particles of corn, etc., can be readily recognised; in the second colon the material is becoming more fluid, whilst at the pelvic flexure the contents are invariably in a liquid pea-soup like condition, and the particles of which they are composed are not readily recognised. In the third colon the material becomes firmer, but only slightly so, and bubbles of gas are being constantly given off from its surface; in the fourth colon the entire ingesta are like thick soup, and the material composing it is in a finely comminuted condition, the surface being covered with gas bubbles; for the first foot or so of the single colon this condition is maintained, when quite suddenly the contents are found solid and formed into balls. The remarkable suddenness of this change is invariable in a state of health, and indicates either most active absorption, or that the contents are subjected to great compression.

The entire contents of the colon are yellow in colour or yellowish green, rapidly becoming brown or olive-green on exposure to light; the colour is due to the chlorophyll of the food. The contents of the colon are normally alkaline throughout; we once, however, found them acid.

The muscular movements of the large intestine are much slower than those of the small bowels; possibly one reason for this may be that the food has to remain a longer time

in contact with the absorbing surface, viz., for at least forty-eight hours.

The digestive changes in the large intestines have by some been regarded as insignificant, but this cannot be, for it is impossible, as has been suggested, to regard these large bowels as simply reservoirs for ingesta. Such a view is incompatible with their structure or the appearance of their contents.

Owing to the fact that no secretion other than the succus entericus is poured into the large bowels, some physiologists have considered that the digestive changes which take place here, are occasioned by fermentative or putrefactive processes brought about by organisms which are taken in with the food and water.

Later in this work we will draw attention to the fact that the ferments made in the body are spoken of as enzymes or unorganized; the ferments which according to some observers do the work in the large intestines are organized ferments, viz., the various kinds of bacteria; these are believed to have the power of acting on starch, fat, cellulose, and proteids.

Whether this explanation be correct or not, it would appear certain that some or all these substances are digested in the large intestines, but how much is due to organized and how much to unorganized ferments we cannot say.

Perhaps the chief action of the colon is directed against cellulose; whether this substance furnishes its own ferment is not known, but such has not yet been found in hay. Landois says that the *bacillus butyricus* and *vibrio rugula* partly dissolve cellulose, and further, that in herbivora no digestive juices can digest cellulose so long as putrefaction does not take place in the mixture. Bunge believes that the epithelial cells of the intestine dissolve cellulose, but the entire question of cellulose digestion is still wrapped in obscurity, and no positive statements can as yet be made. What we do know for a certainty is that the result of cellulose digestion is the evolution of a quantity of gas, consisting of equal volumes of carbonic acid and marsh-gas.

Bunge* considers that cellulose is absolutely essential to animals with a long intestine, as it acts as a natural stimulus to the bowel, and promotes peristalsis.

Throughout this chapter repeated reference has been made to the digestion of cellulose by herbivora, from which it may be imagined that its value in a diet depends upon the energy it is capable of contributing to the body; but this is not so, the importance of cellulose digestion depends upon the fact that it encloses in its framework the proteid, starch, and fat, contained in vegetable substances, and until this framework is broken down the food stuffs cannot be acted upon. It is for this, and other reasons, that digestion in the large intestines of the horse cannot be regarded as of minor importance, and further it is evidence that proteid, fat, and sugar, can be absorbed from them as in the small intestines.

In the **single colon** we have noted the remarkable and sudden change of highly fluid, thick, soup-like ingesta, into comparatively dry fæces. As the material moves towards the anus it becomes drier and drier, and more thoroughly formed into balls by the action of the bowel-sacs, which squeeze the mass into a round or oval shape. The contents of this portion are still alkaline, or slightly so, as we approach the rectum a distinctly acid reaction is obtained on the surface of the fæces, though at this time the interior of the ball may be, and often is, alkaline; the converse of this may also be obtained. In the rectum the single balls collect in masses, to be forced out of the body at the next evacuation; the reaction of this mass is acid, the colour depends on the food, and on an ordinary diet is of rather a reddish-yellow or brownish tint due to altered chlorophyll.

Absorption from the single colon and rectum is very rapid; animals may be killed by the rectal injection of strychnine, narcosis can also be produced by the rectal administration of ether, and life may be supported, at any rate for a little time, by means of nutritive enemata.

* 'Physiological and Pathological Chemistry.'

Intestinal Digestion in Ruminants.—Though intestinal digestion is so important in the horse, it would appear that in ruminants it occupies a subordinate position ; the rumen of the ox corresponds to the large intestines of the horse. It is curious why in one animal the changes should occur at the anterior part of the digestive tract, and in the other at the posterior part, but there can be no doubt that the difference in the arrangement for digesting cellulose depends upon one being capable of rumination and the other not.

The intestines of the ox are of extreme length but small in calibre, they are half as long again as those of the horse and it would appear that their chief function is that of absorption. It is in this immense length of absorbent surface that the food substances capable of being utilized are taken up by the bloodvessels and villi.

It is clear, however, that certain digestive changes do occur in the small intestines, into which as in other animals the pancreatic and biliary fluids are poured; here the proteids which have escaped the stomach, and the fats and starches are rapidly changed and rendered fit for assimilation; the cellulose in all probability only finds its way here when fit for absorption after its digestion in the rumen.

If we are to judge from an experiment made on a sheep, intestinal digestion in ruminants must be short. Meade Smith who quotes the experiment, says that the hay received by this sheep remained in the first three stomachs for twenty hours, in the fourth stomach for 1·2 hours, in the small intestines 2·3 hours, cæcum 7 hours, and colon 5·5 hours.

Intestinal Digestion in other Animals.—**In the pig** intestinal digestion is said to be of short duration, and absorption very rapid. **In the dog** the material passes out of the stomach slowly and only in small quantities into the small intestines, which are usually found collapsed. It is in the small intestines of this animal that the chief absorption occurs, as the large ones are rudimentary.

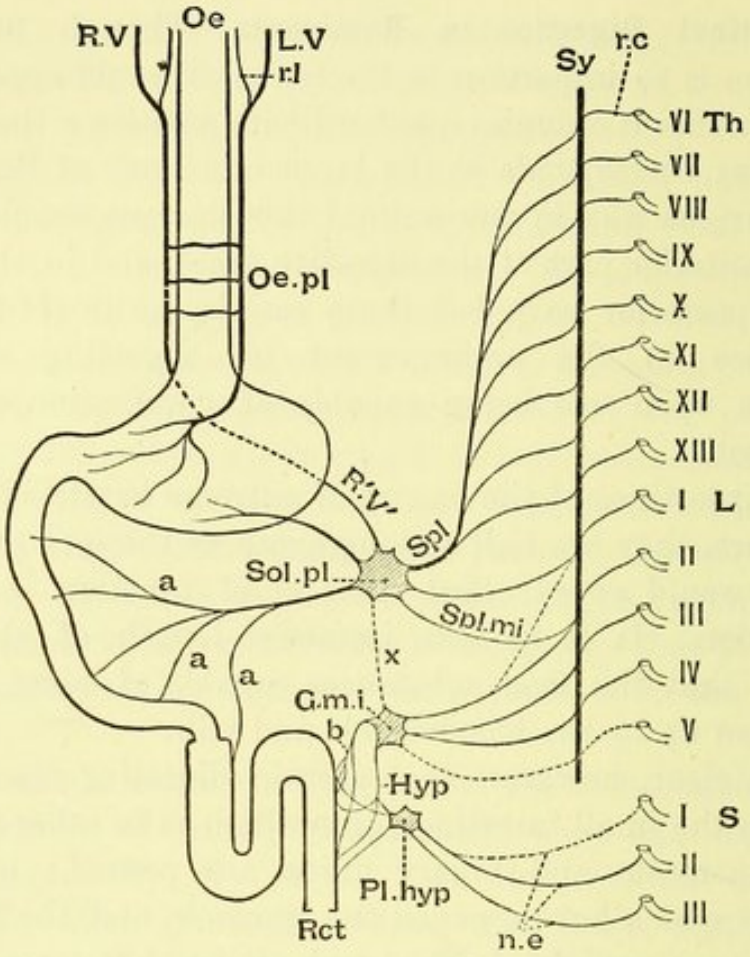


FIG. 27.—DIAGRAM TO ILLUSTRATE THE NERVES OF THE ALIMENTARY CANAL OF THE DOG (FOSTER).

(The figure is very diagrammatic and does not represent the anatomical relations.)

Oe. to *Rct.* The alimentary canal from the œsophagus to the rectum.

LV. Left vagus nerve ending on the front of the stomach. *rl.* Recurrent laryngeal supplying upper part of œsophagus. *R.V.* Right vagus joining left vagus in the œsophageal plexus *Oe.pl.*, supplying the posterior part of the stomach, continued as *R'.V'.* to join the solar plexus, *Sol. pl. here represented by a single ganglion*, and connected through *x* with the inferior mesenteric ganglion (or plexus) *G.m.i. a*, *a*, *a*, branches from the solar plexus to stomach and small intestines, and *b* from the mesenteric ganglion to the large intestines.

Spl. Large splanchnic nerve arising from the thoracic ganglia of the sympathetic *Sy.* and rami communicantes *r.c.* of the dorsal nerves.

Spl.mi. Small splanchnic nerve. Both the large and small splanchnics join the solar plexus and thence make their way to the alimentary canal.

G.m.i. Inferior mesenteric ganglion formed by nerves running from the dorsal and lumbar cord, and thence by the hypogastric nerve *Hyp.* and the hypogastric plexus *Pl.Hyp.* to the circular muscle of the rectum.

n.e. Nervi erigentes arising from the sacral cord and proceeding by the hypogastric plexus to the longitudinal muscle of the rectum; they also supply the bladder and genital organs.

In the sheep, ox, pig, and dog, the reaction of the small intestines is acid anteriorly and alkaline towards the ileum; probably in all animals the large intestines are alkaline in reaction.

Munk gives the following statistics respecting the intestinal canal. In the tiger and lion the whole digestive tract is 3 times the length of the body, in the dog 5 times, man 9 times, horse 12 times, ox 20 times, and pig 16 times; the comparative shortness of the intestinal canal of the horse is compensated for by its enormous capacity which is 352 pints, in the ox 140 pints, pig 47 pints, dog 14 pints. The superficial area of the intestinal tract is also given by the same observer; horse 550 square feet, ox 160 square feet, pig 32 square feet, and dog 5½ square feet (M'Kendrick).

Nervous Mechanism of the Intestinal Canal.—This is furnished by the vagus and sympathetic. Fibres from the vagus pass to the solar plexus (Fig. 27), from whence branches are distributed to both the small and large intestines by means of the mesenteric nerves. Stimulation of the vagus produces active contraction of both the large and small intestines; contraction and regular peristalsis may occur not only when the vagus is divided, but when every source of nerve supply is severed.

This points to the existence of local ganglia, and such are found in the form of the plexus of Auerbach which can be traced throughout the intestinal canal, and to which fibres of the vagus pass; it is considered by some that these local ganglia do not play any important part in the production of peristalsis.

Owing to the fact that peristalsis may occur after the vagus is divided, the action of the latter nerve is regarded in the light of an augmentor rather than a motor nerve.

But there are other sources of nerve supply than that furnished by the vagus; coming out from the spinal cord in the dorsal and lumbar portions, are branches of nerve

which form the splanchnics of the sympathetic system, and join the solar and mesenteric plexuses; from these plexuses or ganglia fibres are given off which supply the intestines (Fig. 27). The function of these fibres is mainly inhibitory, irritation of them stops the active contractions produced by the vagus; in addition the sympathetic supplies constrictor fibres to the walls of the bloodvessels of the intestine, the vagus probably supplying the dilator mechanism to the vessels.

From the sacral cord nerves run out which pass to the hypogastric plexus, they are known as the *nervi erigentes*, and their function is to supply the longitudinal muscle of the rectum; the circular muscle is supplied from a distinct source the fibres for which are derived mainly from the lumbar cord, and reach the hypogastric plexus through the hypogastric nerve. Though we have no evidence in any other part of the intestinal canal that the circular and longitudinal muscles have a separate nerve supply, yet such is most likely to exist.

Under ordinary circumstances the normal stimulus to promote peristalsis is furnished by the food passing along the bowel, in the dog it has been observed that even the sight of food has caused increased peristalsis. But besides this the character of the circulating blood has some effect, venous blood or blood deficient in oxygen and containing an undue proportion of carbonic acid causes active peristalsis, and the cutting off suddenly of the blood supply to the bowels causes pronounced peristalsis and even evacuation of the contents of the rectum.

The vermicular movements seen after death are supposed to be due to the absence of blood from the bowel, and the evacuation of the contents of the rectum in animals destroyed by injuring the brain may probably be brought about in the same way.

Under normal conditions the mind is not aware of the peristaltic process which is constantly occurring, but when this is very energetic and the bowel powerfully constricted pain is produced, which reaches the brain through the

abdominal splanchnics and the spinal cord; thus the splanchnics may convey impressions in both directions.

Exercise is an important source of intestinal peristalsis especially in horses; this is very evident in the case of the rectum.

Under the influence of nervous excitement, rapid and frequent evacuations of the bowels may be obtained especially in horses, this may be due either to increased peristalsis, or to an increased secretion into the intestines owing to derangements of the vaso-motor supply.

Secretion of intestinal fluid may be obtained by chemical, thermal, and other stimuli. Irritation of the vagus produces no increase in the secretion, but extirpation of the solar and mesenteric plexuses causes a profuse secretion; in the same way division of the nerves leading to a loop of intestine produces a considerable outpouring of intestinal fluid. As it is through these plexuses and nerves that the vaso-motor supply is obtained, it is possible that the secretion which follows interference with the nerve supply is due to paralysis of the intestinal vessels.

Finally, turning once more to the natural stimulus of peristalsis, viz., the food in the intestinal canal, it cannot be too distinctly understood in the feeding of herbivora how necessary it is that moderate bulk should exist in their diet. Bunge has shown that rabbits die from intestinal obstruction if cellulose (and lignin) be withheld from their diet, and it is quite impossible to keep horses in condition on concentrated food. It is the cellulose and lignin in the diet which provide the needful stimulus to the intestines of herbivora, though, like everything else, in excess it may produce the opposite effect.

Putrefactive Processes in the Intestinal Canal.—We may now consider the nature of the putrefactive processes occurring in the digestive canal, the presence of which is recognised by the production of foul-smelling gases.

In the anterior part of the small intestine no putrefactive

odour is obtained, but after the admixture and action of the pancreatic juice a distinctly fæcal odour is given to the contents, this is due to the formation of indol and skatol. There can be no doubt that a large number of organisms are found in the intestines, and these, to a certain extent, may be useful in assisting digestion, especially that of proteids, and perhaps of fats. By means of organisms leucin and tyrosin, indol and skatol, lactic and butyric acids, may also be formed (Halliburton), and the function of these organisms may further—according to the same observer—be protective by destroying poisonous products, such as cholin (the alkaloid derived from lecithin).

The decomposition of proteids in the large intestine leads to the formation of carbonic acid, sulphuretted hydrogen, ammonia, phenol, kresol, skatol, and certain organic sulphur compounds; the latter, with phenol and indican, are excreted by the kidneys, and in carnivora and omnivora are regarded as a measure of the putrefactive processes occurring in the bowel. This, however, will not hold good for the herbivora, as with them phenol is principally derived from the food. The longer the food remains in the bowel, the more indol and phenol is formed; these are decomposition processes, and have nothing to do with nutrition. In flesh-feeders the products of these decompositions are got rid of by disinfecting the intestinal canal with calomel.

According to Tappeiner phenol is found in the stomachs and intestines of cattle, skatol in the rumen, and indol in the small and large intestines. In the horse indol is present up to the cæcum; in the colon its place is taken by skatol, whilst phenol and ortho-kresol are found throughout the large intestines.

According to Ellenberger the fermentation in the intestines of the horse may be either acid or alkaline, both leading to the production of marsh gas; but the acid fermentation occurs in the presence of skatol, whilst the alkaline occurs in the presence of indol. Intestinal fermentation in the horse is allied to that occurring in the

rumen of cattle; in all cases the fermentation can occur without the presence of oxygen.

By the decomposition of starchy matters lactic, formic, acetic, butyric, and propionic acids are formed; it is to some of these that the acid reaction of normal fæces is due.

In the large intestines of horses Colin describes no less than eight or ten species of Infusoria. The most characteristic of these are the **Colopodes**, recognisable by their ovoid form with lateral indentation, at the base of which the mouth is found. Others are ovoid but lack the lateral indentation of the previous species; some have an elongated rectangular form, and others are unsymmetrical in shape. All these infusoria are found in the cæcum and anterior parts of the double colon; they die in the last part of the intestine, and leave nothing more than their débris in the excreta; in ruminants similar organisms are found in the rumen. As to the action of these organisms we know nothing.

The largest amount of gas found in the intestinal canal is in the cæcum and colon; the small intestines do not naturally contain much, whatever is formed there being probably rapidly passed into the large bowels. In the large intestines marsh-gas commonly exists, forming with carbonic acid the bulk of the gases present. The pathological conditions arising in the large bowels of horses, and in the rumen of cattle, as the result of the fermentation of food—particularly green grass—and the enormous size to which these animals may be distended, are matters of common clinical experience. In both horse and ox the gas may generally be ignited a short distance away from the cannula which has been passed into the parts to give relief, the marsh-gas igniting readily on meeting with the proper proportion of oxygen.

Tappeiner, quoted by Ellenberger, gives the following analysis of intestinal gases in the horse:

SMALL INTESTINES (HAY DIET).

	Anterior portion.	*Posterior portion.*
Carbonic acid - - - -	72	15
Sulphuretted hydrogen and hydrogen -	19	24
Nitrogen - - - - -	37	59

LARGE INTESTINES (HAY DIET).

	Cæcum.	*Colon.*	*Rectum.*
Carbonic acid and sulphuretted hydrogen - - -	85·0	55·5	29·0
Hydrogen - - -	2·0	1·7	1·0
Marsh-gas - - -	11·0	33·0	56·0
Nitrogen- - - -	·9	10·0	13·0

ON CORN AND HAY DIET.

	Small Intestines.	*Colon.*	*Rectum.*
Carbonic acid - - -	11·0	75·00	45·0
Hydrogen - - -	4·0	·38	3·0
Nitrogen - - - -	84·0	6·00	12·0
Oxygen - - - -	·7	—	—
Marsh-gas - - -	—	17·00	40·0

The gases found by Tappeiner in the intestine of the ox were as follows :

	Small Intestines.	*Large Intestines.*
Carbonic acid - - -	17 to 92	14 to 81
Hydrogen - - -	·04 ,, ·44	·36
Marsh-gas - - -	6 ,, 64	17 ,, 44
Nitrogen - - -	·29 ,, 1·2	2 ,, 41

The intestinal gases of the dog depend upon the character of the diet ; this causes considerable variation in the nature and quantity of the gases found ; for example, on a flesh diet the hydrogen amounts to 13·9 per cent., on a diet of bread 6·3 per cent., and on one of peas 48·7 per cent.

The above analyses show that intestinal digestion is carried on in the absence of oxygen.

The Fæces.

The fæces consist of that portion of the food which is indigestible, together with that part which though digestible has escaped absorption; mixed with these are water, colouring substances, mucin, organic matters in great variety, inorganic salts, bile pigment, volatile fatty acids, remains of digestive fluids, organisms, etc.

The composition of the fæces depends largely on the diet. The following table from Gamgee* can only give a general idea of their nature:

Approximate Composition of the Fæces of the

	Horse.	*Cow.*	*Sheep.*	*Pig.*
Water - -	76·0	84·0	58·0	80·0
Organic matter	21·0	13·6	36·0	17·0
Mineral ,, -	3·0	2·4	6·0	3·0
	100·0	100·0	100·0	100·0

Considerable differences exist amongst animals in the consistence of the fæces; they are moderately firm in the horse, pultaceous in the ox, and hard in the sheep. These differences depend upon the amount of fluid they contain. In the pig they are human-like and very offensive; in the dog, soft or hard, dark or light, depending on the diet, the mineral matter of bones producing the light-coloured fæces. It is necessary to remember that the proportion of fluid in the fæces does not depend upon the amount of water which is drunk, but rather on the character of the food, the activity of intestinal peristalsis, and the energy with which absorption is carried on in the digestive canal. Succulent food in horses produces a liquid or pultaceous motion; other foods, such as hay and chaff, have a constipating effect, the fæces being small and firm; excess of nitrogenous matter in the food produces extreme fœtor of the dejecta, and frequently diarrhœa, probably due to putrefactive processes. Nervous excitement rapidly induces a free action of the bowels, accompanied by very liquid fæces;

* 'Our Domestic Animals in Health and Disease,' p. 253.

this latter is explained by the increased production of peristaltic action probably associated with vaso-motor paralysis.

The fæces always float in water so long as cohesion is maintained.

The colour of the fæces in the horse is yellowish or brownish-red; they rapidly become darker on exposure to the air; when the animal is grass-fed the fæces are green, and when fed wholly on corn they become very yellow and like wet bran in appearance.

The colour of the fæces of animals receiving hay or grass is due to altered chlorophyll.

The fæces of the horse are moulded into balls in the single colon, an intestine where, as we have previously indicated, either most active absorption of fluid occurs or the contents must be exposed to great compression.

The fæces of the horse are always acid, the acidity probably depending upon the development of some acid from the carbo-hydrates of the food.

Fæces contain amongst the indigestible portion of the ingesta, lignin, a proportion of cellulose, husks of grains, the downy hair found on the kernel of oats, vegetable tubes and spirals, starch and fat granules, gums, resins, chlorophyll, etc.; unabsorbed proteid, carbo-hydrate and fatty material; products of digestive fermentation, such as lactic, malic, butyric, succinic, acetic, and formic acids; leucin, tyrosin, indol, skatol, and phenol; biliary matters and altered bile pigment, stercobilin, which gives the colour to the dejecta in the dog but not in herbivora; and, lastly, mineral matter in varying proportions. In the dog portions of muscle fibre, fat cells, tendinous and fibrous tissue, are found in animals fed on flesh.

Of the inorganic matter silica exists in largest amounts in herbivora, then potassium and phosphoric acid; sodium, lime, magnesium, and sulphuric acid, forming a smaller but still important proportion.

The horse excretes but little phosphoric acid by the kidneys, but considerable quantities pass with the fæces in the form of ammonio-magnesium phosphate. This salt is

derived principally from the oats and bran of the food, and it frequently forms calculi through collecting in the colon and becoming mixed with organic substances. Other intestinal calculi are formed from lime deposits in the bowel, while collections of the fine hairs from the kernels of oats form oat-hair calculi.

The following table by Roger gives the mineral composition of the fæces in every 100 parts of the ash: *

	Horse.	*Ox.*	*Sheep.*
Sodium chloride -	·03	·23	·14
Potassium - -	11·30	2·91	8·32
Sodium - -	1·98	·98	3·28
Lime - - -	4·63	5·71	18·15
Magnesium - -	3·84	11·47	5·45
Oxide of iron - -	1·44	5·22	2·10
Phosphoric acid -	10·22	8·47	9·10
Sulphuric acid - -	1·83	1·77	2·69
Silica - - -	62·40	62·54	50·11
Oxide of magnesium -	2·13	—	—

Roger observed that the ash of the fæces of herbivora contained scarcely any alkaline carbonates.

The **amount of fæces produced** in 24 hours varies with the quantity and nature of the food given. We have observed that on a diet consisting of 12 lbs. of hay, 6 lbs. of oats, and 3 lbs. of bran, the average amount of fæces passed by fifteen horses during an experiment lasting seven days, amounted to 29 lbs. 13 ozs. in 24 hours, the fæces being weighed in their natural condition, viz., containing 76 per cent. water; the dry material of this bulk of fæces is about 7¼ lbs. More fæces are passed during the night than during the day; in the above experiment, during the 12 hours (6 p.m. to 6 a.m.), the average amount of fæces per horse was 18 lbs. 3 ozs., whilst from 6 a.m. to 6 p.m. the amount was 11 lbs. 10 ozs. The largest amount of fæces we have known a horse produce was an average of 73·3 lbs. (weighed in their natural state) for the 24 hours; the diet consisted of 12 lbs. of oats, 3 lbs. of bran, and 28 lbs. of hay.

* Quoted by Ellenberger.

In an experiment carried out for several months with different horses all receiving 12 lbs. hay and varying proportions of bran and oats, the average daily amount of fæces, weighed in their natural state, amounted to 24 lbs.

A horse will evacuate the contents of the bowels about ten or twelve times in the 24 hours, and the food he consumes will take at least four days to pass through the body.

In the ox the amount of fæces is between 70 lbs. and 80 lbs. in the 24 hours.

In the sheep the fæces vary from 2 lbs. to 6 lbs. daily, in swine 3 lbs. to 6 lbs., depending on the nature of the diet; in a dog fed on meat the fæces amounted to 1 to 2 oz. per diem, but this must vary with the size of the animal.

The **odour of fæces** is distinctly unpleasant, due to the presence of indol and skatol. In disease the fæces are often extremely fœtid; the odour probably depending upon indol and skatol and the decomposing unabsorbed proteid.

The act of **defæcation** is performed by a contraction of the rectum assisted by the abdominal muscles, the glottis being closed. In the horse the contraction of the rectum alone is sufficient to expel its contents; this is proved by the fact that this animal can defæcate while trotting, showing there is no necessity to fix the diaphragm and hold the breath, though at rest this does occur. The anal sphincter dilates under the pressure of the fæces, the tonic contraction of the sphincter muscle—the centre for which exists in the lumbar cord—is relaxed, the longitudinal muscular fibres shorten the bowel, while the circular muscle, which receives an independent nerve supply, contracts from before backwards and expels the contents. So marked is the shortening of the longitudinal fibres in the horse that the mucous membrane is often everted.

If the defæcating centre in the cord be destroyed the anus becomes flaccid and the rectum remains full, showing that the mechanism which contracts the anus also contracts the rectum; in the dog, however, division of the spinal cord in the lumbar region does not interfere with the act of defæcation, which is then carried on as a purely reflex act.

Probably owing to the horizontal position of the body the rectum in the horse possesses considerable power which the animal can apparently exercise at will. As far as one can reach forward with the hand in the rectum the bowel appears to be capable of exercising a voluntary contraction; the strength of these contractions is sufficient at times to numb the fingers and arm of the examiner.

Meconium is the dark-green material found in the intestines of the fœtus. It consists of biliary matters, both acids and pigments, fatty acids, and cholesterin; whilst the salts of magnesium and calcium, phosphoric and sulphuric acids, sodium chloride, soda, and potash are also found in it. Meconium is the product of liver excretion.

CHAPTER VII.

THE LIVER AND PANCREAS.

In considering the function of the liver it is necessary to bear in mind its peculiar blood supply. Most glands of the body which are called upon to produce a secretion are furnished with arterial blood for the purpose, but the liver is an exception to this rule; the entire blood returning from the splanchnic area, viz., the bowels, stomach, spleen, pancreas, etc., constitutes the material with which the liver is flooded. Such a mixture of blood derived from a peculiar and considerable area must be charged with many products, some the result of secretory activity, others the soluble constituents of the elements of food, especially proteid and sugar, or again other substances absorbed from the intestinal canal, which are bye-products produced during the gradual breaking-down of the food substances, and in other ways. It is from this blood that the liver performs its various functions, and one of the most evident, viz., the secretion of bile, will be dealt with first.

Bile.

The bile is a fluid of an alkaline reaction, bitter taste, a specific gravity in the ox of 1022 to 1025, in the sheep from 1025 to 1031, and in the horse 1005. The colour is yellowish-green or dark-green in herbivora, reddish-brown

in the pig, and golden-red in carnivora. These differences in colour depend upon the character of the pigment present.

Bile taken direct from the liver is watery in consistence, that taken from the gall-bladder is viscid, due to admixture with mucin during its stay in the latter receptacle. The secretion contains no proteid, which is somewhat remarkable, it contains mucin (derived from the gall-bladder), biliary pigments, bile acids, fats, soaps, lecithin, cholesterin, a small quantity of diastatic ferment, and inorganic salts. By standing in the gall-bladder the solids are considerably increased, owing to an absorption of part of the water of the bile. The secretion in the horse contains no mucin, and, according to Ellenberger, there is very little mucin in the bile of sheep.

The dried alcoholic extract of bile contains in the ox 3·58 per cent. of sulphur, sheep 5·71 per cent., and pig ·33 per cent.* The gases found in bile are CO_2, and traces of O and N.

The chief inorganic salts are sodium chloride and sodium phosphate, besides which are found lime, magnesium, potassium, iron, phosphoric and sulphuric acids; the sodium salts always exist in the largest proportion. The iron, which is found as phosphate, is probably derived from the hæmoglobin of the blood during the formation of the bile pigments.

The following analysis of ox-bile is given by Berzelius :†

Water - - - -	90·4
Solids - - - -	9·6
Bile salts - -	8·0, cholesterin 2·5 per cent.
Lecithin, cholesterin, fats, soaps -	
Mucus and pigment - -	·3
Inorganic salts - - -	1·3, including iron ·003 to ·006.‡

* Quoted by Halliburton.

† Quoted by M'Kendrick.

‡ Young, quoted by Halliburton.

The following table is compiled from Ellenberger:

	Ox Bile.	*Sheep Bile.*	*Dog's Bile.*	*Pig's Bile.*	*Horse Bile.*
Water	92·91	86·90	95·3	88·8	Water 95 per cent.
Bile acids	5·61	16·69			Solids 5 ,, ,,
Bile pigments	·32	·29	3·9	8·0	
Fat	·03	(?)			
Mucus	·51	·94	·2	·3	
Salts	1·30	11·83	·6	1·3	

Percentage Composition of the Ash of Ox Bile.

Sodium chloride	27·7	Manganese peroxide	·12
Potassium	4·8	Phosphoric acid	10·45
Sodium	37·7	Sulphuric ,,	6·39
Lime	1·4	Carbonic ,,	11·26
Magnesia	·53	Silica	·36
Iron oxide	·23		

The differences found in the composition of bile, probably depend upon whether it be taken from the gall bladder or from a fistula, the former being the more concentrated.

The fat present in bile is in the form of lecithin, a complex nitrogenous substance united with phosphoric acid, and found in several of the tissues and secretions of the body.

Cholesterin, another singular substance, is an alcohol and not a fat, though from its appearance it has been termed bile-fat, it is found in very regular quantities and forms the principal constituent of certain gall-stones; it is kept in solution in the bile by means of the bile salts.

The **Bile Pigments** are two in number bilirubin and biliverdin, the latter is produced by oxidation from the former. Bilirubin is the colouring matter of human bile and that of carnivora, whilst biliverdin is the pigment of the bile of herbivora. It is not uncommon to find both pigments in the same specimen of bile.

These pigments are insoluble in water but soluble in alkalies; in the bile they are held in solution by the bile acids and alkalies. Bilirubin may be obtained from the gall-stones of the ox in the form of an orange-coloured

powder, which can be made to crystallize in rhombic tablets and prisms. If an alkaline solution of bilirubin be exposed to the air it becomes biliverdin by oxidation, and this latter pigment by appropriate treatment may be obtained as a green powder.

Both colouring matters of the bile behave like acids, forming soluble compounds with metals of the potassium group, insoluble ones with those of the calcium group (Bunge).

On the addition of nitric acid (containing nitrous acid) to the bile pigments a play of colour is observed, this is known as Gmelin's test. In the case of bilirubin the colours pass from yellowish-red to green, then to blue, violet, red, and yellow; each of these colours is indicative of a different degree of oxidation of the original bilirubin. Biliverdin gives the same play of colours excepting the initial yellowish red which is absent.

Although bilirubin has not been obtained from hæmoglobin, there appears to be no reasonable doubt that this is the source of the pigment, for if hæmoglobin be liberated in the blood and enter the serum, bile pigments appear in the urine; further, hæmoglobin may be readily decomposed yielding a proteid and hæmatin, and if this hæmatin be deprived of iron, the residue thus obtained is not very dissimilar in composition to bilirubin. We have previously mentioned (p. 10) that old blood-clots contain an iron free substance known as hæmatoidin, which is practically identical in composition with bilirubin. Part of the iron which is found in the bile probably arises from the hæmoglobin after it has become converted into the iron-free substance bilirubin.

Though biliverdin is the colouring matter of the bile of herbivora, yet the gall-stones found in the ox consist very largely of bilirubin combined with chalk; in the pig the same combination is observed.

Bilirubin is said by Hammarsten to be constantly present in the serum from horse's blood though not in that of the ox, and Salkowski states that it is a normal constituent of the urine of the dog during the summer.

The actual production of bile pigments takes place in the liver, but the means by which the latter organ is furnished with free hæmoglobin for the purpose is still obscure; it has been supposed that through the destruction of red blood cells in the spleen and elsewhere hæmoglobin is liberated, but the subject is one on which very little is definitely known.

The **Bile Salts** are two in number glycocholate and taurocholate of soda; they are formed in the liver by the union of cholalic acid with glycin or taurin, and exist in combination with soda. These salts are found in varying proportions in different animals, thus, glycocholate of soda is largely found in herbivora, taurocholate principally in carnivora, while in the pig hyoglycocholic and hyotaurocholic acids are found. Both salts are soluble in water, have a markedly alkaline reaction, rotate the plane of polarized light to the right, and may be obtained in a crystalline form of highly deliquescent acicular needles.

Glycocholic acid is the chief bile acid in herbivora, it is produced by the union of glycin with cholalic acid; it is diminished by an animal diet, and increased by a vegetable one. Taurocholic acid is produced from taurin and cholalic acid and exists principally in carnivora, though small quantities may be found in the ox. The acid differs from the first characteristically by containing sulphur, by which it shows its proteid origin.

In the intestine the constituents of the bile are absorbed, both acids are decomposed or split up by ferments into cholalic acid and glycin or taurin, the two latter being reabsorbed.

Glycin or glycocoll originates from proteids, and if administered it reappears externally as urea. It cannot be traced in the free state in the body, but occurs with benzoic acid from which combination hippuric acid is formed.

In Pettenkofer's test for bile acids the reaction obtained is due to cholalic acid; the test is performed as follows: A drop of the fluid is placed on a white earthenware surface, and to it is added a drop of a strong solution of

cane-sugar, and a similar quantity of strong sulphuric acid; a beautiful purple-red colour forms, which may be assisted by warming; this test is not solely indicative of bile acids, other substances also give it.

The origin of the bile acids is wrapped in obscurity, taurin is formed in the body probably also glycin, and cholalic acid is formed in the liver. Beyond this we know but little, not even why glycin should predominate in some animals and taurin in others, but we do know that after extirpation of the liver no bile salts are formed.

Bile is secreted under a very low pressure, which is the reverse of what occurs in the saliva; but low as the pressure is (·58 inch of mercury), it is higher than that of the blood in the portal vein, in fact double. If the pressure in the bile duct be raised the bile is reabsorbed, being taken up by the lymphatics of the liver and so conveyed to the blood stream. It is probable that the majority of cases of jaundice are of an obstructive nature, though exceptions to this rule occur.

The secretion of bile is a continuous one, whether the animal be in full digestion or fasting the flow does not intermit like the saliva; but though continuous, it is not uniform, it reaches its maximum in the dog between the second and fourth hours after a meal, this is followed by a fall, and again about the seventh hour by a rise. A similar curve is given by the pancreatic secretion.

In those animals possessing a gall-bladder this receptacle is filled with bile during abstinence, or if it be empty it is filled even during digestion. The bile is propelled along the bile ducts by a contraction of the muscular coat of the tubes, but doubtless both the forcing onward of the bile and the circulation through the liver are largely assisted by the respiratory movements, during which the liver is compressed between the abdominal viscera and the diaphragm. The gall-bladder is emptied through the muscular contraction of its walls; the reflux of bile from the biliary duct to the gall-gladder is supposed to occur either from a contraction of the duct or from a constriction

of that portion of it penetrating the wall of the intestine, by which means the bile is driven back through the cystic duct to the gall-bladder. Under any circumstance the whole of the bile during abstinence is not forced into the gall-bladder, but a certain proportion of it continues to trickle into the intestine.

Quantity of Bile.—The amount secreted varies, but is greater in herbivora than carnivora. Colin's experiments gave him the following amounts as hourly secretions:

Horse	-	-	$8\frac{3}{4}$ ozs. to $10\frac{1}{2}$ ozs. per hour.
Ox	-	-	$3\frac{1}{2}$ ozs. to $4\frac{1}{4}$ ozs. ,, ,,
Sheep	-	-	$\frac{1}{4}$ oz. to $5\frac{1}{2}$ ozs. ,, ,,
Pig	-	-	$2\frac{1}{2}$ ozs. to 5 ozs. ,, ,,
Dog	-	-	$\frac{1}{4}$ oz. to $\frac{1}{2}$ oz. ,, ,,

The flow of bile is influenced by the nature of the food, proteid products in the portal vein stimulate the flow, while fat which enters the system by another channel than the portal vein has no such effect. An acid fluid passing over the intestinal opening of the bile duct produces a flow of bile.

The nervous influence controlling the secretion of bile is unknown, the nerve supply is from the vagus and solar plexus. Stimulation of the medulla, spinal cord, or splanchnics, stops or checks the flow.

The **Use of the Bile** from a digestive point of view is very disappointing, inasmuch as it does not digest in the sense that pepsin and trypsin do. That it is intimately connected with the function of the pancreas would appear from the fact that the secretions are poured out either close together in the bowel, or, as in some animals, by a duct practically common to the two glands.

As the horse possesses no gall-bladder the secretion as fast as it is prepared is poured into the intestine; not so with the ox, sheep, pig and dog, where the bulk of it is stored up in a capacious receptacle until required. The reason offered for the horse having no gall-bladder is that as digestion under ordinary circumstances is always going

on, the bile is poured into the bowel as fast as it is secreted, but that in the case of other animals it is only poured out to any extent when the contents of the stomach are passing out into the intestine; this explanation, however, does not meet all the difficulties of the case.

The bile being alkaline its first action on the chyme is to precipitate the acid albumin which has escaped the process of peptonizing in the stomach. One effect of this is probably to protect the pancreatic ferments from the pepsin of the gastric juice, and further, to delay the progress of the chyme along the bowel, by which means the pancreatic juice has time to act.

On proteids the bile has no digestive action; on fats, however, it has a solvent and emulsifying effect, being more active in the presence than in the absence of pancreatic juice. Bile cannot split up fats into fatty acids and glycerine as the pancreas does, but if free fatty acids are present the bile salts are decomposed, their soda set free, and soluble soaps formed; the soaps so formed assist in rendering the emulsifying effect of the bile permanent and the absorption of fat much easier. Fat will not readily pass through a membrane, but if the latter be first moistened with bile the passage is readily effected. In Voit's experiments on dogs it was found that by cutting off the flow of bile to the intestine the absorption of fat fell from 99 per cent. to 40 per cent.

According to Hofmeister the bile of the ox, sheep, and horse, converts starch into sugar, whilst the bile of the pig and dog possesses no such action or only to a limited extent.

It has been said that bile has an action on the intestinal contents, keeping them from putrefaction and promoting peristalsis, for it has been found that when it is prevented from entering the intestines, constipation and extreme fœtor of the intestinal contents result. Bunge states that the clay-coloured fæces obtained in jaundice are due to the presence of unacted-on fat, the fat encloses the proteids which putrefy, hence the odour. The bile, he states, is

not an antiseptic, but acts as a natural purgative and keeps up intestinal peristalsis, and by so doing hurries the food out of the system before it undergoes putrid decomposition.

Whatever value the bile may be, it appears certain that its working constituents are the bile salts.

Fate of the Bile.—Some of the constituents of the bile are broken up in the bowel, for instance, the bile acids yield cholalic acid setting free glycin and taurin; the two latter being absorbed again are carried to the liver, and may probably there excite the further secretion of bile acids, while cholalic acid is excreted with the fæces. It has been suggested that the rapid secretion of bile which follows the first outpouring into the bowel, is due to the re-absorption of the glycin and taurin.

In the bowels the pigments also undergo change, yielding stercobilin (the colouring matter of the fæces in carnivora and omnivora) and urobilin (the colouring substance of the urine).

Glycogen.

It is quite certain that the largest gland in the body must have some other function than that of the secretion of a fluid of comparatively unimportant digestive power, and such is the case; the liver manufactures and stores up in its cells a peculiar substance known as glycogen or animal starch. Though glycogen is spoken of as animal starch, yet in some respects it differs from vegetable starch; thus, it is soluble instead of insoluble in cold water, and it is stained reddish-brown instead of blue by iodine.

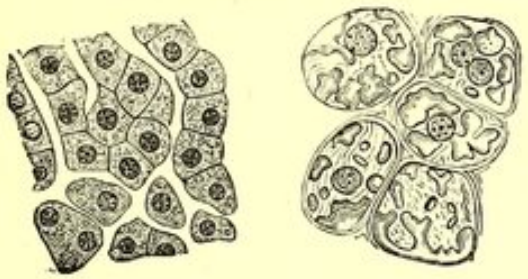
The literature of glycogen is extensive, perhaps no substance has given rise to greater controversy; all we can attempt here is to give a general and brief outline of a complicated subject on which much diversity of opinion has existed.

The sugar in the food, or that derived from starch-conversion, finds its way by means of the intestinal vessels into the portal vein, from here it passes into the liver;

under ordinary circumstances it is stored up in the liver as glycogen, being, in fact, reconverted into a kind of animal starch, and gradually doled out to the system as sugar when required.

The liver regulates the amount of sugar which should pass into the blood, so much and no more is admitted to the circulating fluid, the amount varying between ·05 and ·15 per cent. The sugar in the blood of the ox was estimated by C. Bernard at ·17 per cent., in the calf ·1 per cent., and in the horse ·09 per cent. When the liver fails to regulate the amount of sugar in the blood diabetes is produced.

The glycogen which is thus stored up in the liver for future use may be made to disappear by starving the animal, the material in this way escaping from the liver as sugar and passing into the general circulation through the hepatic veins; if food, particularly carbo-hydrate, be now given the store of glycogen is rapidly replenished, and the sugar-liberating functions once more established (Fig. 28).



FASTING. AFTER FOOD.

FIG. 28.—LIVER CELLS FROM THE DOG DURING FASTING AND AFTER FOOD. (WALLER, AFTER HEIDENHAIN.)

During fasting the cells contain no glycogen, after receiving food they become swollen with this substance.

This storing up of starch and its subsequent utilization is very closely allied to a similar process in the vegetable kingdom; the starch in the leaves of plants may pass down the stem as sugar and so nourish the plant and again form starch. It is certainly curious to observe that starch must be first converted into sugar before the bloodvessels of the

bowel can take it up, then in the liver once more converted into a kind of starch, and lastly again into sugar before being finally used by the tissues.

The sugar formed from starch in the bowel is maltose, while that formed in the liver from glycogen is glucose. This conversion of glycogen into glucose is due to the activity of the protoplasm of the liver cells (Noël Paton),* and not necessarily to the presence of a ferment, such as until lately was believed to be essential to the conversion. A ferment capable of converting starch into sugar has been described as existing in blood and lymph, but as a matter of fact all the tissues are capable of yielding a starch-converting ferment.

The total amount of glycogen obtained from a given quantity of food is not wholly stored in the liver, as the latter organ cannot contain more than about 10 per cent. of this substance, which would represent only a small amount of the soluble carbo-hydrates passing into the blood. We know as a fact that the liver, having taken up all the sugar it can from the portal vessels and converted it into stored-up glycogen, allows the balance to pass through the hepatic veins into the general circulation as sugar, and that it is deposited in other organs (principally the muscles) as glycogen for future use. The muscles of the horse contain in this way a considerable quantity of glycogen, even after nine days' starvation from 1 per cent. to 2·4 per cent. were found by Aldehoff.†

The glycogen thus stored up in the muscles is utilized during the act of contraction, and in this way much of it may disappear; but its presence in muscle is not essential to contraction, for there are muscles in which no glycogen is found, and in which active contraction takes place.

In the muscles of the embryo before striation has occurred the amount of glycogen existing is something considerable, as much as 40 per cent. of the dry material of the embryo muscle consists of this substance; as striation

* Philosophical Transactions, 1894.

† Quoted by Bunge.

appears the glycogen leaves the muscles to a great extent and the liver takes on the process of production.

The existence of glycogen in the embryonic muscle points to its use in active nutrition and rapid growth, further it is found in the placenta where it is used for the nourishment of the fœtus, and also in rapidly developing cells such as some found in cartilage and the white cells of the blood, in all these and other places it is simply stored for future requirements.

In the adult the chief use of glycogen is to supply muscular energy and animal heat, but Foster warns us against regarding the glycogen of muscle as of any value in the production of muscular energy until it has actually become part of the muscle, as he expresses it, 'It cannot be fired off in a contraction while it lies as raw glycogen, or even as dextrose, in the interstices of the muscle fibre.'

The source of glycogen is a disputed point, carbohydrates no doubt contribute largely to its production, but there is very good reason to believe that proteids also assist in its formation. Every proteid consists of a nitrogenous and a non-nitrogenous portion, this latter may be available for glycogen production, and quite lately Pavy has shown that the non-nitrogenous moiety of the proteid may be split off by a laboratory process, and that from it a something resembling sugar may be obtained.

Further evidence of the formation of sugar from proteid is afforded by the disease diabetes, in some forms of which as much sugar is passed on a proteid as on a carbo-hydrate diet. If a starving animal be rendered diabetic by the administration of phloridzin, more sugar is excreted by the urine than is contained in the drug, and this sugar is believed to originate from the proteid tissues.

Most observers agree that fat takes no part in the production of glycogen.

When the liver is removed from the body the glycogen in it diminishes and sugar increases; this sugar is considered to be formed in the first instance by the action of the living liver cells, and later on by the activity of an enzyme.

If the liver on removal from the body be boiled no sugar appears but glycogen is found, as by the process of boiling both the activity of the cells and the production of the ferment are prevented. Paton has shown that by pounding the liver with fine sand, so as to destroy the liver cells, the post mortem conversion of glycogen into sugar is stopped.

If arsenic be administered to an animal the power of storing up glycogen in the liver cells is prevented, and if glycerine be given it prevents the conversion of the liver glycogen into sugar, so that the post-mortem conversion of glycogen does not take place; further, glycerine prevents the diabetes which follows an injury to the medulla of the rabbit.

It would appear that a provision exists in the system for the destruction of any glucose in the blood in excess of the requirements. A glucose-destroying ferment has recently been described in the blood, and support is given to this view by the fact that extirpation of the pancreas causes diabetes; it is probable, therefore, that a glycolytic ferment is formed in this gland.

Diabetic Puncture.—Bernard discovered that if the floor of the fourth ventricle be punctured in a well-fed rabbit, the glycogen stored up in the liver was rapidly converted into sugar and passed off in the urine; no sugar or very little followed puncture in an ill-fed animal.

The explanation afforded of this diabetic puncture is that paralysis of the vessels occurs leading to engorgement of the liver, but this is not considered by some to be satisfactory, for if the vessels of the liver be dilated by dividing the splanchnics no diabetes occurs, in fact division of the splanchnics prevents the puncture of the medulla from producing diabetes.

Kaufmann* has recently shown that if the nerves of the liver in the dog be cut diabetes does not result, though it follows on puncture of the medulla, but the puncture of

* Quoted by N. Paton, 'The Physiology of the Carbo-hydrates,' *Edinburgh Medical Journal*, December, 1894.

the medulla will not succeed if the nerves of the pancreas be previously divided. In the same way, if the nerves of the pancreas be divided and those of the liver left intact glycosuria is caused.

Kaufmann believes that Bernard's puncture has a double action, (1) stimulating the formation of sugar in the liver, and (2) inhibiting the 'internal secretion of the pancreas,' viz., the sugar-destroying substance produced by this gland.

In our remarks upon the origin and use of glycogen we have represented the views of Claude Bernard, who nearly fifty years ago discovered this curious substance; these views have not always been accepted, and in this country Pavy has been their most obstinate opponent. This observer regards Bernard's teaching as wrong, he says that the liver is not the source of sugar, and that instead of throwing sugar into the circulation it checks its progress by abstracting it from the portal blood; if this abstraction fails to take place diabetes results. The glycogen which is stored up in the liver Pavy considers is not doled out to the system as sugar, but is applied to the construction of proteid, or of fat, or both. Finally, he states that the glycogenic theory is incompatible with the observed order of things in the animal economy.*

Probably the majority of physiologists accept the teaching of Claude Bernard.

Further Uses of the Liver.

We have studied two uses of the liver, viz., the formation of bile and the storing up of glycogen, but there are other uses of this gland to consider.

The material carried by the portal vein to the liver contains besides peptones some other ultimate products of proteid digestion, viz., leucin, tyrosin, and other bodies; these are conveyed to the liver, and the leucin contributes to the formation of urea. Possibly many of the antecedents

* Croonian Lectures, *British Medical Journal*, July, 1894.

of urea in the body are in the liver converted into this substance. This is a point to be dealt with more fully in the chapter on the urine, all we wish to impress here is the share the liver takes in converting into urea and uric acid certain nitrogenous products.

As the result of proteid decomposition in the intestinal canal certain aromatic compounds are formed; these are united with sulphuric acid and got rid of by the kidneys as conjugated sulphuric acids. In this combination the originally poisonous proteid products are converted into non-poisonous ones, and this change is effected in the liver (Bunge). Here we have a very important function of the liver demonstrated, viz., as a neutraliser of poisons introduced into the blood by the intestines. It is a noteworthy fact that many metallic poisons are also arrested in the liver, for example mercury and arsenic.

The numerous and complicated changes produced by the liver may thus be summarised: It forms bile, regulates the supply of sugar to the system, storing up as glycogen what is not required; it guards the systemic circulation against the introduction of certain nitrogenous poisons, such as ammonia, by converting them into urea and uric acid, and against other poisons of proteid origin by converting them into harmless products, by conjugation with alkaline sulphates.

The Pancreas.

The fluid secreted by the pancreas performs certain important functions in digestion. It is remarked by Bunge that there is scarcely any animal which does not possess a secretion allied to the pancreatic, even those invertebrates without a peptic or biliary apparatus are in possession of one. From the resemblance of the pancreas to the salivary glands it has been termed the abdominal salivary gland.

The pancreatic fluid from herbivora can only be obtained with extreme difficulty; to establish a pancreatic fistula in the horse is a formidable operation, necessitating an

incision from the sternum to the pubis and the turning back of the bowels. Colin has established these fistulæ both in the horse and ox, but the profound impression on the nervous system produced by such extensive interference, must considerably affect the character of the secretion and the amount manufactured.

Pancreatic fluid is an alkaline, clear, colourless fluid like water, and though viscid in some animals is not so in the horse. It has a saltish unpleasant taste, and a specific gravity of about 1010; the viscid secretion of the dog has a specific gravity of 1030.

The following analysis of the fluid in the horse is given by Hoppe-Seyler :*

Water	982·53			
Solids	17·47	Organic matter	8·88,	containing 8·6 of ferments.
		Salts	8·59,	,, much sodium phosphate.
	1000·00			

Schmidt found the fluid of the dog to have the following composition :

Water	900·0			
Solids	99·2	Organic matter	90·4	
		Salts	8·8,	containing much sodium chloride.

The salts present are sodium chloride in abundance, potassium chloride in traces, sodium carbonate and phosphate, calcium and magnesium phosphates in small quantities. The organic solids are remarkable for the amount of proteid present in them, and for the extreme variations in the amount in different animals, for example 90 per cent. in the dog and 9 per cent. in the horse.

Uses of the Secretion.—The pancreatic juice is poured into the bowel in the horse and sheep by an opening common to the pancreas and liver; in the ox, pig, and dog, the two are separate, and open within a short distance of each other.

* Quoted by Halliburton.

Pancreatic juice is essentially a digestive fluid, acting on all the elements of food, viz., proteids, fats, and carbo-hydrates ; all of these undergo certain changes, the proteids are converted into peptones, the fats into fatty acids and glycerin, and the carbo-hydrates into sugar. These changes are so definite that it has been assumed, with very good reason, that each is brought about by a distinctive enzyme, though every attempt to isolate such has failed. It is convenient, however, to speak of them as separate ferments, the total amount of which in the horse has been estimated by Hoppe-Seyler to be 8·6 per 1000, forming, in fact, nearly the total organic matter existing in the secretion.

The ferments found in the pancreatic fluid are :

Trypsin—which converts proteids into peptones.
Amylopsin—which converts starch into sugar.
Steapsin—which splits up fat into fatty acids and glycerin.

A milk-curdling ferment has been described, but in adult digestion there can be but little need for one.

The action of the ferment on proteids is much the same as we have previously studied in the gastric juice, proteids being converted into peptones, especially those difficult of conversion in the stomach, while the hemi-peptones of the stomach are carried a stage further and split up into leucin and tyrosin. There are certain important differences which serve to distinguish between proteid digestion in the stomach and that in the intestines, thus :

1. Peptic digestion is an acid one, pancreatic is essentially alkaline.

2. During the action of the ferment the fibrin digested by trypsin does not swell up as in peptic digestion ; further, it is eroded by the action of trypsin rather than dissolved as in peptic digestion.

3. The outcome of pancreatic digestion is an alkali-albumin and not an acid one as in the stomach ; the proteids in the case of pancreatic digestion undergo a change not only into peptones, but a portion of them are further converted into leucin, tyrosin, and other substances. The production of indol, phenol, and skatol which gives to

pancreatic proteid digestion its offensive odour, cannot be regarded as due to the pancreas but to the presence of micro-organisms and consequent putrefaction.

By these differences it is easy to distinguish between a peptic and pancreatic digestion ; it is very remarkable that peptone products can be obtained through the action of two such apparently opposite secretions as gastric and pancreatic juice.

The action on starchy food is to convert it into sugar, and this it is capable of doing either on boiled or unboiled starch with extreme rapidity; 15½ grains of pancreatic juice can convert in half an hour 71 grains of starch into sugar ; the form of sugar produced is maltose, with a little glucose. The pancreatic fluid has no action on cane-sugar.

On fats the action is very marked, the fats are first converted into an emulsion by which means the particles of oil are finely divided ; in the next stage the fat itself is split up into its constituents, viz., fatty acids and glycerin, and the former in the presence of an alkali forms soaps. The alkaline salts of the pancreatic juice, especially the sodium carbonate, assist in this action. It is said that the pancreatic juice of the horse emulsifies less completely than that of other animals.

Fats are chemically neutral in reaction but if rancid they are acid ; if carbonate of soda be added to a fat containing even a small proportion of free fatty acid, the latter unites with the alkali and forms a soap, this soap envelops the fat globules and a true emulsion results. If the fat acted upon be a neutral fat, nothing less than a free alkali, such as caustic potash, can liberate the fatty acids.

Pancreatic juice, however, can attack perfectly neutral fats, splitting them up into free fatty acids and glycerin, and this it is enabled to do by means of the fat-splitting ferment it contains.

The most important action on the fat is probably the formation of the minute oil globules or emulsionising, by which means rapid absorption through the intestinal villi occurs.

Colin's experiments on horses and other animals, showed that fats were as perfectly absorbed from the intestine in the entire absence of pancreatic juice as in its presence, and this he attributed to the alkaline intestinal fluid.

The ferments of the pancreas which bring about all the changes we have described do not exist ready formed in the gland, but they are produced from a mother-substance termed Zymogen, which is manufactured in the cells of the gland; this zymogen by decomposition yields the ferments.

The **changes occurring in the cells** of the gland correspond very closely with those described in the salivary secretion. During the period of rest the gland is rapidly forming the mother-substance of the ferments, which can be seen as minute granules filling the cells, during activity the gland is discharging its manufactured products. In the herbivora the gland is practically constantly secreting, but periods of rest and activity still occur for the reason that all the lobes are not active at the same time.

When a pancreas or lobe of a pancreas has been at rest for some time the cells forming it are rendered very indistinct, the lumen of the alveolus is nearly obliterated by the swollen condition of the cells, and the latter are seen crowded with granules, which are so arranged as to form on the margin next the basement membrane a clear or fairly clear zone, and within this an intensely granular zone (Fig. 29, *A*). When activity commences the granules appear to pass centrally towards the alveolus, leaving the cell comparatively clear excepting that portion immediately abutting on the alveolus, which even in the exhausted condition is still granular. These changes have resulted in the cells becoming distinct and clearly defined from each other, and moreover, as they have emptied their granular contents into the alveolus as pancreatic secretion, they have consequently become much smaller; the narrow clear zone seen in the resting gland now becomes a broad one, the previously choked alveolus is readily defined, whilst the nucleus of the cell, which was hidden in the charged condition, is now distinctly seen (Fig. 29, B). These changes have been

worked out on the pancreas of the living rabbit by Kühne and Sheridan Lea.

Amount of Secretion.—From the investigations of Colin and others we know that in all animals the secretion of pancreatic juice is continuous though not uniform; in ruminants the largest secretion is towards the end of rumination; in the dog the maximum is reached between the second and fourth hours after feeding, this maximum is followed by a fall and about the seventh hour by a rise; it will be remembered that the bile gives a similar curve.

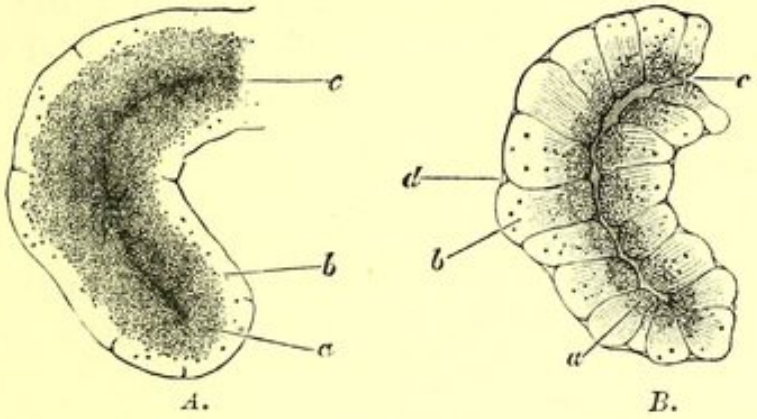


FIG. 29.—A PORTION OF THE PANCREAS OF THE RABBIT (KÜHNE AND SHERIDAN LEA). A, AT REST; B, IN A STATE OF ACTIVITY (FOSTER).

a, The inner granular zone, which in A is larger and more closely studded with fine granules than in B, in which the granules are fewer and coarser. *b*, The outer transparent zone, small in A, larger in B, and in the latter marked with faint striæ. *c*, The lumen, very obvious in B but indistinct in A. *d*, Indentation of the junctions of the cells seen in the active but not in the resting gland.

In the ox the maximum secretion is between 7 and 9 ozs. per hour, in the horse the hourly secretion is much the same, in the sheep and pig about $\frac{1}{4}$ oz. per hour, and in the dog still less.

There is no ratio between the size of the animal, the weight of the gland, and the amount of pancreatic fluid secreted; relatively carnivora secrete more than herbivora.

The pressure under which the pancreatic juice is secreted is low, it is said to be equal to ·67 inch of mercury which is very little greater than that of the bile.

Pancreatic Diabetes.—Nearly forty years ago Colin concluded from his experiments on dogs, that the entire pancreas might be removed without subsequent ill effect. This is now known to be incorrect, for if every trace of the pancreas be removed the animal dies from diabetes; the explanation of Colin's dogs surviving, is doubtless due to the fact that small pieces of the gland were left behind which were sufficient for the purpose of nutrition.

Shortly after the pancreas is removed there is a great increase in the amount of urine, and sugar is found in it, there is also an increase in the nitrogen of the urine; great muscular weakness and wasting follow, and a fatal result ensues.

It is suggested by some that the increase of sugar is due to an increased formation, and as the blood will not hold more than ·3 per cent. of sugar without excreting it with the urine, the glycosuria is accordingly due to this fact, especially as ·3 to ·46 per cent. of sugar have been found in the blood in this disease.

Other observers believe the diabetes is due to the want of a glycolytic ferment, which in a normal state is always being formed in the pancreas, from which it is poured into the blood through the lymph stream and there destroys the sugar (see p. 202). One strong piece of evidence in favour of the existence of such a ferment, is that if pieces of pancreas be grafted into the abdominal walls after the operation of extirpation, the development of diabetes is hindered.

Nervous Mechanism.—The pancreas is supplied by the solar plexus and probably by branches of the vagus. If the medulla or spinal cord be stimulated an increased secretion follows; if the central end of the vagus, sciatic, or other efferent nerve be stimulated the secretion stops. Nothing is known for certain of the nervous mechanism of pancreatic secretion.

CHAPTER VIII.

ABSORPTION.

Lymph.

Lymph may be regarded as the material by which the tissues are directly nourished, and by which effete material is collected from them and taken back into the blood; further, there are certain non-vascular tissues, such as the cornea, cartilage, etc., where the lymph circulation is the only means by which the part is supplied with nourishment. Speaking generally, however, the lymphatic system may be described as the drainage system of the body, in contradistinction to the blood or irrigating system.

The tissues are bathed in lymph, which is contained in the lymphatic spaces existing between the capillary bloodvessels and capillary lymph-vessels. There is a constant passage of material from the blood into the tissues, and from the tissues through the capillary lymphatics into the main lymphatics, and thence through the thoracic duct into the venous system.

The **Lymph Spaces** are irregular passages in the connective tissue, the larger ones being lined by epithelioid plates of a peculiar irregular outline; these spaces exist outside the bloodvessels, and the material they contain, viz., lymph, finds its way from the bloodvessels into the lymph space. From the lymph spaces the fluid reaches the lymph capillaries, but the means by which it gets there is not clear, for it appears certain that excepting in a few cases there is no

direct communication between the space and the capillary. In the vessels of the brain a peculiar arrangement is present, the lymphatic vessel surrounds the artery and obtains its lymph direct; such are known as peri-vascular lymphatics.

The lining of the **Lymph Capillary** is composed of the same epithelioid plates with irregular outline which are found in the spaces, and it is believed that at the junction of the plates, crevices or intervals may exist through which fluid may find its way by the simple process of transudation. From the lymph capillary begins the **Lymphatic Vessel** which in addition to an epithelioid lining has also a muscular coat, more marked in the large than in the small vessels, and a connective-tissue covering. In the interior of these vessels valves are found which produce a beaded appearance when the lymphatic is distended.

The whole of the lymphatics of the body converge towards a central vessel, those from the left side of the head and neck, the left fore limb, the chest, abdominal cavity, and hind limbs, open into the thoracic duct at different points, and this in turn opens into the anterior vena cava; whilst from the right side of the head and neck, and right fore limb, the vessels collect and pour their contents by a separate duct into the same vein. The thoracic duct is nothing more than a large lymphatic vessel, possessing the same structure as the lymphatic vessels above described, the muscular coat especially being well marked.

The thoracic duct receives the lymph not only from the ordinary tissues but also from the intestinal canal; during starvation the mesenteric lacteal vessels convey to the duct a fluid which is essentially lymph, but during digestion this clear fluid is replaced by a turbid white fluid known as chyle; at this period then the lacteal vessels are carrying not only lymph but also the products of digestion.

The **Serous Cavities** of the pleura, pericardium, and peritoneum, may be looked upon as large lymphatic spaces; the fluid they contain is lymph, and they are in direct communication with lymphatic vessels, especially those of

the diaphragm. In the diaphragm slits or stomata exist, and into these the lymph readily finds its way, being aspirated into the vessels during the respiratory movements of this muscle; so readily is this effected that the diaphragm may be artificially injected in a recently dead subject, by placing some milk on its surface and establishing artificial respiration.

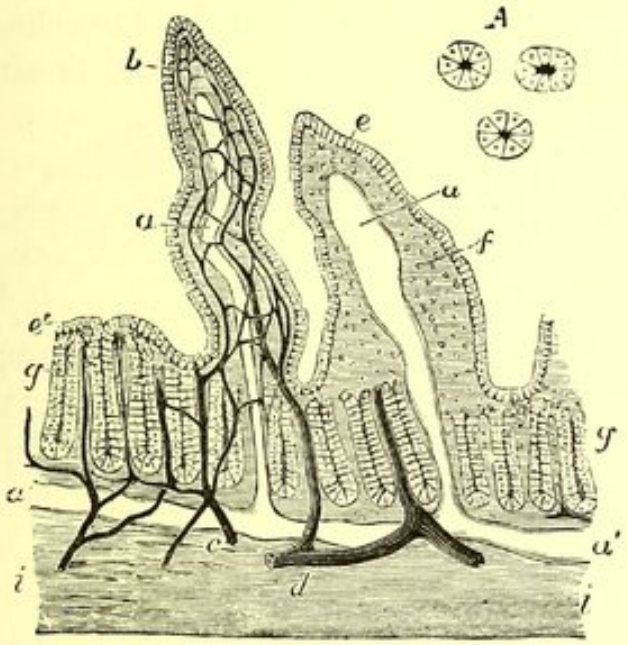


FIG. 30.—SECTION OF THE MUCOUS MEMBRANE OF THE SMALL INTESTINES, SHOWING THE VILLI. (LOWNE.)

a a, The lacteal vessels; *b*, the capillaries of the villus terminating at *c* in the veinlet *d*; *e*, the epithelium of the villus; *f*, adenoid tissue; *g*, Lieberkühn's glands; *i*, submucous tissue. *A*, transverse section of Lieberkühn's glands.

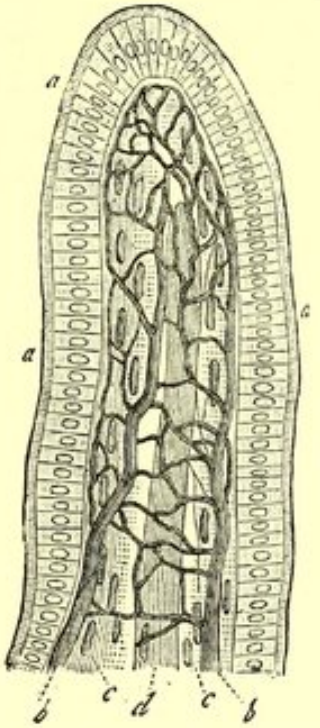


FIG. 31.—A SINGLE VILLUS HIGHLY MAGNIFIED. (LOWNE.)

a a, Epithelium with striated border; *b b*, bloodvessels; *c c*, non-striated muscle fibres; *d*, lacteal vessel.

We have mentioned that in the ordinary tissues the radicles of the lymph vessels are the lymph spaces, but in the wall of the small intestines, the origin of the lymph vessels are highly differentiated structures known as villi and solitary glands.

The Villi (Figs. 30 and 31) are innumerable projections from the surface of the mucous membrane shaped like minute fingers; in the interior and central part of the

villus is a vessel termed the lacteal, it may be single or multiple, straight or branched, and at the base of the villus it opens by a valvular arrangement into the lymphatic system. Surrounding the lacteal is a network of capillary bloodvessels which is better marked close to the apex of the villus than below, and filling up the cavity of the villus not otherwise occupied by vessels is a peculiar structure, found especially in lymphatic glands, known as adenoid tissue; this tissue is relatively larger in the villi of carnivora than in herbivora (Fig. 32). Covering the entire villus is a basement membrane on which is set

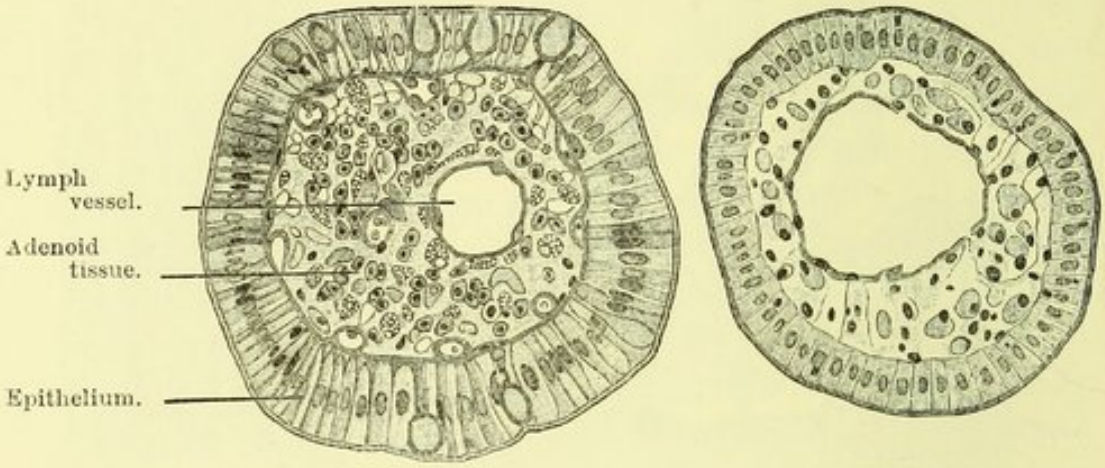


FIG. 32.—TRANSVERSE SECTION OF VILLI OF CARNIVOROUS AND HERBIVOROUS ANIMALS. (WALLER, AFTER HEIDENHAIN.)
The large cells in the epithelial zone of the dog are the goblet cells.

a layer of columnar cells, so placed that their narrowest end is next the basement membrane and their broadest next the interior of the intestine. The cells at their narrowest part are in touch with the adenoid tissue of the villus.

Each cell contains a nucleus, and on that edge next the interior of the bowel is a clear band bearing fine striations. Lying between the columnar cells are others which from their shape are spoken of as 'goblet cells'; by means of a pore they extrude their contents into the intestine, which consists of a transparent material known as mucin. Within the villus are bands of involuntary muscle fibre, by the contraction of which certain movements are obtained.

This, then, comprises the essential features of an intestinal villus, the function of which will be dealt with presently.

The other lymph radicles found in the intestine are the *Solitary Follicles* which are found studding the whole of the mucous membrane of the small intestines; these solitary follicles are at certain places in the ileum collected into masses where they are known as *Peyer's Patches.*

The **Solitary Follicle** is essentially a lymphatic structure and is not concerned like the villus in absorbing anything from the food; it consists of a mass of adenoid tissue, the network of which is filled with leucocytes, within the network are capillary vessels, and surrounding the whole is a space across which branches of the adenoid network pass; this space is known as a *lymph space* or *sinus*, it is lined, liked those we previously described, with epithelioid plates and opens into a lymphatic vessel. The blood brought to one of these masses passes through the vessel wall, and through the adenoid tissues to the lymph sinus; on its way through the adenoid tissue some of the corpuscles found in the meshes of the network are added to it and become lymph corpuscles. The corpuscles in the network give indication of growth and development, and many are seen in a state of division, in fact, there can be no doubt this is one seat of their manufacture, from which they are carried into the blood stream through the lymphatic system.

The lymphatic vessels in their course pass through bodies known as **lymphatic glands**, entering at one side and emerging at the other, and experience shows that in the passage through these glands the lymph has corpuscles added to it which ultimately become white blood corpuscles, and moreover it becomes coagulable.

The gland consists of a capsule within which is a mass of adenoid tissue divisible into a cortex and medulla. The capsule sends in bands of tissue which divide the gland into septa; the septa form spaces or alveoli, those in the cortex being much larger than those in the medulla; the

alveoli contain a mass of adenoid material. The latter, however, does not occupy the entire alveolus, but fills up the centre, and is maintained in position by bands passing to the wall of the alveolus, in this way a space or channel is formed between the mass of adenoid tissue and the wall of the alveolus, this channel is known as a lymph

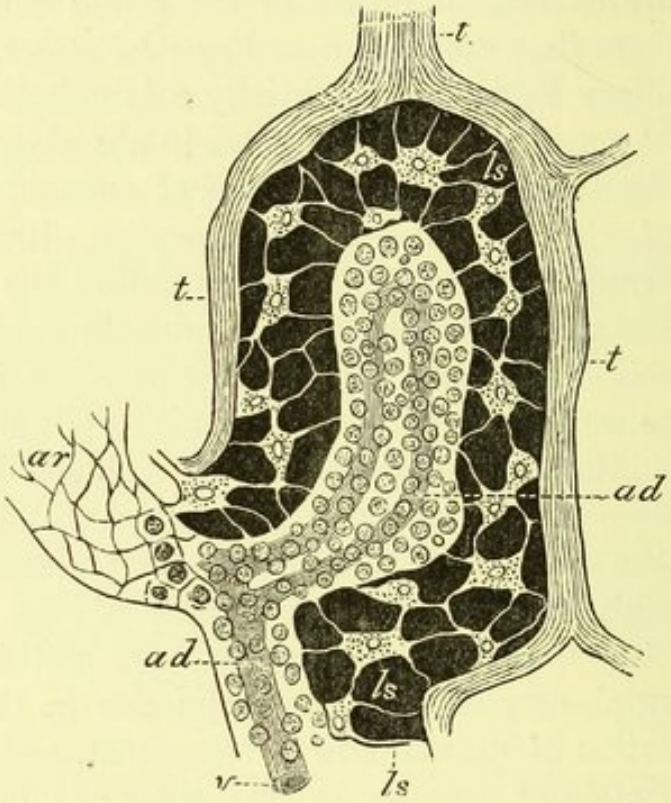


Fig. 33.—Diagrammatic Section of Lymphatic Gland.

ad, Adenoid tissue containing lymph corpuscles, excepting to the left of the figure *ar* where they are omitted in order to show the adenoid reticulum.* In the adenoid tissue may be seen a capillary vessel *v*. Outside the core of adenoid tissue is the lymph sinus or space *ls*, across which runs branched nucleated corpuscles, which are simply an open network of adenoid tissue. These corpuscles are shown on a black ground in order to better distinguish the lymph space. Surrounding the whole is the trabecular framework *t*.

channel or sinus (see Fig. 33). It is through the lymph sinuses of the cortex that the gland is in direct communication with the efferent lymphatic vessels. In the mass of adenoid tissue is found a network of bloodvessels, the tissue itself being filled with corpuscles, and these are

* It was intended to represent the region *ad* as densely packed with corpuscles; this the figure fails to convey.

also found in the bands which extend across the lymph sinus. The medulla of the gland has no essential difference in structure from the cortex, excepting that the reticular network is more complex, closer, and more extensive; from the medulla arises the efferent lymphatic vessels.

Lymph is a slightly yellow-coloured fluid, alkaline in reaction, with a specific gravity of 1012 to 1022, and possessing the power of spontaneous clotting. The clot it yields is not so firm as that of blood, and takes longer to form, moreover, the bulk of fibrin is much smaller. Lymph may be regarded as blood minus the red corpuscles, it contains, therefore, the proteids of that fluid, cells resembling the white cells of the blood, extractives, salts, and gases; the fluid in which these are contained may be spoken of as lymph plasma.

The gases consist principally of carbonic acid, which is greater than in arterial, but less than in venous blood, a small quantity of nitrogen, and traces of oxygen; in the dog the gases consist of CO_2 40 per cent., N 1·2 per cent., and traces of O.

In the lymph plasma the fibrin factors are found, hence the power the fluid possesses of spontaneous clotting.

Amongst the extractives some observers have found urea, a substance which exists more largely in lymph than in blood, and which is said to be always present in the cow. The salts are distributed much as those in blood, viz., potash and phosphoric acid in the corpuscles, and soda in the serum.

The lymph cells possess amœboid movements and are identical with white blood cells; they are more numerous in those vessels which have passed through lymphatic glands, as it is these latter which principally add the corpuscles to the lymph. The cells consist of proteids, lecithin, cholesterin, and fat, and their nuclei contain nuclein. Owing to their power of movement they are able to pass through the bloodvessels into the tissues and *vice versâ*. The proportion of lymph corpuscles to fluid is about the same as the proportion of white corpuscles to blood.

The lymph corpuscles originate in the lymphatic glands, the mucous membrane of the intestines, the red marrow of bone, and in the spleen; in the body they undergo decay and death, and are then broken up and help to form the fibrin factors.

ANALYSIS OF THE LYMPH OBTAINED FROM THE LYMPHATICS OF A HORSE* (C. SCHMIDT).

Constituents in 1,000 *parts.*	I.	II.
Water	963·93	955·36
Solid matters	36·07	44·64
Fibrin, Albumin, Fats and fatty acids, Other organic matters	28·84	34·99
Inorganic matters	7·22	7·47
Sodium chloride	5·43	5·67
Sodium	1·50	1·27
Potassium	0·03	0·16
Sulphuric acid	0·03	0·09
Phosphoric acid combined with alkalies	0·02	0·02
Calcium and magnesium phosphate	0·22	0·26
In the serum from 1,000 parts of lymph Schmidt found:		
Albumin, Fats and fatty acids	23·32	30·59, 1·17
Other organic matters	4·48	1·69

ANALYSIS OF THE LYMPH OF A COW (C. SCHMIDT):

Serum	95·52
Clot	4·42

	In 100 *parts serum.*	*In* 100 *parts clot.*
Water	95·76	90·73
Fibrin	—	4·86
Other albumins	3·20	—
Fats	0·12	3·43
Organic matter	0·17	—
Salts	0·74	0·96
Sodium chloride	0·56	0·60
Soda	0·13	0·06
Potash	0·01	0·10
Sulphuric and phosphoric acids and earthy phosphates	0·04	0·23

* I am indebted for these analyses of lymph and chyle to Gamgee's 'Physiological Chemistry' and Colin's 'Physiologie Comparée.'

The chief points brought out by analysis are the small proportion of solids in lymph compared with blood, there being practically half the amount of total solids, half the amount of proteid, and a larger proportion of water.

In can be easily understood that the chemical composition of the lymph will depend upon the nature of the food supplied, and also the sources from which it is obtained. The following table illustrates the differences in the lymph of the horse, depending on its source :

	Lymph collected from the Femoral Vessels. (Gmelin.)	*Lymph collected from the Cervical Vessels. (Leuret and Lassaigne.)*	*Lymph collected from the Vessels of the Foot. (Geiger.)*	*Lymph from the Vessels of the Foot of an Ass. (Rees.)*
Water - -	964·30	925·00	983·70	965·36
Solids - -	35·70	75·00	16·30	34·64
Fibrin - -	1·90	3·30	0·40	1·20
Albumin and extractives -	23·17	57·36	8·90	27·59
Fats - -	traces		traces	traces
Inorganic matters -	10·63	14·34	7·00	5·85

The **Quantity of Lymph** in the body is very difficult to arrive at, and varies considerably; 13¼ lbs. of lymph have been collected in two hours from a lymphatic vessel in the neck of a horse (M. Smith); Landois mentions that 2½ to 3½ ozs. have been collected from the same place in 1½ to 2 hours; Colin obtained from a lymphatic in the neck of horses a quantity which varied between 1 to 4 lbs. in 24 hours; the mean amount was 2 lbs. 6 ozs. for the same period, but he notes that the variations are very wide, and that herbivora secrete more than carnivora, and young animals more than adults. The amount of material collected from the thoracic duct of a cow in 24 hours has been found to be 209 lbs.! but this is no guide to the quantity of lymph in the body, as the material in the thoracic duct is mixed with the chyle from the intestines. It is usual, however, in this vessel to consider two-thirds of the contents to represent chyle and one-third lymph.

The quantity of mixed chyle and lymph obtained by Colin some hours after the animals had been fed was as follows:

Horse, 30 lbs. to 90 lbs. in 24 hours.
Ox, 46 lbs. to 209 lbs. ,, ,,
Sheep, 6½ lbs. to 10 lbs. ,, ,,
Dog, 3 lbs. to 6 lbs. ,, ,,

The Formation of Lymph.—It is far from settled how the lymph passes from the bloodvessel into the lymph space, both physical and vital theories have been put forward to account for the process.

The process of transudation is one which doubtless takes a greater or less share in the phenomenon of lymph production, and transudation may be brought about either by filtration or diffusion.

For the process of filtration to have any effect it must be shown that there is a greater pressure on one side of the tissue than on the other, the material passing from the higher to the lower pressure. There is no difficulty in demonstrating that the needful pressure exists in the blood capillaries which will produce a material closely resembling lymph in composition, but a dead filter and a living one are two different things, and an increase of pressure in the capillaries by no means necessarily indicates a large secretion of lymph; further, through the dead filter material only passes in one direction, whilst in the living one fluid and substances may pass in both directions, viz., from the vessel to the lymph space, or from the lymph space to the vessel, being in the first instance tissue food, and in the second tissue waste.

The process of diffusion as a purely physical one gives us but little more assistance than filtration; it is true that two saline fluids of different densities separated by a partition will pass through, the salt from the stronger to the weaker, the water from the weaker to the stronger until equilibrium is established, and this will occur in spite of any difference in pressure which may exist; but diffusion will not account for the proteid in lymph, proteid

being practically indiffusible, so that, for this and other reasons which cannot be entered on here, it fails as a theory to explain some of the essential features in lymph production.

It would appear that neither of these purely physical processes is wholly capable of explaining all the facts connected with lymph formation, and Heidenhain's view that lymph production is an act of secretion on the part of the endothelial cells of the capillary wall, materially assists us to a better understanding of the subject.

This observer has shown that there are two classes of bodies, termed by him **Lymphagogues**, which when injected into the circulation largely increase the flow of lymph. In the first class is included peptone, leech extract, decoction of intestinal wall, liver, etc. These increase the exudation from the blood and thereby augment the flow of concentrated lymph ; their manner of action is by increasing the secretory activity of the endothelial cells lining the bloodvessels. The second class of lymphagogues are crystalline bodies such as sugar and neutral salts. These rob the tissue elements (cells, fibres, etc.) of water, and pass it into the lymph space, so that both lymph and blood are rendered more watery.

According to Heidenhain, both classes of lymphagogues operate through the action they produce on the cells lining the capillary bloodvessels, in the one case the blood, in the second the tissues providing the secretion, but Starling* draws a different conclusion ; he believes lymph formation to be the function of two factors, (1) permeability of the vessel wall, and (2) intra-capillary blood-pressure. He states that Heidenhain's first class of lymphagogues act by increasing the permeability of the hepatic capillaries, and that the increased flow of lymph comes from the liver, whilst the members of the second class attract water from the tissues, thereby increasing the total bulk of the blood and raising the capillary pressure. Starling concludes that

* *Journal of Physiology*, vol. xvii.

the secretory hypothesis of lymph formation is unnecessary, and that filtration accounts for its production.

As fast as the lymph finds its way into the spaces it is passed on to the capillaries, so that the rate of output is equivalent to the rate of income; when however the output is less than the income the lymph accumulates in the tissues and **Œdema** results. It is conceivable that the output need not necessarily always be at fault, but that the rate of secretion may be so greatly increased that the outgoing channels are not equal to the demands made upon them. Such an increased secretion of lymph lies on the shoulders of the vascular system; an increase in the size of the bloodvessels, alterations in the capillary wall, or in the character of the circulating blood, leading to an increased formation of lymph.

Experience shows that in the majority of cases increased formation of lymph is a more common cause of œdema than defective drainage.

It is well known that interference with the venous circulation is productive of œdema, disease of the right side of the heart or portal obstruction is a fruitful source of trouble; the explanation is that there is not only an increase of pressure in the capillaries as the result of the venous obstruction, but also a back flow of venous blood which is kept in contact with the wall of the capillary, and induces changes in the epithelioid cells resulting in lymph formation.

The swollen legs so common in horses kept idle in the stable are practically due to the same cause; the venous blood ascending the limbs against gravity and at a low pressure, exercises on the capillaries of the legs below the knees and hocks a pressure which is equivalent to the height of the vein; the cells of the capillary wall bathed in venous blood take on a process of exudation and the legs accordingly 'fill,' a condition removable by exercise.

Experiment however has shown that simple obstruction of the venous outflow from any given area is insufficient to account for all lymph formation; if Wooldridge's tissue

fibrinogen be injected into the circulation after ligature of a vein the operation is followed by œdema, while no such œdema is produced by the simple ligature of the vein; the only explanation here is that the tissue fibrinogen causes damage to the capillary wall, so that the œdema is really an act of secretion.

Ranvier showed that the posterior vena cava of the dog might be tied without the production of œdema, provided no injury were inflicted to the vaso-motor nerves; if, on the other hand, these were divided and the vein ligatured marked œdema was produced.

In pleurisy we meet with an effusion of inflammatory lymph into the pleural lymph space, a process brought about not only by primary alteration to the wall of the vessels of the pleura, but also by the character of the circulating blood.

All observations to determine the existence of special lymph secretory nerves have failed, but with the above facts before us, we are warranted in believing that lymph formation is an act of secretion *assisted by filtration and diffusion*, that is to say the secretory act may call in processes to its assistance allied to filtration or diffusion, but these are subordinate and not paramount.

The **Movement of Lymph** in the vessels is due to several causes, of which by far the most important are the muscular contractions in the neighbourhood of the vessels, by which they are compressed and their contents forced along, the valves which the vessels contain preventing any attempt at a back flow.

The obstruction caused by the lymphatics passing through glands is more apparent than real, the glandular network does not offer a serious resistance, and the involuntary muscle fibres in its covering more than compensate by their contraction for any resistance in the gland.

Capillary pressure is very difficult to ascertain, but whatever it is it is certainly higher than the venous pressure in the jugulars; the pressure of the lymph in the lymph spaces is also no doubt higher than that in the jugular

vein, so the flow of lymph from the tissues to the vein is assisted by the fact that the fluid is passing from a region of higher to one of lower pressure.

The walls of the lymphatic vessels contain muscular fibre, it is not known how far they may be under the control of the nervous system, but experiments on the dog indicate that when by the division of certain nerves the bloodvessels become dilated the flow of lymph increases, and when the bloodvessels are contracted the flow of lymph slows off. This does not necessarily prove that the walls of the lymphatic vessels dilate and contract, for inasmuch as the amount of lymph in the tissue depends largely upon the amount of blood present, the dilated vessels would increase the flow while the contracted ones would diminish it.

The movements of the diaphragm, tendons, and fasciæ produce an aspirating effect on the lymph circulating through them. In the case of the diaphragm, as previously mentioned, the lymphatic vessels drain the two large lymphatic sacs, the pleura and peritoneum. Owing to the direction taken by the fibrous tissue of the diaphragm, compression is exerted on the lymph spaces during its contraction, forcing the fluid onwards, whilst a sucking action is produced when the part relaxes by which the vessels are filled. This pumping arrangement exists in tendons, fasciæ of muscles, etc., and is a valuable aid in lymph circulation.

Once the lymph has found its way into the thoracic duct, its passage into the general circulation is not only favoured by gravity, and by the muscular contraction of its coats, but also by the negative pressure produced in the jugular vein by the process of inspiration, the result being that the lymph is aspirated out of the duct into the vessel. This aspirating influence has been proved on the horse by experimental inquiry, a negative pressure in the thoracic duct having been observed during inspiration, and a positive pressure of ·5 inch of mercury during expiration.

Colin states that the mixed chyle and lymph rose in five minutes to a height of over three feet, in a manometer

tube placed in the thoracic duct of the ox; this pressure is one third of the blood pressure in the aorta, and appears to be excessive. The lateral pressure in a lymph vessel in the neck of the horse amounted to from one half to three quarters of an inch of a weak solution of soda; in the dog the lateral pressure was half that found in the horse.

The thoracic duct terminates in the jugular confluent in a variety of ways; its most usual method is that before entering the vein it dilates, and from the dilatation one or two very short vessels are given off which enter the anterior cava, the entrance being guarded by a valvular arrangement. The right lymphatic channel also opens into the anterior cava at the jugular confluent, the entrance being furnished with a double semilunar valve. The blood in the jugular vein is prevented from passing into the thoracic duct by the presence of these valves, which normally only allow fluid to pass in one direction, viz., from the duct into the vein. Colin has observed that it is not uncommon in the horse to find the lymph in the thoracic duct slightly blood-stained, a slight leakage from the vein into the duct being liable to occur in this animal, though such has never been seen in the ox.

The lymph moves slowly in its vessels; Weiss has observed 9 inches to 11 inches per minute in a large lymphatic in the neck of the horse, but the velocity in the small vessels is very much less.

Chyle.

In the thoracic duct the lymph from the body meets with the lymph coming from the intestines, termed here chyle. Chyle is closely allied to lymph in its chemical composition, but it differs from it in containing a quantity of neutral fat, which gives it its milky appearance. The amount of this fat in dogs will vary from 2 per cent. to 15 per cent. or even higher. The fat is in the condition of fine particles, owing to the change it has undergone passing through the villi (see p. 233); these fine particles of fat give

to chyle what is known as the molecular basis, it is the molecular basis which distinguishes chyle from lymph.

The following analyses of chyle will give an idea of its composition:

Analyses of Chyle of the Horse (Hoppe-Seyler).

Constituents in 1,000 *parts.*	I. *Chyle of Horse.*	II. *Chyle of Horse.*	III. *Blood-serum of Horse.*
Water	960·97	956·19	930·75
Solids	39·03	43·81	69·25
Fibrin	2·57	1·27	—
Albumin	22·60	29·85	56·59
Fat, cholesterin and lecithin	0·09	0·53	—
Fatty acids in the form of soaps	0·76	0·28	1·57
Other organic matters	5·37	2·24	3·85
Hæmatin	0·05	0·06	—
Mineral salts	7·59	7·49	7·14
Sodium chloride	5·76	5·84	5·74
Sodium	1·31	1·17	0·87
Potassium		0·13	0·14
Sulphuric acid	0·07	0·05	0·11
Phosphoric acid	0·01	0·05	0·01
Calcium and magnesium phosphates	0·44	0·25	0·26
Carbonic acid	1·02	0·82	0·56

Chyle from the Thoracic Duct (Wurtz).

	Ox.		Cow.	Dog (Munk).
	Before Rumination.	*After Rumination.*	*Fed with Hay and Straw.*	
Water	950·89	929·71	951·24	912·0
Fibrin	1·76	1·96	2·82	1·0
Albuminoids	39·74	59·64	38·84	27·0
Fats	0·81	2·55	0·72	49·0
Salts (soluble in alcohol)	2·47	2·50	2·77	8·0
Salts (soluble in water)	4·33	3·61	3·59	

Chyle contains more solid material than lymph, and more fat; but the amount of its constituents must depend upon the nature of the diet, for instance on a hay diet the fat is small, but on oats it increases considerably. Though the proteids from the intestinal canal are absorbed as peptones, yet no peptones are found in chyle, owing to the fact that these pass away by the bloodvessels, after undergoing a change in the intestinal wall which we shall presently indicate. It is said that no sugar, or but very little, is taken up by the lacteals from the bowels, the bulk of the carbo-hydrates being carried off by the portal vein to the liver; but Colin states that sugar is found in the chyle of the horse, ·12 to ·14 per cent., and that this amount is increased by the introduction of glucose into the bowels.

The gases in chyle are much the same as in lymph, viz., a considerable quantity of carbonic acid, a little nitrogen, and a mere trace of oxygen.

Chyle is a turbid fluid of alkaline reaction and a specific gravity of 1007 to 1022. In starving animals it is transparent owing to the absence of fat, and it is, in fact, at this time practically pure lymph. Colin observes that the chyle of herbivora is yellowish or yellowish green: it is possible that this colour may be due to chlorophyll taken up from the food. In the horse it is often reddish, due, no doubt, to a slight leakage from the jugular, such as has been previously noted.

The chyle while passing upwards through the mesenteric glands receives from them numerous lymph corpuscles, and it now possesses the power of spontaneous clotting.

The movement of chyle is due to the muscular contraction of the intestinal villi forcing it onwards, the valves in the lacteals preventing its return. Intestinal peristalsis may also assist, and the negative pressure in the thoracic duct during inspiration must largely help in aspirating the contents of the chyle vessels upwards.

Absorption in General.

The activity of absorption in the horse has been made known to us by the experiments of Colin.

Absorption from the Respiratory Passages is remarkably rapid; stimulated by Colin's researches, we have for years administered certain alkaloids by the trachea rather than by the skin.* Colin showed that potassium ferrocyanide could be detected in the blood 2 minutes after being injected into the trachea, and that it appeared in the blood before it was found in the chyle; the same salt was also found in the urine 8 minutes after being introduced into the trachea. A solution of nux vomica injected into the trachea produced tetanic symptoms in 3 minutes; turpentine, alcohol, and ether were also rapidly absorbed, but oil could not be taken up, and it was rejected by the nostrils.

Such drugs as morphia, pilocarpine, physostigmin, etc., are all rapidly absorbed from the air-passages, and according to our observations they produce their therapeutical effect in a shorter time than when simply injected under the skin; further, the lungs have the power of absorbing certain poisons like curare, which are not absorbed when introduced into the digestive canal. The absorption of water from the trachea is also very rapid; Colin introduced 6 quarts of water per hour into the trachea of a horse, the animal was destroyed at the end of 3½ hours and no fluid was found in the bronchi; he also poured into the air-passages one pint of water at a time, repeating this without intermission, in this way he poured in 74 pints of water before he caused death.

So rapid is absorption from the trachea, that a horse may be placed under chloroform almost instantaneously by an intra-tracheal injection of the drug.†

* It is interesting to observe that the injection of liquids into the trachea (either high up, or as low as its bifurcation) excites the reflex act of swallowing, probably due to stimulation of the recurrent or other laryngeal nerve.

† It is not intended here to recommend the intra-tracheal administration of chloroform, which is not only dangerous but produces the greatest excitement.

The rapidity of absorption is therefore remarkable, but in spite of the facility with which drugs are absorbed the lining membrane of the bronchial tubes is remarkably tolerant of such irritating agents as turpentine, strong liquid ammonia, acetic acid, etc., and offers in a state of health an almost impassable barrier to putrid organic infusions, or at any rate these do not appear to produce any local irritation.

Absorption from the Cellular Tissue is very active, and it is certain that both the bloodvessels and lymphatics take part in the process; ferrocyanide of potassium injected into the face has been detected in a carotid lymphatic in 7 minutes. The rapidity of cellular tissue absorption is hastened by muscular movement.

Absorption from the Conjunctiva is very pronounced for some drugs such as atropine and certain organic poisons, but there are others which are not absorbed in this manner. Curare is not absorbed through the conjunctiva, and Colin could not infect horses with anthrax by placing anthracoid blood and fluids in the conjunctival sac.

Absorption by the Skin if the surface be unbroken is slow even for those drugs which will pass through it, while there are many organic and inorganic substances which refuse to pass through the unbroken epidermis. Colin kept the lumbar region of a horse wet for 5 hours with a solution of ferrocyanide of potassium; the salt was detected in the urine in $4\frac{1}{2}$ hours, although the skin was quite unbroken.

From a wound or abraded surface absorption will occur rapidly with some agents, slowly with others. Colin placed a horse's foot with a wound on the coronet in a solution of ferrocyanide of potassium, in 20 minutes he detected the salt in a lymphatic of the thigh. In connection with absorption from a wounded surface, he found that the poison was taken up quite as readily by the lymphatics as by the bloodvessels.

The mucous membrane of the vagina is found by experiment to absorb very slowly.

Experiments made on **Absorption from the Pleural and Peritoneal Cavities** showed that such drugs as strychnine rapidly produced fatal symptoms when injected into these sacs, even in such a short time as from 3 to 7 minutes tetanic symptoms may supervene; potassium iodide injected into the peritoneal cavity of a sheep may be detected in the thoracic duct 5 to 8 minutes after the operation. When we consider the numerous connections these large lymphatic cavities have with the lymphatic system, the rapidity of absorption cannot be wondered at.

In some recent work on absorption from serous cavities Starling and Tubby* have shown that the active agents in absorption from these sacs are the bloodvessels, and that the share taken by the lymphatics is insignificant.

Further they observed that an interchange took place between the fluid in the cavity and the blood in the vessels, so that equilibrium occurred between the fluids on the two sides of the pleural endothelium; if however the fluid in the chest presents the same composition as the circulating blood absorption is very slow.

We have here one explanation of the extreme difficulty with which serous effusions are absorbed.

Intestinal Absorption.

The remarkable fact that no absorption occurs from the stomach of the horse and very little, if any, from that of the ox, points to intestinal absorption as being of considerable importance in herbivora. That this absorption is very rapid is proved by Colin's experiments; hydrocyanic acid injected into the small intestine of a horse caused death in 1 to 1½ minutes, and potassium ferrocyanide injected into the bowel, after tying the mesenteric lymphatics, was detected in the blood 6 minutes afterwards.

The Paths of Absorption.—The paths by which intestinal

* *Journal of Physiology*, vol. xvi.

absorption occurs are (1) through the villi into the lacteals, and (2) through the bloodvessels into the venous system.

The villi are found only in the small intestines, they are ·04 to ·07 inch long, and possess a diameter of from ·02 to ·04 inch. They are comparatively small in herbivora, and their number in the horse and ox, according to Colin, is from 45,000,000 to 55,000,000.

The structure of a villus has been previously dealt with (see p. 213).

The lacteals pass up the mesentery, and each of the 1,200 vessels counted by Colin passes through a lymphatic gland before gaining the receptaculum chyli; here the chyle mixes with the lymph coming from the posterior extremities, and the whole is passed into the anterior vena cava.

The material absorbed by the bloodvessels passes into the portal vein and reaches the liver before entering the general circulation. This arrangement would point to the fact that there are certain substances which need only pass through a lymphatic gland before being suitable for the blood, whilst others must pass through or undergo changes in the liver previous to being rendered fit for the system. Physiologists have therefore devoted considerable consideration to this subject, but it is far from being in a satisfactory condition.

In the small intestines of the horse, it has been observed by Colin that, almost immediately after food has been given, waves of chyme are passed into the duodenum, and at once the lacteals in the mesentery in connection with this portion of intestine become opaque, though previously they were filled with a colourless fluid. As the chyme passes along the bowel the other lacteals in their turn become opaque, until at last the whole of them are filled with this milky fluid. Colin draws especial attention to this regular invasion of the lacteals from the duodenum to the ileum.

In the large intestines there are no villi. It must not, therefore, be supposed that absorption is here exclusively carried on by the bloodvessels, for remembering the large

chain of glands along the colon in particular, it is probable that the material absorbed passes through these glands to a greater or less extent, as in the mesentery, before entering the circulation. There is, at any rate, a well-developed lymphatic system in the walls of the large intestines, and it is certain that material is taken up both by the blood-vessels and lymphatics, and that the amount of this is something considerable, may be readily understood when we remember the size of these bowels and the character of their contents.

That substances can be taken up with extreme rapidity from the large bowels is a well-known fact, Colin observed that 18 minutes after injecting a solution of nux vomica into the cæcum of the horse convulsions began, and 8 minutes later the animal was dead; anæsthetics, such as ether, may also be administered to the horse per rectum and produce narcosis.

Absorption of Fat.—Experimental inquiry, limited almost entirely to dogs, points to the lacteals as the means by which the fatty part of the food is taken up. It has been observed that these vessels after a diet rich in fat are filled with a milky fluid containing the same substance, whilst the blood in the portal vein does not contain more fat than that of any other vein in the body. Clearly, therefore, in dogs at least, the lacteals take up the fat; but what about herbivora, the diet of which contains but little fat, that of the horse in particular? Exactly the same appearance of milky lacteals is obtained in the horse after feeding on a diet notoriously deficient in fat; it is possible, therefore, that in the horse the lacteals may take up other substances than fat, and that the milky appearance is not due to fat alone.

Colin expressly states that proteids and sugar are absorbed by the lacteals in the horse, and on this point we are certainly inclined to agree with him, in spite of experiments to the contrary on dogs. This observer injected glucose into the intestine, and the chyle contained in a short time a decided increase in sugar.

It is curious to observe that in dogs only about 60 per cent. of the fat absorbed can be recovered from the thoracic duct, and none, as we have mentioned before, enters the blood; the missing 40 per cent. cannot be accounted for.

The method by which the fat passes into the lacteal is interesting; the fat globules are seized upon by the columnar cells of the villus, their passage into the cell may be assisted by the striated border previously described, but how this is brought about is unknown. The fat globule passes through the length of the cells and escapes at the inner edge into the adenoid tissue of the villus, the passage being effected by the direct connection existing between these two; through the adenoid tissue of the villus it passes to the central lacteal, having in its course become changed from fat to milky chyle, the fat globules being in a minute state of division, the so-called molecular basis.

The central lacteal is emptied into the lymphatic vessel at its base, partly through the assistance received by the intestinal movements, and partly by means of the muscular fibre found in the villus, by which means the villus is shortened and compressed.

The lacteal of the villus empties into one situated at its base belonging to the intestine, a reflux being prevented by means of a valvular arrangement. The lymphatic vessel runs up the mesentery, passing through the mesenteric glands where certain additions are made to the stream in the shape of cells, and the whole is poured into the general circulation.

It is a well-known fact in human surgery that fat embolism is not an infrequent accompaniment of certain injuries, fractures, etc.; the fat of the body being taken into the bloodvessels blocks the capillaries, especially those of the lungs. Fat embolism in lacteal absorption is prevented by the fine emulsion produced in the intestines, for no emulsion can occur in any other part of the body, in spite of the alkaline nature of the blood, owing to the

fact that the body fat is neutral, and neutral fats can only be emulsified by free alkalies, and not by their carbonates (Bunge).

Absorption of Sugar.—The sugar formed in the bowel is said to reach the general circulation *viâ* the portal vein and liver. We have reason, however, to believe that some portion of it may in the horse find its way into the lacteals; but the bulk of it must of necessity be absorbed by the bloodvessels of the villi, and pass by the portal vein to the liver. We have seen, in speaking of the liver, how important the function of this gland is in regulating the supply of sugar to the system, and the method it possesses of storing it up.

The **Absorption of Proteids** is said to be exclusively by the bloodvessels of the villi, from which they are conveyed to the liver by the portal vein; but here a curious point arises, little or no peptone can be found in the portal vein or even in the general mass of blood. If peptone be experimentally injected into the blood it is rapidly excreted by the kidneys, so that it is evident the peptone taken up from the intestinal canal must undergo some important and rapid change before entering the portal system. Hofmeister's work in this direction has shown that the peptone is converted once more into proteid, and that this change occurs in the intestinal mucous membrane, so that peptones enter the system in the form of proteid. The process is analogous to that we have previously dealt with in speaking of glycogen, where the starch enters the blood as sugar, is again converted into a kind of starch in the liver, and is here converted into sugar for the use of the blood. Similarly the proteids are converted into peptones in the intestine in order that they may be more readily absorbed by the intestinal walls, but they are no sooner in the capillaries of the villi than they are found to be proteid once more.

The blood of the portal vein does, however, contain a small portion of peptone which appears to have escaped this conversion; but instead of passing out of the blood by

means of the kidneys, as injected peptones do, it is enabled to circulate in the stream by being lodged in the white cells of the blood, and Hofmeister and his pupils have shown that the number of white blood cells depends upon the proteid matter in the food, and is not affected by carbohydrates, fats, salts, or water.*

We are in ignorance of the causes which induce some substances to select the vessels and others the lacteals in order to gain the circulation.

* Bunge.

CHAPTER IX.

THE SKIN.

It is obvious that one important function the skin performs is that of affording cover to the delicate parts beneath; wherever the chance of injury is the greatest the skin is the thickest, whilst in those parts where sensibility is most required it is thinnest. The skin of the back, quarters, and limbs are good examples of the first type; on the back especially is found a protective covering which, in some horses, is as much as a quarter of an inch in thickness; the face and muzzle are a good example of the latter variety, the skin in some parts being as thin as paper. In those regions not exposed to violence it is also thin, as on the inside of the arms and thighs.

In spite of the thinness of the skin its strength is remarkable; a horse's body may be dragged along by the thin skin of the head.

The skin as an organ of touch is of great importance, all animals appear most sensitive to even slight skin irritation; flies will cause horses considerable suffering, and the elephant, with its thick hide, is quite as intolerant of these tormentors as a well-bred horse.

The skin is highly endowed with sensory nerves, particularly in those parts connected with the organs of prehension; here also the long hairs growing from the part are brought into contact with distinct nerve-endings.

The skin is a bad conductor of heat, and this is considerably assisted by the layers of fat found beneath or at

no great distance from it, as in the abdominal region; the subperitoneal fat protects the viscera of animals living in the open and lying in wet places.

The epidermal covering of the skin relieves the part from excessive sensitiveness, such as would occur to an exposed sensory surface; through the sebaceous secretion it assists in preventing loss of heat, whilst the greasy covering helps to throw off the rain, prevents the penetration of water, and thus saves the epidermis from disintegration.

Hair.—By means of the hair growing from the skin the heat of the body is maintained and prevented from passing off too rapidly. The thickness of the hairy covering varies considerably with the class of horse, the better bred the animal the finer the coat. We have obtained from draught horses between 7 lbs. and 8 lbs. of hair by clipping, in a well-bred horse this would be reduced to 10 ozs., or even less; the mean amount of hair of the mane and tail, weighs 1½ lbs.

It is a well-known fact that, excepting the hair of the mane and tail, that of every other part of the body has only a temporary existence, and is changed twice a year, once for a thick, and once for a fine coat.

The growth of the hair depends upon the surrounding temperature; if horses in the depth of winter are placed in a heated atmosphere, such as a horse deck on board ship, they commence to shed their heavy winter coat in a few days, though the temperature of the outside air may be at freezing-point; similarly, if taken from a warm to a cold place the hair at once responds by becoming longer.

The permanent hair of the body, viz. the mane and tail, may grow almost any length, but the temporary hair of the surface of the body only grows a definite length, and in the same way as the shedding of the hair is affected by temperature so is the growth. Nothing will make a short summer coat grow longer; yet if the horse be shaved hair at once grows rapidly, but only to its original length; in other words, everything is present for the needful growth to occur, but there is a restraining influence which appears

to be the surrounding temperature acting on the nerves of the skin.

Of the pigment in hair which gives the colour to the coat we know nothing; with the exception of black horses which are liable to turn grey, all other colours are practically permanent even to old age. It is presumed that the pigment is derived from hæmoglobin, but there are no pathological conditions which either point to this or suggest the seat of elaboration.

We do know, however, that injuries to the skin of horses, even of a slight character, are commonly followed by a growth of perfectly white hair, which never regains its pigment.

It is found that the heavy coat grown by horses is the cause of considerable sweating at work, and the general practice of clipping has been introduced; of its value there can be no doubt, it considerably reduces the risk of cold and chest disease, for animals instead of coming in from work with a wet skin, which in some cases will not dry for hours, are readily dried and easily protected against inclement weather.

Horses which sweat freely at work lose condition; it has been shown that this is due to the proteid lost by the skin, for, as we shall presently see, proteids are regularly found in the sweat of the horse; clipping largely prevents this loss. As to the influence of clipping on temperature, see 'Animal Heat.'

In some animals, for instance the dog and cat, the hairs are rendered erect under excitement; this is due to the involuntary muscle attached to the hair follicle, and the process is under the influence of the sympathetic nervous system. The fibres for the body hair escape from the spinal cord by the inferior roots, pass to the grey ramus of the sympathetic chain, and run to the skin by the dorsal cutaneous nerves; the fibres for the head and neck are in the cervical sympathetic.

By means of glands in the skin an albuminous fluid termed 'sweat,' and a fatty material known as 'sebum,' are secreted.

Sweat, or perspiration, is not found to occur over the general surface of the body in any other hairy animal than the horse. The ox sweats freely on the muzzle, and even sweating from the general surface of the body has occasionally been observed; it has been said that sheep perspire, while it is certain that both the dog and cat, especially the latter, sweat freely on the foot-pads though not on the general surface of the body; the sweating of the pig is confined to the snout.

Sweat exists in two forms: viz., the invisible vapour which is always rising from the surface of the skin, and distinguished as the 'insensible perspiration,' and the visible material, which is termed 'sweat.'

Colin gives various figures representing the insensible perspiration, from which we gather that 14 lbs. of water probably represent this loss in the horse for 24 hours; Grandeau* puts the loss by the skin and lungs in a state of rest at 6·4 lbs. daily. Much depends upon the humidity and temperature of the atmosphere, the drier and hotter it is within certain limits, the greater the insensible perspiration.

Sweat obtained from the horse is always strongly alkaline; after filtration it is the colour of sherry, which is probably accidental, and due to contamination with dandruff which contains a pigment, chlorophyll; it possesses a peculiar horse-like odour, and has a specific gravity of 1020. An analysis of horse's sweat gave the following result:

Water		94·3776	
Organic matters		·5288	Serum albumin · ·1049
			,, globulin · ·3273
			Fat · · · ·0020
Ash		5·0936	Chlorine · · ·3300
			Lime · · · ·0940
			Magnesia · · ·2195
			Phosphoric acid · traces
			Sulphuric ,, · ,,
			Soda · · · ·8265
			Potash · · · 1·2135

* 'Horse-feeding,' R. Warrington, F.R.S., *Live Stock Journal*, January, 1894.

The proteids are thus seen to be serum albumin and globulin, and their constant presence has been determined by a number of observations; the mineral matter is very high and consists principally of soda and potash, especially the latter. It will be observed that the mineral matter exceeds the organic matter; in horses which have sweated freely the matted hair (which is due to albumin) is often seen covered with saline matter, looking like fine sand. There appears to be some complemental action between the skin and the kidneys in the elimination of soda and potash; during rest the kidneys eliminate these salts, whilst during work they are assisted by the skin.

It is difficult to see why horses should excrete albumin by the skin; the loss thus produced accounts for the great reduction of vitality and strength in animals which sweat freely at work, and for which clipping is the only preventive.

Nervous Mechanism of Sweating.—A skin may sweat under quite opposite conditions, viz., both with a hot flushed skin and a bloodless cold skin, in other words an animal may sweat when it is hot or when it is cold. The former is a physiological condition and regulates, as we shall see, the body temperature; the latter is abnormal, but it occurs and disproves at once any notion of sweating necessarily depending upon an injected condition of the vessels of the skin.

Experiments show that most of the features of sweating can be accounted for through the agency of the nervous system, and though we are ignorant of the manner in which the nerves terminate in the sweat glands, still it is certain that there are special branches of nerves, the function of which is the secretion of sweat, and these are quite independent of any which regulate the vascular supply. If the peripheral end of the divided sciatic in the cat be stimulated the foot-pads sweat; the proof that this reaction is a nervous one is easy, for the sweating will occur when the vessels of the skin are empty or when the aorta has been tied, and it is absent when the vessels of the part are dilated under the influence of atropine. The effect

of atropine on the sweat glands is very closely allied to its effect on the salivary glands; atropine though inducing well-marked vaso-motor effects, prevents the sweating which follows stimulation of the sciatic.

It has been considered that a high temperature favours the activity of the epithelium lining the sweat glands, for if the limb of a cat be kept warm a larger secretion of sweat is obtained on stimulating the sciatic than in a limb kept cold, in which stimulation of the sciatic may produce no secretion whatever; further, if a cat in which one sciatic has been divided be placed in a hot chamber profuse secretion will occur on the foot-pads of the limbs not subjected to interference, while on the side on which the sciatic has been divided no sweating occurs.

It has been thought that the sweating which takes place at death is due to a dyspnœic condition of blood and in many cases this may be so, but it is difficult to account for the profuse cold sweating in ruptures of such viscera as the stomach and intestines, or the hot sweating which is often so well marked in horses immediately after they are destroyed.

Thrombosis of both iliac arteries may occur in the horse, and a marked symptom of this trouble is the peculiarity in sweating; the general surface of the body will sweat freely but not the hind-quarters. It is probable in these cases that the effect on the sciatic produced by an absence of blood supply is equivalent to division of the nerve, which as we saw in the cat admits of no sweating, for it can be readily shown that in some animals compression of the posterior aorta is followed by paralysis of the hind-quarters.

In comparing the sweat glands with the salivary we must be careful not to draw too close a parallel, for though in some features they agree, in others they are very different; for instance in the horse pilocarpine produces as in other animals a profuse salivary flow, but unlike its action on man, the dog, and cat, it has no effect whatever in producing sweating in the horse.

By the use of drugs it has been ascertained that sweating may be produced either by a direct action on the nerves of the sweat glands, or even after the nerves to them have been divided; this has suggested a central origin for sweat glands, or sweat centres, and such are supposed to exist in the cord or in the medulla.

The peculiar breaking out into sweats which occurs in horses after work has no parallel in man; some animals will break out two and three times for hours afterwards, even after having been rubbed quite dry.

Another peculiarity in sweating of the horse is the patchy perspiration observed occasionally, such as a wet patch on the side or quarter which never dries, and may remain for several days in this condition.

Finally, there is no drug, so far as we are aware, which produces sweating in horses; this is an explanation of the common use of nitre in veterinary practice, the kidneys having to do the work of the skin.

The sweat nerve supply to the fore and hind limbs passes out of the cord by means of the *rami communicantes* of the sympathetic system, and so reaches the brachial and sciatic plexus respectively; the sweat fibres for the head and neck are in the cervical sympathetic; those for the face in the horse, the muzzle in the ox, and snout in the pig, run in the branches of the fifth pair of nerves.

Division of the cervical sympathetic in the horse produces profuse sweating of the head and neck limited to the side operated upon; this in all probability is due to vasomotor paralysis, though a different interpretation has been placed on it, viz., that the sympathetic carries inhibitory impulses to the sweat glands of the head, so that on division the secretory fibres act without opposition.

In the ox Arloing has shown that division of the cervical sympathetic causes the muzzle on the same side to become dry; stimulation of the cut end of the nerve is followed by secretion, but this is not so when the nerve degenerates, though even then the glands respond to pilocarpin.

The changes occurring in the secreting cells of the sudo-

riferous glands of the horse are described by Renaut;* when charged the cells are clear and swollen, the nucleus being situated near their attached ends; when discharged they are smaller, granular, and their nucleus more central.

The **amount of sweat** secreted daily can only be roughly guessed at; there are many conditions which affect it, such as the length of coat, nature of the work, and pace; but we are of opinion that a minimum secretion would be about 1 pint, and this was arrived at by brushing a horse lightly over with water.

Grandeau† by estimating the total water consumed in the food and drink, and that voided in the urine and fæces, arrived at the amount of vapour passing away in the breath and perspiration.

The mean amount of water evaporated daily by these two channels under different conditions of work was as follows:

At rest - - - -	6·4 lbs.
Walking exercise - - -	8·6 ,,
At work walking - - -	12·7 ,,
Trotting - - - -	13·4 ,,
At work trotting - - -	20·6 ,,

In each case the distance walked and trotted, and the load drawn were the same.

It is unfortunate that we have no means in the above experiments, of determining the proportion which the water of respiration bears to that of perspiration.

The compensating action existing between the kidneys and skin observed in men exists also in the horse, viz., when the skin is acting freely less water passes by the kidneys, and *vice versâ*.

There are certain parts of the skin which sweat more readily than others; the base of the ears in the horse is the first place for sweating to begin, the neck, side of chest, and back follow, lastly the hind-quarters. No sweating takes place on the legs, the fluid found there has run down from

* Halliburton, *op. cit.* † *Op. cit.*

the general surface of the body. Mules and donkeys sweat with difficulty and then principally at the base of the ears.

Sebaceous Secretion or **Sebum** is a fatty material formed in the sebaceous glands of the skin, which in the horse are freely distributed over the whole surface of the body. Though it is spoken of as a secretion, yet the process involved is not one which generally occurs in a secretion, inasmuch as the cellular elements of the gland are not actively employed pouring out a material, but are themselves shed after undergoing fatty metamorphosis.

The greasy material thus produced saves the epithelium from the disintegrating influence of wet, keeps the skin supple, and gives the horse a glossy coat; from its greasy nature it must assist in preventing the penetration of rain and thereby saves to an extent undue loss of heat.

Dandruff.—The material removed from horses by grooming consists of a white or grey powder which can readily be moulded by pressure into a dough-like mass. It consists of epithelial scales, fat, largely in the form of lanolin, salts, and a considerable amount of silica and dirt, the two latter depending upon the cleanliness of the animal.

The amount of dandruff lost in an ordinary grooming will vary from 20 to 60 grains for clean horses, and 170 to 200 grains for very dirty animals.

An analysis of dandruff from the horse gave the following composition :

Water - - -	17·96	
Fat - - -	12·40	
Organic matter - -	56·22	containing 1·07 of urea.
Ash - - -	13·42	,, 2·45 ,, silica.
	100·00	

The fatty matter in the skin proves to be lanolin, the same as that found in the fleece of sheep; it explains the reason why horses living in the open should not be too freely groomed, and supports the prejudice which has always existed against this practice. It is evident that with free grooming the loss in fat alone is something considerable, and the animal exposed to chill. The amount of

fat depends upon the diet; on hay alone there is very little in the dandruff, whilst on oats there is a considerable amount.

The dandruff contains a colouring matter found to be chlorophyll, which has undergone a modification by passing from the digestive canal to the skin. The use of this pigment is unknown, in fact the horse is the only vertebrate in which chlorophyll has been found in the tissues.

In certain places, as in the prepuce, considerable quantities of sebum are found; the sebaceous secretion of the prepuce of the horse consists of 50 per cent. fat, and also contains calcium oxalate (Lehmann). The ear-wax and eyelid secretions are also of a sebaceous nature.

In the sheep a considerable quantity of fatty substance is found in the wool; it exists in two forms, (1) as a fatty acid united to potash to form a soap, and (2) a fatty acid combined with cholesterin instead of glycerin; the latter is known as lanolin, and is largely used as a basis for ointments. It is also found in hair, horn, feathers, etc.

The fatty substance in the fleece is known to shepherds and others as 'suint'; in merino sheep it may amount to more than one-half the weight of the unwashed fleece, but in ordinary weather-exposed sheep it may be 15 per cent. or less. The large amount of potash in unwashed wool is very remarkable; a fleece sometimes contains more potash than the whole body of the shorn sheep (Warrington).*

Respiratory Function of the Skin.—Certain vertebrates like the frog can respire by the skin in the entire absence of lungs; in this way they absorb oxygen and excrete carbonic acid. Observations made on animals and men enclosed in air-tight coverings, have demonstrated that a loss of oxygen and an increase of carbonic acid take place, but there is nothing to show that this change of gases occurs through the skin, or may not have resulted from decompositions taking place in the sweat.

Gerlach† is said to have collected ½ oz. of carbonic acid in 24 hours from the skin of horses at rest, and 3 ozs. at

* 'The Chemistry of the Farm.' † Quoted by M'Kendrick.

work; it is difficult to know how these figures were arrived at unless the horse were enclosed in a rubber bag.

Varnishing the skin will rapidly cause death in rabbits, and more slowly in horses. Death is due to loss of body heat, and not to suffocation as was at one time supposed. Bouley* states that horses shiver when varnished, and the surface of the body and expired air become cold, the visible membranes violet, and the animals die after several days; according to Ellenberger, if only partly varnished they do not die, but exhibit temporary loss of temperature, and show signs of weakness.

For absorption from the skin, see ' Absorption,' p. 229.

* Colin's ' Physiologie.'

CHAPTER X.

THE URINE.

The urine is sometimes spoken of as a secretion, but this is not strictly correct; speaking broadly, we may say a secretion is something which is formed in a part for the purpose of being eventually utilised by the system. This does not apply to the urine, the chief constituents of which are not even formed in the kidneys, but only separated by them; moreover, the urine having once been formed is of no further use to the body, and is excreted. An excretion, therefore, is a something removed from the system as being no longer required, and the retention of which would be harmful.

The kidneys may be regarded as the filters of the body, and one of the channels by which waste and poisonous products are removed or filtered off from the blood, by which means the latter fluid is maintained in a healthy condition. We have seen how both nourishment and waste materials are poured into the circulation, and have studied several of the channels by which the latter are removed, viz., by the lungs, skin, and intestinal canal; we have now to examine the last excretory path, viz., the kidneys.

The kidneys are not only the path by which the waste products of the body are removed, but also the means by which the normal constituents of the blood are got rid of if in excess; for, according to Bunge, by the selective power which the epithelial cells of the tubules possess, the

alkalinity of the blood is maintained, alkali being got rid of or sent back to this fluid as it needs it.

Secretion of Urine.—The vascular arrangements of the kidney are intimately connected with the function of the organ. The renal artery is short, it comes off close to the posterior aorta, and the pressure within it is practically the pressure in the posterior aorta; the pressure in the renal vein on the other hand is low, nearly as low as that in the posterior vena cava. It will be observed that the same amount of blood-pressure required to fill the vessels of the lumbar region and hind limbs, is expended on driving the blood through the kidneys.

At every increase in the amount of blood in the kidney the organ swells, at every decrease it contracts. These movements on the part of the kidney have been carefully studied by means of Roy's oncometer, viz., a metallic capsule in which the living kidney is enclosed, and which registers the expansion and collapse of the organ. The tracing given by the use of this instrument shows that the volume of the kidney is affected by every beat of the heart, and even shows the respiratory undulations.

The branches of the renal artery break up at the boundary of the cortical and medullary portions; the cortex of the kidney is the essential secreting region, and it is here that the Malpighian tufts are found. These consist of small balls of capillaries derived from the renal artery; the artery entering the Malpighian tuft is larger than the vein leaving it, the result is that a high blood-pressure is maintained in the glomerulus. The vessel which supplies these tufts also sends branches, which do not enter the Malpighian body, to form a plexus around the uriniferous tubes. The whole glomerulus is contained in a capsule in which it is suspended by its afferent and efferent vessel; when the vessels are dilated the tuft fills the capsule, when they are collapsed there is a space between the two (Fig. 35).

The minute vein or efferent vessel leaving the tuft breaks up into capillaries around the uriniferous tubule, so the plexus of capillaries around the tubule is composed of

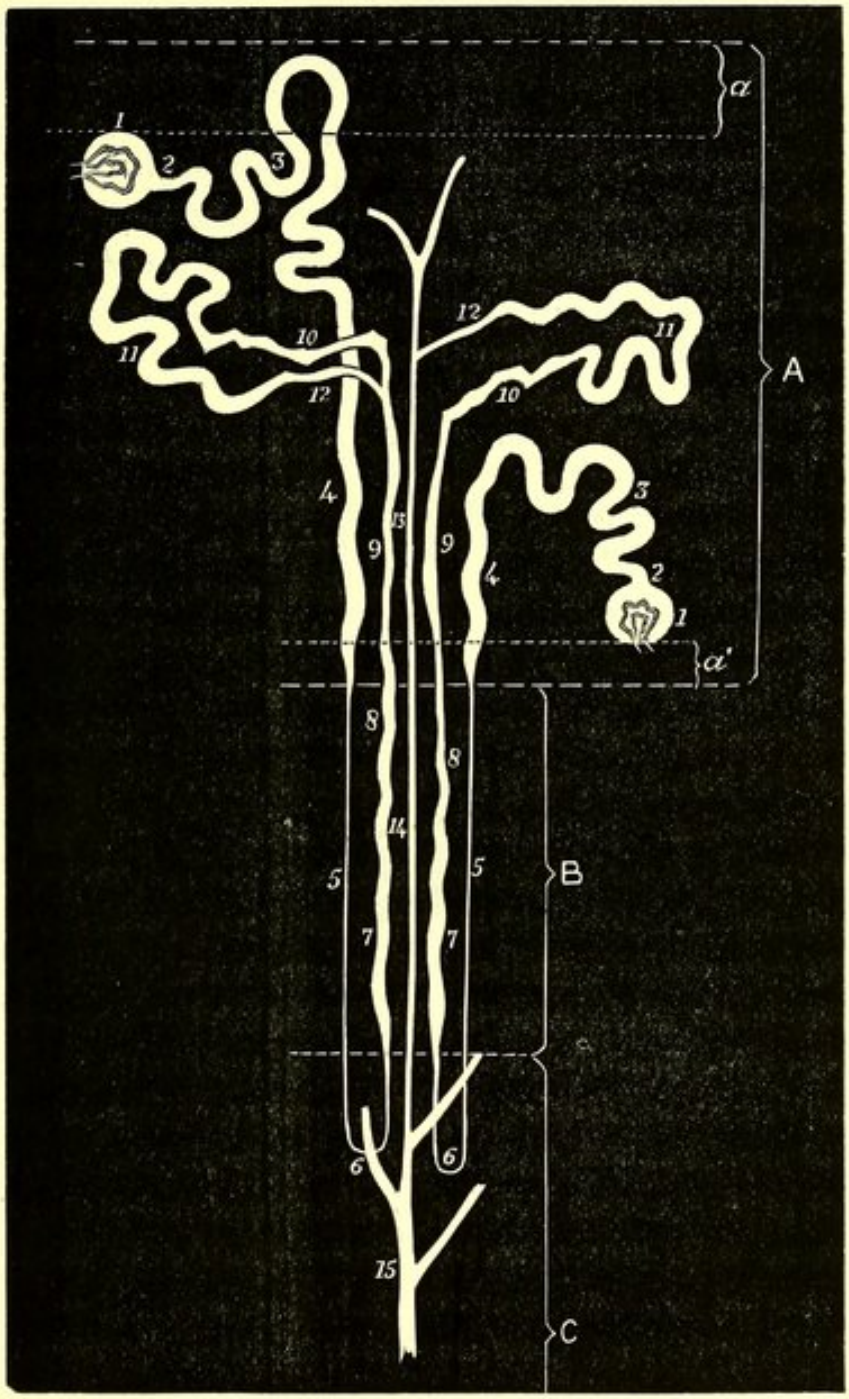


FIG. 34.—DIAGRAM OF THE SECTIONS OF URINIFEROUS TUBES. (KLEIN AND NOBLE SMITH.)

A, cortex of kidney; *a*, subcapsular layer not containing glomeruli; *a'*, inner structure of cortex also without glomeruli; B, boundary layer of medulla; C, papillary part of the medulla; 1, Bowman's capsule of the glomerulus; 2, neck of capsule; 3, proximal convoluted tube; 4, spiral tube; 5, descending limb of Henle; 6, loop of Henle; 7, thick part of ascending limb; 8, spiral part of ascending limb; 9, narrow ascending limb in the medullary ray; 10, the irregular tubule; 11, distal convoluted tube; 12, curved collecting tube; 13, straight collecting tube; 14, collecting tube of boundary layer; 15, large collecting or discharging tubule of papillary layer.

vessels from the tuft, and with these are united vessels direct from the renal artery which have not passed through the Malpighian body.

The capsule of Bowman which surrounds the tuft is lined by a material resembling the epithelioid plates seen in capillaries; they are flat polygonal cells containing a nucleus. The capsule is practically the dilated beginning of a uriniferous tubule, and this latter is continued from the capsule taking a course of extraordinary complexity in order to reach the pelvis of the kidney; further, the cells found

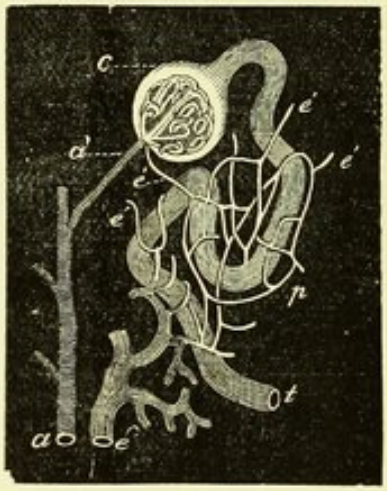


FIG. 35.—DIAGRAM SHOWING THE RELATION OF THE MALPIGHIAN BODY TO THE URINIFEROUS TUBES AND BLOODVESSELS. (KIRKE, AFTER BOWMAN.)

a, an interlobular artery; *a'*, branch of artery passing into the glomerulus; *c*, capsule of the Malpighian body forming the commencement of, and continuous with *t*, the uriniferous tube; *e'e'e'*, vessels leaving the tuft, forming a plexus *p* around the tube, and finally terminating in *e*, a branch of the renal vein.

in the tubule are no longer the flat polygonal cells of the capsule, but a something special to the tubule and even to different parts of it.

If we briefly follow the course of a uriniferous tubule (Fig. 34), it is found that on leaving the capsule it becomes twisted in the cortex forming the *convoluted tube*, it then forms a *spiral tube*, becomes suddenly very narrow, and leaving the cortex runs straight into the medulla; it now makes a sharp curve, the loop of Henle, and travels back to the cortex in the same way that it left it, the one is called the *descending* the other the *ascending limb of Henle;* whilst

the descending limb is straight the ascending limb is wavy in character and enlarges, and having reached the cortex it becomes distinctly wider and twisted, forming the *zigzag* or *irregular tubule;* from this a tubule is continued which resembles in its contortions the first convoluted portion, it is termed the *second convoluted tubule*, this now leaves the cortex and enters the medulla as a straight tube known as the *collecting tube*, running towards the apex of the pyramid it joins other collecting tubules and so becomes larger, until it reaches the apex where it is known as a *discharging tubule*.

It has been supposed that the reason why the tubules pursue such an erratic course and alter in calibre, is to assist in the reabsorption of some of the water passing along them, or even, it has been said, to reabsorb albumin which has been considered by some to be secreted in the Malpighian tuft.

The epithelial cells lining the tubules are not of the same character throughout, those found in the convoluted and irregular tubules are irregularly-shaped or cubical cells, containing a nucleus, possessing striation in the cell substance, and staining readily with reagents. These are features which are suggestive of secreting cells, whilst those found in the collecting and discharging tubes are cubical cells, containing a nucleus and transparent material which stains with difficulty, features which are characteristic of epithelium lining ducts, rather than secreting alveoli.

The vascular arrangements of the kidney are under the control of the vaso-motor system; if the general blood-pressure be constant dilatation of the renal vessels means an increased secretion of urine, contraction of the vessels means a reduced secretion. An increase in the general blood-pressure produces an increase in the amount of blood in the kidney, and this is rendered evident by the swelling of the organ in the oncometer; if the increased general blood-pressure is accompanied by a *contraction* instead of a dilatation of the renal vessels, as for instance when the

blood-pressure curve is complicated by Traube-Hering waves (p. 68), then the increased blood-pressure cannot stimulate secretion, but on the contrary the amount of urine becomes less and the kidney *shrinks*.

A fall in blood-pressure, such as is caused by dividing the spinal cord, brings about a reduction in the flow through the kidney, and the blood-pressure may become so low that the secretion of urine is almost entirely suspended.

It is evident, therefore, that the vaso-motor influence over the kidney is of the greatest importance, and practically regulates the amount of urine manufactured.

In the dog it has been determined that by the inferior spinal roots of the eleventh, twelfth, and thirteenth dorsal nerves, both vaso-constrictor and dilator fibres pass to the kidney, after having previously passed through the solar plexus, and then by the abdominal splanchnics to the renal plexus; the nerves having entered the kidney their method of termination is unknown.

Dilatation of the kidney may be produced by other causes than an increase in general blood-pressure; if water or urea be injected into the blood the kidney first temporarily shrinks and then swells, this swelling is accompanied by an increased flow of urine; in some way or other these substances have caused a local determination of blood to the part, and that their effect is produced on the nerve terminations within the kidney appears certain, as the phenomenon is present after all the nerves to the kidney have been divided.

The alterations in the vascular supply have been woven into a theory of urinary secretion which is known as the filtration theory, by which it has been supposed that owing to the high pressure exercised in the Malpighian tufts, the fluid portions of the urine are forced through the capillary wall into the capsule of Bowman.

Valuable as this pressure is for the purpose intended, it is impossible to believe that the separation of water from the blood can be brought about by a process which is not of the nature of a secretion, though there can be no doubt

that the secretion in the tufts is not of such a high character as that met with further on in the uriniferous tubule.

No doubt whatever is entertained of the power possessed by the epithelium of the tubule, especially of the convoluted portion of the tubes, to carry out an act of secretion. If the spinal cord be divided and the blood-pressure rendered so low that the secretion of urine practically ends, the injection into the blood of urea, urates, etc., produces a profuse secretion; this secretion is not due to any increase in the amount of blood sent to the kidney, such as we noticed previously in a somewhat similar experiment, for the amount of blood passing to the kidney is insufficient to account for the increased flow. By this and other experiments in which certain colouring matters injected into the vascular system, have been arrested in the tubules and have not stained the glomerulus, it has been proved that the cells of the tubules take an active share in secretion, the most active parts being the two convoluted tubes, the zig-zag tube, and the ascending limb of Henle; the active share taken by the tubules is quite independent of what is occurring in the glomerulus.

This view is strongly supported by the evidence afforded by the kidney of amphibia in which, owing to the peculiarity of their vascular supply, it is possible to cut off the blood from the tufts without interfering with that of the tubules.

Experiments conducted on these lines have shown that urea is separated from the blood by the epithelium of the tubules and not by the glomerulus, and further that the separation from the blood is attended by an outpouring of water which is also secreted in the tubules.

Other substances, such as sugar and peptone, which readily appear in the urine of the normal kidney, are not excreted when the glomerular blood supply is cut off, the obvious deduction from this experiment being that under normal conditions these substances are separated in the glomerulus and not in the tubule.

But the function of the cells does not end with the removal from the blood of the substances presented to

them, they are capable of originating substances on their own account, thus the union of glycin with benzoic acid, resulting in the formation of hippuric acid, takes place in the cells of the tubules, and observations have shown that providing the benzoic acid be presented to it, the kidney is capable of providing the needful glycin. It can hardly be doubted that what is true of glycin and benzoic acid may also be true of other substances, and that transformations may occur in the cells leading to the production of colouring matters, etc., a knowledge of which is at present obscure.

We may summarise what has been said about the secretion of urine as follows :

There are no known secretory nerves of the kidney, the vessels are under the control of the vaso-motor system, and depending upon whether they be dilated or constricted so there is a greater or less secretion of urine ; in other words, the nervous system can only influence the secretion of urine by altering the vascular conditions.

Broadly speaking there are two distinct parts of the kidney where secretion occurs, viz., in the glomerulus and the tubules ; in the first water, sugar, peptones, etc., are separated by the process of secretion assisted by that of filtration, the needful pressure in the glomerulus being insured by the high blood-pressure in the renal artery, and the small size of the vein leading from the glomerulus. The dependence on blood-pressure for the secretion of urine forms a great contrast to the secretion of bile, saliva, and gastric juice, but the filtration theory is incomplete if we fail to take into consideration the vital activity of the cells of the capsule.

In the tubules the secretive power of the cells is undoubted, and affords a reasonable explanation of the presence in urine of a large amount of urea and other substances which only exist in traces in the normal blood ; the cells have the power of selecting this and other substances out of the blood stream. The peculiar selective power of the animal cell is nowhere better seen than in the kidney ; the tubules are largely supplied with blood by a plexus

formed by the vein leading from the glomerulus, yet the glomerulus elects to secrete principally water, while from the same blood the tubules elect to remove principally the organic and inorganic solids.

The amount of blood passing to the kidney is something very considerable; it has been calculated that in 24 hours 146 lbs. of blood will pass through the kidneys of a dog weighing 66 lbs.

Reference has been made to the secretion of proteid in the tuft and its reabsorption later on in the tubule; physiologists are not agreed about the accuracy of this statement, and inasmuch as no proteid is found in the normal urine of any animal, it is safe to assume that in an undamaged state the epithelial cells of the glomerulus allow none to pass.

The **Composition of the Urine** depends upon the class of animal; in all herbivora, with certain minor differences, the urinary secretion is much the same, but not so with omnivora or carnivora, which possess a distinctive urine, especially the latter. When herbivora live on their own tissues, as during starvation, they become carnivora, and their urine alters completely in character corresponding to the urine of flesh feeders; the young of herbivora, if still sucking, have a urine possessing much the same properties as that of carnivora.

But apart from this general statement, it is necessary to point out that in animals of the same class the composition of the urine will vary within very wide limits, depending upon the nature of the diet. This is a practical point of importance, and as examples occur they will be alluded to.

Urine consists of:

Water.	
Organic matter	Nitrogenous end products: urea, uric acid, hippuric acid, creatin, creatinin.
	Aromatic compounds: benzoic acid, ethereal sulphates of phenol, cresol, etc.
	Colouring matter and mucus.
Salts	Sodium, potassium, calcium, and magnesium, combined with chlorine, sulphuric and phosphoric acids.

Urea.—When the complex proteid molecule is taken in as food it eventually forms part of the body, and after performing its function is removed by the kidneys. During its passage through the system it has undergone many changes, some of which are known to us, others we can only guess it, but all the changes tend step by step to break down this complex body into simpler substances, and the end products are found in the urine as urea, uric acid, hippuric acid, etc.; these substances, therefore, represent the waste nitrogenous products of the body.

Urea is the chief of these; it represents the wear and tear of proteid tissue, but in spite of this fact it does not represent the amount of muscular work performed.

The muscles are constantly streaming out into the circulation a something which becomes urea, as it leaves the muscle it is a nitrogenous substance but it is not urea; this is quite certain for no urea can be found in muscle. The question then which has puzzled physiologists for years, and is not yet definitely settled, is how urea is formed in the body.

Urea is considered to be formed in two or three ways:

1. From the nitrogen of the food split off during pancreatic digestion in the form of leucin, glycin, aspartic acid and asparagine. These amido-acids when introduced into the body leave it as urea; they are probably broken down into an ammonia stage, and urea subsequently formed by synthesis.

2. But the amido acids will not account for the whole of the urea formed, so we are compelled to look to other substances as helping to furnish it; one of these is creatin. Creatin is found in well-marked proportions in muscle, so it is evident that it is always being formed and as rapidly carried away. By a certain line of treatment creatin may be made to yield urea, and this and certain other facts point to it as being one of the sources of urea, and the form in which this substance leaves the muscles.

3. It is possible that a portion of the nitrogen may leave the muscles as ammonium carbonate (though there is no

evidence of this) the ammonia carbonate being dehydrated into urea.

In whatever form the nitrogen leaves the muscles the synthesis into urea takes place in all probability in the liver, while according to some even the spleen and lymphatic glands may participate.

The origin of urea from carbonate of ammonia, is a practical point worth bearing in mind in examining the urine of a patient receiving this drug.

In the urine the urea exists in a free and uncombined state, though it is capable of forming salts with acids (Fig. 36). It is a substance very soluble in water.

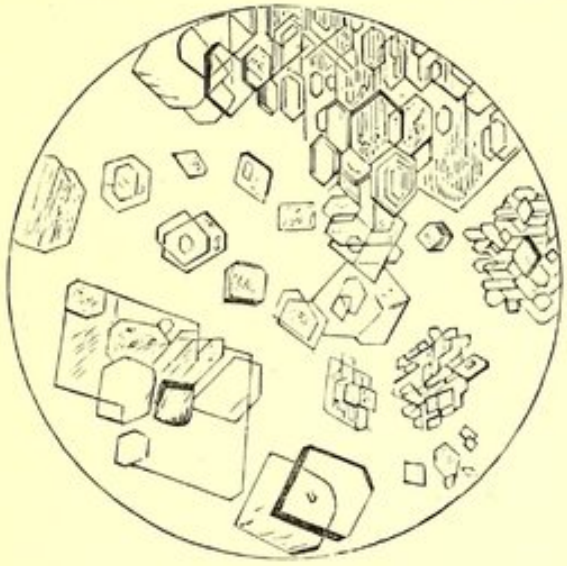


FIG. 36.—CRYSTALS OF NITRATE OF UREA (FUNKE).

The amount of urea excreted is largely influenced by the diet, we have found $3\frac{3}{4}$ ozs. as a mean daily excretion in the horse. Tereg and Munk placed it at $4\frac{1}{4}$ ozs., the weight of the horse being 880 lbs. and the diet consisting of 10 lbs. oats and $5\frac{1}{2}$ lbs. hay. On a diet consisting principally of hay these observers have shown that more urea is excreted than on one containing oats as well as hay; but even on a rigid diet great variation in the amount of urea may be met with in different horses. Speaking somewhat broadly we may say the urea of the horse varies between 3 per cent. and 4 per cent.; that of other animals will be dealt with under their respective headings.

Uric Acid.—In carnivora this substance next to urea carries off the most nitrogen from the body; in reptiles and birds it is the chief nitrogenous product.

The production of uric acid is affected by the diet, being largest on animal food and smallest on vegetable. The acid is therefore present in the dog fed on meat and in the pig, but entirely absent, so far as our observations go, in the horse in health, and probably in all herbivora unless still suckling the mother.

It is important to note that during sickness, especially when there is fever and the animal living on its own tissue, uric acid may be readily found in the urine of

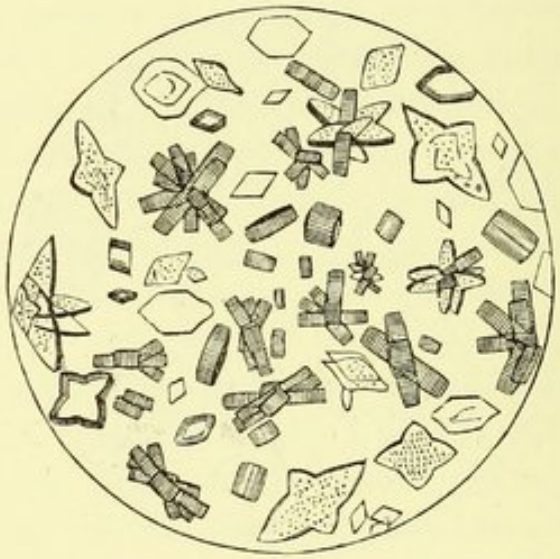


Fig. 37.—Crystals of Uric Acid (Funke).

herbivora; the explanation is simple, the animal for the time being is practically carnivorous.

Uric acid does not occur free in the urine, but in combination with soda and potash: its crystalline formation is shown in Fig. 37; it is a substance very insoluble in water, but soluble in alkaline solutions.

The acid is not manufactured in the kidney, and the exact seat of its formation in mammals is unknown, though in birds it is known to occur in the liver.

Hippuric Acid.—This acid replaces uric in the urine of the herbivora, and it may arise in two or three different ways.

It is known that hay, grass, and grains, contain in their cuticular covering a substance which yields hippuric acid in the body; if these foods be extracted with caustic potash the hippuric forming substance is removed, and if animals are fed on forage so treated no hippuric acid is formed in the body; even, it has been said, if the husk be removed from grain the latter is incapable of forming hippuric acid.

The hippuric acid found in the urine is produced by the synthesis in the system of benzoic acid and glycin (glycocoll); hay and grass yield not only benzoic acid but quinic acid, which is readily convertible into benzoic; so the initial stage in the formation of hippuric acid from hay, grass, and grain, in the production of benzoic acid.

A second source of hippuric acid is the aromatic (benzoic) products formed in the intestinal canal as the result of the putrefaction of proteids; lastly it is believed by some that hippuric acid may be formed from the aromatic residues of tissue proteids.

The chief source of hippuric acid in the herbivora would then appear to be from the benzoic acid derived from various aromatic combinations contained in plants, and this latter is combined with glycin which in all probability arises from the decomposition of albuminous tissues.

The seat of this synthesis for the dog has been ascertained by Bunge and Schmiedeberg* to lie in the kidney, and here it is brought about by the living cells of the tubules in conjunction with the oxygen of the red blood corpuscles.

In rabbits, however, it has been found that hippuric acid can be formed even when the kidneys are removed, so that it is possible the seat of the synthesis in herbivora may not entirely lie in the kidney.

Hippuric acid never exists in the free state in the urine, but either as hippurate of lime or potash, probably the former. Crystals of hippuric acid are shown in Figs. 38 and 39.

* 'Physiological and Pathological Chemistry,' Bunge.

The amount of hippuric acid excreted varies with the diet, it is increased by using meadow-hay and oat-straw, and decreased by using clover, peas, wheat, oats, etc.; as the urea rises the hippuric acid falls.

According to Munk, a horse fed on meadow-hay excretes

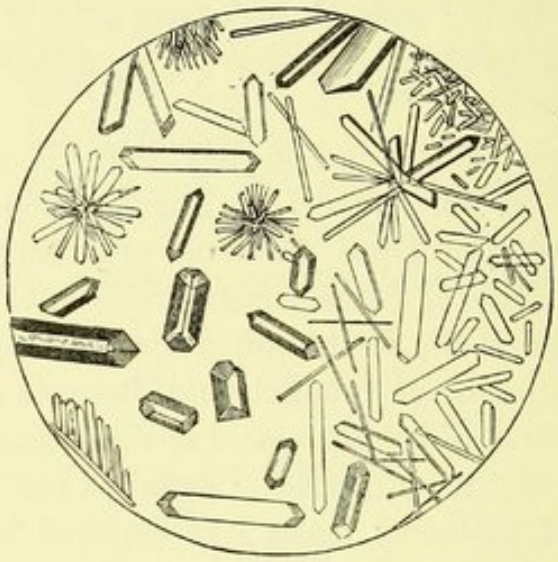


Fig. 38.—Crystals of Purified Hippuric Acid (Funke).

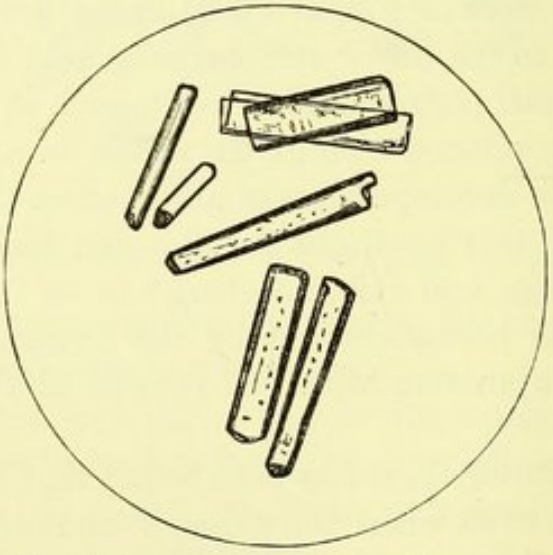


Fig. 39.—Crystals of Impure Hippuric Acid.

1·76 ozs. of hippuric acid per diem, fed on oats and a moderate amount of hay $\frac{1}{2}$ oz. to $\frac{3}{4}$ oz. per diem is yielded; this was the mean amount we found in horses fed on the same diet.

Liebig many years ago started a theory that benzoic

acid was found in the urine of working horses, and hippuric acid in the urine of those at rest; we have endeavoured to find out what truth there was in the statement. Our observations show that hippuric acid is generally found in the urine of working horses, and seldom found in the urine of horses at rest—in fact, the reverse of Liebig's theory. Hippuric acid is rarely to be found in urine 24 hours old, in fifty-four specimens we only found it eight times, this is due to its fermentative decomposition.

Benzoic Acid is the antecedent of hippuric, as just mentioned it is derived from the benzoic-acid-forming substances in vegetable food; its crystalline formation is

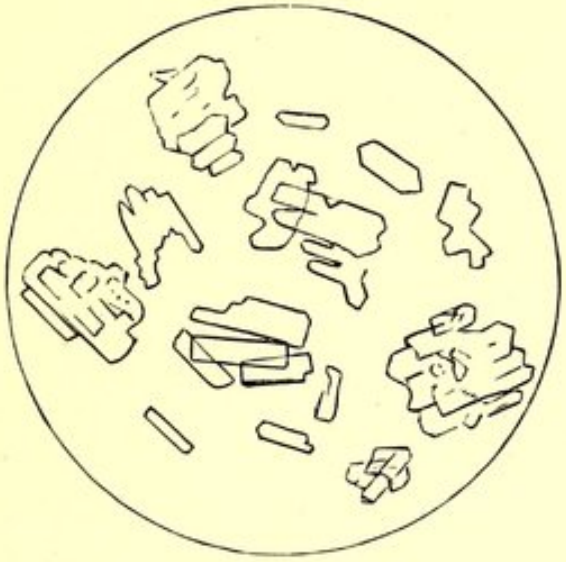


Fig. 40.—Crystals of Benzoic Acid.

shown in Fig. 40. The amount found in the urine of horses at rest is about $\frac{1}{4}$ oz. per diem.

Creatinin is found in urine, being derived from the creatin of muscle; the special interest of creatin lies in its contributing to the formation of urea, and this we have previously touched on.

Sulphuric Acid exists in the urine in two forms, first as an inorganic compound, second as ethereal sulphates. Both are derived from the decomposition of proteids, but the ethereal sulphates, or sulphonates, are combined in the form of a potash salt with phenol, cresol, catechol (pyrocatechin), indol, and skatol.

These ethereal sulphates occupy an important position in the composition of the urine of herbivora, as they are largely derived from the aromatic substances found in their food, or from the splitting up of the complex proteid molecule during pancreatic digestion. In carnivora and omnivora the ethereal sulphates are a measure of the amount of decomposition occurring not only in the proteids of the body, but of active putrefactive changes occurring either in the intestinal canal or outside it, such as in septic and suppurative diseases. This will not hold good for herbivora, as much of the material excreted does not arise from putrefaction, but is taken in with the food.

The union of the ethereal sulphates with aromatic compounds takes place in the liver. When the phenol sulphate is excreted it undergoes change in the presence of the oxygen of the air, forming, amongst other bodies, pyrocatechin which gives the brown colour to stale urine. The daily amount of ethereal sulphate compounds is about $\frac{1}{4}$ oz.

Another sulphur compound of the urine is **Sulphocyanic Acid**, found regularly in the urine of herbivora.

Indoxyl or **Indican** is formed from indol, and yields on oxidation indigo blue; it is commonly found in the urine of the horse and other animals.

Oxalic Acid in combination with lime is constantly found in the urine of herbivora, its deposit presenting a characteristic microscopical appearance (Fig. 41).

In dogs it has been produced in considerable quantity by feeding on uric acid; its origin in the herbivora is doubtless from the oxalates contained in the food.

The **Colouring Matter of the Urine** is generally regarded as being due to urobilin,* which is a decomposition product of hæmoglobin; the change may take place in the liver or kidney, though it is generally supposed to occur in the small intestines, where it is believed to be brought about by the bile pigment being acted upon by the nascent

* Quite recently Garrod has denied that urobilin is the pigment of the urine; he considers the yellow colour is due to urochrome.—*Proc. Royal Society*, vol. lv., 1894.

hydrogen, the product being absorbed and excreted by the kidneys. It is generally considered that there is only one urine pigment, but it is certain that in diseased conditions other decomposition products of hæmoglobin appear. The whole question of urinary colouring matters is in such an unsettled state that no positive statements can be made on the subject.

The Inorganic Substances found in the urine are calcium, magnesium, sodium, and potassium, existing in the form of chlorides, sulphates, phosphates, and carbonates.

The origin of these salts is from the food taken into the body, and from metabolic processes occurring in the tissues.

The nature and amount of the salts vary with the class of animal and the character of the food. In the horse potassium salts predominate, sodium and magnesium are small, phosphates are practically absent, whilst sulphates and chlorides are in considerable quantity.

It has been found that in ruminants the calcium salts are mostly excreted with the fæces, whereas in the horse they principally pass through the kidneys; in the same way it is said that sheep excrete nearly all the potassium of the food by the kidneys? whilst the horse only excretes about half by this channel. It is certain that phosphoric acid, which forms such a prominent feature in the urine of carnivora and omnivora, is in the horse almost wholly excreted by the intestines.

Calcium.—More lime exists in the urine of the horse than is soluble in an alkaline fluid, so that both suspended and dissolved lime exist, the former increases with the age of the urine, owing to the development of ammonia, until nearly the whole of the lime is precipitated. The lime exists in combination with oxalic, carbonic, hippuric, and sulphuric acids; all these combinations do not necessarily exist in one specimen of urine, the salts formed depend upon the amount of lime and the affinity it possesses for the unsaturated acids. The amount of lime in the food does not influence the production through the kidneys, but more lime is found in the urine of horses at work than of

those at rest. Oxalate and carbonate of lime crystals are common microscopic deposits in the urine of the horse (Figs. 41 and 42).

Magnesium in the urine is also suspended and dissolved,

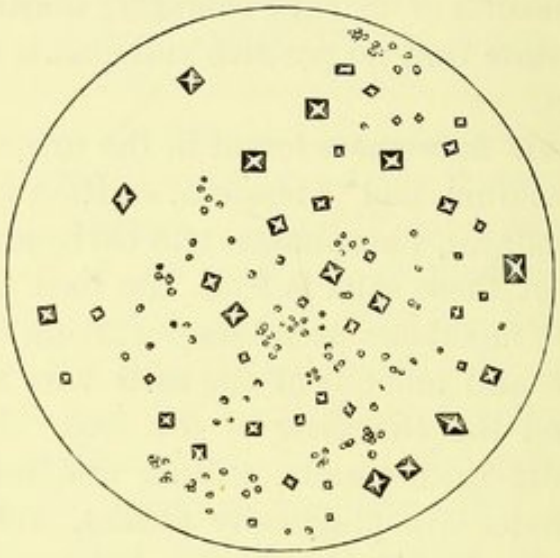


FIG. 41.—CRYSTALS OF OXALATE OF LIME (FUNKE).

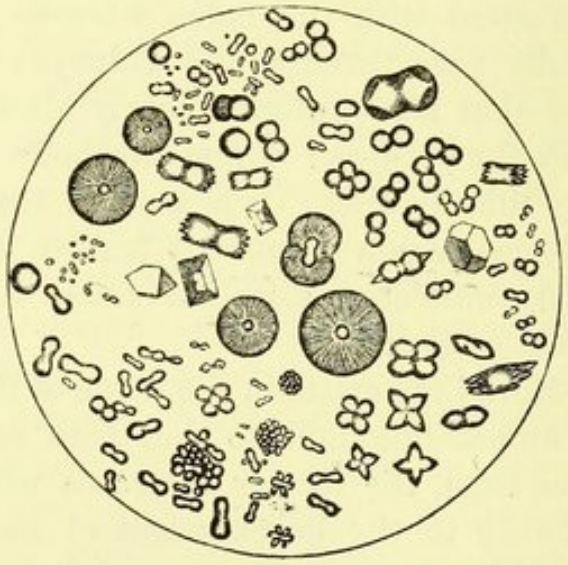


FIG. 42.—CRYSTALS OF CARBONATE OF LIME (FUNKE).

the amount which is suspended being increased by the ammonia generated as the urine gets older.

Potassium exists largely in the urine of herbivora, derived from the potash of the food; it forms numerous combinations, the one with carbonic acid being the cause of the fixed alkalinity of the urine in the horse. There is more

potash found in the urine of horses at rest than of those at work, which is explained by the considerable amount of potassium excreted with the sweat.

Sodium only exists in the urine of herbivora in small quantities, which is due to the fact that very little sodium is found in vegetable food.

Sulphuric Acid in its organic combination has been dealt with previously; the inorganic sulphur is combined with alkalies.

Chlorine is supplied by the chlorides of the food. The proportion of chlorine in the food of herbivora is not very high; the amount excreted by horses, united to the small amount of sodium present, was found by us to equal a daily excretion of 85¼ grains of common salt. In the analysis of horse's urine by Salkowski, the amount of sodium chloride excreted was put at rather more than ¾ oz. daily.

Phosphoric Acid, though existing largely in food such as oats, passes off almost wholly by the alimentary canal; sometimes only traces are to be found in the urine of herbivora, at others the amount is marked, but never considerable. Work does not influence its production.

In the urine of carnivora the phosphates are an important constituent. They exist in the urine in two forms, viz., alkaline phosphates, such as phosphate of soda or potash, and earthy phosphates, as phosphates of calcium and magnesium; these triple phosphates are common in the decomposing urine of the horse (Fig. 43). The phosphates are derived from the food and tissues.

Munk, quoted by M'Kendrick, states that if there is an abundance of lime salts in the diet, as in vegetable food, the phosphates are not eliminated to any extent by the kidneys, for the reason that they combine in the intestinal canal with lime and magnesium and pass off by that channel; if on the other hand there is but little lime and magnesium in the intestines the phosphates, united to soda and potash, pass into the blood and are eliminated by the urine.

Ammonia.—We believe that free ammonia exists in the

urine of herbivora. It may be that, owing to the amount of mucin, the urine has undergone ammoniacal fermentation in the bladder, but it is certain that perfectly fresh urine gives marked evidence of the presence of free ammonia. On standing a short time, especially in summer weather, the urea decomposes and carbonate of ammonia is largely formed.

The **Reaction** of the urine of herbivora is alkaline, the alkalinity being due to carbonate of potash. The urine of all vegetable feeders is alkaline, owing to the excess of alkaline salts of organic acids, such as malic, citric, tartaric and succinic contained in the food; by combustion in the

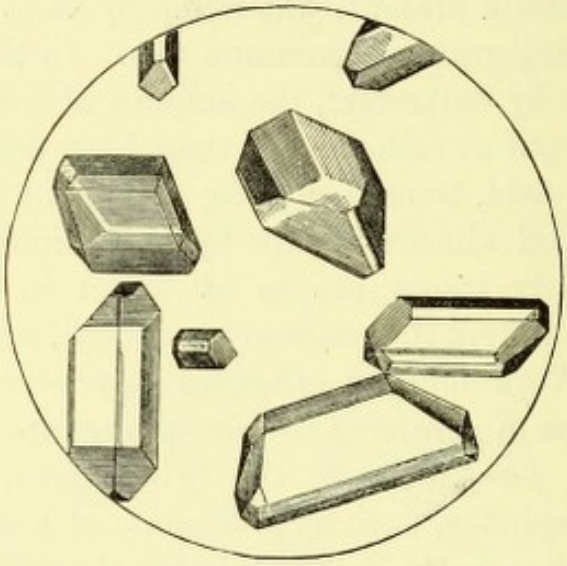


Fig. 43.—Crystals of Triple Phosphate (Funke).

system these salts are converted into carbonates, and appear in the urine where they produce considerable effervescence on the addition of an acid. The nature of the food influences the reaction, for it is stated that the urine of the horse may be rendered acid by feeding entirely on oats. A considerable quantity of the alkalinity present in stale urine of the horse is due to the exceedingly rapid change which occurs in it on standing, leading to the breaking up of part of the urea and the formation of ammonia carbonate. The fixed alkalinity of the urine for the twenty-four hours in the horse is equivalent to the excretion of between 45 grains to 60 grains of potassium oxide.

In the dog the urine is acid due to the acid phosphate of soda, and not to any free acid; no free acids exist in the urine of any animal.

In the pig the reaction is either acid or alkaline depending on the diet; an animal diet producing an acid and a vegetable diet an alkaline urine.

Urine of the Horse.

Specific Gravity.—This varies considerably depending on the diet. The mean of a large number of observations was 1036, the highest registered was 1050 and the lowest 1014.

The Quantity of urine is liable to very considerable variation depending on the diet; the more nitrogen the food contains the larger the amount of urine excreted. The mean of a large number of observations was 8½ pints in 24 hours, the diet being moderately nitrogenous, but in individual instances very much more than this may be met with, viz., 12, 15, or even 20 pints.

Horses at work excrete less urine than those at rest, probably owing to the loss by the skin.

Of the total water consumed, about one-fifth passes away in the urine, though Munk* considers that one-third passes away by the kidneys and two-thirds by the lungs. An interesting point is the ultimate disposal of the water consumed by various animals; it has been found that carnivora excrete by the kidneys the greater part of the water they drink, whilst herbivora excrete the greatest part by the lungs.

Here is Munk's table:

Man: 60 per cent. of water escapes by the kidneys, and 40 per cent. by the lungs and skin.

Carnivora: 70 per cent. of water escapes by the kidneys, and 30 per cent. by the lungs and skin.

Herbivora: 30 per cent. of water escapes by the kidneys, and 70 per cent. by the lungs and skin.

---

* Quoted by M'Kendrick.

The *Odour* of urine is said to be due to certain aromatic substances of the phenol group. Perfectly fresh urine has a most distinct though faint smell of ammonia.

The normal fluid is always turbid, some specimens more so than others; very rarely is it clear, and then only for a short time. The turbidity is due to the amount of suspended carbonate of lime and magnesia which exists in it: as the urine cools, particularly if it undergoes ammoniacal fermentation, the amount of turbidity becomes intense.

The *Consistence* of the fluid depends upon sex, and perhaps on the season. It is certain that some mares excrete a glairy tenacious fluid which can be drawn out in strings, due to the amount of mucin it contains; it is very common to find it as thick as linseed-oil, and very rare to find it fluid and watery. During œstrum the urine is of the consistence of oil.

The *Colour* of the urine is yellow or yellowish-red, rapidly turning to brown, the dark tint commencing on the surface of the fluid and gradually travelling into its depth. The cause of the colour is due to the oxidation of pyro-catechin (see p. 262).

The *Total Solids* of the urine consist of organic and inorganic matter, of which on a mixed diet 5 ozs. are organic and 3 ozs. inorganic; they are liable to great variation, sometimes being found to be greatly in excess of that mentioned.

The total solids are considerably affected by the diet; E. Wolff* found that when he reduced the hay and increased the corn ration the solids in the urine decreased, whereas on a diet consisting principally of hay and but little corn the solids increased; for example, on a diet of 17·6 lbs. hay and 4·4 lbs. oats the urinary solids for 24 hours amounted to 20 ozs., whilst on a diet of 8 lbs. hay, and 13·2 lbs. oats, the total solids fell to 16¼ ozs.; this is an important point to bear in mind.

The composition of the mineral matter excreted is given

* Ellenberger.

in the following table by Wolff. In every 100 parts of mineral matter there are found:

Potassium	36·85 per cent.
Sodium	3·71 ,,
Calcium	21·92 ,,
Magnesium	4·41 ,,
Phosphoric acid	—
Sulphuric ,,	17·16 ,,
Chlorine	15·36 ,,
Silicic acid	·32 ,,

In the following table are given the results obtained by us in the examination of the urine of rest and work:

TABLE SHOWING THE MEAN COMPOSITION OF THE TWENTY-FOUR HOURS' URINE OF HORSES AT REST AND WORK.

	Rest.	*Work.*
Quantity	8·689 pints	7·877 pints
Specific gravity	1036	1036
Total solids	8·114 ozs.	8·188 ozs.
Organic solids	5·155 ,,	5·368 ,,
Inorganic solids	2·94 ,,	2·820 ,,
Urea	3·4744 ozs.	
Ammonia carbonate as urea	·4626 ,,	
Ammonia	·887 ,,	·187 ,,
Benzoic acid	·23 ,,	
Hippuric acid		·549 ,,
Phosphoric anhydride	·046 ,,	·067 ,,
Sulphuric ,,	·375 ,,	·539 ,,
Other sulphur compounds	·258 ,,	·271 ,,
Chlorine	1·118 ,,	·775 ,,
Calcium oxide	·121 ,,	·067 ,,
Magnesium oxide	·105 ,,	·093 ,,
Potassium ,,	1·290 ,,	·954 ,,
Sodium ,,	·088 ,,	·064 ,,

A special study has been made of the urine by Salkowski, who has examined that of the horse. The animal experimented upon was fed on 4·4 lbs. oats, 4·4 lbs. hay, 2·2 lbs. bran, and an unmeasured amount of straw-chaff. The reaction of the 24 hours' urine was neutral, the quantity was $3\frac{1}{2}$ pints, and the specific gravity 1046.

It presented the following composition:

Water - - - -	3·5 pints
Organic solids - - -	6·25 ozs.
Ash - - - -	1·60 ,,
Urea - - - -	3·25 ,,
Ammonia - - -	5·53 grains
Hippuric acid - - -	·49 oz.
Phenol - - - -	37·89 grains
Organic sulphur - -	208·69 ,,
Inorganic ,, - - -	85·77 ,,
Phosphoric acid - - -	3·40 ,,
Lime - - - -	88·50 ,,
Sodium chloride - -	·87 oz.

In the following summary of the urine of animals other than the horse, the analytical tables are those given by Tereg.*

The Urine of the Ox.

This is much the same as that of the horse, excepting that it is secreted in larger amounts, 10 to 40 pints, the differences largely depending upon the amount of nitrogenous matter in the diet, for it has been shown that the more nitrogen a diet contains the larger the amount of water consumed.

The fluid is clear, yellowish, and of an aromatic odour; it is of a lower specific gravity than the horse, 1007 to 1030 (in milch cows, according to Munk, 1006 to 1015), owing to the larger amount of water secreted, and the smaller quantity of solids contained.

The nitrogenous matter in the urine, mainly represented by urea and hippuric acid, varies according to the diet. On a diet of wheat straw, clover hay, beans, starch, and oil, the amount of urea was found to be 4·06 per cent.; whilst on one of oat straw and beans it fell to ·84 per cent.; when the urea is high, the hippuric acid is low, and *vice versâ*. The largest amount of hippuric acid is

* Ellenberger's 'Physiologie.'

produced by feeding on the straw of cereals, the smallest by feeding on leguminous straw, whilst a medium amount is produced by feeding on hay.

The urine of ruminants contains less aromatic sulphur compounds than that of the horse, and more of the inorganic sulphur, but, like the horse, the phosphates are either absent or only occur in small amounts.

Here is a table of Tereg's showing the composition of the urine of the ox on different diets, the observations extending over four months:

	lbs.	*lbs.*	*lbs.*	*lbs.*
Total quantity of urine -	26·026	31·174	29·986	18·326
,, ,, dry matter -	1·716	1·518	1·408	1·144
,, ,, ash - -	·880	1·012	1·034	·660

Calves still sucking excrete an acid urine rich in phosphates, uric acid, creatinin, and a peculiar substance allantoin; it is poor in urea, and, according to Moeller, contains hardly 1 per cent. of solids.

The Urine of the Sheep.

This has an alkaline reaction, a specific gravity 1006 to 1015, and the amount excreted is from ·5 pint to 1·5 pints. Tereg gives the following percentage composition of a sample:

Water - - - -	86·48
Organic matter - - -	7·96
Inorganic matter - -	5·56

The organic matter contained:		*The inorganic matter contained:*	
Urea - - -	2·21	Chlorine - - -	1·05
Hippuric acid - -	3·24	Potassium chloride -	1·84
Ammonia - -	·02	Potassium - -	2·08
Other organic substances -	2·07	Lime - - -	·07
Carbonic acid - -	·42	Magnesia - -	·20
		Phosphoric acid - -	·01
	7·96	Sulphuric ,, - -	·24
		Silica - - -	·07
			5·56

In sheep urea and hippuric acid stand in the proportion of 2 to 3, whereas in cattle on the same diet the proportion is 16 or 20 of urea to 11 or 13 of hippuric acid.

The food most productive of hippuric acid in the horse is old meadow hay, whilst *new* meadow hay has this effect on sheep.

In sheep there is very much more magnesia than lime in the urine, consequently the reverse obtains in the fæces of the same animal.

The Urine of the Pig.

This resembles that of carnivora, but its composition, etc., depends on the character of the food. The specific gravity is 1003 to 1025, it is either acid or alkaline; the amount excreted varies between 2½ to 14 pints, and it contains uric acid, hippuric acid, xanthin, guanin, and much urea.

Here is an analysis, the diet of the animal being one of peas, potatoes, and sour milk:

Total urine	7 pints
Sp. gr.	1018
Dry substance	2·768 per cent.
Total nitrogen	·604 ,,
Ammonia	·024 ,,
Ash	1·234 ,,

The ash consisted largely of phosphates and potassium, a fair amount of magnesia, but very little sodium and calcium.

The Urine of the Dog.

It is impossible to give any idea of the composition of the urine of the dog, as the daily amount of constituents secreted vary considerably depending upon the nature of the diet.

The urine is acid in reaction on a flesh diet, the acidity

being due to acid phosphate of soda; on a vegetable diet it may be alkaline. The amount excreted is from $\frac{3}{4}$ to $1\frac{3}{4}$ pints daily, but varies with the size of the animal and the nature of the diet; the specific gravity is from 1016 to 1060 depending on the diet; the colour is yellow to golden yellow; the urea varies from 4 per cent. to 6 per cent. On an animal diet uric acid is excreted but disappears on giving vegetable food; hippuric acid in small quantities appears with fair regularity; indigo and phosphoric acid are well-marked constituents, and a substance known as glycuronic acid may be found which exercises a reducing action on salts of copper. The presence of bilirubin in the urine of the dog has been noted by Salkowski (see p. 193).

As an illustration of the variation of the dog's urine depending on the nature of the diet, we may take an example from a long series of experiments by Bischoff and Voit.

On a diet consisting of meat ·57 lbs., starch ·71 lbs., salts 77·5 grains, the urine gave the following composition:

Amount	·44 pint
Sp. gr.	1049
Urea	326·6 grains
Salts	85·6 „

On a diet consisting of meat 2·75 lbs. and fat ·55 lbs., the following was the composition:

Amount	1·23 pints
Sp. gr.	1054
Urea	1,351 grains
Salts	189 „

Glycuronic acid exists only in traces, but after the administration of camphor or chloral it is obtained in well-marked quantities. The point of practical importance is to avoid regarding dog's urine which reduces salts of copper as necessarily containing sugar.

The Discharge of Urine.—The secretion of urine is continuous; from the pelvis of the kidney it is discharged into the ureter, and its descent to the bladder is favoured by the

action of gravity. Apparently the action of gravity is insufficient for the purpose, for in the rabbit rhythmical contractions of the ureters are observed to occur, which pass from the kidney to the bladder, and are repeated at regular intervals.

On reaching the bladder the urine falls drop by drop into its cavity from the mouth of the ureters; the latter pierce the bladder wall obliquely, so that as the bladder becomes distended there is no reflux into the ureters.

The bladder consists principally of involuntary muscle fibre arranged in a longitudinal, circular, oblique, and spiral manner; the former being, at any rate in the dog, the best developed. The sphincter of the bladder is formed by Wilson's muscle, which encircles the membraneous urethra, and not by the circular fibres of the bladder.

The nerve supply to the bladder is of a double origin, viz., through the hypogastric nerves from the sympathetic system, and through the sacral nerves direct from the spinal cord; it is supposed that the sympathetic supplies the circular, whilst the sacral supplies the longitudinal fibres of the bladder.

In the spinal cord there exists a centre for micturition which is under the control of a higher centre in the medulla, though this control is not essential, at any rate in some animals, for the full development of the act of micturition. In the dog, for example, micturition occurs perfectly after the spinal cord is divided between the dorsal and lumbar portion; the process is here carried out as a reflex act.

In the horse we have observed that severe injury to the spinal cord in the lumbar, and even in the dorsal region, is not always immediately followed by loss of power over the bladder or rectum, and such may not occur until inflammation and degeneration take place.

Either as a reflex or volitional act the micturition centre, through its afferent and efferent nerves, keeps control over the sphincter of the bladder, tightening its grip as the organ advances in the pelvis through distension, and, by

means of this centre, acquainting the mind with the degree of distension which exists.

When the process of micturition commences the sphincter relaxes, the involuntary muscle of the bladder wall contracts, the diaphragm is fixed, and the abdominal muscles contract; the urine is thus forced into the urethra, along which it is pressed by the accelerator urinæ muscle.

During the act both the horse and mare stand with the hind-legs extended and apart, resting on the toes of both hind feet, thereby sinking the posterior part of the body; the male animal also often advances the fore-legs in order to avoid getting them splashed, in this position the penis is protruded, and the tail raised and quivering. The stream which flows from the two sexes is very different in size, depending on the relative diameters of the urethral canal. The mare after urinating spasmodically erects the clitoris, the use of which it is difficult to see; it may be due to the passage of a hot alkaline fluid over a remarkably sensitive surface.

The horse can under ordinary circumstances only pass urine when standing still, though he can defæcate while trotting; but, if considerably excited, the bladder can be emptied even at a canter.

In the ox the urine simply dribbles away, owing to the curves in the urethral canal, and is directed towards the ground by the tuft of hair found on the extremity of the sheath. The ox can pass his urine while walking.

The cow arches her back to urinate, but instead of extending her hind-limbs as does the mare, she brings them under the body, at the same time raising her tail.

CHAPTER XI.

NUTRITION.

Wear and tear is momentarily taking place in the bodies of all animals, and as fast as destruction occurs repair must follow.

We have previously studied the various channels in the body which supply the income and furnish an outlet for the expenditure, but this is only the beginning and the end of the process; to attempt to trace the exact changes which occur, say in the body of a pig, in producing 100 lbs. of living material from 500 lbs. of barley-meal, is an impossibility; all we can do is to interpret the coarser or more obvious processes which take place, the conversion of food into living tissues being quite beyond our knowledge.

Composition of the Body.—The animal body consists of proteids, fats, salts, water, and a very small proportion of carbo-hydrate. Every food must either contain these principles, or be capable of conversion into them within the animal body.

Here is a table from Lawes and Gilbert, showing the relative proportion of these various tissues in oxen, sheep, and pigs, in store condition:

	Ox.	*Sheep.*	*Pig.*
Water - -	60·8	63·5	61·2
Proteids - -	18·0	15·0	14·0
Fat - - -	16·0	18·0	22·0
Ash - - -	5·2	3·5	2·8

The water is always in the largest and, excluding the carbo-hydrate, the salts in the smallest proportion. The

amount of fat depends upon the condition, in fat animals it may, roughly speaking, be double the amount given in the above table.

The great bulk of the body is represented by the muscles, and these hold half the water and half the proteid found in the system.

The following table shows the proportion of the chief body constituents of an adult horse weighing 1,100 lbs., and it may be compared with that of a cat:

	Horse.	*Cat.*
Muscles and tendons	45 per cent.	45 per cent.
Bones	12·4 ,,	14·7 ,,
Skin	6·02 ,,	12·0 ,,
Blood	5·90 ,,	6·0 ,,
Abdominal viscera	5·49 ,,	
Thoracic ,,	1·60 ,,	

According to Lawes and Gilbert the following table shows the relation of parts in the ox, sheep, and pig for every 100 lbs. of living weight:

	Ox.	*Sheep.*	*Pig.*
Heart, lungs, liver, blood and spleen	7·0	7·3	6·6
Internal loose fat	4·6	6·9	1·6
Stomach and contents	1·6	7·5	1·3
Intestines ,, ,,	2·7	3·6	6·2
Other offal parts	13·0	15·0	1·0
Muscle, bone and surrounding fat	59·3	59·2	82·6

Income and Expenditure.—In order to arrive at a knowledge of the processes involved in nutrition, tables of the income and expenditure of the body have been drawn up.

The *Income* of the body consists of carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, salts and water; these are contained in the food, the oxygen being mainly supplied by the air taken in at the lungs.

The *Expenditure* consists of the same elements, which are got rid of by the lungs, urine, and skin.

The nitrogen is excreted almost wholly by the urine, excepting in the horse where there is a loss by the skin. It is usual to regard the urine nitrogen as a measure of the proteid changes in the system, and this nitrogen is got rid

of mainly as urea, and in smaller proportion as uric and hippuric acids, and minor nitrogen compounds. The hydrogen is excreted as water by the lungs, skin, and urine, and very small quantities by the respiratory passages. The carbon is largely got rid of by the lungs, by the carbon compounds found in the urine, and in the horse by the skin. The salts are excreted by the kidneys, skin, and in the form of secretions. The sulphur is lost through the kidneys, epithelium, hair, and horn.

It is hardly necessary to add that in calculating the total income of the body the fæces must be subtracted; though existing in the alimentary canal they are outside the body and form no part of it.

When the income balances the expenditure the body is in equilibrium; if the expenditure exceeds the income the body loses weight, and if the income is in excess of the expenditure the animal gains weight.

Income and expenditure experiments have been made on all animals, mainly to determine the actual amount of food required to maintain the body weight; such experiments are extremely difficult and tedious, especially on animals; the composition of everything passing into and out of the body must be ascertained, and if the body remains exactly in equilibrium the amount of the elements found in the expenditure must equal that occurring in the income.

For this reason slight analytical errors may lead to very considerable error in calculation, and as we believe that error does exist in those tables already compiled they are not reproduced.

Metabolism.—By this term is understood the changes occurring in living tissues.

It is evident from all that has been said that constant breaking down and building up is occurring in the body; every muscular contraction, every respiration, the beating of the heart, and the movements of the bowels, all mean wear and tear, and as rapidly as a part is destroyed it must be replaced. The process of construction is known as **anabolism**, and of destruction as **katabolism**, in a perfect

state of health these should be in equilibrium. Both repair and destruction are dependent upon definite chemical changes occurring in the system, some of which we have a fair knowledge of, others are wrapped in obscurity.

We must not lose sight of the fact that the metabolism of the tissues is under the influence of the nervous system, by which is regulated apparently both their nutrition and the rate of their destruction. We have previously studied a good example of this in dealing with the secretory nerves of the submaxillary gland, and it is probable, though our information on the point is very defective, that under the guiding influence of the nervous system the nutrition of the body is largely maintained.

We constantly observe muscular wasting in some forms of lameness and injury in the horse, which is out of all proportion to the atrophy a part suffers by being simply thrown out of use, and it can only be explained by injury to the trophic nerves which regulate the nutrition of the part.

Even a better example are the peculiar changes which sometimes follow direct injury to trophic nerves, as in plantar neurectomy of the horse; the sloughing of the entire foot, or gelatinous degeneration of the phalanx, is due to injury of the trophic nerves.

Injuries to the fifth pair of nerves have been followed by sloughing of the cornea, and pneumonia has followed division of the vagi, but in these cases the resulting disease may be due to mechanical irritation from dust in the one case, and food falling into the air-passages in the other, and it is not possible to determine to what extent loss of trophic influence is responsible.

But disordered nutrition of a tissue may show itself without any obvious injury to trophic nerves, as for example in the phenomenon known as inflammation, or the well-known sympathy existing between the digestive system of the horse and the laminæ of the feet, or between a chronic eczema of the skin and a brittle condition of the horn of the foot.

Further evidence of nervous action is afforded in nutrition which is normal in character, such as the change of the

coat with the season of the year. The influence of light on metabolism is also probably effected through the nervous system; also it appears certain that a connection between visual sensations and the nutrition of the skin occurs in blind men and animals, and the popular belief that a blind horse carries a heavy coat in summer and a short one in winter may be something more than mere superstition.

But in making these statements we must guard against the error of considering that no growth, repair, or reproduction can take place excepting under the influence of the nervous system; the trophic influence exercised by nerves appears to be directed to maintaining in equilibrium the processes of building up and breaking down which are occurring in all tissues.

Though the metabolism of the body is largely regulated by the nervous system, yet the process cannot be carried out without food. It is true that metabolism is carried on during starvation, but even then food is being supplied, inasmuch as the animal is living on its own tissues.

The food must contain the elements required by the tissues, referring to the table on page 276, we may say that every food must supply the principles found in the body, viz., water, proteid, fat (or carbo-hydrate) and salts; each of these must be in proper proportion neither deficient nor in excess of the animal's requirements; each must be present, fat cannot be substituted for proteid, nothing can take the place of salts, and a water-free diet would not sustain life long.

We have, therefore, to inquire why it is these substances are absolutely essential in every diet, and how they behave in the system.

Nitrogenous Food.—If an animal be fed exclusively on proteid, it is found in the first instance that practically the more it eats the more nitrogen it excretes by the kidneys; at last a period arrives when the amount of nitrogen passing by the kidneys equals the amount being taken in at the mouth, and such an animal is said to be in 'nitrogenous equilibrium.' A dog requires $\frac{1}{20}$ of its weight daily in lean meat to attain nitrogenous equilibrium.

It is only possible to carry out this experiment on dogs, and even with them nitrogenous equilibrium can only be maintained for a short time; it is impossible to obtain it unless the animal starts the experiment with some stored-up fat in its body.

Before commencing the experiment, the amount of nitrogen daily excreted by the dog during starvation is ascertained—let us assume this amount to be 77 grains per diem. If we now wish to establish nitrogenous equilibrium and give a meat diet equivalent to 77 grains of nitrogen, it will be found insufficient for the purpose; instead of storing up nitrogen as we might expect the animal to do, more will pass off by the kidneys than is entering by the mouth; in fact, to obtain nitrogenous equilibrium three times the amount of nitrogen must enter the body as food, compared with the amount lost during starvation, viz., 231 grains instead of 77. With a flesh diet containing 231 grains of nitrogen the above dog will be in nitrogenous equilibrium, for the same amount of nitrogen will be recovered from the urine as enters as food.

In studying the changes produced by the above diet, we observe that the effect of proteid is to stimulate tissue metabolism, that is the reason why in the first instance more nitrogen is given off by the kidneys than entered by the mouth, even though we give in food the amount of nitrogen which experiment has shown to be lost during starvation.

Such a diet as we have spoken of is seriously deficient in carbon, and the reason why the animal has to eat so much to balance its nitrogen output, is owing to the fact that the excess of flesh consumed is required to supply the necessary carbon. Proteid contains 15·53 per cent. nitrogen and 53 per cent. carbon; the carbon of proteid is an expensive and wasteful method of supply. The supply of carbon required by the body is essentially the function of non-nitrogenous food, and as a matter of fact if carbon be given to the above dog in the form of fat, a very much smaller diet of flesh will place its body in nitrogenous equilibrium.

Returning, however, to a purely proteid diet, it is found from experiment that if an amount be supplied equivalent to that required for nitrogenous equilibrium, the animal gains weight and is evidently storing up something in its body. It is found that this something stored up is fat, and that it is derived from the carbon portion of the proteid; it has been calculated that 100 parts of proteid are in this way capable of furnishing 42 parts of fat.

From these observations it has been determined that proteid breaks up in the body into two portions, one the nitrogenous portion which is excreted as urea, the other the non-nitrogenous portion which is stored up in the system as fat.

Under the circumstances of an ordinary nutritive diet the whole of the nitrogen of the proteid is not excreted as urea, a portion remains in the system and is converted into tissue. According to some observers the nitrogenous portion which gives rise to urea has been termed 'the circulating albumin,' the other or smaller portion which is stored up 'the tissue albumin.'

Considerable discussion has occurred with reference to Voit's theory of circulating and tissue albumin, and it is generally considered that the line drawn by this observer between the two does not hold good, and that he is not warranted in stating that urea is derived from that portion of the proteid which never becomes a part of the living body, viz., from the 'circulating albumin.' It is undoubted that under ordinary circumstances a portion of the nitrogen taken in does form urea and allied substances, whilst another portion is converted into tissue; but it by no means follows from this that the urea moiety is not derived from living tissue.

So long, therefore, as we are careful not to regard the circulating albumin as so much dead substance, no harm can arise from the use of the terms 'circulating' and 'tissue albumin,' as expressing the idea that part of the proteid is retained in the body and part cast off from it.

The metabolism of proteid material results in urea, we

have previously considered (p. 256) the sources of this substance in the body; to follow step by step the breaking down of the complex proteid molecule to the simpler substance urea, is not possible in the present state of our knowledge, but the channels through which this substance travels from complexity to simplicity are (1) by the breaking up of proteid in the intestine, the formation of leucin and tyrosin, and the conversion of these into urea in the liver; or more largely by (2) the circulating proteid, and to a limited extent only by (3) the tissue proteid.

All true proteids are equally capable of becoming part of the tissues when taken as food, but when albuminoids, like gelatin are consumed, they produce the same amount of urea as an assimilable proteid, but the animal loses flesh, viz., none of the material is stored up in the system; when gelatin is mixed with proteid it exercises a sparing action upon the latter, and less of it is used up in the body.

Non-nitrogenous Food.—When animals are fed on an exclusively fat or starch diet they soon succumb; it is impossible to maintain life on a nitrogen-free food. In experiments made with fat and starch some proteid must therefore always be given at the same time.

The most remarkable effect of proteid and fat being given together, is that much less proteid is used in the system when fats are given than without them; this is spoken of as the proteid-sparing action of fats, and we drew attention to it in speaking of the dog in nitrogenous equilibrium. The amount of proteid required by the system is diminished by the presence of carbo-hydrates; this is an important feature in the feeding of herbivora, in the food of which very little natural fat exists. It has been suggested that the proteid-sparing action of carbo-hydrates and fats is due to the fact that they are oxidized more readily than albumin, and that they thus prevent the action of oxygen on proteid. Conversely it has been found that the administration of considerable amounts of proteid hasten the destruction of fat, as in Banting's system of treating obesity. The practical point is that the non-nitro-

genous substances spare the nitrogenous, whilst the latter hasten the destruction of the non-nitrogenous material.

The formation of fat occurs in three ways: (1) From the fat which enters the body, which in the herbivora is small unless fed on oilcake; (2) from the carbonaceous residue of the proteid substances; (3) from the carbo-hydrates of the food. It has been clearly shown by experiment that animals have stored up fat on a purely proteid diet, and that without doubt the vast quantities of fat found in highly-fed animals have their origin in the proteid and carbo-hydrate substances of the food. Further evidence on this point is the fat found in milk, which greatly exceeds in amount any fat which may be partaken of in the diet.

Apparently the fat is not deposited in the tissues in the form in which it is received. The fat of the body varies in composition in all animals, horse, dog, ox, sheep, and pig, and it is not affected by the animal receiving fats foreign to the body; none of these foreign fats are deposited as such, the animal's body converts them into the fat peculiar to itself before they are stored up, so that nothing like a direct deposition of the fat received in the food occurs. The dog fed on fats of high-melting point, like those of the ox, converts them into fats of low melting-point, and the ox converts low melting fats into fats of high melting-point. This is evidence that the fats are not directly deposited, but have to pass through the laboratory of the organism.

Owing to the large amount of carbo-hydrate food used by herbivora, and to the fact that carbo-hydrates require less oxygen for their oxidation than fat, more of the oxygen consumed finds its way back in the carbonic acid of the egesta with herbivora than is the case with carnivora, where the greater portion of the oxygen leaves the body combined with hydrogen in the form of water. Herbivora therefore use less oxygen than carnivora, and the respiratory quotient, as seen in the chapter on 'Respiration,' p. 87, is consequently greater.

Inorganic Food.—The salts in the body perform important functions in connection with secretion and excretion;

as Foster expresses it, they direct the metabolism of the body, though how they do so is unknown. Their distribution throughout the structure is remarkably regular, sodium and chlorides being found in the blood-serum, potassium and phosphates in the red cells, sulphur in hair and horn, potassium in sweat, sulphur and phosphorus in proteid tissue, phosphates and lime in bones, etc.

When a deficiency in salts occurs, the body apparently for some time draws on its own store, and then certain nutritive changes follow; animals fed on a diet which is as far as possible rendered free from salts soon die. Both organic and inorganic salts are required by the body.

The chief salt used by herbivora is potassium, whilst sodium is used by carnivora. Both carnivora and herbivora obtain in their natural diet a sufficiency of these salts, though the general impression is, that the wild herbivora long for sodium. It is quite certain that under the conditions of domestication horses can be kept in perfect health without receiving any sodium chloride, other than that contained in the food, and the amount of this in vegetable substances is small.

It is evident that the daily quantity of salts required must depend upon the age of the animal, young growing animals requiring more than adults.

Water consumed in considerable quantities increases metabolism; the amount ordinarily partaken of depends upon the work performed and the nature of the diet.

Starvation.—When an animal is starved it lives on its own tissues; in the herbivora the urine becomes acid, hippuric is replaced by uric acid, and the secretion becomes clear. The elimination of nitrogen in the starving animal at first falls rapidly, then gradually, and shortly reaches a fluctuating daily quantity. During starvation the carbonic acid excreted falls in amount, and the oxygen absorbed becomes reduced, though not in proportion to the fall of carbonic acid.

If water be given life is considerably prolonged; Colin records a case (to be mentioned presently) where a horse

receiving water lived thirty days without food. It is notorious that herbivora, though they lose less proteid during starvation than carnivora, do not withstand starvation so well; nor need we go so far as a starvation experiment to ascertain this fact; when men and horses are being hard worked, the loss in condition amongst the horses sets in early, and is extremely marked for some time before the men show any appreciable muscular waste. One explanation offered as to the reason why herbivora withstand starvation so badly, is that they possess less circulating and less tissue albumin.

Horses have been known to live without food or water for as long as three and dogs for four weeks; but it is said that if horses have suffered 15 days' starvation, the administration of food after this time will not save them.

Dewar* records two remarkable instances of the length of time sheep will withstand starvation; in one instance eighteen sheep were buried in the snow for six weeks and only one died, and that was the day they were released; the other animals were scarcely able to walk. In the second case seven sheep were buried for eight weeks and five days, and all were recovered alive and eventually did well.

Colin records an experiment where a horse weighing 892 lbs. was starved for 30 days, only being allowed 2·46 pints of water per diem. The animal was nourished on its own tissues, the daily loss in weight being 5·9 lbs., which must be considered as exceptionally small.

When this horse died the body weight was 715 lbs., and it was found that of all the organs the kidneys had suffered the greatest loss, 41·6 per cent. of their weight; next the lungs, 38 per cent.; the stomach and intestines (empty), 35 per cent; the skeleton, 26 per cent.; skin and hoofs, 21 per cent.; muscles, 19·6 per cent.; heart, 17·8 per cent.; pancreas, 17 per cent.; spleen, 16 per cent.; liver, 12 per cent.; brain and spinal cord, 2·3 per cent.

It is most remarkable that the muscles should have suffered so little. It was found that the amount of fat

* *Veterinarian*, May, 1895.

after 30 days' starvation was actually greater than that found in a healthy control animal of equal weight destroyed for the purpose of comparison; the case must therefore be regarded as exceptional, but is introduced here as being probably the only experiment of its kind made on horses.

In some very accurate experiments on a starving cat, it has been shown that the principal loss occurs in the fat, 97 per cent. of which disappeared in 13 days; here is a table showing the percentage of dry solid matter lost by the tissues:

Fat	97 per cent.
Spleen	63·1 ,,
Liver	56·6 ,,
Muscles	30·2 ,,
Blood	17·6 ,,

The loss in the glandular organs is very heavy, next follow the muscles, and then the blood. The central nervous system suffers no loss; it is evident that its nutrition is kept up at the expense of other tissue of less importance.

It has been found by experiment that old animals bear starvation much better than young growing ones, as their requirements are smaller.

Cause of Body Waste.—The work of the body may be described as internal and external, by internal work we refer to respiration, the action of the heart, movement of the bowels, animal heat, etc., by external work is understood those movements of the muscles which transport the body; in both cases the work results in the production of heat and motion.

Every diet given to an animal must take these two factors into consideration; the ration of subsistence is for the internal work of the body, the ration of labour supplies the external.

The changes in the tissues resulting in heat and motion occur principally if not exclusively in the non-nitrogenous elements, this has been settled beyond all doubt. Considering that no animal can live on a nitrogen-free diet, and that the harder the work performed the larger the amount

of nitrogen required, one would have thought, as Liebig did years ago, that the source of energy in food was the proteid substance; this is not so, therefore the urea is no measure whatever of the work performed, in fact is hardly affected by work, though, as we have shown in the dog, it is largely affected by the amount of nitrogen received in the food.

The explanation of the necessity for proteid food is far from known, one reason offered is that it determines the absorption of oxygen, but this is by no means a complete explanation of one of the fundamental facts in feeding.

During work the heart and respirations are quickened, the horse sweats, and a larger volume of air is warmed in the lungs, all this means a loss of heat to the body; in addition the muscles produce heat as the result of contraction, in fact every process seems to tell essentially on the non-nitrogenous elements of the body, which is the explanation why carbo-hydrates are so necessary in the diet of hard-worked horses.

The **Energy yielded by Food** has been ascertained by burning the substance in a calorimeter and measuring accurately the amount of heat given off; in this way has been ascertained the potential energy of each food substance, proteid, fat, and carbo-hydrate. Every 1 gramme (15·432 grains) of water in the calorimeter raised 1° C. (1·8° Fahr.) is called a heat unit, by this method of investigation it has been found that

15·432 grs.	of	proteid	evolve,	when	oxidised,	4,500	heat units.
,,		fat	,,	,,	,,	9,000	,, ,,
,,		carbo-hydrate	,,	,,	,,	4,000	,, ,,

In the body proteid is never fully oxidised as one-third of it passes away from the system as urea, in the above table a correction on this account has been made.

If the number of heat units a substance is capable of affording be known, we can readily calculate the amount of energy the food can yield. Joule demonstrated that to raise the temperature of 1 lb. of water 1° Fahr. was equivalent to raising 1 lb. 772 feet high. The foot-pound is

therefore the unit of work, and 772 foot-pounds are the mechanical equivalent of 1° Fahr., from this we get the following table:

1 oz. of proteid oxidised in the system yields					170	foot tons of	energy.	
,,	fat	,,	,,	,,	,,	380	,,	,,	,,
,,	carbo-hydrate	,,	,,	,,	,,	130	,,	,,	,,
,,	carbon converted into CO_2				,,	311	,,	,,	,,

As the result of contraction muscles liberate heat and mechanical energy, and the relative proportion of these produced is not without interest. In the construction of steam engines the great object in view is to obtain from the fuel the largest amount of energy and the smallest amount of heat; the heat is of no use, it is the energy which is wanted. In some of the best triple expansion engines the proportion of energy liberated is twelve and a half per cent., while eighty-seven and a half per cent. are lost as heat; in the ordinary locomotive only four per cent. of the total energy is liberated as work.*

Turning now to muscle, it has been found as the result of the most recent investigations by Chauveau, that from twelve to fifteen per cent. of the total energy contained in the food is produced as work; this is a lower estimate than that originally made by Fick, who fixed it at twenty-five per cent., while M'Kendrick calculates that in man a little over seventeen per cent. is produced as work, and the remainder in heat.†

It would appear that compared with an ordinary engine the muscles are economical machines.

The Amount of Food required.—As previously pointed out, the majority of the experiments made in the feeding of horses appear to have been directed towards ascertaining the minimum amount of food required during idleness; the amount of food required for work is extremely difficult to determine, and must of necessity be liable to considerable variation.

Subsistence Diet.—The most recent experiments bearing on this subject were made in France by Grandeau and

* 'Life in Motion,' M'Kendrick. † *Ibid.*

Leclerc, and the labours of these investigators have been brought before the horse-owning public of this country by Professor Warrington, to whose articles on 'Horse Feeding'* I am indebted.

Three horses maintained their weight unaltered, for a period of from four to five months each, on a diet consisting of 17·6 lbs. of meadow hay; the animals led a life of idleness with the exception of receiving half an hour's walking exercise daily.

The 17·6 lbs. of hay furnished as a mean 7·02 lbs. of dry digestible organic matter for every 1,000 lbs. of body weight; the 7·02 lbs. of organic matter contained ·538 lb. of digestible proteid.

From this the subsistence diet for a horse for 24 hours is as follows for every 1,000 lbs. of body weight:

Proteid - - - -	·538 lbs.
Non-nitrogenous - -	6·482 ,,
	7·020 lbs.

This amount of hay contains the following elements:

Carbon - -	3·533	lbs.
Hydrogen - -	·385	,, (6·16 ozs.)
Oxygen - -	2·986	,,
Nitrogen - -	·08608	,, (1·377 ozs.)

Assuming the correctness of Grandeau's observations, we may accept the above amounts of carbon, hydrogen, and nitrogen, as approximately representing a horse's requirements for 24 hours during idleness, the animal neither gaining nor losing weight.

The ratio of nitrogen to carbon in the above diet is 1 : 41; the albumenoid ratio is 1 : 12.

From a table furnished by Grandeau and Leclerc, it would appear that no matter what the nature of the diet may be, horses require between 7 lbs. and 8 lbs. of dry *digestible* organic matter daily for every 1000 lbs. of body weight, to maintain their weight during idleness; here is the table:

* *Live Stock Journal*, January, 1894.

Diet.	In the Ration.	Amount digested.	Amount for 1,000 lbs. of body weight.
Hay alone - - -	14·08 lbs.	6·09 lbs.	7·02 lbs.
Maize and oat straw - -	11·57 ,,	8·33 ,,	8·22 ,,
Maize, oats, hay and straw -	9·48 ,,	7·30 ,,	7·50 ,,
,, ,, ,, ,, -	9·49 ,,	6·74 ,,	7·45 ,,
Oats alone (crushed) - -	8·59 ,,	6·41 ,,	7·02 ,,

In some German experiments made by Wolff on the subsistence ration, 8·3 lbs. of digestible dry organic material were found necessary to maintain the body weight, and from this the digestible fibre, 1·6 lb., was deducted, as in the experience of Wolff the fibre digested by horses was of no value as sustenance either at work or rest; there can be no doubt that this latter is incorrect.

In speaking just now of the minimum dry food required to maintain the body during idleness, we said it had been fixed by experiment at between 7 lbs. and 8 lbs. daily, but this presupposes that the diet possesses a sufficient proportion of digestible proteids; in one of Grandeau's experiments a horse received 33 lbs. of wheat-straw per diem which furnished 13 lbs. of digestible matter daily, nearly twice the amount actually required, but these 13 lbs. of material only furnished ·157 lb. of digestible proteids, or less than one-third of the minimum, the result being the horse died from starvation.

The subsistence diet for an ox weighing 1,000 lbs. is, according to the experiments of Wolff, ·5 lb. to ·6 lb. of proteid, and 7 lbs. to 8 lbs. of non-nitrogenous matter reckoned as starch; this gives an albuminoid ratio of 1 : 14.

According to the same authority sheep require a relatively larger subsistence diet, owing to the growth of the wool and its accompanying fat, viz., for 1,000 lbs. of live weight ·9 lb. of proteid and 10·8 lbs. of non-nitrogenous matter, the albuminoid ratio being 1 : 12.

Working Diet.—The ration for working horses has not yielded satisfactory results to experimental inquiry; as might be expected, it was found in the French experiments

that work at a trot and at a walk gave very different results. A horse walking 12½ miles was kept in equilibrium on 19·4 lbs. of hay, while 24 lbs. were found insufficient when the same distance was performed at a trot. In another experiment a horse walked 12½ miles dragging a load, and was kept without loss of body weight on 26·4 lbs. of hay; but the largest amount it could eat, viz., 32·6 lbs., would not enable it to do the same work at a trot.

It has been assumed by some Continental observers, but in our opinion incorrectly, that if the amount of digestible proteids required during rest be given in a diet, a horse may be worked without loss of body weight provided the food has added to it sufficient non-nitrogenous matter; in other words, labour does not necessitate an increased supply of albuminoid material.

On this point the theory and practice of feeding are diametrically opposed; the harder the work performed the greater need there appears to be for nitrogen, in spite of the fact that it is the non-nitrogenous substances of the body which supply both heat and motion. It is possible that in this country we may have carried this to an extreme, and that our diets are wastefully nitrogenous, but though Wolff tells us that starch when burned in the body of the horse is capable of yielding nearly half its full energy, so that 1 lb. produces 1,232 foot-tons of work, yet experience would not admit of our endeavouring to train a horse for the Derby on ½ lb. of digestible proteids and a few pounds of starch per diem!

Fattening Diet.—The amount of material stored up by animals during the period of fattening was worked out in this country by Lawes and Gilbert; their figures are only approximate, and presuppose food of good quality is used, and that the conditions present are favourable for fattening.

Every 100 lbs. increase in the live weight of the fat pig consists of 73·8 lbs. of dry material, that of the sheep 72·5 lbs., and of the ox 68·6 lbs.

Oxen.

To produce 100 lbs. of live weight the following amount of food is required: Oil-cake 250 lbs., clover-chaff 600 lbs., swedes 3,500 lbs.; the increase in weight is mainly fat, viz., 58 per cent., the proteid matter stored up is 9 per cent., the mineral matter 1·6 per cent.

Sheep.

To produce 100 lbs. of live weight, oil-cake 250 lbs., clover-chaff 300 lbs., swedes 4,000 lbs., are required; the increase consists of fat 63 per cent., proteid 7·5 per cent., ash 2 per cent.

Pigs.

To produce 100 lbs. of live weight 500 lbs. of barleymeal suffice; the increase consists of 66 per cent. fat, 7 per per cent. proteid, and ·8 per cent. ash.

These observers in analysing the results of their investigations, point out that the pig only requires 420 lbs. of *dry* substance in food to produce 100 lbs. increase in body weight, while the sheep requires 912 lbs., and the ox 1,109 lbs. The explanation of the difference in the amounts required is that the food of the pig is practically of a concentrated kind, whilst that of the herbivora contains a large amount of woody fibre and crude succulent roots.

The proportion of fat stored up is greatest in the pig and least in the ox; but the ox lays up the largest amount of proteid 9 per cent., while the pig stores the least 7 per cent. Both of the herbivora store up more mineral matter than the pig, and the sheep rather more than the ox; this is due to these animals developing more bone during the fattening period than pigs.

Lawes and Gilbert have further shown that a pig increases 6 to 6½ per cent. of its weight per week, the sheep only 1¾ per cent., and the ox little more than 1 per cent., hence the herbivora require much longer to fatten.

In the following table Wolff shows the amount of food required for every 1,000 lbs. of body-weight in different animals:

Animal.	Total amount of Organic Matter.	Assimilable Matter.				Albuminoid Ratio.
		Proteid.	Carbo-hydrates.	Fat.	Total.	
	lbs.	lbs.	lbs.	lbs.	lbs.	
Horses at light work -	21·0	1·5	9·5	·40	11·40	1 : 7·0
,, moderate work -	22·5	1·8	11·2	·60	13·60	1 : 7·0
,, hard work -	25·5	2·8	13·4	·80	17·00	1 : 5·5
Oxen at moderate work -	24·0	1·6	11·3	·30	13·20	1 : 7·5
,, hard work- -	26·0	2·4	13·2	·50	16·10	1 : 6·0
Milch cows- - -	24·0	2·5	12·5	·40	15·40	1 : 5·4
Fattening oxen : 1st period	27·0	2·5	15·0	·50	18·00	1 : 6·5
,, ,, 2nd ,,	26·0	3·0	14·8	·70	18·50	1 : 5·5
,, ,, 3rd ,,	25·0	2·7	14·8	·60	18·10	1 : 6·0
Fattening sheep : 1st period	26·0	3·0	15·2	·50	18·70	1 : 5·5
,, ,, 2nd ,,	25·0	3·5	14·4	·60	18·50	1 : 5·4
Sheep fed for wool :						
Stronger breeds -	20·0	1·2	10·3	·20	11·70	1 : 9·0
Finer breeds - -	22·5	1·5	11·4	·25	13·15	1 : 8·0

It will be observed that the quantities given in the above table are of 'assimilable' or digestible matter. It is a well-known fact that animals can only obtain from food a certain proportion of its nourishment; the 17 lbs. of assimilable matter in the above table for horses doing hard work, would probably only be extracted by the administration of 25 lbs. of food.

Each food and each proximate principle has a digestive co-efficient of its own, and before any opinion can be formed as to the amount of nourishment a food is capable of supplying, we must apply to it the digestive co-efficients which have been obtained as the result of direct experimental inquiry.

Digestibility of Food.—Every diet should contain proteid, fat, carbo-hydrates, and salts; of each of these proximate principles there is a distinct proportion absorbed, and the

remainder rejected and excreted with the fæces; the percentage which represents the quantity absorbed is spoken of as the digestive co-efficient (p. 296).

The methods employed by which these results have been obtained, have been to feed animals on food of known composition and analyse the excreta ; the difference between the amount of proteid, fat, starch, sugar, cellulose, etc., taken in by the mouth, and that rejected from the body by the fæces, is the amount digested by the system.

The digestibility of a food depends upon its age, growth, mode of preparation, and condition ; well-saved hay, for example, is better digested than hay which has been washed by rain. The admixture of other substances with a food also affects its digestibility ; the addition of starch or sugar to a diet of hay and straw, if it exceeds 10 per cent. to 15 per cent. of the dry forage, decreases its digestibility; small quantities of oil aid digestion, large quantities retard it; the addition of oats to a ration of hay increases the amount of hay digested.

Grandeau and Leclerc* determined the effect of work on digestibility ; they found that a horse receiving moderate exercise digested its food better than one absolutely idle; on the other hand when the animal was called upon to work either at a walk or trot the amount of food digested fell off.

This reduction in the amount digested during work was not equally distributed over the whole of the proximate principles ; the same amount of starch and sugar was digested no matter whether during idleness or work, but a reduction occurred in the proteids and cellulose, the digestion of which rose with moderate exercise but fell off considerably during hard work.

Contrary to expectation, experiments made by the French and Germans have shown that neither crushing oats nor cutting hay increases the proportion assimilated by the system. It is certain as a practical matter that both these

* *Op. cit.*

methods of preparing food for horses are highly appreciated in this country, and we think with good reason.

Experiments have shown that the same amount of proximate principles are not digested by all classes of animals; a sheep, for instance, digests hay better than a horse, and this digestion is not limited, as one might expect, to the cellulose only, but is extended to the other proximate principles excepting the proteids, of which both animals digest the same amount.

The following table shows the average percentage of each proximate principle digested by animals. The figures are the mean of a mixed diet:

	Horse.	*Ox.*	*Cow.*	*Sheep.*
Proteids - -	69	65	57	57
Fatty matter	59	64	65	61
Carbo-hydrates	68	66	70	73
Cellulose and fibre	33	60	61	58

It is evident that every food, no matter how well-balanced in its proximate principles, will contain a certain proportion of digestible and indigestible matter; the latter, no doubt, largely depends upon the amount of cellulose and lignin. The herbivora, though adapted to digest these, cannot obtain from their food the full amount of nutriment if either of them be in great excess.

CHAPTER XII.

ANIMAL HEAT.

One of the important divisions of the animal kingdom is into warm-blooded and cold-blooded creatures.

Poikilothermal or cold-blooded animals, are those whose internal temperature depends upon their external surroundings, so that when these are cold the bodies of such animals are cold, being about a degree or so higher than the medium in which they are living.

Homoithermal or warm-blooded animals, are those whose temperatures do not depend upon the temperature of the medium in which they are living; whether this latter be high or low makes little difference, as the warm-blooded creature possesses certain mechanisms by which the heat of its body is maintained uniform.

Source of Heat.—The heat of the body is the result of tissue metabolism, in reality of chemical action occurring in the tissues, such action being generally of the nature of oxidations, for example, the combustion of carbon into carbonic acid and of hydrogen into water. Fifteen and a half grains of carbon when fully oxidised will yield 8,080 heat-units, while a similar quantity of hydrogen converted into water yields 34,460 heat-units.

Any change such as muscular contraction, the secretory activity in glands, growth and repair of tissues etc., all lead to the production of heat.

The chief seat of heat production is the muscles, where

no less than four-fifths of the entire heat of the body is generated; at every muscular contraction heat is produced which is carried off by the veins of the part, and in this way the whole mass of blood may have its temperature raised. It has been observed that a thermometer placed in the masseter muscles of the horse during mastication, has shown an elevation of 5° Fahr. over that of rest.

A sufficient number of experiments have been made on horses to place beyond doubt that during active exercise the temperature of the body rises, though to a variable extent in different animals. Half an hour's trotting has been known to raise the temperature ·7 to 2·7° Fahr. above the normal, and this in spite of the mechanisms which exist in the body for getting rid of heat, and ensuring an even temperature being maintained. If it were not for these mechanisms, sufficient heat would be produced, even during idleness, to raise the entire body to boiling-point in less than two days.

The liver furnishes ample evidence of the heat which is generated as the result of glandular activity; it is certain that secretory changes cause the temperature of the blood in the hepatic vein to be higher than that of the portal, or even of that of the aorta. Claude Bernard showed that in a dog during active digestion the temperature of the blood in the portal vein was 103·5°, whilst that in the hepatic vein was 106·3° Fahr.

Some recent work by Bayliss and Hill* has cast a doubt on the heat liberated in the submaxillary gland during activity, though at one time it was generally believed that such was the case.

Loss of Heat.—It is certain unless some conditions exist in the body for the regulation of the temperature, that with all this metabolic activity occurring, the heat would continue to steadily rise until it accomplished the destruction of the animal. Mammalian muscle coagulates at a temperature of 122° F., and this and other important changes would occur, both to the central nervous and cir-

* *Journal of Physiology*, vol. xvi.

latory systems, unless some heat-regulating mechanisms existed. Some of these mechanisms are obvious, others are not so evident, but it is quite certain that a rise in body temperature must be met by increased dissipation of heat if a normal temperature is to be maintained; in other words, loss of heat must balance heat production.

The skin is the chief means by which the heat of the body is dissipated. If the vessels in it dilate a larger amount of blood is admitted to the cooling surface it affords, if the vessels contract less blood is admitted, less cooling from the surface occurs, and a larger quantity of blood is sent to the hotter parts of the body.

When the vessels of the skin dilate heat is lost by radiation, but in addition a vascular skin is in some animals an actively secreting skin, and the sweat which is poured out is an important means of cooling by the abstraction of heat which occurs during its evaporation.

Evaporation from the surface of the skin is a most important source of loss of heat, so marked is this in the horse that the resulting fall in temperature may even carry it below the normal if the sweating be very profuse, or the wetted area a large one.

The peculiar breaking out into sweats in the horse after return from work may be connected with a discharge of heat, which as we previously mentioned rises above the normal during work, in some cases, it is said, as much as 4° Fahr. to 5° Fahr., and remains so for some short time afterwards.

Animals varnished so as to prevent evaporation from the skin soon die; it was supposed at one time that the cause of death was due to suppressed skin excretion, but it is now known to arise from cold. The effect of the varnished skin is to conduct heat rapidly away from the body so that the loss exceeds the income; if this rapid loss be prevented by rolling the animal up in cotton-wool, death may be prevented.

The hairy covering on animals prevents a loss of heat by conduction, but when hair is wet by rain or sweating it

becomes a good conductor, and a considerable amount of heat may be lost; hence we see another reason of the value of clipping working horses (p. 238).

Influence of Heat and Cold.—Moderate cold applied to the external surface of the body increases the production of heat; moderate heat applied to the body lowers the temperature. It is believed that the skin may reflexly influence the body temperature by exciting or inhibiting the activity of the heat-forming mechanisms.

A rise or fall in body temperature by no means indicates an increase or diminution in the *production* of heat. In the above cases the rise in temperature due to moderate cold, might be caused by a contraction of the vessels of the skin sending a larger quantity of blood into the internal and therefore hotter parts of the body; or the loss of temperature due to the external application of heat may solely be due to the greater cooling which occurs when the vessels are dilated. To demonstrate increased heat-production we must be able to show that the metabolism is increased, that more oxygen is absorbed, and more carbonic acid produced.

During summer the metabolism is diminished and during winter it is increased; therefore the probable explanation of the influence of heat and cold on the body temperature is that the production of heat is affected; Waller* states the same fact another way, 'If it is cold outside the fire burns high within, if it is warm outside the fire burns low.'

Continuous and intense application of cold to the external surface of the body lowers the temperature by the conduction of heat, in spite of the increased amount which is produced. Continuous heat at a much higher temperature than that of the body may stop the discharge of heat, which becomes stored up as in sunstroke; but at moderately high temperatures and especially in a dry heat, the profuse perspiration produced is sufficient to maintain the body temperature by evaporation.

A loss of heat by lying out at night on the bare ground

* 'Human Physiology.'

is provided against in the herbivora by the thick layer of fat found beneath the peritoneum, this forms a protective covering which renders the conduction of heat from the body extremely difficult.

Clipping.—Siedamgrotzky has observed the effect on the temperature of clipping horses. He found that the temperature rose after clipping, and fell to normal about the fifth day. It was observed that clipped horses had during exercise a higher rectal temperature by 1·8° Fahr. than unclipped horses, and the return to normal temperature was more steady and regular with them than with unclipped.

The rise in temperature after clipping may be due to vaso-motor action; less blood being in the skin more will find its way to the viscera, viz., to parts of the body which have a naturally high temperature, the result being the total mass of blood will have its temperature raised. Another way of accounting for the rise in temperature after clipping, is by supposing that an actual increase in the production of heat occurs. This may be due to stimulation of the skin influencing the heat-forming mechanism reflexly.

Colin clipped a horse on one side of the body and not on the other; the *subcutaneous* temperature in the stable was:

Clipped Side.	*Unclipped Side.*	*Difference.*
86·9°	95°	8·1°

The animal was now taken out into cold air of three degrees below freezing-point.

	Clipped Side.	*Unclipped Side.*	*Difference.*
In 30 minutes the subcutaneous temperature was - -	85·1°	94·1°	9·0°
2½ hours later - - -	79·9	95·0	15·1
1 hour „ - - -	83·3	95·5	12·2
1 „ „ - - -	85·1	96·1	11·0

The cooling of the clipped side is remarkable, and the temperature continued to fall for three hours, whilst the

slight fall in the temperature of the unclipped side was recovered from in three hours.

This experiment shows the enormous loss of heat over the clipped surface, a condition which though valuable during work is obviously a serious tax on the system during rest, and has to be met by clothing and in many cases an increased diet.

Evaporation by the Lungs.—Under the influence of increased respiration the amount of air passing in and out of the lungs becomes augmented; the warming and evaporation which thus occurs in the respiratory passage is a very important source of loss of heat, this loss principally occurs in the nasal chambers, mouth, and perhaps trachea, but not in the depth of the bronchi. In animals which do not sweat, such as the dog, the panting and evaporation from the open mouth practically take the place of sweating; in the panting of sheep and cattle in show condition we have a very evident means of getting rid of body heat by increased respiratory movement. The same fact is brought before us clinically in the hurried respirations of the animal with a high temperature.

Effect of Feeding and Drinking.—Feeding has the effect of raising the temperature of the body; in the dog the maximum is reached from six to nine hours after a meal, during which time from 20 per cent. to 25 per cent. more heat may be produced; after the ninth hour it falls. In the horse, feeding has been observed to cause an elevation of the body temperature by as much as from ·4° to 1·4° Fahr., but not so in the ox (Siedamgrotzky).

In the horse a fall in temperature is observed as the result of drinking, and there can be no doubt that the bulk of water consumed by this animal and by cattle receiving a succulent food, must prove an important source of loss of heat. Drinking a pailful of water at a temperature of 50° has caused the body temperature to fall ·5° to ·9° Fahr. In this way drinking and feeding act antagonistically and so help to neutralize each other.

The shivering indicative of cold is a method of increasing

heat production by muscular contraction. The shivering seen in some horses after drinking is explained by this fact; it is an attempt to restore the heat which has been lost by warming a large volume of cold water.

There are other causes influencing the loss or production of heat. Severe hæmorrhage causes a loss of temperature; transfusion of blood produces a rise. Starvation causes a fall, while food, by increasing the metabolism, causes a rise. Chloroform, alcohol, quinine, aconite and digitalis produce a loss of heat, whilst strychnine, veratrin, and nicotin cause a rise.

Probably in all animals there is a slight decrease in temperature from birth to old age.

Influence of the Nervous System.—An important controlling influence is exercised over heat production by the nervous system; it is supposed that a mechanism exists by which the heat production in a muscle is regulated, so that a lowering of the temperature of the skin leads to an increased production of heat, whilst a rise in the skin temperature leads to a reduction of muscle metabolism.

This controlling nervous influence has been termed the THERMOTAXIC nervous mechanism, it is of the very greatest importance, especially when we bear in mind the fact that the muscles are the chief sources of heat; that it has more than a hypothetical existence is proved by the fact that it is possible to suspend its operation in an animal poisoned by urari, so that in such a urarized animal the temperature and metabolism fall. If an animal so poisoned be exposed to an increased surrounding temperature the muscle metabolism increases, and if to a reduced temperature the metabolism falls; in other words it behaves in exactly the opposite manner to a normal warm-blooded animal, and this is caused by the thermotaxic mechanism being in abeyance, owing to the action of the urari on the motor nerve-endings in the muscles.

Direct experimental inquiry on the brain has shown that injury to certain parts not yet agreed upon, corpus striatum or optic thalamus, is followed by a high temperature; it is

possible that these are the heat centres which control the muscle metabolism.

Waller* is of opinion that heat production, unless as the consequence of mechanical and chemical action, is inconceivable through the nervous system, and that there are no such things as thermogenic nerves or heat centres; he does not deny that heat production, dissipation, and distribution are under the control of the nervous system, but only through the medium of the vaso-motor and trophic nerves.

In fever the metabolism of muscle is increased, and this is recognised by the body waste which occurs, and the increase of urea in the urine. It would appear to be beyond doubt that the temperature in fever is brought about by an increased production of heat and not by a diminished loss of heat. A continuous high body temperature leads to fatty degeneration of the heart, liver, etc.

The **Amount of Heat produced** by animals depends upon the rate of their metabolism and the surface area of their bodies. A large animal actually but not relatively produces more heat than a small one; a small animal has a greater body surface relative to its weight than a large animal, and in this way its loss is more rapid. As heat production must balance heat loss, the small animal must lose more heat, and therefore produce more heat, than a large animal.

The heat produced is measured as heat-units or calories,† and the amount produced per hour for every 2·2 lbs. of body weight is given by Colin as follows:

Horse - - -	2·1 calories.
Sheep - - -	2·6 „
Dog - - - -	4·0 „

A horse loses according to Colin 20,684 large calories per

* *Op. cit.*

† There are two calories a large and a small, the large calorie is the amount of heat necessary to raise 1 kilogramme (2·2 lbs.) of water 1° C. (1·8° Fahr.); the small calorie is one thousand times smaller, viz. the amount of heat required to raise 1 gramme (15·5 grains) of water 1° C. (1·8° Fahr.). The calorie referred to in the text is the *large*.

diem, or sufficient heat to raise 4,550 gallons of water 1·8° Fahr., or to raise 44 gallons from freezing to boiling point.

Wolff, quoted by Tereg,* gives a table showing the heat lost by cattle, horses, sheep, and pigs, for every 1,100 lbs. of body weight:

Horse at moderate work	24,500 calories (large).
,, hard ,,	37,200 ,,
Ox resting and on moderate diet	18,600 ,,
Sheep, with fine wool	27,700 ,,
Pigs, fattening	35,000 ,,

According to Despritz a dog loses 393 calories (large) in 24 hours, and a man 2,700 in the same time.

The Normal Temperature of Animals.—It is remarkable the wide differences which exist in the normal temperature of animals of the same class. The following observations were made principally by Siedamgrotzky.

Horse.—The temperature varies between 100·4° to 100·8° Fahr. Age has a slight influence:

From 2 to 5 years old the temperature is	100·6°
,, 5 ,, 10 ,, ,, ,, ,, ,,	100·4
,, 10 ,, 15 ,, ,, ,, ,, ,,	100·8
,, 20 ,, ,, ,, ,, ,,	98·4 to 100·2

Horses living in the open have a temperature of ·9° Fahr. lower than those in stables.

Sex appears to slightly influence the temperature:

Stallions	100°
Mares	100·8
Geldings	100·4

The time of day is important, the lowest body temperature of the day is at 4 a.m., the highest at 6 p.m. It is not at all clear what causes these daily variations; they are seen in all animals, and in disease as well as in health. It has been observed in the human subject that the diurnal variations are reversed when a person sleeps during the day and works during the night, so that they may be accounted for in part by muscular activity.

* Ellenberger's 'Physiologie.'

Cattle.—The normal temperature is from 101·8° to 102° Fahr. Compared with the horse the daily variations are small.

Sheep.—In these animals the greatest variation in temperature occurs, viz., 101·3° to 105·8°, probably the majority of temperatures lie between 103·6° to 104·4°. The cause of the variation is unknown.

Shearing like clipping causes the temperature to rise, but only temporarily.

Swine.—The average temperature is 103·3° Fahr., varying from 100·9 to 105·4° Fahr.

Dog.—The dog is liable to important variations depending on the external temperature; according to Dieckerhoff it varies from 99·5° to 103° Fahr., other observers put it at 100·9°, 101·3°, and 101·7°. Feeding raises the temperature, and there is also a rise towards the evening.

Temperature Topography has occupied the attention of several observers, and both the fluids and organs of the body have had their temperature taken. According to some physiologists the warmest organ in the body is the cerebrum; in the table of the sheep quoted below, the lungs were the warmest, but this is not the rule; the liver both from its position and activity can probably in all animals claim to have the highest temperature.

The temperature of the blood in the right and left hearts has been a fruitful source of discussion; there certainly is a difference, in some animals the right in others the left is the highest; in the horse Colin found as a rule that the blood in the left heart was warmer than that in the right. Here is a table by Berger* giving the distribution of temperature in a sheep:

Subcutaneous tissue	99·1°	Rectum	105·1°
Brain	104·4	Right heart	106·9
Liver	106·2	Left heart	105·6
Lungs	106·5		

The surface temperature of animals must depend largely upon the length of the covering, and the character of the

* Landois and Stirling.

underlying tissue. Where the parts have little or no muscle, the normal temperature of such is low; for example, the legs of the horse consisting solely of bone and tendon are always cold to the feel in a state of health. Colin found in a horse with a long winter coat (the thermometer standing at freezing-point), that a difference of 44° Fahr. existed between the temperature of the pasterns and that in the rectum; a difference of 35·1° Fahr. between the knee and the rectum, and 5·4° Fahr. between the temperature of the skin covering the chest and that of the rectum. As we might naturally expect, he found from direct experiment that in extremely cold weather those horses with the longest coat had the warmest skins, the difference being as great as 9° or 10·8° Fahr.

Hybernation.—The effect of lowering the temperature of the bodies of animals is to produce a depression of metabolism. This is well seen in some mammals like the dormouse which sleep all the winter, during which time they live upon the store of fat laid up in the tissues during the summer. Owing to their depressed metabolism this store is found sufficient to keep them alive, though they wake up at the end of the winter mere skeletons.

Post-mortem Temperatures are frequently observed. The explanation afforded of a post-mortem rise in temperature is that metabolism is still occurring in the tissues, but there being no circulation to carry the heat away the temperature of the part rises.

CHAPTER XIII.

THE MUSCULAR SYSTEM.

The muscular system is the largest in the body; the skeletal muscles alone represent 45 per cent. of the body weight.

The movements of the skeleton, the contraction of the heart, and the transport of the ingesta along the intestinal canal, are all examples of muscular movement, and further they are examples of different kinds of movement; the owly moving intestina l canal is very different from the active skeletal muscles, and these with their long periods of activity and rest are greatly in contrast with the rhythmical movements of the heart.

Structure of Muscle.—The structure and appearance of muscle differs according to the nature of the work it has to perform; the muscles of the skeleton are red in colour and as a rule bulky, the muscle of the intestine is pale and in thin sheets; further, the skeletal muscles when examined under the microscope are found to be striated, whilst the pale muscle is not. Lastly the skeletal muscles are capable of voluntary contraction, while the pale muscles are not in any way under the control of the will; the heart muscle, as we shall again point out, is an exception to the above, it is striated and red in colour yet involuntary.

A primitive red muscle fibre is enclosed in a sheath termed the sarcolemma, and supplied by a medullated nerve which enters the fibre generally about the middle, terminating in what is known as an end-plate. By entering the fibre near its centre the impulse of contraction travels towards each end, and as a muscle is made up of

a number of these fibres we can understand that by this arrangement the entire length is at once innervated on receiving an impression, by which means one part does not contract before another.

Two views are held as to the structure of striped muscle. The one most generally accepted is as follows: The striation observed in red muscle is due to bands in the elementary muscle-fibre; these bands are of two kinds, one bright and the other dim, they are placed end to end and run the entire length of the fibre (Fig. 44).

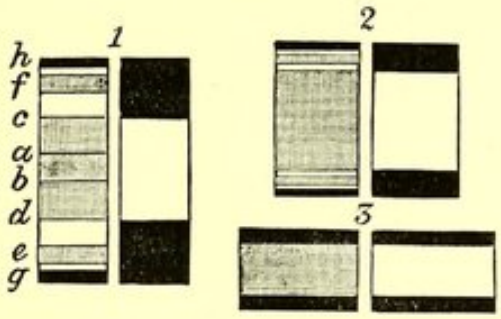


FIG. 44.—THE MICROSCOPIC APPEARANCE DURING A MUSCULAR CONTRACTION IN THE INDIVIDUAL ELEMENTS OF THE FIBRILLÆ. (LANDOIS AND STIRLING, AFTER ENGELMANN.)

1.—From *h* to *c* and from *d* to *g* are the bright bands, and between them is situated the dim band *c* to *d*; the lines *f* and *e* are only found in the muscles of insects. The entire sarcous substance of the muscle is contained from *h* to *g*, but the broad dim band *c d* constitutes the contractile part of the sarcous substance; this commonly shows a stripe in its centre *a b*. When the muscle element is examined by polarised light, the whole of the contractile substance being doubly refractive becomes bright, the other part being singly refractive is black; this is shown in 1 on the right. 2 illustrates what is known as the transition stage and 3 the proper stage of contraction of the muscle element; in both cases the figure on the right is viewed in polarised light.

When a muscle contracts the bright and dim bands become shorter and broader, and the dim band increases in volume at the expense of the bright band. By the use of the polariscope it can be shown that the bright band is singly refractive while the dim band is doubly refractive (Fig. 44). It is believed that during contraction fluid passes from the singly refractive substance to the doubly refractive, so that the former shrinks and the latter swells;

in this way the increase in the volume of the doubly refractive disc is accounted for.

The other view of the structure of striped muscle is that expounded by Haycraft.* This authority shows that the fibrils of a muscle are *varicose* threads of tissue, presenting alternate swellings and constrictions of their substance (Fig. 45). The bright and dim bands correspond to thickenings or constrictions of the fibrillar



FIG. 45.—DIAGRAMMATIC REPRESENTATION OF THE MINUTE STRUCTURE OF STRIPED MUSCLE. (HAYCRAFT.)

Part of a muscle fibril is represented; it will be noticed that the striping of the fibril corresponds with the position of inequalities in its thickness.

substance, and are simply optical effects due to varicosity. This was conclusively proved by taking a mould of a muscle fibre in collodion, which gave the usual appearance of bright and dim bands as in the muscle itself.

The alterations in the striping due to contraction are simply due to *change in the form* of the muscle fibre, and not to any change within the fibril itself, such as is believed by the upholders of the first theory we described.

Haycraft regards the fibrils as composite structures, and

* 'On the Minute Structure of Striped Muscle, etc.' J. B. Haycraft, M.D., *Proceedings of the Royal Society*, vol. xlix.

this he believes is indicated by their varicosity; each fibril has practically undergone segmentation into a series of minute particles (the sarcous elements of Bowman), and each of these is capable of contracting on its own account. In this way we can account for the rapidity of muscular contraction, for the larger the contractile element the longer time will it take to reach its maximal degree of shortening, but by segmentation of the fibril into smaller particles, each one contracting and relaxing on its own account, a considerable saving in time is effected.

This view of Haycraft's simplifies considerably our knowledge of the structure of striped muscle.

It is observed that all muscles are striped where rapidity of contraction is required; in fact the great characteristic difference between red and pale muscle, is the slow and deliberate movements of the latter compared with the rapid movements of the former.

Plain or unstriped muscle consists of nucleated spindle-shaped cells, the nucleus is rod-shaped, and the cells being dovetailed are held together by a cement substance. The nerves supplying them are of the non-medullated kind, and terminate in minute bulbs, somewhat resembling the motor end-plates in voluntary muscle.

When a red muscle is stimulated it contracts, and the contraction shows itself as a wave which runs rapidly along it at the rate of about 33 feet per second; this wave is not propagated from fibre to fibre, and in this respect it differs widely from the wave in pale muscle which has an influence on neighbouring fibres, and moreover travels very slowly. Further the pale fibres can originate a contraction within themselves, whereas the red fibres must receive a stimulation before they contract.

In heart muscle is found an exception to the usual structure of red or so-called voluntary muscle, for though we know the heart to be involuntary yet it is red and striped, but the fibres instead of being straight are branched, and each possesses a nucleus; further there is no sheath or sarcolemma to the fibre.

Histologists have therefore considered the heart muscle to occupy a position midway between red and pale muscle.

Chemical Composition.—Muscle when examined chemically is found to consist principally of proteids and salts, in addition to which may be found a small quantity of acid, glycogen, traces of urea, and carbonic acid gas. By suitable precautions a yellowish neutral or alkaline fluid, termed muscle plasma, can be obtained from perfectly fresh muscle; this undergoes coagulation like blood, and yields a clot known as myosin and a serum called muscle serum.

Myosin is a substance obtained after the death of the muscle; there is every reason to believe that during the life of the muscle it does not exist as myosin, any more than fibrin exists in living blood as fibrin. The living muscle therefore contains myosinogen, or myosin precursor, bearing the closest resemblance to the fibrin of the blood. Myosin differs from blood fibrin by being soluble in a dilute solution of common salt and dilute hydrochloric acid.

The muscle serum consists of three proteids, two being globulins and one an albumin; it possesses an acid reaction, which is due to the presence of lactic acid formed as the result of the process of coagulation.

In muscle are also found small quantities of volatile fatty acids, such as acetic, butyric, and lactic; the latter acid exists in two forms. Carbo-hydrate substances, such as glycogen and sugar, are also found in muscles, their function is the liberation of muscular energy; the muscles of the horse contain a considerable quantity of glycogen even after starvation (see p. 200).

Certain extractives can be obtained from muscular tissue, such as creatin, creatinine, carnin, a variable amount of glycogen and sugar, together with a trace of urea.

The salts of muscle are principally those of potassium. The gases in muscle are carbonic acid, together with a small proportion of nitrogen, but no oxygen.

The Changes in Active and Resting Muscles.—The changes occurring in muscles are remarkably active; the so-called explosions which result in muscular contractions use up at

every moment the combustible material of the structure, and the products arising from their combustion have to be got rid of at once and repair brought about; changes are constantly occurring even during the period of muscle rest. Muscle activity is characterized by muscle waste, muscle rest is characterized by a preponderance of the process of repair. We must therefore learn the nature of the waste and repair occurring in muscles, and the physical and electrical phenomena exhibited by muscular tissue during the period of rest and activity.

The oxygen carried to resting muscles by the blood is absorbed by them in considerable quantities, and a volume of carbonic acid, in less quantity than corresponds to the oxygen absorbed, is returned to the venous blood. Whether a muscle be at rest or active, it is always absorbing oxygen and giving up carbonic acid, and, moreover, it is always storing up oxygen. The absolute amount of oxygen stored up and carbonic acid produced varies considerably during rest and work; during work more carbonic acid is given off than oxygen absorbed.

In an active muscle the bloodvessels are more dilated than in the muscle of rest, and this dilatation corresponds to the increased quantity of blood sent to the part. By means of the blood the irritability of the muscle, or its power of contraction, is maintained; whatever leads to a smaller quantity of blood being sent to an active muscle, produces partial or complete paralysis of the group or groups of muscles affected. This is well seen in the horse when suffering from thrombosis of the iliac arteries; the blood supply to the muscles of the horse with thrombosis is sufficient during the time the animal is at rest, or even at a walk, but if called upon to trot muscular cramps occur followed by paralysis.

Muscles in a state of activity contain less glycogen and sugar than those in a state of rest, due to the amount utilized during muscular activity; but glycogen is not necessarily the source of the energy, since muscles free from glycogen can work normally. Glycogen as we shall

learn later is rather a convenient accessory than a necessary factor in the production of energy in muscle.

Active muscle presents an acid reaction due to the formation of sarcolactic acid, while resting muscle is alkaline.

During muscular activity heat is produced, the blood returning from a muscle has a higher temperature than that going to it; this explains why Colin found the temperature of the masseter muscle of the horse to rise 5° Fahr. through feeding.

Heidenham points out that more heat is evolved in the contraction of a stretched than in that of an unstretched muscle, and further that more heat is evolved by a muscle which contracts without doing work than by a muscle which does work.*

The explanation of the first fact is obvious, the greater the resistance the muscle experiences in contraction the greater the energy set free, the less resistance the less energy evolved. The second fact is explained by saying that a muscle which contracts without doing work liberates its energy as heat, while the muscle which does work liberates part of its total energy as heat and part as work. A muscle in a state of tetanus does no work; during the act of contraction work is performed, but not so when the muscle finally ceases to shorten. This is the probable explanation of the high temperatures registered in cases of tetanus.

The **Nerve Supply of Muscles** is both sensory and motor, through the sensory nerves the brain is made acquainted with the position of the body and the state of the muscles, viz., relaxed or rigid, cramped or fatigued. The amount of ordinary sensibility in muscle is not very great unless it be cramped or inflamed; under these conditions acute muscular pain may be manifest, as we see in the painful lameness of thrombosis in the horse. The special function, however, of the sensory nerves is to keep up communication between the muscles and the brain.

* Waller, *op. cit.*

By means of the motor nerves the muscles are supplied with the needful stimulus which brings about contraction; division of the motor nerves or interference with their function leads to muscular paralysis, of which the best example in the horse is the left laryngeal paralysis resulting from pressure on or disease of the recurrent nerve.

Irritability or Excitability of Muscle.—Muscles possess, in common with some other tissues of the body, the phenomenon of irritability or excitability, viz., the power of contracting when irritated; the movement shows itself by the contraction or shortening which occurs. The normal stimulus to muscle is imparted to it through the nerves, but chemical, mechanical, and electrical stimuli also lead to a contraction even in the absence of nerves, or when applied to a muscle removed from the body.

When a muscle contracts it becomes shorter and thicker; there is a decrease in length but not in bulk; after contraction the muscle returns to its original length. Contraction may follow contraction, until at last the muscle becomes fatigued, it now contracts more slowly, and is not capable of performing the same amount of work. If the contractions in a muscle succeed each other with considerable rapidity, there is no period of relaxation, and the part is thrown into a condition of tetanus or cramp. During the time of the muscular contraction a sound is produced, which under suitable conditions may be heard.

All these changes can be studied with considerable accuracy by employing muscles isolated from the body, which are placed in contact with an apparatus on which they can describe their movements when irritated, and at the same time we can study the electrical phenomena in nerves.

Muscle Currents.—Great controversy has taken place over the question as to whether currents of electricity exist in muscle independently of those which make their appearance when the muscle is stimulated. It has been found, for instance, that a muscle isolated from the body, and placed under suitable precautions in connection with a galvano-

meter, demonstrates the presence of electric currents which behave in a perfectly regular manner, viz., under certain conditions they are always weaker, and under others stronger, in passing from one definite point on the muscle to another. They are spoken of as the natural *muscle currents*, or the *currents of rest*, and they always pass in

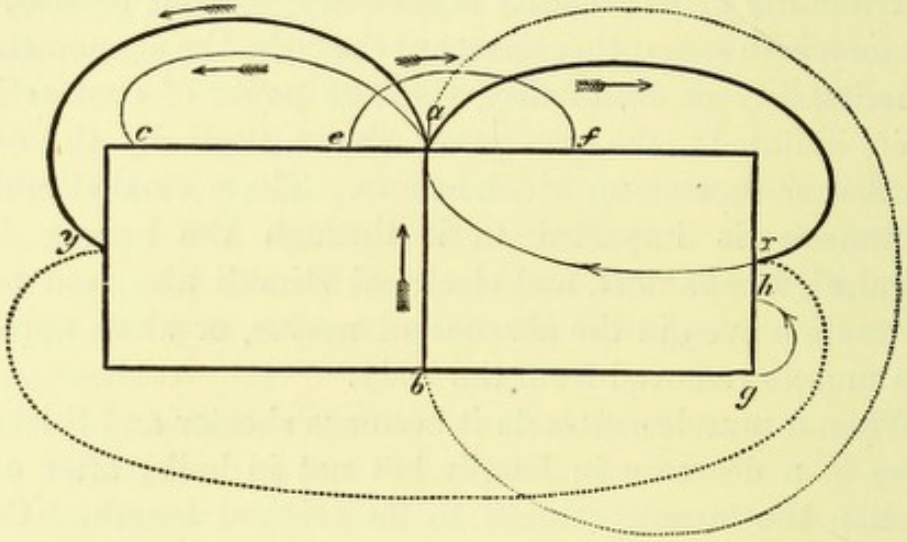


FIG. 46.—DIAGRAM ILLUSTRATING THE ELECTRIC CURRENTS OF REST OF NERVE AND MUSCLE. (FOSTER.)

Being purely diagrammatic, it may serve either for a piece of nerve or muscle, excepting that the currents at the transverse section cannot be shown in a nerve. The arrows show the direction of the current through the galvanometer.

a, *b*, the equator. The strongest currents are those shown by the dark lines, as from *a* at the equator to *x* or to *y* at the cut ends. The current from *a* to *c* is weaker than from *a* to *y*, though both, as shown by the arrows, take the same direction. A current is shown from *e*, which is near the equator, to *f*, which is farther from the equator. The current (in muscle) from a point in the circumference to a point nearer the centre of the transverse section is shown at *g*, *h*. From *a* to *b*, or from *x* to *y*, there is no current, as indicated by the dotted lines.

a definite direction, viz., from the surface of the muscle to the cut extremity (Fig. 46).

If while the galvanometer is registering the direction of the natural muscle current we stimulate the muscle preparation, a backward swing of the needle of the instrument indicates a current passing in an opposite direction to the natural muscle current; it is termed the *negative variation* of the muscle current, or the *current of action*.

The existence of currents of rest in living muscle is denied, and it would appear that they are purely post-mortem phenomena, or when obtained in living muscle are the result of injury due to the needful preparation for the experiment. But there can be no doubt that currents are developed in muscle during contraction, and these are spoken of as the currents of action.

The current of action travels with great rapidity from the nerve termination in the muscle known as the motor end-plate; a contraction now follows, produced by a decomposition of the muscle substance, the contraction being in

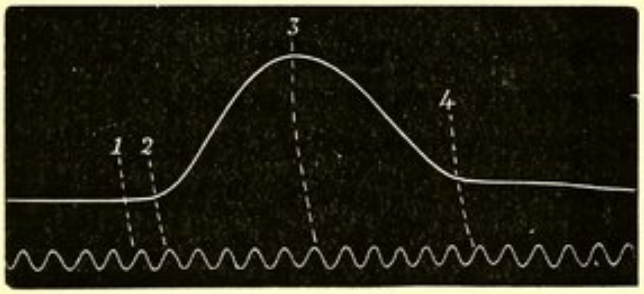


FIG. 47.—A MUSCLE CURVE FROM THE GASTROCNEMIUS OF THE FROG. (WALLER.)

From 1 to 2 is the latent period; from 2 to 3 the period of shortening; from 3 to 4 the period of relaxation.

the form of a visible wave which leads to swelling and shortening of the muscle fibres. The velocity of the muscle wave varies in different animals, in human striped muscle it is about 30 to 40 feet per second, in pale muscle it is very slow.

The electrical changes in nerves are practically the same as those occurring in muscles, and as this question has to be dealt with more fully under the nervous system, we shall postpone any further consideration of the subject until then.

Muscular Contraction.—If a muscle preparation be arranged so as to record its movements on a revolving drum, and a single shock from an induced current be passed into it, a single contraction follows which traces an upstroke on the drum, and the muscle then relaxing makes a downstroke; in this way is obtained a muscle-curve. It is found on examining this that the muscle does not contract imme-

diately the stimulus is applied, but that a perceptible period elapses before contraction occurs; this is called the *latent period*, or physiological lost time (Fig. 47). During the latent period, although the muscle is not moving, yet it is possible to determine that the natural muscle current is diminished, or suffers a negative variation, viz., a momentary reversal of the natural current. The latent period differs in various muscles, and depends also on their condition; in the frog it is estimated at $\frac{1}{100}$ of a second, or even much less.

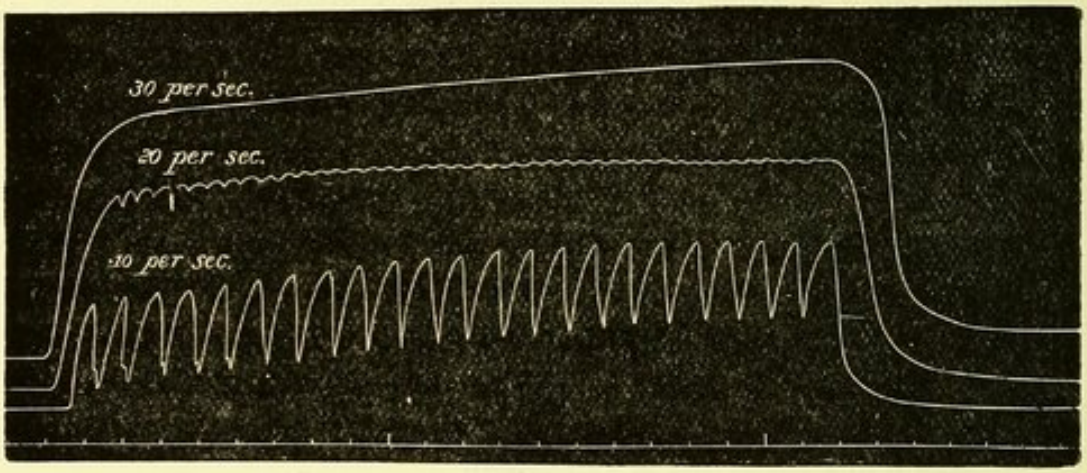


FIG. 48.—CURVES OF MUSCLE CONTRACTION. (WALLER.)

The lower curve is one obtained by stimulating the muscle ten times every second, the intervals of relaxation are clearly seen. In the middle curve the shocks were twenty times per second, and the relaxation is only of a very partial kind. The upper curve is that of tetanus.

Succeeding the latent period is the second stage or stage of contraction, at first slow, then rapid, then again slow till extreme contraction has been produced; this is followed by the third stage, viz., that of relaxation or elongation of the muscle, which is slow at first and then rapid.

As the muscle becomes fatigued the latent period becomes longer, and the contraction slower and shorter.

If the interval between simple shocks be reduced so that the latent period of one occurs at the maximum of its predecessor, the muscle curve of the second shock will run higher than the first as it starts not from the base but from the maximum of its predecessor; if another shock be sent

into the muscle the third curve will be higher than the second and so on, each movement of the lever describing a curve higher than the preceding one, until a maximum is reached when the muscle can lift the lever no higher; the tracing thus produced is a gradually rising undulating curve (Fig. 48).

If a succession of more rapid shocks be passed into the muscle, say twenty per second, there is no time for complete relaxation, and small waves are produced on the curve showing where attempts at relaxation occur (Fig. 48). If the number of shocks be still further increased, say up to thirty per second, complete tetanus of the muscle is produced (Fig. 48). Tetanus consists, therefore, of a series of short contractions with an insufficient interval for complete relaxation.

All the ordinary voluntary contractions of muscles are of a tetanic nature, a single contraction, such as is shown in Fig. 47, is only obtained by experimenting on a muscle outside the body.

A muscle cannot continue permanently in tetanus, fatigue soon occurs followed by relaxation, even though the stimulation be kept up. The relaxation is at first rapid, and then slows down. When muscles have been strongly and directly stimulated, and are greatly fatigued, they remain partially shortened for some time before they regain their original length; this shortening is described as the *contraction-remainder*. If a muscle preparation be considerably stretched, it may remain elongated for some days; this is known as the *elastic after-effect*.

A muscular contraction of striped muscle is modified by temperature, by certain drugs, and by fatigue.

The effect of cold on a muscular contraction is to prolong the latent period, and while the muscle is cooling to prolong and heighten the contraction. When the muscle is very cold the latent period is still further increased, and the contraction is considerably prolonged but not so high. With a rise in temperature above the normal each contraction becomes shorter and smaller, the excitability diminishes,

and finally if the temperature be raised to 104°—120° Fahr. rigor occurs and the muscle shortens.

Veratrin and calcium salts have the effect, especially the former, of considerably prolonging the muscular contraction.

Muscle fatigue is brought about by the presence of fatigue products formed as the result of muscle activity. It has been said that a solution of these products injected into the vessels of a fresh muscle depress its excitability, and that symptoms of fatigue are induced in the body of a fresh dog by transfusing into it the blood of a dog exhausted by excessive exercise.

In studying graphically the effect of fatigue on muscle it is observed that in the first instance the contractions increase in height and duration, and that this is followed by a decrease in height and a more prolonged contraction. The tracings thus obtained closely resemble those given by a muscle while passing from the cooling to the very cold stage.

Nerves are held to be inexhaustible, muscle on the other hand is readily exhaustible, though it possesses considerable power of self-restoration even after removal from the body. It is generally considered that fatigue begins in the motor end-plates of the muscle.

The ordinary method by which restoration in fatigued muscle occurs is through the circulatory system, by which the products of activity are removed; but a bloodless muscle outside the body may be exhausted, and yet is capable of self-restoration if given time.

A muscular contraction can occur even when the nerve ending is exhausted. This latter fact can be proved by paralysing the motor end-plates of muscle by poisoning them with urari, the muscle now cannot respond to nerve stimulation, though it can to direct stimulation of the muscle substance.

The influence of resistance to muscular contraction is demonstrated by loading a muscle preparation with different weights, and observing the height to which they are lifted. It is found that up to a certain maximum the load absolutely

increases the amount of work done by the muscles, the tension thus exercised on the fibres appearing to stimulate the changes occurring in the muscle substance which lead to a contraction. By gradually increasing the weight it is lifted to a less height, and the amount of work performed falls off; finally by overloading the muscle the weight is no longer lifted and the muscle may even become elongated.

The relaxation of a muscle follows contraction, and is partly brought about by the action of antagonistic muscles; but it is observed that an active muscle relaxes more readily than a tired one, and there are reasons for believing that obscure chemical changes, the reverse of contraction, facilitate the production of relaxation.

On electrical or other stimulation, involuntary muscle behaves much the same as voluntary, excepting that the contractions and relaxations are much slower and longer, and the stimulation required to tetanise pale muscle is twice as strong as that required for red. The intestinal movements seen in a horse recently destroyed exhibit perfectly the latent period, the stage of contraction, and that of relaxation. If the bowels or stomach be very irritable the lightest touch provokes a contraction, and in the case of the stomach particularly, large weals may occur on its surface by lightly drawing the finger over it.

The Cause of a Muscular Contraction.—We are now brought to a consideration of an exceedingly difficult problem, viz., the cause of a muscular contraction.

It is supposed that in the substance of a muscle is manufactured a complex material a compound of carbon and hydrogen; this compound is lodged in the muscle and it, and not the muscle fibre itself, is used up in a muscular contraction. The complex body is broken up and carbonic acid liberated not by the direct action of oxygen, for no free oxygen occurs in muscle, but by oxygen stored up at an earlier date in the muscle substance, and apparently available for this particular purpose only (see p. 90). The decomposition of this complex body, or as it has been

termed *inogen*, is fittingly described as an explosive decomposition.

We have previously seen that the nitrogen of the urine is not the measure of muscular activity, further that the non-nitrogenous substances in food are those which furnish muscular energy. These facts would support the view that the explosive 'inogen' of muscle is of a non-nitrogenous nature, and yet so closely allied is muscular contraction in the living body, to muscular contraction in the dead body (rigor mortis), that the view is forced on one that the 'inogen' when decomposed yields a nitrogenous body (like the solid myosin of rigor mortis), which is soluble, and can either be utilized in the muscles or elsewhere; while the non-nitrogenous residues, viz., carbonic acid and sarco-lactic acid are got rid of from the system through the blood stream.

As the result of a contraction we have seen that certain physical and chemical changes occur in a muscle. (1) The muscle becomes shorter and thicker, but with no decrease of volume. (2) The ultimate fibrils of which it is composed change shape, so that the parts which previously bulged now become the thinnest; or if Englemann's view be adopted, the dim band becomes broader and shorter. (3) Heat is generated during contraction. (4) The natural muscle current undergoes a negative variation. (5) The muscle becomes more extensible and less elastic. (6) Carbonic acid is produced in increased quantity and oxygen absorbed, but the amount of the latter absorbed is not in proportion to the carbonic acid given off. (7) Finally, the muscle may become acid as the result of the lactic acid produced.

The **Elasticity** in muscle depends upon its condition. In a resting muscle it is small but perfect, that is to say, it readily stretches and regains its natural length when released ;* a working muscle owing to fatigue is less elastic

* The stretching of muscle or other tissue is best defined as *extensibility*, whilst the power to return exactly to its former shape is *elasticity*.

than a resting one. The great advantage to the animal machine of the elasticity of muscles, is the reduction in concussion to the skeleton during progression; further, the skeletal muscles in the living body are always slightly on the stretch, at any rate they are not slack, and in this way no loss of time occurs before they can act. This condition of tension is known as muscular tone.

There are certain muscles in the machine where the strain on them is so considerable that tendinous material is intimately mixed up with the muscular tissue; this is well seen in the masseters, the muscles of the back, forearm, and thigh. In the horse provision is made for the muscles of the limbs being rested without necessitating the animal assuming a recumbent position, viz., by the check ligaments in the leg; by which means a horse can sleep standing, and may remain standing for some weeks without suffering.

During progression the entire strain of the body comes on the feet and the muscles of the limbs, and in such paces as galloping the strain is enormous. During the canter and gallop a weight equivalent to that of the whole body is imposed on one foreleg; it is very easy, therefore, to understand why horses 'break down,' for as the muscles become fatigued they lose their elasticity, and the strain is now thrown on the flexor tendons, which possessing little, if any, elasticity give way under the weight.

Muscle Fatigue.—As previously explained, fatigue in muscle is due to excess of work; the products arising from muscular contraction accumulate faster than they can escape, the irritability of the muscles decreases, and they require a greater stimulus to induce them to respond. The fatigued muscles are also acid from sarcolactic acid, which probably produces the soreness and stiffness resulting from overwork. Hand-rubbing and shampooing the tired body muscles, as is practised on both man and horse in India, and followed by such good results, is explained by the fact that the lymph vessels are stimulated to further absorption, and the lactic acid and other fatigue products

are got rid of. This is also the explanation of the value of hand-rubbing the legs of horses.

Condition.—That remarkable state of the body described as 'condition,' into which horses can be brought by care in feeding, general management, and carefully-regulated work, must be regarded as the highest pitch of perfection into which muscles can be brought; it is not a permanent state, no horse can remain in it for any length of time, and many can never be got into it at all. It is easy in the training of horses to overstep the mark and produce 'staleness,' a result due to over-training, but which, unless it be gone too far, is in both men and horses recovered from by a short judicious rest, when the system immediately responds.

It is necessary, however, to remember that condition though judged of largely by the state of the muscles has a very important claim on the respiratory and circulatory systems. To sustain severe and prolonged muscular exertion an adequate supply of oxygenated blood must be sent to the muscles; this necessitates a rapid flow of blood through the lungs, strong regular pumping power in the heart, and adequate ventilation in the lungs. All these factors must work in harmony, and though long walking exercise is given as a muscle developer, and judicious gallops to give the animal its 'wind,' yet as a matter of fact the 'wind' is largely a question of heart. As the circulatory pump works at higher pressure the bloodvessels must be fit to stand the strain, and to return to the heart by both auricles the amount of blood leaving by both ventricles. A deficiency in this mechanism leads to 'loss of breath'; clogging in the lungs means deficient oxygenation, and without an adequate supply of hæmoglobin saturated with oxygen the muscles are practically powerless to contract.

Rigor Mortis.—After death a muscle passes into the condition of rigor or stiffening, by which it changes both in its physical and chemical aspect. The muscle becomes firm and solid, loses its elasticity, and no longer responds

to electrical stimuli; further, it loses its alkaline reaction, and in course of time becomes acid owing to the formation of lactic and other acids. Through the death of the muscle the fluid myosin becomes coagulated, it is this coagulation which produces the stiffening; the analogy between rigor mortis and blood-clotting is very marked. During rigor mortis heat is developed, and some after-death temperatures are remarkably high.

The rapidity with which rigor mortis sets in differs according to the mode of death. If an animal in perfect health be destroyed the muscle stiffening is slow to set in and very persistent; where death is produced by debilitating disease, or in cases where severe muscular exhaustion has preceded death, the rigor mortis may occur so suddenly and pass off so rapidly as occasionally to escape observation, and decomposition also sets in early.

The muscles of the tongue, pharynx and œsophagus appear to be the only ones where rigor mortis occurs incompletely; the extremity of the tongue in a dead horse is nearly always flaccid, and hanging out of the side of the mouth.

After a certain length of time rigor mortis passes off and decomposition commences.

CHAPTER XIV.

THE NERVOUS SYSTEM.

Nerves.—Various classifications have been adopted for nerves. Anatomically they are known as cranial, cerebro-spinal, and sympathetic, but for physiological purposes they are classified according to their structure and function. Thus, from a structural point of view there are (1) medullated, (2) non-medullated nerves, while classified according to their function there are (1) afferent, frequently called sensory, and (2) efferent, commonly called motor. The division into motor and sensory is so obviously incomplete, confining the function of nerves to simply conveyers of motor impulses, or carriers of sensation, that the terms afferent and efferent have been adopted.

Afferent nerves are those conveying an impression from the periphery of the body to a nervous centre, that is to say conveying centripetal impulses. The centre may be situated in the brain or spinal cord, and the afferent impressions thus conveyed may be nervous impulses of (*a*) special sense such as sight, hearing, taste, smell, etc.; (*b*) impulses conveying the impression of sensation pleasurable or painful, from skin, muscle, and viscera; (*c*) impulses conveying the impression of heat and cold, or (*d*) impulses leading to a reflex act without affecting consciousness at all.

Efferent nerves are those conveying impulses from a centre to the periphery, that is conveying centrifugal impulses; these impulses in the main are of a motor nature

evoking from the muscles, bloodvessels, and viscera movements and contractions; they may also be of an inhibitory or controlling character, such for instance as the impulses which slow the heart, dilate the bloodvessels, or restrain the peristaltic contraction of the bowels. But besides these, centrifugal impulses may be of such a nature as to cause glands to secrete, or to regulate the metabolism of a part, or control, stop, or augment any other efferent act.

Though afferent and efferent nerves have all these varied functions assigned them, it does not follow that in every case distinct nerves exist for each function; for instance, we know that in the case of the nerves of special sense distinct channels exist which are of no other use than that for which they were designed; but we have no evidence that separate nerves exist which carry, say to a horse's brain, the fact when he is being 'fired' (1) that pain is being inflicted, and (2) pain accompanied by burning; in other words, it is probable that no matter what the sensory impressions may be, painful or pleasurable, hot or cold, rough or smooth, they are all conveyed from a part by the same afferent channel and differentiated elsewhere.

On the other hand, we know that the nerves which cause constriction of the arteries are not the same which cause contraction of adjacent muscles, and in the same way we know that division of the optic nerve gives rise to no pain and only a luminous sensation, irritation of the auditory to the sensation of sound and sound only, and so on.

Again, there are afferent nerves conveying to centres impressions which are totally unrecognised unless they get out of order. Take for instance the impulses passing from the bowels, the existence of these one may remain in ignorance of all their life, or may be made painfully aware of their presence by an attack of colic.

Thus there are distinct channels for (1) centripetal (2) centrifugal impulses; but there are not distinct channels for every kind of nervous impulse, though in some cases distinct channels exist.

Structure of Nerves.—Medullated nerves, often spoken of as white nerves owing to their colour, are distinguished microscopically by the fact that they possess a white fatty sheath enveloping the essential nerve-substance or axis-cylinder, which lies like a core within it. The axis-cylinder is the true nerve-substance, and is in connection with either the brain or spinal cord, depending upon the position of the nerves. In these organs are situated cells with processes, the processes become the axis-cylinders of nerves, so that the cells of the brain, and especially of the spinal cord, may be looked upon as possessing processes of immense length.

The white fatty sheath, known as the medullary sheath, which covers the axis-cylinder does not extend continuously along the nerve, but is broken at intervals termed nodes; the portion of nerve included between two nodes has somewhere in it a cell. It is at the nodes where the fatty sheath is absent, that the material which supplies the nerve with nutrition gains access. Covering the medullary sheath is a delicate membrane which envelops the fatty matter, it is known as the neurilemma. Such is the structure of a single nerve-fibre; bundles of such fibres, enclosed in an appropriate material, constitute a nerve.

The non-medullated nerves, often spoken of as sympathetic or grey fibres, possess no white fatty cover around their axis-cylinder; they are freely nucleated at intervals, and made up in bundles like medullated nerves.

The essential feature in the nerve is the axis-cylinder, it is the true impulse-conducting substance, while fatty sheaths can only be looked upon as a means of insulation or support.

From what has been stated about the nature of the axis-cylinder, it can be readily understood that every nerve runs direct from its origin to its termination, there is no union of nerve-fibres, each and every one is distinct, though numerous divisions may exist at their termination.

In certain cases medullated nerves enter nervous bodies known as ganglia and leave them as non-medullated fibres;

all medullated nerves before breaking up in the tissues they are intended for, lose their fatty sheath and eventually their neurilemma, nothing but the bare axis-cylinder being left.

Ganglia on Nerves.—Placed on certain nerves, somewhere in their course, are masses of nervous tissue called ganglia; these ganglia are composed of nerve-fibres embracing nerve cells; the latter are of a particular shape depending upon whether the ganglion examined be from the cerebro-spinal or sympathetic system. In the former the nerve cells are round and possess a projection or pole, which not unfrequently coils before issuing from the cell, and after running a short distance divides T-shaped into two branches which travel in opposite directions; such a body is known as a unipolar cell.

The ganglia belonging to the sympathetic differ in the shape of their cells, for these instead of having one pole like the cerebro-spinal, have two, three, or more poles, known as bi-polar or multipolar cells.

We may here say, though the subject will be touched on again, that the cells of the brain, spinal cord, and sympathetic system, are mainly multipolar, whilst those of the spinal and cranial ganglia are unipolar. Bi-polar cells may be found in the spinal ganglia of fishes.

One process of a nerve-cell is the axis-cylinder of a nerve, the other processes branch, dividing and subdividing like a root, and become primitive fibrils.

Nerves are remarkable for their want of elasticity, they do not retract on being divided; further they are capable of very considerable stretching without breaking; in the human subject the nerves of the limbs require a force of from 40 lbs. to 120 lbs. to break them.

There are nerves supplying nerves, the *nervi nervorum*, and the rationale of nerve-stretching in painful diseases is probably accounted for by the damage done to these minute nerves during the process.

Nerve trunks receive a poor blood supply, though ganglia and grey matter are richly vascular; it is possible that

the numbness produced in a sensory nerve by pressure is due to its blood supply being temporarily cut off, the nerve thus losing its irritability. The lymphatics are numerous, and exist within the lamellæ of the perineurum or covering of the nerve bundle.

Excitability.—We have no means of distinguishing microscopically between an afferent and an efferent nerve, there is nothing in the structure of a motor, sensory, or secretory nerve, which enables its function to be determined. Further, we know that though in the body impulses pass only in the one direction through a nerve, yet removed from the body and tested electrically it is as easy to pass impulses in one direction as another.

Nerves however are excitable, the living nerve can be made to react by means of chemical, mechanical, or electrical stimuli, and when so excited appear to transmit the same impulses as when irritated physiologically, viz. as when the normal body impulses are being transmitted; thus the stimulation of a sensory nerve gives rise to pain, of a motor nerve to muscular contraction, and of a secretory nerve to secretion.

The conductivity of nerves is diminished by cold, compression, or injury, but it is noteworthy that even after long-continued excitation nerves are found practically inexhaustible. Impulses are no longer transmitted when nerves are ligatured or divided.

Electric Phenomena of Nerves.—Some very definite facts are known in connection with the electric currents in nerves, and the effect on the excitability of the nerve by transmitting currents through it; these facts have been ascertained with the nerves of the frog, and so far as can be proved apply to the higher animals.

If a nerve be removed from the body and suitably applied to an instrument which is capable of measuring delicate electric currents, the galvanometer, the needle of the instrument will be found to be deflected, showing the passage of a current; it is spoken of as the *current of rest*, and by many physiologists grave doubts have been expressed as to

whether this is a natural current in nerves or not. It is practically identical in direction with the natural muscle current described on p. 315.

If while the current of rest is passing shocks be sent into the nerve from an induction coil, the needle of the galvanometer is found to indicate a momentary current in the opposite direction to the current of rest. This momentary opposite current is spoken of as *negative variation* or the *current of action.* If, instead of passing into the nerve shocks from an induction coil, we pass into it a continuous current of voltaic electricity, certain phenomena will occur, to explain which we must suppose the nerve experimented upon to be in connection with a muscle.

With such a preparation the electrical stimulation employed is the make and break of a constant (voltaic) current, such as is produced by connecting two wires with a suitable battery, and in addition an induced current (faradic), which is obtained by means of a battery and an induction coil.

If a moderate constant current be passed into the nerve by connecting it with the poles of the battery, at the moment the connection is made the muscle gives a twitch or contraction, and then remains perfectly quiet though the current is still streaming through it; if the connection be broken by removing one pole of the battery, the muscle gives another contraction. This is termed 'a making and breaking contraction,' viz., a contraction produced on closing and opening the electric circuit. If instead of a moderate constant current a weak or strong one be used, the results on making and breaking may not be the same.

During the period of apparent quiescence following the closing of the circuit, though the muscle is giving no indication of the current, yet changes are occurring in the nerve; if it be tested by passing into it an induced current, it is found that the irritability is diminished in the neighbourhood of the positive pole of the continuous current, and increased in the neighbourhood of the negative pole. This condition is known as **electrotonus**, the diminished irritability being known as **anelectrotonus**, the increased ex-

citability as **kathelectrotonus.** Between the increased and reduced irritability, is a zone of unaffected irritability known as the **neutral point.**

During the condition of electrotonus there is no interruption to the natural nerve current, which is simply increased

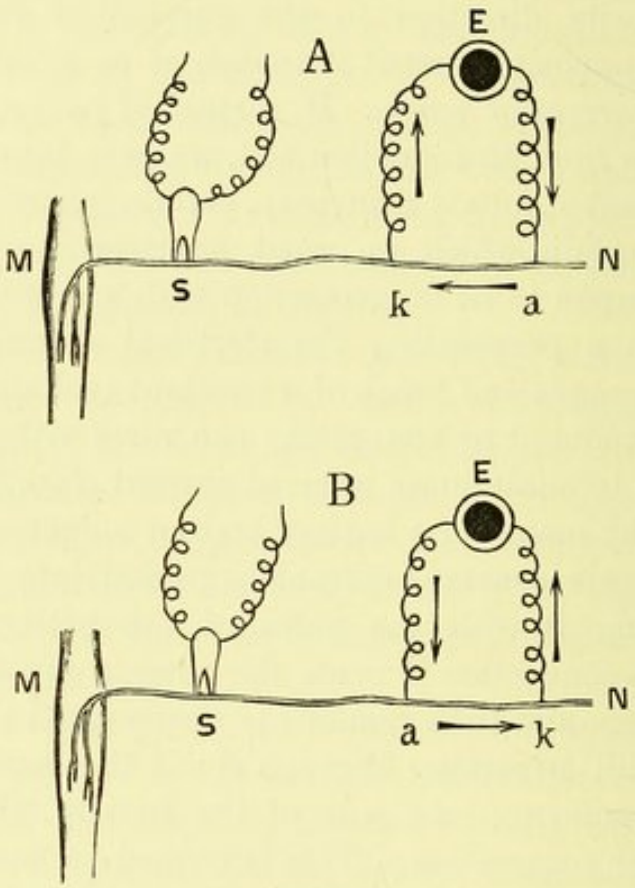


FIG. 49.—DIAGRAM OF ELECTROTONUS.

N, the nerve running to the muscle M; E, an element for the production of a constant current, the positive pole or anode (a) in A being placed furthest from the muscle, the current consequently flowing down the nerve, and in B being placed nearest to the muscle, the current flowing up the nerve; at S the nerve is stimulated by an induced current, and its irritability determined by the contraction of the muscle M; the irritability is increased in A, kathelectrotonus, and decreased in B, anelectrotonus.

if the constant current takes the same direction as the current of rest, but if the constant current be passed in the opposite direction to the nerve current, the latter is diminished.

To state this matter more clearly, imagine a nerve

running to a muscle, Fig. 49; at a certain part of the nerve a continuous current of electricity generated at E is passed through it, the application and withdrawal of which gives rise to the making and breaking contraction previously mentioned; during the passage of the current the muscle is perfectly quiet, in spite of important changes occurring in the nerve. Shocks are now sent into the nerve from an induction coil at a place between the muscle and the continuous current; as the result of the stimulation the muscle either responds more than it should do for the strength of the stimulus employed, viz., there is increased excitability of the nerve (kathelectrotonus), or the muscle does not respond as strongly as it should, viz., there is decreased excitability of the nerve (anelectrotonus). The increase or decrease of excitability in the nerve depends upon whether the continuous current is passed down it, as in Fig. A, or up it, as in B; with a descending current the excitability is increased, with an ascending one it is decreased.

The explanation of electrotonus in nerves is that it is a vital phenomenon, viz., the irritability of the nerve is increased when its molecules pass from their ordinary condition to one of greater mobility (kathelectrotonus), or it is diminished when its molecules pass from their ordinary condition to one of less mobility (anelectrotonus) (Cyon). Hermann considers that it is a purely physico-chemical phenomenon, due to the electric current generating acids at the positive pole, and alkalis at the negative; the effect of the acid is to lower the excitability of the nerve, and of the alkali to increase it.

The practical application of this law is that the excitability of a part, pain, cramp, etc., may be removed by passing a current up the nerve, viz., by placing the positive pole nearest the muscle, and producing anelectrotonus; or by reversing the process and throwing the current down the nerve, so that the negative pole is nearest the muscle, the irritability of the part is increased.

The Nature of Nervous Impulses is quite unknown, excepting

that they travel in the form of waves, but a wave which is smaller and more rapid than that which traverses a muscle. It is impossible to tell what influence is passing along a nerve in obedience to a physiological stimulus, that it is not due to the passage of an electric current appears for many reasons quite certain, amongst others being the slow rate of a nerve impulse compared with that of an electric current.

At one time it was believed that the nerve impulse gained strength the longer the stretch of nerve it had to travel, hence the 'avalanche theory' of Pflüger that impulses increased in the nerve as it passed towards the muscle; it is now known that this is not the case, but the greater contraction obtained by stimulating a nerve some distance from its muscle, is explained by the fact that the further the nerve is from the muscle the nearer it is to the spinal cord, and the excitability of a nerve is greatest near its nerve centre.

Impulses are not transmitted from one fibre to another in a nerve bundle; in medullated nerves this may be accounted for by the good insulation provided by the medullary sheath.

Conductivity of Nerves.—Compared with electricity a nervous impulse travels very slowly, and it is necessary to bear this in mind as comparisons between electric currents and nerve impulses have been made.

The velocity of nervous impulses in motor nerves has been stated between 111 to 140 feet per second, whilst through sensory nerves it is said to be faster 160 to 320 feet per second; in visceral nerves the velocity is less, Chauveau ascertained in the pharyngeal branches of the vagus that the velocity amounted to 26 feet per second.

Degeneration of Nerves.—When nerves are cut they degenerate, the degeneration always taking place in the portion cut off from its nutrient centre. The nerve fibre, as has been stated above, is but a branch of a nerve cell; if a portion of a cell be separated from the rest containing the nucleus of the cell it soon dies. Thus, when a large

amœba, or a Radiolarian, is torn up into several pieces, the portions containing no nucleus degenerate and die; but that portion containing the nucleus repairs itself and reforms a perfect cell. The nerve fibre dies down after being cut, just in so far as it is a piece of cell cut off from its nucleus.

The sensory nerve divided in neurectomy, as practised on the horse, degenerates towards the foot and not up the limb, for it is the piece below the wound which is cut off from its nutrient centre and not the portion above; had this been a motor nerve the degeneration would still have taken place below the wound and for the same reason. All spinal nerves have their seat of nutrition either in the spinal cord or just outside it; the nearer to the spinal cord at which the section is made the greater the length of nerve which degenerates, the further away from the cord at which section is practised the shorter the length which degenerates.

When the nerve degenerates the fatty medullary sheath breaks up forming globules around the axis-cylinder, this latter also degenerates and afterwards breaks off. The remarkable fact about these changes is the rapidity with which they occur, ten days is sufficient to show their commencement; small nerve fibres degenerate more quickly than large.

By suturing divided nerves union occurs, and though the act of division causes degeneration, yet when union takes place regeneration of fibres occurs; a fresh axis-cylinder grows through the length of the degenerated nerve, and after some weeks and often months motion or sensation is restored, the former always much later than the latter.

Even suture of divided nerves is not always necessary for union; we know clinically that the plantar nerves of the horse will often unite in a few months in spite of a piece being excised, the portion of nerve above growing down an axis-cylinder which soon finds out its divided portion below.

Not only is the nutrition of the nerve itself affected

by nerve division, but also the nutrition of those parts supplied by it; ulceration more or less severe has been known to follow injury of certain nerves, sloughing of the cornea occurs in animals when the ophthalmic division of the fifth is divided, and many are practically acquainted with the sloughing of the entire foot which sometimes, though fortunately rarely, follows the operation of neurectomy.

It is undoubted that nerves influence the nutrition of a part, nowhere is this better demonstrated than in cases of intense muscular atrophy due to nerve injury; these trophic nerves also take an important part in the metabolism of the body.

Nerve Terminations.—There are some structures like glands where the nature of the nerve termination is not satisfactorily made out, there are other places like muscle where definite and distinct motor nerve-endings have been found; and on many sensory and sympathetic nerves special terminations known as Pacinian corpuscles and Krause's end-bulbs exist.

Nerve terminations are found in the muzzle of animals, in tendons, in muscles, in the generative organs, conjunctiva, mouth, tongue, epiglottis, etc.; some are known as Krause's end-bulbs, those in tendon are described as the organ of Golgi, in muscle they are known as end-plates, whilst in the skin of the muzzle the nerves terminate in small swellings or enlargements known as tactile cells, which are placed between the epithelial cells of the epidermis; cells of this kind also exist in the foot of the horse.

The nerves of special sense have each a distinct termination peculiar to themselves, such as the hair cells of the internal ear, the rods and cones of the retina, taste bulbs of the tongue, etc.

Spinal Cord.

The spinal cord extends from the atlas to about the second or third sacral vertebra, and is completely enclosed in a dense membrane, the dura mater. The canal in which it is lodged is very much larger than the cord, especially at those parts where the greatest amount of movement occurs, as in the neck. The cord is not the same shape nor the same size throughout; oval in the cervical region, it becomes circular in the dorsal, and again oval in the lumbar portion. It is largest where any considerable bulk of nerves is being given off, and thus there is an enlargement corresponding to the fore, and another to the hind limbs. On exposing the spinal canal, a large number of nerves are found to be passing through the dura mater either outwards or inwards, and these gain an exit from or entrance to the spinal canal by means of the foramen formed at the junction of the vertebræ.

Spinal Nerves.—On opening the dura mater, it is observed that the nerves divide in such a way that part of them run to the superior, and part to the inferior surface of the cord; these are spoken of as the superior and inferior roots of the spinal nerves. In the horse the number of branches of nerve thus formed is considerable, for both the superior and inferior enter the cord not by a single root but by several.

On the superior root, but outside the dura mater, is found a nervous body termed a ganglion; each branch of a superior spinal nerve has a ganglion on it: no such body exists on the inferior root. Both inferior and superior roots unite below the ganglion to form a mixed spinal nerve (see Fig. 51).

The function of these two sets of nerve roots is entirely different; the superior root, possessing the ganglion, conveys sensation and sensation only; the inferior roots convey motion, in addition to certain other functions to be shortly alluded to: the superior roots are passing into the cord, the inferior roots are passing out of it.

Passing out with the inferior root of the spinal nerve, but indistinguishable from it, is a branch of nerve known as the white ramus communicans, which leaves the main trunk after the mixed nerve has formed, and runs to a distinct system known as the sympathetic. One part of the latter, the gangliated cord, runs under the arches of the ribs and back as far as the loins; to this cord the white ramus

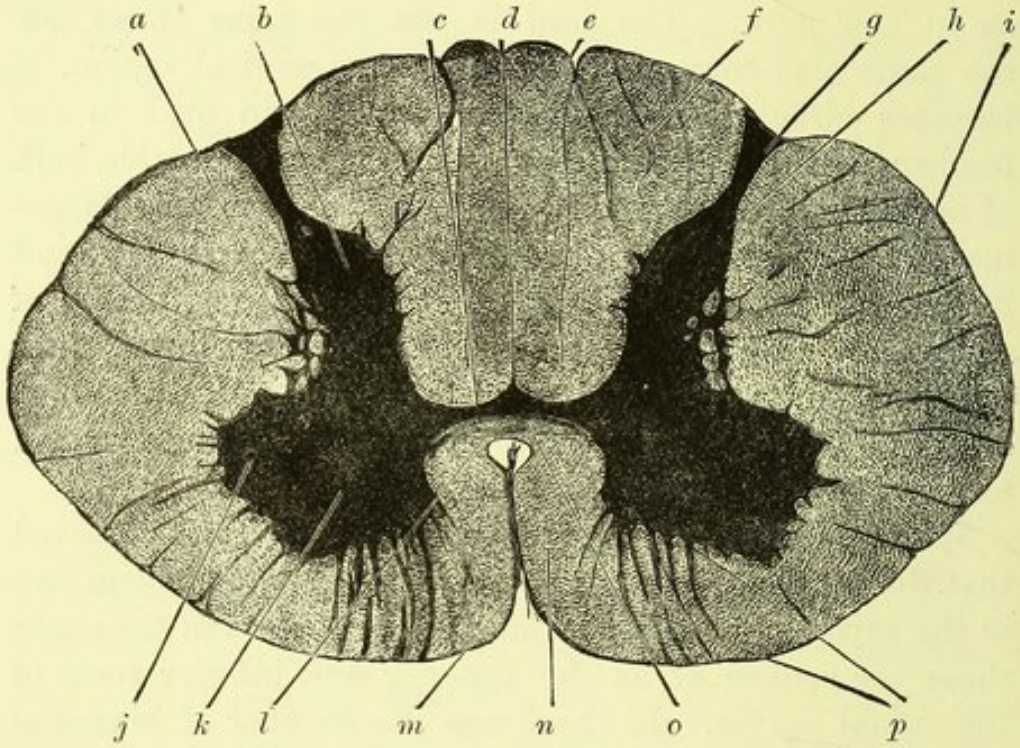


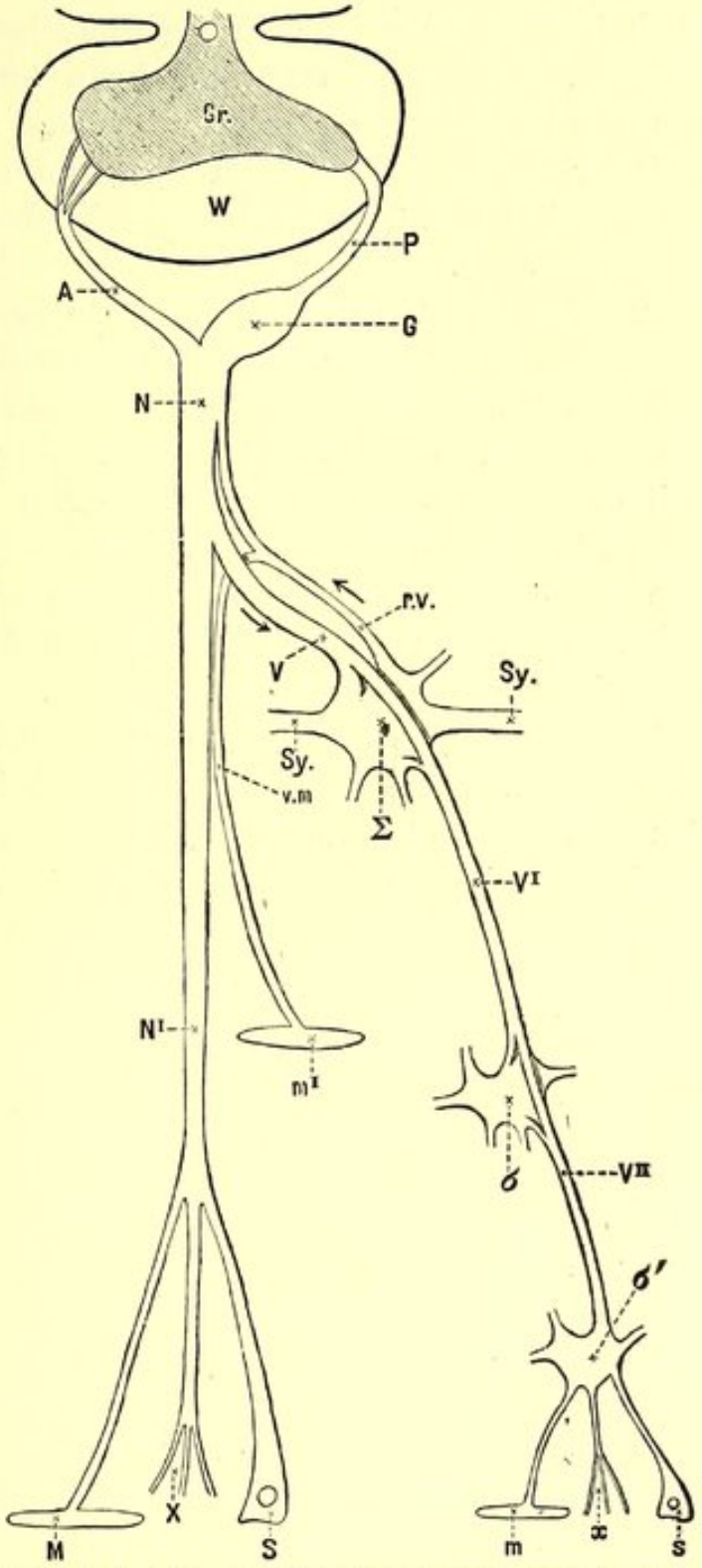
FIG. 50. — TRANSVERSE SECTION OF THE SPINAL CORD IN THE CERVICAL REGION ×8D. THE LINES IN THE LATERAL AND SUPERIOR COLUMNS RUNNING FROM THE OUTER MARGIN ARE LAMINÆ OF THE PIA MATER. (M'KENDRICK.)

a, Processus reticularis; *b*, superior horn; *c*, grey commissure; *d*, superior septum; *e*, Goll's column; *f*, superior column; *g*, superior root; *h*, substantia gelatinosa; *i*, lateral column; *j*, large multipolar nerve cells; *k*, inferior horn; *l*, white commissure; *m*, inferior longitudinal fissure; *n*, inferior column; *o*, central canal; *p*, inferior roots.

runs, and establishes a communication between the cerebro-spinal and sympathetic system; moreover, in this branch are the nerves which constrict the bloodvessels. A careful study of Fig. 51 is necessary for the clear elucidation of the arrangement of the spinal nerves.

Arrangement of the Cord.—If a cord be suitably prepared,

FIG. 51.—SCHEME OF THE NERVES OF A SEGMENT OF THE SPINAL CORD (FOSTER).



Gr., grey; W, white matter of spinal cord; A, inferior; P, superior root; G, ganglion on the superior root; N, mixed nerve, consisting of sensory and motor branches with fibres passing into the sympathetic system at V; N^1, spinal nerve, consisting of sensory and motor branches, terminating in M, skeletal muscles, S, sensory cell or surface, and X, in other ways. V, white ramus communicans uniting the cerebro-spinal with the sympathetic system; it runs out from the cord with the inferior spinal nerve, and is given off from the mixed nerve at V, from whence it passes to Σ, a ganglion on the sympathetic chain, and thence on to V^I to supply the more distant ganglion σ, then to V^{II} to the peripheral ganglion σ′, and ends in *m*, a visceral muscle, *s*, a visceral sensory cell or surface, and *x*, other possible visceral endings.

From Σ is given off a branch, r.v., known as the grey ramus communicans, which partly passes backwards towards the spinal cord, and partly runs, as v.m., in connection with the spinal nerve to supply vaso-constrictor fibres to the muscles of bloodvessels, m^1, in certain parts, for example in the limbs.

Sy, the sympathetic chain (gangliated cord of the sympathetic) uniting the ganglia of the series Σ. The terminations of the other nerves arising from Σ, σ, σ′, are not shown.

it is found to consist of a superior, lateral, and inferior column, each being separated by a longitudinal groove. On the superior and inferior surface is a fissure; the inferior fissure is wide and does not reach down to the centre of the cord, whilst the superior fissure is narrow and deep (Fig. 50).

A section of the cord shows it to be made up of both white and grey matter, the latter internally placed, forming the medulla, is arranged something like two commas placed back to back, the tail of the comma being uppermost. The tail of the comma corresponds to the incoming sensory fibres, the head of the comma to the outgoing motor ones; the two commas anatomically known as cornua, are connected by a band of grey matter called the grey commissure, in the centre of which is a canal.

The white substance of the cord is not the same thickness throughout, stated generally the cord increases in white matter from the tail to the head; the grey matter is largest in the cervical and lumbo-sacral enlargements, and this increase and decrease in size corresponds with the increase and decrease in the number of nerves entering and leaving the cord.

The white substance of the cord is found microscopically to consist of longitudinally arranged medullated nerve fibres, very much like those previously described, excepting that the fatty white substance has not the same covering found in other medullated nerves, but is enclosed in a sheath of neuro-keratin which is peculiar to the nerves of the spinal cord. Between groups of fibres exist peculiar branched corpuscles known as glia cells; these belong to a connective tissue peculiar to the cord, called the neuroglia.

The grey matter of the cord consists of cells, many being large multipolar; amongst these are very fine fibres either the delicate processes of the cells, or of medullated or non-medullated fibres derived from the white substance of the cord, and terminating in the grey matter: the whole is held together by neuroglia.

The nerve cells of the grey matter of the inferior cornua

arrange themselves into certain groups in various parts of the cord, those situated at the lower part of the cornua run the entire length of the cord, but others are limited to certain regions, being at some parts strongly in evidence, at others almost or entirely absent. The cells are very large, and possess numerous branched processes or poles known as multipolar cells. In the superior cornua the cells are not in groups, and moreover they are much smaller.

A peculiar column of cells known as Clarke's column is limited to three portions of the spinal cord; the cells are found lying above the inferior cornua towards the middle line of the cord, and are related to the endings of sensory nerves entering the cord. The cells of this column have few processes, and their long axis lies in the long axis of the cord.

Distribution of Nerves in the Cord.—The superior spinal nerve root joins the superior cornu, the inferior proceeds from the inferior cornu. We must now learn how the fibres composing these roots are disposed with reference to the cord itself.

Recent work in connection with the arrangement of the nerve fibres in the spinal cord has thrown fresh light on this subject, and produced a modification of our previous knowledge.

The fibres of the superior spinal nerve root grow from the spinal ganglion, enter the superior column of the white matter of the cord, and some travel forwards others backwards in its substance; after running a short distance the fibres bend at right angles, enter the grey substance of the cord, and end not in nerve cells but simply in fine branches (Fig. 52). During their course, before the final bending occurs, they all give off collateral fibres at right angles to the main trunk, which enter the grey matter, and connect the parent fibre with various segmental levels of the cord. In this way all the sensory fibres reach the grey matter of the superior and in some cases the inferior cornua, terminating in numerous fibrils close to but not in continuity with the nerve cells (Fig. 53). The superior

column of white matter is made entirely of the fibres of the superior roots arising in the cells of the spinal ganglion.

The fibres of the inferior spinal nerve roots may be traced into the grey matter of the inferior cornua. There each has its origin, for it really arises in one pole of the large multipolar cells situated there, the remaining poles of the cells giving off small branched fibres (Fig. 53 and 54).

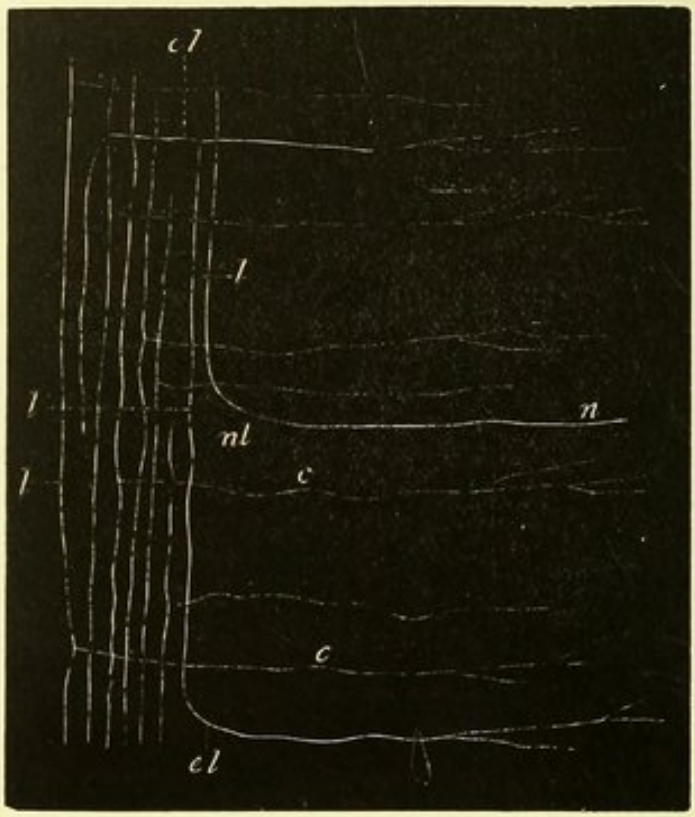


FIG. 52.—LATERAL COLUMN OF A NEW-BORN RABBIT TO SHOW THE COLLATERAL FIBRES, AND THE MANNER IN WHICH THE LONGITUDINAL FIBRES BEND ROUND AND END FREE IN THE GREY MATTER. (LANDOIS AND STIRLING, AFTER RAMON Y CAYAL.)

c, collateral fibres, *cl* bending round of the longitudinal fibres, *l*, to end in the grey matter; *n*, axis cylinder process of nerve-cell bending in amongst the longitudinal fibres of the white column.

The axis cylinder process of the inferior cornual cell is, excepting in very rare instances, without collaterals (Fig. 54).

The inferior and lateral white columns are composed of fibres which originate from nerve cells in the grey matter of the fibres in the cord; the fibres in these columns give

off collateral fibres which again enter the grey matter, and finally the fibre itself, as we saw in the superior column, bends round and terminates in the grey matter of the cord; it is observed that none of these fibrils are in continuity with nerve cells nor do the fibrils anastomose among themselves. The inferior and lateral columns of one side of the

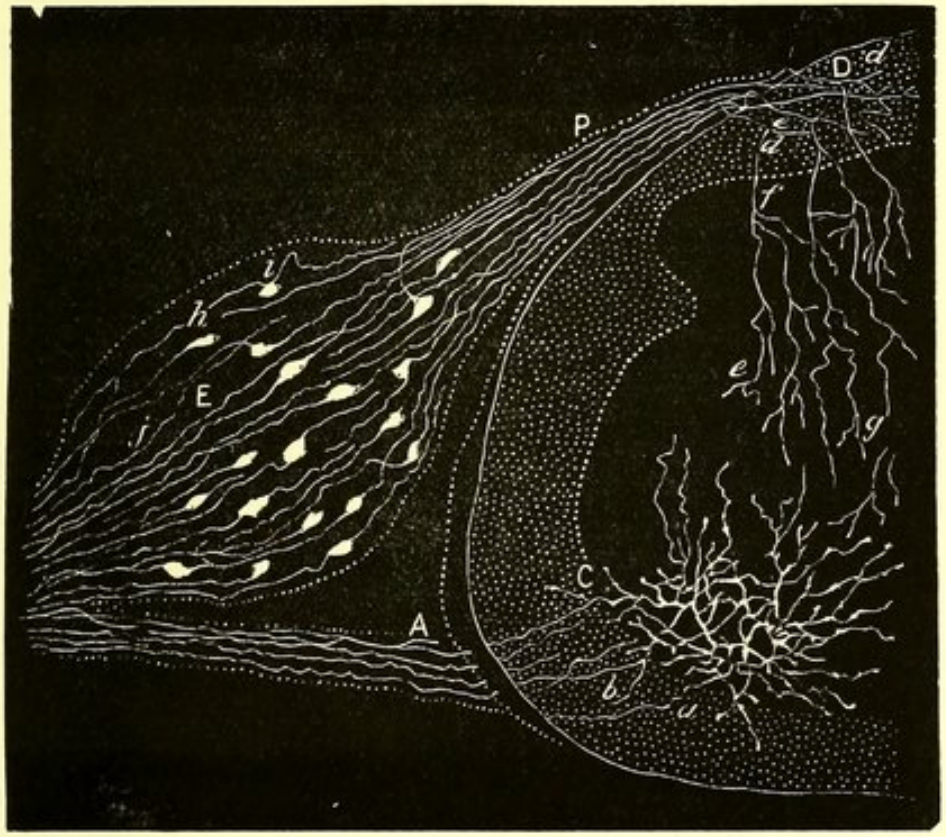


FIG. 53.—TRANSVERSE SECTION OF THE SPINAL CORD IN THE THORACIC REGION OF AN EMBRYO FOWL, AT 9TH DAY OF INCUBATION. (LANDOIS AND STIRLING, AFTER RAMON Y CAYAL.)

A, inferior root; P, superior root of spinal nerve; C, axis cylinder of a motor nerve cell, issuing from the large cells of the inferior cornu; D, intra-medullary part of the superior root; *e*, origin of a collateral branch, which ramifies as *f g*, the terminal ramifications of the collateral fibres; *d*, final bifurcation; E, ganglion on superior root; *h*, bi-polar ganglionic cells; *i*, a unipolar nerve cell like those in mammals.

cord receive fibres from the opposite side, and these, with the aid of the collateral fibres which are returning in the opposite direction, help to constitute the anterior commissure.

Corresponding to this arrangement of the fibres it is found that three different kinds of nerve cells exist in the

grey matter: (1) the large multipolar cell of the inferior cornua in which the motor fibres begin, (2) cells supplying the fibres which pass into the inferior and lateral columns of the cord, and (3) cells found only in the superior cornua, giving off a process which is confined entirely to the grey matter and breaking up in it. In connection with all these cells it is important to bear in mind that the branched processes do not anastomose, although they are often continued for a considerable distance.

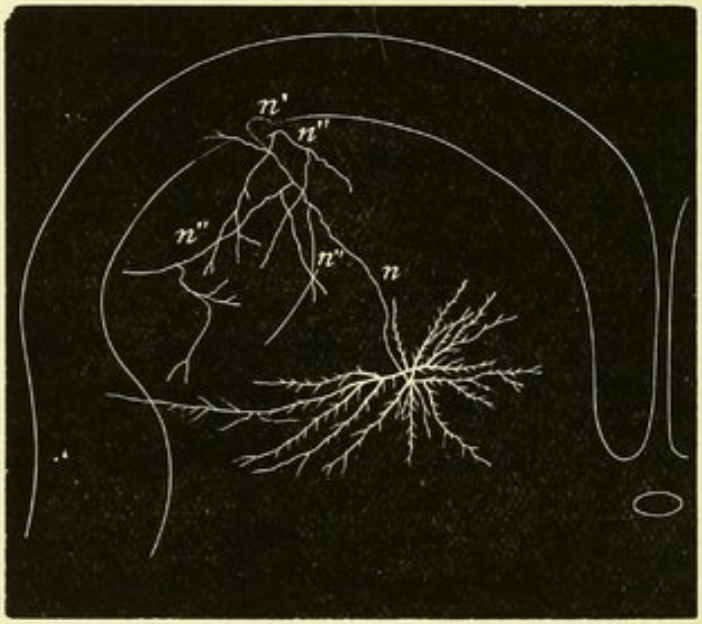


FIG. 54.—A NERVE CELL IN THE INFERIOR CORNU OF THE LUMBAR REGION OF AN OX EMBRYO. (LANDOIS AND STIRLING, AFTER GOLGI.)

n, axis-cylinder process passing at *n'* into a longitudinal fibre of the inferior column; *n''* much branched lateral process of *n*.

The chief features which recent inquiry has brought to light are the collateral branches of fibres; these fibrils do not anastomose, but terminate by surrounding and perhaps coming into contact with nerve cells.

This latter fact would go to show that many of the impulses conveyed to the cord can only act on the nerve cells by contact without continuity.

Function of Spinal Nerves.—If the superior spinal roots be divided it causes great pain, all parts supplied by them below the division lose sensation, but if the portion of

nerve in connection with the spinal cord be irritated pain is produced.

If the inferior roots be divided all parts supplied by the nerves below the seat of division suffer motor paralysis; if the cut end of the nerve still in connection with the tissues be irritated the muscles contract vigorously, whilst if the piece of nerve in connection with the cord be irritated nothing happens.

In this way it is demonstrated that the sensory impulses pass into, whilst the motor impulses pass out of the cord.

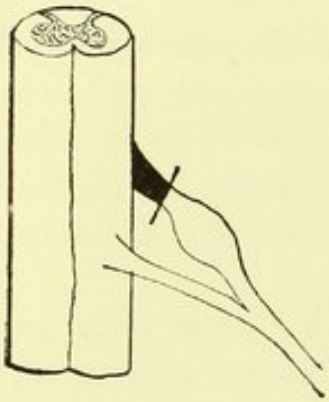
Sometimes pain is felt when the motor roots are divided, due to one or two branches of the sensory nerves finding their way in by this channel; the phenomena is known as *recurrent sensibility.*

The function of the inferior or motor roots is to supply all the voluntary muscles with the power of movement, the bladder, uterus, intestines, and other hollow viscera and the blood-vessels, with the power to contract and dilate, secretory fibres to the sweat-glands of the skin, and perhaps 'nutritive' nerves to the tissues. Many of the nerve fibres of the efferent or inferior roots are distributed *viâ* the sympathetic system; from which nerve cells in the cord they arise is not at present known, but after leaving the cord in the inferior roots they join the vertebral ganglia of the sympathetic under the name of the 'rami communicantes' of those ganglia, thus establishing a communication between these two important systems (see p. 338).

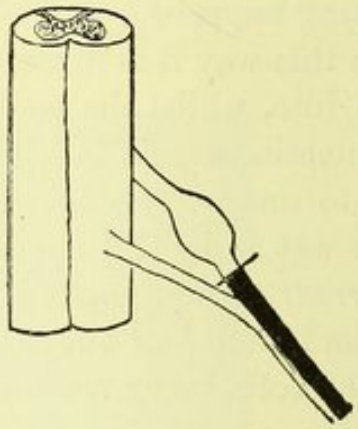
The spinal sensory fibres endow the whole of the body with sensation, with the exception of certain parts of the face.

Wallerian Degeneration.—As the result of dividing the spinal nerves degeneration of them occurs; if the superior root be divided *above the ganglion* degeneration occurs upwards into the spinal cord, and there affects certain bundles of fibres, which are really the fibres of the superior roots continued into the spinal cord, and running especially forward towards the head (Fig. 55—1). If the root be divided *below the ganglion* the degeneration takes

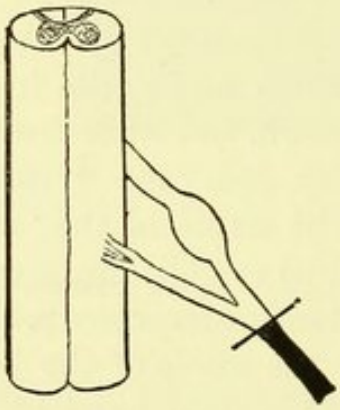
place in a downward direction, involving the whole length of the nerve below the ganglion (Fig. 55—2); if the trunk be divided both above and below the ganglion degeneration above and below occurs, but the ganglion remains unaffected. If the mixed nerves be divided below the ganglion, both roots degenerate (Fig. 55—3).



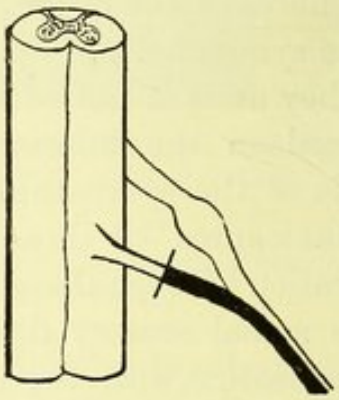
No. 1.—Degeneration of afferent fibres caused by a section of superior root above the ganglion.



No. 2.—Degeneration of afferent fibres below a section of superior root below the ganglion.



No. 3.—Degeneration of efferent and afferent fibres below a section of the entire nerve.



No. 4.—Degeneration of efferent fibres below a section of inferior root.

FIG. 55.—DIAGRAMS TO ILLUSTRATE WALLERIAN DEGENERATION OF NERVE ROOTS. (WALLER.)

All this is explained by saying that the ganglion is the seat of nutrition of the superior spinal nerves, and whichever part of the nerve is cut off from its nutritive influence degenerates; or in other words, the ganglion contains the

nerve cells, of which the sensory nerve fibres of the nerve are the axis cylinder processes.

If the inferior nerve roots be divided degeneration of them also occurs, but the degeneration extends *down* the trunk of the nerve, and does not run up into the spinal cord (Fig. 55—4), the explanation being that the seat of nutrition of the motor nerves lies in the spinal cord, so

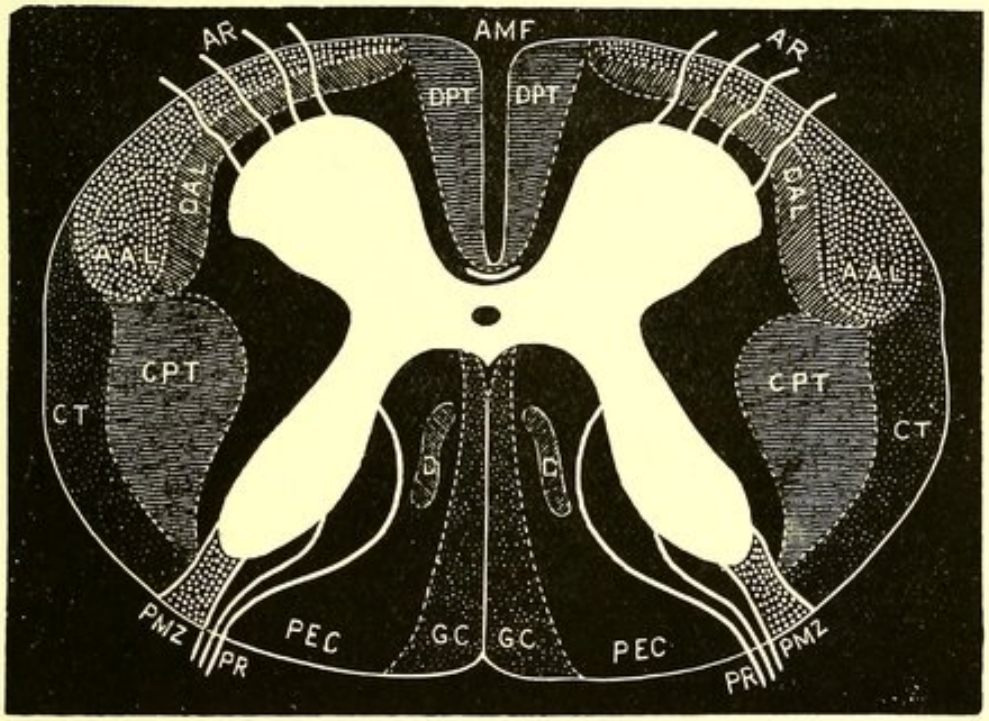


FIG. 56.—SCHEME SHOWING THE DEGENERATION TRACTS, AND THE PATHS WHICH DO NOT UNDERGO DEGENERATION IN THE CORD. (LANDOIS AND STIRLING.)

AMF, inferior median fissure; DPT and CPT, direct and crossed pyramidal tracts. AR, inferior root; PR, superior root of spinal nerves; AAL and DAL, ascending and descending infero-lateral tracts; CT, cerebellar tract; GC, column of Goll; D, comma-shaped tract; PMZ, superior marginal zone; PEC, posterior-external column. The parts left black do not undergo degeneration; the ascending degenerations are shaded with dots, the descending with lines.

that degeneration occurs below the cut part and not above it.

These degenerative changes were first described by Waller and bear his name.

Tracts in the Cord.—The white matter of the cord can be mapped out into columns or tracts, which are quite distinct from the columns into which the cord is

anatomically divided. Some of these tracts convey impulses from the cord to the brain and are known as ascending tracts; others convey impulses from the brain to the cord and are known as descending tracts.* These descending and ascending tracts have not been made out by ordinary observation, but by experimental inquiry and embryology. It was found that after division of certain nerves, or injuries to certain parts of the brain or spinal cord, particular tracts became degenerated either in a forward or backward direction. By this and other means, it was ascertained that certain paths or tracts exist in the white matter of the cord, connecting the brain with the cord and *vice versâ*. It must not be supposed that the function of an ascending or descending tract is necessarily entirely exerted in the direction given to it by its name; the tracts are called ascending or descending according to the direction taken by the degeneration.

The following are the tracts in the cord (see Fig. 56):

Descending Tracts.	*Ascending Tracts.*
Crossed pyramidal tract.	Direct cerebellar tract.
Direct pyramidal tract—column of Türck (not generally found in animals).	Median superior tract — column of Goll.
Infero-lateral descending tract.	Lateral superior tract—column of Burdach.
Comma tract (limited to cervical and anterior thoracic regions).	Infero-lateral ascending tract.

These paths, known to various observers by somewhat different names, are distributed between the superior, lateral, and inferior columns. The tracts are not found throughout the entire length of the cord, and those descending diminish in size from the head to the tail, those ascending diminish from tail to head.

The *crossed pyramidal tract* is large in man but small in the monkey and dog (Fig. 57); it is in connection with the motor region of the brain, and its great size in man

* We have hesitated to adopt the terms ascending and descending, as not harmonising with the terms employed in dealing with the cord of the quadruped, but it is difficult to find a suitable substitute.

appears to bear a distinct relation to the complexity of the motor region; the more intricate the changes in the central nervous system the larger the pyramidal tract. (Foster.)

The crossed pyramidal tract is the great motor path; the fibres which form it arise in the motor areas of the cerebrum and find their way to the bulb (medulla), where they cross at the pyramids to the opposite side of the cord, and descend in a region external to the superior cornu.

The *infero-lateral descending tract* arises from the cere-

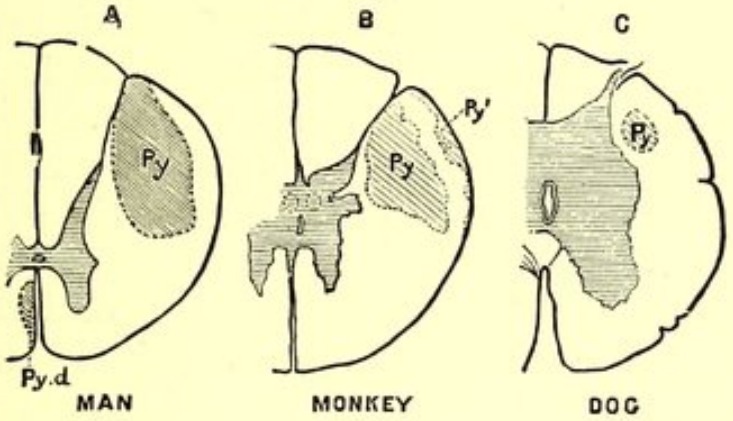


FIG. 57.—DIAGRAM TO ILLUSTRATE THE RELATIVE SIZE OF THE CROSSED PYRAMIDAL TRACT (Py) IN THE DOG, MONKEY, MAN. (FOSTER, AFTER SHERRINGTON.)

In B, Py' is an outlying portion of the pyramidal tract separated from the rest by the cerebellar tract. Py.d in A is the direct pyramidal tract only present in man.

brum, but not in the cells of the cortex: it travels on the same side of the cord.

The *comma tract* is a small one and its origin is not clear.

The *direct cerebellar tract* is supposed to be connected with the cells of Clarke's column, the fibres composing it are very large and they terminate in the cerebellum.

The *median superior tract* occupies a position on the superior part of the cord on either side of the median fissure, it is a sensory tract and is affected in locomotor ataxia of the human subject. The fibres composing it are small and the tract terminates at the bulb;* degeneration

* The word 'bulb' is used throughout to indicate the medulla oblongata.

of this tract follows division of the superior spinal roots, and the fibres composing it have their trophic centre in the ganglion of these roots, being cell processes from the cells of the ganglion.

The *lateral superior tract* is made up of the fibres of the sensory roots, some of these fibres plunge into the grey matter at once and end there, others pass in the preceding tract, the median superior, and run for a great distance forward, many even reaching the medulla oblongata.

The *infero-lateral ascending tract* runs the entire length of the surface of the cord; the origin of it is not clearly known, degeneration cannot be brought about by dividing the superior roots, so that its origin must be in the cord. It is supposed to terminate in the cerebellum.

It has not been found possible to divide the whole of the white matter into tracts; even after all the above have been defined, there is still much left unaccounted for.

When the various tracts in the spinal cord reach the bulb they undergo change in form, position, and distribution, in order that they may arrive at the various parts of the brain to which they are proceeding. Two tracts, however, are known to pass unbroken through the bulb, viz., the pyramidal tract to the cerebrum and the cerebellar tract; all the others are broken up.

Afferent and Efferent Paths in the Cord.—By experimental inquiry certain paths have been made out in the cord whereby impressions are transmitted from the centre to the periphery and from the periphery to the centre. We have previously spoken of the ascending and descending tracts, as probably representing the direction in which impulses travel along given portions of the cord. The remarks on the paths in the cord are only supplemental to our knowledge of the tracts.

By the superior columns of the cord such impressions as temperature, pressure, and muscular sense are conveyed to the cerebrum, running along the same side of the cord on which they entered, and when reaching the bulb crossing over to the opposite side (Fig. 58).

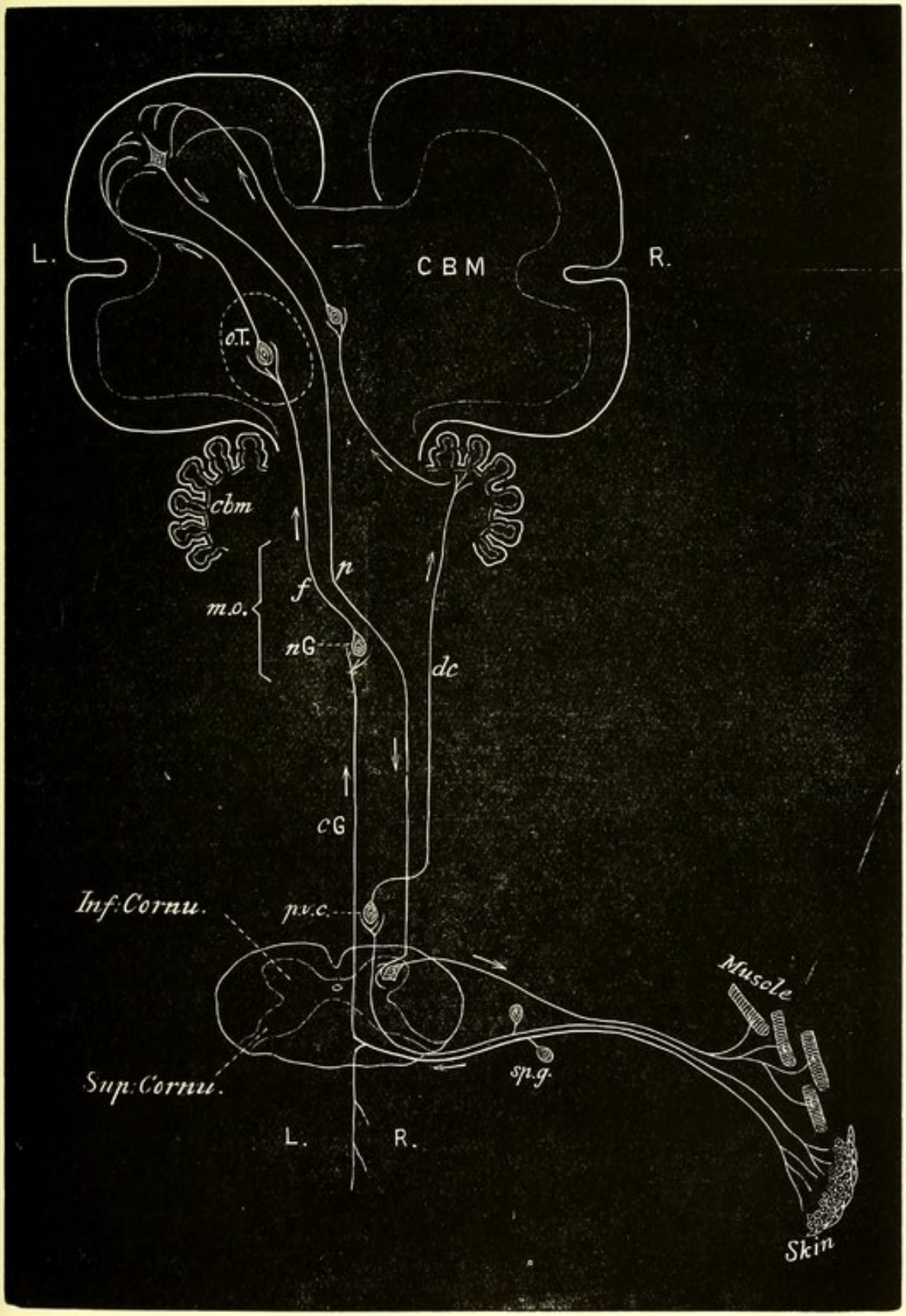


FIG. 58.—DIAGRAM OF THE AFFERENT AND EFFERENT PATHS IN THE CORD. (SHERRINGTON.)

L left, R right; CBM, cerebrum; cbm, cerebellum; mo, medulla oblongata containing the decussation of *p*, the pyramidal tract, and of

f, the fillet; the decussation of *f* should really be a little higher instead of a little lower than that of *p*; *ng*, nucleus gracilis (Goll's); ot, optic thalamus; *pvc*, the posterior vesicular column, or column of Clarke; *sp g*, spinal ganglion; cg, median posterior column (Goll's); *dc*, direct cerebellar tract.

The arrows show the direction of the impulses. A centripetal impulse, say from the skin, passes up the afferent nerve, through the spinal ganglion, and enters the superior columns of the cord; it may pass to the cerebrum direct *viâ* the medulla by cg, the median posterior column, which crosses in the bulb and so gains the opposite side of the brain: or the impulse may pass by *dc*, the cerebellar tract, to the cerebellum, entering it on the same side, and from here crossing over to the opposite cerebral hemisphere. A centrifugal impulse originates in the cerebral cortex, gains the pyramidal tract, passes through the bulb to the *opposite* side of the cord, enters the cells in the inferior cornu of the grey matter, and passes out of this as the inferior spinal nerve.

In the lateral columns painful sensations are transmitted, and it is supposed that on entering the cord a small number of the fibres cross over to the opposite side so that both sides of the cord are transmitting painful impulses. Those fibres which do not decussate in the cord do so in the bulb.

The whole of the afferent fibres entering the cord do not reach the brain, many of them enter the grey matter and terminate by breaking up around cells, and in this way the afferent fibres contract connections with many of the spinal segments in front of it.

In the direct cerebellar tract, fibres believed to be connected with the maintenance of the body equilibrium are transmitted to the brain; the whole of the fibres composing this tract do not reach the cerebellum some, as just indicated, terminating in the cord itself. All voluntary motor impulses originate in the cerebrum and travel direct to the bulb; here they cross over and run down the opposite side of the cord, travelling by the crossed pyramidal tract to the multipolar cells of the inferior cornu of the grey matter, from which the motor nerves arise (Fig. 58).

These efferent fibres are the longest in the cord, for unlike the afferent fibres they have few connections with spinal segments, and practically run direct from their origin to their termination.

It will be observed that all sensory impressions enter the brain on the side opposite to their origin, whilst all motor

impulses leave the brain on the opposite side to which they are distributed, so that injury to a motor area of the right brain leads to a left body paralysis.

In the lateral columns of the cord both vaso-motor and sweat nerves travel, decussating in the cord they enter the grey matter of the opposite inferior cornu, and pass out with the motor nerves from the spinal cord.

Reflex Action.—Nerve fibres are incapable of *generating* impulses, they can transmit them but without modifying them; such can only occur in nerve centres, as the brain and spinal cord, and these centres always consist largely of the bodies of nerve cells, of which the nerve fibres leaving or entering the centre are simply processes or branches. Dealing at present solely with the spinal cord, it may be described not as one long centre, but a series of centres lying end to end, each capable to a greater or less extent of acting independently of its neighbour, and each centre possessing its afferent and efferent roots.

In these segments of spinal cord, complex acts can be initiated by the arrival of simple centripetal impulses; such acts may be carried out without any assistance from the brain, for they can readily be demonstrated in an animal where the brain has been destroyed. These acts are known by the name of reflex, from which we must not infer that an afferent impulse is simply reflected into an efferent channel, but rather that an afferent impulse reaches the cord, and passing into the grey matter stimulates the ganglionic cells which generate the efferent impulse.

The structures necessary for a simple reflex act are (1) an afferent nerve to convey the impression to a nerve centre; (2) a nerve centre in which the outgoing impulses are generated; (3) an efferent channel for their transmission (Fig. 59). More complex acts may need more afferent nerves, a larger number of excitable centres, and a greater number of efferent fibres (Fig. 60).

A classical example of a reflex act, is the drawing up of the leg when the foot is pinched in a frog from which

the brain has been entirely removed. Depending upon the degree of pressure applied to the foot, it draws up either one leg or both, viz., unilateral or symmetrical reflex movements, according to the number of ganglionic centres in the cord which have been stimulated.

Still greater violence applied to the foot of this brainless frog will affect a larger number of centres further forward in the cord, so that the fore-limbs may share in the reflex,

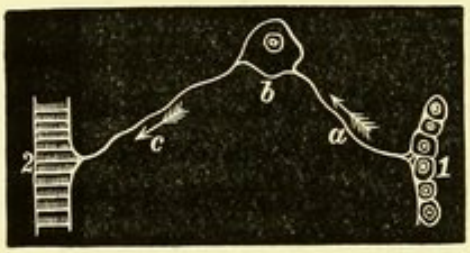


FIG. 59.—SIMPLE REFLEX ACTION. (M'KENDRICK.)

1, Sensory surface ; 2, muscle ; *a*, sensory nerve ; *b*, nerve cell ; *c*, motor nerve. The arrows indicate the direction in which the influence travels.

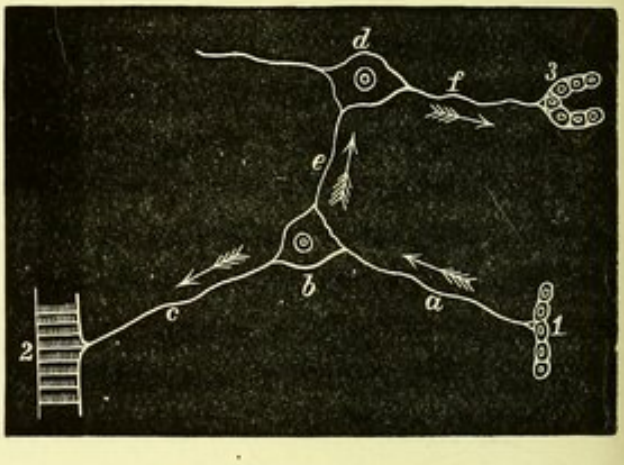


FIG. 60.—DIAGRAM ILLUSTRATING A COMPLEX REFLEX MECHANISM. (M'KENDRICK.)

The arrows indicate direction of impulses. 1, Sensory surface ; 2, muscle ; 3, gland ; *a*, sensory nerve ; *b*, reflex centre, connected with another reflex centre, *d*, by internuncial fibre *e* ; *c*, motor or efferent nerve ; *f*, secretory nerve passing to gland 3. From the other side of *d* is seen a fibre passing to the brain, and there exciting changes which result in a sensation.

such is known as *irradiation* ; still further excitation may produce convulsive movements of the entire body, known as *general action*. It is noteworthy that the direction taken by the irradiation of reflex action is up and down one side of the cord, more readily than across the cord from one side to the other.

The brainless frog reacts more regularly to this experiment than one possessing a brain, which is evidence that

the brain is capable of exercising a controlling influence or inhibitory effect over reflex actions.

One very prominent feature of a reflex act is its apparently intentional character; turning once more to the brainless frog, if an acid be applied to the skin of the flank the foot endeavours to remove the source of irritation, and if this foot be restrained an endeavour is made to use its fellow.

In the dog very characteristic reflex actions occur after division of the cord, such as those of micturition and defæcation; in this animal after division of the spinal cord in the dorsal region the hind limbs are at first rendered flaccid, incapable of any important response to a stimulus such as we have seen may be evoked in the frog, and it would seem as if its spinal cord were incapable of any reflex act. In course of time, though no regeneration of the cord occurs, reflex acts become established, and the muscular movements are not irregular but co-ordinate, so that tickling the skin causes the animal to scratch the part with the hind feet.

The higher we ascend in the animal scale the less marked is the complexity of the spinal reflexes, which may perhaps be owing to the inhibitory influence exercised over them by the brain. Still, the reflex acts in locomotion are very complicated, for instance the tactile and muscular sense required, the exact grouping of muscles, and the regulation of the degree and rapidity of contraction, would appear at first sight to need the supervision of the higher centres in the brain, but such is not the case; a pigeon will fly after decapitation, and if a horse had to think of every step it had to take it would soon be worn out and blunder. That the higher centres do at times come into play is shown by the judgment which the horse exercises when jumping, viz., the proper distance to take off at, the amount of muscular contraction required to lift the body, and the needful height to which it should be raised, etc., are all evidence of this.

But the reflex acts carried out by the cord are not

limited to those affecting voluntary muscles, the act may be a secretory or nutritive one, or involving the contraction or relaxation of pale muscle; for example, the contraction and dilatation of the bloodvessels under the influence of the vaso-motor system, the peristaltic movements of the intestines, the contraction of the bladder and uterus, and the secretions from the various abdominal glands, are all examples of reflex acts.

The time occupied by a reflex act varies depending upon the strength of the stimulus and the nature of the reflex; the sharper the stimulus the more rapid the reflex, the more active the centre the more rapid the response; impulses which have to cross the cord take longer than those which enter and return from the same side. It is mainly during the appreciable delay, as measured by delicate apparatus, that the changes are occurring in the grey substance which lead to an efferent response. In the dog the time occupied by a reflex on the same side is estimated at ·022 to ·04 seconds, and for a reflex on the opposite side ·048 to ·058 seconds.

Tendon Reflexes.—The muscle and tendon reflexes, so well known in the human subject, have not, so far as we are aware, been studied in the ungulates; nor do we know whether the existence of any reflexes has been demonstrated, if, perhaps, we except the immediate lifting up of the foot, which generally follows pressure on the so-called 'chestnut' found on the inside of the fore-arm of the horse.

One of the best known of the tendon-reflexes is the knee jerk, a jerking forward of the leg when the straight ligament of the patella is struck. This is caused by a momentary single spasm of the extensor muscles of the knee, and although often called a reflex act cannot truly be so, because the time between the blow and the jerk is too short for any reflex act. It is well seen in the dog, cat, rabbit, etc. Although not a reflex action it is dependent on the reflex-tonus that is maintained in the muscles by the spinal arcs connected with them; if that tonus be much lowered, as by severance of the nervous reflex arc, the jerk can no

longer be elicited. The jerk is a good index of the condition of the reflex arc, and therefore of the condition of the activity or depression of the segments of the cord by which the extensor muscles are innervated. It is depressed during sleep or anæsthesia, and by anæmia of the cord; it is intensified when the cerebral restraint is removed from the lumbar spinal segments by diversion or attention to another part, or by severance of the cord in the dorsal region. Another brisk 'jerk' in the dog is the ischial, obtained from the hamstring muscles by tapping the tuberosity of the ischium.

By a **Co-ordinate movement** is meant one in which the contraction of various related groups of muscles is so adjusted that the extent of their contraction, and everything necessary for a perfect movement is present and faithfully carried out. This co-ordination of movement we have seen may occur even without the assistance of the brain, and we have alluded to the complex co-ordinate movements of locomotion as an example of this. In the spinal cord, therefore, not only reflex but co-ordinate movements are generated, even the crossed or diagonal movements of locomotion in quadrupeds are of this nature, and are carried out by the spinal cord.

Movements which are irregular and purposeless, or in any way fail to co-ordinate, are termed inco-ordinate.

Automatic Action.—Nerve centres are capable of issuing impulses which are not the result of an afferent stimulus; the impulse originates in the centre. The respiratory centre in the bulb is the best example of automatism, but even in the cord there is some evidence to show that automatic action may be present. If the spinal cord of a dog be divided the muscles are left in a flaccid state, but in course of time the condition known as muscular tone, or the firmness of muscle to external pressure, becomes to an extent established though not completely so. It is supposed that the maintenance of muscular tone depends, at any rate to some extent, upon impulses originating in the spinal cord. In the same way the tone

of the vascular system, or the force which keeps the muscular wall of the vessel in the necessary condition of constriction, is in part brought about by automatic impulses from the cord. Some physiologists do not regard the cord as a seat of automatic action, but consider muscular tone, and the tone of the muscular walls of the vascular system, to be due to tonic (permanent) reflex actions, the same as the tone shown by the sphincters of the bladder, anus, and pylorus.

Special Centres in the Spinal Cord.—In the cord certain centres exist, which though ordinarily under the control of a chief centre in the bulb, yet are capable of carrying on peculiar reflex action even after the cord has been divided, and thus separated from the controlling influence of the bulb.

The *cilio-spinal centre* lies between the cervical and dorsal portions of the cord; in it originate fibres which through the cervical sympathetic supply the dilator muscle of the iris. Destruction of the region in question causes a contraction of the pupil, whilst irritation of it causes the pupil to dilate.

The *ano-spinal* centre, found in the lumbar portion of the cord, controls the act of defæcation; it would appear to be highly developed in herbivora, which possess the power of bringing it into play not only when the body is at rest but during movement. The functions of the ano-spinal centre are rather complex, inasmuch as it has not only to maintain the tone of the sphincter, but also to relax it during defæcation, and under the latter condition contracts both the wall of the intestine and the abdominal muscles.

The *vesico-spinal* centre also exists in the lumbar portion of the cord, it governs micturition; its action is like that of the ano-spinal centre.

In the lumbar portion of the cord other centres are found, for example, the *erection* centre, the *genito-spinal* centre which contains the nervous apparatus employed in the emission of semen, and the *parturition* centre.

Vaso-motor centres are found throughout the cord; they

are principally under the control of similar centres in the medulla, but may act independently. *Sweat* centres are probably closely connected with the vaso-motor centres. *Trophic* centres for the nutrition of the tissues also exist in the cord; destruction of parts by ulceration, or great muscular wasting, may follow injury of the trophic nerves.

The Functions of the Spinal Cord may be summarised as follows: The cord is the central seat of numerous reflex actions, some of these are intermittent and occasional, others permanent or tonic, such as the maintenance of muscular and arterial tone. There is evidence that it assists in co-ordinating movement, and it is also the path by which the brain and the body are brought into connection, both in an upward and downward direction and from side to side.

Medulla Oblongata or Bulb.

Situated at the top of the spinal cord, and forming the connection between it and the brain, is the medulla oblongata. It is composed of white and grey matter, but not arranged with the regularity found in the cord; the columns of the latter are continued into it, and give rise to certain columns in the bulb larger and more prominent than those of the cord. The inferior columns form the inferior pyamids of the bulb, the superior form the superior pyramids, and the lateral columns dividing into three parts help to form the restiform bodies.

As the main paths or highways in the cord are either going to or coming from the brain, it is interesting to briefly study their distribution in the bulb.

Of all the paths known in the cord only two pass for certain through the bulb to higher centres in the brain, viz., the pyramidal tract the fibres of which are descending to the cord from their origin in the cells of the cerebral cortex, and the cerebellar tract which passes upward through the medulla to reach the cerebellum.

All the other tracts in the cord terminate in groups of cells in the bulb, and act as carriers between it and cord.

The grey matter of the cord does not maintain its characteristic appearance in the bulb, the inferior cornua disappear, while the superior cornua enlarge. Owing to the decussation of fibres in the inferior pyramid the grey and white matter get mingled up, and nuclei and masses of nerve cells are formed as the result; from these nuclei the cranial nerves arise.

This arrangement leads to considerable complexity in the grey matter of the medulla, and a markedly intricate arrangement of the fibres of the white substance.

The tracts passing through the bulb are composed of motor and sensory nerves, or, more correctly, afferent and efferent nerves; these decussate in the medulla, and in this way account for a right brain lesion producing a left body paralysis. But besides these tracts, there are reflex and other centres so numerous and widespread, that it is remarkable how the varied functions carried out by them can be performed within such a limited area.

Centres in the Medulla.—The various centres found in the bulb are of such importance to life that an injury to this part generally means instantaneous death. The whole of the rest of the brain may gradually be removed without destroying life, but the medulla itself will not tolerate interference.

The centres localised in the bulb are those for mastication, swallowing, sucking, vomiting, respiration, phonation, coughing, the movements of the heart, bloodvessels, and iris, the secretion of saliva, the diabetic centre, and a centre for the sweat glands of the head.

Though all these functions have been more or less clearly referred to the bulb, we must avoid falling into the error that a definite representation exists for each of them; and though the term centre is employed, it is more as a convenient mode of expression, than as absolutely establishing the fact that any particular group or groups of cells are responsible for one function more than another. Perhaps

the only exception to this is the respiratory centre, which has been defined with a certain amount of exactitude.

The *mastication* and *swallowing centres* lie in the floor of the fourth ventricle; they have for their afferent nerves the inferior division of the fifth, glossopharyngeal, and the superior laryngeal of the pneumogastric; whilst the motor branches are in the motor parts of the fifth for mastication, and in the fibres of the pharyngeal plexus of the vagus for swallowing. All the muscles of mastication, except the diagastricus, receive motor nerves from the inferior maxillary division of the fifth pair. It would appear that the reflex act of swallowing may be excited not only by the presence of food in the pharynx, but even by irritating portions of the respiratory apparatus; touching the rima of the glottis excites the act, and so does touching the interior of the trachea, even as low down as the bronchi; on the other hand, stimulation of the glossopharyngeal does not cause swallowing.

A *vomiting centre* exists in the bulb, which in the horse and ruminants is certainly most imperfectly developed. We have previously (p. 161) drawn attention to the fact that there is no drug which has the power of exciting vomiting in the horse; tartar emetic has not the slightest action, and the effect of apomorphia is only to produce the most alarming symptoms of cerebral excitement, but no attempt at vomiting.

In the dog and pig the vomiting centre is well developed. The afferent nerves may be those of the pharynx, palate, and root of tongue, viz., the glossopharyngeal, or those from the mucous membrane of the stomach, for example, the vagus and sympathetic; the impression having been carried to the bulb the efferent nerves are the phrenics for the diaphragm, and vagus for the stomach and œsophagus.

The vomiting centre may be directly stimulated by irritating the central end of the vagus.

Secretion of Saliva.—The centre for this lies in the floor of the fourth ventricle at the origin of the seventh and ninth

pair of nerves; the afferent nerves are those of taste, viz., the gustatory branch of the fifth and glossopharyngeal, whilst the chorda tympani is the efferent nerve for the submaxillary and the superficial petrosal that for the parotid gland.

Other centres exist in the bulb which depend upon automatic action, for example the cardiac and respiratory centres.

For the *respiratory centre* see p. 94.

For the *cardio-accelerator* and *cardio-inhibitory centre* see p. 39.

For the *vaso-motor centre* see p. 66.

For the *diabetic centre* see p. 202.

Functions of the Medulla.—The medulla apart from the brain cannot elaborate sensation or voluntary movement. It forms a pathway to the brain for the columns in the spinal cord, and is a conductor of centripetal and centrifugal impulses; it gives origin to all the cranial nerves but those of smell, sight, and the motor nerves of the eyeball; finally it is the supreme reflex centre for the nerves governing respiration, circulation, the action of the heart, and the digestive apparatus from the mouth to the stomach.

The **Pons Varolii** conducts centripetal and centrifugal impulses to and fro and up and down; it connects the brain with the medulla and cerebellum, and several of the cranial nerves arise in connection with the grey matter of the various nuclei found in it. When stimulated, pain and muscular spasms are produced.

The **Crura Cerebri** connect the cerebellum with the cerebrum, and the basal ganglia with the pons and bulb. They conduct both centripetal and centrifugal impulses, and are connected with the complex movements of the eyeball. Division of one peduncle leads to what is known as circus movements, the animal travelling round and round in a circle towards the opposite side to that on which the injury was inflicted.

The basal ganglia are composed of the **corpora quadrigemina, thalami optici**, and **corpora striata.** Destruction of

the anterior pair of corpora quadrigemina causes blindness; removal of one part causes circus movements or rolling, or, at any rate, destruction of equilibrium and want of muscular co-ordination. These results are not confined to the corpora quadrigemina alone, for the same inco-ordinate movements will occur on injury to the crura cerebri, optic thalami, corpora striata, etc. Irritation of the corpora quadrigemina causes contraction of the pupil, whilst removal of these bodies produces dilatation.

The **Thalami Optici** are connected with vision, but are mainly supposed to be the centres for tactile impressions which they transmit onwards to the cerebral cortex (Fig. 58 OT).

The **Corpora Striata** are interesting clinically on account of the comparative frequency with which they are diseased in the horse. They are considered to be the centres for co-ordination of motor impulses; when they are destroyed the animal has an irresistible tendency to move forwards.

We have certainly seen this latter symptom shown in the horse in disease of the corpora striata, but it is far from invariable. It is remarkable how extensively the parts may be affected and pressed upon by tumours without symptoms being exhibited; the gradual progress of the pressure or destruction may account for this.

The corpora striata are also considered to be concerned in heat production; there appears to be no doubt that experimental injury of these bodies produces a high temperature. Nothing is known of the mechanism, but it is supposed that impulses pass from the corpora striata to the muscles, the result being a great increase in the amount of heat produced.

It is of interest to remember that the corpora striata, unlike the optic thalami, are shown by their developmental history to be really portions of the cortical grey matter.

Cerebellum.

In the cerebellum is found a collection of fibres and ganglion cells in direct communication with the bulb and cerebrum. It is the first piece of nervous tissue we have studied where the grey matter is externally placed and not internally as in the cord; the surface being folded and doubled in on itself to a considerable extent, forming convolutions.

The functions of the cerebellum are principally concerned in the co-ordination of movement, viz., harmony and rhythm in muscular actions; it is enabled to carry out this function through its connection with the superior columns of the cord, which keep the cerebellum informed of the position of the limbs. There can be no doubt that in co-ordinating muscular movement, the cerebellum is assisted both by the sense of sight, and by the lymph in the semicircular canals of the ear; an animal walks with uncertainty when the eyes are covered up, and disease of the internal ear is a well-known cause of vertigo in the human subject.

Injury of the cerebellum produces no sensory disturbance, but entails defects of movement. When sliced away in birds they lose the power of flying, walking, or preserving their equilibrium; there is no loss of consciousness or intelligence, but an inability to co-ordinate the skeletal muscles. Injury to one of the crura of the cerebellum produces 'forced movements' as they are termed. The animal rolls over and over around the long axis of the body, and always from that side on which the injury has been inflicted, or else circus movements or somersaults are performed.

In dogs superficial injury to one of the processes of the cerebellum causes only temporary disturbance, whilst deep injury or removal of a hemisphere, causes rigidity of the legs and shaking of the head; more extensive injury is followed by disturbance of co-ordination.

The entire cerebellum has been removed in the dog, the

animal living for eight months; in the first instance spasms of the muscles of the head, neck, and fore legs, and weakness of the hind legs were present; when the eyes were closed standing was impossible. These symptoms gradually gave way, and the animal was left with a deficiency of muscular tone, and a tremor in the muscles which increased on the performance of voluntary movement; it could swim but was muscularly weak, and eventually died from marasmus.

The cerebellum influences movement by re-inforcing the activity of the opposite hemisphere of the cerebrum (Luciani), especially of the 'motor area.' The movements produced by the opposite cerebral hemisphere become wanting in steadiness and power when half of the cerebellum has been removed, and the muscles innervated by that hemisphere are deficient in tone. No direct downward connection of the cerebellum with the cord is known to exist, though, as previously mentioned, the cord in an upward direction is connected with the cerebellum.

Cerebrum.

The cerebrum is composed of grey and white matter, the grey being externally placed and thrown into convolutions. These convolutions, though well marked in the lower animals, are by no means regular in their position or direction, thereby forming a great contrast to the brain of man. The use of the convolutions is no doubt to increase the surface of the brain, and the deeper and more complex they are, the greater, as a rule, is the intelligence of the animal. In the horse the convolutions are comparatively very shallow.

Use of the Cerebrum.—In the grey matter of the cerebrum is located the seat of intelligence and the higher faculties, the white matter is simply the conducting paths along which the impulses are distributed. In man it has been supposed that from the anterior part of the cerebrum proceed consciousness and intelligence, from the middle

and lateral portions motor impulses, whilst sensory impressions are implanted on the posterior half, but there is little ground for such a phrenology.

In attempting to define to what extent the higher faculties exist in animals, we are treading on distinctly controversial ground. Have they a moral sense of right and wrong? Probably this question can only be positively answered in the affirmative for two animals, viz., the elephant and the dog. With the horse the moral sense is very small, we do not think he knows he is doing anything wrong when he kicks his stable down once or twice a week, or when he 'runs away,' but he does understand that he should not refuse a jump, and a horse careless in his walk or trot knows exactly what every stumble will be followed by, and anticipates matters accordingly.

Strength of will most animals lose as the result of domestication. They become mere reflex machines or automata, but there are notable exceptions, for instance the ass, mule, and occasionally the horse.

The so-called stupidity of the ass and provoking obstinacy of the mule are not indications of want of intelligence, on the other hand they show a determination of purpose and strength of will, which if these animals understood how to combine against man, would obtain for them their complete freedom from civilization.

The majority of horses on the other hand have no great strength of will, they can be rendered docile and tractable, they will gallop until they drop, work at high pressure when low would suffice, can never apparently learn the obvious lesson that it is the 'willing horse' which suffers, and that the harder they work the more they get to do. All this is due to defective intelligence and a want of the higher faculties, they cannot reason like the dog or elephant, and are more flexible than the ass or mule.*

* We are aware that the majority of people will not agree with these views of the defective intelligence of the horse, but we are not alone in our judgment; see 'The Points of the Horse,' by Captain Hayes, whose experience amongst horses in all parts of the world is very considerable.

Some horses do show signs of reasoning and are capable of grasping a position. A load so heavy as to be beyond the limit of his power, or from some other cause, has taught him to refuse to work; to use the familiar expression he 'jibs,' he has learned to disobey, he has learned his own strength, and the comparative powerlessness of his master, and this through an exercise of reason. In other words, the horse which refuses to wear himself out in the service of man is one possessing too much intelligence and strength of will for a slave; a 'jibber' is an intelligent and not a stupid horse.

As a rule the intelligence and affection of the horse only exist in books and the imagination of those who have the least to do with him; whatever region of the brain affection is located in, it does not occupy much space in the equine. Taking the dog as the standard to judge by, it may be said with the greatest truth that the large majority of horses have no affection whatever, either for their own kind (excluding maternal affection) or for human beings. Two strange horses cannot as a rule be put together without disagreeing, and no one ever heard of a horse pining away through the prolonged absence of its master! The often quoted example of a horse jumping over a man on the ground rather than treading on him is an act misunderstood; it is true the horse jumps over the man, but he does so because he is taught to jump over every obstacle, and the man on the ground might for all he knows be a bush. In other words it becomes largely a reflex action, and only to a very limited extent a volitional act.

If the horse possesses but little affection it is compensated for by cherishing no resentment; he will kick his friend as readily as a foe, or in many cases his groom with as much cheerfulness as a perfect stranger; to all his hard life and the abominable cruelties of civilization he shows no sign of resentment, water and feed him, and give him a place to lie in, and he forgets the past in his anxiety for the present.

He is a peculiar mixture of courage and cowardice; physical suffering he can endure, no animal bears pain

better; when his blood is up nothing is too big or too wide for him in the hunting field, he has a keen enjoyment for both chase and race in spite of the punishment they may entail; but the same horse is frightened out of his life by a piece of paper blowing across the road, or at his own shadow, and an unusual sight or a heap of stones on the side of the road has cost many a man his life. No animal is more readily seized with panic, and this spreads amongst a body of horses like an electric shock.

The horse has an excellent memory for locality, probably nearly equal to that of the dog or cat; he never forgets a road, and automaton-like if he has once stopped at any place on it, he wants to stop at the same place next time no matter how long the interval may be between the visits.

Reasoning power in the majority of horses is small; an animal runs away because he is seized with panic, or his spirits are bubbling over, but with few exceptions distinct acts of reasoning are rare. Of this we daily see examples in our infirmaries, horses injured in the most severe manner through their own struggles when placed in a little difficulty, such as a head rope around the leg, or unable to rise when down owing to being too close to the wall, or some trifling circumstance of this kind, where if he employed any reasoning powers he would remain quiet until released, instead of which he behaves like a lunatic, inflicting in a short time injuries which may lay him up for months. Or take the case of a horse which gets its tail over the reins when being driven, instead of lifting the tail in response to the exertions of the driver he draws it closer down to his quarters, gripping the reins as in a vice, and is so astonished and frightened at the new state of things that he becomes uncontrollable. We can hardly point to a single act in the horse in which the powers of reasoning are clearly brought into play, unless it be that he knows punishment follows refusal to obey, and he learns to 'jib.'

The horse is very conservative, he likes nothing new nor

any departure from his ordinary mode of life ; he will starve himself for days rather than take a new feeding grain, and he dislikes a change of stable or a new place.

His gregarious instincts are proverbial; he frets at the absence of his companions, and if used to work amongst a body of horses, as in cavalry, he will take any degree of punishment rather than leave them for five minutes. During absence from his companions he neighs, sweats, paws with the forelegs, and almost screams with delight on rejoining them, not because he loves them, but because he dislikes being alone.

Finally, his predominant feature, and the feature of all animals below adult man, is the childishness present throughout life, probably the absence of care, worry and anxiety may account for this ; the horse will play all day with a piece of rope, or nibble his neighbour persistently, even the oldest horses when 'fresh' will perform the antics of a foal, and imitation amongst them is so great that if one of a string of horses being led along should happen to kick out, it repeats itself all along the line as if by preconceived arrangement.

Sydney Smith defined the difference between reason and instinct as follows : 'If in order to do a certain thing certain means are adopted to effect it, with a clear and precise notion that these means are subservient to that end, the act is one of reason ; if, on the other hand, means are adopted subservient to an end, without there being the least degree of consciousness that these means are subservient to the end, then the act is one of instinct.'

Morgan* believes that between instinct on the one hand, and reason on the other, we may insert as a middle term 'intelligence,' while Romanes and others use the word 'intelligence' as synonymous with 'reason.'

Morgan defines instinct as a motor response to a certain stimulus, viz., a reflex act but one accompanied by consciousness. Animals come into the world endowed with

* *Fortnightly Review*, August, 1893. It is from Professor Morgan's paper that we have obtained the views of Sydney Smith and Romanes.

this innate capacity for motor response; but these instincts are not quite perfect, they need training and experience, and their instructor is 'intelligence.' Intelligence, according to this observer, does not imply a conscious knowledge of the relation between the means employed and the end attained, such a conscious knowledge would be reason.

We are asked in other words to regard animals as simply reflex machines, their brain being very little higher in the scale than their spinal cord, and for some animals such a position probably meets their case, but certainly not for all.

If we accept Morgan's definition of instinct and intelligence, it offers no reasonable explanation why dogs fight, and why they worry cats; why a horse so inclined will turn his quarters towards another as he passes and rapidly let both hind legs fly in the direction of his objective, nor will it explain why a horse will use his fore legs to strike when he knows his hind legs cannot reach the object of his irritation. It is absolutely impossible to believe that such acts imply no conscious knowledge of the relation between the means employed and the end attained.

The higher animals are capable of a limited amount of reasoning; with some it is even well developed, with others it is extremely imperfect. The elephant and dog occupy the top of the scale, the ox and sheep the bottom, the horse comes midway.

We do not see how to separate reason from intelligence, but there is no difficulty in separating them from instinct.

Animals are born with such complicated reflex acts as walking, galloping, jumping, etc., so highly developed that they are employed at once; no member of the human family has been seen to walk and run about a few hours after leaving the womb, for both brain and spinal cord are incompletely developed and the acts have to be learned. This is not so with animals (excepting the dog and cat) foals, calves, lambs, goats, etc., are born prepared to at once feel their feet, they require no teaching and no imitation, their

senses are perfect, they can recognise their mother or a stranger, can smell, see, hear, in fact they have nothing to learn for they are born with as much intelligence as their parents, and only differ from them in one respect, and that is they are born wild, and so have to learn confidence. Domestication and obedience are not properties transmitted from parent to offspring.

It is quite possible for an animal to perform acts which look as if executed by intelligence, or to undertake movements which need precision, in spite of the fact that it is without a cerebrum.

Some very curious observations have been made on the frog in which the cerebral hemispheres have been removed. If stimulated the frog springs, if thrown into water it swims, if placed on its back it recovers its normal position, and if stroked it croaks. All these actions would indicate the presence of consciousness but such is not so; the frog without its cerebral lobes will remain, unless stimulated, in one position until it dies, it appears to possess no power of spontaneous movement, or power of will.

A remarkable experiment performed on a frog in this condition consists in placing it on a board which is gradually brought from the horizontal to the vertical position; during the movement the animal crawls up the inclined plane, and when the board is vertically placed it sits on the top perfectly balanced; as the board is lowered to the opposite side from which it was raised the creature descends. It is only during the time the board is being raised or lowered that the frog moves, but the movements are executed with precision.

It is evident that these acts which strike one as being intelligent are really reflex, and are executed by the spinal cord the animal being absolutely unconscious of what is going on, and it may be even amongst the higher animals, that some acts regarded as volitional are in reality reflex.

Motor and Sensory Areas.—So far as we are aware no observations have been made on the motor and sensory areas of the cerebrum of ungulata, but the dog has on this point

been very carefully examined, and the following account of the position of the areas in the brain of this animal, and the effect of ablation, is taken from Landois and Stirling,* where the subject is very fully dealt with.

The dog's brain is marked by two primary fissures, one known as the sulcus cruciatus (Fig. 61 S), the other as the fossa Sylvii (Fig. 61 F). Between these fissures are arranged four primary convolutions I., II., III., and IV. (Figs. 61 and 62).

In the anterior part of the fourth or superior convolution is found from before backwards—

(*a*) The motor areas for the muscles of the neck (Fig. 61—1).

(*b*) The motor areas for the extensors and abductors of the fore-leg (Fig. 61—2).

(*c*) The motor areas for the elevation of the shoulder and extension of fore-limb movements as in walking (Fig. 61—8).

(*d*) The motor areas for the flexors and rotators of the fore-leg (Fig. 61—3).

(*e*) The motor areas for the muscles of the hind-leg (Fig. 61—4).

(*f*) The motor areas for the retraction and abduction of the fore-leg (Fig. 61—7).

(*g*) The motor areas for the lateral switching movements of the tail (Fig. 61—6).

Close to No. 2 area (Fig. 61) is one *d* (Fig. 62) stimulation of which causes the eye to turn to the opposite side, opens the eyelid and dilates the pupil.

In the third convolution is situated an area 9, 9, 9 (Fig. 62), stimulation of which controls the movement of the orbicularis muscle, produces an upward movement of the eyeball, and a narrowing of the pupil; behind this is *e*, *e*, *e*, an area which represents vision.

In the second convolution is an area *a a* (Fig. 62), which produces retraction and elevation of the angle of the mouth with partial opening of it. Behind this is *c c*, stimulation of which retracts the mouth owing to the action

* 'A Text-Book of Human Physiology.'

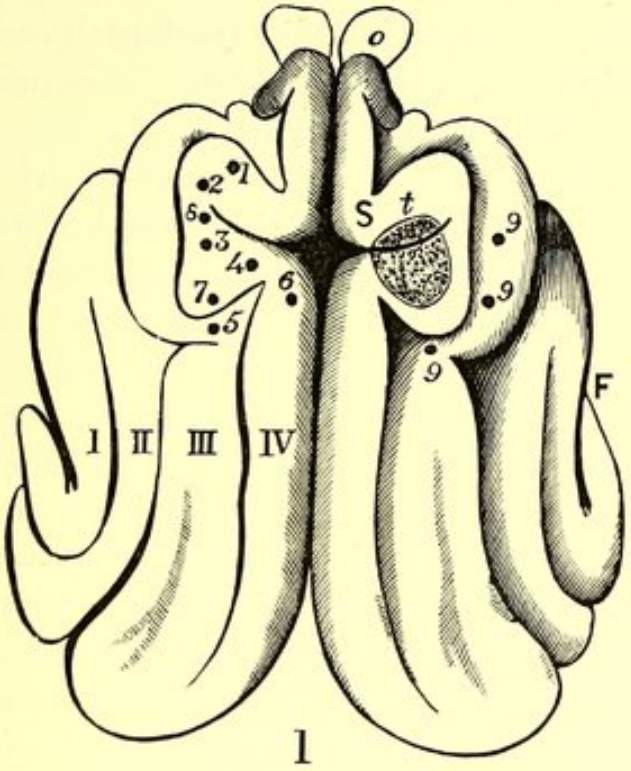


FIG. 61.

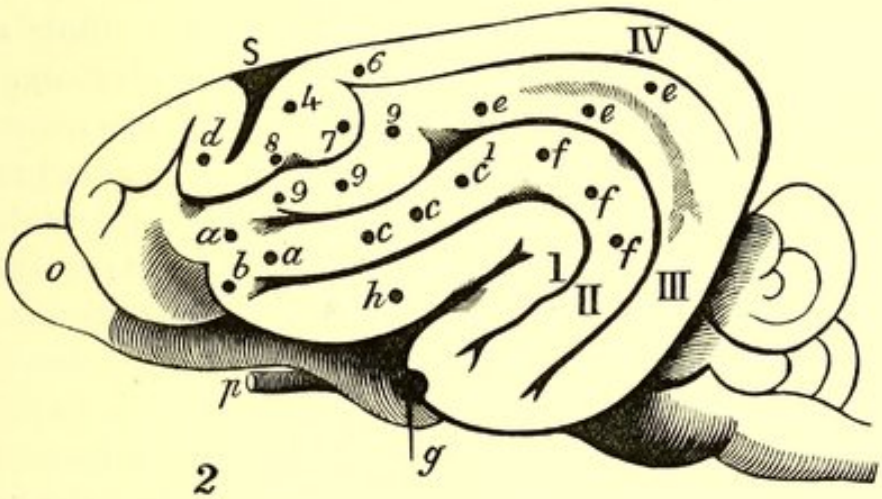


FIG. 62.

TO ILLUSTRATE THE MOTOR AREAS IN THE BRAIN OF THE DOG. (LANDOIS AND STIRLING.)

Fig. 61, cerebrum of the dog from above. Fig. 62, cerebrum from the side. I., II., III., IV., the four primary convolutions; S, sulcus cruciatus; F, sylvian fosse; *o*, olfactory lobe; *p*, optic nerve. The positions of the areas are described in the text.

of the platysma; then an area c^1 which like 9 (Fig. 62) causes elevation of one angle of the mouth and of one half the face until the eye is partly closed. Behind this is *f f f* which is the auditory centre.

In the first convolution is the oral centre (*b* Fig. 62), stimulation of which opens the mouth, protrudes and retracts the tongue, while the dog not unfrequently howls.

All these centres have been indicated, but it is necessary to remember that though in area they may be as large as a pea, yet to an extent they overlap. The higher the animal is in the scale the greater the complexity observed in the areas, as for instance in the monkey, where the skilled movements of the hands and feet are largely represented in the cortex. The size of an area bears no relation to the size of the part supplied, but does bear a relation to the complexity of movement which the part is intended to produce. Thus the thumb area in the cortex of the monkey is relatively larger than the shoulder or hip area.

A so-called *heat centre* has been discovered in the cerebrum of the dog, it is situated at *t*, Fig. 61 in the fourth convolution, and is in the fore and hind limb area. Destruction of this part leads to a rise in temperature.

The effect of removing the motor areas differs according to the animal, in the monkey it results in permanent motor paralysis of hand or foot, but not of parts with less skilled movement, *e.g.*, shoulder or knee. In the dog paralysis is not necessarily produced, and it has been supposed that the basal ganglia are capable in this animal of taking on the duties of the cortex.

If this is so it throws some light upon the destruction which has been observed at times in the cortex of the horse, and unaccompanied by any symptoms until shortly before death.

Strong stimulation of the motor areas produces epilepsy in all animals. By observing the groups of muscles first affected and knowing the region of the cortex to which they are related, it is possible, certainly in man, to localize with considerable exactitude the seat of the trouble.

Removal of the anterior or frontal convolutions in the dog leads to unilateral motor and sensory paralysis, from which the animal recovers with the exception that there is loss of muscular sense. If the operation be performed on both sides there is an exaggeration of the symptoms, and the animal becomes vicious.

Removal of the posterior or occipital lobes leads to blindness, no loss of motion or of muscular sense, and the dog remains obedient and lively.

Removal of a large mass of the cerebral cortex causes the animal to become intensely stupid, it walks slowly, the head hangs down, sensibility is diminished; the dog sees but cannot comprehend, it howls from hunger and eats until its stomach is full, it exhibits no sexual excitement, and becomes, in fact, an eating, complex, reflex machine.

Colin draws attention to the difficulty in producing paralysis experimentally in the horse from lesions of the hemispheres. Neither the artificial production of a clot in the falciform sinus, nor the introduction of pieces of lead the size of a pea into the convolutions, gave rise to hemiplegia. This quite bears out what we know to be a clinical fact, that it is possible for horses to have in their lateral ventricles tumours the size of an egg without producing any disturbance. We have seen such cases, the tumours being of variable size, and the clinical history has never given more than a few days' illness, though the growths must have been forming for a considerable period.

The **Circulation in the Brain** is peculiar, the veins or so-called sinuses, are enclosed in very rigid membranous walls formed by the dura mater; the blood is driven through these not only by the force from behind, but by the aspiratory effect produced by inspiration.

Coverings of the Brain.—The dura mater is a dense fibrous membrane, probably endowed with sensation, which acts the part of the periosteum of the skull, and a protective covering for the brain; between it and the arachnoid a lymphatic space known as the subdural exists. The arachnoid contains but few vessels and no nerves and

covers the extremely vascular pia mater; between these is formed the subarachnoid space, which contains the subarachnoid or cerebral fluid.

Cerebral Fluid.—The subarachnoid space communicates with the ventricles of the brain, the lymph in it is also shown to be in communication with the perivascular spaces of the cerebral vessels, and the lymphatic spaces in the perineural covering of nerves. Through the fourth ventricle it communicates with the central canal of the spinal cord, and there is also a connection between the cerebral spaces and those formed on the exterior of the cord. The subdural and to an extent the subarachnoid fluid communicates with the sinuses of the dura mater.

The cerebral fluid is secreted by the pia mater and choroid plexus.

The use of this cerebral fluid, which normally in horses amounts to 80 or 90 grains, is to equalize the pressure on the brain, afford protection to the latter, and through the manner in which the organ is suspended inside the skull by the dura mater, to save it from jar and concussion; both cerebrum and cerebellum half float on water-cushions. Withdrawal of the cerebral fluid leads to convulsions, and an increase in the amount may cause coma owing to the pressure it exercises.

Movements of the Brain.—When the brain is exposed it rises and falls during each respiration, rising with expiration and falling during inspiration; the cause of this is the respiratory rise and fall of blood pressure.

Alterations in the volume of the brain have been observed; the brain expands under a rise in pressure of the systemic arteries, such as is produced by stimulating the central end of the sciatic. Ether and particularly strychnine cause a considerable expansion; chloral hydrate and especially chloroform cause a marked contraction.

No vaso-motor fibres have been discovered in the vessels of the brain.

Cranial Nerves.

These are divided into nerves of special sense, sensory nerves, motor nerves, and mixed nerves. Altogether they make twelve pairs, and all but Nos. 1, 2 and 3 arise from the medulla.

For nerves Nos. 1 and 2 see the Senses.

Third Pair, or Motor Oculi, is one of the motor nerves of the eyeball; it supplies with motor power all the muscles (excepting the external rectus and the superior oblique), also the muscle of the upper lid. Through its connection with the lenticular ganglion it supplies fibres to the iris and ciliary muscle; it is also connected at its origin with two other motor nerves of the eyeball, viz., the fourth and sixth pairs.

The deep-seated origin of the third pair is from the corpora quadrigemina and peduncles of the cerebrum. Division of the nerve causes the eye to turn upwards and outwards, owing to the unbalanced action of the superior oblique and external rectus; there is also depression of the upper lid, immobility of the eyeball, and dilatation of the pupil. The action of the third pair will be discussed again in connection with the physiology of sight.

Fourth Pair, or Pathetic.—The motor nerve of the superior oblique muscle of the eyeball; it has a deep-seated origin in the valve of Vieussens, and is the smallest cranial nerve.

Fifth Pair, or Pars Trigemini, resembles a spinal nerve in having two roots, a motor and sensory; and the resemblance is carried still further by the sensory root having a large ganglion on it, the Gasserian. The motor root arises from the trigeminal nucleus of the medulla, and is connected with the cerebral cortex on the opposite side. The sensory fibres arise from the sensory trigeminal nucleus; but fibres in connection with the origin of this branch can be traced upwards into the cerebrum and cerebellum, and downwards into the grey matter of the cord.

This nerve also has connections with all the nerves arising from the medulla, excepting the abducens; in this way can be explained the extensive connections and varied reflex acts of the fifth pair.

There are three divisions of the fifth pair of nerves, viz., the inferior maxillary, the ophthalmic, and the superior maxillary division.

The *inferior maxillary* division is a mixed nerve, it supplies motor power to the muscles of mastication, viz., the masseters, buccal muscles, internal pterygoid, part of the temporalis, and the mylo-hyoid muscle of the tongue. By means of its great gustatory branch, which enters the tongue in conjunction with the chorda tympani of the seventh nerve, and proceeds throughout the length of the organ, sensation is supplied to the anterior two-thirds of the tongue, and in addition the special sense of taste.

Besides the above, sensory branches are supplied to the teeth and lips near the commissures, and filaments to the parotid, molar, and buccal glands.

The *ophthalmic* division is the smallest of the three furnished by the Gasserian ganglion, it is exclusively sensory supplying with sensation the structures over the brow, the lachrymal gland, membrana nictitans, and the pituitary membrane on both sides.

The *superior maxillary* division is wholly sensory and supplies part of the orbit, eyelids, skin, hard and soft palates, pituitary membrane of the nostrils, and teeth (molars, incisors, and canine), whilst the terminations of the main trunk are extended over the face, upper lip, and nostrils, by means of a considerable plexus of nerves which issues from the infra-orbital foramen.

Each of these main divisions of the fifth nerve possesses a ganglion on it, viz., the ophthalmic on the ophthalmic branch, the spheno-palatine on the superior branch, and the otic ganglion on the inferior branch. All these ganglia receive branches of nerve from the sympathetic and cerebro-spinal system.

It is from the ophthalmic or ciliary ganglion that the

ciliary nerves of the iris and ciliary muscle arise, the motor root of the ganglion being supplied by the third nerve, and the sensory from a branch of the ophthalmic of the fifth.

The ganglion on the superior branch is known as the spheno-palatine; it receives its motor supply through the Vidian nerve from the facial, its sensory roots being numerous and supplied by the spheno-palatine branch of the fifth. This ganglion supplies branches to the blood-vessels of the orbit, and Chauveau (whose description has been followed) states that branches go to the oblique muscles of the eye, and others to the palate through which motor power is supplied to the muscles of the soft palate.

On the inferior division of the fifth is sometimes found a ganglion known as the otic, the motor root of which is derived from the seventh pair, and the sensory from the inferior branch of the fifth. This ganglion gives branches which supply the tensor tympani of the internal ear, and some branches to the pterygoid muscles, Eustachian tube and tensor palati.

In the dog and cat is found the submaxillary ganglion, or more correctly, according to Langley, the sublingual; it is supplied by the chorda tympani of the seventh pair with secretory fibres for the gland and dilator fibres for the bloodvessels; to this ganglion also runs a branch of the sympathetic. All the fibres of the chorda do not enter the gland, some supply the tongue.

A submaxillary ganglion exists in both dog and cat, it lies in the hilum of the gland of the same name.

Division of the superior maxillary division of the fifth in the horse (Bell's experiment), prevents the animal from grasping food with its lips; not for the reason that they are deprived of motion, but owing to loss of sensibility the animal is unaware of how to take hold of the food. The relation of the fifth to muscular movements is that it keeps the muscles aware of the position of objects.

Complete section of the fifth pair causes loss of sensation to one side of the face, lips, mouth, and temple, part of the ear, cornea, conjunctiva, nasal mucous membrane, and

anterior two-thirds of the tongue. There is paralysis of the muscles of mastication, and the mouth becomes injured by the teeth owing to loss of sensibility; the food collects on the paralysed side, where it decomposes and produces local irritation. Section of the fifth nerve causes the animal to frequently bite the tongue as its position in the mouth cannot be felt. The cornea becomes cloudy and ulcerates, the eyeball destroyed owing to loss of its trophic fibres, and not, as was at one time taught, to injury due to its insensibility. Vaso-motor paralysis also occurs in such parts as the eye and pituitary membrane.

As an afferent nerve in reflex acts the fifth nerve is most important; without it there would be no closure of the eye nor sneezing; irritation of the conjunctiva would produce no tears, and no saliva, or but little, would be secreted.

Sixth Pair, or Abducens, rises from the floor of the fourth ventricle, and supplies the external rectus muscle of the eye with motor power. Paralysis of this muscle causes internal squint.

Seventh Pair (Portio Dura), **or Facial.**—Arises from the medulla, passes through the internal auditory meatus in company with the eighth pair which it leaves behind in the internal ear, whilst the seventh nerve escapes by the aqueduct of Fallopius, passes beneath the parotid, and finds its way on to the cheek over the external masseter muscle, and is eventually distributed to the upper and lower lips, and the alæ of the nostrils. It essentially supplies the muscles of expression and not those of mastication.

In its course it is joined by branches from the fifth pair and vagus, and gives off to the lingual of the fifth, as previously mentioned, a branch known as the chorda tympani, supplying a portion of the tongue with sensation and taste.

It is a motor nerve to the muscles of the middle ear, external ear, cheeks, lips, nostrils, and orbicular muscle of the eye. Through the chorda it supplies sensory fibres derived from the vagus to the tongue, taste fibres probably from the glossopharyngeal, and secretory and vaso-dilator fibres to the submaxillary gland.

Division of the seventh nerve leads to alterations in sight, taste, hearing, smell, and facial expression. As it supplies the muscle which closes the eyelids (the orbicularis palpebrarum), conjunctivitis occurs from exposure of the eyeball; hearing is affected owing to paralysis of the muscles of the internal ear; smell is impaired due to the paralysed condition of the nostrils; taste is affected through paralysis of the chorda.

The expression of unilateral facial paralysis in the horse is characteristic; the upper lip drawn to one side, the elongated nostril, the pendulous lower lip, escape of saliva and food from the mouth, the vacant look, the open eye, and the drooping ear, point clearly to the extensive distribution of this nerve.

Bernard pointed out that horses were suffocated if galloped after division of both facial nerves, owing to the fact that the nostrils were no longer capable of dilatation.

Eighth Pair, or Portio Mollis.—Arises by two roots, one the nerve for the special sense of hearing, the other distributed to the semicircular canals, and assists through these in maintaining the equilibrium of the body.

Injury to the semicircular canals produces giddiness, not deafness, and certain movements (termed 'pendulum-like') of the head occur; the direction in which these are made depends on the direction in which the canals have been injured.

Ninth Pair, or Glosso-Pharyngeal, arises from the medulla, it is a mixed nerve, and supplies motor power to the muscles of the pharynx, and sensory fibres to the posterior third of the tongue, soft palate, part of pharynx, and anterior surface of the epiglottis. It is also a special nerve of taste, supplying the posterior third of the tongue, and having special nerve-endings, known as 'taste-bulbs,' in the circumvallate papillæ.

Tenth Pair, or Pneumogastric.—This is both a sensory and motor nerve. At its origin in the medulla it is intimately mixed up with the ninth, eleventh, and twelfth pairs of nerves, and later on with the sympathetic. It is the most

extensively distributed nerve in the body, supplying the œsophagus, pharynx, lungs, bronchi, trachea, heart, stomach, and intestines.

The sensory branches of the nerve are not highly endowed with sensation, probably for the reason that their chief function as sensory nerves is as afferent channels for reflex action. The motor fibres are derived from the spinal accessory nerve.

In the foramen lacerum the vagus is joined by the jugular ganglion, and for a very short distance it is intimately connected with the accessory nerve, here it receives filaments from the accessory, sympathetic, hypoglossal, and two first cervical nerves. The vagus now descends behind the guttural pouch and joins the cervical portion of the sympathetic nerve, from which results in the horse and most other animals a single cord which passes down the neck above the carotid artery; as the vagus enters the chest it separates from the sympathetic. The arrangement of the right and left nerves is different, the right gives off the right recurrent which passes around the dorso-cervical artery, whilst the main trunk terminates above the origin of the bronchi; the left gives off its recurrent branch opposite to the aorta, and also terminates on the bronchi, forming with the right nerve the bronchial plexus and œsophageal nerves, the latter passing to the stomach and from thence to the solar plexus.

The various branches of the vagus may best be studied in the order in which they are given off.

The *pharyngeal nerve* originates at the superior cervical ganglion and passes to the pharynx, where it forms with the ninth pair the pharyngeal plexus. It is a mixed nerve, and supplies the middle and constrictor muscles of the pharynx, and the cervical portion of the œsophagus with motor power.

The *superior laryngeal* nerve supplies the mucous membrane of the larynx with remarkable sensibility, and gives a motor branch, the external laryngeal, to the crico-pharyngeus. In most animals the superior laryngeal supplies the

crico-thyroid muscle of the larynx with motor power, but in the horse this is supplied by the first cervical nerve.

It is the superior laryngeal nerve which reflexly excites coughing, the coughing centre being situated in the medulla; further, it contains afferent fibres in connection with the respiratory centre, which when stimulated cause arrest of respiration, they are therefore inhibitory fibres.

Section of the superior laryngeal causes pain, and produces in dogs a deeper and hoarser voice due to paralysis of the crico-thyroid muscle, which can no longer render the vocal cords tense. The absence of sensibility in the larynx allows food to pass into the trachea, and thus produces pneumonia.

The *inferior laryngeal*, or *recurrent*, is given off from the main trunk within the chest, on the left side winding around the aorta from without inwards, and on the right side passing around the dorso-cervical artery; both branches return up the neck and supply all the muscles of the larynx (excepting the crico-thyroid) with motor power.

The recurrents are of great practical interest, inasmuch as they are affected (especially the left) in that common form of disease in the horse known as 'roaring,' which is generally due to paralysis and atrophy of the muscles which dilate the laryngeal opening. After division of the recurrent nerves death by asphyxia is likely to follow. We have however observed complete bilateral paralysis of the larynx in horses without asphyxia being produced. In such cases it has been shown that the age of the horse is the saving factor, the rigidity of the cartilages preventing the arytenoids from completely collapsing over the opening of the glottis.

Division of the recurrent also leads to a partial loss of voice, and a peculiar cough is produced owing to paralysis of the laryngeal muscles. As the recurrent supplies sensory branches to the tracheal portion of the œsophagus and trachea, division of these nerves causes loss of sensation in these parts.

It is curious that the recurrent laryngeal should contain

motor fibres, not only for the dilator but also the constrictor muscles of the larynx; it has been observed that when this nerve gets out of order, it is the *dilator* muscles which first become paralysed and later the constrictors. Irritation of the peripheral end of the recurrent produces spasm of the larynx. There are certain poisons, such as that contained in *Lathyrus sativus* and others of the Leguminosæ, which appear to have a special action on this nerve, or at any rate on the larynx, spasm of the larynx being one of the earliest symptoms of poisoning.

The cardiac branches of the vagus contain the fibres which exercise a controlling and inhibitory power over the heart (see p. 39). They also contain the depressor nerve which is leaving the heart to run up the neck with the pneumogastric, entering the medulla by means of the superior laryngeal branch; for the effect of this nerve on the heart see p. 44. The depressor nerve is present as a distinct branch in the rabbit and cat, but in other animals it is mixed up with the vagus. Lastly, the cardiac branches contain fibres from the sympathetic which supply accelerator fibres to the heart (p. 39).

The pulmonary branches supply both sensory and motor branches to the trachea and motor fibres to the bronchi.

Through these branches are transmitted to the medulla impressions which are continually in action, and by which the respiratory centre is stimulated. Through other branches centripetal impulses are transmitted to the vaso-motor centre by which the general blood-pressure is regulated.

The thoracic œsophageal branches supply the œsophagus with motor power; so that division of the vagus causes food to accumulate in the lower part of the tube.

The œsophageal nerves after uniting in pairs in a peculiar manner run along the œsophagus one superiorly the other inferiorly, and passing through the diaphragm they enter the abdominal cavity. The superior nerve supplies the left sac of the stomach and enters the solar plexus, from which it runs to the intestines and other organs (p. 179); the inferior

nerve terminates in the walls of the stomach at its cardiac or right extremity.

Division of both vagi in the horse causes the breathing to become much deeper, more prolonged, and suffocation may result owing to loss of motor power in the larynx. Through the absence of sensation in the larynx, trachea, bronchi, and lungs, food is apt to find its way into the respiratory passages and produce pneumonia. The lungs likewise undergo congestion owing to the laboured and difficult respiration, and the parts become œdematous. In the horse the respirations have been known to fall to five per minute, but the heart beats rapidly owing to the unbalanced action of the sympathetic. Through paralysis of the œsophagus and stomach food collects in the latter, and may extend throughout the entire length of the œsophagus up the neck.

Apparently this effect of engorgement of the stomach in the horse is not invariably produced, for some observers have noted no difficulty in this respect, but experiments made by Colin have shown that division of the vagi paralyses the stomach, so that poisons may remain there and cause the animal no inconvenience as they never pass into the intestine, and thus cannot become absorbed (see p. 157). This is a point of practical importance, and warns us how useless drugs administered by the mouth may be in some digestive troubles of the horse, especially those of the stomach.

Eleventh Pair, or Spinal Accessory, arise by two roots, one from low down the cervical portion of the cord, the other from the medulla. It is essentially a motor nerve, but through being intimately connected with the pneumogastric it also possesses sensory fibres. The use of this nerve is to supply motor power to the sterno-maxillaris, trapezius, and a portion of the levator humeri muscles; at its origin it supplies most of the motor fibres found in the vagus, and also furnishes the latter with its cardio-inhibitory fibres.

The accessory is considered also to possess an influence

over the larynx; division of it produces no difficulty in breathing, as in the case of the recurrent laryngeal, but it causes loss of voice due to paralysis of the motor fibres of the vagus.

Twelfth Pair, or Lingual.—The branches of this nerve supply the tongue with motor power, and fibres to the muscles which depress the larynx. Section of the nerve on both sides causes paralysis of the organ; dogs are unable to lap, and injure the protruding tongue with the teeth.

The Sympathetic System.

An extensive system of nerves exists in the body, the function of which is mainly to supply the bloodvessels, viscera and glands. At one time owing to its peculiar distribution the sympathetic system was regarded as distinct from the cerebro-spinal, this is now known to be incorrect; the two are intimately connected, in fact the sympathetic system is entirely derived from the spinal cord and brain.

The sympathetic is composed of nerves and ganglia; the nerve fibres are remarkable for their fineness and are both medullated and non-medullated; the ganglia consist of multipolar cells and nerve fibres. The numerous processes belonging to the cells serve to increase the number of tracts along which impulses travel, so that these are able to pass out in several directions. There is no evidence that these ganglia can originate impulses, but they serve to transmit nerve impulses, and can modify them in transmission. Until lately there was nothing to show that they were capable of performing a reflex act, but this would now appear to be possible.*

Medullated nerves by passing through a sympathetic ganglion lose their medulla, and Langley has shown that nearly all the nerve fibres entering a ganglion terminate in the nerve cells of that ganglion, though some pass through without communicating with the cells. Nicotin applied to

* Langley and Anderson, *Journal of Physiology*, vol. xvi.

a ganglion paralyses the cells but not the nerve fibres. By this method of inquiry, which is due to Langley, it is possible to demonstrate what nerve fibres do and what do not end in the various sympathetic ganglia.

The number of fibres in a nerve is increased by passing through a ganglion, and further, the ganglion exercises a nutritive effect over such of the nerve fibres as are branches from the cells of the ganglion.

Gaskell has shown that the extensive sympathetic system is capable of classification into three groups: (1) *Vertebral ganglia*, which run on either side of the vertebral column practically throughout its length; below and in connection with these are the large nervous plexuses and ganglia of the chest and abdomen, such as the cardiac, solar, and mesenteric plexuses, these are known as (2) the *Collateral ganglia*; from these are given off fibres which terminate in the tissues supplied by them and known as (3) *Terminal ganglia*. On reference to Fig. 51, p. 339, this distribution is shown in a diagrammatic form Σ being the vertebral, δ the collateral, and δ' the terminal ganglia.

It is through the vertebral ganglia that the sympathetic is mainly brought into connection with the cerebro-spinal system. White medullated nerve fibres run out from the spinal cord, especially in the dorsal and lumbar regions, to join the ganglia on the vertebral chain, this branch is known as the *white ramus communicans* (V Fig. 51). After passing through the vertebral ganglia it loses its medulla, and a branch, the *grey ramus communicans* (rv Fig. 51), leaves the ganglion, returns to the spinal cord, and again issues from it in a manner previously described (p. 69), to supply the bloodvessels of the spinal cord, and those of the fore and hind limbs with constrictor influence.

Those fibres of the white ramus which do not return pass through the vertebral ganglia, become non-medullated, and join the collateral ganglia. White rami are found running out from the spinal cord of the dog from the second dorsal to the second lumbar nerve; in front and behind these points there are no white but only grey rami. In the cervical

region, though there is no white ramus yet fibres run out from the cord by means of the spinal accessory nerve, a division of which enters the vagus and supplies the heart with inhibitory nerves (Fig. 3, p. 40); from the second and third dorsal nerves are given off white fibres which pass through vertebral sympathetic ganglia, and finally reach the heart exercising an augmentor effect (Fig. 3). In the cervical sympathetic are found fibres supplying constrictor influence to the bloodvessels of the head and neck, dilator fibres for the iris, fibres causing the eyelids to open, the eyeball to come forward, and the third eyelid to be retracted in the cat, dog and rabbit; besides these there are sweat fibres for the head and neck, secretory fibres for the salivary glands, and for the glands in the muzzle of the ox. In both the ox and dog trophic fibres are found supplying the muzzle, and in the horse there are fibres for the sebaceous glands of the skin of the ear.

Arloing has shown that in both the ox and dog division of the cervical sympathetic has been followed by a dry, papillated, and hypertrophied condition of the skin of the nose and muzzle, due to damage to the trophic fibres.

From the spinal cord between the sixth and thirteenth dorsal and the first and second lumbar nerves in the dog, are given off the greater and lesser splanchnic nerves, which run to collateral ganglia, the solar plexus; from the first to the fifth lumbar nerves in the dog, are also given off fibres which form the inferior mesenteric ganglion; see Fig. 27, p. 178. From these plexuses are given off fibres supplying the muscles of the stomach and intestines with inhibitory power, so that stimulation of the splanchnics causes the viscera to cease moving (see p. 180).

The splanchnics are also the chief vaso-motor nerves to the vessels of the abdomen; section of them gives rise to great dilatation of the vessels of the intestines, liver, kidneys, etc., due to vaso-motor paralysis, this causes a great fall in blood pressure; stimulation of the peripheral end of the divided nerve causes the vessels to contract and raises the general blood pressure.

The splanchnics contain sensory fibres, it is through these that abdominal pain is felt.

Extirpation of the solar and mesenteric plexuses produces a great outpouring of intestinal fluid, this is probably of paralytic origin, just as section of the chorda tympani causes a paralytic flow of saliva. For further remarks regarding the nerve supply of the viscera, see p. 179.

The sympathetic system also furnishes the pilo-motor fibres in the cat and dog (see p. 238).

The functions of the sympathetic may thus be summarised: This nervous system supplies the bloodvessels with constrictor and dilator fibres, the viscera with motor and inhibitory fibres, accelerator fibres to the heart, dilator fibres for the pupil, secretory fibres for sweat, salivary, and sebaceous glands, motor fibres to the muscles of the hair, and fibres which exercise an effect on the nutrition of a part.

CHAPTER XV.

THE SENSES.

Sight.

The delicate structures composing the eye receive a very thorough protection by the anatomical arrangement of the parts. The orbital cavity, for example, is nearly surrounded by incomplete bony walls, and the layers of fat within it assist the muscles in protecting the globe and the optic nerve. The eyelids sweep the cornea and protect the part from dust and exposure; the tears keep the face of the cornea brilliant; the membrana nictitans removes particles of solid matter which would otherwise produce irritation; and the eyeball can be retracted to a considerable extent to assist it in withdrawing from injury. The size of the orbit is such that ordinary blows inflicted upon the eye are expended on the margin of the orbital cavity, and not on the eyeball itself, so that the risk of injury is less from large than from small bodies.

The shape of the eyeball is not (in the horse) quite spherical, the vertical axis is greater than the horizontal, and the posterior face of the eyeball is distinctly less convex than the anterior.

Optic Nerve.—Issuing from the back of the eyeball, very low down and inclined to the temporal side of the globe, is the optic nerve, which after describing a peculiar curve upwards, runs in the substance of the retractor muscle to enter the cranium through the optic foramen. This curve in the optic nerve (Fig. 63) is necessitated by the horizontal

movements of the eyeball; if the eye looks backwards the curve is increased, whereas if it looks forwards the 'slack' is taken out of the nerve and the curve entirely disappears.

The optic or second cranial nerve has a deep-seated origin in the corpora quadrigemina, and a representation in the occipital region of the cerebral hemispheres (see p. 372).

The fibres forming the optic nerve decussate, those from the left brain passing to the right eye and vice versâ. In some animals this decussation is complete such as the horse, sheep, and pig; but in others a certain number of fibres decussate, whilst some enter the nerve on the same side of the brain as that on which they originate; this is the arrangement in the dog, cat, rabbit, monkey, and man.

This partial decussation is considered in man to play an important part in the production of sympathetic ophthalmia, the inflammatory trouble running along the optic nerve to the commissure, and so finding its way to the other eye. It is quite certain in the horse, where the decussation is complete, that sympathetic ophthalmia from an injury is unknown.

Division of the optic nerve causes no pain but only the sensation of light, stimulation of the nerve causes flashes of light to be perceived by the brain, in fact the optic nerve conveys nothing but luminous impressions to the brain which the consciousness perceives as vision.

Structure of the Eye.—The globe of the eye is anteriorly made up of a transparent convex surface known as the cornea, whilst the remainder of its walls are opaque and formed by the sclerotic, choroid, and retina. The sclerotic is the tunic on which the strength of the eyeball depends, the choroid may be regarded as that which principally attends to the vascular supply, while the retina is the sensitive expansion of the optic nerve on which the picture is imprinted.

The shape and tension of the eyeball is maintained by means of its humours, which are known as the aqueous and vitreous.

The *aqueous humour* occupies the space between the cornea and the lens, it is a watery fluid, poor in solids, and is in reality lymph. It is constantly being secreted, probably by the ciliary processes, and as constantly carried away by the lymphatic channels with which it communicates through the spongy ligamentum pectinatum ; these channels empty themselves into the anterior system of veins. If the anterior chamber be evacuated it is refilled in about twenty-four hours.

The use of this fluid is to maintain the convexity of the cornea ; after death the process of drainage still appears to occur, though, of course, there is no reproduction, the result being that in a day or two the cornea falls in through loss of the aqueous.

The *vitreous humour* is a viscid, tenacious material, contained within the hyaloid membrane, which permeates its substance. The vitreous contains mucin but a very small percentage of solids. The use of this humour is to maintain the intra-ocular pressure, by which the proper tension of the globe is brought about.

Between the two humours is situated a diaphragm known as the iris, which regulates the amount of light passing into the eye, and behind this is a focussing arrangement or lens. The cornea, lens, and media constitute the refracting apparatus of the eye.

The whole of the vitreous chamber is rendered dark by the liberal application of pigment, with the exception of a surface above the optic nerve which is brilliant and iridescent in appearance, and known as the tapetum lucidum.

The similarity in construction between the eye and the apparatus known as a camera is very marked ; both have a refracting surface anteriorly placed, a diaphragm to cut off superfluous rays of light, an arrangement for focussing, a dark chamber in which is placed a sensitized surface, and on which a reduced and inverted image of the picture is impressed.

By means of the muscles of the eye the globe is given a considerable range of movement, and in addition it can be

retracted within the orbital cavity; further, these muscles afford some protection to the optic nerve.

Though we have thus briefly run over the leading features of the eye, yet there are structures which need some detailed description if we are to clearly understand the phenomena attending perfect vision.

The **Cornea** in most animals is circular in outline, in the horse it is somewhat egg-shaped; when viewed from the front and divided into two halves by a vertical line, it is distinctly larger on its nasal than on its temporal side.

When viewed from the side the cornea is seen to be convex, but measurement shows that in the majority of horses the curvature of the cornea taken in its horizontal and vertical meridian does not exactly agree, as it would do supposing the surfaces were perfectly convex. The excess of curvature of one meridian of the cornea, over that of the surface at right angles to it, produces a defect in vision which is known as astigmatism; the meridian in the horse which is nearly always the flattest in the horizontal.

The cornea is very tough, non-vascular, richly supplied with nerves, and nourished by the lymph which freely circulates in it. It may be regarded as the chief refractive apparatus of the eye.

The **Lens** is composed of various onion-like layers of different refractive powers. In shape it is bi-convex, the convexity of its posterior face being greater than the anterior. It is held in its place by a capsule which really suspends the lens in the eye, the capsule receiving attachment to some long processes behind the iris known as the ciliary. In the horse the lens is in contact with the ciliary processes, in most other animals there is a small space between the two.

The lens possesses inherent elasticity, which admits of its surface undergoing an alteration in shape, flatter at one time more convex at another. This alteration in shape occurs through the ready manner in which the lens by its elasticity lends itself to the pressure exercised on it through its capsule, so that if the tension of the capsule be relaxed

the lens bulges, or if the tension be applied it flattens. In this way the eye is focussed or accommodated to various distances, a subject which will be dealt with presently.

The **Iris** is a curtain with a hole in the centre called the pupil. The shape of the pupil varies in different animals; in the dog it is circular, in the horse, sheep, ox and cat elliptical; in the latter animal the elliptical slit is placed vertically in the others horizontally.

The iris is mainly a collection of bloodvessels and muscular fibres, the whole being heavily coated with a brown pigment in the horse, though occasionally this pigment is wanting, giving the iris a bluish-white streaky appearance as in the so-called 'wall-eyed' horse. In the ox and dog the iris is a brighter brown than in the horse, while in the sheep it is brownish yellow.

The muscular fibres of the iris are commonly described as circular and radiating; a contraction of the circular muscle contracts the pupillary opening, a contraction of the radiating fibres dilates it. Great discussion has taken place as to whether a dilator muscle exists. Langley and Anderson* from their observations on the cat, dog, and rabbit, are distinctly of opinion that one does exist, and that dilatation of the pupil is partly due to the action of this muscle, and partly to inhibition of the circular muscle.

The nerve supply to these circular and radiating fibres is not the same; the circular fibres are supplied with motor power through the third cranial nerve, whilst the dilator muscle is supplied by the sympathetic. The latter fibres come out from the spinal cord at the first three thoracic spinal nerves, from a part known as the cilio-spinal centre; from here they travel up the neck in the cervical sympathetic, and reach the iris through the ciliary ganglion.

If the third nerve be divided the radiating muscular fibres of the iris contract under the unbalanced action of the sympathetic, and thus dilate the pupil; if the sympathetic be divided the pupil contracts under the unbalanced action of the sphincter fibres.

* *Journal of Physiology*, vol. xiii., No. 6.

Stimulation of the retina by light is the natural method by which alterations in the size of the pupil are brought about, the act is a reflex one; in a brilliant light the pupil contracts, in a low light it dilates. In the horse this is not strictly true; in direct sunlight the pupil of this animal is a mere narrow chink, but in ordinary daylight the pupil barely responds to artificial light, or if it does contract it is so little as not to materially reduce the size of the pupil. Even when the light is concentrated on the eye, either by means of a mirror or a lens, the iris practically remains unchanged. Owing to this phenomenon the eye of the horse can be examined by the ophthalmoscope without the use of atropine, or even without artificial light.

There are certain drugs which dilate the pupil such as atropine and cocaine, and others which contract it such as morphia and eserine. It is curious to observe in the horse that though the pupil is elliptical, yet when it is dilated by atropine it becomes circular; the chief radiating fibres would therefore appear to be above and below and but very few on the sides.

Eversbusch* has worked at the question of the iris of the horse, and states that the elongated form of the pupil is due to the presence of an accessory apparatus on the posterior surface of the iris, which he calls the ligamentum inhibitorium; through this ligament the sides of the iris are not pulled in by the contraction of the sphincter muscle.

The direction of the pupil in the horse is always horizontal, or practically so, no matter what the position of the head may be; this is a point which will be touched on again in dealing with the muscles of the eyeball.

The pupil of the horse is said to dilate after the animal has been galloped; *immediately* after death it dilates, but gradually, in the course of twenty-four hours or so, it contracts until the pupil is of normal size.

In the horse there exists on the edge of the iris, at the centre and upper part of the pupil, one or more large soot-like bodies known as **corpora nigra**, a small one may be

* *Zeitschrift für Vergleichende Augenheilkunde*, Heft 1, 1882.

found on the lower margin of the iris, but the upper ones are the most prominent. When the pupil is strongly contracted in direct sunlight, the centre of it is entirely blocked out by these pigmentary masses, and divided into an inner and outer portion. It would appear as if this caused an imperfect image to be imprinted on the retina, and this view we at one time held, but on subjecting the question to actual experiment no broken image was found to result from the use of a diaphragm the centre of which was blocked out.

The use of these bodies is doubtless to assist in absorbing rays of light, but their position in the centre of the pupil would theoretically not appear to be the most suitable position, and they must have some other function. The horse appears to be the only animal possessing them.

Ligamentum Pectinatum.—Around the attached margin of the iris, viz., at the corneo-scleral border, a peculiar spongy tissue exists which gives the iris at this part a distinctly elevated rim; this is known as the ligamentum pectinatum. Roughly speaking it is a rim of spongy iris traversed by canals, crevices, and spaces, which lead into the lymphatic system of the eye; the function of this tissue is to carry off the aqueous humour as rapidly as it is worn out and replaced, by which means the normal tension of the anterior chamber is maintained.

The **Choroid** coat contains the vessels which nourish the retina, it possesses innumerable nerves, numerous lymphatics, and further it is an elastic coat. Anteriorly behind the iris it forms the peculiar plaited body known as the ciliary processes, and in front of this it furnishes the tissue which is called the iris; the iris and ciliary processes are therefore part of the choroid coat.

With the exception of one area the whole of the interior of the choroid is covered with pigment, and the same extends on to the processes and iris. The area which is an exception lies on the posterior wall of the eyeball above the optic nerve; it is of a brilliant colour, in the horse a mixture of green, yellow, and blue, and is known as the

tapetum lucidum. This is found in both herbivora and carnivora; in the former it is due to the interference of light causing iridescence, produced by the arrangement of the connective tissue of the choroid, and not to the presence of any pigment; in carnivora it is due to minute crystals in the cells of the part, the crystals causing the interference.

The use of the tapetum is generally supposed to enable animals to see in the dark; this of course is impossible, but it is probable that the presence of a tapetum may enable an animal to see better in a low light, and it has been said that this is accomplished by the tapetum acting as a concave reflector, causing the rays of light to traverse the retina a second time.

The **Ciliary Zone** is a peculiar and important part of the eye, formed on the one hand by the junction of the cornea and sclerotic, and on the other by the iris and ciliary processes. Between these lies a muscle known as the ciliary, which is firmly attached to the corneo-scleral margin, and running backwards into the choroid is there attached. In man the **ciliary muscle** consists of both circular and longitudinal (or meridional) fibres; in the horse, and probably all the lower animals, only meridional fibres exist.

The muscle is composed of unstriped fibres, and its use is to pull the choroid forward; the object of this will be apparent when we discuss the question of accommodation.

The Vitreous is enclosed in the hyaloid membrane; anteriorly this membrane, here known as the *Zonula of Zinn*, becomes dovetailed into the ridges formed by the ciliary processes, and enveloping the lens forms its suspensory ligament. If the amount of vitreous humour present is sufficient in quantity, this ligament of the lens must always be tense, and as it is very inelastic it tends to keep the lens flattened; we shall refer to this again in speaking of accommodation.

The **Retina** lies within the choroid and outside the vitreous, it spreads out from the entrance of the optic nerve of which it is the expansion. Microscopic examina-

tion shows this membrane to be composed of seven layers, of which the most important is one termed from its appearance the layer of rods and cones. It has been shown conclusively that these rods and cones are the essential elements of the retina, and that wherever they are absent the part is insensitive to light, as for example in the blind spot of man, and over the entrance of the optic nerve in probably all animals.

Though this layer is the most important, it is not placed, as one would suppose, next the vitreous, but next the choroid, whilst the layer next the vitreous is composed of nerve fibres and ganglion cells. Rays of light have, therefore, in the first place to pierce the entire thickness of the retina to arrive at the rods and cones, here they give rise to a nervous impulse which retraces its steps in the retina, until it arrives at the layers next the vitreous, from which it is carried off by the optic nerve to the brain.

The entrance of the optic nerve within the eyeball is spoken of as the optic disc; it is a concave oval surface surrounded by a white ring formed of sclerotic. It lies, in the horse, towards the bottom of the eyeball and inclined to the temporal side. There is no yellow spot in animals, in man this exists and is the area of the most acute vision. A line drawn through the centre of the cornea to the yellow spot is called the visual axis of the eye. The visual axis in man does not quite agree with the optic axis, viz., a line drawn exactly through the centre of curvature of each refractive medium. In the lower animals we have no means of knowing whether the optic axis is also the visual axis, but from the absence of the yellow spot it is assumed to be so.

The Ophthalmoscope.—We may here describe in outline the theory of this instrument, and the appearance of the picture presented by it.

To examine the eye, a mirror with a hole in the centre is applied to the eye of the observer; from a suitable source of light rays are thrown through the pupil on to the retina to be examined. When a light is thrown into the eye, the

rays are reflected back through the pupil in the direction in which they entered, and pass through the hole in the mirror into the eye of the observer. This is the principle of the ophthalmoscope.

On looking at the retina of the horse, a remarkable golden-yellow or greenish-yellow surface is illuminated studded with minute dots; this is the tapetum. Examination shows this surface to be situated above the optic papilla, and to be somewhat half-moon shaped; below it the optic papilla comes out of a reddish or pink colour,

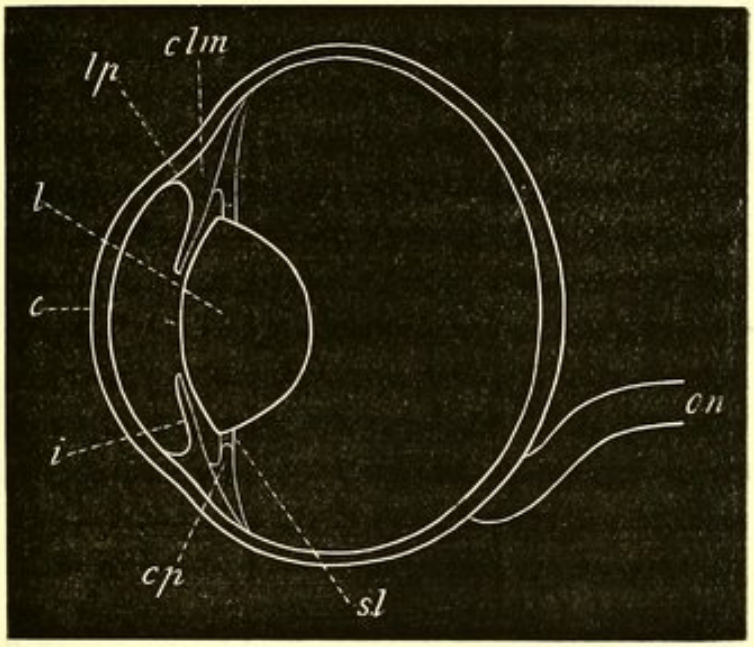


FIG. 63.—VERTICAL SECTION OF THE EYE OF THE HORSE, NATURAL SIZE.

c, Cornea; *l*, lens; *i*, iris; *cp*, ciliary process; *lp*, ligamentum pectinatum; *cl m*, position of ciliary muscle; *sl*, suspensory ligament of lens; *on*, optic nerve showing its curve.

with a slightly raised whitish margin. It is so difficult to study the eye, owing to its frequent movement, that only occasional glimpses of the papilla can be obtained. From the optic papilla a dense network of vessels may be seen radiating, but extending no great distance from it; this is characteristic of the retina of the horse. The remainder of the fundus is purple or brown, but owing to its extent very little of it can be seen. In other animals the vessels radiating from the disc are wider apart and more regular,

and several of them have received names; moreover, the arteries can be distinguished from the veins, which is not possible in the horse.

Owing to the presence of the tapetum in the horse, a perfect examination of the lens and fundus may be made without the aid of artificial light; under the influence of artificial light the pupil dilates so much that there is no need for the use of atropine.

Accommodation.—All rays of light proceeding from a distant object may be regarded as parallel, and all those proceeding from an object within twenty feet of the eye may be regarded as divergent. A distant object is one situated

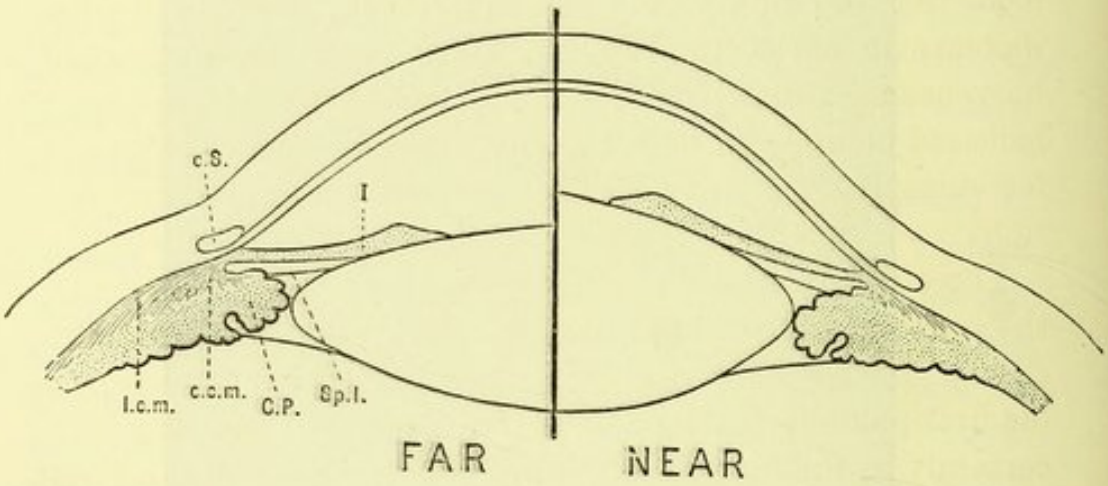


FIG. 64.—DIAGRAM TO ILLUSTRATE ACCOMMODATION. (FOSTER AFTER HELMHOLTZ.)

C.P., ciliary process; I, iris; Sp.l., suspensory ligament; l.c.m., longitudinal ciliary muscle; c.c.m., circular ciliary muscle; c.S., canal of Schlemm.

The left half represents the shape of the lens for viewing far objects, and the right half that for viewing near objects.

anywhere between twenty feet from the eye and infinity; an object closer than twenty feet to the eye is called near, and this point increases up to four or five inches, at which distance no object can any longer be distinctly seen. The nearest distance at which objects can be distinctly seen is called the near point.

Parallel rays need no focussing on the retina other than that provided by the cornea; but rays from near objects do

require focussing owing to their divergent nature, and it is evident that the nearer the object to the eye the greater the focussing required.

This focussing is brought about by a change in the shape of the lens, it becomes more convex for near objects, and this increase in convexity is due to the ciliary muscle drawing forward the choroid coat, and with it the ciliary processes. By this means the tension exercised through the Zonula of Zinn (the suspensory ligament of the lens) is relaxed, and the lens of its own inherent elasticity bulges forward and so increases the curvature of its anterior face (Fig. 64). A more convex lens is a more convergent one, and its focus is therefore shorter; in this way near objects are brought to a focus on the retina and distinctly seen, whereas if this increase in curvature had not taken place, nothing could have been distinctly seen, and the picture would have been focussed behind the retina. The power the eye possesses of focussing itself is known as the mechanism of accommodation.

The ciliary muscle is governed by the ciliary nerves. In the human subject the constrictor fibres of the iris and the ciliary muscle are paralysed by atropine, but in the cat (as first pointed out by Lang and Barrett*), the dog, and certainly in the horse, there is no evidence that any paralysis of the ciliary muscle takes place under atropine, though the pupil dilates. Under the full effect of atropine all these animals can see objects quite close to the eye, and this they could not do if the ciliary muscle were paralysed.

Eyes which possess the power of seeing objects distinctly a few inches from the eye to infinity are known as **Emmetropic** (Fig. 65); but all eyes do not possess this range of vision owing to their shape, or more correctly, to the length of the eyeball.

Myopia or short sight is due to the eyeball being too long, whereby the picture is formed in front of the retina, and only a confused and blurred image falls on the retina (Fig. 65).

* 'The Refractive Character of the Eyes of Mammalia,' *Royal London Ophthalmic Hospital Reports*, vol. xi., part ii.

Hypermetropia or long sight is due to the eyeball being too short, whereby, though vision may be perfect for distant objects, those situated near at hand are not distinctly seen, as the picture is brought to a focus behind the retina (Fig. 65).

It is obvious that a concave glass which scatters rays is the remedy for myopia, whilst a convex lens which converges them is the appropriate glass for hypermetropia.

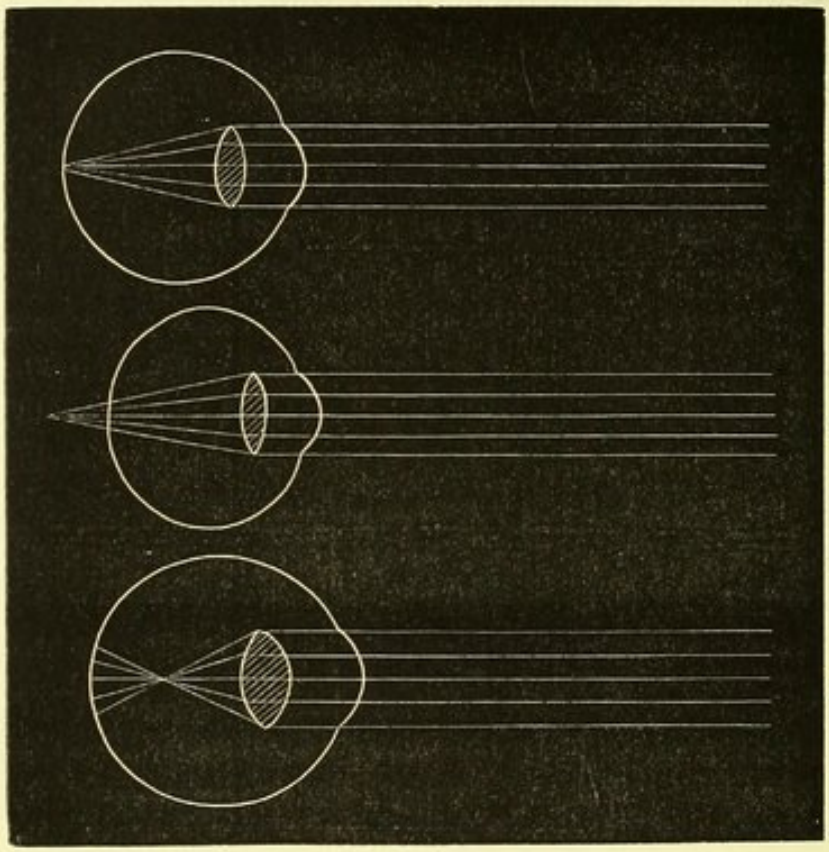


FIG. 65.—DIAGRAM OF AN EMMETROPIC, HYPERMETROPIC AND MYOPIC EYE, TO ILLUSTRATE WHERE THE FOCAL POINT EXISTS (KIRKE).

In 2 the short eyeball causes the focus to form behind the retina; in 3 the long eyeball causes the rays to come to a focus in front of the retina.

Our observations show that the majority of horses are slightly short-sighted.

Astigmatism is another error of refraction, due to irregularities in the curvature of the cornea or lens, generally the former. The effect of this condition is that the rays of light passing through one meridian of the eye, are brought to a focus earlier or later than those passing through the

meridian at right angles to it. The horse is very commonly astigmatic; the horizontal is generally the meridian of least curvature, and corresponds to the long diameter of the pupil.

Errors of Refraction.—In the following table is given the proportion of eyes affected with errors of refraction in the horse.

Out of 100 eyes (54 horses):

51 were myopic and astigmatic.
2 were hypermetropic and astigmatic.
6 were affected with mixed astigmatism.
39 were affected with myopia.
1 was hypermetropic.
1 was emmetropic.

The amount of error of refraction is as a rule small, the chief visual defect being myopia with or without astigmatism. The number of astigmatic horses is remarkable.

According to Lang and Barrett's observations,* the cow would appear to be hypermetropic, and the eye also suffers from astigmatism. In dogs and cats the refraction closely approaches emmetropia. In nearly all the wild animals examined by these observers the refraction was hypermetropic.

Katoptric Phenomena.—When a candle is held opposite to the eye three images of the flame are seen; one a very sharp bright one, obviously reflected from the cornea; a second much duller, but also large, reflected from the anterior surface of the lens; and a third very small, brighter than the middle one, and *inverted*, reflected from the posterior part of the lens (Fig. 66). In a normal eye these are seen perfectly and move in a definite direction when the candle is moved, the inverted image passing in an opposite direction to the two erect images, and all are equally visible at any point on the surface of the lens.

This phenomenon has been taken advantage of in determining the clearness of the media of the eye, and though superseded by the greater accuracy of the ophthalmoscope it is still a valuable aid; in cataract one or more of the

* *Op. cit.*

reflections become blurred, and sometimes the image is duplicated.

The first and second images are erect inasmuch as they are reflected from a convex surface, but the third image is inverted, being reflected from the posterior surface of the lens which viewed from the front is concave. During the act of accommodation the relative position of these images alters, the second advancing nearer to or receding from the first, as the anterior face of the lens becomes more convex or flatter as the case may be.

The **Movements of the Eyeball** are brought about by means of the ocular muscles; in this way the globe of the eye can

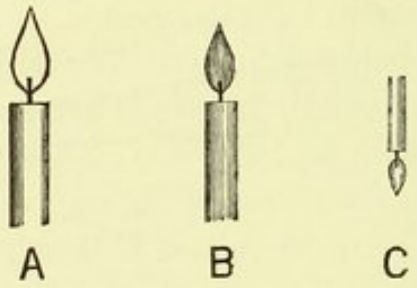


FIG. 66.—DIAGRAM OF THE KATOPTRIC TEST.

A, from the anterior surface of the cornea; B, from the anterior face of the lens; and C, from the posterior face of the lens.

be rapidly turned in any direction. But the movements are somewhat complex, for in some of the lower animals, for example the horse, the eyes are laterally placed in the head, so that vision is commonly single-eyed and not binocular as in man. The eye that is viewing an object situated to one side and moving to and fro, is being followed in this muscular movement by the eye which does not see; the movements are conjugate, but this only occurs so long as monocular vision is practised. If both eyes be directed to an object situated to the front binocular vision becomes possible, and now the movements are no longer conjugate but opposite, for while the left eye is inclined to the right the right eye is inclined to the left.

Another complication in the ocular muscles is due to the movement of the head; it was first pointed out by Lang

and Barrett,* that in the rabbit and guinea-pig no matter what position the head occupied the pupil was always kept vertical. If the head of the horse or ox be raised or depressed to the fullest possible extent, at one time the muzzle being on the ground, at the next the muzzle being high in the air, it will be found that the eyeballs rotate like a wheel, so that the pupil is still kept horizontal; if it were not for this the pupil in the uplifted head would be vertical and in the depressed head oblique.

When the head is elevated the eyeball becomes depressed

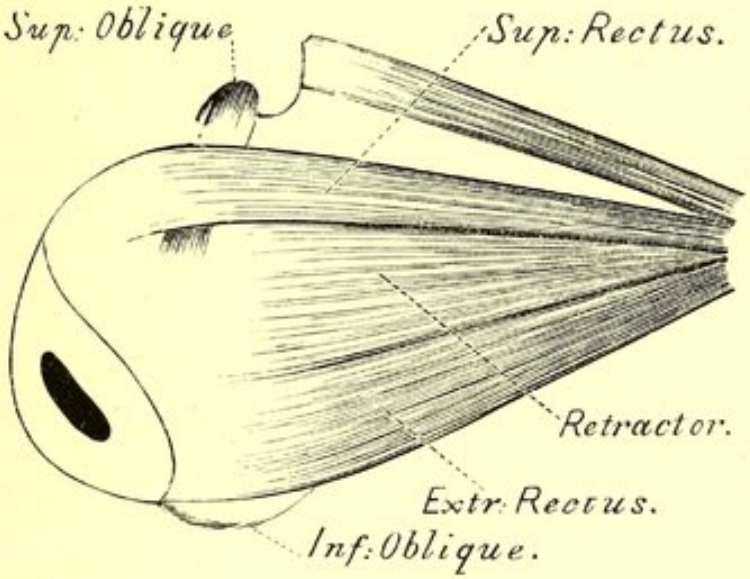


FIG. 67.—THE MUSCLES OF THE LEFT EYEBALL OF THE HORSE VIEWED FROM THE TEMPORAL SIDE.

to such an extent that the sclerotic largely shows above, whilst the cornea partly disappears beneath the lower eyelid. When the head is depressed to the ground no more sclerotic shows than with it in the ordinary position; the probable cause of this will be mentioned presently.

The muscles of the eyeball (Fig. 67) are seven in number, viz., four recti, two oblique, and one retractor. The use of the recti is clear enough, they rotate the eye in four directions, outwards, inwards, upwards and downwards. The two oblique muscles rotate the eye in opposite directions around

* *Op. cit.*

its antero-posterior axis; when the superior oblique contracts it pulls the temporal side of the pupil upwards, and if it were not counteracted by the inferior oblique it would continue to contract until the pupil became vertical like that of the cat; the inferior oblique pulls the temporal side of the pupil downwards, in other words these oblique muscles produce a torsion of the globe or swivel rotation. The retractor partly withdraws the eye in its socket.

The nerves supplying these muscles with motor power, are the third pair to all the muscles excepting the external rectus and superior oblique; the external rectus being supplied by the sixth pair or abducens, and the superior oblique by the fourth pair or pathetic.

The chief movements of the eyeballs are backwards and forwards, corresponding to the directions described as outwards and inwards in man. During these movements it is evident that the external rectus of one eye is acting in conjunction with the internal rectus of its fellow, and such is always the case in monocular vision.

Animals with the eyes laterally placed have, however, the power of monocular and also of binocular vision, but the latter is only produced by an internal squint, and the movement of the muscles are now no longer conjugate, for both internal recti are acting together (Fig. 68). Sometimes, then, the group of muscles employed in turning the eyeballs are the same in each eye, at other times they are not.

The torsion produced by the superior and inferior oblique muscles is of value in the binocular vision of animals, and in the vertical movements of the head. When the muzzle is raised, as previously described, the superior oblique muscle revolves the eyeball in its socket until the pupil is horizontal; the explanation of the cornea partly disappearing under the lower lid, and the sclerotic showing extensively above, appears to be due to a conjugate action of the inferior rectus muscle whenever the superior oblique is so employed. The inferior oblique is mainly employed with the internal rectus in pulling the eyes inwards for binocular vision,

also, as mentioned above, for maintaining the horizontal pupil when the head is depressed or raised.

The orbicularis palpebrarum, which closes the eyelids, is supplied by the seventh nerve, and the muscle which raises the upper lid derives its nerve supply from the third pair.

Monocular and Binocular Vision.—When a horse directs both eyes to the front (Fig. 68) he produces a well-marked internal squint, and is then capable of binocular vision.

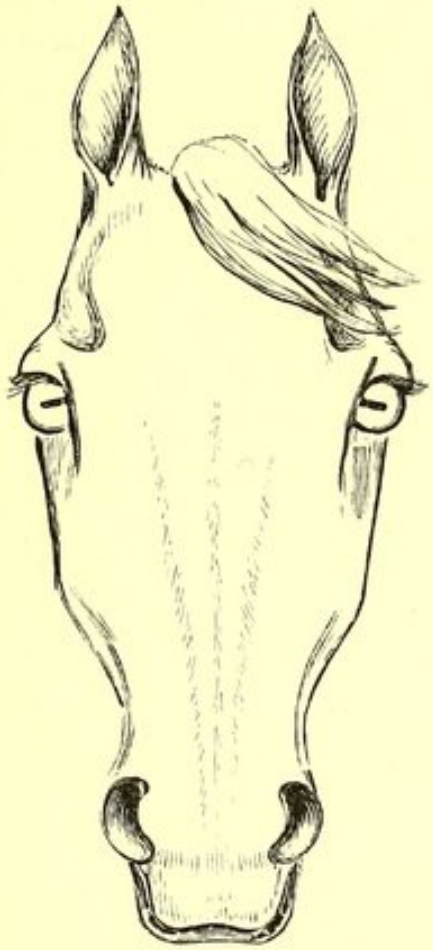


Fig. 68.—The Position of the Head and Eyes in Binocular Vision.

The eyes are rotated inwards and slightly upwards by the combined action of the inferior oblique and internal rectus; the pupils are not perfectly horizontal but nearly so, and the pupillary opening is brought so far to the front that the inner segment of the cornea and iris entirely disappears beneath the inner canthus.

In no other position than this has the horse binocular

vision, viz., single vision resulting from the employment of a pair of eyes, and it is curious to observe that the condition of eye which gives a horse single vision causes in man double vision.

Animals with their eyes situated on the lateral side of the head are capable of exercising monocular vision for all objects placed to one side of them; monocular would appear to be for them as perfect as binocular, but on this point it is difficult to judge. It is certain in the horse when the attention is *particularly* directed to an object, that it is viewed with *both* eyes, the head being held very high, and the ears 'pricked' and turned to the front.

Though ordinary vision is monocular, yet the right eye blinks when an attempt is made to strike the left, though it cannot possibly see what is going on.

In man binocular vision is perfect, and the explanation afforded is that any part of one retina corresponds to the same part of its fellow; so that if the retinas be laid over one another, the left portion of one will lie exactly over the left portion of the other, and their upper and lower parts will equally correspond; but the temporal side of one eye does not correspond to the temporal side of its fellow but to the nasal side. In Fig 69, the two circles represent the two retinas divided into quadrants, L being the left and R the right eye; a and c in the left eye, correspond to a′ c′ in the right eye; and b and d in the left, correspond to b′ and d′ in the right eye, but the optic nerve o is in the left segment of one eye, and the right segment of the other.

When the two images of an object fall on corresponding points of the retina, vision is binocular and only one object is seen; thus, if the rays fall on the right side of one retina, they must fall on the right side of its fellow; in Fig. 69 this is shown, v l from x to x′, and x to x are the two visual axes; if the object y x z be looked at, z in each case falls on the left of the retina, and y on the right, viz., on corresponding points, by which means the object is seen as a single one. Owing, then, to the manner in which the

human eyes are placed in the head, and the convergence of axes of the eyeball, a ray of light from any point is imprinted upon the same side of the retina in both eyes, and we see the object not as a double image, but as a single one.

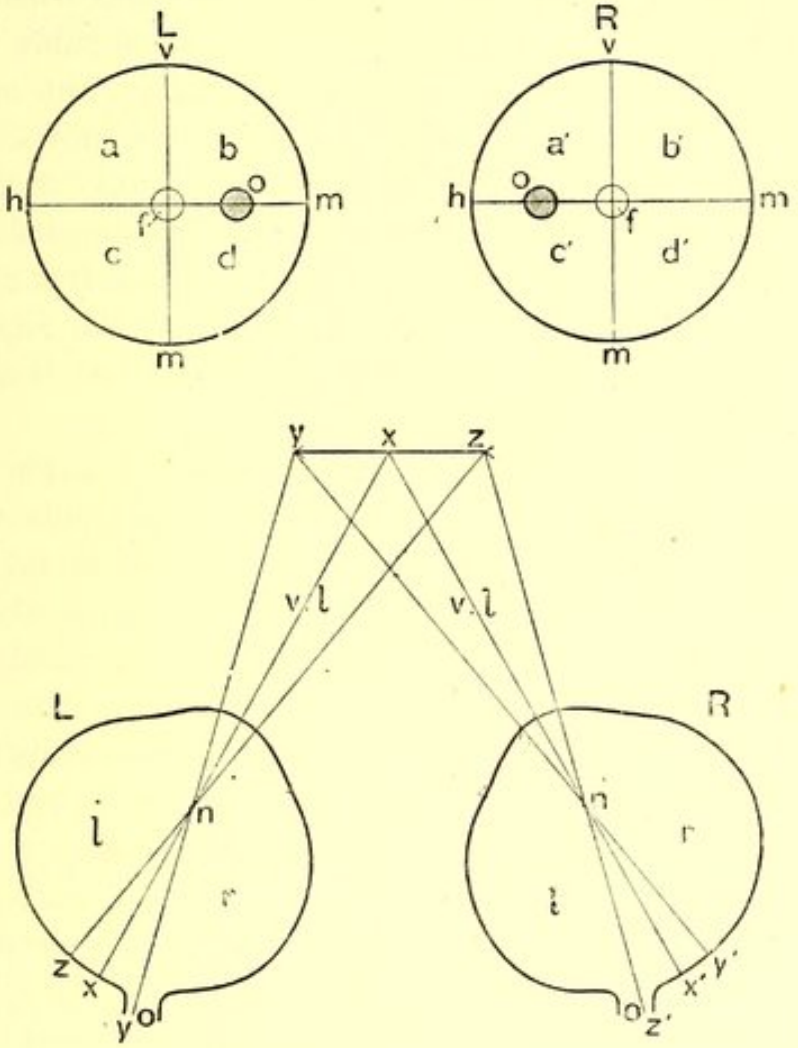


FIG. 69.—DIAGRAM ILLUSTRATING CORRESPONDING POINTS IN THE HUMAN EYE (FOSTER).

z′ x′ y′ are points in the right eye corresponding to z x y in the left eye; v l, visual axis. The two figures above, illustrate the corresponding points on the retina described in the text.

This explanation does not apply to the herbivora; no matter how greatly the eyes may be converged in order to see an object, the rays of light do not fall on the same side of the retina, but on *opposite sides* of it. The diagram (Fig. 70) will make this point clear.

The outer part or temporal side of the retina in the horse, corresponds with the temporal side of the opposite eye; while the nasal side cannot correspond with the nasal side of its fellow, as it is not possible for a ray of light from an object to strike both nasal sides at one time (Fig. 70).

Cartilago Nictitans.—The retractor muscle of the eye

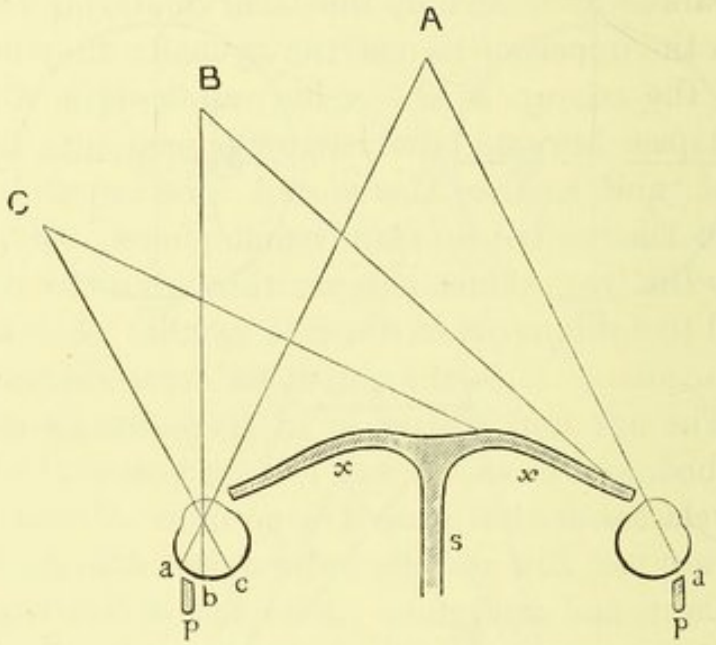


FIG. 70.—DIAGRAM OF HORIZONTAL SECTION OF THE HEAD PASSING THROUGH BOTH EYEBALLS, TO ILLUSTRATE CORRESPONDING POINTS IN THE RETINA OF THE HORSE.

x x, the frontal bones; p p, portion of malar bone entering into the formation of the outer rim of the orbit; s, the nasal septum. Rays of light proceeding from A are seen by both eyes, being imprinted on the temporal side of each retina at a; rays from B are seen at b in the left eye, but are not seen with the right eye; in the same way rays from C are imprinted at c in the left eye, but cannot be seen with the right eye.

withdraws the eyeball within the orbit, and the pressure thus produced within the cavity forces the cartilago nictitans forward, so that it may be made to sweep nearly the whole corneal surface.

The reason why the cartilage is pressed forwards is due to the fact that though naturally curved, it becomes flattened by the pressure caused by retraction and shoots forward; when the pressure is removed it retires through its own elasticity, and becomes curved once more.

On the cartilago of some animals is a small gland termed the Harderian; its use is to prepare an unctuous secretion, probably of a protective nature.

In the eyelids are found numerous glands, the Meibomian, which furnish an oily secretion, and prevent the overflow of tears.

The **Tears** are secreted by the lachrymal gland which is placed on the upper surface of the eyeball; they find their way into the conjunctival sac by numerous small tubes. The tears pass through the narrow puncta into the lachrymal sac, and so into the nostril; once in the sac the descent to the nostril is readily understood, but it is not clear why the tears prefer passing through a narrow slit in the eyelid to running over the side of the face; probably the only explanation is the unctuous secretion mentioned above. The use of the tears is to keep the cornea moist and polished, and to wash away foreign bodies.

The **Eyelashes** of the horse are peculiar. Those on the lower lid are very few and fine, whilst on the upper lid they are abundant, and exist not as a single row but as a double one; the rows cross each other like a trellis-work, but without interlacing; these eyelashes are very long and strong. A few protective hairs grow from the brow and below the lower eyelid, in some horses they are four or five inches in length; they appear to be in connection with nerve terminations, for their delicacy to the sense of touch is remarkable. The function of these hairs is doubtless protective, and to give the eyes warning of danger.

Physiological Optics.—When a ray of light enters the eye it has to pass through four surfaces, and including the air four media. There are two surfaces to the cornea anterior and posterior, and two surfaces to the lens anterior and posterior; each of these surfaces differs in curvature. As media there are the aqueous and vitreous humours and the crystalline lens; the latter is further complicated by not being of the same refractive index throughout.

The formation of an image in such a complex optical system would be difficult to understand, were it not possible

to construct theoretically from it a simplified eye, or, as it is known, a *schematic* eye. The basis of this construction is, that so long as a complex system has its surfaces and media 'centred,' that is symmetrically disposed around the optical axis, it is possible to deal with it as if it consisted of two surfaces and two media, viz., the *schematic* eye, and even to simplify it still further to one surface and two media, the *reduced* eye, the media in the latter being air and water.

In such a simple optical system it is readily possible to

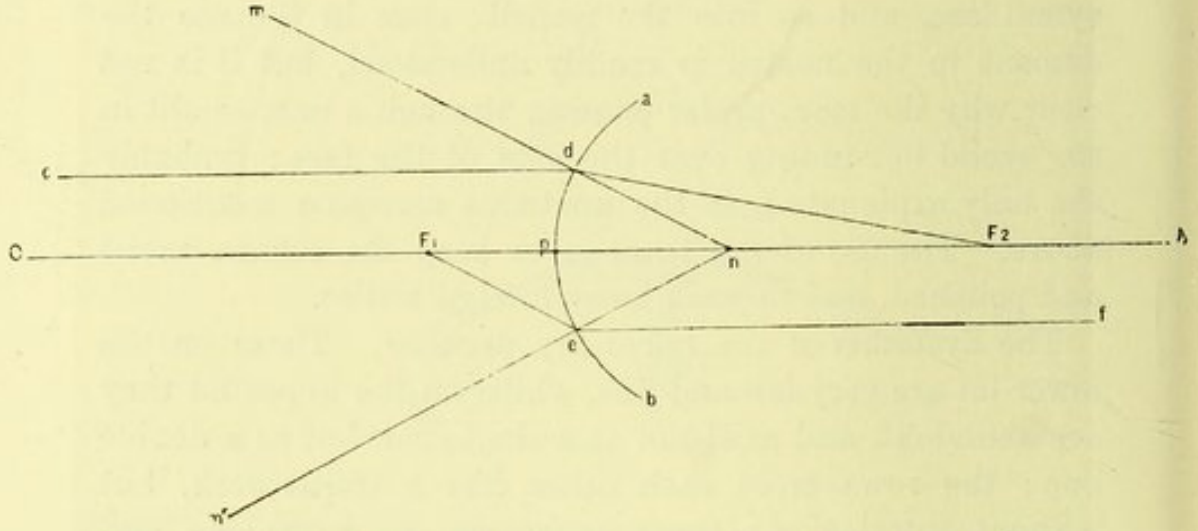


FIG. 71.—THE CARDINAL POINTS OF A SIMPLE OPTICAL SYSTEM (FOSTER).

O A, optic axis; a p b, a curved spherical surface; n, nodal point; F_2, principal posterior focus; F_1, principal anterior focus; e f, rays proceeding from F_1, rendered parallel to the optic axis; p, the principal point; the rays m d, O p, and m′ e, pass through the nodal point n and undergo no refraction; the rays c d, parallel to the optic axis, are refracted and meet at F_2.

trace the paths taken by the rays of light, and so understand the formation of an image on the retina of the eye.

Cardinal Points.—The most simple optical system which can be devised has an *optic axis* (O A Fig. 71), viz., a line passing through its centre perpendicular to its refractive surface (a b); on the optic axis is situated the centre of curvature of the refracting surface, this centre is known as the *nodal point* n. All rays of light which strike the refractive surface perpendicularly, such as O, m′, pass through the nodal point and are not refracted; all rays of light

parallel to the optic axis, such as c d, strike the refractive surface obliquely and are refracted, and the point where they meet is called the *principal posterior focus*, F_2. On the optic axis, in front of the refractive surface, is situated a point F_1 known as the *principal anterior focus*, rays proceeding from this strike the surface obliquely, and are so

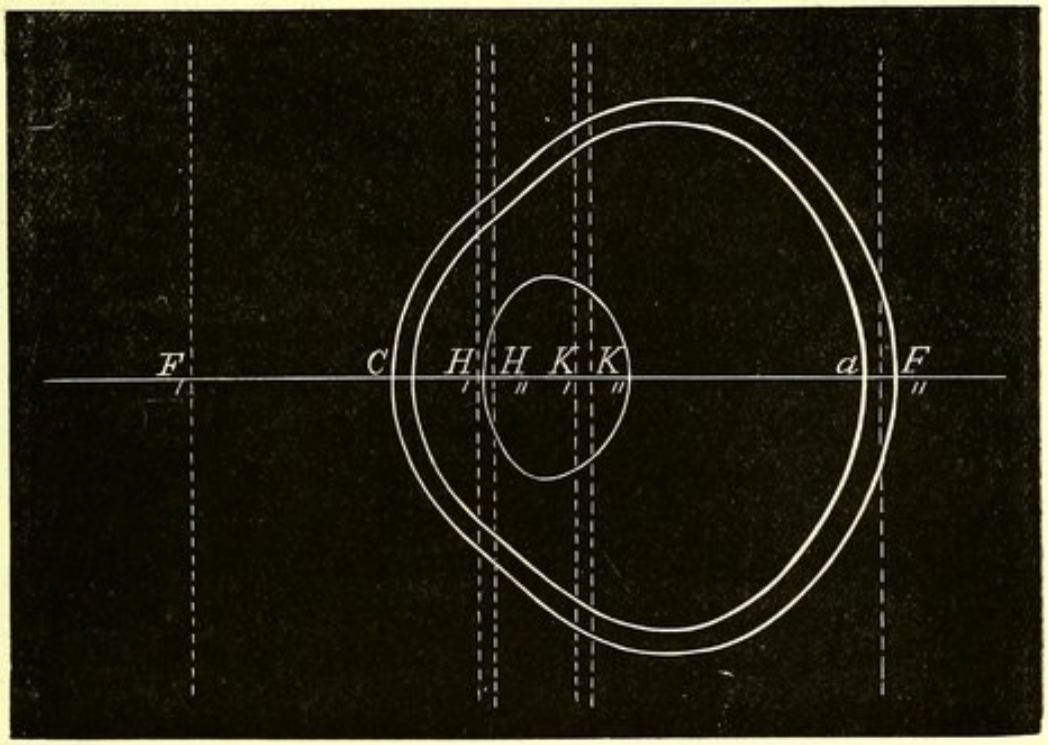


FIG. 72.—THE CARDINAL POINTS OF THE EYE OF THE HORSE (BERLIN).

F_I is the first principal focus, situate ·7244 inch in front of the cornea.
C is the anterior principal point.
H_I the first principal point, distant from the cornea ·3201 inch.
H_{II} the second principal point ,, ,, ,, ·3641 ,,
K_I the first nodal point ,, ,, ,, ·6693 ,,
K_{II} the second nodal point ,, ,, ,, ·7157 ,,
K_{II} to *a* is the distance of the retina from the second nodal point ·8000 inch.
C to F_{II} is the distance from the cornea to the second principal focus (which Berlin shows to be behind the retina) 1·7594 inches.

refracted as to be rendered parallel (e f) to the optic axis (O A). To these must be added the *principal point* p, that is the point where the refracting surface cuts the optic axis.

These various points are known as the *cardinal points* of the simple optical system we have imagined. For a more complex system like the eye, even when simplified, there

are two nodal points, two principal foci, and two principal points; but with the reduced eye where we have but one surface and two media, the two nodal points become one, and the two principal points one.

Dioptrics.—In order to be able to calculate the position of the cardinal points of the eye certain data must be known, such as the refractive index of the media, the radius of curvature of each refracting surface, the distance from the cornea to the lens, and the thickness of the latter. A very

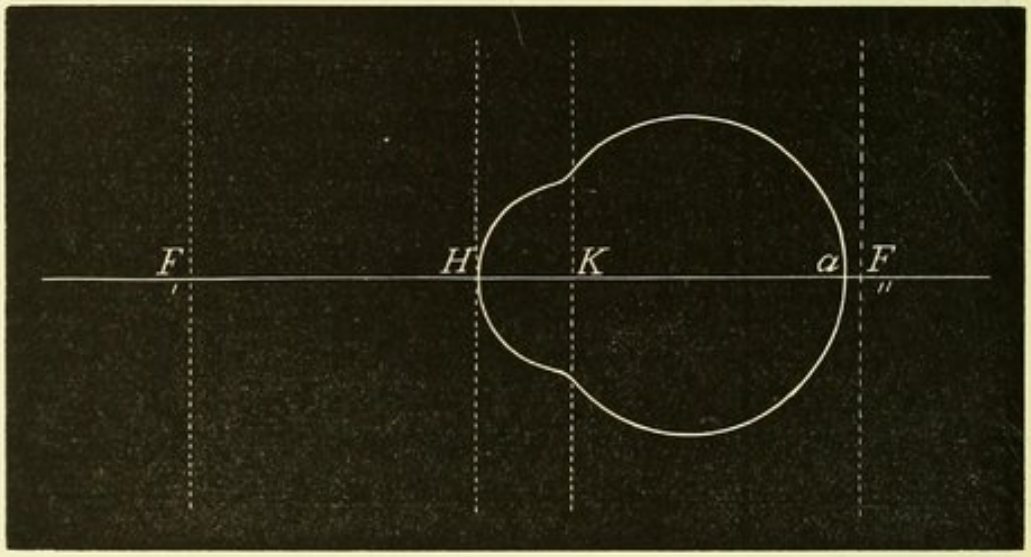


Fig. 73.—The Cardinal Points of the Reduced Eye of the Horse. (Berlin.)

slight error in the determination of these may produce a considerable error in calculation, so that all measurements made by us on the frozen eyes of horses are rejected as wanting in accuracy, but as an illustration of the measurements of the actual and reduced eye, those furnished by Berlin* are here given, though even these are not free from error.

According to Berlin the horse is normally long-sighted, the retina being in front of the second principal focus. What may have been true for the eye he examined is not universally true, for as we have previously stated the majority of horses are slightly short-sighted, therefore the point $F_{''}$ will fall in front of the retina.

* *Zeitschrift für Vergleichende Augenheilkunde*, Heft 1, 1882.

The simplified or reduced eye (Fig. 73) consisting of one surface and two media, gives for the horse, according to Berlin, the following values:

$F_{'}$ the first principal focus is situated 1·063 inches in front of the cornea.
$F_{''}$ the second principal focus is situated 1·427 inches behind the cornea; (in the diagram it falls outside the eye, but this is not normal, see above remarks).
K to *a* is the distance from the nodal point to the retina 1·004 inches.
H to *a* the distance from cornea to retina 1·3683 inches.

Passage of Light through Lenses.—In nature all rays of light are diverging, but so slight is the divergence of the rays from distant objects, that for the purposes of the eye they are practically regarded as parallel. All rays, then, proceeding from an object situated in front of the eye

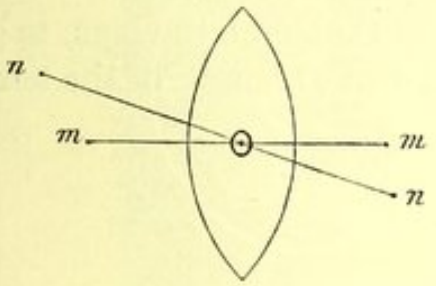


Fig. 74.

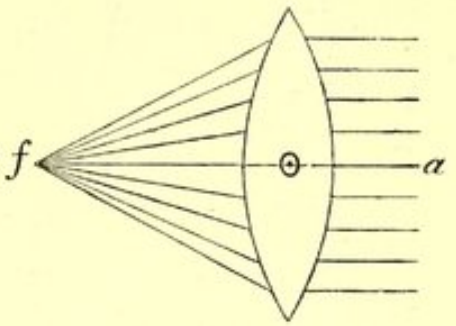


Fig. 75.

Figures illustrating the Action of Lenses upon Rays of Light passing through them. (Landois and Stirling.)

Fig. 74.—Biconvex lens; O, optical centre; *m*, *m*, chief or principal axis; *n*, *n*, secondary axis.

from 20 feet to infinity, are considered as *parallel rays*, all rays within this distance to the cornea are *diverging rays*. Obviously the nearer the object to the cornea the greater the divergence, so that there is more divergence in the rays proceeding from a body 1 foot from the eye than in one 10 feet from the eye; conversely, the further the object is from the eye the less divergent the rays, until we reach that point (20 feet) where the rays may be regarded as parallel.

A convex lens has two curved surfaces, and a line drawn through the centre of these two surfaces is known as the **principal axis** of the lens (Fig. 74, *m m*). The essential

idea of a double convex lens, is that it is thicker at the centre than at the edges.

Situated on the principal axis of a biconvex lens at a point in its interior is the **optical centre** (Fig. 74, O); any straight line passing through the optical centre is termed a **secondary axis** (Fig. 74, *n n*).

When *parallel* rays of light (Fig. 75, *a*) pass through a convex lens they are refracted and brought to a point *f* on the opposite side of the lens known as the principal focus; the only rays not refracted are those passing through the centre of the lens, viz., those coinciding with the principal or secondary axes. The converse of this is also true, viz., *divergent* rays proceeding from the principal focus of a lens *f*, pass through and are rendered parallel (Fig. 75).

The distance from O, the optical centre of the lens, to *f*, its principal focus, is known as the focal length of the lens.

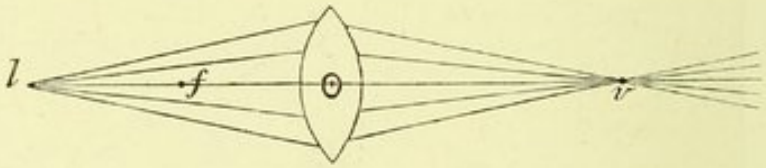


FIG. 76.—Rays of light passing through a convex lens from *l*, at a point beyond the focus *f*, cross at some point *v*, and invert the image (Landois and Stirling).

If the divergent rays instead of proceeding from the focus of the lens (Fig. 76, *f*) proceed from a point *beyond the focus l*, then the rays on passing through the lens are not rendered parallel but *convergent*, (as the refractive power is more than sufficient to render them parallel), and they come to a focus again on the other side of the lens at the point *v*. The distance from the lens at which they come to a focus depends upon the distance of the luminous point from the lens on the opposite side; thus the nearer the luminous point *l* to the principal focus *f*, the further will the focus on the opposite side recede, and *vice versâ*. The two foci *l* and *v* are termed *conjugate foci* and as we have shown they have a definite relationship.

If the rays of light proceed from a point L (Fig. 77), which is nearer to the lens than the principal focus F, the lens

is unable to refract the rays sufficiently and they issue from the opposite side divergent (Fig. 77, *d d*).

Parallel rays of light passing through a concave lens, instead of being refracted to a focus are refracted away from a focus, viz., caused to become divergent, so that a concave lens has no real focus; but if the divergent rays be produced backwards on the principal axis of the lens, the point where they meet is called the *negative focus* of the lens.

A knowledge of these laws is essential if we are to understand how an image is formed on the retina, and why the eye should have to focus itself for near objects.

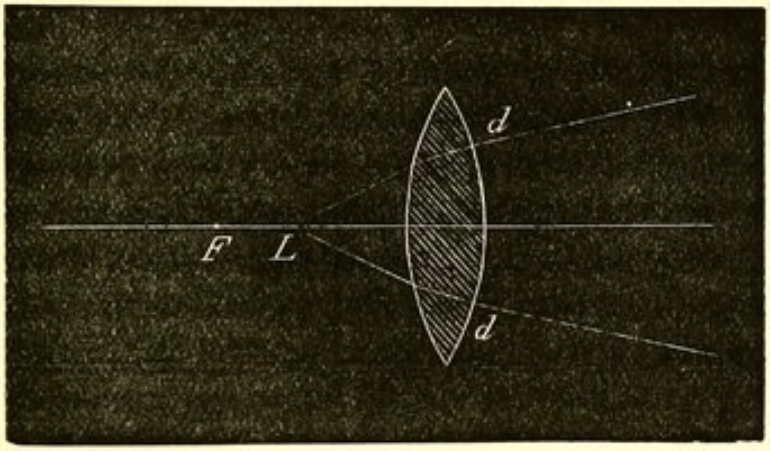


Fig. 77.—Rays of light passing through a convex lens from a point L within the focus F, diverge.

Formation of a Retinal Image.—Rays of light falling on the eye, as from the arrow X O Y (Fig. 78), issue as a pencil of rays from every point of the arrow, the pencil containing a central core known as the principal ray. All principal rays *a a'* pass through the nodal point *n* without undergoing refraction, whilst the rays *b c*, and *b' c'* are refracted to a greater or less extent, so that in this way the retinal image becomes inverted, and very much smaller than the object it represents; it is a miniature though perfect representation of the object presented to the eye.

The chief refraction undergone by these rays is in the cornea, doubtless the other media also refract, the lens for example, but an eye can have very good distant vision without a lens.

Though the retinal picture is so completely inverted that the right hand of the object becomes the left of the image, and the top becomes the bottom, yet the mind does not perceive the image inverted, but mentally refers the picture not to the retina but to the object.

Turning once more to Fig. 78 we observe that the angle X n Y is equal to the angle Y n X. The angle X n Y is spoken of as the **Visual Angle**, and all objects having the same visual angle form the same sized picture on the retina.

By the aid of the visual angle the size of an image on the retina may be calculated, provided we know the distance of the nodal point from the retina; thus at the distance of a mile, a man six feet high is represented on the retina of the

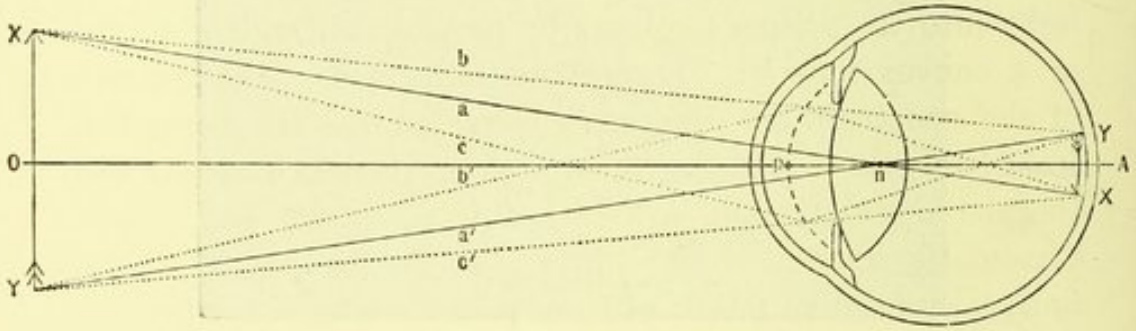


FIG. 78.—DIAGRAM OF THE FORMATION OF A RETINAL IMAGE (FOSTER).

a, principal ray of the pencil of light proceeding from X; a′, principal ray of the pencil of light proceeding from Y; the principal rays pass through the nodal point *n* without being refracted; the other rays b, c and b′, c′ are refracted. In this way the arrow X Y forms a smaller inverted image of an arrow on the retina Y X.

horse by an image $\frac{1}{880}$ of an inch in height, in the human eye at the same distance the picture of the man would be $\frac{1}{1300}$ of an inch, or about the size of a red blood corpuscle. The nearer the object the larger the image; taking the six foot man again at a distance of 10 yards, his height on the retina of the horse would be $\frac{1}{3}$ of an inch, whilst on the retina of a man it would be rather over $\frac{1}{8}$ of an inch.

Spherical Aberration.—The rays of light passing through a convex lens are not all equally refracted, those passing through the circumference being more bent than those

passing near the centre; the result is that the rays do not all meet in the same point, those passing through the circumference of the lens coming to a focus earlier than those passing nearer the centre. This defect, known as 'spherical aberration,' is remedied in the eye by the introduction of a diaphragm or iris, which prevents some of the rays of light from passing through the circumference of the lens; spherical aberration is further prevented by the fact that the refractive index of the central part of the lens is greater than that of the circumference.

Spherical aberration produces indistinctness of vision by the production of circles of diffusion, caused by those rays which meet too early crossing each other and forming a circle.

Chromatic Aberration is due to the decomposition of white light into its primary colours by passing through a prism or a convex lens, viz., a spectrum is formed. The colours of the spectrum are differently refracted, the red being the least bent, the violet the most; when therefore we can see the red distinctly the eye is not focussed for the violet. Chromatic aberration is prevented in the eye by the unequal refractive power of the various media.

Smell.

The nasal chambers are divided by a septum, and each chamber contains the convoluted turbinated bones. It has been observed that acuteness of smell is often associated with large and extremely convoluted turbinated bones.

By the arrangement of these bones the nasal passage may be divided into two channels, one which lies next the floor of the chamber, which from its obvious communication leads directly to the respiratory passages, and another channel which lies above it and leads to structures situated very high in the face and nose, but with no outlet save

what is furnished it from below. But apart from this there are other reasons for dividing the nasal chamber into a lower part through which the air travels, and into an upper part which is devoted to the sense of smell; the one is known as the respiratory and the other the olfactory portion.

In the horse the nasal chambers are of extreme importance, inasmuch as it is the only animal we are called upon to deal with which is unable under ordinary circumstances to breathe through the mouth; the majority of animals can breathe through both nose and mouth, but owing to the extreme length of the soft palate in the horse this is under ordinary circumstances impossible. So far as respiration is concerned the question of the nostrils has been dealt with (p. 84), but the arrangement of that portion devoted to the sense of smell has yet to be touched upon.

From the olfactory tracts in the brain are formed the olfactory lobes, which in some animals possess a well-marked cavity, in others only a canal; in the cavity is contained some fluid which communicates with the cerebro-spinal, and notably in the horse with that contained in the lateral ventricles.

From the olfactory bulbs are given off nerve-fibres which penetrate the cribriform plate of the ethmoid, and ramify over the mucous membrane covering the superior portion of the septum, the superior turbinated bone, and the superior third of the superior and middle meatus. The mucous membrane of this olfactory region differs from that of the respiratory portion in being not only thicker but of a yellowish tint; it is in this membrane that the fibres of the olfactory nerve are distributed.

This nerve is non-medullated, and in the surface of the membrane where it terminates are to be found two or three different kinds of cell. One known as a *rod cell* is generally believed to be the terminal cells of the olfactory nerve, though this has also been attributed to a *cylinder cell* which is likewise found in the membrane; other observers consider that both cells are the terminal organs of the olfactory nerve. No definite statement can be made on this point, but perhaps

the balance of opinion is in favour of the rod cell being the chief agent whereby odours give rise to nervous impulses termed smell.

Before an odour can be perceived by the olfactory nerves it has to diffuse into the higher cavities of the nasal chambers, and become dissolved in the fluid which bathes these surfaces.

We have no idea of the nature of the particles which constitute an odour, but it is certain that before they can make any impression on the olfactory nerve endings, they must become dissolved in the fluid covering the nerve terminations, for a dry olfactory surface is insensible to smell; on the other hand one too moist is equally insensible, as we know in the case of nasal catarrh.

There are certain odours which excite the olfactory organs more readily than others, thus flesh, blood, or offal have a remarkably stimulating effect on the carnivora, whilst grass, grain, and vegetable products generally stimulate the herbivora. The odour of blood or flesh is evidently repulsive to the herbivora, and may even cause nervousness and fright; there are exceptions to this, for we have known a horse eat meat with evident pleasure.

Some of the herbivora have a remarkably keen scent, antelope and deer have the power of detecting the presence of man even a considerable distance away, and it is evident that in most animals the sense of smell plays a more important part in their daily lives than with ourselves.

It is through the sense of smell that the male is attracted to the female during the 'rutting' season, and not only can the odour of a female in this condition be detected at a considerable distance, but the smell is evidently most persistent.

The organ of Jacobson, which is well marked in herbivora, is said to have some connection with the sense of smell. Cuvier regarded it as the means by which the herbivora distinguished between poisonous and non-poisonous plants; this can hardly be correct, for cattle-poisoning is comparatively common.

The odour of a body can be detected with greater accuracy by 'sniffing'; by this inspiratory act no time is lost in diffusion occurring between the respiratory and the olfactory region, as the odoriferous particles are forcibly drawn upwards.

The sense of smell rapidly becomes blunted, at any rate in ourselves; any offensive odour is always most marked when first detected.

By the sense of smell animals have the power of recognising their own offspring; a cow which has lost her calf will yield milk for weeks to a 'dummy' clothed in the skin of the dead calf, and she can recognise the difference between her 'dummy' and that belonging to another cow.

It is possible that everything and everybody has a peculiar odour, at least it would appear to be so from the remarkable manner a dog will follow a scent, or recognise its own master in the dark from amongst a crowd of other persons.

By the sense of smell animals have the power of distinguishing eatable from noxious, though it is probable that the sense of taste here takes an important share in the process. A substance need not necessarily be noxious to be rejected, a horse will starve itself rather than accept an alteration in its diet which introduces something new; conversely, noxious material may be partaken of freely, as in the common cases of yew poisoning in cattle.

Both the respiratory and olfactory portion of the nasal chambers are supplied with sensation by the fifth pair of nerves.

Taste.

The sense of taste is nearly though not quite dependent upon the sense of smell. There are certain substances which cannot be distinguished when the nose is closed, there are others which can be readily distinguished by the tongue alone.

This has led to a classification of taste sensations of which four qualities exist, viz., sweet, bitter, acid, and salt. Animals are certainly capable of distinguishing all these sensations.

On the tongue are found certain papillæ which are intimately connected with the sense of taste, viz., the filiform, fungiform, and circumvallate; the latter are probably the most important in connection with the sense of taste, but the others are most numerous.

In both circumvallate and fungiform papillæ, but especially the former, are found structures known as **taste buds**, bulbs, or taste goblets. They are balloon or barrel-shaped bodies, the walls of which are formed of elongated cells resembling the staves of a barrel; this structure is open top and bottom; the nerve fibrils enter below, whilst above is formed the gustatory pore, or opening into the interior of the body by which fluid finds its way in. Within the goblet or barrel are other cells, processes from which may be projecting at the pore. It appears to be essential to taste that fluid should readily find its way into the pore, and as a provision to ensure this the papillæ containing the buds are situated close to glands.

M'Kendrick states that in a single circumvallate papilla of the ox 1,760 taste-goblets have been counted, in the papilla foliata of the sheep and pig 9,500, and in that of the ox as many as 30,000 goblet-cells.

The nerve supplying these taste-buds is the glossopharyngeal, which is essentially the nerve of taste, and mainly distributed to the posterior part of the tongue; if this nerve be divided the taste-bulbs degenerate.

The glossopharyngeal nerve consists of a medullated and non-medullated portion; the former terminates in the tongue in end bulbs, whilst the latter proceeds to the taste goblets.

The goblet cells are not strictly limited to the tongue, but have been found in the palate, and close to the epiglottis; they have not been found on the anterior two-thirds of the tongue, a region which we know to be also

possessed of the sense of taste, and one not supplied by the glossopharyngeal nerve. This area of the tongue is supplied by the gustatory branch of the fifth, and it is to this nerve (which probably receives its taste fibres from the chorda tympani of the seventh) that the sensation of taste is here imparted.

Sensation to the tongue is supplied by the lingual branch of the fifth pair, whilst motor power is furnished by the hypoglossal or twelfth pair.

It is necessary for the purpose of taste that the substance should be dissolved; this is one of the functions of saliva, and experiments on herbivora show that taste produces an abundant secretion from the submaxillary and sublingual glands, though not from the parotid.

It is probable that each distinct taste affects a particular part of the tongue; in man it has been shown that the back part of the tongue is sensitive to bitter tastes, the tip to sweet and saline tastes, the sides to acid tastes, while the middle portion of the tongue is insensitive to any taste. The *flavour* of a substance is not obtained by the sense of taste alone, but by the union of the senses of smell and taste.

Touch, Temperature, and Painful Sensations.

The skin is capable of distinguishing these three sensations, for which purpose it is provided with special sets of nerve fibres. The touch fibres are distinct from the temperature fibres, the heat are distinct from the cold, and the fibres of general sensation, with which are included those of painful sensations, are distinct from the others.

There are good reasons for believing that the nature of painful sensations is quite different from those of touch and temperature, the latter being comparable with the special sensations of vision and hearing; but the whole

question is one of considerable complexity, and it is not intended here to institute any inquiry into the subject.

Tactile sensations play a very important part in the lives of animals. In the lips and muzzle, which correspond to the fingers of the biped, are located the touch organs proper; the parts are endowed with exquisite sensibility, and enable the animal to be kept acquainted with the nature of its surroundings and the character of its food. The long feelers or hairs growing from the muzzle and face of the horse are in connection with nerves in the skin, and are valuable for tactile purposes.

The tactile sensibility of the foot, by informing the animal of the character of the ground it is travelling over, is useful though not absolutely essential in locomotion; nor is the tactile sensibility in the foot of the horse absolutely essential to its safety in progression, as is clearly proved by the results of plantar neurectomy.

Temperature sensations doubtless do exist in animals, but nothing is known of them. It is curious to observe in the human subject that the skin contains 'hot spots' and 'cold spots,' viz., areas which are sensible to heat and not to cold, and *vice versâ*.

Painful sensations are of various characters, hence such terms as stabbing, boring, burning, throbbing, etc., to express the impression imparted. It is presumed that amongst the lower animals these different qualities of pain exist; it is quite certain, for instance, that the pain exhibited by a horse during an attack of colic, is very different from that shown when pus is forming in the foot.

Pain is transmitted by those nerves which convey common sensibility; it can only be regarded as being due to a stimulus which is stronger than that required for common sensation.

Pain may be conveyed by channels which under ordinary conditions convey no sensation, especially is this the case in disease. The normal heart, liver, muscles, bones, etc., may be handled, pinched, wounded, and cauterized, without exhibiting much or any sensation, but under the condition

of inflammation they become acutely sensitive, and the same applies to such viscera as the intestines, kidneys, bladder, etc.

Of the nature of pain nothing whatever is known.

Muscle Sense.

This is the sense by which we are aware of the movements and position of the body, and the amount and character of resistance which it experiences in its transport.

Centripetal impulses passing to the central nervous system keep it acquainted with the muscle sense; the afferent channels which have been suggested as taking part in this may be located in the muscles, tendons, the movements of the skin which occur over joints, in the joints themselves, and in the foot.

As to the relative share taken by these afferent channels, that of the muscles, tendons, and joints, would appear to be the most important: the skin plays the least important part, that is if we are to judge from the movements exhibited by animals which have had the skin removed.

The influence of the foot, say that of the horse, in supplying muscle sense is less than one would expect judging from the results of neurectomy. Whether it supplies it or no, it is certain after division of the afferent nerves of the foot, that the loss is soon compensated for in some other way.

Though we have spoken of these centripetal impulses as if their existence had been proved, yet it is essential to bear in mind that other views are held, notably that muscle sense originates in the centre and not in the periphery, and that it is furnished by changes in the motor areas of the cerebrum.

Thirst.

Thirst is referred to the palate; observations show that moistening the palate allays thirst, while on the other hand, the filling of the stomach with water through a fistula does not immediately allay the anxiety for fluid.

The loss of water caused by sweating, purging etc., is made good to the blood by taking up water from the tissues, in this way the drain on the lymph may be considerable. It has been supposed that the sensation of thirst referred to the palate may be brought about by a deficiency of water or lymph in the part.

Hunger.

Hunger is referred to the stomach. The close approximation of the stomach walls is not necessary for the production in all animals of the sensations of hunger, for some of the herbivora may be very hungry even when the stomach contains a moderate amount of food, the horse and rabbit for example; further, the sensations of hunger may be removed though the walls of the stomach remain in opposition, viz., by the introduction of nutritive enemata.

The reason why the sensations of hunger are referred to the stomach wall is unknown.

Hearing.

The Nature of Sound.—The vibrations produced by an elastic membrane, or other vibrating body, are communicated to the air, and cause this to be thrown into waves which travel at a definite rate in a longitudinal direction and thus produce sound. The pitch and loudness of this sound are governed by the character of the air-wave produced; thus, the higher the wave the louder the sound, whilst the longer the wave the higher the pitch of the note.

Sounds are simple or compound; a simple sound consists of a single pitch as in the vibrations of a tuning-fork, a compound sound consists of the fundamental tone, and in addition certain other sounds termed harmonics or partial tones, which closely follow on the fundamental tone in a series of waves. The quality of a sound depends upon these partial tones, where they are absent the tone is thin, where they are present they give richness.

From observations on the human subject it has been ascertained that the smallest number of vibrations audible are thirty per second, whilst the average human ear can recognise up to 30,000 vibrations per second. It is undoubted that some animals can recognise a smaller number of vibrations than thirty per second. Galton shows that the cat is capable of recognising sounds inaudible to the human subject.

External Ear.—The vibrations of sound are collected by a freely moving funnel-shaped body or external ear; it is composed mainly of cartilage, which is curved and hollowed out in such a way as to form a good collector, while several muscles enable it to assume considerable change in direction. The two chief directions taken by the ears are backwards and forwards; judging from the behaviour of many horses in carrying one ear backwards and the other forwards, it would appear that they are capable of hearing and appreciating sound in two opposite directions at one and the same time; we say appreciating, inasmuch as something more than mere hearing is required for auditory judgment.

The funnel formed by the external ear leads somewhat indirectly to a canal known as the external auditory meatus; in and around this is found an unctuous secretion, and above it in the funnel of the ear are many hairs which evidently have a protective effect.

The movements of the ears give evidence of what is passing through the mind of an animal. The ears of the horse are turned well to the front and closely pricked, viz., the points approximated, when he is attentive, whether the

attention be devoted to a something he is alarmed at or pleased with. The ears are laid back in sourness of temper and in vice; they are moved rapidly to and fro when a horse is anxious either from impending danger or other cause; one ear carried forward and the other backward is considered by some the sign of a good stayer and willing worker, whilst the ears drooping are indicative of muscle fatigue or debility.

Why the ears should be laid back in temper is difficult of explanation, the same thing exists in the cat.

At one end of the external auditory canal is a piece of membrane stretched completely across it known as the tympanum, it separates the external from the middle ear.

The **Middle Ear** is on the opposite side of the tympanum from the external ear; it consists of a cavity containing a chain of very small bones, known as the malleus, incus and stapes, which stretch across the space from the tympanum to the third or internal ear. The middle, like the external ear, is in communication with the external air, but by means of a passage known as the Eustachian canal which opens into the pharynx.

The tympanum has, therefore, air on both sides of it, the object of which is to ensure that the atmospheric pressure on either side is equal, and by this means undue depression is prevented. The air finds its way into the Eustachian tube during the act of swallowing, and at the same time air is conveyed in the horse to the guttural pouches.

The **Tympanum** is concave towards the external ear; in the middle ear the handle of the malleus is fixed to the central bulging part of it, and as this bone articulates with the incus, and the latter with the stapes, any alteration in the shape of the drumhead, such as is produced by the vibrations of sound, causes the bridge of bones to move; further, their movement is assisted by some small muscles which are attached to them.

The **Internal Ear**, known as the labyrinth, is composed of the semicircular canals, the vestibule, and the cochlea;

these are contained in a solid piece of bone in which exist two small foramen or windows, one known as the fenestra ovale, the other the fenestra rotundum; the base of the stapes or third bone of the ear rests over the fenestra ovale.

All three parts of the labyrinth communicate, but it is quite certain that all three do not take an equally active part in hearing. The evidence on this point is quite clear so far as the semicircular canals are concerned, and some have even included the vestibule, regarding the cochlea as the essential organ of hearing.

The whole of the internal ear is lined by a membrane containing a fluid known as the peri-lymph, this peri-lymph has free access to all parts of the inner ear. Within this membrane is a membranous labyrinth, the counterpart of the semicircular canals and vestibule, and this also contains fluid known as endo-lymph.

The membranous labyrinth is composed of two pouches, the saccule and utricle; with the latter the membranous semicircular canals are connected, while the former communicates with the middle canal of the cochlea.

On both utricle and saccule is an area known as the macula acustica, on this branches of the auditory nerve are distributed to some cells known as hair cells; similar areas exist on the semicircular canals.

Leaving the membranous and returning to the bony labyrinth, we must glance at the two windows existing in it which have been previously mentioned. The foot of the stapes lies over the fenestra ovale, and between the stapes and the peri-lymph is the membrane which lines the internal ear. Every movement of the tympanum causes the bony bridge to oscillate, and every oscillation of this thrusts the stapes against the membranous window, and so sets up oscillations in the peri-lymph which are transmitted throughout the internal ear.

The cochlea resembles in appearance the shell of a snail, its interior consists of three spiral channels which wind their way from base to apex like a circular staircase. The number of twists in the cochlea is two and a half, the axis

around which these wind is composed of soft bone, having canals up which the auditory nerve travels.

If a spiral of the cochlea be cut across (Fig. 79) the three canals it contains are seen, these are divided by septa; one septum, known as the *lamina spiralis*, separates the upper canal or *scala vestibuli*, from the lower one or *scala tympani;* the third, or middle canal, is of a triangular shape and called the *cochlear canal*, it contains the essential organs of hearing, and it lies between and to the outside of the other two. The roof of the cochlear canal is formed by a piece of tissue known as the *membrane of Reissner*, whilst its floor, on which is situated the essential organs of hearing, is formed by the *membrana basilaris*, which connects the outer wall of the cochlea to the lamina spiralis. The cochlear canal is the continuation of the membranous labyrinth.

The upper passage of the cochlea, viz., the scala vestibuli, is continuous with the lymphatic peri-lymph space of the vestibule, whilst the scala tympani, or lower passage, ends at the base of the cochlea in a blind extremity in which is a membranous window, the fenestra rotundum, which separates the scala tympani from the cavity of the tympanum. The cochlear canal terminates suddenly at the summit of the cochlea, and at this point the two scalæ, which in their windings have been decreasing in size from base to apex, meet and communicate, and the fluid of the one mixes with that of the other.

It would be outside the scope of this work to give anything like a full account of the important cochlear canal, all we can do is to glance at its arrangement in order to better understand its function. Its position, shape, and boundaries have already been touched on, and we have mentioned that on its floor, or basilar membrane, is arranged the essential organ of hearing known as the Organ of Corti.

Organ of Corti.—This consists of a triangular-shaped tunnel (Fig. 79), the base of which rests on the basilar membrane; the tunnel is composed of certain rods arranged

side by side, inclined from both sides towards each other and meeting superiorly like an inverted V. At this point the rods, known as the rods of Corti, fit into each other in a peculiar manner. Flanking either side of the tunnel are certain cells of two distinct kinds; those nearest to the tunnel are somewhat flask-shaped and having hairs growing from their summit are spoken of as *hair cells*, outside these are tall conical cells known as *Hensen's cells*.

It will be remembered that the auditory nerve ascends the axis of the cochlea, in its passage it gives off fibres which ramify over the lamina spiralis, at the outer edge of which the above-described organ of Corti exists; having reached this the fibres lose their medulla, and the naked axis cylinders pass into the cells flanking the triangular tunnel, some fibres cross the tunnel to reach the cells on the opposite side (Fig. 79). How the nerve terminates in the hair cells—for it is to these that it is distributed—is unknown, but that the hair cells are the organs of hearing is undoubted; Hensen's cells are probably only of a nutritive nature and unconnected with auditory impulses.

This description of the organ of Corti is as it presents itself in transverse section; if, however, we look at the tunnel from above where the rods from either side meet, it is observed that in their union the rods of the outer wall of the tunnel fit into the heads of the rods of the inner wall, and the squareness of their heads is such that the arrangement is very like the keyboard of a piano.

Auditory Sensations.—Any analysis of these is hardly necessary in a work dealing with the lower animals, we have no direct evidence that they understand or appreciate the difference between music and noise; a dog will howl at one as readily as another. At the same time it is certain that animals can learn to recognise sounds and associate them with certain ideas, as for instance the commotion and excitement amongst the horses of a regiment when the trumpet sounds 'feed,' and again the recognition by a dog of its master's voice. Further, we have undoubted evidence that sounds which are so feeble as to unaffect the human

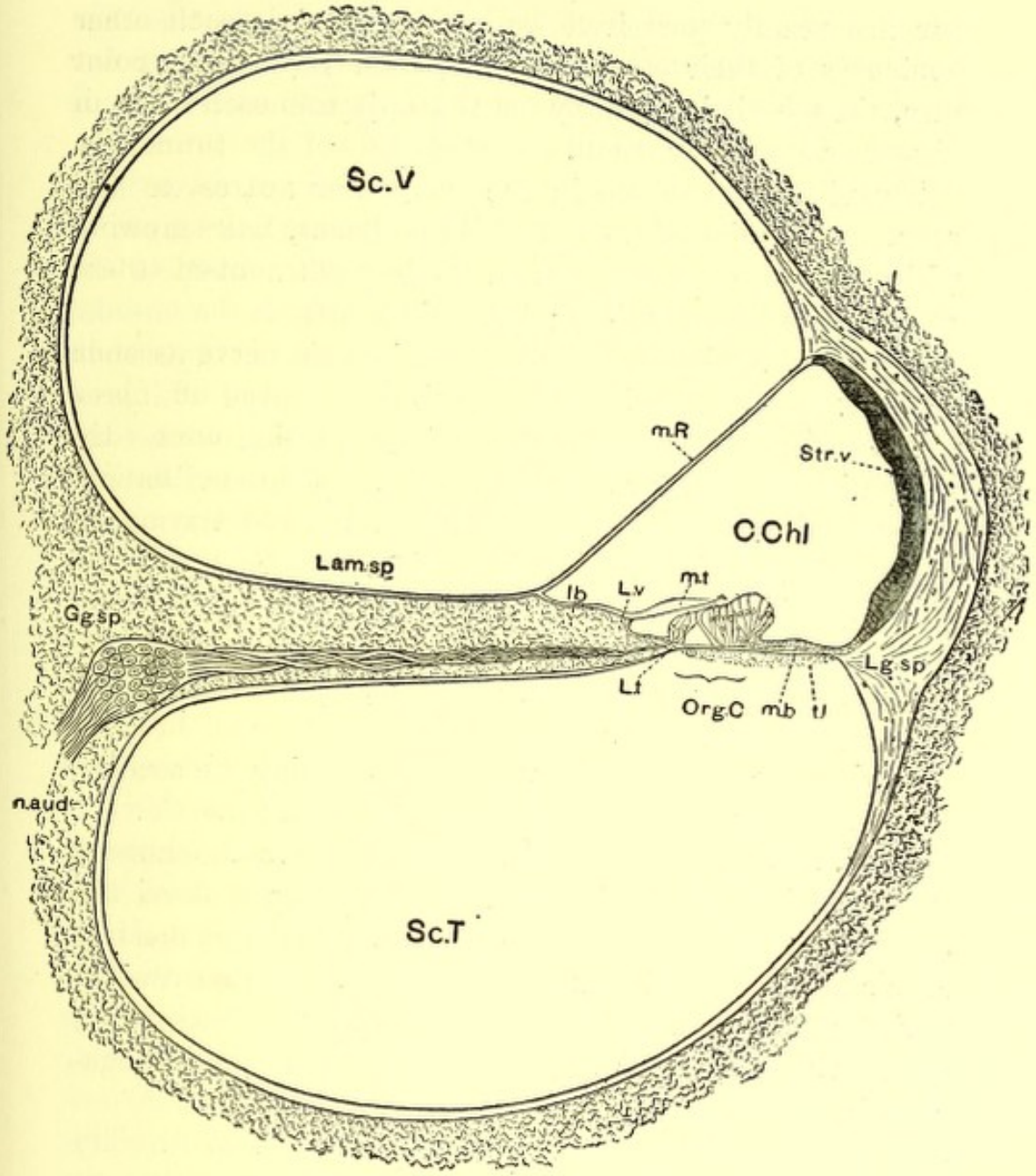


FIG. 79.—DIAGRAM OF A TRANSVERSE SECTION OF A WHORL OF THE COCHLEA (FOSTER).

Sc.V, scala vestibuli; Sc.T, scala tympani; C.Chl, canalis cochlearis; n.aud, auditory nerve; Gg.sp, spiral ganglion; Lam.sp, lamina spiralis; lb, limbus; m.t, tectorial membrane; Org.C, organ of Corti resting on mb, the basilar membrane; m.R, Reissner's membrane. In the organ of Corti can be seen the ∧ tunnel, formed of inner and outer rods, and flanked on either side by hair cells, into those on the left the auditory nerve may be seen running.

ear are readily perceived by some animals, so that the acuteness of their sensations is greater than that of our own, though their capacity for the enjoyment of music is absent or extremely small.

The vibrations set up in the tympanum are, as we have seen, communicated to the chain of bones, the stapes of which through the fenestra ovale imparts a push to the perilymph of the labyrinth; this fluid transmits the impulse through the vestibule, and from here into the scala vestibuli of the cochlea. The vibrations ascend the spiral staircase, set in motion the membrane of Reissner, which causes the lymph in the cochlear canal to vibrate, and these vibrations through the basilar membrane reach the scala tympani. The lymph in this is now set in motion, with the result that at its blind extremity the membrane of the canal is pushed outwards at the fenestra rotundum. Every push inwards at the fenestra ovale causes, therefore, a push outwards at the fenestra rotundum.

During the time the vibrations are crossing the cochlear canal from one scala to another the organ of Corti is affected, and by means of the auditory nerve the impulse is conveyed to the brain. It is in this organ of Corti with its nerve endings, that the complex sounds which make up even a single note of music are analysed, and this analysis was at one time supposed to be effected by the rods of the organ, which were believed to vibrate to their own particular tone, in the same way as a tuning fork will pick out its own tone from sounds in its vicinity and vibrate to it. This view, tempting as it is, is negatived by the fact that the rods of Corti do not exist in birds, and it has therefore been supposed that the vibrations to the nerves terminating in the organ are set up by the vibration of the basilar membrane on which the organ is built, but the question is far from settled.

Even the function of the vestibule is disputed, while some hold from analogy that it is connected with auditory sensations—through the nerves terminating in hair cells which are found on the areas previously described as the

macula acustica—others believe it is wholly devoted to the movements of the body, by which means the animal is informed of the extent and direction of its own movements.

It would appear at present to be best to regard both the cochlea and the macula acustica of the membranous labyrinth as the essential organs of hearing.

The semicircular canals, though they undoubtedly take some part in hearing, are particularly connected with maintaining the equilibrium of the body, and of keeping the mind acquainted with its position. This remarkable function is probably carried out by alterations in the position and pressure of the fluid contained within them, such as results from every movement of the head. Division of these canals causes the most remarkable irregularity in the movements, and a side-to-side or upward movement of the head.

Within the membranous labyrinth are found certain calcareous particles termed otoliths, which are supposed to act the part of ' dampers.'

Whatever part those remarkable sacs, the **guttural pouches** (confined solely to solipeds) are intended for, it is probable, from their anatomical connection, that they take some part in the sense of hearing, perhaps that of supplying the needful amount of air to the middle ear. The actual use of the guttural pouches is involved in obscurity, but we may provisionally consider them as part of the middle ear. In man acuteness of hearing is produced by listening with an open mouth; the fact that the horse cannot breathe through the mouth may explain the presence of these large air-sacs beneath the skull; in other words, they are probably associated with acuteness of hearing.

CHAPTER XVII.

THE LOCOMOTOR APPARATUS.*

The muscles are attached to bones, and these by their movements on each other form angles of varying size. These angles are opened and closed during progression, and the mechanical aid which is introduced to effect this is that of the lever.

The **Lever** is composed of a power, fulcrum, and weight, and according to the relative position which these occupy, is formed a lever of the first, second, or third order.

In a *lever of the first order* the power is at one end, the weight at the other, and the fulcrum between the two. The muscles which extend the head act as a lever of this order, the head being the weight, the occipito-atloid articulation the fulcrum, and the muscles of the neck the power. In extension of the hind-leg the gastrocnemii muscles are the power, the hock-joint the fulcrum, and the leg below the hock the weight.

A lever of the first order is principally a lever of extension, and exists all over the body; it is also a lever of power, for if the long-arm be 5 feet, and the short-arm 1 foot, a power of 1 lb. at the long-arm will support a weight of 5 lbs. on the short-arm. It is to be noted that as a lever increases in power it loses in speed.

* The importance of this subject, in the correct appreciation of the causes leading to lameness, has necessitated this chapter being slightly enlarged with material from an article on 'Joint Diseases,' published by the author in the *Journal of Comparative Pathology and Therapeutics*, 1893-1894.

In the *second lever*, which is a rare one in the body, the weight is placed between the fulcrum and the power as in a wheelbarrow, the wheel being the fulcrum.

When the leg is fixed on the ground and the body passing over it a lever of the second order is formed, the ground being the fulcrum, the triceps or gastrocnemii the power, and the body through the elbow or hock-joints the weight.

The *third order of lever* is the lever of flexion; the power is placed between the fulcrum and weight; the nearer the power is to the fulcrum, the greater the flexion obtained with the least amount of muscular force. This lever is one of speed, and what it gains in speed it loses in power; it is therefore a wasteful lever, but an essential one in the limbs. Examples of it in the body are numerous; in the flexion of the elbow joint, the weight is the leg below the elbow, the power is the flexor brachii muscle at its insertion into the radius, whilst the elbow-joint forms the fulcrum. In the flexion of the hock the power is the flexor metatarsi, the fulcrum is the hock-joint, the weight being represented by the limb below the hock.

The reason why the third lever is more frequent than the others, is due to the fact that the chief movements of the limbs are directed to moving comparatively light weights through a great distance, or through a certain distance with great precision, rather than moving heavy weights through a short distance (Foster). In connection with this we may say that the weight of the fore-leg of a cavalry horse cut off at the elbow was found to be 17 lbs. 8 ozs.; cut off at the knee, through the upper row of bones, it was found to weigh 7 lbs. 10 ozs.; one fore-foot with corona weighed 2 lbs. 3 ozs., and the hind-leg, cut of at the hock-joint, weighed 10 lbs. 9 ozs.

Stillman* points out that the terms flexor, extensor, adductor, and abductor, cause the chief function in muscles to be lost sight of, viz., the power of propelling; it is necessary, however, to remember that propelling is not a power apart from flexion and extension, but the result of them.

* 'The Horse in Motion.'

Co-operative Antagonism.—As a rule, to which there are certain exceptions, the contraction of any group of muscles is attended by a contraction and not a relaxation of their antagonists. This is described by Waller* as 'Co-operative Antagonism.' The amount of contraction thus exhibited by antagonistic muscles is insufficient to neutralize the effect of the direct motors, but it would appear that for the due performance of such movements as flexion, extension, etc., the antagonistic group of muscles should offer some slight opposition. This can readily be demonstrated by flexing the fingers and grasping the arm with the opposite hand; both extensor and flexor muscles will be felt to harden. Moreover the opposition of antagonistic muscles appears in many cases to be essential to the due performance of movement; Waller quotes as an example of this the fact that in lead palsy only the extensor muscles of the arm are affected, yet the flexors are powerless to act.

Though antagonistic muscles contract yet they gradually yield to their opponents, and eventually undergo an elongation.

The difference existing between the articulation of the fore and hind limbs with the body, has until recent years been the cause of considerable error being promulgated. It was previously supposed that the muscular attachment of the fore-leg to the trunk indicated that the body was simply slung between the fore-legs, the latter acting as props whilst the hind-limbs did the work. Instantaneous photography has shown us that the fore-limbs not only act as props but as propellers of the body, especially is this seen in the gallop, where by measurement it has been shown that one fore-leg will propel the body a distance of 10 feet, and in so doing will raise it 4 inches in height in a vertical direction.†

By means of the fore-legs also, the horse is enabled in draught to assist its hind-legs in stopping weights.

Joints are formed wherever two bones come into contact. Dealing only with those joints in the limbs which are of

* *Op. cit.* † Stillman, *op. cit.*

the most practical interest, it is observed that ball-and-socket joints (as in the hip), hinge-like joints (as in the hock), and gliding joints (as in the knee), are found; all these are coated with articular cartilage and lubricated with synovia.

Synovia is a viscid, yellow, alkaline fluid containing proteids, mucin, and salts. The viscidity of synovia is due entirely to the mucin it contains, and this confers on synovia its slippery nature. There is no difference between the synovia of joints and that of bursæ.

It is said that the amount of synovia in a joint is greater in animals at rest than in those at work, but the extra bulk appears to be due to an increase in the watery material, whilst the proteids are decreased; the salts, on the other hand, especially those of sodium, exist in a larger proportion than in the synovia of working animals.

The bursæ in the limbs of the horse are very important structures; they are placed where the tendons pass through bony channels, and without them the rapid movements of the limbs would be impossible; that the strain on them from wear and tear is considerable we know from practical experience.

Hock Joint.—Solipeds appear to stand alone in having the ridges of the astragalus obliquely placed, instead of vertically as in other animals; the oblique ridges in the horse occasion some considerable difference in the action of the limb. It is usual to speak of a screw action of the hock produced by the oblique ridges of the astragalus, this screw action, we believe, is an entire misconception. The ridges on the astragalus do act as a screw but not on the hock; *the effect is on the stifle*, and produces that remarkable stifle action particularly well seen in trotters. If the ridges on the astragalus turned the hock outwards, every horse would travel as if it were 'cow-hocked.' The leg below the astragalus is carried directly forwards; when, however, it comes to the ground, and the body passes over it, it is not uncommon in some horses to observe a considerable twist *outwards* of the hock-joint, the toe being

turned in; this is due to the *ascent* of the tibia on the astragalus *turning in the stifle*, the result of the leg being extended.

The object of the stifle being turned outwards during the flexion of the leg is to clear the abdominal wall, and the reason why solipeds have oblique ridges on the astragalus and ruminants and carnivora vertical ones, is that the ribs of the latter class are short and do not come near the pelvis (as in the horse), and therefore the abdominal wall is not in the way.

A spring or automatic flexion action in the hock has been described, such as may readily be observed in the dead leg, when if the hock be flexed slightly it either flies back or completes its revolution with a jerk. This condition does not exist during life, nor after death until rigor mortis occurs; it is produced by the lateral ligaments of the hock-joint, and is purely a post-mortem condition.

The flexor metatarsi muscle is remarkable in having a tendon running its whole length, so that from the origin at the femur to the insertion at the front of the hock is a stout tendinous cord. A somewhat similar arrangement exists in connection with the gastrocnemii muscles. When the flexor metatarsi acts the hock is flexed, but the use of the tendon running from origin to insertion is not at first sight quite clear. Chauveau considers that it automatically flexes the hock, but tendons are devoid of any such power; it would appear that its function is to relieve the muscle when the animal is standing, or sleeps standing.

When muscles which perform flexion and extension are acting together with equal force no movement results; such is the case when the weight is on the limbs and the animal at rest. When a horse is at rest his gastrocnemii muscles and flexor metatarsi are acting in opposite directions and equally, the one is trying to close the femoro-tibial angle, the other is keeping it open. It is the function of the tendinous portion of the flexor metatarsi and gastrocnemii muscles to assist in keeping the leg fixed without any great muscular effort.

The chief movement of the hock occurs between the tibia and astragalus. Though the range of motion between these bones is considerable, yet it is not fully exercised in all paces; it is only in the jump and gallop that the angle formed between the tibia and metatarsal is closed to any great degree. When the joint is completely closed in the dead dissected limb, if we look at the posterior part, viz., the now uncovered ridges, we find that when the joint is flexed to the utmost the *tibia and astragalus are no longer in opposition*, the tibia has left the astragalus and a space exists between them. To prevent flexion to a dangerous degree two stops are placed on the anterior face of the inferior extremity of the tibia, one outside the other inside, the outside being the larger of the two; these stops come into contact with two rests on the astragalus, and in this way we think a certain amount of jar may be imparted to this bone. As the inside stop comes into contact with the astragalus slightly before the outside stop, we conceive it possible that the inside of the astragalus receives more concussion than the outside. Can this help to offer any explanation of the position of spavin?

Looking at the ridges on the astragalus, one is narrow the other broad; the narrow one is the inside ridge, and it runs completely down to the surface which articulates with the magnum, and sometimes considerably overlaps it.

The movement in the true hock-joint is very simple as well as extensive; but the movements between the small bones composing the joints are complicated. In the first instance they are very limited; the astragalus moves on the magnum, the magnum on the medium, and the medium on the large metatarsal; but the amount of movement in these is not the same, the astragalus and magnum movement being the greatest. One would consider that the movement in this part was rather of a front to rear, viz., to and fro character, though the ligamentous attachment between the bones being situated at the central part, would show that this was probably not the case. Pathology

proves the correctness of this latter supposition. An examination of the face of these bones when affected with articular disease exhibits well-marked, sharp, and rather deep grooves, which run *obliquely* across the surface of the bones, and are better seen between the astragalus and magnum than elsewhere. The grooves are the result of friction during the movement of the joint, and they tell us that the motion of these bones on one another is more of the nature of a rotation.

Again, these grooves tell us where the greatest amount of pressure normally comes on the bones; it will always be found that the greatest damage in disease is on the anterior and internal surface, and this rule holds good whether it be the astragalus, magnum, medium, or head of the large metatarsal which we are examining.

If we make a longitudinal section of the leg from the thigh to the fetlock, we observe that the line of weight on the bony column mainly falls through the anterior part of the hock-joint.

There can be no doubt that this pressure is removed by resting the leg, viz., flexing the hock, and this is probably the reason why no horse ever stands resting equally on both hind-legs.

The **Stifle** is the largest joint in the body; the cause of its rotation has been previously described. One function of this joint is that of rendering the limb firm and rigid when the foot is on the ground, and this it does by the contraction of the muscles inserted into the patella; if the latter bone be kept fixed on the upper part of the trochlea of the femur, no flexing of the hock or stifle can occur. This experiment can be readily tried on a horse just destroyed; the limb having been extended, the simple pressure of the hand on the crural muscles is sufficient to prevent the bending of the hock unless considerable force be employed. No bending of the hock can occur if the foot be kept extended; the first movement in the advance of the leg and the flexing of the hock and stifle, is that the foot is flexed.

In a certain surgical condition, commonly known as dislocation of the patella, the limb is rigid from the femur to the metatarsus; but, though the foot may be flexed, neither hock nor stifle responds, owing to the patella being fixed. We believe that in the majority of these cases the patella is not fixed from dislocation, but from some other cause.

The amount of movement in the stifle is considerable, and to admit of it being carried out with perfect freedom, the convex condyles of the femur play in cups formed of cartilage on the upper surface of the tibia.

The **Hip** is a cup and ball joint; the range of outward movement obtained by it in the horse is limited by the insertion of the ligamentum teres (and pubio-femoral ligament) into the inner side of the head of the femur, and not into its centre as in most other animals. This is said to be the reason why the horse rarely 'cow-kicks.' The lengthening of these ligaments accounts for 'cow-hocks' in horses.

The **Shoulder-joint** is remarkable for the considerable surface afforded by the humerus and the small surface of the scapula, the object being to obtain a large range of motion.

The **Elbow** presents an articulation with ridges which influence the turning outwards of the knee in progression; if the knees are turned out too much the leg below is thrown in as it is brought forward, and in this way one cause of 'brushing' and 'speedy cutting' is produced.

The **Knee** consists of three main joints and numerous minor ones; the upper joint possesses the largest range of motion, whilst the lower joint practically does not open. Probably such defects as 'speedy cutting' and its opposite condition, 'dishing,' are influenced not only by the elbow, but by the shape of the articular surfaces between the radius and upper row of bones.

The radius is peculiar in presenting on that articular surface next the knee a concave surface anteriorly and a convex one posteriorly; these form two condyles, of which the inner is more curved than the outer. The outer

condyle plays on the trapezium, cuneiform, and lunar; the inner condyle plays solely on the scaphoid. When the knee is flexed the influence of the condyles is seen, the concave articular surface of the radius is removed from the surface of the bones of the knee, and the convex articular surface appears as the joint grows wider; the inner condyle being larger than the outer depresses the scaphoid, so that a very important movement occurs between the scaphoid and lunar. This action of the radius on the scaphoid throws the foot slightly outwards, probably with the object of enabling it to clear the opposite limb. We believe that an examination of the knees of 'dishing' horses will show that extreme curvature of the inner condyle of the radius is the cause of the action, in the same way that turned-in elbows, and alterations in the curvatures of the radius and humerus, will probably account for horses throwing the foot inwards, and thus 'brushing' or 'speedy cutting.'

The **Fetlock Joint**, owing to the presence of the sesamoid bones, forms a yielding articulation. In a state of repose the greater part of the horse's weight is borne on the posterior half of the metacarpal articulation, and the articular surface of the sesamoids. One great advantage gained by the articulation of the fetlock being yielding, is to destroy the concussion of impact when the body comes to the ground; a similar condition will be observed in the joint of the foot, for which see the chapter devoted to that subject.

The **Function of the Suspensory Ligament** has been a fruitful source of discussion; its chief use, no doubt, is to support the fetlock, in no other way could a joint placed in this part of the limb, possessed of so much motion, and exposed to such concussion be supported. Though ligaments and tendons are held to be non-elastic, yet we must claim for the suspensory ligament a little more elasticity than would be obtained if the sesamoids were united by bony tissue to the metacarpal, and the pleasantness and freedom from jar experienced in the riding-horse are due to the suspensory ligaments.

Stillman claims for the suspensory a function which he believes to be demonstrated by instantaneous photography, viz., that it acts the part of a spring, flexing the fetlock sharply when the weight is taken off it, and explaining why the dirt is thrown out of the feet of a galloping horse.

We have no evidence of the correctness of this statement, the sharp picking up of the foot from the ground in walking, (a movement so rapid as almost to defy detection), must rest with the flexor muscles.

Besides these functions, the suspensory ligaments assist the horse to stand whilst sleeping.

If the suspensory ligament be divided, the fetlock sinks but does not come to the ground; if the perforans be divided a slight sinking of the fetlock is the only change. To bring the fetlock to the ground, both flexors and suspensory ligament must be divided, which demonstrates that all three support the weight while standing.

Function of the Check Ligaments.—Horses are enabled to sleep standing, and remain for some considerable time without lying down, by means of a singular arrangement of check ligaments which exists in both fore and hind limbs; we have previously touched on this question so far as the hind-limb is concerned. The flexor tendons of the fore-limb support the weight, the extensors keep the limb rigid. In order that the strain of supporting the weight may not be placed solely on the muscles of the arm, both flexor and extensor tendons receive branches of ligament from the radius and metacarpus. These are attached to the tendons in such a way as to cut off the muscles, at any rate to a considerable extent, from the strain of standing in one position for a length of time.

In the act of standing the rigidity of the bony column of the leg is maintained by the extensor tendons, each phalanx having an extensor attached to it, viz., the extensor metacarpi leading to the large metacarpal bone, extensor pedis to the corona and pedis, (receiving also a slip from the suspensory ligament), and extensor suffraginis to the suffraginis. This latter receives a strong slip of ligament from the out-

side of the carpus, which entirely takes off the strain from the muscle, and keeps the tendon taut during sleep.

Further, the horse is enabled to stand whilst sleeping by means of the fascia of the arm and thigh; both of these are attached to the muscles and tendons of the part, affording them considerable support of a non-muscular nature.

Centre of Gravity.—The centre of gravity at rest is fixed, but during motion it oscillates from front to rear, depending on the position of the body and the pace.

Owing to the fact that more weight is carried on the fore than on the hind legs, the centre of gravity lies nearer to the elbow than the stifle. If a vertical line be dropped just behind the ensiform cartilage of the sternum, and intersected by a horizontal one passing through the lower part of the middle third of the body, the point of intersection is the centre of gravity of the body at rest; this is the rule given by Colin. We may say, speaking roughly, that the vertical line passes about six inches behind the elbow, the horizontal just below the shoulder-joint; the centre of gravity is where these intersect. It is obvious that the position of the centre of gravity will vary with different horses, but not to such an extent as to seriously affect the truth of the above statement. During locomotion the centre of gravity moves to the front and rear of the normal at rest; it is in front of it when the fore-legs are coming to the ground, behind it when the hind-legs are coming to the ground; it is in front of it during draught, behind it during backing.

Distribution of the Weight of the Body.—The fore-legs carry more weight than the hind, which is perhaps the reverse of what might be expected; but if a horse be carefully weighed, it is found that the fore-legs take more than one-half the body weight. The position of the head (which weighs between 40 and 50 lbs.) considerably affects the weight on the legs. Thus, if the head be raised up when the fore-legs are weighed, the latter will be found to be carrying over 20 lbs. less weight than if the head were

dependent. The practical application of this fact is obvious —keep a stumbler well in hand.

When a man is on the horse's back, it is found that 66 per cent. of his weight is carried on the fore-legs, and 34 per cent. on the hind; the amount of weight on the fore-legs is increased by leaning forward in the saddle, and decreased by leaning back.

An explanation why fore-legs are worn out earlier than hind, is afforded us by what we now know of the physiology of locomotion, viz., the fore-legs act as propellers of the body, and owing to their being nearest to the centre of gravity, they bear the largest share of the weight of the body and the weight of the rider.

The Structure and Function of the Limbs in Relation to the Production of Lameness.—As high as the shank we may say that there is no practical difference in the anatomical arrangements of the fore and hind limbs, and yet we know how commonly the foot and coronet of the fore-leg are affected with lameness, and how rarely in comparison the hind one. In comparing the knee and hock great differences are observed; it is true that in both a number of pieces of bone enter into their formation, but here the likeness ends; the small bones of the knee have considerable movement, the small bones of the hock only a trifling amount. The lower row of knee bones, so far as movement is concerned, are the nearest approach to the movement of the small bones of the hock, yet the latter are frequently diseased, the former rarely affected. Evidently, then, the presence of small and comparatively immobile bones in the hock cannot constitute an explanation of the frequency of hock disease. Does the manner in which the joints are flexed, throw any light on the acknowledged fact that knee disease is rare and hock disease frequent? It will be observed that these two joints bend in opposite directions; the knee opens in the front when flexed, the hock opens at the back; we have given reasons for believing that some injury may be inflicted on the hock joint by its method of closing.

Continuing this comparison of the fore and hind leg, it

may be remarked that the stifle corresponds to the elbow, and the patella to the ulna; during flexion of these joints the elbow opens at the back whilst the stifle opens in front; in other words, though corresponding joints—the elbow and the stifle, the hock and the knee—yet they do not agree in the direction in which their movement is made.

The hip-joint corresponds to the shoulder-joint, and though in the hip all the movement is done by one bone instead of two, yet the to-and-fro movement is practically the same in each.

When the fore-leg comes to the ground, no matter what the pace may be, the limb must be straight in order that the foot may be placed down flat, or, as in the faster paces, heel first. This straightening of the knee renders the bony column of the leg rigid for the time being; the shock of impact is therefore greatest at that part of the column nearest to the point of impact, and decreases as it passes up the leg.

It would be anticipating our subject to attempt to deal with the various means which exist in the foot to render this shock as little destructive as possible; we can only allude to the weight being supported on the laminæ, to the presence of a foot articulation which is yielding posteriorly, the existence of an elastic movement of the posterior part of the foot, and the presence of an elastic and indiarubber-like cushion the foot pad.

There are, however, two distinct strains imposed on the same limb, viz., the shock or concussion when the foot comes to the ground, and the strain or compression occasioned when it is leaving the ground; one is the concussion of impact, the other the compression of propulsion.

The hind-leg differs from the fore-limb in its method for providing for the concussion of impact; here we find that the limb instead of being straight—as the fore-leg is from the elbow to the foot—is bent, and it is bent at the hock, at a point which we may take to be midway between the stifle and the ground. The shock of impact comes, therefore, largely on the hock.

The fore-leg in providing for propulsion rotates over the foot, the limb still being straight from the elbow to the ground, and the shock of rotation is mainly confined to the lower end of the bony column. In the hind-leg propulsion is obtained not only by the foot remaining fixed on the ground, but also at the same time by a straightening or unbending of the hock, which gradually opens until the tibia forms with the metatarsal bone the nearest straight line it is capable of making.

In this way we may say that the hock performs twice as much work as the knee, and such a statement throws some possible light on the frequency with which this joint is affected with disease.

The anti-concussion mechanisms existing in the limb are roughly speaking of two kinds, viz., (1) those for receiving the weight of the body on the leg when the foot comes to the ground, without the part suffering from the concussion of impact, and (2) those which admit of propulsion by one fore-limb without the parts suffering from the compression of propulsion. The first is principally provided by the yielding joints formed in the pedal and fetlock articulations, by the arrangement of the foot, and by the tendinous and ligamentous material at the back of the limb; the second is provided by the column of bones forming the limb being broken up from the scapula to the pedis, and progressively increasing in size from the seat of the largest amount of compression, viz. the foot, to the least amount in the shoulder.

Probably the coronet and pastern represent the weakest part of the fore-limb, and their small size in comparison with the weight they have to support is evidence of this.

To ease the skeleton from concussion the muscles and tendons are brought into play and rendered taut; we know for instance how much better we are prepared to stand a sudden shock if we get sufficient warning, and, further, we recognise the risk of damage incurred to bones and ligaments if weight is suddenly imparted to a limb without the needful preparation for its reception.

The tendons and muscles of the limbs help to take the shock. So long as the muscles maintain their elasticity the work done by their tendinous attachments is comparatively slight; as the muscles tire the strain on the tendons increases, and in consequence they may give way, and this will occur at their weakest part. In this tired condition of limb the skeleton also suffers, the bones forming the column receive more shock than normal, and the smallest and shortest bones situated nearest to the seat of concussion, viz., the ground, may even fracture under the strain, and under any circumstance run a grave risk of becoming inflamed.

This argument is based on clinical observation; we do not believe that any riding horse sprains its back tendons or suspensory ligament until the muscles tire, and are no longer capable of exhibiting that perfect elasticity inherent in muscular tissue. We do not, however, say that no horse suffers in its pastern bones until the muscles tire (for example the cart horse), though the strain on them is undoubtedly greater at this time than any other. The strain on the pastern bones during draught depends upon the force exerted, viz., the compression of propulsion, that this is something considerable may readily be seen in any heavy draught work.

Fractures of the pastern also teach us some useful lessons, we may regard them for our purpose as experimental evidence of the shock inflicted on the lower bones of the limb. This shock is caused when the foot comes to the ground not when it leaves it, and it may occur on hard ground or on sand; in the former case the cause of the concussion is obvious, in the latter at first sight it is not so clear, yet when we remember how rapidly horses tire working at any fast pace over sand, and, owing to the nature of the ground, the manner in which they must misjudge applying the muscular bracing which saves the skeleton from concussion, it is not difficult to explain the well-known fact that pasterns fracture on sandy soil. That direct concussion, in a horse which is not tired and not

working on sand, may also produce a fracture of this region is equally undoubted.

Our only object in dealing with a subject which appears to be foreign to the one under consideration, is to bring some light to bear on the strain to which the skeleton is exposed. This strain would appear to be greatest on the suffraginis in the fore-limb, for fracture of this bone is incomparably more common than fracture of the corona, though this might be accounted for by the density of the latter and the absence of a medullary canal. In concluding these remarks on fracture of the pastern, we would draw attention to the fact that the strain imposed on the bones in all cases is probably nearly identical in direction, for there is a remarkable similarity in appearance presented by fractures of either the corona or suffraginis, the fractured portions agreeing in shape and size in some cases almost piece for piece.

In spite of what we have said about direct concussion affecting the pastern bones, we do not think that this is necessarily the only factor present in the production of ringbone. The compression of propulsion must take a part; we mean by this, the shock imparted to the pastern bones while the foot is on the ground and the body is passing over it. The fore-leg from the knee to the foot is only intended to open and close in one direction, we can readily make the foot touch the point of the elbow, but we cannot make it touch the front of the fetlock. Now if we study the movement the limb makes from the time the foot comes in contact with the ground, we observe that the fetlock at first descends and then ascends, and having reached the desired point the limb passes over the foot which remains fixed on the ground, and at this moment an important movement occurs in the pastern, viz., its rotation from rear to front. While the fetlock is ascending the meta-carpal is moving on the suffraginis, the suffraginis on the corona, and the latter on the pedis; but as soon as the limb becomes vertical (in the rotation of the body over the foot), the movement between the suffraginis and corona becomes

exceedingly limited, and for all practical purposes, owing to their immobility, the two may be regarded as one bone; thus the remaining rotation of the body occurs between the corona and pedis. It is only possible to understand this by following it out on the dead limb, the leg being upright and the foot fixed.

The important point is this—during the rotation of the body over the foot considerable compression and strain must be experienced in the pastern; this strain is most severely felt at the articulation between the suffraginis and corona, owing to the fact that these are locked together during the main extension of the limb. Further, as the upward and forward propulsion to the body is given as the foot is leaving the ground, much of the shock resulting from it must be expended on the pastern bones.

In the **act of Standing** the body is supported on four props; two of them have only a muscular attachment to the trunk, the other pair are united by a ball and socket joint. It is unnecessary to allude by name to the muscles connecting the fore-leg with the trunk, excepting to mention the serratus magnus through the medium of which the body is principally slung on the scapula.

No matter what the position of standing may be, the horse never in a state of health keeps its fore-feet in any other position than together; one fore-limb advanced in front of the other is abnormal excepting when grazing. On the other hand, it is very rare to see a horse standing squarely on both hind-legs, he is invariably resting the limbs alternately. Some years ago we drew attention to this as being an explanation of the exemption of the hind-limbs from navicular disease; by this process of resting, the compression of the navicular bone (through the body weight above, and the perforans tendon below) is relieved. The horse only learns to rest the fore-feet when too late.

In **Lying down** the horse brings the four legs together under the body, and bends both knees and hocks, the knees and chest touch the ground before the hind-quarters. Whilst down he either lies extended on one side or seated

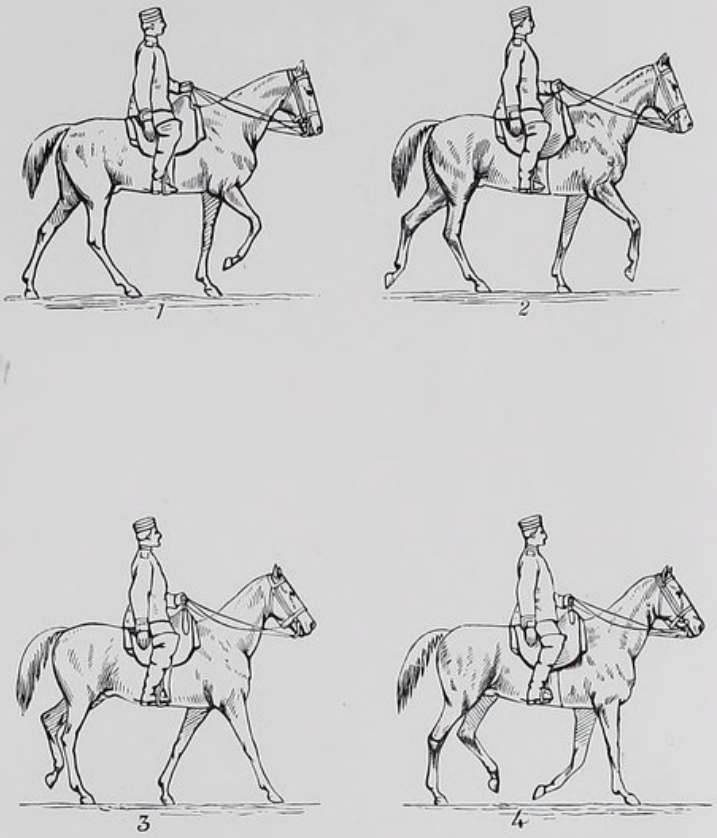


PLATE I.—THE WALK.

[*A folding-plate to face p.* 453.]

on the chest, two lateral legs being under thebody and two outside it. If resting on the chest inclined to the near side, the near fore-foot is placed close to the breast-bone, the elbow touching the ground, the near hind-foot is under the abdomen; the off fore-foot lies close to the off elbow but outside it as a rule, and the point of the off hock touches the ground. A horse does not lie long in one position owing probably to the enormous weight of his body.

It will be observed that the horse lies on the point of the elbow which is underneath the body. This is the cause of 'capped elbow,' and not that usually assigned, viz., resting on the heel of the shoe.

In **Rising** the horse can only get up by extending both fore-feet in front of the body. The hind-quarters are now pressed upwards assisted by the muscles of the back, and the animal is immediately on its feet, the fore-part always rising before the hind.

The cow rises quite differently, in fact the reverse of the horse, the hind-quarters being the first to ascend.

Locomotion.—We have now to study the question of locomotion in the horse, and describe how the legs are moved during the different paces. It will be remembered that our knowledge of this subject chiefly depends upon graphic records and instantaneous photography, the pioneers in the field being Marey* in France, Stanford, Stillman, and Muybridge in America.†

The **Walk** (Plate I.) is the slowest pace, the movements are somewhat complex, and may roughly be divided into four stages. In the first stage the body is balanced on three legs, in the second stage on two diagonal legs, in the third stage on three legs, in the fourth on two lateral legs, and the next movement brings it back to the first stage, only with different legs employed.

Tracing the movements in each stage, the horse advances one fore-leg—say, the off (Plate I., Fig. 1) and is left standing on the near fore, near hind, and off hind; in the second

* 'Animal Mechanics,' International Scientific Series.

† 'The Horse in Motion.'

stage the near hind is picked up, and the animal is standing on the near fore and off hind, viz., on diagonal legs (Fig. 2); in the third stage the off fore has come to the ground, and the animal is balanced on both fore and the off hind leg (Fig. 3); in the fourth stage the near hind is advanced to be placed over, or in advance of, the track of the near fore; to make room for it the near fore is advanced, and the horse is left standing on two lateral legs, viz., off fore and off hind (Fig. 4); the next movement brings the animal into the first position, with the near fore leading instead of the off fore.

The fore-leg remains on the ground for a longer time than it takes passing through the air, and comprises the period during which the body is passing over the limbs. The movement in the air both of fore and hind legs is so extremely rapid as almost to defy detection.* The snatching up of the foot from the ground is the quickest movement, Stillman refers it to the spring or rebound of the suspensory ligament, but it is doubtless due entirely to the flexor muscles.

In walking on level ground the majority of horses rarely extend the knee any great distance beyond a vertical line dropped from the point of the shoulder. A sudden movement of the extensors now straightens the leg, and the foot is placed down flat or heel first. If the leg is not fully straightened by the extensor muscles, the foot comes to the ground toe first, with the knee slightly bent, and a stumble follows. In heavy draught work it is no uncommon thing to see the toe put down first, but here the conditions are very different.

It appears to be a matter of indifference with which fore-leg an animal starts the walk.

Figs. 80 and 81 show the curves or paths described by both fore and hind limbs in the walk, after Marey and Pages. Examining these curves *from the time the fore-limb*

* Stillman points out that if the speed of the horse be 25 miles an hour, the foot which is in the air and travelling forward is moving at the rate of 50 miles an hour.

leaves the ground until it touches it again (Fig. 80, B), we find that the shoulder-curve runs slightly upwards, due to the limb being advanced; the elbow-curve runs rather downwards, due to the limb being extended; the knee shows a marked upward curve, and then a fall as extension occurs; the fetlock also shows a well-marked curve, due to its flexion and then extension. The curve shown by the foot is a large and gradually increasing one; it then rapidly descends as extension occurs.

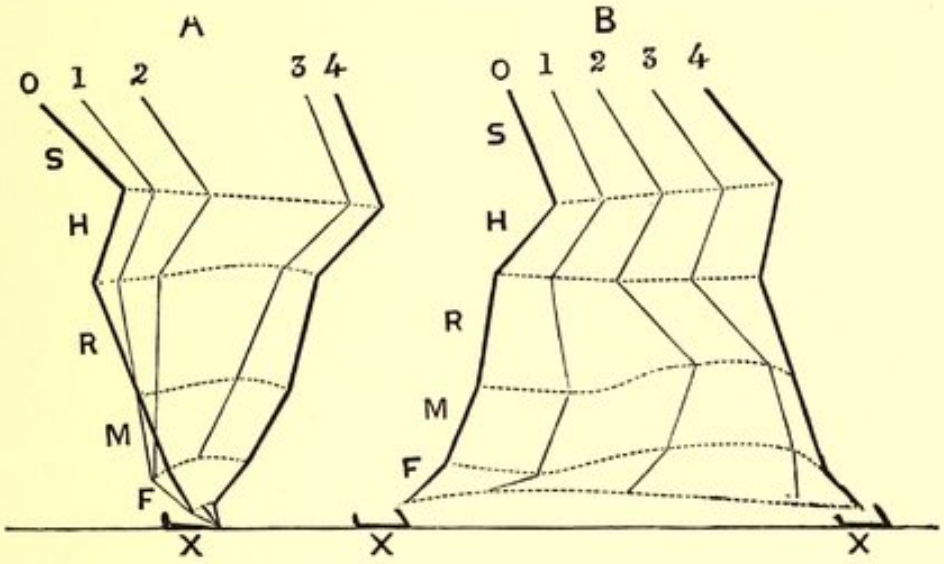


FIG. 80.—PATH DESCRIBED BY THE JOINTS OF THE FORE-LIMB AT THE WALK: A, WHILE THE FOOT IS ON THE GROUND; B, DURING THE TIME IT IS IN THE AIR.

S, scapula; H, humerus; R, radius; M, metacarpus; F, fetlock; in Fig. A—0 is the position in which the leg makes contact with the ground; 4, the position at which it leaves it; in Fig. B—0 is the position in which the limb leaves the ground, and 4 at which it meets it; X is the foot; 1, 2, and 3, various phases during progression. Observe the sinking of the fetlock at A, 1 and 2, as the weight comes on the limb. (Marey and Pages.)*

The foot-curve obtained by Marey and Pages by means of photography, agrees with results obtained by us by walking the horse past a piece of prepared canvas with a blacklead pencil attached laterally to the foot, by which means the path of the foot was readily traced on the canvas.

The curves described *by the fore-limb from the time it touches the ground until it leaves it* are shown in Fig. 80, A.

* Goubaux and Barrier, 'L'Extérieur du Cheval.'

The shoulder sinks, the joint coming nearer the ground due to the forward movement of the body. While the body is passing over the leg the elbow slightly rises, due to the ascent of the fetlock; this also produces a well-marked curve in the path of the knee, though the fetlock-curve is naturally the steepest. It will be noticed that there is first a sinking in the fetlock curve before it rises; this occurs at the moment the weight of the body commences to pass over the foot (Fig. 80, A, 1 and 2).

Following now the curves of the hind-limb *from the time*

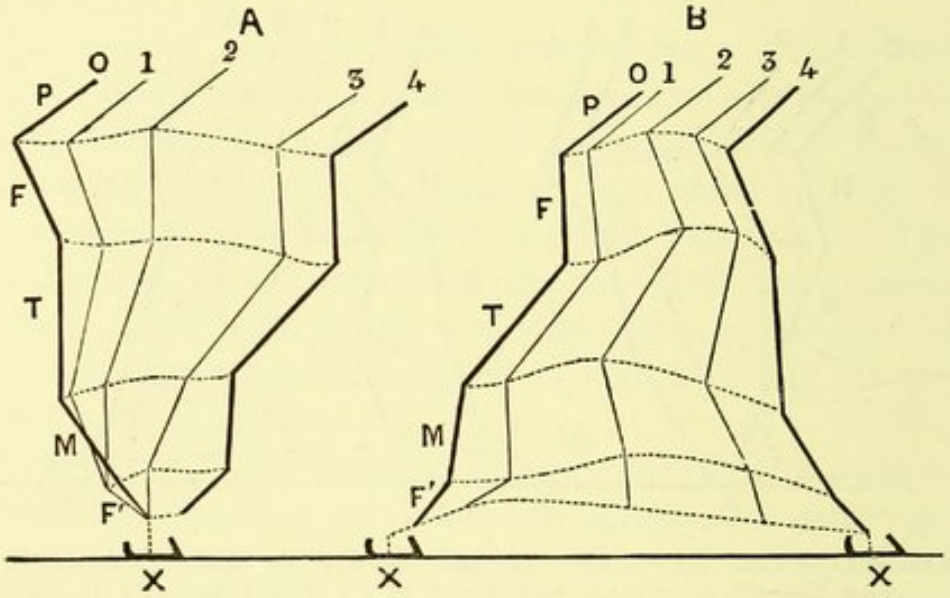
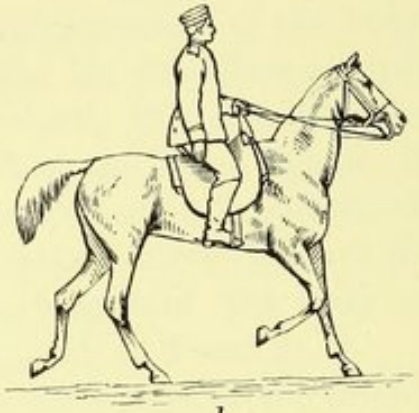


FIG. 81.—PATH DESCRIBED BY THE JOINTS OF THE HIND-LEG DURING THE WALK.

P, pelvis; F, femur; T, tibia: M, metatarsus; F', fetlock; X, foot. In other respects the description of Fig. 80 applies. (Marey and Pages.)

it leaves the ground until it meets it again (Fig. 81, B), it will be observed that the stifle-curve rises and then sharply falls as the leg touches the ground; the hock-curve is highest at the first half of the movement, and then gradually falls; the fetlock-curve rises, being greatest at the middle of the movement, and then falls; the foot-curve is greatest at the commencement of the movement.

In examining the curves of the same limb *from the time it reaches until it leaves the ground* (Fig. 81, A), there is a well-marked curve in both hip and stifle; the hock-curve



1



2



3

PLATE II.—THE TROT.

From instantaneous photographs by O. Anschütz. (*Ellenberger.*)

[*To face p.* 457.]

rises the whole way, while the fetlock-curve is rather a flat one compared with that of the fore-leg.

The **Trot** (Plate II.) is a very simple pace to analyse, the body is supported on diagonal legs (Fig. 1), which by their propulsion drive it off the ground, during which period all the legs are in the air (Fig. 2); when the body comes to the ground again the next pair of diagonal legs receive it (Fig. 3), and once more propel it off the ground. There are thus three stages to the trot, the body in two of them is supported by diagonal legs, and in one of them it is in the air.

The trot appears to be the only pace in which instantaneous photography has supported the conventional

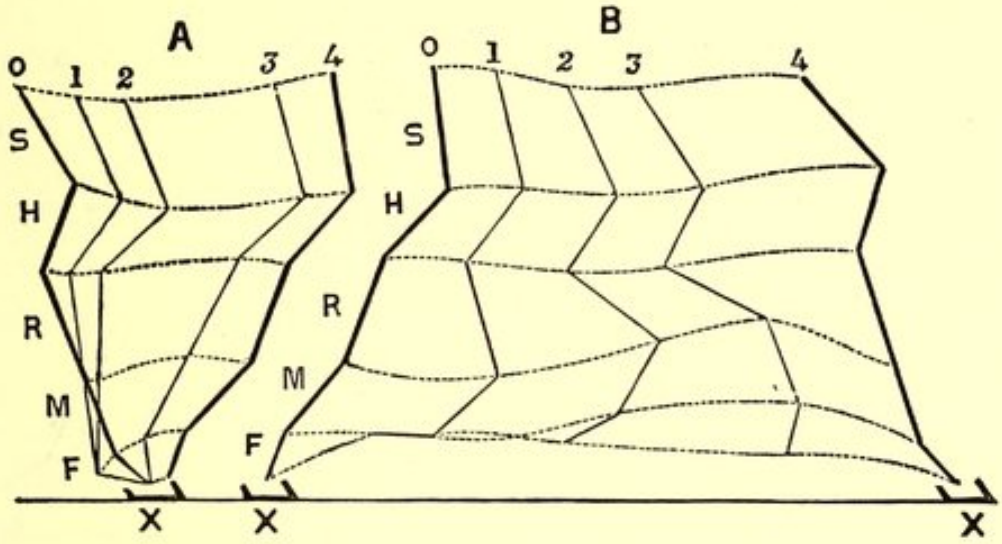


FIG. 82.—CURVES DESCRIBED BY THE FORE-LEG DURING THE TROT. The description of Fig. 80 applies. (Marey and Pages.)

notions of this movement. We can see the trot, first because it is a simple pace, and secondly because the body is comparatively long in the air.

When a horse falls at the trot, he does so through not flexing his knee sufficiently before bringing the leg forward, and the toe touches the ground; further, if the extension of the knee is not perfect he also falls. When the knee has been well bent and the leg brought forward, the limb is then sharply extended, well braced, and the foot placed down flat or heel first.

Marey and Pages' curves of the fore and hind limb during the trot are seen in Figs. 82 and 83. Observe the

knee-curve as the limb is in the air; the hock-curve in Fig. 83 is much flatter than one would have expected, whilst the foot-curve is a big one.

In the **Amble** the horse, instead of using diagonal legs uses the lateral limbs, so that off fore and off hind are on the ground instead of off fore and near hind. A horse may amble both at the walk and trot, in this respect resembling a camel; there is no doubt that it is a perfectly natural pace for some horses, others are taught it as it is a particularly pleasant one for the rider.

In the **Canter** (Plate III.) the body is pushed upward off the ground by one fore-leg—we will say the off-fore (Fig. 1)

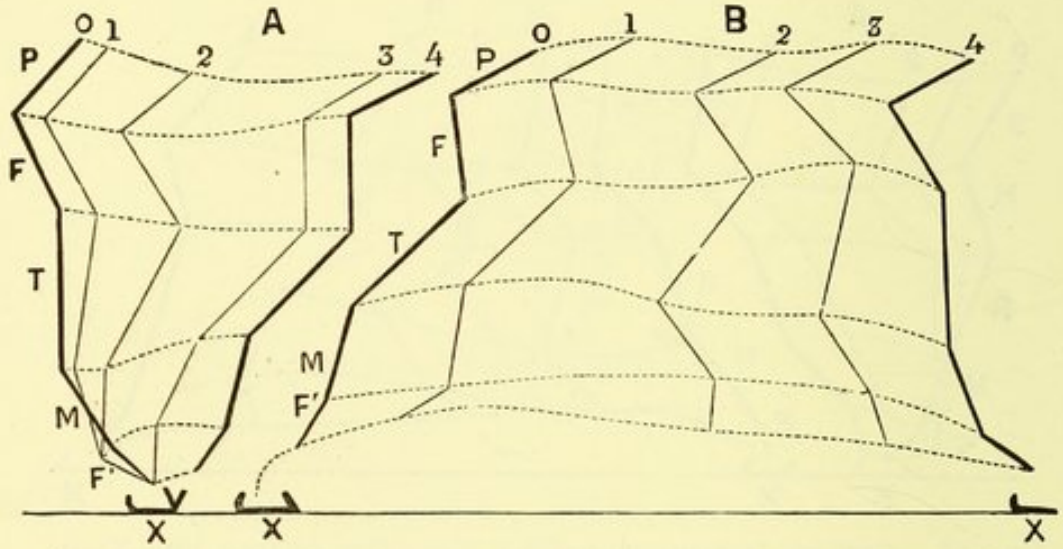


Fig. 83.—Curves Described by the Hind-leg during the Trot. The description of Fig. 81 applies. (Marey and Pages.)

—the near fore and both hind being off the ground; in the next stage all the legs are off the ground though the feet are no great distance from it (Fig. 2); in the third stage the body returns to the ground, alighting on the near hind-leg, which is not placed under the centre of gravity as in the gallop, but behind it, the animal being balanced on one limb only (Fig. 3); in the fourth stage the off hind and near fore come to the ground together, so that the body is now balanced on three legs, viz., near fore and both hind (Fig. 4); in the fifth stage the off fore comes to the ground, but as it does so the near hind rises; the animal is still left on

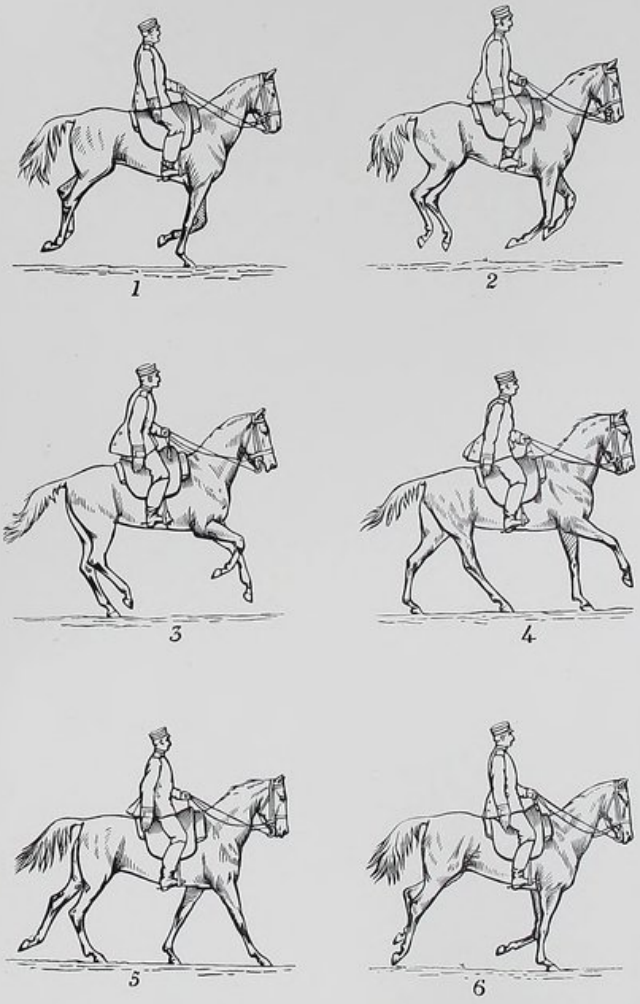


PLATE III.—THE CANTER.

From instantaneous photographs by O. Anschütz. (*Ellenberger.*)

[*A folding-plate to face p.* 458.]

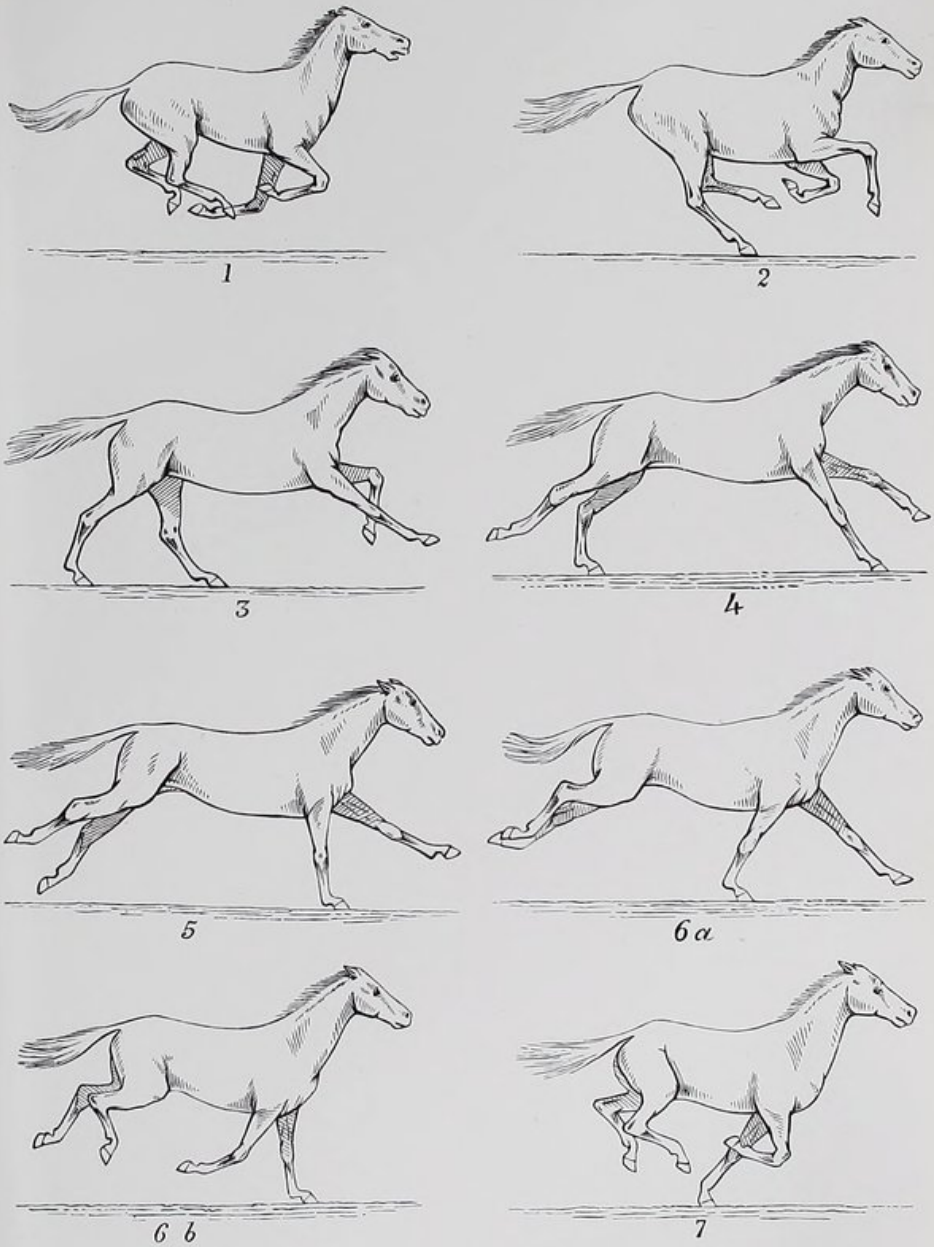


PLATE IV.—THE GALLOP.

After Stanford, Muybridge, and Stillman. (*'The Horse in Motion.'*)

[*A folding-plate to face p.* 459.]

three legs, viz., both fore and off hind (Fig. 5); in the sixth stage the near fore and off hind leave the ground, the horse being balanced on the off fore only (Fig. 6); the next movement is a repetition of the first, the off fore pressing the body upwards.

In the example quoted the off fore is the leading leg, and it will be seen that it is this which gives the final propulsion to the body. This is the explanation why the leading leg tires so early.

Though it is a matter of indifference which leg a horse leads off with in the walk and trot, this is not the case in the canter or gallop. There are some animals which so long as they are leading with the leg of their own choice are pleasant in their paces, but if forced through fatigue or other cause to lead with the opposite fore leg, the movements are rough and clumsy and wanting in co-ordination. It should form part of the training of every horse to be able to change its leading leg in the canter or gallop with facility. This education would prevent many cases of sprain.

The **Gallop** is a very difficult pace to describe, and the analysis I give of it here is from one of Mr. Muybridge's numerous instantaneous photographs.

The Gallop (Plate IV.) consists of seven stages; we will elect to describe it from the time the animal is in the air no legs being on the ground, but all four of them brought well under the body; this is the first stage (Fig. 1); in the second stage one hind-leg, say the off, comes to the ground, the foot being placed down close under the centre of gravity and not behind it as in the canter (Fig. 2); in the third the near hind comes to the ground, the horse now being balanced on two hind-legs, both fore being in the air (Fig. 3); in the fourth stage the off fore comes to the ground, but the horse is not balanced on three legs as in the canter, for at the moment the off fore comes to the ground the off hind is extended, leaving the animal on diagonal legs, viz., off fore and near hind (Fig. 4); in the fifth stage the near hind leaves the ground, the animal being balanced on the

off fore-leg (Fig. 5); in the sixth stage the near fore comes to the ground (Fig. 6*a*), and the off fore leaves it (Fig. 6*b*) —the body is still supported on one fore-leg; in the seventh stage the body passes over the near fore-leg (Fig. 7), and by a contraction of its muscles the entire weight is lifted off the ground, and propelled forwards and upwards (Fig. 1).

The points of importance in both the gallop and canter are that the heel of the foot comes to the ground first, that the hind-legs break the shock of the falling body, and that the fore-legs take the largest share in propelling the weight. Two of these facts were described years ago by Lupton, but were then disbelieved; see p. 486.

In examining the track of a galloping horse it is remarkable to observe what a very straight line the hoof-marks leave, showing that each foot is brought well under the middle line of the body.

When a horse gallops, no matter how fast the pace, the fore-feet never extend beyond a vertical dropped from the muzzle.

In the **Jump** (Plate V.) the horse rises to it by the propulsion upwards which the fore-legs give to the body (Fig. 1), the knees at the same time being flexed to enable the feet to clear the obstacle. Both hind-legs being fixed on the ground, the body is through these propelled forwards (Fig. 2). In alighting on the other side the animal does so through the medium of both fore-legs, one following the other (Fig. 3). Instantaneous photography disproves the theory that in the jump a horse naturally alights on the hind-legs, though it is true that some clumsy horses do.

In **Rearing** the hind-legs are brought well under the body, the head and neck are thrown up, and the propelling power of the fore-legs directs the body upwards, where it is sustained by the muscles of the back and loins. So long as the centre of gravity falls within the base formed by the hind-feet, the body is in a position of stable equilibrium; but if it passes outside this base, the horse comes down on to the point of both hocks, and may either roll over on its side or go directly backwards. If the latter,

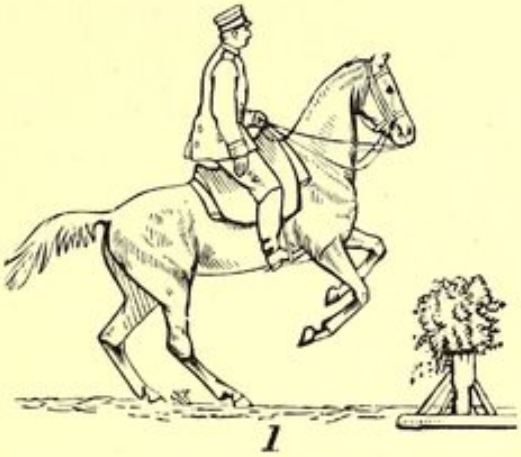






PLATE V. — THE JUMP.

(*Anschütz-Ellenberger.*)

[*To face p.* 460.]

the first part of the body to strike the ground is the occiput; in this way fracture of the base of the skull may occur.

In **Kicking** with both hind-legs the head is depressed, and a powerful contraction of the muscles of the quarter and back throws the croup upwards, and at the same time both legs are violently extended. A horse appears to have very little power of kicking if the head be kept up, or the tail be fixed down.

In **Buck-jumping** the animal springs bodily off the ground, the back is violently arched, and the head depressed between the fore-legs.

The Normal Daily Work of Horses, the rate at which they are capable of performing it, and the power they exercise in doing so must now be briefly considered.

Rankine has laid down that the **mechanical daily work** is the product of three quantities: (1) the effort; (2) the rate; (3) the number of units of time per day during which the work is continued. Our only difficulty here is in obtaining the value of the effort, which it is clear must depend upon the nature of the work, the character of the ground, the weight carried or drawn, and the physical fitness of the animal.

The normal work of horses would appear to be 3,000 foot-tons per diem; a hard day's work is equivalent to 4,000 foot-tons, and a severe day's work is 5,000 foot-tons. Redtenbacher* places the daily work of a horse for 8 hours at 6,700 foot-tons, and Rankine's tables† show that a draught horse exercising a force of traction of 120 lbs. for 8 hours a day, performs 6,200 foot-tons of work. I think both these estimates are without doubt too high. The co-efficients of resistance employed in our calculations, were those determined for man by the Rev. Professor Haughton, we know of none especially calculated for the quadruped. Assuming the weight of the animal, plus the weight carried or drawn, to be equal to 1,000 lbs., then

* Quoted by M'Kendrick.

† 'Encyclopædia Britannica,' art. 'Animal Mechanics.'

3,000 foot-tons of work will be obtained by the following work:

Walking	at	3	miles	per hour	for 8·7	hours.
,,	,,	4	,,	,,	5·3	,,
,,	,,	5	,,	,,	3·7	,,
Trotting	,,	8	,,	,,	1·5	,,
Cantering	,,	11	,,	,,	1	,,

This table is only given as a means of conveying to the mind the value of 3,000 foot-tons of work.

The **Velocity** of the gallop has been variously stated, but it is certain that no horse has galloped 1 mile in 1 minute as is reported of Flying Childers. Firetail's mile in 1 minute 40 seconds in 1772, was beaten in 1890 in the United States by Salvator's mile in 1 minute 35½ seconds. This horse was galloped on a straight course against time, the weight carried being 7 stone 12 lbs., the age of the animal four years. The best time in a race has been quoted at 1 minute 39¼ seconds for 1 mile, and 3 minutes 2¼ seconds for two miles.

At Carlisle in 1761 owing to six heats being run the winner galloped 24 miles; but the most severe galloping ever recorded was performed by Quibbler in 1786, who galloped 23 miles round the flat at Newmarket in 57 minutes 10 seconds.

The fastest pace at which trotting has been performed is 1 mile in 2 minutes 8¼ seconds; the horse was Sunol, the match taking place in the United States in October, 1891. The celebrated American trotting-horse Tom Thumb trotted 100 miles in 10 hours 7 minutes, including a stoppage of 37 minutes; an English mare did the same distance in 10 hours 14 minutes, including a stoppage of 13 minutes, while Sir E. Astley's Phenomenon trotted 17 miles in 53 minutes.

The walking performances are not numerous. Twenty-two miles in 3 hours 52 minutes was done by Sloven in 1793.

All the old performances here quoted are from Youatt's work on 'The Horse.'

Turning now to what may be expected of ordinary horses, we find that the average walk of a cavalry horse is 3·75 miles per hour; the average trot is 7·5 miles per hour, or a mile in 8 minutes, and a fast trot is 8½ miles per hour. A cavalry gallop is from 12 to 14 miles per hour.

The stride of horses at various paces was measured in a very ingenious manner by Stillman and Muybridge.* They give the stride at the walk as 5 feet 6 inches; at the trot between 7 feet and 8 feet; at the canter about 10½ feet; and the gallop varies between 16 feet and 20½ feet, and they even speak of a stride of 25 feet.

The question of the **Weight** which a horse can carry is one affecting the vital interests of the cavalry service; there is a great difference between the weight a horse can carry and the *effective* weight it can carry. It has been stated by Desaguliers† that a horse at Stourbridge carried 1,232 lbs. of iron for a distance of 8 miles! This either exceeded or must have equalled its own body-weight, and the case is probably without parallel.

The entire question of the weight a horse can carry must depend upon the pace at which it has got to be carried, but under any circumstances is largely influenced by the weight of the animal's own body. We are not far from the truth in saying that the mean weight of a riding horse is 1,000 lbs., and the question is what proportion should the weight carried bear to its own body-weight. On this point we have made some observations, through its important bearing on the cavalry service, and have shown that cavalry horses should not be asked to carry more than one-fifth of their body-weight, and this conclusion will doubtless apply to all riding horses. One-fifth of the body-weight of a cavalry horse is roughly 14½ stones; instead of carrying this, they carry at least 20 stone.

We found in a cavalry regiment that the effective carrying capacity of the horses was between one-fifth and one-sixth of their body-weight, and that if the horse's weight were divided by 5·67, we got a figure which represented the

* *Op. cit.*

† 'Expt. Philos.,' vol. i.

weight it should carry. These results were arrived at by weighing a large number of horses, the weight each being 'up to' having been previously estimated by an independent observer.

The physiological features of **Draught** can only be glanced at. The subject of draught is a big one, and our information is still very incomplete.

Quadrupeds appear to be designed for the purpose of draught, a horizontal spine is not intended for carrying weight; such can only be satisfactorily met by an upright column, as in man, who, from his conformation, is essentially devised for carrying a burden; the horse, on the other hand, is constructed for hauling or draught. Brunel, in his article on 'Draught,'* points out that the reason why a horse is more suited for draught than for carrying weight, is that he can throw his weight considerably in front of his centre of gravity, the feet forming the fulcrum, and 'allowing the weight of the body in its tendency to descend, to act against the resistance applied horizontally and drag it forward; as the resistance yields the feet are carried forward and the action continued.'

Such is the theory of draught; the nature of the vehicle, the condition of the roads, the angle the trace forms with the horizontal, the presence or absence of springs, four wheels or two, high or low front wheels, and the width of the track, so complicate the question as to take it at once into the domain of pure mechanics, into which we cannot follow it.

The force exerted in draught depends upon the load and the pace; in the light or mail stage-coach, where 10 and 11 miles an hour were attained, the strain or force of traction employed by each horse was only 40 lbs.; in the heavy coach it was 62½ lbs. for each horse. The higher the velocity the less the force of traction which can be employed, and the shorter the duration of labour.

For slow draught work at 2½ to 3 miles per hour, and for 8 hours a day (which appears to be the most suitable

* 'Book of the Horse,' Youatt.

pace and duration of labour), a force of traction of from 100 lbs. to 125 lbs., or 150 lbs., is quoted by Brunel as being the most suitable. We have previously stated that a force of traction of 120 lbs. for 8 hours a day is too much to expect from a horse.

Watt found that a horse could raise a weight of 150 lbs. passed over a pulley, 220 feet per minute. This, as applied to engines, is termed 'horse power,' and is equal to 33,000 lbs. lifted 1 foot high per minute, viz., 33,000 foot-pounds per minute. This standard of comparison cannot be generally applied to horse labour, as it is much too high. An animal could only perform this amount for $3\frac{1}{2}$ hours per diem, whereas its most useful work is performed in 8 hours.

The actual dead pull which a horse can exert depends upon his body-weight; no animal tested by me against a dynamometer has pulled its own weight, nor should we expect it.

A very big railway horse tested against a dynamometer pulled 16·4 cwt.: a powerful van horse notorious for its strength pulled 11 cwt., the body weight being a few pounds under 14 cwt. It is probable that the greatest effort a horse weighing about 10 cwt. can exert for a few seconds as a steady pull is from 8 cwt. to $8\frac{1}{2}$ cwt.

CHAPTER XVII.

THE FOOT.

The foot is largely a modified form of skin, the vascular tissues represent the corium, whilst the horny represent the epidermis. It is no uncommon thing to have a horn-like tissue produced by the skin, as, for example, in the human nail, in the hand of the labourer, and in the chestnut and ergot found on the limbs of the horse. In spite of its origin from the skin, the foot is a specialized structure presenting not only a surface for wear and tear, but mechanisms for supporting the weight, and others devoted to warding off from both the foot and limb the concussion and jar to which such a structure is necessarily exposed.

If it were not for the mechanisms just alluded to, and were the foot a structure simply devoted to offering a surface of sufficient density for the horse to stand upon, it would present little of special interest.

The foot may primarily be divided into two parts, the insensitive or horny foot and the sensitive or vascular foot. The horny is produced from the vascular foot, but the latter does not exist solely for the production of horn, but is provided with a fibrous pad, elastic tissues, a peculiar arrangement of joint, and a remarkable corium, the collective function of which is devoted to saving the parts from destruction during the battering process to which the foot is exposed, and further to support the weight. These two feet the sensitive and insensitive are closely united, in their general configuration one is an exact counterpart of the

other, and one fits into the other much as a finger fits into a glove.

It would be out of place here to give anything like a detailed account of the anatomy of the foot, but there are certain structural features so intimately associated with the physiology of the organ that it is impossible to separate them.

Bones of the Foot.—The core of the foot consists of bone around which all the other structures are moulded. The bone is not one solid piece, as we might imagine was necessary in such a position, but on the other hand consists of three pieces. One of these is the pedal bone which in shape resembles a miniature foot, and the substance of which is rarefied in such a manner as to resemble pumice stone in appearance; a second bone, the navicular, is very small, of peculiar shape, dense in structure, rests slightly on the pedal bone, and is mainly held in position by ligamentous tissue. The third bone only partly belongs to the foot and partly to the limb.

One would suppose that the pedal bone should occupy the whole of the interior of the hoof, as high as the coronary edge and as far back as the heels, but this is not so. It only occupies a comparatively small portion of the internal foot (Fig. 90), and that portion is mainly situated towards the anterior and lateral parts; the posterior part of the foot practically contains no pedal bone, but the deficiency is made up by the introduction of two large plates of cartilage attached to the bone, and over which the structures are reflected as on the bone itself.

This singular deficiency of bone, in a part where one might be led to regard its existence in large amounts as a necessity, and the presence of large cartilaginous plates to take its place, is due to the various movements which the foot has to perform, and which could not be carried out if the bone of the foot were relatively proportioned to the structure within which it fits.

The Foot Joint.—Three bones form the foot joint; the question naturally arises why the joint was not com-

posed of two bones instead of three, and what advantage is gained by the introduction of a small dense bone like the navicular into the articulation ?

The articulation furnished by the pedis is much smaller than that furnished by the corona, but by the introduction of the navicular, the pedis plus navicular surface is nearly but not quite equal to the corona surface; one use, therefore, of the navicular bone is to increase the articular surface of the pedis.

But it is conceivable that this small articular surface of the pedis might have been increased in some other way than by the introduction of a distinct bone and other complicated apparatus, and one is forced to recognise that the value of the navicular articulation does not depend entirely on the fact that it increases the size of the joint, but that it supplies what elsewhere we have spoken of as a yielding articulation. The value of this yielding articulation appears to be in the saving of direct concussion; the weight through the corona comes in the first instance mainly on the navicular, which under its influence yields slightly in a downward direction; from the navicular the weight is transferred to the pedis itself, which, as we shall later have more particularly to point out, also yields slightly under its influence, and in this way it is undoubted that direct concussion to the joint is prevented.

The Navicular Bone and Bursa.—It is quite certain that the navicular would be very little use for the above purpose, if it depended on being kept in position solely by the delicate ligaments which have origin from it. The chief support to the navicular bone is the broad expansion of the perforans tendon which passes beneath it; between the tendon and the bone the most intimate fitting occurs, and a synovial apparatus exists here to save friction. It is probable that the perforans tendon and the inferior face of the navicular are more closely adapted to each other than any articulations in the body, excepting those found in the knee and hock joints.

Briefly, then, the small dense navicular bone is enabled

to form a yielding articulation in the foot, owing to the manner in which it is supported in position by the powerful perforans tendon.

One might almost argue on purely theoretical grounds that a small bone thus placed in the foot would be very liable to damage, and such we know practically to be the case. It is not our intention here to touch on the subject of navicular disease, excepting in so far as it helps to elucidate the physiology of the part, but it is permissible to regard the lesions of navicular disease in the light of an experiment, and we learn from them how intimately the freedom and elasticity of a horse's action depend upon the navicular bone, and the stilty, pottering, shuffling gait conferred on the animal when the navicular bone is no longer capable of properly performing its functions.

The very close support afforded to this bone by the perforans tendon may possibly be the cause of the disorder, for the conclusion has been forced on us that under the influence of the weight of the animal, and the counteracting influence of the perforans tendon, the navicular bone must be exposed to considerable compression. This view is mentioned here not so much as a pathological as a physiological factor.

We cannot recognise in the navicular bone any pulley function in connection with the perforans tendon, such as has been usually described, that is if by the use of the term pulley it is sought to convey the impression that some mechanical advantage is obtained. It is true that by passing beneath the navicular bone the direction of the pull of the tendon is slightly altered, but no mechanical advantage is thereby derived.

The perforans tendon at its insertion spreads out fan-shaped, and is attached over a considerable semilunar surface of the pedal bone; so extensive is this attachment that it is erroneous to believe the tendon plays over the navicular bone. It is true that movement does occur between the tendon and the bone, but the tendon is passive, while the yielding of the navicular bone under the influence of

the body-weight is the active agent. It is curious to observe the direction in which the largest amount of friction occurs between these two surfaces. Reasoning from the position of the parts one would think the greatest amount of wear would occur at the moment the foot came to the ground, but if the eroded tendon of navicular disease be examined, it will be observed that the fibres are all stripped *upwards* and rarely or never downwards. This would point to the greatest friction occurring, not when the bone yields under the weight, but when it returns to its place as the body passes over the foot; but it may be that the fact is capable of a different explanation.

The frequency with which the central ridge of the navicular bone is affected with disease, would point to this part as being the position of the largest amount of pressure.

Lateral Cartilages.—Attached to the heel of each pedal bone is a large curved plate of cartilage, in parts fibrous, in others hyaline in nature. So extensive is this plate that it reaches high above the margin of the hoof, viz., outside the foot in an upward direction as far forward as the coronet and as far back as the heel (Fig. 90). There is no other structure in the body with which it can be compared; a bone possessed of two large cartilaginous wings is a something peculiar to the foot.

The use of these cartilages is intimately connected with the main principles of the physiology of the foot, but the time has not yet arrived for their discussion.

Plantar Cushion.—Placed between the two plates of cartilage, is a large somewhat pyramidal-shaped body known as the plantar cushion. In appearance it resembles a fibro-fatty mass, composed of interlacing fibres and fat, pale yellow in colour, almost destitute of bloodvessels, firm to the touch yet yielding in its nature. It occupies the posterior part of the foot, rising above the hoof into the hollow of the heel, whilst its inferior face is V-shaped, and a complete counterpart of the horny cushion or foot-pad which covers it.

The **Corium** of the foot covers completely the structures just described, viz., the whole of the pedal bone, a large surface of the lateral cartilages, and the plantar cushion. This tissue has received various names, viz., from its colour the vascular foot, from its appearance the fleshy, from its character the velvety foot, whilst from one of its functions it has been termed the horn-secreting foot.

The **Vascular Wall** or laminal tissue is composed of a number of leaves lying side by side, which run from the coronet downwards and forwards to the edge of the wall. In number there are about 500 or 600 of these leaves, and they invest the entire surface of the pedal bone and the greater part of the lateral cartilages, their extreme vascularity giving the appearance of a thin layer of muscle. The leaves at the toe are longer than those at the heel, where they are short and turned in under the foot, running forwards beneath it to form the sensitive bars.

If a single leaf, say at the toe, be removed and examined, it is found to commence immediately under the thick cornice-like structure known as the coronary substance, and to be most firmly attached to the pedal bone ; in fact, so intimate is the attachment that it is almost impossible to cleanly remove this tissue from the bone. The edge of the leaf is not regular but denticulated, and when viewed from the side it is observed that it is narrower near the coronet than at its inferior part, at which latter place it terminates in five or six papillæ.

The leaf is extremely vascular, in fact quite scarlet in colour, the effect on the whole mass of leaves being very striking in appearance. If the tissue be examined microscopically it is found that part of its substance is devoted to leaf formation, whilst the remainder is a sub-laminal tissue, the function of which is to secure the laminæ firmly to the wall of the pedal bone.

This sub-laminal tissue has been described by Moeller as consisting of two layers, one nearest the bone which he designates the *stratum periostale*, presenting the appearance of fibro-cartilage and evidently acting as the periosteum of

the bone. Outside this is a layer of fibrous connective tissue and elastic fibres, arranged in bundles, crossing and forming networks, and containing few cellular elements, though more than were found in the periosteal stratum ; this layer is extremely vascular and has been designated the *stratum vasculosum*. Outside this are the laminæ formed of elastic and connective tissue fibres as in the previous layer, only the network is much finer ; in the laminæ may be found numerous bloodvessels and nerves.

If a horizontal section of the laminæ be made and examined microscopically, it can easily be seen that each lamina has growing from its free edge a number of delicate processes which are miniature laminæ, or as they have been termed secondary laminæ or lamellæ; in number they are from 100 to 120 on each leaf, depending upon the size of the primary lamina.

The appearance thus presented (Fig. 84, d) is very characteristic, and has been likened by Chauveau to a feather, the barb being the lamina and the barbules the secondary laminæ.

The **Wall-secreting** or **Coronary Substance** is a thick, half-round, cornice-shaped welt of material situated above the laminæ ; it has received several names, the most rational being that based on its function as the wall-secreting substance. Externally this body is covered with long papillæ which are highly vascular, whilst the body itself on section is fibro-fatty in appearance. It extends all round the coronet from heel to heel, and here joins the plantar cushion. On its superior margin is a narrow groove marking off a distinct part of the body from which the periople is secreted, and which runs almost imperceptibly into the skin.

The entire coronary substance fits into a half-round groove in the horny wall, and the papillæ on its surface are lodged in canals formed in the horn. Beneath the coronary welt is a well-developed subcutis, which unites it to the tissues covering the corona and to the lateral cartilages.

The **Vascular Sole** is scarlet in colour, and covered by

long papillæ which are lodged in the horny sole. In each papilla an artery and one or more veins may be found.

The corium covering the plantar cushion is similarly arranged, the papillæ being lodged in the foot-pad or horny frog.

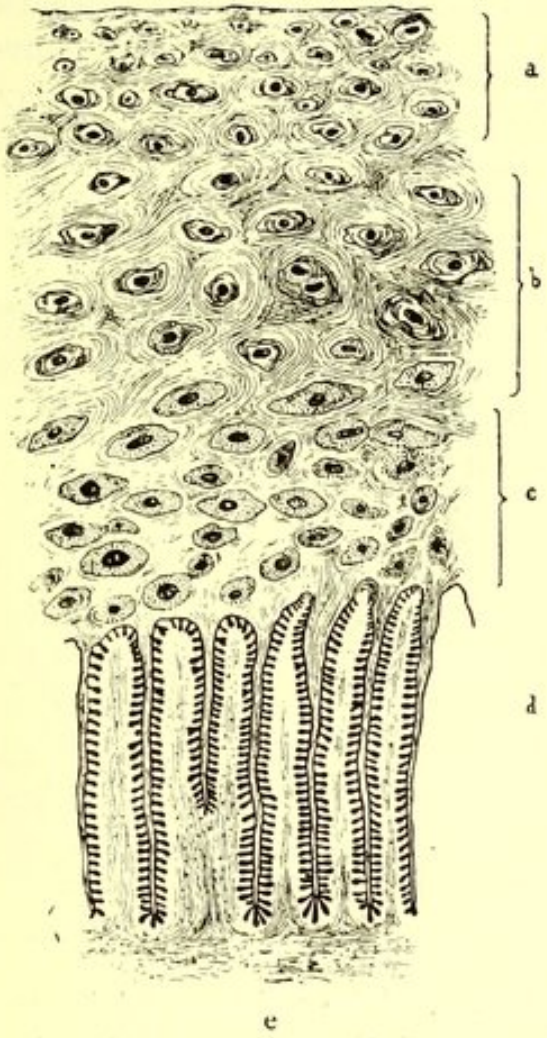


FIG. 84.—HORIZONTAL SECTION OF THE HORNY AND VASCULAR WALL OF THE HORSE'S FOOT.

a, *b*, *c*, The outer, middle and inner portions of the wall, showing the canal system with the tubular and intertubular horn; *d*, the horny laminæ bearing on their side the lamellæ, shown black; there are sometimes a few short laminæ to be seen, one is shown in the figure; *e*, the sub-laminal tissue, from which the sensitive laminæ may be seen dovetailed between the horny laminæ, and from the sides of which grow the sensitive lamellæ.

The **Vascular Supply** to the foot is exceedingly rich. We have alluded to the scarlet appearance presented by the laminæ, the vascular sole, and the tissue covering the

plantar cushion; but besides these the coronary cushion, pedal bone, etc., are richly supplied with blood. The pumicestone-like appearance presented by the latter, is for the purpose of affording passage to the innumerable vessels which are passing from the interior of the bone in an outward direction to reach the vascular tissues; in fact, no description or drawing can adequately convey an idea of the appearance presented by this vascular body. The veins are large and numerous (Fig. 85) and are not provided with valves; some pass through the substance of the lateral cartilage, and a large plexus exists both outside and

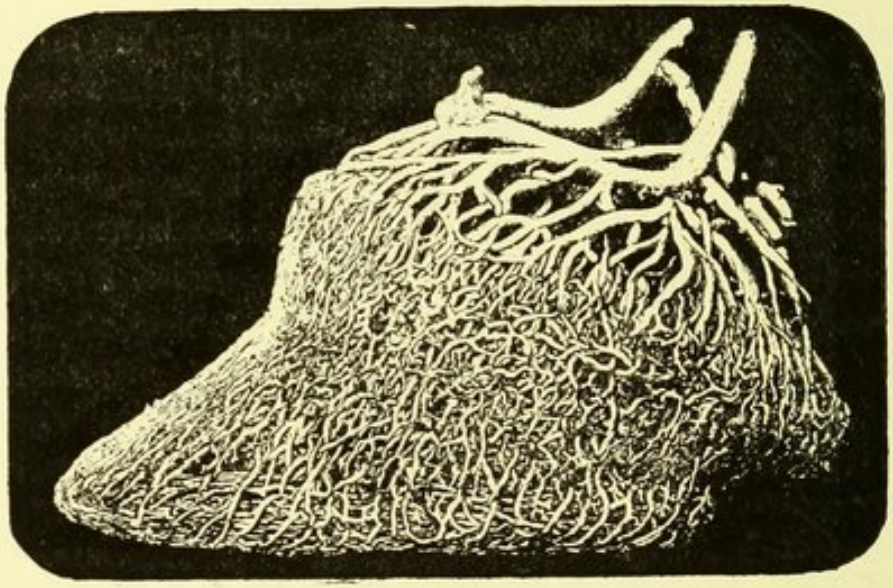


FIG. 85.—THE VENOUS SYSTEM OF THE HORSE'S FOOT. (STORCH.)

inside the cartilage. The relation of these vessels to the lateral cartilages and the absence of valves, are points which will occupy our attention again when we deal with the use of the various parts of the foot.

Such, then, is a brief account of the structure of the internal foot, sufficient to enable us to deal with its physiology, but before doing so we must glance at the arrangement of the capsule within which this internal foot is contained, viz., the external, insensitive, horny foot, or hoof.

The insensitive foot or **Hoof** is moulded over the sensitive structures in such a way as to completely cover them, and

form in horn a perfect counterpart of the sensitive foot. The hoof is composed of a wall with its inflections the bars, a sole, and a foot-pad or frog; each of these parts must be considered separately.

The **Wall** is that part of the hoof which can be seen when the foot is on the ground; its division into toe, quarters, and heels is for convenience of description, as no natural division exists.

On the exterior of the wall is a layer of horn known as the periople, which is more apparent near the coronet where it is white, soft, and thick, than lower down where it is extremely thin and more of the nature of a varnish, while at the toe it is practically absent. This layer is formed from the upper edge of the coronary substance.

A foot which has been poulticed causes the periople at the coronet to stand out as a white band running from heel to heel; this appearance is due to the absorption of water by the layer of soft cells of which it is composed at the coronet. The use of the periople appears to be to cement over the junction of the skin and hoof, and by the covering it affords the wall to prevent evaporation from its surface.

The wall is thickest and longest at the toe, thinnest and shortest at the heel. A gradual decrease in thickness occurs from front to rear, but if a section of the wall be made in the direction of its fibres, it will be found that whatever the thickness may be at that particular part, this thickness is maintained from the coronet to the ground surface.

The greater thickness of the wall at the toe and quarters as compared with the heels, is connected with the wear and tear of the hoof, and the movements which the latter undergoes under the influence of the body weight. If the wall were as thick at the heels as at the toe it would have been a rigid box; we shall have to show that it is a yielding box, and that the yielding which occurs corresponds to the thin wall of the heels. The reason why the wall is thick at the toe is that this is the region of the greatest friction.

The wall at the heels is suddenly inflected, running under the foot in a forward direction for a short distance, and forming an acute angle with the wall. This inflected portion of the wall is called the **Bars**, and in the gap formed by the inflection is lodged the foot-pad.

Thus the wall is an incomplete circle of horn, the circle being broken at the posterior part of the foot, and the piece of wall which might have completed the circle is bent on itself and caused to run in practically the opposite direction.

When we consider this arrangement it is easy to see the object with which it was devised; the foot is not a rigid body but a yielding one. It would be difficult to understand how any lateral movement could occur to it had the wall been a complete circle.

The value of the inflected portion of the wall is rendered evident when we bear in mind the lateral movement of the foot. From their position the bars afford additional strength; they knit the structures together at the heel in a remarkable way, and prevent any rupture between the wall and foot-pad during the lateral movements of the foot, such as would undoubtedly have occurred had the wall and foot-pad been directly united.

On examining the inside of the hoof-wall a very complex arrangement presents itself. At the upper edge, corresponding to the coronet, is a deep semicircular groove, deepest at the toe and narrowest at the heels, in which is lodged the thick welt of tissue previously described as the wall-secreting substance. Covering the entire surface of this groove are innumerable pin-point holes, into which it is easy to see the papillæ which project from the substance are lodged. The thickness of the wall at any one place corresponds to this coronary substance, and from it the entire horny wall is secreted.

The most perfect contact exists between the wall-secreting substance and the horny groove in which it is lodged, and this contact is further assisted by the vascular papillæ which run for a short distance into the depths of the horny wall.

Horny Laminæ.—On the inside of the wall of the hoof are found a number of leaves arranged side by side, running all round the foot from heel to heel, and composed of delicate plates of horn. It is easy to see they correspond in size, direction, and length, with the vascular or sensitive laminæ previously described, and like them they possess secondary horny laminæ or lamellæ.

These insensitive and sensitive laminæ are arranged towards each other in a peculiar way, by which an enormous amount of strength is obtained, viz., by the process of dovetailing. Each horny lamina fits in between two sensitive laminæ, and so powerful is this union, that in endeavouring to separate them the vascular laminæ will often tear from the pedal bone rather than rupture the dovetail. In this way the most intimate and perfect union between the vascular and horny wall is brought about, and in addition other advantages are obtained which will be dealt with shortly.

The horny laminæ as their name implies are composed of horn, but the secondary laminæ which invest them are composed of cells which are a something between horn and epithelium, viz., the cells have not undergone a true horn conversion but remain protoplasmic in nature; this is recognised by the fact that they readily stain with carmine whereas horn does not.

If our description has been made clear, it will be observed that though the sensitive and insensitive laminæ dovetail yet they are never in actual contact, for between them are the lamellæ both sensitive and insensitive, and it is actually through these structures that the intimate union is maintained (Fig. 84, d).

It will be remembered in speaking of the vascular laminæ that we described some as being found beneath the foot; in the same way horny laminæ corresponding in position and number to these are also found under the foot, and are situated at that part which has been described as the bars. Clearly, therefore, the bars though situated under the foot at its posterior part, are a part of the wall, inasmuch as

they possess all the essential anatomical elements of the wall proper.

The **Sole** of every normal foot is concave, that of the hind feet being more concave than the fore. This concavity agrees with the concavity of the solar surface of the pedal bone; it is ample evidence of itself that the general surface of the sole is not intended to bear weight. Soles vary in thickness, some being very rigid and firm others very thin and yielding; the sole cannot be too thick. The growth of the sole is peculiar, in exactly the same way as we noticed in the wall, the papillæ from the vascular sole fit into pin-point holes in the horny sole, and horn is developed around them. But here the resemblance ends, whilst the horn of the wall is capable of growing to almost any length, until in fact the direction of the foot causes it to curl like a ram's horn, the horn of the sole can only grow a very short distance before the fibres break off, and scales or flakes of horn are the result; these either fall out or are pulled out. In other words, the foot determines for itself how thick the sole shall be, and without any assistance the fibres break off when the proper thickness has been obtained, and allow the part to drop out.

This shelling out of the sole is necessary, inasmuch as the part not being exposed to friction cannot wear away. In those parts of the foot like the wall, which in the unshod foot are exposed to friction, no breaking off of horn fibres is required, as the wear and tear maintain the part at its proper length and thickness.

The sole and wall are united, the place of union being marked by a white line which extends around the complete circumference of the hoof. That part of the sole situated just inside the white line is capable of bearing weight, inasmuch as it is not immediately under the vascular sole.

The arrangement of horn at the junction of the wall and sole is peculiar. It will be remembered that the horny laminæ have on them secondary laminæ, these secondary laminæ exist wherever the sensitive horny laminæ digitate. But in the horn of the line of junction of the wall and sole

there are obviously no sensitive laminæ, and though the horny laminæ are there and can be distinctly seen with the naked eye, there are no traces of secondary laminæ on them; these have been left behind in the sensitive foot as the wall grows down.

The horn formed between the junction of the wall and sole is softer than that of any other part of these two structures; this softness allows of a slight yielding of the sole in an up and down direction, and this we will find actually occurs.

The Foot-Pad* or 'frog,' as it is vulgarly known, is a pyramidal-shaped piece of horn, accurately moulded over the plantar cushion, and filling up the space left by the inflection of the wall at the posterior part of the foot.

In the foot-pad we meet for the first time with a peculiar soft elastic horn, possessing something of the characters and appearance of indiarubber; nothing in its microscopical appearance accounts for this physical difference in the horn of the pad as compared with that of the wall. Chemistry, however, comes to our assistance, and shows that the horn of the pad contains much more moisture than that of any other part of the foot, and it is the moisture which confers on it, its peculiar soft pliable condition.

The foot-pad grows from the vascular membrane covering the plantar cushion, in the same way as we have already seen in the wall and sole.

At the heels of the foot where the wall is inflected, the soft horn of the pad not only fills up the gap between them, but plasters over the inflected edge of the wall for some little distance, so that an inspection of the heel gives the impression that the horn found at the posterior part of the hoof is a continuation of the wall.

The overgrowth of the foot-pad is provided for by a method which is a combination of that found in the wall and sole, viz., it is cast off after growing a certain thickness, whilst that part next the ground gets worn away by

* The term 'Foot-pad' is introduced not only to define the function of the part, but in order to eliminate the senseless language of the stable from scientific discussion.

friction; in consequence, owing to its rubber-like nature, rags of horn along the edges of the foot-pad are a common and natural condition.

The Structure of Horn.—The horn of the foot consists of epithelial cells which have undergone compression and hornification, by which latter process they become hard and tough. It is possible to have horn in the foot which has undergone no hornification, and the two are very readily distinguished by the process of staining.

The double stain picro-carmine has a selective affinity

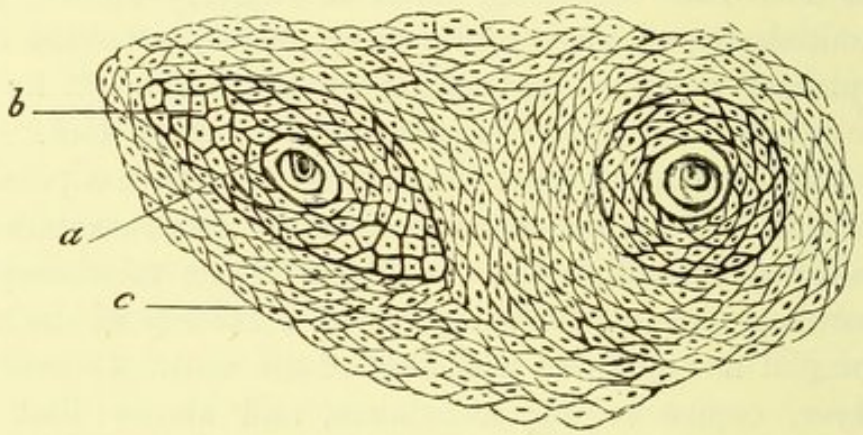


Fig. 86.—Horizontal Section of the Horn of the Wall, Highly Magnified.

a, Horn tube, a canal containing cellular elements; *b*, the tubular horn, viz., the horn secreted from the papillæ, forming an oval or circular nest of cells around the canal; *c*, the intertubular horn.

for each kind of horny tissue; the carmine picks out the protoplasmic and non-corneous cells and stains them red, whilst the picric acid stains all tissue which has undergone the process of hornification of a yellow colour. By means of this stain we possess a very easy means of determining the character of the horn under examination.

The ultimate horn cell is a very thin, spindle-shaped, oblong, or irregular body, containing granular matter, a nucleus, and frequently pigment (Fig. 86). In all cases the cells are united at their edges and sides by a cement substance.

By acting upon horn with caustic alkalies the cells are in the first instance rendered clear, they then gradually

dissolve, are converted into a gelatinous mass, and finally they disappear. There is no necessity to use a caustic alkali to destroy horn, any alkali has the effect of eroding it. Bearing in mind the highly alkaline nature of the horse's urine, the practical application of this fact in the care and management of the feet is very obvious.

If a portion of horn be examined microscopically, it is found that the compressed epithelial structure is tunnelled in such a way as to form canals or tubes, or, at any rate, to form a structure which is tube-like in nature. These tubes exist wherever the growing surface is invested with papillæ or projections, so that where the papillæ are numerous the tubes are numerous, where they are absent the tubes are absent. The only horny structure not secreted from a papillated surface is the horny laminæ, and here consequently we find no horn tubes, but everywhere else the horn is found to possess a more or less tubular structure.

The method of tube formation in horn is very simple; the papillæ growing from the various secreting surfaces are lodged in depressions in the horn, in this way a canal is formed for the reception of the papilla. As the horn grows down from the surface which secretes it, the canal lodging the papilla is gradually carried off it, but throughout the length of the horn a tubular appearance indicates where the papilla was at one time lodged, and the cells of these tubes from their reaction with carmine prove themselves to be different to true horny structure.

The horn which is secreted in the foot is therefore formed (1) from papillæ found on the secreting surface, and (2) from the spaces between the papillæ. The papillæ form tubular horn, the spaces between them form intertubular horn (Fig. 86, b and c). The tube or canal in horn is the outcome of the existence of papillæ.

The horn formed by the papillæ is arranged in an oval or circular manner around the canal (Figs. 84 and 86); the cells composing it are so placed that their edges are towards the papillæ or canal, with the exception of a layer of cells which actually form the wall of the canal, and these are

arranged with their sides next it; or, to put it another way, they stand on their edges.

The horn formed by the papillæ is therefore arranged concentrically, and this gives a laminated appearance around the canal, which is best seen in the external and middle layers of the wall (Fig. 84, a, b). In the deep layer of the wall the papillæ produce a much larger secretion, and here the circular or oval mass of cells investing the canal is more prominent, and further, unlike those in the anterior and middle parts of the wall, they need no reagent to identify their cellular nature (Fig. 84, b).

If a section of wall be stained with picro-carmine only the canal contents of the external and middle wall stain with carmine, all the remaining substance takes up the picric acid. In the deep wall this is different, here the whole of the cellular material secreted by the papillæ is stained red, showing that these cells are protoplasmic rather than horny, and partly accounting for the fact that this deep horn is always softer than the middle or external horn of the wall.

The horn formed between the papillæ surrounds and knits together that formed by the papillæ.

If a section of horn be examined without undergoing any special preparation, it is quite impossible to see the cells of which it is composed. Fig. 84 gives a good idea of this, and conveys faithfully the fibrous appearance presented by a horizontal section of the wall. To see the cells the preparation has to be treated with a solution of potash or other reagent, when the appearance presented in Fig. 86 is obtained.

It is not necessary to enter here upon the differences which exist in the horn of the various parts of the foot; there are differences present which enable a section of the foot-pad to be distinguished from that of the sole, or the sole from that of the wall, but such differences do not influence the physiology of the part and are only of subordinate interest.

At the junction of the wall and the sole the horn of the

laminæ is firmly interdigitated with the soft horn of the margin of the sole. This can be perfectly seen microscopically, and further it may be demonstated that the portion of the sole thus thrust between the horny laminæ, is perforated in five or six places for the reception of the papillæ which grow from the inferior extremity of the sensitive laminæ.

If a vertical section of horn be made, we can study the canals now divided in their length. It is readily seen that though spoken of as canals or tubes they are really not empty, but throughout their entire length they contain cells which are protoplasmic in nature. These, owing to the manner in which they reflect light, give to the part a beaded appearance. The cells contained within the canal are secreted by the apex of the papilla; they do not fill up the entire lumen of the canal (Fig. 86, a).

The use of the canal system in horn is for the purpose of irrigation; the horn must be supplied with moisture, the bulk of this is obtained through these imperfect canals, the soft protoplasmic canal wall readily admitting of transudation. It is not intended to represent that anything like a fluid is circulating along the tubes, but moisture certainly does find its way down, and is readily imbibed by the surrounding cells. Besides this arrangement for maintaining the moisture in horn, there is no doubt that in the intertubular horn, moisture passes from the secreting surface from cell to cell, and in this way is transmitted throughout the length of the foot.

Constant evaporation is taking place from the foot, and the loss is made good in the manner indicated.

In one part of the foot we have undoubted evidence that sweat glands exist, these are found in a particular part of the plantar cushion near and on the sides of the cleft. The glands are very large, coiled, and a spiral duct passes through the horn of the foot-pad and opens on the surface. Fig. 87 is after Franck who carefully described these structures, though the original discovery was made by Ercolani.*

* *Veterinary Journal*, vol. i., No. 1.

If the invisible moisture which is always escaping from the foot be hindered in its evaporation, the horn becomes sodden, crumbles away, and closely resembles a grey cheese. This experiment can readily be performed on the sole and foot-pad, by accurately moulding to their surface a sheet of gutta-percha and leaving it there. The practical lesson is obvious, no impervious material should be applied to the foot as a protection, or if used it should be ventilated.

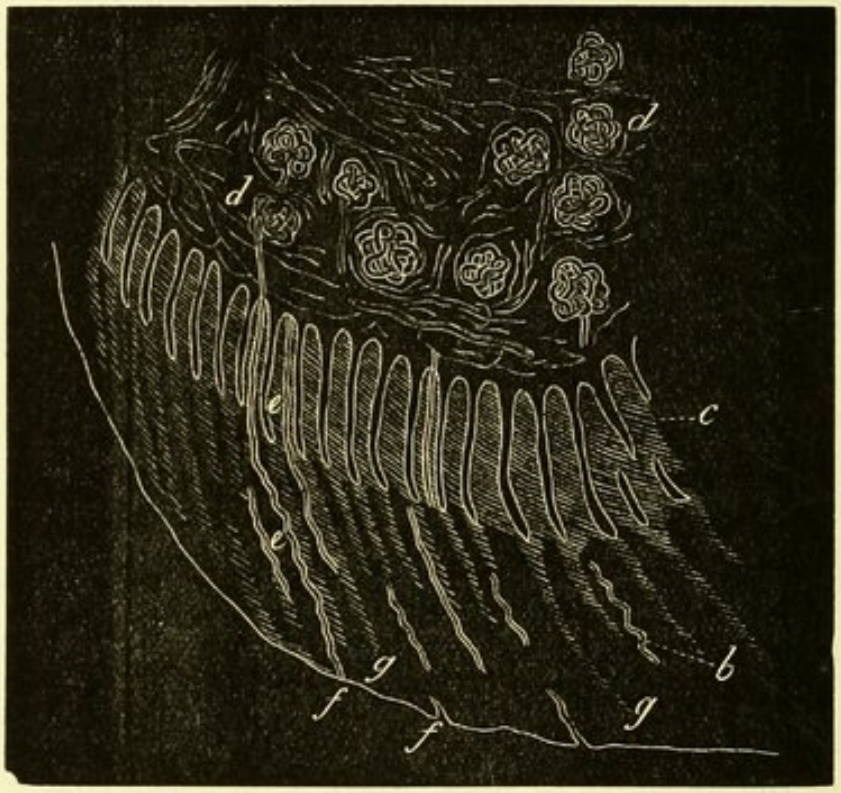


FIG. 87.—THE SWEAT GLANDS OF THE PLANTAR CUSHION. (FRANCK.)

d, *d*, The glands, the corkscrew-like ducts of which (*e*, *e*, *b*) pass out through the horn of the foot pad, opening at *f f* on to the surface of the foot. At *c* is the deep-seated portions of the horn of the foot pad, where it grows from the papillæ of the corium of the plantar cushion; *g*, *g* are horn tubes seen in longitudinal section.

Use of the Moisture in Horn.—The amount of moisture contained in horn is something considerable, and the rate at which it evaporates is quite extraordinary. If portions of the foot-pad be inclosed in a bottle, in a short time the interior will become bedewed with moisture.

The use of moisture in horn is to keep the foot elastic and prevent it from becoming brittle. The agency which is at work to prevent the too rapid evaporation of moisture

from the wall is the periople, which can only be seen in the unmutilated foot; in the case of the sole, the layers of exfoliated material which accumulate as the result of the breaking off of the horn fibres prevent undue evaporation.

Horn containing but little moisture is in an abnormal condition, it is rigid and brittle, nails driven into the part cause it to crack, and that elasticity on which so largely depends the natural shape and usefulness of the foot becomes impaired, or even destroyed. A museum specimen of a foot will very clearly illustrate our meaning; in its dried condition it is so brittle that if dropped it will occasionally fracture like a piece of glass; but if this foot be placed in water for a few days, it comes out as fresh and elastic as though it had just been removed from the body instead of being probably twenty years old. All that the horn has done is to imbibe water, and the previously brittle substance now becomes yielding and elastic. The entire physiology of the horse's foot is centred around this question of the moisture contained in horn.

We can see how necessary elasticity is in the foot, when we consider the concussion to which it is exposed during work, which would inevitably lead to its destruction by fracture or otherwise unless this provision were present. Clinically we are perfectly acquainted with the fractures which occur in the wall of the hoof from violence.

One of our main objects in shoeing should be to protect the wall from unnecessary interference; the removal of the varnish layer formed by the periople, and the cutting across of some thousands of horn-fibres by the unnecessary use of the rasp, lead to considerable destruction owing to the evaporation of water.

Chemistry of Horn.—An analysis of the horn of the foot has given the following results:

	Wall.	*Sole.*	*Foot-Pad.*
Water - -	24·735	37·065	42·54
Organic matter -	74·740	62·600	57·27
Salts - -	·525	·335	·19
	100·000	100·000	100·00

The pad contains the largest amount of moisture, and the wall the least.

The salts are small, and consist principally of those of sodium, magnesium, iron and silica.

Hoof consists of a horny material or keratin, which replaces the protoplasm in the cells furnished by the horn-producing surface. Keratin is an albuminous substance found in hair, nails, and even, in a modified form, in the nervous system; it consists of Carbon 51·41, Hydrogen 6·96, Nitrogen 17·46, Oxygen 19·49, and Sulphur 4·23 per cent.

The sulphur is loosely combined, and it is this in combination with hydrogen which causes horn undergoing decay or disease to have such an offensive odour, sulphuretted hydrogen being formed.

Keratin is a very insoluble substance, but is dissolved by strong and boiling acids and by alkalies. With sulphuric acid it yields leucin, tyrosin, and volatile substances; the latter conferring the peculiar odour on burnt horn, feather, nail, etc.

The Wall.—From what we have previously said, it can be seen that it is on the wall of the foot where the horse's weight is supported. On examining the horny wall we found that it was thickest at the toe, thinner at the quarter, and thinnest at the heels; it is thickest at the toe owing to the wear and tear of the foot at this part. As the pad and posterior part of the foot are the first to make contact with the ground (at any rate in all fast paces), so the toe is the last part to leave it, and as the final propulsion is given to the body by the toe, as we have seen in studying locomotion, we can readily understand how necessary it is for this part to be thick and strong.* The object of the wall becoming thin towards the posterior part of the foot,

* While these sheets were passing through the press, our attention has been drawn to the fact that as far back as 1858, Mr. J. Irvine Lupton, in vol. xxi. of the *Veterinarian*, communicated a paper on 'Physiological Reflections on the position assumed by the fore foot of the Horse in the varied movements of the limbs.' In this paper

is to allow of the elastic movement which we have yet to describe.

Two physical conditions have, therefore, to be provided for in the wall, viz., elasticity of the posterior part, and toughness of the anterior portion. The first is provided by the wall being thinner at the heels than elsewhere; but besides being thinner, the wall of the heel contains more moisture than the wall of the toe, and this moisture ensures its elasticity. The younger the horn, viz., the nearer to the coronet at which it is examined, the more moisture it contains; the further away from the coronet the less moisture and the tougher and more resisting the horn.

The wall grows evenly from the coronet all the way round; if it grows half an inch in the month at the toe, it grows the same length at the quarters, and the same at the heels. The anterior part of the wall is longer than the posterior, therefore the anterior is tougher than the posterior, for the reason that the horn is much older at the extremity of the toe than it is at the heel, and being further away from the coronet, it contains less moisture.

The wall at the heel is some months younger than that at the toe; it is thinner, and contains more moisture, therefore it is more elastic but not so tough.

The age of the wall is an important factor in the wear of the foot. If it takes from nine to twelve months for the wall to grow from the coronet to the toe, the piece of the wall at *f*, Fig. 88, is, say, twelve months old, whilst that at *a′* is less than six months old. The horn of the quarter is older than the horn of the heel, and the horn of the toe older than that of the quarter.

This excellent provision admits in the unshod foot of

Mr. Lupton states that the heel comes to the ground before the toe; further, he clearly and expressly describes the use of the foot-pad, the expansion of the foot, and the final propulsion given by the toe.

Mr. Lupton's advanced views did not meet with approval thirty-seven years ago; to-day they are accepted facts. We can only accord him tardy though full recognition.

considerable friction occurring at the toe without producing undue wear, for the part is hard and tough; while the younger and moister horn at the posterior part of the foot allows of expansion. In this way varying degrees of toughness and elasticity are provided in the wall.

The toe of the wall appears to grow faster than either the quarters or the heels, but this is more imaginary than real; it is the tendency of the foot to grow *forward* as well as downward which produces the illusion. That the foot does grow forward may readily be determined by experiment, for if we cut or saw a groove in the wall at the coronet, say an inch or so from the heels, the groove will

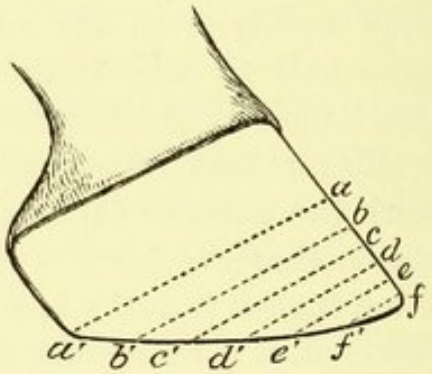


FIG. 88.—DIAGRAM ILLUSTRATING THE AGE OF THE WALL.

a, *b*, *c*, *d*, *e*, *f*, are circles drawn round the hoof parallel to the coronet; in this way it is ascertained that the age of the wall at *a* is the same as the heel at *a'*, the age of the wall at *d* corresponds with the age of the quarter at *d'*. Every portion of the ground surface of the wall is of a different age, being oldest and hardest at *f'*, and youngest and most elastic at *a'*.

in course of time be carried some considerable distance towards the toe; the exact amount can be determined by observing the obliquity of the horn fibres.

How the Weight is carried by the Foot.—We have now to consider the means by which the weight of the body is supported within the foot. It is universally recognised that this is carried out by the union of the horny with the sensitive laminæ. That the enormous weight of the horse's body should be carried upon—or, rather, slung upon—thin delicate strips of sensitive material on the one hand, and correspondingly delicate strips of horn on the other, is

perhaps the most remarkable feature in the physiology of the foot. We know how firm the union is, the extreme difficulty in separating these two parts even by mechanical means in a state of health, and we readily recognise the delicate structure of the parts yielding this firm connection.

The weight is carried on 1,000 or more primary laminæ, and 150,000 or more secondary laminæ. Those laminæ situated at the anterior part of the foot are exposed to more strain than those posteriorly placed, for the reason that they are longer, and they have no plantar cushion and foot-pad to assist them as the shorter posteriorly-placed laminæ have. Moreover, during progression the final propulsion of the toe on the ground comes entirely on them.

The short posteriorly placed laminæ have their strength increased by the direction in which the weight of the body comes upon them. Instead of bearing the weight on the length of the laminæ, as at the toe, they carry it on the side, in such a manner that where we have, say, one laminæ at the toe, there are twenty at the quarter. It is not possible to clearly describe this condition, but Fig. 89 will help to explain it.

It will be remembered that the laminæ are attached at the anterior and part of the lateral face of the foot to bone, but for the remaining lateral face and posterior part of the foot they are attached to stout cartilage;* if a line be drawn through the foot separating the osseous attachment of the laminæ from the cartilaginous attachment (see Fig. 90), it will be found that roughly speaking one-half is cartilaginous and one-half osseous; the cartilaginous portion is situated just where elasticity is required, viz., the posterior face of the wall. One function of the lateral cartilages of the foot is to afford a movable wall attachment to the sensitive laminæ, and enable them to be carried outwards during expansion.

A knowledge of the relation of the posterior laminæ to the lateral cartilage explains the cause of lameness in side-

* Some of the laminæ are attached to the tendon of the extensor pedis, and the lateral ligaments of the foot joint.

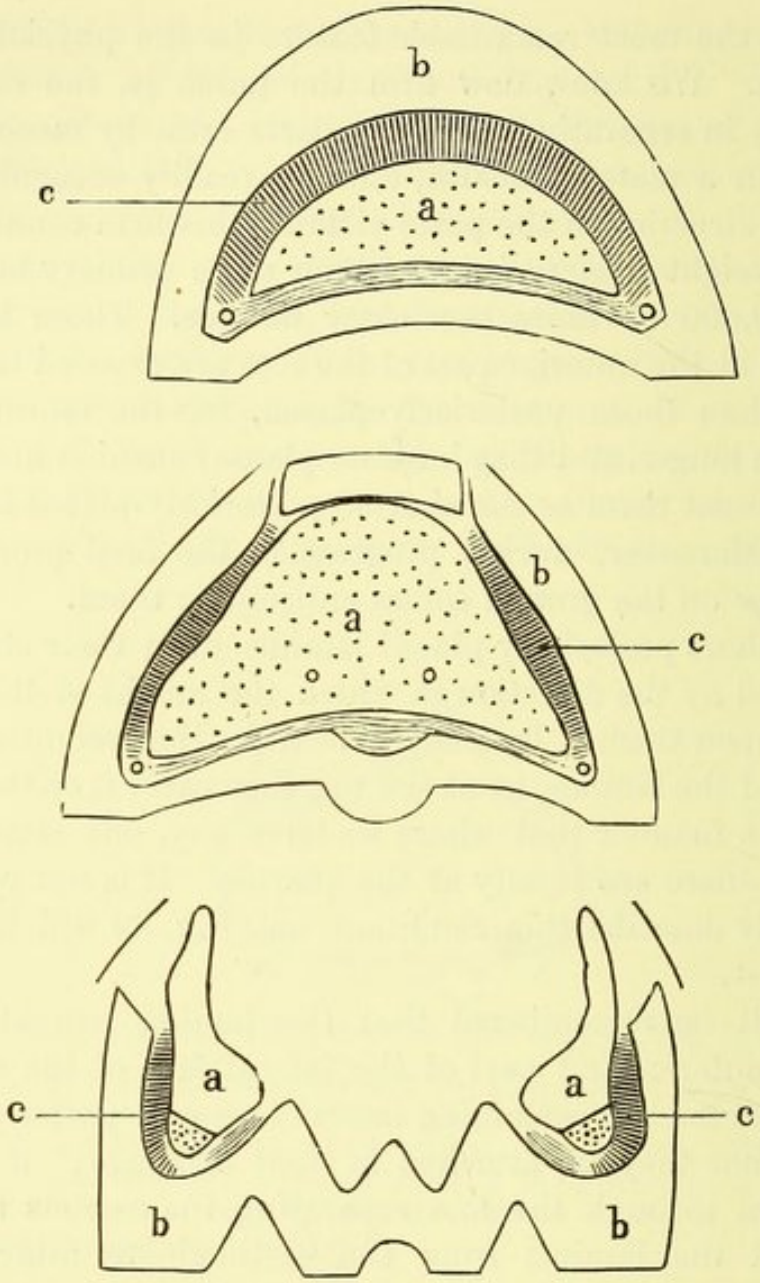


FIG. 89.—DIAGRAMS TO ILLUSTRATE THE DIRECTION TAKEN BY THE LAMINÆ AT DIFFERENT PARTS OF THE FOOT, AS SEEN IN TRANSVERSE SECTION.

In the upper figure the section is made through the toe of the foot: a, being part of the pedal bone; b, the horny wall; c, the laminæ, the latter are practically straight, the weight being imposed from top to bottom in their length. The middle figure is a vertical section just behind the point of the frog: the laminæ, c, give the appearance of being placed above one another. The lower figure is a vertical section through the posterior part of the foot: a, being the lateral cartilage, and c, the laminæ. It will be observed that the laminæ, as in the previous figure, are placed one above the other; this arrangement gives strength, and is a compensation for shortness.

bone, viz., the squeezing of the sensitive laminæ between the wall on the one hand, and the ossifying cartilage on the other.

The folding up of the horny and sensitive leaves in the foot, in the manner above described, has another function besides that of merely supporting the weight and rendering the union firm.

The first thing which strikes one in the foot is its remarkably small size in proportion to the size of the body. Comparing the horse's foot, so far as size is concerned, with the human foot, the advantage in the majority of cases lies on the side of the biped. The most interesting fact which physiology has to demonstrate is, that though the foot presents a small circumference, in reality it encloses a vast area due to the anatomical arrangement of the laminæ.

It is clear that by folding up this amount of material the surface of the foot is considerably increased. In other words, by this arrangement the foot has been kept within small proportions without affecting its strength. A book, say of 500 pages, may, by placing one leaf on the other, be made to occupy a bulk represented by a few inches; but if each page be laid out separately on the ground, and made to touch one another, the surface covered will be considerable. This is exactly what occurs in the foot, the horny and sensitive leaves by their singular arrangement increase the surface of the foot, and yet keep it within reasonable limits. Bracy Clarke, who first had a calculation made as to the increased surface afforded by this arrangement, came to the conclusion that it was equal to $1\frac{1}{2}$ square feet; but Moeller* has estimated that it is equivalent to 8 square feet, whilst Gader's estimate† is $10\frac{3}{4}$ square feet. For safety we will adopt Moeller's number.

The bearing surface afforded by each foot is equivalent to 8 square feet, giving a total area of 32 square feet; but it is evident that as feet vary greatly in size, this surface must be greater or less depending on the size of the foot.

* *Veterinary Journal*, vol. v.

† Quoted by Goubaux and Barriere.

The physiological function of the leaves of the foot is demonstrated by pathological observation. Inflammation of the laminæ occurs either through over-work, or through an animal standing too long in one position ; in either case the parts get strained, and resent it. We all know the practical value of exercising horses which from any reason have to stand for a length of time; the exercise overcomes the tendency of the laminæ to congestion from continual strain, and the feet not only become cool, but the animal may continue standing for a considerable time if daily exercised. The treatment of laminitis by exercise, first taught by Mr. Broad, of Bath, possesses a sound physiological basis.

If any doubt exists as to the function of the laminæ in supporting the weight of the horse's body, we have only to look at the processes which occur in them as the result of disease. Laminitis is often attended by separation of the horny and sensitive laminæ, when the horse's weight being no longer properly supported, the pedal bone under its influence is actually forced through the sole of the foot.

No one doubts that the wall grows from the coronet, but great controversy has taken place over the origin of the horny laminæ, some saying they grow like the wall from a part of the coronary cushion, and others affirming they obtain their origin from the sensitive laminæ.

If we were to judge solely by the result of pathological processes, one would be inclined to say that the sensitive secreted the horny laminæ ; but Moeller* points out that the sensitive and insensitive laminæ are never in actual contact, but that between them are placed the secondary laminæ both vascular and horny. Therefore he argues, and with very great weight, that the vascular cannot secrete the horny laminæ, but that the secondary vascular secrete the secondary horny laminæ.

If a portion of wall be removed experimentally and the vascular laminæ exposed, in the course of a short time the part becomes covered with a layer of horn, and this has

* *Op. cit.*

been used as a strong argument in favour of the secretion of horny from sensitive laminæ; but the horn which is thus secreted is derived from the secondary vascular laminæ, and no one contends that these secrete the primary horny laminæ.

Moeller's argument indeed is fatal to the theory that the vascular secrete the horny laminæ, and we must fall back on the coronary substance as the available source of the secretion. The only part of this body which could furnish the horn leaves, is that portion of it insinuated between the vascular leaves where the two structures meet.

As the wall grows down the horn leaves are carried with it, so that there is a perpetual movement occurring between the slowly-travelling horny and the fixed vascular laminæ. The rate of this movement is probably about ·0125 inches in twenty-four hours, on the assumption that the wall grows $\frac{3}{8}$ of an inch in the month.

During the time the horny are gliding through the sensitive leaves the vascular lamellæ furnish them with horny lamellæ; and, as we have previously seen, when the wall reaches the sole the horny lamellæ are left behind, and the laminæ emerge with the wall destitute of these structures.

The Use of the Bars.—The inflected portion of the wall, known as the Bars, runs, as we have previously mentioned, forwards under the foot instead of completing the circle of the wall. The object of turning aside from the complete ring the wall looked like forming, is to make room for the elastic posterior foot, viz., the plantar cushion and foot-pad; and the reason why the wall is turned in instead of ending abruptly, is to afford a solid bearing to the posterior part of the foot, to give additional strength, and to secure a more intimate union with the sole.

The bars being part of the wall are intended to bear weight; in the foot of the wild horse and zebra, the bars present the most extraordinary development the result of weight-bearing.

The Use of the Sole is quite clear, its function is protection

to the sensitive parts above. Its normally concave shape proves that it is not intended to bear on the ground, and the acute lameness which results from a stone in the foot gives further proof, if any were required, of its indifferent weight-supporting properties; that margin, however, in contact with the wall can bear weight (see p. 478).

Under the influence of the body-weight the sole becomes slightly flatter, especially that portion of it situated posteriorly, viz., the horns of the crescent. When we come to study the expansion of the foot the object of this flattening will be more apparent.

The sole grows from the sensitive sole, as previously described.

The Use of the Foot-pad.—This is one of the chief anti-concussion mechanisms in the foot; it is there to break the jar, and it does so by receiving in conjunction with the posterior wall the impact of the foot on coming to the ground. This is imparted to the plantar cushion, and through the lateral cartilages to the wall of the foot, which bulges, or, as it is termed, expands. In breaking the jar (not only to the foot but to the whole limb), it is assisted by its elastic rubber-like nature, and these properties are also of the highest value in causing it to have a grip on the ground and thus prevent slipping, in which function its peculiar shape helps considerably.

The foot-pad needs for its perfectly healthy condition contact with the ground; it is strange that in this respect two structures situated side by side, viz., the sole and pad, should be so opposed in function. We know practically that if the latter be kept off the ground the part atrophies, the heels contract, the foot is rendered smaller, and the pad becomes diseased. This wasted condition of the pad and narrow foot may be restored by pressure, but that pressure must be ground pressure. It is possible by means of a bar-shoe to throw considerable pressure on the pad and heels, but the foot still contracts; it is only when the pad is bearing on the ground that it continues in a healthy condition, and retains its normal size. Foot-pad pressure is, therefore, one

of the golden rules in shoeing if the part is to exercise its natural functions.

The Lateral Cartilages. — We have dealt with certain functions of the lateral cartilages, but it will not be amiss to summarise our knowledge of their use.

1. They form an elastic wall to the sensitive foot, and afford attachment to the vascular laminæ.

2. As the foot increases in width (expansion), the cartilages carry outwards the sensitive laminæ which are attached to them, and so prevent any disturbance of the union of the horny and sensitive laminæ.

3. Large venous trunks pass through and close to the cartilages of the foot, and the movements of the cartilages assist the venous circulation.

4. The object of having lateral cartilages in the foot is to admit of expansion under the influence of the body-weight. This increase in the width of the foot is brought about by pressure on the pad, which widens and presses on the bars at H, Fig. 90, and at the same time tends to flatten the plantar cushion, both of which factors force the cartilages slightly outwards. When the posterior wall retracts the cartilages are carried back. When this elastic cartilage becomes converted into bone, its functions are destroyed, and lameness occurs. By a simple operation relief from this lameness may, in a large proportion of cases, be secured; it is possible to demonstrate that by surgical interference the hoof may be made permanently wider, and thereby rendered capable of accommodating, without inconvenience to the animal, lateral cartilages which have undergone an increase in size as the result of ossification. This operation is based on physiological principles.

Anti-Concussion Mechanism.—Practically the whole physiology of the horse's foot is a consideration of the factors whereby the parts are saved from concussion, in spite of wear and tear, batter and jar.

The weight carried on each fore foot when the horse is standing is rather more than one quarter the weight of the

body; during locomotion the amount varies from half the weight in the trot, to the entire weight in certain stages of the canter and gallop.

The mechanisms which exist in the foot to save concussion, are not only intended for the protection of the

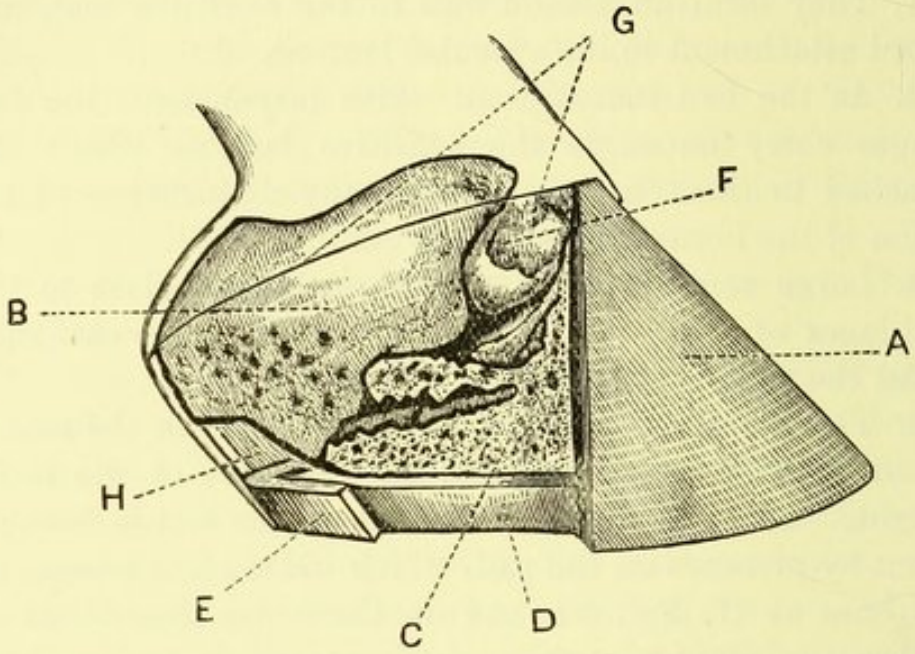


FIG. 90.—PORTION OF THE WALL REMOVED, TO SHOW THE POSITION OF THE RIGID AND ELASTIC SENSITIVE FOOT.

A, wall of the foot; B, the lateral cartilage; G, a line which represents the coronet; C, the pedal bone—the line of union between the pedal bone and lateral cartilage is well seen; F, is a portion of the corona; D, a portion of the sole exposed by the removal of the wall; E, the heel of the wall left at its plantar surface to show the arrangement of the bar, H, which passes behind and within the lateral cartilage B. The figure, which is accurately drawn from a photograph, is intended to show what an extensive surface the lateral cartilage presents, and the variety of surfaces to which the sensitive laminæ are attached; they cover B, C, and F, the latter in the living animal being the position of the extensor pedis tendon and lateral ligament of the foot, to which the laminæ are attached. Further, the figure shows the division of the internal foot into an elastic and a rigid portion.

foot but also to save the limb, and they may be tabulated as follows:

1. The yielding articulation in the pedal joint.
2. The increase in the width of the foot when the heels come to the ground, known as expansion.

3. The elastic foot-pad.

4. The slight descent of the pedal bone and with it the sole.

Some of these we have already considered, the others will now be dealt with.

Expansion.—We have here retained a word warranted by custom though perhaps not free from objection. By its use is indicated the fact that the wall of the foot opposite to the heels becomes wider when the weight comes on the part, Fig. 91. The increase in the width of the foot is not

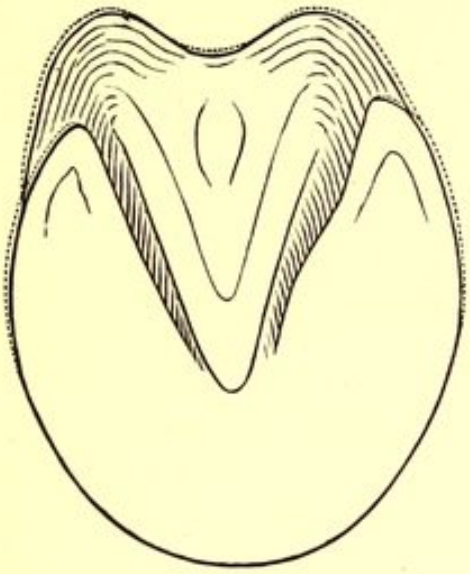


FIG. 91.—DIAGRAM TO ILLUSTRATE THE EXPANSION OF THE FOOT. (LUNGWITZ.)

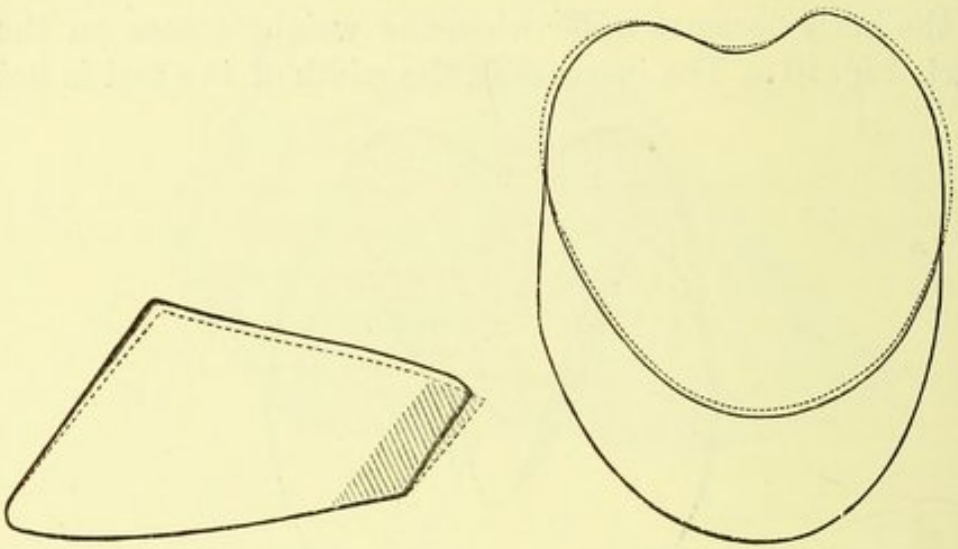
The unbroken outline illustrates the shape of the foot at rest; the dotted outline shows the portion of the foot which has yielded laterally under the influence of the body weight.

due to a something being added to it, but to an alteration in the shape of certain structures already existing in it; if, therefore, the foot becomes wider it does so at the expense of other parts altering their shape.

As a matter of fact an increase in the width of the foot is not the only change which occurs, it can be shown that the heels at the coronary edge sink closer to the ground, whilst the coronary edge of the wall in line with the toe of the foot retracts, or travels backwards and downwards, Fig. 92 A.

When the foot comes to the ground the posterior wall and frog, in all fast paces, first receive the weight. Under the

influence of the body-weight the foot-pad is compressed and becomes wider, the plantar cushion with which it is closely in contact is also compressed and becomes wider. The effect of this increase in width is that the foot-pad presses on the bars, whilst the plantar cushion presses on the cartilages both of which yielding laterally force apart the wall at the heels. When the weight is taken off the foot



A. B.

FIG. 92.—DIAGRAMS TO SHOW THE AREA OVER WHICH THE WALL EXPANDS, AND TO ILLUSTRATE THE RETREAT OF THE ANTERIOR CORONARY EDGE OF THE HOOF, AND THE SINKING OF THE HEELS.

A. The unbroken outline shows the shape of the foot with no weight on it; the dotted outline illustrates the retreat of the coronary edge in front and sinking of the heels.

B. In this figure the hoof is looked at from above; the unbroken outline is the coronary edge from heel to heel. The dotted line shows the change in shape it undergoes under the influence of the weight of the body.

In A the shaded part of the wall is to illustrate the area which expands.

the heels return to their original position, and the foot becomes narrower.

The increase in width which the foot undergoes is something very small, this is probably the reason why for years it has never been accepted as a fact, and that in this country in particular few were found who gave the theory any support. The employment of delicate apparatus such as

that used by Lungwitz* and others, and experimenting upon feet which have not been mutilated in shoeing, have placed the question beyond all doubt.

The area over which the wall expands can be seen in Fig. 92 A, the shaded portion of the heel represents the part which yields laterally. At times expansion is obtained at the coronet and little or none on the ground surface, but as a rule the amount obtained at the coronet can also be obtained near the ground.

As to the amount of expansion no definite statement can be made, it is small but is influenced by the shape of the foot; horses with low heels and full well-developed frogs register a larger amount than where the heels are high and rigid. The measurements obtained by us with very delicate apparatus were smaller than those obtained in Germany by Lungwitz. On an average we obtained an expansion of $\frac{1}{30}$ of an inch for half the foot, or $\frac{1}{15}$ of an inch total increase in width, by simply lifting up one fore foot, and so causing the horse to throw double weight on the limb. Doubtless during locomotion a greater expansion than this occurs.

The question may be asked what advantage can be gained by such a small increase in the width of the foot? Small as the increase is, yet it makes all the difference between a yielding and an unyielding block of horn being brought to the ground; it 'gives' instead of offering resistance, and this 'give' is sufficient to prevent the hoof from being fractured, whilst the pad which caused the expansion has acted as a buffer and assisted to destroy concussion.

There is no point in the physiology of the foot which has given rise to greater discussion than this question of expansion, but we submit that its existence is not only proved, but that it is provided for by the anatomical construction of the part and the elastic nature of horn.

The retraction of the coronary edge of the foot in front, and the sinking behind (see Fig. 92), are accompanied by a

* *The Journal of Comparative Pathology and Therapeutics*, vol. iv., 3.

tense condition of the coronary substance which Lungwitz describes as an elastic ring; Macdonald* in this country regards it as a hydraulic ligament which supports the pedal joint under the strain to which it is exposed. The tense state of the coronary substance is probably due to the alteration in the shape of the coronary edge of the foot, whilst the value or existence of any hydraulic support in connection with the joint has yet to be demonstrated.

In addition to the changes in the coronary edge of the foot during the period of expansion, another condition is present, viz., a *compression* of the wall under the influence of the body-weight, which produces a diminution in its height. This can be roughly demonstrated in the following manner: If a portion of the wall, say between the heel and quarter, be cut away so as just to clear the shoe when the latter is fitted, it will be found on placing weight on the limb by lifting up the opposite fore-foot, that the wall has now descended sufficiently to touch the shoe.

The only explanation which can be afforded is that given above, viz., the wall has undergone sufficient compression to allow the part which was originally clear of the shoe to come in contact with it, and to produce this it must have diminished in height.

The Descent of the Pedal Bone is the last factor employed in saving concussion, and the existence of this has been as strenuously denied as the expansion of the wall; there is however no difficulty in demonstrating it, and we can readily see the value of this function.

Concussion to the sensitive foot is prevented by a slight up-and-down play between the sub-laminal tissue and the pedal bone; as the weight comes on the foot the pedal bone slightly descends, to rise again when the weight is taken off it. As the pedal bone descends, the horny sole on which it is resting also slightly descends and comes nearer to the ground; this is one reason why the sole is concave instead of flat. The descent of the internal foot saves concussion, in the same way that it is easier to catch a cricket-

* *Veterinary Record*, No. 145, 1892.

ball with a retreating movement of the hand than by rigid opposition; further it facilitates the circulation.

The descent of the pedal bone is one of the safeguards of the sensitive foot.

Vascular Mechanism.—Lying as the foot does furthest from the heart, we are led to inquire why it is that the blood is able to circulate through it so thoroughly, and whether other means are at hand for assisting the force of the heart in facilitating the circulation. Such means, we know, do exist.

Though the contraction of the left ventricle is sufficient under ordinary circumstances to bring the blood back to the right side of the heart from any part of the body, (as we have pointed out in dealing with the circulation), it is doubtful whether this would be wholly sufficient to empty the foot of blood or keep the considerable plexus of veins full. This plexus is shown in Fig. 86, which is a reproduction from a photograph of a corrosion injection.* The figure conveys very accurately an idea of the remarkable venous arrangement of the foot.

The venous circulation is assisted by two movements in the foot, viz., the expansion and contraction of its posterior wall, and the descent and elevation of the inner foot.

There is no difficulty in seeing the movement imparted to a column of fluid circulating in these parts, for if a plantar vein be divided and the horse made to walk, every time the foot comes to the ground the blood spurts out from the vein as if from an artery; when the foot is taken off the ground the stream of blood becomes greatly reduced. A perfect pumping action is in this way produced.

We must accept it, therefore, as a proved fact that the venous circulation is largely facilitated by the expansion and contraction of the posterior part of the foot; during expansion the blood is being driven upwards, and during

* The figure appeared in an article by Dr. C. Storch, of Vienna, on the Venous system of the Horse's Foot, 'Oesterreichischen Monatschrift für Thierheilkunde,' 1893.

contraction the veins relaxing aspirate the blood into their interior.

So perfect are these changes that, as previously pointed out, there are no valves in the veins of the foot, and none are found nearer than the middle of the pastern. To assist the circulation, the large venous trunks at the postero-lateral part of the foot are in close connection with the lateral cartilages, and some even pass through their substance.

We may now with advantage summarise what has been said about the anti-concussion mechanisms:

When the weight comes on to the foot, it is received by a yielding foot articulation, an elastic wall, bars, pad, and through this the plantar cushion. The elastic posterior wall is pressed outwards by the compressed indiarubber-like pad and plantar cushion, and it slightly expands from the ground surface to the coronet. At the moment of expansion, the bulbs of the heel of the foot at the coronary edge sink under the body-weight and come nearer the ground, and as a result of this the anterior coronary edge retracts. The pedal bone slightly descends through its connection with the sensitive laminæ, and presses the sole down with it, while the wall of the foot diminishes in height under the compression to which it is exposed. Under these conditions the blood-pressure in the veins of the foot rises, and the vessels are emptied. When the weight is removed from the foot the bloodvessels fill, the pad and posterior walls contract, the bulbs of the heel rise, and the foot becomes narrower from side to side; at the same time the anterior edge of the coronet goes forward, and the pedal bone and sole ascend.

Such are the physiological features of the foot which facilitate the circulation and help to counteract concussion. Foot-lameness is only too frequent, but if it were not for the mechanisms we have described, it would not be possible for horses to work for a single day.

Physiological Shoeing.—It is impossible to conclude this chapter on the foot without some mention of what might be termed physiological shoeing.

We all recognise the evils of shoeing as strongly as we recognise its necessity. By bearing in mind the functions of the various parts of the foot, we can certainly reduce these evils to comparatively narrow limits. The following rules form the basis of physiological shoeing;

1. The reduction of the wall to its proper proportions, such as would have occurred through friction had no shoe been worn.

2. Fitting the shoe accurately to the outline of the foot, not altering the latter to fit the shoe. Rasping away the exterior of the crust to fit the shoe, not only renders the horn brittle, but is so much loss of bearing surface.

3. The exterior of the wall should be left intact. The practice of rasping the wall for the sake of appearance destroys the horn, and allows of so much evaporation from the surface of the foot that the part becomes brittle.

4. The sole should not be touched with the knife; it cannot be too thick, it is there for the purpose of protection.

5. The bars should not be cut away, they are part of the wall, and intended to carry weight. The shoe should rest on them.

6. The foot-pad should not be cut, but left to attain its full growth. No foot pad can perform its functions *unless on a level with the ground surface of the shoe.*

7. The pattern of shoe is immaterial so long as it has a true and level bearing, and rests well and firmly on the wall and bars. We believe the simpler the shoe the better, viz., one plain on both ground and foot surface. It should be secured with no more nails than are absolutely necessary, as the nails destroy the horn. The nails should not be driven higher than needful, for high nailing is ruinous to feet.

Such, briefly, are the conditions which fulfil physiological shoeing.

CHAPTER XVIII.

GENERATION AND DEVELOPMENT.

The **Spermatic Fluid** is alkaline or neutral in reaction, of viscid consistence, and was found by Lassaigne, who examined the material taken from the vesiculæ seminales of the horse, to contain a large quantity of water, an abundance of a substance termed by him spermatin, mucus, soda, chloride of sodium, and phosphate of lime. Colin describes the spermatic fluid of a bull to consist on standing of two parts, the upper stratum colourless and transparent, the lower milky and opaque. He regards the former as prostatic fluid, the latter as spermatic. More recent analyses of this fluid show it to contain serum and alkali albumin, nuclein, lecithin, cholesterine, fat, leucin, tyrosin, kreatin, inosit, sulphur, alkaline earths, and phosphates.

The essential element of the spermatic fluid is the spermatozoa, without which the fluid is not fertile. These exhibit spontaneous movement, the long tail moving from side to side, by which means the organism is propelled when placed in the body of the female. The vitality of the spermatozoa is considerable under suitable conditions, and when placed in the body of the opposite sex they have been found very active seven or eight days after copulation. Colin has found them in a similar state in the vesiculæ seminales eight days after castration. The spermatozoa are readily killed; Colin says that those of the ox, horse, and carnivora are killed immediately by ordinary or acidulated water, glycerine, etc.

The prostatic fluid precedes the spermatic in ejaculation, and in stallions and bulls, when excessive daily demands are made, the fluid ejaculated is largely prostatic and infertile.

The testicular products of hybrids, such as the mule, are infertile and said to be devoid of spermatozoa.

The act of copulation consists in the introduction of the penis of the male into the vagina of the female. With some animals, as the dog, the introduction is facilitated by the presence of a bone in the substance of the penis; but in all the penis has to become erect and larger before it is fit for penetration.

The **Phenomena of Erection** is produced by a gorging of the vessels of the penis, caused by a dilatation of the arteries, and pressure on the veins. This condition is brought about by the nervi erigentes, the fibres of which contain dilator nerves for the walls of the bloodvessels. An erection centre also exists in the spinal cord, which is normally under the control of the vaso-motor centre in the medulla, though it may act independently of it as in persistent erection after laceration of the cord.

Stimulation of the centre may even at the moment of death lead to erection and ejaculation. Colin has observed this in stallions destroyed by section of the medulla, injuries to the head, or even simply by bleeding. Contraction of the bladder and evacuation of the contents of the intestines in horses which have been killed by destroying the brain, is a regular accompaniment of this mode of death; and whatever it is which leads to a contraction of these parts, also apparently leads to a contraction of the seminal vesicles and urethra. It has been supposed that the phenomenon may be due to asphyxial blood stimulating the centre, but this cannot be a complete explanation, in fact in the case of the horse the bowels and bladder are emptied almost instantaneously with the stroke which destroys life.

The influence of the cerebrum on the mechanism of erection, viz., in stimulating the centre in the cord and medulla, is well known.

The first portion of the penis which receives the excess of blood in erection is the corpus cavernosum; the spongiosum and glans are not fully erect in the stallion until the penis is introduced into the vagina; at the moment of ejaculation in this animal the glans swells enormously, apparently to cover or grasp the os uteri. The blood sent to the penis for the purpose of erection is practically, though not completely, imprisoned by the compression exercised by the muscles of the perinæum on the veins of the part, and this mechanism further maintains the blood pressure.

If the nerves of the penis be divided in the horse, erection is impossible though desire may be intense. Gunther's and Colin's experiments have placed this beyond doubt.

Though the organ in the horse assumes such considerable proportions, in the bull this is not so marked. The peculiar penis in this animal comes to a narrow point without any of the swelling observable in the stallion. In the ram, also, the penis is narrow and pointed, and the vermiform appendage at its extremity appears essential for successful impregnation, for if it be removed, it is said the animal proves sterile. In the dog the increase in the size of the penis is mainly at its posterior part, and the bulbous swellings there observable are the portions grasped by the spasm of the sphincter cunni of the female, rendering withdrawal impossible until complete relaxation occurs.

Sexual Intercourse is of short duration in the majority of animals, excepting the dog and pig. Colin places it at 10 to 12 seconds for a vigorous stallion; it is exceedingly rapid, almost instantaneous, in the bull and ram, probably from the peculiar shape of their intromittent organ.

The spermatic fluid is forced into the vagina, or even directly into the uterus; the peculiar termination of the urethra of the horse, and the bulbous enlargement of the glans during the act of coition, would rather point to the fluid in this animal being, at any rate to some extent, directly passed into the os uteri, and the pointed penis of

the bull and ram makes it nearly certain that much of the fecundating fluid passes directly into the uterus.

At the moment of intercourse the uterus becomes erect, and the introduction of the male element into it is assisted by the aspiration following its subsidence. It would appear necessary in the lower animals for the fluid to pass into the mouth of the uterus, and there is probably a great deal to say in favour of the common practice of preventing the mare from straining immediately after copulation, and thus rejecting the spermatic fluid.

The actual mechanism of ejaculation is produced by a contraction of the vesiculæ seminales, and probably of the vasa deferentia, through the reflex action of the ejaculation centre in the lumbar and sacral portions of the cord. By this means the seminal fluid is forced out of the vesiculæ into the urethra, and by means of the muscles of the perinæum is forcibly ejected from the urethra.

In animals possessing no vesiculæ, such as the dog, ejaculation takes place direct from the testicle and vas deferens.

The period of heat manifests itself at certain periods; the mare is 'in season' during the spring and summer, the period lasting two to four days, and recurring every three or four weeks; during the interval the male is not accepted. The cow is much the same as the mare, while sheep take the ram in the autumn. The male is attracted to the female by a peculiar smell, which can be detected by the former at some considerable distance.

The number of ova discharged at each period varies; one for the mare and cow is generally the rule, though two may be discharged; the sheep discharges one to four ova at a time, while the pig discharges ten or more.

The **Period of Puberty**, or that time in the animal's life when it is capable of procreation, has been put at 1½ years for the horse, 8 to 12 months for bovines, and 6 to 8 months for the sheep, pig, and dog. There is, however, a great difference between capability and *fitness* for procreation; the horse is fit at from 4 to 5 years old, ruminants from

1½ to 2 years, the pig at 1 year, and the dog from 1 to 2 years.

Breeding from immature mares is one explanation of a great deal of the worthless material in the shape of horses which may be seen in this country.

The advent of maturity is marked by certain changes in form, particularly in horses. They lose their awkwardness, the outline of the frame becomes more consolidated and in greater unison. In the male the neck becomes thick and curved, the voice deepens, and the whole appearance denotes life and vigour; the temper is usually irritable and uncertain, and often extremely vicious.

The age at which procreation ceases is not known. Fleming* says that mares have been known to produce foals at 28, 32, and 38 years of age, and it is certain that some of our best stallions are well advanced in years.

The life of all things must necessarily be limited, tissues waste and decay, and the various organs become unfitted to perform their several functions. That the species may not become extinct provision must be made for its permanence, and the living body sets aside cells or accumulations of cells in ordered sequence to form organs. The duty of these specialised cells is to provide material for the new being.

Copulation is not necessary in all animals, nor indeed in any. What is required is merely an interchange of elements from the nucleus of two different cells. To this last statement a slight exception might be taken, because there is known a condition, parthenogenesis, where the access of a second element is not required, but this method of development is unknown in the higher animals.

The essential elements for procreation are the male unit, the sperm cell or spermatozoon, and the female cell, the egg or ovum. The fusion of the nuclear elements of these two different cells results in a new structure, the fertilized ovum, and from this the embryo develops, embodying in itself the hereditary properties of both parents.

* 'Veterinary Obstetrics.'

The sperm cells are developed in the testes of the male, the ovum is derived from and matured in the ovaries of the female.

The Ovaries.—The ovaries are abdominal organs situated behind the kidneys, and attached to the extremities of the broad ligaments of the uterus. They are solid organs and about half the size, or a little less than half the size, of the testicle of the male. An exception to this must be made in the case of the sheep, here the ovary is very small compared to the testicle of the ram, this animal for its size having probably the largest of testicles, certainly among the domestic males.

The ovaries of the mare, cow, and sheep, are somewhat ovoid with a slight depression termed the hilum; the ovaries of the pig and dog are lobulated and resemble a bunch of grapes; the ovary of the cat and rabbit is more or less lenticular. Covering the ovary is found a modified endothelium, the germinal epithelium. The substance of the ovary is divided into cortex and medulla; the cortex being that portion containing the developing eggs or ova, the medulla being the solid, connective tissue, vascular core.

Germinal Epithelium.—This is of the columnar type (a modification of the endothelium of the body cavity), and is found over the whole ovary except where the ligament of the ovary passes to the uterine horn, and where the broad ligament of the uterus is attached to the ovary itself. The epithelium is called germinal because from it the eggs are developed, though it is probable that no new ova are formed after birth.

During development the germinal epithelium grows into the body of the ovary as a long cylinder of cells. These cells eventually are cut off from any connection with the epithelium covering the ovary, and one cell, it may be two, takes on the appearance and characters of an ovum. The other cells that have accompanied and been constricted off with the ovum, take on the duties of the membrana granulosa, which is merely a cellular sphere containing the

ovum. The earliest ova are found in the cortex as large cells enclosed in the simple one-layered membrana granulosa.

The changes that occur from this primitive condition until the ovum is mature, are chiefly indicated in the wall of the structure containing the egg, the so-called Graafian follicle. This at first is purely epithelial, as mentioned above, but the cells of the original single layer divide rapidly, and thus the ovum comes to lie within a solid cellular sphere. In the meantime a connective-tissue capsule, the tunica fibrosa, has originated around the sphere, and finally a cavity appears owing to a splitting of the membrana, a cavity containing a fluid under pressure, the liquor folliculi. The ovum continues to grow slowly until it reaches about $\frac{1}{125}''$ in diameter, and is found in an upheaval of the cells of the membrana granulosa known as the discus, or cumulus proligerus.

The mature Graafian follicle consisting of the above-mentioned parts, (from without inwards, tunica fibrosa, membrana granulosa with its cavity containing liquor folliculi and ovum) and containing the ovum, extends throughout the thickness of the cortex of the ovary, and daily becoming larger it appears eventually as a vesicle on the surface. The formation of the liquor folliculi under pressure, and its tendency to move in the direction of the least resistance will influence the point of rupture, which is said generally to occur at the hilum or thereabouts.

When rupture of the Graafian follicle occurs the ovum is flushed out, and at the same moment, according to Henson, the fimbriated extremity of the Fallopian tube becoming erect grasps the ovary, and thus the escaping ovum is received into its 'duct.' Probably the converging furrows found on the plicated extremity of the Fallopian tube may assist in directing the ovum to the ostium abdominale. If by chance the ovum be not caught and carried away to the uterus as described, it may fall into the peritoneal cavity and perish, or if it has been already fertilized abdominal fœtation may occur, the peritoneum acting as a matrix in which the embryo may develop.

The Ovum.—With the exception of those produced by the *prototheria* (duck-mole and spiny ant-eater), the mammalian ova are extremely small. They vary in size from $\frac{1}{150}$ to $\frac{1}{120}$ of an inch, and although not to be compared to those of birds, reptiles, or amphibians, yet they are undoubtedly the largest cells found in the mammalian body. The greater size of the eggs of birds, reptiles and amphibians is due to the quantity of deutoplasm or yolk contained therein. In mammals this is small in amount, owing to the speedy union of the developing ovum to the uterine wall, and intimate connection with an abundant food supply.

The ovum is a typical cell, it is spherical and more or less translucent. It has a thick cuticle or zona radiata, within which lies the protoplasm and vitellus or yolk, confined, as Van Beneden pointed out some time ago, in a special membrane, the vitelline membrane. Within the vitellus or yolk is the germinal vesicle or the nucleus of the cell, and in this the germinal spot or nucleolus. This is the structure of the ovum prior to its extrusion from the Graafian follicle; but either just before or immediately after escape from this, and prior to impregnation, a change or changes must occur. This change more especially involves the nucleus or germinal vesicle—the germinal spot or nucleolus being according to some authorities merely a storehouse of nourishment for the nucleus—and is known as the formation of the polar bodies.

The extrusion of the **Polar Bodies** has been studied by Van Beneden in the ova of the *ascaris megalocephala* of the horse. The first stage is that of indirect division of the nucleus, and movement of this towards the periphery of the cell. The nucleolus probably divides in a similar manner, but its fate is not known. The nucleus having divided, one half is extruded into a space beneath the zona radiata and above the vitelline membrane, the perivitelline space. The half still remaining in the ovum divides, and a second time a daughter nucleus is extruded, forming the second polar body. It is extremely probable, and generally

believed, that similar phenomena take place in the mammalian ovum.

What is the significance of the polar bodies? There have been many explanations offered, and as many rejected. Two, however, are important and worthy of mention. Minot and Balfour believed that they were intended to prevent parthenogenesis, or the possibility of a new creature developing from an ovum that had never received a male element. Weismann believes that by the loss of certain elements by means of the polar bodies, the ovum is rendered receptive for characters of the male; in other words, it has a bearing upon the hereditary properties of ovum and sperm, the polar bodies carrying away superfluous histological and genetic properties. In Weismann's own words, 'Only one polar body can signify the removal of the ovogenetic nucleoplasm from the mature egg, and the second is obviously a reduction of the germplasm itself to half of its original amount.'*

As a result of the rupture of the Graafian follicle, a rent is made in the ovary. This wound fills with blood from the opened vessels, and for some time afterwards appears as a pigmented spot. If pregnancy has not supervened, it undergoes a retrogressive metamorphosis and soon disappears. If, however, the ovum is fecundated, the corpus luteum, as this pigmented spot is termed, continues to grow, and may be observed in the ovary even near term. The corpora lutea 'consist of columns of large yellowish cells, with intervening vascular fibrous tissue, which converge to a central strand of connective tissue occupying the axis of the nodule' (Schäfer). The ovum, having got rid of the polar bodies, is now ready for the sperm-cell—it is the female pronucleus.

The Testicles.—If the developing embryo be examined in early life, we find the genital ridges arising from the mesoblast (the middle germ layer) on either side of the mesenteric insertion. Soon the epithelial cells of these genital ridges are observed to take on different characters, some becoming

* Weismann, 'Essays,' second edition, vol. i., p. 357.

large, and eventually known as primordial or primitive ova. At this stage of development it is impossible to predict the future sex of the creature. These primitive ova are the forerunners of the ova proper, and are mother cells of those that give rise to spermatozoa. Thus the ova and sperm-cells have a similar origin.

The testicles are developed in the same position as the ovaries, but during fœtal life they move down into the scrotum, being directed by the so-called gubernaculum testis. The testicles are solid organs with an external covering of serous membrane, and possessing a tunica albuginea, and a stroma or framework of fibrous tissue. This stroma is thickened (in the horse) in the interior of the body of the testicle to its anterior and superior part, forming the corpus Highmori, but in 'the dog, cat, bull, pig, rabbit, etc., it (the corpus Highmori) is central in position' (Klein). The spaces of the meshwork are occupied by the seminiferous tubules. These tubules are highly convoluted in the parts immediately concerned in the formation of spermatozoa, and commence usually by blind extremities.

If the changes in the cells found on the basement membrane of the tubules be followed until the seminal elements are ready for discharge, we find that the cells of the lining epithelium divide into two daughter cells, one remaining attached to the basement membrane, the sustentacular cell, the other becomes a spermatogen. The spermatogen-cells divide and subdivide to form other cells that are recognised as spermatoblasts. These spermatoblasts elongate and pass into spermatozoa, collecting into sheaves as they do so, and becoming attached to the sustentacular cells that are placed on the basement membrane. These sustentacular cells minister to the needs of the developing sperms until they are fully matured. The latter are then set free, and pass into the lumen of the tubule.

A mature spermatozoon under favourable conditions is active, moving about rapidly by means of its long vibratile tail in the seminal fluid. It is formed of a head, a middle

piece or body, and a tail. The head corresponds to the nucleus, and is constantly present, the middle piece and tail is developed to a varying degree in different animals. In the horse the length of the head, which is bluntly pear-shaped, is about 5 μ, the tail is eight or nine times as long as the head. It is supposed that the sperm-cell extrudes polar bodies as does the ovum, but they have not been recognised. The head of the sperm may be considered as the male pronucleus. When access has been gained to the uterus, the spermatozoa journey along the horns and into the Fallopian tubes, where the ova are fertilized.

Impregnation.—The spermatozoon encounters the ovum in the Fallopian tube, and passes through the zona radiata, one of the fine pores present doubtless facilitating the passage. It then reaches the vitelline membrane, which moves slightly towards it. When within the vitellus, the middle piece and tail are lost sight of—probably they fuse with the protoplasm—and the head alone is seen. The two pronuclei (male and female) come together, and apparently form a single nucleus, though it is affirmed that the chromatin elements of the two remain separate. A single spermatozoon alone suffices; if two should gain access to an ovum a monster is said to result, and it is believed that a spermatozoon cannot enter an egg that is already fertilized.

Segmentation of the Ovum.—Ova are holoblastic or meroblastic according to the method of segmentation. This depends upon the amount of yolk contained in the egg, if very little or none the segmentation is holoblastic and complete as in the eggs of mammals; if abundant as in birds, the segmentation is meroblastic and partial. Ova with little or no yolk are alecithal, with yolk are centrolecithal or telolecithal according to distribution.

After fusion of the two pronuclei the resulting nucleus begins to divide, and there first results two cells which are not equal in size. These also divide, each into two, and the inequality of size of the first generation is impressed upon the second, and after the third division, when eight cells have resulted, we find four large cells and four some-

what smaller. From this time the smaller cells divide more rapidly than the larger and become superficial, the larger cells remaining in the centre (Fig. 93, I.). Thus as the result of repeated division there results a mulberry mass of cells, the small cells being external, the large cells internal. (It is at this stage that the segmenting ovum

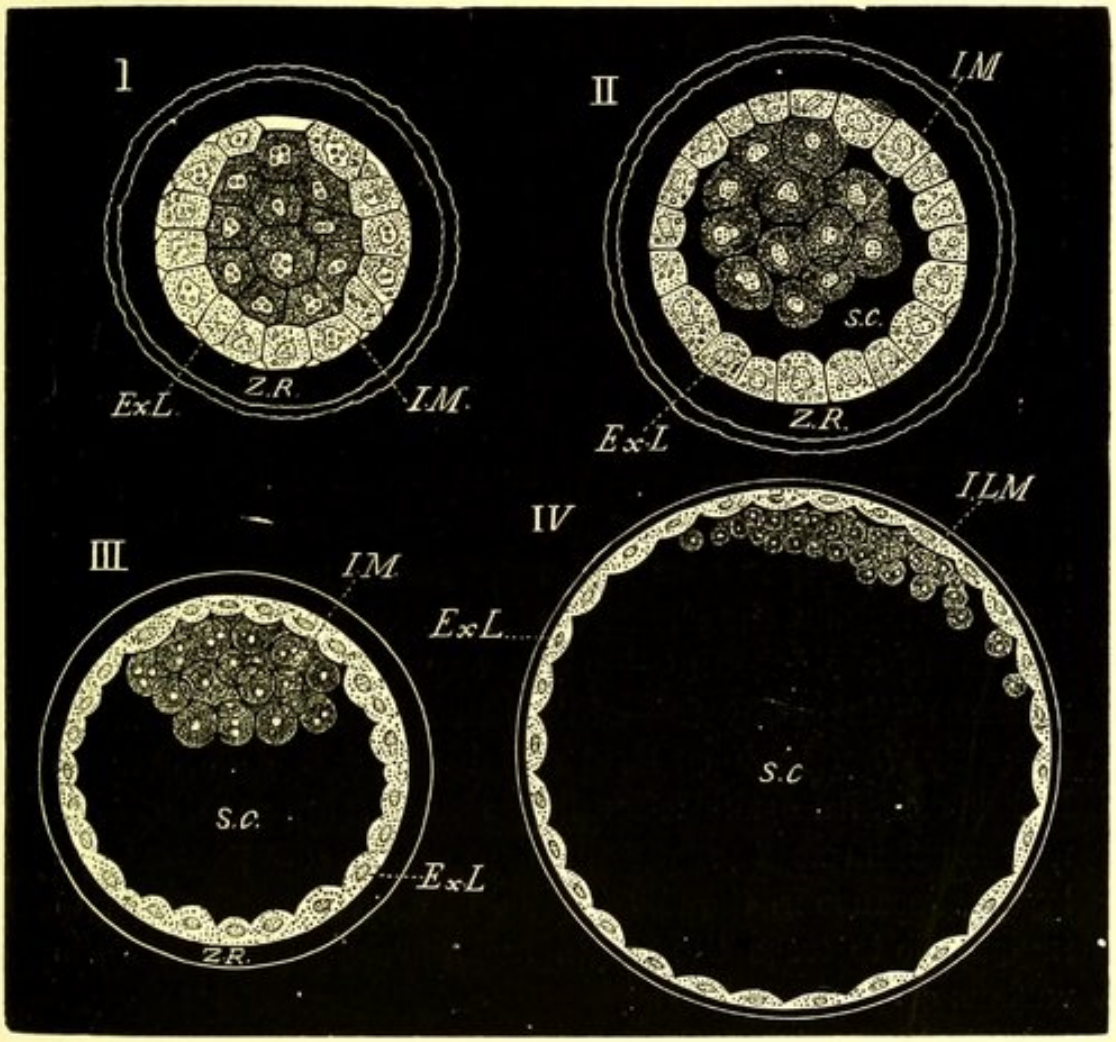


FIG. 93.—SECTION OF A RABBIT'S OVUM AT THE CLOSE OF SEGMENTATION. II., III., IV., STAGES IN THE FORMATION OF THE BLASTODERMIC VESICLE. (E. v. BENEDEN.)

Z.R., Zona radiata; *Ex.L.*, External layer of cells; *I.M.*, Inner mass of cells; *I.L.M.*, Inner lenticular mass of cells; *s.c.*, Segmentation cavity.

enters the uterine horn from the Fallopian tube; such has been observed in the rabbit.)

The next change observable is the appearance of the segmentation cavity (Fig. 93, II.). This first appears as a cleft between the inner large cells and the outer small cells,

this rapidly increases in size at the expense of the inner cells, which are pressed together forming a disc-like patch within the now hollow sphere of small external cells. This is the blastodermic vesicle, and is much larger than the original ovum. The lens-like mass of inner cells flattens somewhat, still however remaining thicker in the centre; this central thickening being the first sign of the embryonic or embryonal area (Fig. 93, III. and IV.). The spherical blastodermic vesicle rapidly becomes ellipsoidal, and the membranes or coverings of the ovum become thin and attenuated; the vitelline membrane indeed may have disappeared.

The next stages in the blastodermic vesicle are not clearly understood, but it appears that the wall of the vesicle is one cell thick except at the embryonal area, where two layers are to be seen. This is the bilaminar blastoderm, the superficial layer of which is epiblast, the inner hypoblast. If the embryonal area be examined from a surface view it is seen to be pyriform in outline, and in its posterior part the primitive streak appears. This streak is due to a thickening—to the appearance of the third permanent layer of cells—of the mesoblast, which is derived probably from both epiblast and hypoblast. These three layers constitute the trilaminar blastoderm, and here we may summarise the various organs derived from these layers, because in the short space at our disposal it will be impossible to trace the origin and development of all the various organs.

From the *epiblast* the following develope: The whole of the nervous system, including the brain, spinal cord, peripheral nerves, and sympathetic system. The epithelial structures of the organs of special sense. The epidermis and its appendages, including hairs, hoofs and nails. The epithelium of all glands opening upon the surface of the skin, including mammary glands, sweat glands and sebaceous glands. The epithelium of the mouth (except that covering the tongue and posterior part of the mouth which is hypoblastic) and glands opening into it. Epithelial

covering of anus. The enamel of the teeth. The epithelium of the nasal passages, upper part of pharynx, and cavities and glands opening into the narial passages, *e.g.*, sinuses of head, etc.

From the *mesoblast:* The urinary and generative organs (except epithelium of urinary bladder and urethra). All the voluntary and involuntary muscles of the body. The whole of the vascular and lymphatic system, including serous membranes and spleen. The skeleton and all connective tissues. The amnion is partly epiblastic and partly mesoblastic.

From the *hypoblast:* The epithelium of the alimentary tract from the back of the mouth to the anus, and all the glands opening into this part of the tract, such as the liver, pancreas, etc. The epithelium of the Eustachian tube and tympanum. The epithelium of the bronchial tubes and air-sacs of the lungs. The epithelium lining the vesicles of the thyroid body. Epithelial nests of the thymus. Epithelium of the urinary bladder and urethra. The allantois is partly hypoblastic and partly mesoblastic.*

At the stage mentioned in a previous paragraph, viz., the appearance of the mesoblast, the hypoblast has grown along the inner surface of the epiblastic layer, and nearly lines the whole blastodermic vesicle, which now becomes ellipsoidal and filled with a coagulable fluid. In front of the primitive streak, the primitive groove appears as a linear depression bounded by two ridges, known as the medullary ridges, the groove is the medullary groove. The ridges continue to grow upwards, and then to curve inwards and approximate in the middle line from before backwards, forming a tube the foundation of the cerebro-spinal nervous system.

If a section of the embryo be taken at this stage across the medullary groove and ridges, we find placed beneath the groove and derived from the hypoblast, a mass of cells circular in section the notochord or chorda dorsalis (Fig. 94). The notochord, which is rod-like, gives rise to

* Schäfer, Quain's 'Anatomy,' Part I., Vol. I.

nothing, but around it the vertebral column develops, and rudiments of it are found even in adult life in the pulpy centre of the intervertebral disc. The mesoblast has been rapidly growing as a sheet between the epiblast and hypoblast, and if the young embryo be examined from above it is seen to be broken up into 'quadrangular masses' the protovertebræ or somites. These somites give rise to portions of the vertebræ and to the muscles of the trunk.

During the growth of the mesoblast the embryo, which is developing in front of the primitive streak, is being gradually lifted from off the blastodermic vesicle. This is brought about by a process of tucking or folding off, and first appears at the tail-end of the embryo, and extends along either side to the head; as a result there is a distinct depression or 'sulcus' surrounding the embryo. The remainder of the blastodermic vesicle is filled with fluid, and forms the *yolk sac* (Fig. 94) and this may persist in some animals, as the dog, until birth. Many believe that this yolk sac, which is absent in mammalia generally, and so abundant in birds and reptiles, points to the fact that the ancestors of mammals had large eggs even as the monotremes (prototheria) have to-day. The eggs of the ornithorhynchus or duck-mole are as large as a hazel-nut.

The *medullary* or *neural groove* which has now been converted into a canal, becomes dilated and vesicular in the head region. These vesicles are at first three in number, then five, and give rise to various parts of the brain. The lumen of the canal and vesicles persists, and we see them in the adult as the minute central canal of the cord, and the ventricles of the brain. The nervous structures of the eyeball are derived as outgrowths of the brain; the organ of smell is the nasal pit innervated from the fore part of the brain; the ear is an involution of the epiblast that also speedily receives a nervous supply from the brain.

The mesoblast about the time of the formation of the cerebral vesicles splits into two laminæ, and the space between becomes the *cælom* or body cavity (Fig. 94). The upper lamina, consisting of epiblast and mesoblast, is

known as the somatopleure; the lower lamina, consisting of mesoblast and hypoblast, becomes the splanchnopleure.

Arising from the somatopleure, at first posteriorly and then at the sides of the embryo, are ridges that grow upwards over the embryo towards the head region, to fuse and form the amnion (Fig. 94). In front of the head the mesoblast has not as yet extended, and the epiblast and

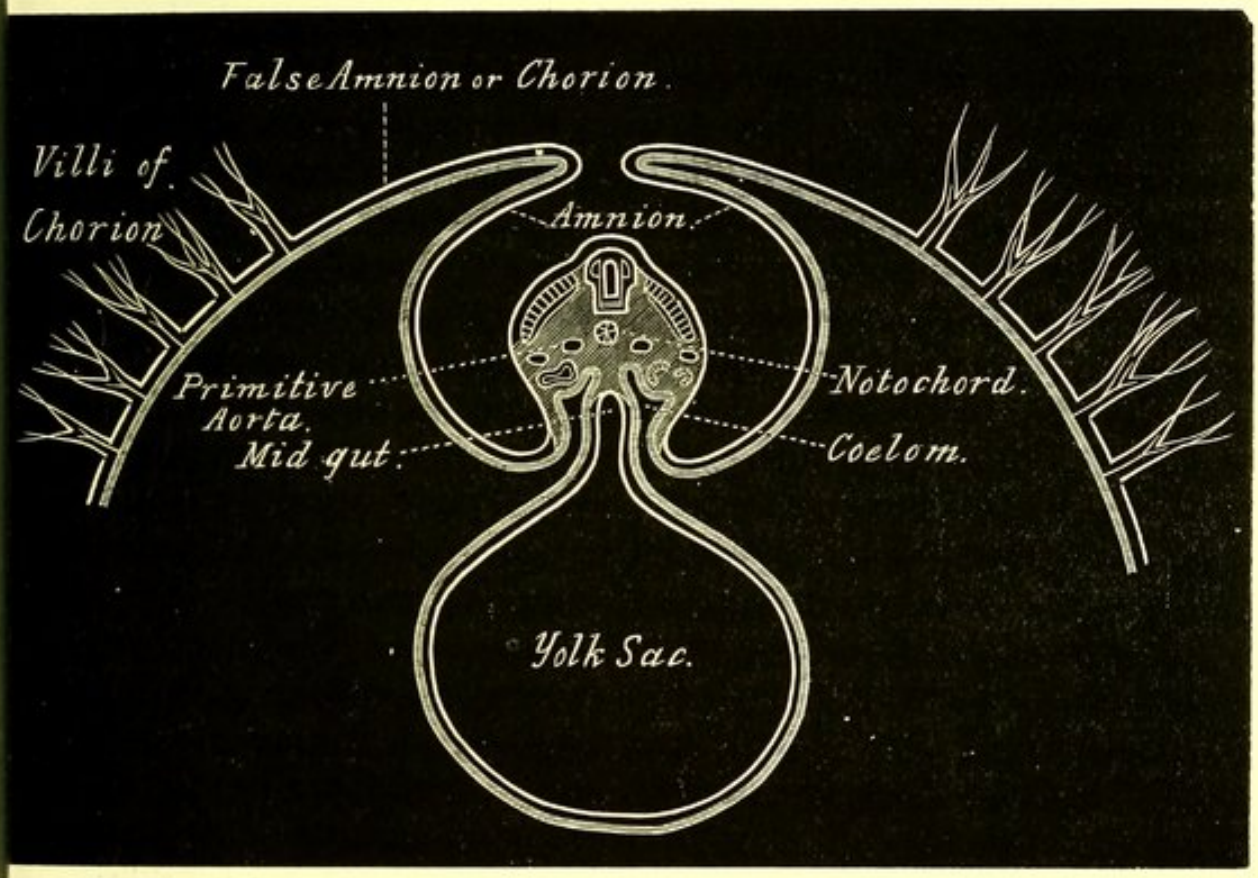


FIG. 94.—DIAGRAM OF A TRANSVERSE SECTION OF A MAMMALIAN EMBRYO, SHOWING THE MODE OF FORMATION OF THE AMNION. (SCHÄFER.)

The amnion folds have nearly united in the middle line.

hypoblast are united forming the pro-amnion. This however soon disappears, and a ridge developed here grows over the head of the embryo to meet those advancing from behind. This fuses with those from the tail and sides, and as a cavity appears in the ridges the embryo has a dorsal covering (Figs. 94 and 95) of two layers, that next the embryo being the true amnion, and this separated from the outer or false amnion (the chorion) by a cavity

into which the allantois grows. Thus the amnion arises from the same portion of the embryo as gives rise to the body wall, and it is well to remember the disposition of the laminæ. Next the embryo we have epiblast, then mesoblast cavity, followed by the mesoblast and epiblast of the false amnion.

Prior to the formation of the amnion, the zona radiata which has become much thinned and attenuated, has formed on its outer side a number of processes or villi, and when the false amnion unites with it, it forms the chorion or subzonal membrane; the villi then become the chorionic villi. These villi are received into folds of the uterine mucous membrane, or into uterine crypts, and thus attachment to the mother is secured, Figs. 94 and 95.

During the formation of the amnion the splanchnopleure grows inwards, curving beneath the embryo and thus giving rise to the rudiment of a gut (Fig. 95). From the part recognised as the hind gut, a hypoblastic outgrowth occurs into the mesoblast carrying this before it. This outgrowth is the initial stage of the formation of the allantois, and it rapidly pushes its way into the cavity between the true and false amnion, and fuses with the subzonal membrane or chorion (Fig. 95). During development to this stage bloodvessels have formed in the mesoblast, and two are easily recognised one on either side of the notochord, Fig. 94, but since the embryo has become more and more cylindrical, owing to the somatopleure beyond the point of origin of the amniotic outgrowths curving downwards and inwards to close in the body wall, the two bloodvessels under the head have fused to form a single vessel, the tubular heart, Fig. 95.

In the head region the tubular heart splits to form two ventral aortæ, and these give off laterally branches, branchial arteries, that encircle the fore-gut or anterior part of the alimentary tube. Part of the blood is carried to the head and brain, but the remainder is received into two dorsal arteries that have arisen to traverse the trunk of the embryo posteriorly, subjacent to the neural canal and its contents.

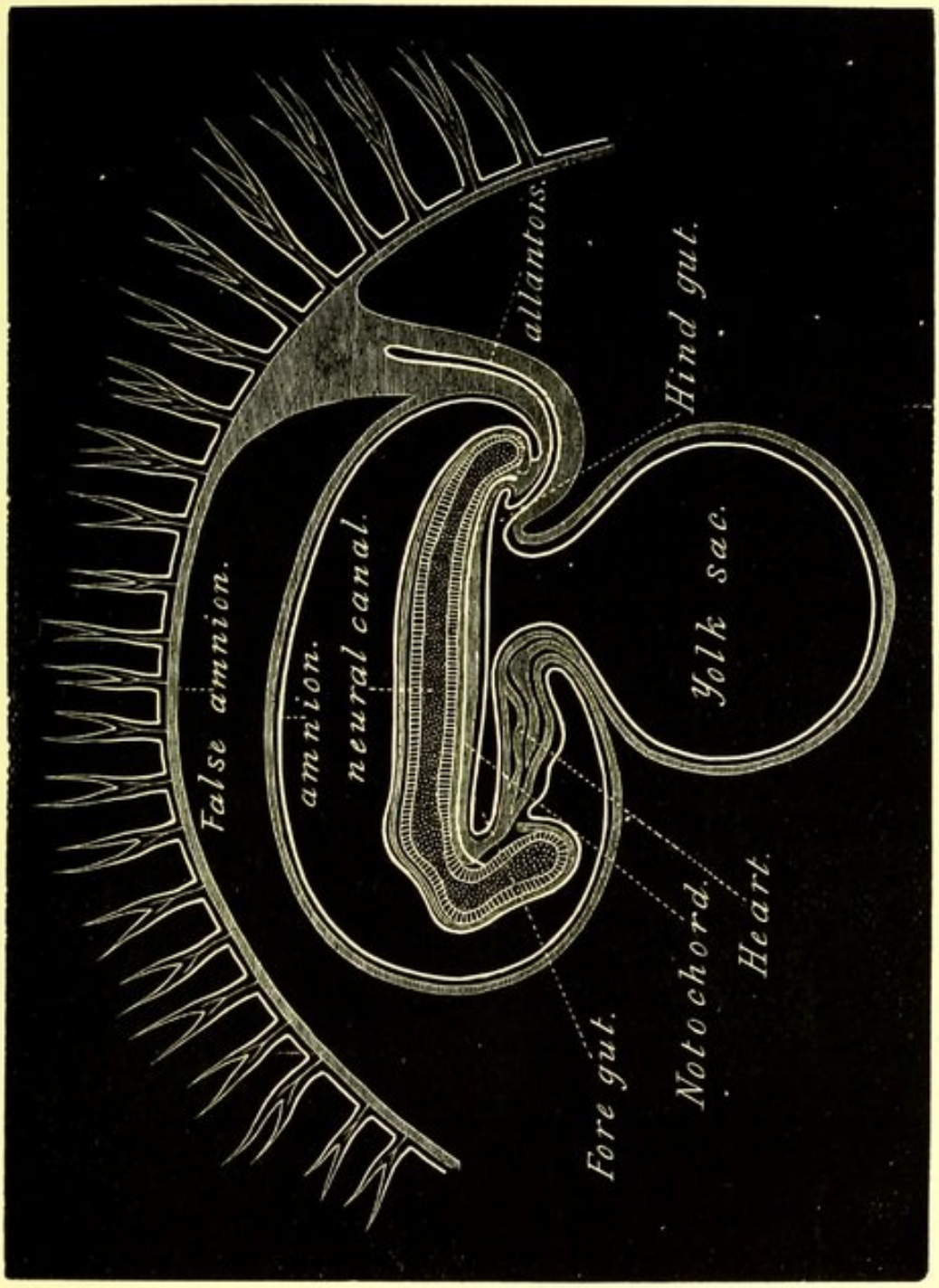


FIG. 95.—DIAGRAM OF A LONGITUDINAL SECTION OF A MAMMALIAN OVUM, AFTER THE COMPLETION OF THE AMNION. (SCHÄFER.)

These aortæ are at first two, but as development proceeds they meet and fuse so that a single vessel results. A case has been recorded in which the aorta of an adult when cut into, was found to be divided longitudinally by a mesial partition, the remains of the approximated walls of the primitive aortæ. Posteriorly the tubular heart receives the two vitelline veins.

The terminations of the aortæ are carried out by the

hypoblast as the allantoic vessels (umbilical), and by these the fœtal blood is carried to the allantois and subzonal membrane. As a result of this the false amnion and chorionic villi become vascular, and the fœtal blood is brought near to but not in connection with the maternal. The chorionic villi within the maternal crypts may be simple as in the diffuse placenta, or arborescent as in the cotyledonary placenta. They are surrounded by a plexus of maternal vessels. In the zonary placenta the crypts are large and the maternal capillaries are distended, and according to some authorities this type of placenta is deciduate, or partly so.

Placentæ, or those structures developed during intra-uterine life for the purification and nourishment of the fœtal blood, are of two types, deciduate or nondeciduate. Deciduate placentæ are those in which new maternal tissue is formed in connection with the uterus during the period of gestation, and which is lost at parturition. The best example is found in the human family, where, after delivery, owing to loss of this tissue the womb is little better than an open wound. In the domestic animals, with the possible exception of the cat and dog, the placentæ are nondeciduate.

Besides recognising placentæ as deciduate or non-deciduate, they are further classified according to the disposition of the chorionic villi. If the villi are scattered over the whole surface of the chorion the placenta is diffuse, as seen in the sow, mare, and camel. The only parts of the chorion in these animals destitute of villi are the poles, and the smooth patch is very minute. If the villi are gathered into tufts upon the surface of the chorion, and these tufts correspond to elevations of the mucous membrane of the uterus, the placenta is cotyledonary or polycotyledonary. The tufts and elevations are the fœtal and maternal cotyledons respectively, and number sixty more or less. If the villi are disposed in a strap-like manner around the envelopes, leaving the poles for some distance free from villi, the placenta is zonary, and such a condition is found in the placentæ of dog and cat. In the

rabbit and in woman the placenta, from its shape, is discoidal or metadiscoidal. Thus placentæ may be tabulated as follows:

Deciduate.	*Nondeciduate.*
Discoidal or metadiscoidal { rabbit, woman.	Diffuse—mare, sow and camel. Cotyledonary—cow and sheep.

Intermediate.

Zonary—cat and dog.

After the formation of the fœtal envelopes the body-walls rapidly close in, the splanchnopleure being received up into the body to form the primitive gut and its derivatives, the somatopleure forming the body-wall and the limbs. The embryo or fœtus retains its connections with the placenta by means of the **umbilical cord**, which is composed as follows: Structures in connection with the amnion and the body-wall at the umbilicus; structures in connection with the allantois and the urachus, the latter being a funnel-shaped body connected with the urinary bladder, and the remains of which may be seen as a scar on the fundus of that organ, even in the adult; the umbilical arteries and vein, or veins (ruminants). All these are cemented together by an embryonic connective tissue, the Whartonian jelly.

Fœtal Membranes.—We have seen that the ovum is surrounded by certain membranes which form cavities. Immediately enveloping the ovum is the amniotic cavity, Figs. 96 and 97; this sac contains a fluid in which the fœtus lives. The fluid, or liquor amnii, is alkaline in reaction, and yellowish in colour during the early days of gestation, but reddish towards the end of it, probably due to discoloration with meconium.

The amniotic fluid contains albumin, globulin, mucin, urea, sugar, lactic acid, keratin, and some salts; besides these there are also portions of hoof, epithelium, etc., derived from the fœtus. The source of this fluid is probably by transudation from both the fœtus and mother. Indigo blue injected into the vessels of the mother tinges the amniotic fluid, though it does not stain the fœtal tissues.

The function of this fluid is protective to mother and fœtus, and during parturition it assists in dilating the os and lubricating the maternal passage. The allantois grows out from the body of the ovum at the future umbilicus, the part within the body forms the bladder, that outside it forms a sac which in the mare completely envelops the amnion, but in ruminants only partly so; the two are con-

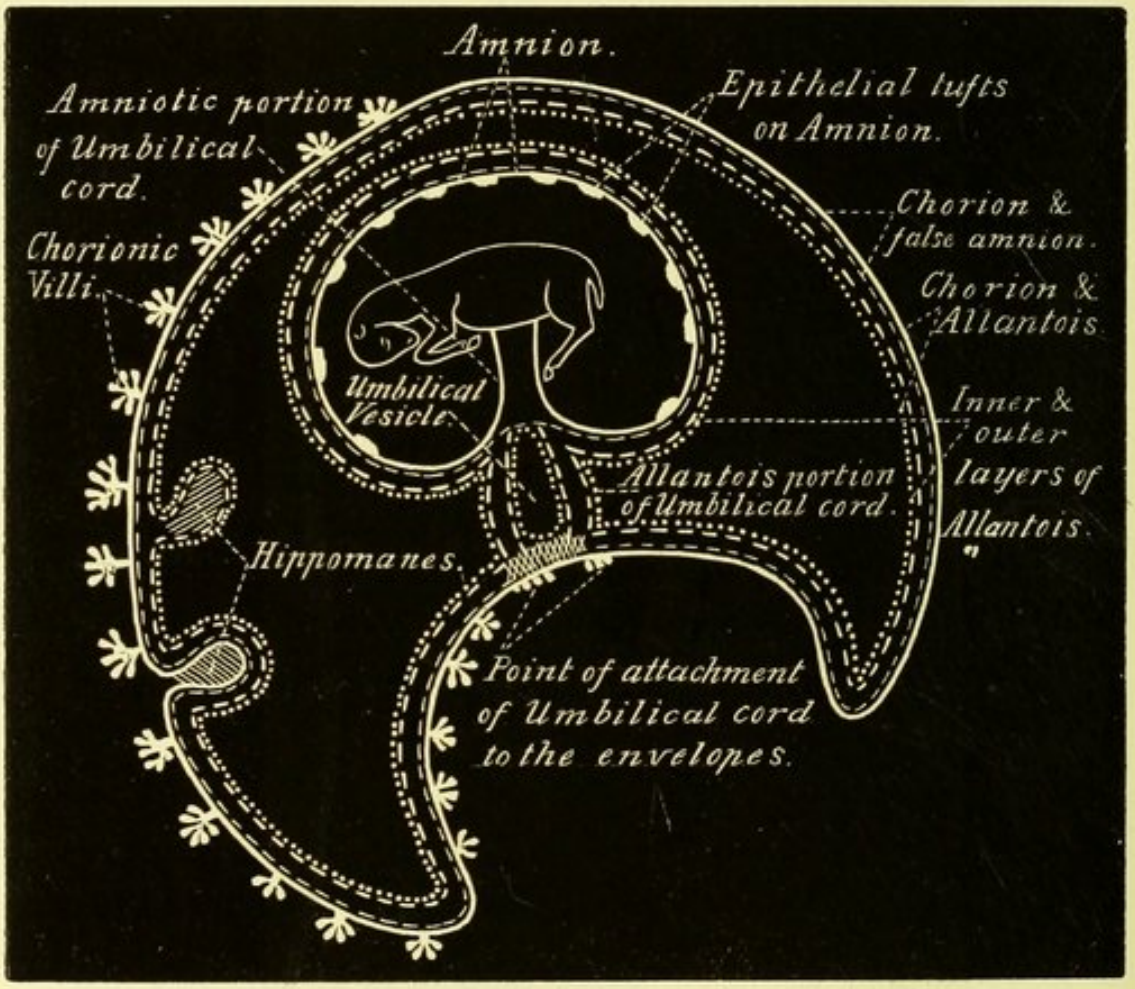


FIG. 96.—DIAGRAM OF THE FŒTAL ENVELOPES OF A FIVE-MONTHS HORSE EMBRYO. (BONNET.)

nected by a canal in the umbilical cord known as the urachus (Figs. 96 and 97).

Fluid is found in the allantois which is derived from the fœtal urine, in the first instance it is colourless or turbid, later on it becomes brown in tint. This fluid contains urea, and a substance allied to it, allantoin, albumin, sugar, lactic acid, and certain salts.

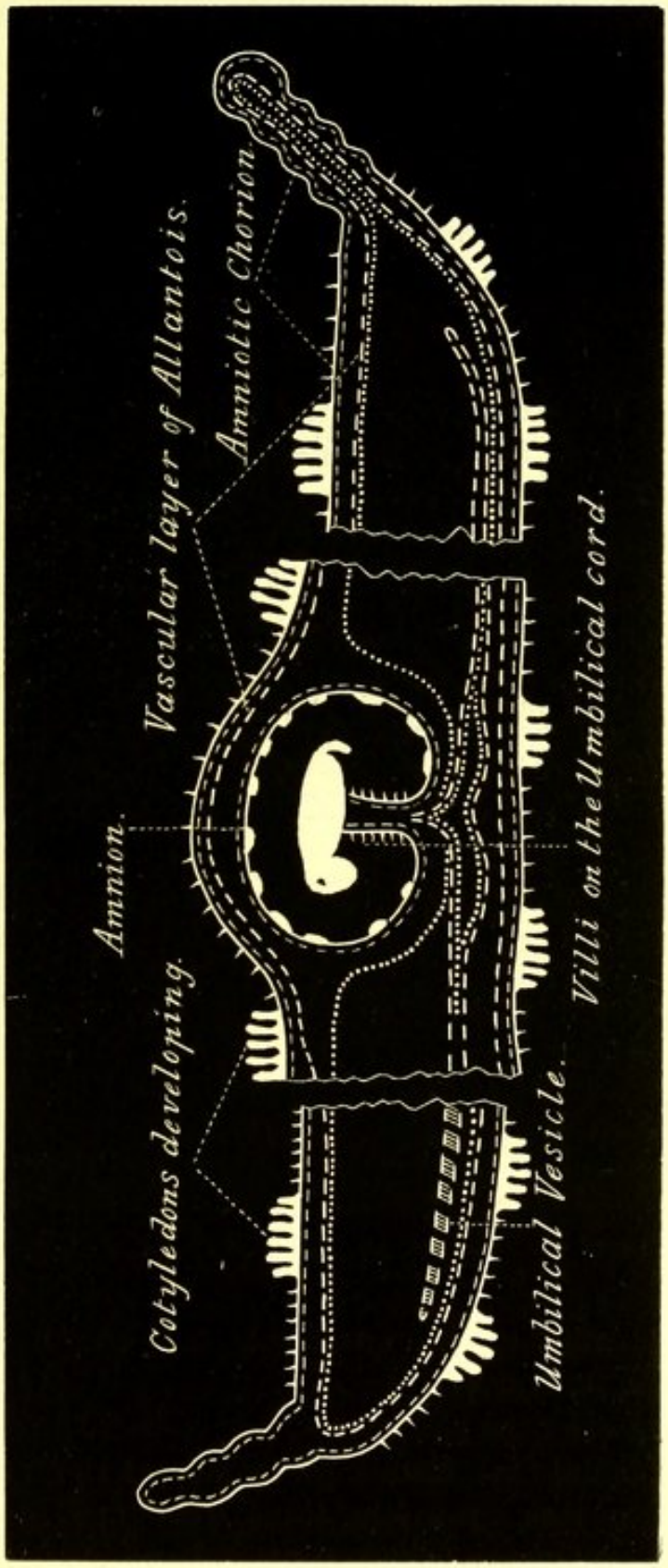


FIG. 97.—DIAGRAM OF THE FŒTAL ENVELOPES OF RUMINANTS. (BONNET.)
Only the central portion and extremities are represented.

Floating in the allantoic fluid of the mare, or attached to the wall of the sac, are certain brown masses termed hippomanes, they contain much oxalate of lime. Their use is quite unknown.

The chorion envelops the two previous envelopes. Through the umbilical cord it forms the vascular connection between the fœtus and the mother, and the arrangement of the villi on its surface have previously been dealt with. The villi project themselves into the mucous membrane of the uterus, not through the medium of a decidua as in the woman, but direct into the uterine wall. The bloodvessels of the chorion and those of the uterus do not anastomose, but the fœtal vessels are bathed in the blood contained within sinuses in the uterus into which they run, and in this way the blood of the fœtus receives oxygen and gets rid of carbonic acid.

The development of the organs of the body hardly enters into a work of this kind; the student, for fuller information, is referred to special works on Embryology, such as Balfour, Schäfer in Quain's 'Anatomy,' Milnes Marshall, Hertwig, and others.

Embryonic Circulation.—It has already been mentioned that the tubular heart arises from the fusion of the two primitive vessels which arise in the mesoblast, while the vitelline veins drain the vascular area. This latter is a more or less circular patch in which the embryo lies, and in its mesoblast the first bloodvessels arise. 'The first appearance of red blood occurs in the form of isolated red points (blood islands of Pander), which are scattered about within this area, and are especially numerous at its circumference, where they form an almost continuous chain' (Schäfer).

The newly-formed vessels anastomose one with another, receiving blood from Pander's blood islands. The vascular area is limited by a bloodvessel, the sinus terminalis, which in mammals is arterial. The heart, which is at first a tube, is developed beneath the head, and commences to beat almost as soon as it is formed. This tube becomes bent upon itself, and by ingrowth along

various constricting lines the cavities of the heart are mapped out. While this is proceeding the head is rapidly growing, and the anterior portion of the alimentary tract is being folded off. The heart is carried down into the developing thorax, and as it moves it carries with it the branches of the pneumogastric nerve known as the recurrents. It is said that during fœtal life the walls of both ventricles are equally thick; the right ventricle is not yet called upon to pump the blood into and through the lungs. The interauricular septum grows downwards from the roof of the auricles, in contradistinction to the septum of the ventricles which grows from the apex towards the auriculo-ventricular zone. It is not uncommon to find near the attachment of the ventricular septum to the zone, a thinning of the septum, or it may be even a foramen, a condition to be explained on the hypothesis that growth has been arrested, and that such growth has been towards the base of the heart.

Fœtal Circulation. — With the formation of the fœtal envelopes and the development of the heart, the circulation takes on a course altogether different from that in the vascular area in early embryonic life.

The placenta—the fœtal structures intimately connected with the tissues of the mother—acts as the fœtal respiratory and food-absorbing organ. Impure blood that has circulated through the tissues of the developing young is brought to the placenta by the umbilical arteries, these acting to the fœtus as the pulmonary arteries to the adult. After an interchange of gases and a renewal of food supply, the blood is carried away to the fœtus by means of the umbilical vein or veins found in the cord. The vein enters the body at the navel or umbilicus, and passes forward along the floor of the abdomen, reaches the falciform ligament of the liver, travels along the free edge of that structure, and empties itself into the portal vein. After birth the remains of the umbilical vein are found as a thickening at the free edge of the falciform ligament, and is named the round ligament of the liver, Fig. 98. In ruminants the umbilical

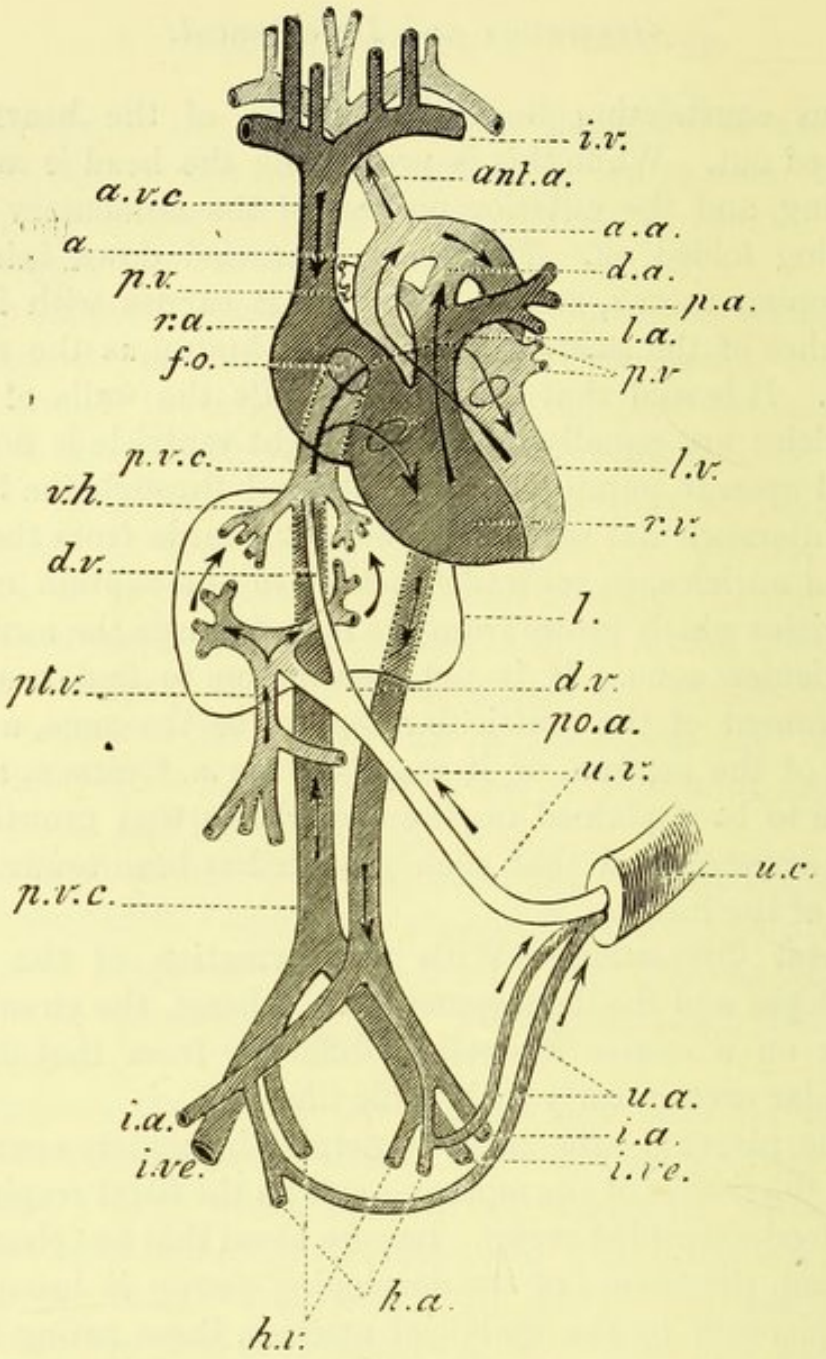


FIG. 98.—DIAGRAM OF THE FŒTAL CIRCULATION. (ELLENBERGER.)

u. v., umbilical vein; *d. v.*, ductus venosus; *pt. v.*, portal vein; *l.*, liver; *v. h.*, hepatic veins; *p. v. c.*, posterior vena cava; *r. a.*, right auricle; *f. o.*, foramen ovale; *r. v.*, right ventricle; *p. a.*, pulmonary artery; *d. a.*, ductus arteriosus; *l. a.*, left auricle: *l. v.*, left ventricle; *a.*, the aorta; *a. a.*, arch of aorta; *ant. a.*, anterior aorta; *i. v.*, innominate veins; *a. v. c.*, anterior vena cava; *po. a.*, posterior aorta; *i. a.*, iliac artery; *h. a.*, hypogastric artery; *u. a.*, umbilical arteries; *i. ve.*, iliac veins; *h. v.*, hypogastric veins; *u. c.*, umbilical cord.

The diagram actually represents the fœtal circulation in ruminants; to make it applicable to the horse the ductus arteriosus (*d. v.*) must be supposed to be removed, the whole of the blood then traverses the liver by the union of the umbilical vein (*u. v.*) with the portal vein (*pt. v.*). The arrows indicate the course taken by the blood: observe that the stream entering the right auricle divides, part passing into the right ventricle, and part into the left auricle through the foramen ovale (*f. o.*).

veins are two in number, but they unite to form a single vessel on entering the body. The vessel thus formed passes along the abdominal floor towards the falciform ligament to occupy the same position as in other animals, but before reaching it, it detaches a large branch the *ductus venosus* Fig. 98 *d v*, which passes upwards to join the posterior vena cava. After the blood has circulated in the liver it leaves by the hepatic trunks, and is poured into the posterior vena cava, where it meets with the blood in that vessel and is thus conducted to the heart.

In the horse the whole of the fœtal blood passes through the liver before reaching the heart through the posterior cava; in ruminants part of the blood passes through the liver, and part goes direct to the systemic circulation of the fœtus through the ductus venosus.

In the fœtal heart the cavities of the right and left auricles are in communication by means of a foramen, the *foramen ovale*. This opening in many animals is provided with a valve, the Eustachian valve, that stretches from the mouth of the posterior vena cava to the annulus or thickened border of the foramen ovale. The function of this valve is to direct the blood-stream into the left auricle; the Eustachian valve is absent from the heart of the fœtal horse and pig. The blood in this way gets into the left auricle, passes into the left ventricle, and thence into the aorta. The greater portion is driven into the vessels that supply the head, neck and fore-limbs (anterior aorta and branches), and is conveyed to the head and anterior portion of the body; the remainder passes backwards in the posterior aorta. The head, it will be noticed, receives almost pure blood.

After the fluid has circulated in this part of the body, it is returned to the right auricle of the heart by the anterior vena cava. From the right auricle it passes to the right ventricle, and from this cavity it is pumped into the pulmonary artery. The lungs, however, are not functional, and are more or less solid organs, consequently they are not prepared to receive the blood as they will be after birth,

when they become distended with air and have taken on their duties as breathing organs. The blood must therefore take another course than through the lungs. This course is provided by the *ductus arteriosus* Fig. 98 *d a*, a short vessel uniting the pulmonary artery to the aorta, and thus bringing their lumina into communication. By this conduit the blood enters the posterior aorta, and is conveyed to the hinder parts of the body and to the placenta.

The allantoic or umbilical arteries convey the blood from the fœtus to the placenta. These arteries are branches of the internal pudics, or of the parent vessels the internal iliacs, and during intra-uterine life they are larger than the parent vessels. Soon after birth, however, their walls become thickened, and their lumina are lost, and they become impervious to the passage of blood. In the adult they are recognised as the thickened cords found in the lateral ligament of the bladder.

The ductus arteriosus just prior to birth has a lumen easily receiving an ordinary cedar pencil, but it steadily diminishes until, at about a month after birth, it is no greater than the diameter of a knitting-needle. It is probable that little blood passes this way after birth, but the exact period of total occlusion is unknown. Similarly the foramen ovale is blocked up by the development of a membrane, which, when pulled out with the forceps, resembles in shape an old-fashioned lace nightcap or cowl. When undisturbed it lies in a heap filling up the foramen. It was quite apparent in the heart of the month-old foal, the ductus arteriosus of which is referred to above.

The **Duration of Pregnancy** for the mare is about 11 months, though it may vary within wide limits; for the cow, about 9 months; sheep and goat, 5 months; pig, 4 months; and bitch, 2 months.

Among the changes which the uterus undergoes after impregnation may be mentioned the great increase in the elements of the muscular wall, enlargement of the broad ligaments of the uterus, and the formation in the mucous

membrane of depressions, or 'crypts,' in which are lodged the villi of the chorion.

Uterine Milk.—If the villi of the chorion be separated from the tubular depressions of the mucous membrane of the uterus, a milky fluid can be expressed known as uterine milk. This is particularly observable in separating the fœtal and maternal cotyledons.

Uterine milk is of a white or rosy-white colour, creamy consistence, and contains proteids, fat, and a small proportion of ash. Examined microscopically it is found to contain globules of fat, leucocytes, rod-like crystals, and

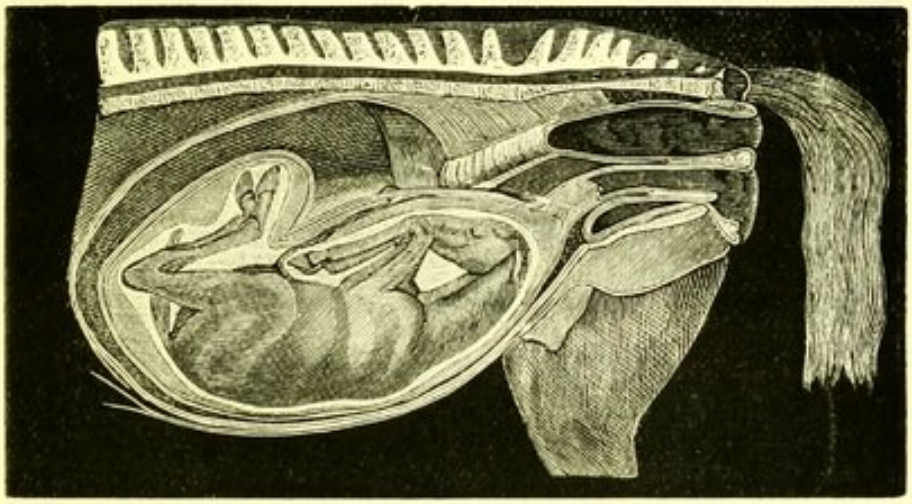


Fig. 99.—The Position occupied by the Equine Fœtus during Intra-Uterine Life. (Franck.)

structureless masses of proteid containing chromatin.* Ellenberger describes the use of the fluid as for the nourishment of the epithelial cells of the chorion.

Parturition.—The fœtus having reached its full stage of development, changes of an obscure nature take place which lead to it being expelled. During uterine life it is lying on its back on the floor of the mother's abdomen, with its chin on its chest, the fore-legs bent at the knee, and the hind-legs in the largest of the two cornua, Fig. 99. Preparatory to birth the fœtus changes position and turns on its side, so as to assume first a lateral position, Fig. 100, and lastly an upright one, Fig. 101, by which the fœtal and maternal spines are brought nearer together. To assume

* Ellenberger, 'Physiologie.'

this position the fœtus has had to make a complete revolution; it is now brought with the muzzle and fore-legs in the direction of the pelvis, Fig. 101, and dilatation of the

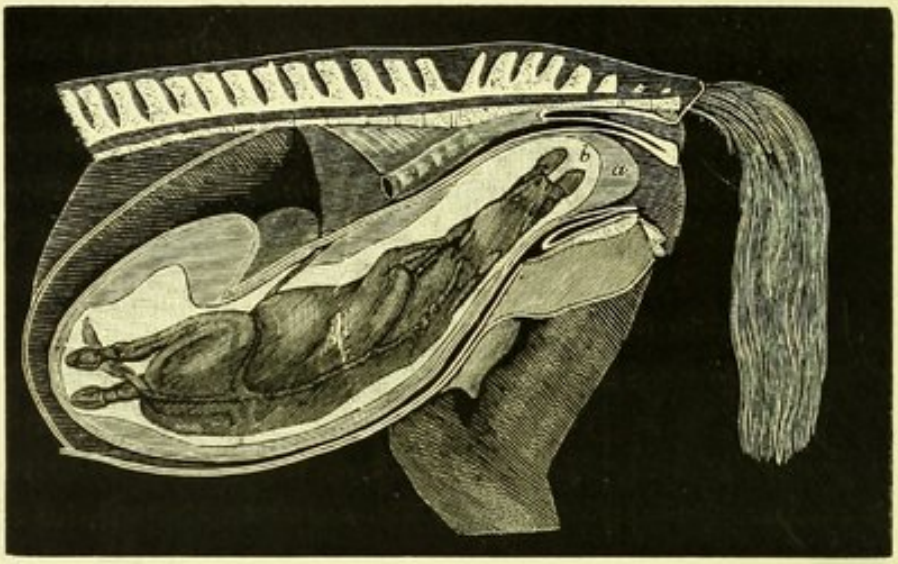


FIG. 100.—THE FIRST STAGE IN THE REVOLUTION OF THE FŒTUS; LATERAL POSITION. THE OS IS DILATED BY THE MEMBRANES WHICH HAVE NOT YET RUPTURED. (FRANCK.)

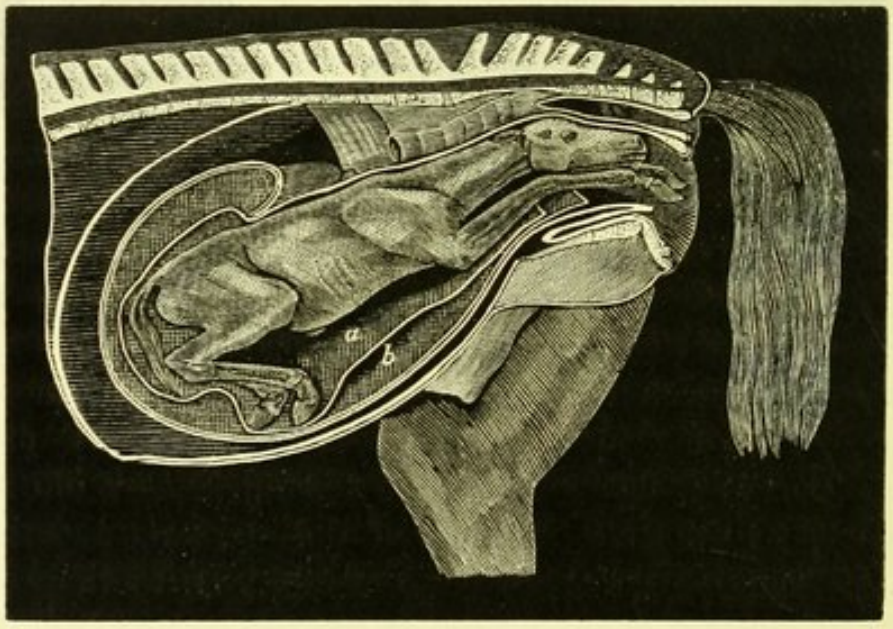


FIG. 101.—THE REVOLUTION COMPLETED, MEMBRANES RUPTURED, AND FOAL IN THE NORMAL POSITION FOR DELIVERY. (FRANCK.)

paggage follows. In the cow the fœtus lies on its back on the floor of the abdomen as in the mare, but lies somewhat crooked, viz., the head inclining towards one side, and the

hind extremities towards the other; in all other respects it resembles the mare. The alteration in the position of the fœtus does not occur through its own movements, but by the contraction of the uterus; on the other hand, the stretching of the limbs is the result of fœtal movement.*

There can be little doubt that the revolution of the fœtus prior to birth is the explanation of the complete torsion of the neck of the uterus and vagina which is sometimes found in both the cow and mare.

The dilatation of the os is assisted by the amniotic and allantoic fluids. Each contraction of the uterus is accompanied by a pain; the pains last from 15 to 90 seconds, and the interval between them is from 2 to 4 minutes.

The mare is remarkable for the rapidity with which delivery is effected; ruminants, on the other hand, are often very slow and in labour for hours. Parturition in the mare is accompanied by a complete separation of the chorion from the uterine walls; this is the explanation why any difficulty in foaling invariably sacrifices the life of the foal. In ruminants, on the contrary, the circulation between the mother and fœtus is kept up to the last by the gradual separation of the cotyledons, so that though calving may be delayed several hours, the calf is generally born alive.

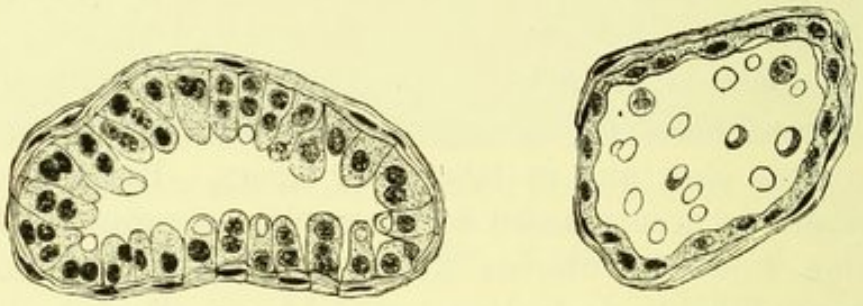
The contractions of the uterus occur through a centre in the lumbar portion of the cord; it is not under the control of the will, and has the power of acting even though the animal be unconscious.

* This description of the change in the position of the fœtus preparatory to birth is taken from Ellenberger's 'Physiologie.'

The Secretion of Milk.

As the period of parturition approaches, the mammary glands become swollen owing to active changes occurring in them, and at or shortly after the birth of the animal milk is formed.

Two processes contribute to the formation of milk, in one the cells lining the alveoli of the gland are bodily shed and form the fat of the milk, whilst in the other the water, proteids, salts, etc., are formed from the lymph in the gland by the ordinary process of secretion. We must



Loaded. Discharged.

FIG. 102.—MAMMARY GLAND OF DOG DURING LACTATION. AFTER HEIDENHAIN. (WALLER.)

examine the first of these processes at somewhat greater length.

If the mammary gland of an animal which has never been pregnant be examined, the alveoli it contains are much smaller and less numerous than those of a secreting gland. The alveoli of the first-mentioned gland are found to be packed with small rounded cells of very slow growth; when the animal becomes pregnant the gland enlarges, the alveoli increase in number, but remain packed with cells until parturition approaches or occurs. The solid masses of cells are now cast off, and leave behind them alveoli lined with a single layer of secretory epithelium, the function of which is to furnish the milk. The shedding of the mass of cells which originally occupied the alveoli supplies the colostrum or first milk.

The appearance presented by the single layer of cells

lining the alveolus of the secretory gland, depends upon whether the gland is loaded or discharged. If the gland be loaded, viz., active secretion occurring, the cells are found to be large and columnar in shape, possessing two or more nuclei, one being at the base of the cell, and the other, giving indications of degeneration, placed near the apex (Fig. 102). In the apex or free portions of the cell can be seen fat globules, which may even have partly extruded themselves from the cell, and besides these there are other particles. Further, the cell gives the appearance of the apex or free border being separated from the base by a process of constriction.

If the gland be examined when discharged, viz., after the milk has been drawn off, the cells lining the alveolus are cubical or flattened, each containing a nucleus; the lumen of the alveolus is also increased in size, and within it may be seen some of the elements of the milk (Fig. 102).

It is evident that the cells in the active gland are loaded with material, much of it being fat, and these cells break off leaving behind them the parent cell containing a nucleus from which another cell grows. In spite of this the formation of fat in milk is really a process of cell secretion, and this is supported by the fact that animals like carnivora, the food of which is deficient in fat, produce a fat containing milk, and the fat is elaborated by the mammary cell from the proteid of the body. A fat diet does not increase the fat in milk, though a proteid diet has this effect.

The proteid, sugar, and salts, found in milk are secreted in the ordinary way from the blood, or rather the lymph circulating in the gland, the cells lining the alveolus being the active factor in the matter, and that these substances are really elaborated by the cell, is evidenced by the fact that neither casein nor milk sugar exists in any other tissue of the body.

Composition.—The milk of herbivora has an alkaline reaction which may readily turn to acid; in carnivora the reaction is acid. In the cow the specific gravity is 1028 to 1034. The secretion contains proteids (casein and albumin), sugar (lactose), fat (butter), and salts.

Under the influence of rennin casein becomes insoluble, and the milk is curdled, resulting in a clot and whey; the clot or insoluble casein is now termed *tyrein.* Neither the albumen nor the casein in milk is precipitated by boiling; on the other hand, colostrum is precipitated by heating, and this is due to the fact that it contains globulin. The albumin of milk offers some peculiarities from ordinary serum albumin, and has been termed *lactalbumin.*

The fats in milk are olein, stearin, and palmatin, and the proportion of these differs in various animals. The fat is contained within fat globules, and these form in milk a true emulsion, each globule being separated by a layer of milk plasma. On standing the globules rise to the surface of the fluid and form cream; by the process of churning the emulsion is destroyed, and the fat is obtained as butter. Butter consists of 68 per cent, of palmatin and stearin, 30 per cent. of olein, and 2 per cent. of specific butter fats.

Milk sugar or lactose is very liable to undergo fermentation, resulting in the production of lactic acid and the curdling of milk. It is not, however, capable of undergoing direct alcoholic fermentation, which would appear to be a provision against fermentative decomposition occurring either in the gland or in the alimentary canal (S. Lea).

The salts of milk are principally calcium phosphate, and salts of sodium and potassium. In the composition of the milk we obtain an insight into the nature and quantity of the salts required by growing animals. Bunge gives the following ash analysis of mare's and cow's milk:

	Mare's Milk.	*Cow's Milk.*
Potassium	1·04	1·76
Sodium	0·14	1·11
Calcium	1·23	1·59
Magnesium	·12	·21
Iron	·015	·003
Phosphoric acid	1·31	1·97
Chlorine	·31	1·69
Total ash per 1,000 ...	4·17	7·97

The phosphates are increased by those contained in the proteids; they are employed mainly in the construc-

tion of the skeleton. The excess of potassium over sodium salts is a feature common to many of the secretions of the herbivora, but in milk, probably in all animals, the ash contains more potassium than sodium. Bunge states that this is due to the fact that as the animal grows it becomes richer in potassium and poorer in sodium salts, depending upon the relative increase in the muscular structure which is rich in potassium, and the relative decrease in the cartilaginous material which is rich in sodium.

Bunge compared the ash of a puppy with the milk of the mother, and the milk with the blood. It was remarkable how closely the composition of the puppy's system agreed with the salts it was receiving in the milk, though when the ash of the milk was compared with the ash of the blood of the mother, the greatest diversity in composition was apparent.

In comparing Bunge's analysis of the ash of cow's and mare's milk, one is struck by the fact that the calf requires much more salts for its nutrition than the foal.

In the following table is given an analysis of the milk of different animals:

	Cow.	*Mare.*	*Sheep.*	*Ass.*	*Dog.*
Water ...	84·28	92·5	82–84	90·5	76·0
Solids ...	15·72	7·5	15–17	9·5	24·0
Casein ...	3·57	1·3	4·7	1·7	10·0
Albumin ...	·75	·3			
Fat ...	6·47	·6	4–8	1·4	10·0
Lactose ...	4·34	4·7	3–4·6	6·4	3·5
Salts ...	·63	·3	·6		·5

These analyses of milk are principally taken from Halliburton.* It will be observed that the milk of the dog and sheep is remarkable for the high percentage of fat it contains; the casein of mare's milk is much less than that found in the cow, and more like that of the human. The milk of the dog is rich in casein, fat, and calcium, but poor in lactose.

The first milk secreted is termed **Colostrum.** The source

* 'Chemical Physiology and Pathology.'

of colostrum, and some peculiarities in its composition, have already been dealt with. In appearance it is a yellowish-white fluid of an alkaline reaction, sweetish taste, and remarkable for the amount of proteid it contains, as much as 15 per cent. whilst ordinary milk only contains 4 per cent. or 5 per cent. Examined microscopically colostrum is found to contain bodies termed 'colostrum corpuscles.' These are large granular corpuscles containing fat.

The use of colostrum is to act as a natural purge, by which means the intestinal canal of the young animal is cleared out.

CHAPTER XIX.

GROWTH, DECAY, AND DEATH.

Growth.—The young of the herbivora very rapidly shake off the helpless condition in which they first find themselves in this world. This is largely due to the fact that they are born with a nervous system in a high state of development; in the course of a few hours they learn to stand and walk, and in a day or two can skip and run. The young animal, moreover, is born in full possession of its senses, such as sight, touch, hearing, smell, taste, and with an amount of intelligence which nearly, if not quite, equals its parents; it practically has nothing to learn but obedience to man.

Not only is the nervous system in an advanced condition, but also the locomotor: the legs of the foal are remarkably long, some of the bones being nearly their full length, though, of course, not their full weight; such joints as the knee and hock have very little to grow. We can understand the reason of this development of the limb from what we have previously said, while the length of leg in the foal is undoubtedly for the purpose of enabling the animal to reach the mammary gland.

The limb, however, is only partially developed; from the knee and hock to the ground it is nearly the length of the adult; from the knee to the elbow and the hock to the stifle it is decidedly below the adult; whilst from the elbow to the withers, and the stifle to the croup, the body has a considerable amount to grow. It has been said, and the

statement appears to be true, that the future height of the foal may be ascertained by measuring the fore limb from the fetlock to the elbow and multiplying it by two.

TABLE SHOWING THE LENGTH OF THE BONES OF THE LIMBS OF THE FOAL AND ADULT HORSE.

	Adult Horse.	*Foal of Six Weeks.*	*Difference.*
Scapula	15 in.	8¼ in.	6¾ in.
Humerus	12 in.	8 in.	4 in.
Radius and ulna	18 in.	12 in.	6 in.
Knee-joint	3½ × 3½ in.	3 × 3 in.	½ in.
Metacarpal	9½ in.	8¾ in.	¾ in.
Suffraginis	3½ in.	3 in.	½ in.
Femur	17 in.	10½ in.	6½ in.
Tibia	13½ in.	9½ in.	4 in.
Calcis to metatarsal bone	6 in.	5 in.	1 in.
Metatarsal	11 in.	10 in.	1 in.
Suffraginis	3½ in.	3 in.	½ in.

The hind quarters of the foal are in a more advanced state of development than the fore; the shoulders are very oblique, the chest contracted and shrunken-looking, and neither contains much muscle. The oblique position of the scapula is due to the weight of the body on the limbs, the weakness of the muscles at this part allowing the angle formed by the scapula and humerus to be considerably closed, and the shoulder joint to bulge.

The head of the foal is prominent over the brain and depressed over the nasal bones. The hair is fully developed but woolly, that of the mane being scanty, and of the tail curly; whilst the colour of the body is light of its kind. A similar deficiency of pigment is observed in the iris.

The rate at which the foal increases in weight, and other circumstances connected with its nutrition, were made the subject of inquiry by Boussingault.* He found that the mean weight at birth was 112 lbs., that during the first three months the daily increase in weight was 2·2 lbs.; from three up to six months the increase was 1·3 lbs., and

* Quoted by Colin.

from six months up to three years of age the increase was at the rate of ·7 lb. per diem.

Calves, according to Torcy,* have a mean weight at birth of 77 lbs., the daily increase during the first two years being 1·5 lbs.

With sheep the daily increase in weight is more rapid; a lamb will in ten days gain 50 per cent. on its original weight, will double its weight at the end of the first month, and treble it at the end of the second.

Swine present, however, the most rapid increase in weight, for, according to the authorities quoted, a pig will increase 20 per cent. in its weight per diem during the first week, and up to the end of the first year will add ·44 lbs. daily to its body weight.

The growth of the body implies an increase in weight and height; from what we have said respecting the limbs, it may be judged that the amount of growth of each part is not the same. The eyes, ears, brain, kidneys, and liver grow less rapidly than the other parts, owing to their relatively large size at birth; the greatest increase is in the skeleton and muscles, and the rate of this increase we have just alluded to; the least increase is in the eyes and the ears, and the limbs below the knee and hock.

But few observations have been made on the rate of growth. Percivall† many years ago drew up a table, which he considered very imperfect, as to the rate at which some horses of his regiment grew, from which he showed that the increase in height between 2 years and 3 years was on an average one inch, between 3 years and 4 years one-third of an inch, and between 4 years and 5 years one-third of an inch. Some of the horses did not grow:

Of 35 two-year-olds, 2 did not grow during the year.
Of 144 three-year-olds, 17 did not grow during the year.
Of 48 four-year-olds, 7 did not grow during the year.
Of 11 five-year-olds, 2 did not not grow during the year.

* Quoted by Colin.

† 'Lectures on Form and Action.'

These numbers are too small to generalize from; there can be no doubt that many horses grow much more than two-thirds of an inch between three and five years old. It is probable that many grow up to their sixth year.

During the time the calf and foal are receiving their mother's milk the urine is acid, for the reason that the animal is practically carnivorous; once a vegetable diet is taken the urine becomes alkaline, and it is probable decreases in quantity.

The activity of certain glands, such as the thymus, becomes considerably reduced as the animal grows, and finally they disappear at the adult period.

One characteristic of the young animal is the necessity for sleep; it is probable that during slumber the tissues make the immense strides noticeable during the first few weeks of life.

Dentition commences immediately at birth, if it has not already commenced *in utero;* the following tables show the period at which changes take place in the teeth from birth to adult age:

HORSE.

	Eruption.	*Change.*
Incisors:		
Central	At birth	2½ years
Lateral	1 to 2 months	3½ years
Corner	7 to 8 months	4½ years
Molars:		
First	At birth	2½ years
Second	At birth	3 years
Third	At birth	About 3½ years
Fourth	About 1 year	
Fifth	About 2¼ years	
Sixth	About 3½ to 4 years	
Canines	About 4½ years	

Ox.*

	Eruption.	*Change.*
Incisors :		
Central	At or soon after birth	$1\frac{9}{12}$ years
Middle		$2\frac{2}{12}$ to $2\frac{6}{12}$ years†
Lateral		$2\frac{6}{12}$ to 3 years†
Corner		$2\frac{10}{12}$ to $3\frac{6}{12}$ years†
Molars :		
First	At birth	About $2\frac{3}{12}$ years
Second		About $2\frac{3}{12}$ years
Third		About $2\frac{6}{12}$ years
Fourth	6 months	
Fifth	About 12 months	
Sixth	21 months	

Sheep.

	Eruption.	*Change.*
Incisors :		
Central	At birth or soon after	About 1 year
Middle		About 2 years
Lateral		Soon after 2 years‡
Corner		About 3 years‡
Molars :		
First	At birth or soon after	Soon after 18 months
Second		
Third		About 2 years
Fourth	3 months	
Fifth	9 months	
Sixth	18 months	

* The age of the ox, sheep and pig is tabulated from the data given by Professor Brown in his 'Dentition as Indicative of the Age of Animals.'

† There is considerable variation in the development of these teeth.

‡ These teeth are liable to great variation in their development.

PIG.

	Eruption.	*Change.*
Incisors :		
Central	1 month	12 months
Lateral	2 months	18 months
Corner	At birth	8 months
Molars :		
First	1 month	About 15 months
Second		
Third		
Fourth	5 months	
Fifth	10 to 12 months	
Sixth	18 months	
Premolars	5 months	
Tusks	At birth	9 months

In all these tables the dates given are those of eruption only ; the teeth are not fully developed for a period which will vary from four to six months in the horse to a month or two in the pig and ruminants.

The influence of feeding on development is most remarkable ; not only does the body increase in size and weight, but the animal presents the appearance of the adult, so that a thoroughbred at two years old is 'furnished' and looks as old as an ordinary horse at four years old.

The completion of dentition marks the age of maturity ; the uncastrated animal presents very distinctive features from the female, viz., greater bulk, a heavy crest and neck, and a harsher voice ; the castrated horse more closely resembles the mare. No such difference as is observable in the human family exists between the male and female of the horse tribe ; the mare arrives at maturity at the same time as the horse, and the castrated animal is not deficient in stamina, strength, or capacity for work ; moreover, castration in the horse does not lead to a deposition of fat in the body.

Decay.—It is doubtful what age a horse would live to if not subjected to civilization, but we may safely say that at seventeen years old the powers of life in the majority of

them are on the wane, though many at this period may be found in full possession of life and vigour. These are probably cases of the survival of the fittest, and cannot be taken as a general guide.

Doubtless the work performed by horses is the chief cause of their rapid decay; but apart from this, changes in their teeth, such as the wearing away of the molars, appear to preclude many of them from reaching a ripe old age, though instances are on record of horses attaining the age of thirty-five, forty-five, fifty, and one animal is known to have lived to sixty-two years of age.

Blaine* appears to have gone very carefully into the question of old age in equines, and he drew the following comparison:

'A parallel drawn between the ages of horses and of men will fully convince us of the error of fixing the decay of the horse at eight years from his birth. A very considerable attention to the subject, over a wide field of observation, has impressed the writer with the propriety of drawing the following comparison between the ages of horses and men:

'The first five years of a horse may be considered as equivalent to the first twenty years of a man; thus, a horse of five years may be *comparatively* considered as old as a man of twenty; a horse of ten years as a man of forty; a horse of fifteen as a man of fifty; a horse of twenty as a man of sixty; of twenty-five as a man of seventy; of thirty as a man of eighty; and of thirty-five as a man of ninety.

'So far from this comparison being too much in favour of the horse, we are disposed to think it too little so.

'Horses of thirty-five years of age are as common as men of ninety, provided it be taken into account there are at least fifty human subjects for every horse; and, unquestionably, a horse of forty-five is less rare than a man of a hundred and ten.'

Death.—Death from natural causes in the horse is a matter of rare occurrence; it is seldom that an animal is

* 'Encyclopædia of Rural Sports.'

taken such care of that the tissues are worn out by age and decay, and the breath of life passes gradually from the body; by far the majority of horses meet either with a violent death or one the result of disease.

Natural death is described as commencing either at the heart, lungs, brain, or blood. Probably in the main most cases of natural death may be attributed to a failure of the heart's action; but from what we know of the physiology of the heart, respiration, and blood, it is very difficult to separate these in discussing the causes of natural death, knowing as we do how completely one is dependent on the other. The cessation of the heart's action may be looked upon as the termination of life.

We cannot enter upon the cause of death the result of disease, excepting to notice the interesting fact that horses seldom die quietly; by far the majority of them leave this world in powerful convulsions, fighting or struggling to the last, lying on their side, and galloping themselves to death. This violent behaviour should not be mistaken for pain, the animal is quite unconscious.

The convulsions and gasping for breath which occur at the last moment are more marked in death from intestinal trouble than from any other cause; they are also more intense where the progress of the disease has been extremely rapid than where it is slow.

Shortly after death *rigor mortis* appears (see page 324). and within an hour or two tympany of the abdomen is apparent in the herbivora, reaching such a degree in a few hours that post-mortem rupture of the diaphragm and other viscera is exceedingly common. The explanation of this disturbance is the considerable amount of gas generated by vegetable food.

APPENDIX.

THE CHEMICAL CONSTITUENTS OF THE BODY.*

A LARGE number of elements enter into the composition of the body. Oxygen, hydrogen, carbon, nitrogen, sulphur, phosphorus, chlorine, fluorine, silicon, potassium, sodium, calcium, magnesium, and iron are found, not, it is true, in a free state or only to a very slight extent, but brought together in such a way as to form compounds, and these may be divided into two classes organic and inorganic.

Carbon exists in nature principally in the form of carbonic acid, viz., united to oxygen; it is only in this form that it can be taken up by plants, which in their special laboratory split off the oxygen molecule and store up the carbon, returning the oxygen to the air, and thus supplying to the atmosphere what animals are momentarily depriving it of.

Carbon enters the animal system with the carbon of the food, and leaves it either as carbonic acid or in compounds, such as urea, which readily yield it; as carbonic acid, therefore, it is again taken up by the plant.

Hydrogen does not occur in a free state in nature, but principally as water, and a very small quantity as ammonia, and it is in these forms that hydrogen is taken up by plants. Animals give off hydrogen as water and ammonia, or as substances which readily yield these.

Oxygen is the most widely distributed of the elements, forming one quarter by weight of the atmosphere, and eight-ninths the weight of water; it also forms, by means of its compounds, one-half the weight of the earth's crust. It is the only element which enters the animal or vegetable body in a free state.

Nitrogen exists largely in a free state, no less than four-fifths of it being in this form in the atmosphere; it has but little affinity for other elements. In the form of ammonia, nitrous and nitric acids, it enters the plant; as proteid it enters the animal, leaving it as urea, etc., which by decomposition yields ammonia. The animal cannot utilise free nitrogen any more than the plant, though the gas is found dissolved to a slight extent in some of the fluids of the body.

Sulphur exists largely in nature in combination as sulphates of alkalies and alkaline earths; in this form it is taken up by the vegetable, and forming a part of the proteid molecule is taken into

* This outline of the chemistry of the body (organic constituents), is a summary of the principal facts contained in Bunge's 'Physiological and Pathological Chemistry,' and Sheridan Lea's appendix to Foster's 'Physiology,' 'The Chemical Basis of the Animal Body.'

the body of the animal, where by splitting up and oxidation it yields sulphuric acid, in which form it is excreted by the urine.

Phosphorus enters plants as phosphoric acid united with alkalies ; in soils it exists in only small quantities, hence the necessity of phosphates as manure. In the plant phosphoric acid forms a part of the complicated compounds known as lecithin and nuclein, in which condition it enters the animal body, forming a part of both the solid and fluid tissues.

Chlorine does not exist in a free state in nature but combined with potassium and sodium, in which form it enters plants and from these passes in the same compounds into animals.

Neither sodium, potassium, nor magnesium enter or leave the body or plant in any organic form, but simply as inorganic salts. On the other hand, Bunge considers that calcium does enter the body as an organic compound.

Iron occurs free and in a ferrous and ferric state in nature ; in the soil it permits the retention of carbon, and also enables it to return to the atmosphere. In the animal it is combined with the highly complex body hæmoglobin, which acts as an oxygen-carrier. Iron furnishes the plant with its colouring matter, for chlorophyll cannot be formed without its aid. It is not known in what form iron leaves the body.

Silicon, in the form of silicic acid, is taken up by plants, and through its aid stems are capable of standing erect. From the plant it is taken into the body and passes into the tissues. It is largely of use in the growth of hair, and much of it passes out of the body of herbivora with the urine ; in sheep, according to Bunge, it sometimes causes stone in the bladder.

Bunge draws a contrast in the following terms, between the methods employed by the vegetable and animal organism in the utilization of the various elements and compounds presented to them :

1. The plant forms organic substances ; the animal destroys organic substances. The vital process in the plant is synthetic, in the animal analytic.
2. The life of the plant is a process of reduction ; the life of the animal a process of oxidation.
3. The plant uses up kinetic energy and produces potential energy ; the animal uses up potential energy and produces kinetic energy.

The organic compounds in the body are broadly divided into nitrogenous and non-nitrogenous.

NITROGENOUS BODIES.

Proteids.—This term has been applied to several substances more or less closely allied, which in one form or other go to make up by far the largest portion of the animal body.

Proteids are highly complex substances, possessing no definite chemical formula owing to the difficulty in obtaining them in a sufficiently pure state for analysis. With few exceptions they have never been obtained in a crystalline condition, and their nature is colloidal, viz., they do not diffuse through an animal membrane.

All proteids contain carbon, hydrogen, oxygen, nitrogen, and sulphur.

Carbon ...	...	51·5 to 54·5 per cent.
Hydrogen	...	6·9 to 7·3 „
Nitrogen	...	15·2 to 17·0 „
Sulphur ...	...	·3 to 2·0 „
Oxygen ...	...	20·9 to 23·5 „

In spite of the fact that proteids exist in several forms in all animal and vegetable bodies, and that it is quite impossible to maintain life without them, yet very little is known of them owing to their extreme complexity. Neither their chemical formula nor their molecular weight is known, and the chemist has never been able to build them up by synthesis.

The decomposition products of proteids are numerous and very varying in nature, in the body carbonic acid, water and urea are the final end products, but between these and proteids are glycin, leucine, uric acid, and other substances. From the non-nitrogenous portions of the proteid fat and glycogen may be obtained, as we have seen in the chapter on nutrition, pp. 201 and 282. Proteids when acted upon outside the body by means of heat, putrefaction, acids, alkalies, and oxidising agents, yield a large and numerous class of substances.

There are several kinds of proteid matter, and such terms as albumin, globulin, albuminoid, albumose, all have their special significance.

In the following table the proteids are classified, and their distinguishing characteristics given.

CLASSIFICATION OF THE PROTEIDS.

CLASS I. *Native Albumins.*

These are soluble in distilled water, and the solutions are coagulated by heat, especially in the presence of dilute acetic acid. Examples of this class are egg and serum albumin, cell, muscle, and lactalbumin.

CLASS II. *Derived Albumins (Albuminates).*

These are obtained by the action of acids or alkalies on albumins. They are insoluble in distilled water, or in dilute neutral saline solutions, but soluble in acids and alkalies, and the solution is not coagulated by boiling, though it is by careful neutralisation. Examples of this class are acid albumin, syntonin, alkali albumin, and casein or native alkali albumin.

CLASS III. *Globulins.*

These are insoluble in distilled water, but soluble in dilute saline solutions ; from these they are precipitated by saturation with common salt or magnesium sulphate. In this class are found the globulin of the crystalline lens (crystallin), the globulin of the blood (para or serum globulin), the fibrinogen of the blood, myosin, the vitellin of egg-yolk, and globin.

CLASS IV. *Fibrins.*

These are insoluble in water, but soluble in neutral saline solutions, and with difficulty in strong acids and alkalies. Examples are the fibrin of the blood, chyle, and lymph.

CLASS V. *Coagulated Proteids.*

Any of the above which have been coagulated by heat or the action of alcohol.

CLASS VI. *Albumose and Peptones.*

Both of these are soluble in water, albumose, being precipitated by saturation with ammonium sulphate, whilst peptones are unaffected.

Peptones are not precipitated by any ordinary proteid precipitant excepting alcohol, and even the prolonged action of alcohol does not coagulate them. Albumoses are precipitated by nitric acid in the cold, but the precipitate disappears on heating to form again on cooling.

Albumoses (or proteoses) are formed as the primary product of the action of enzymes on proteids ; they consist of two varieties, anti and hemi albumose, and the latter consists of four distinct forms.

Albuminoids are substances closely allied to albumins, but differ from them in some important particulars ; they consist of such substances as gelatin, chondrin, mucin, elastin, keratin, and others. Under the influence of digestive enzymes they pass through the albumose and peptone stage in the same way as true albumins, but with certain differences.

The various albumins we have spoken of belong to the animal body, but in the vegetable kingdom proteids are found which do not differ in any important particular from animal proteids. The amount of proteid matter in plants is less than that found in animals ; globulins exist in larger amounts than albumins, in fact there are food substances used by animals, oats, maize, peas, etc., in which it is said the whole of the proteid occurs as globulin and none as albumin.

Some of the plant proteid matter crystallises, vitellin for example. It is this substance which has furnished the so-called 'crystallised albumin,' the existence of which has been known for some time.

Both albuminates and proteoses occur in plants, but peptone does not appear to be found in them.

The process by which plants form proteids is that of synthesis ; it is possible that such substances as asparagine, leucin, tyrosine, etc., which are met with in the plant are on their way to tissue construction, and are not, as in animals, the result of proteid destruction.

A very remarkable fact about proteid substances is that though they constitute the mainspring of organic life, yet they number amongst them, or amongst their decomposition products, some of the most powerful poisons known. Snake poison is a proteid, and even the albumose formed during the peptic digestion of albumin is highly poisonous if injected into the circulation.

The principal tests employed to detect the presence of proteids are as follows :

PROTEID REACTIONS.

1. *Xanthoproteic Reaction.*—Solutions heated with strong nitric acid turn yellow, and on the addition of ammonia or caustic soda are changed to orange.

2. *Millon's Reaction.*—With Millon's reagent they give a precipitate which turns red on heating.

3. *Piotrowski's Reaction.*—To the solution of proteid is added in excess a strong solution of caustic soda, and one or two drops of a weak solution of sulphate of copper ; this gives a violet colour. This test is also used to determine the presence of albumoses and peptones ; the colour reaction given by these is rose-red and not violet, and is termed the *biuret reaction.*

4. *Adamkiewicz's Reaction.*—To a solution of the proteid is added strong sulphuric acid and glacial acetic acid ; a violet colour and slight fluorescence occur.

5. Acetic acid and a solution of ferrocyanide of potassium give a precipitate.

6. Acetic acid and sulphate of soda give a precipitate on boiling.
7. Saturation of the solution with ammonium sulphate precipitates proteids.
8. To a neutral or faintly acid solution of proteid absolute alcohol is added and a precipitate obtained.
9. Heating a solution of proteid (albumin and globulin) causes a coagulum to form. The solution should be rendered faintly acid with acetic acid, any excess of acid being avoided as otherwise no precipitate will be produced.

There are many other tests for proteids, mercuric chloride, lead acetate, etc., but the above are those which are principally employed either to determine their presence, or to entirely free a solution from proteid.

The **Ferments** come under the proteid classification. These are bodies possessing the most remarkable activity, and capable of inducing changes in other bodies with which they come in contact, which result in the production of new substances, without undergoing themselves any appreciable loss. A common illustration of ferment activity is the yeast plant, which is capable of producing alcohol and carbonic acid out of sugar. The action of the yeast plant is due to a living cell, and all ferments produced by living cells are described as **organized**, whilst the action of the cell is spoken of as *fermentation*.

Within the animal body another class of ferment exists which does not depend upon a living cell ; it is described as an **unorganized**, soluble ferment, or **Enzyme**, to use the term by which they are now more commonly known. The changes in the digestive tract which convert starch into sugar, proteid into peptone, fats into glycerine and fatty acids, etc., are all produced by enzymes, and this action is spoken of as *Zymolysis*, to distinguish it from the fermentation produced by the living cell.

The enzymes in tissues do not always exist in a free and active state, but as an inactive antecedent to which the term *Zymogen* has been applied ; a zymogen by appropriate means may be converted into an active enzyme.

The action of enzymes on food stuffs is described as hydrolysis, viz., the fixation of the elements of water, followed by decomposition into simpler products ; thus we speak of the hydrolytic activity of ptyalin.

Both the unorganized and organized ferments agree in so far as their general action is concerned. All of them are destroyed by raising the fluids containing them to a certain temperature ; none of them appear to suffer, that is to be worn out or exhausted, by the amount of work they perform, and in consequence in each case a small quantity of them will produce as great an effect as a large quantity.

The **Pigments** of the body are classed as proteids ; comparatively little is known about them, though they are widely distributed and perform important functions. The best known animal pigment is hæmoglobin, the red colouring matter of the blood ; it is of a proteid nature, yet crystallisable, and it also contains iron. It acts as an oxygen-carrier, and is often spoken of as a respiratory pigment ; it has several derivatives (see Blood), which supply the colouring matter of the bile, urine, and partly that of the fæces.

The next pigment widely distributed is the black pigment of the body, or melanin ; it occurs in the skin, hair, eye, horn, and is the

chief constituent of the melanotic tumours so common in the horse.

Both in the fæces and in the dandruff from the skin of the horse chlorophyll is found ; its function in the body is quite unknown.

There are several other pigments, but none so important as the above.

Nitrogenous Fats. — Though true fatty substances contain no nitrogen, yet there are certain complex nitrogenous fats and their derivatives which are found distributed in the body ; the most important of these is

Lecithin, which is found in the white blood corpuscles, brain, nerves, semen, etc., and also in yolk of egg, where it is united with vitellin. Decomposition products of lecithin are *glycero-phosphoric-acid* and *cholin*. The latter substance is poisonous, and by oxidation with nitric acid yields the extremely poisonous substance muscarin. Lecithin is largely introduced into the body by means of the food ; the poisonous action of the cholin it contains is probably prevented by the substance being broken up by the bacteria of the intestines into carbonic acid, marsh gas, and ammonia.

Neurin is a substance closely related to cholin but much more poisonous ; it is the active principle in the poisonous alkaloids produced by putrefactive decomposition of animal matter.

Amides and Amido-Acids.— To this series belongs some very important substances. *Glycin* (also known as glycocoll and glycocine) is found in the body united with benzoic acid to form hippuric acid, and with cholalic acid to form the glycocholic acid of the bile ; it does not exist in a free state in the body. It is a substance with an acid reaction, a sweet taste, and is capable of crystallising.

Taurin is one of the constituents of the bile acid of carnivora, viz., taurocholic acid. It is a substance with a neutral reaction and very stable, even when exposed to a high temperature and boiling dilute acid and alkalies. In the intestinal canal taurin in some animals, as man, is absorbed and reappears in the urine ; in dogs a large part is excreted unaltered ; in herbivora part is excreted and part oxidised, leading to an increase of sulphates in the urine.

Kreatin is a substance found in muscles and some other parts of the body ; by a certain method of treatment it may be made to yield urea. Kreatinin is readily obtained from kreatin and as readily changed back. It is found in the urine, and is capable of crystallisation.

Leucin is a substance formed during the tryptic digestion of proteids, it may also be readily formed outside the body, and is found in certain glands and also in plants. It is capable of crystallising, the crystals being flat, glittering, and oily to the touch.

Aspartic Acid may be obtained by the decomposition of proteids during pancreatic digestion, it is also found in plants, but forms no part of the animal body. Closely related to this acid is *Asparagin* which is principally of interest in the proteid metabolism of plants, though it does not occur in animals. When taken into the body of the carnivora asparagin is wholly converted into urea ; with herbivora it would appear that a part of the nitrogen of the asparagin can take the place of proteid and be stored up. Considering the frequency with which asparagin exists in plants, the conversion of asparagin into proteid is a valuable provision.

The Urea and Uric Acid Group.—*Urea*, or *carbamide*, is the end product of proteid decomposition, and the chief nitrogenous

constituent of the urine. It has the formula $(NH_2)_2CO$ and is found in minute quantities in some of the tissues of the body, though it is never found in muscle which is the chief seat of its formation. In a pure state it crystallises in long needles, but in the form of nitrate it separates out as six-sided tables arranged in piles (Fig. 36, p. 257), and as oxalate in crystals resembling the nitrate but of prismatic form. Urea is very soluble in water, soluble in alcohol, but insoluble in ether. The crystals have a bitter taste resembling saltpetre.

Urea heated in sealed tubes, or urine allowed to stand, splits up into carbonic acid and ammonia. If urea be heated to a high temperature it yields *biuret* and cyanuric acid.

Uric Acid has the formula $C_5H_4N_4O_3$. It is the chief nitrogenous constituent of the urine of birds and reptiles, but only occurs in small quantities in the urine of the dog, and is absent from that of the herbivora. It is a crystalline substance (Fig. 37, p. 258), odourless, tasteless, and extremely insoluble in water, very slightly soluble in ether and alcohol, but readily soluble in caustic potash.

There is a very close chemical relationship between urea and uric acid, but there is nothing to account for the fact that snakes and birds issue their nitrogenous metabolism as uric acid while mammals get rid of it as urea. Uric acid does not occur free in the urine but as urates combined with bases.

Allantoin is a substance found in the allantoic fluid, especially that of the calf, and in fœtal urine and amniotic fluid. It can be obtained from urine after the administration of uric acid, and from uric acid by oxidation with potassium permanganate.

The Aromatic Series.—Many of these occur in the urine and some in the digestive canal.

Benzoic Acid ($C_7H_6O_2$) is found principally in the urine of herbivora, and more commonly in stale than in the fresh secretion. In stale urine it is derived from the decomposition of hippuric acid. This acid does not exist free in the urine but is combined with alkalies. It may be obtained as fine glistening needles which microscopically give the appearance presented in Fig. 40, p. 261.

This acid is not very soluble in water, but readily dissolves in alcohol and ether; on heating it sublimes, in which respect it differs considerably from hippuric acid. The source of benzoic acid in the body is discussed on p. 259.

Hippuric Acid ($C_9H_9NO_3$).—This acid exists largely in the urine of the herbivora; it is formed within the body by the union of benzoic acid with glycin, and may readily be found in fresh urine, though when decomposition occurs it breaks up into its constituents.

Hippuric acid is found in the urine united to an alkali, but may be obtained as a crystalline substance (Fig. 38, p. 260). The acid is not very soluble in water, but is readily dissolved by alcohol; it is insoluble in petroleum ether, a substance in which benzoic acid is soluble. When heated it yields an odour of new hay. The source of this acid in the body is discussed on p. 259.

Tyrosin ($C_9H_{11}NO_3$).—This is found in many plants, and also in the intestinal canal as the result of the pancreatic digestion of proteids.

It crystallises in fine needles which are sparingly soluble in water, insoluble in alcohol, but soluble in acids and alkalies.

Phenol and *Cresol* are formed in the animal body during the putrefactive decomposition of proteids, and are excreted by the bowels and urine, in the latter being found as an ethereal salt of sulphuric acid.

This phenyl-sulphuric acid is also formed from the aromatic compounds in the food, especially that taken by the herbivora.

Pyrocatechin is found largely in the urine of the horse and other herbivora, and also after the administration of benzol or phenol. The dark colour of urine on standing, such as is well seen in the horse, is due to the oxidation of pyrocatechin. The source of this substance is from the phenol of the intestinal canal, and it may probably be introduced with certain constituents of the food.

Indigo Series.—This contains several substances found in the urine and digestive canal.

Indol is the substance which gives the odour to fæces. It is present during the decomposition of proteids, and may be obtained from an artificial pancreatic digestion, the odour of which is due to this substance.

Part of the indol leaves the body by the urine as a potassium salt of indoxyl-sulphuric acid, and if this be oxidised it may be made to yield indigo blue ; if indigo blue be acted upon by powerful reducing agents it yields indol.

Indol administered to animals increases the output of indican, and whatever increases intestinal putrefaction increases the output of this substance ; this is the reason why it is found more largely in herbivora than in carnivora.

The presence of indican in the urine of the horse can readily be demonstrated by mixing the urine with an equal volume of hydrochloric acid, and adding a solution of hypochlorite of calcium until a blue colour appears.

Skatol is a substance closely allied to indol ; it has much the same odour, and if excreted with the urine it passes off as a potassium salt of skatoxyl-sulphuric acid.

The Bile Acids.—These have been sufficiently dealt with on p. 194.

THE NON-NITROGENOUS BODIES.

Fats.—Fat is composed of a mixture of fatty acids and glycerin, the fatty acids being palmatin, stearin, and olein. Special fatty acids are found in butter and milk ; they are known as caproic, caprylic, and capric acids.

Fat is insoluble in water and only slightly so in alcohol, but freely soluble in ether, chloroform, benzol, etc. When pure it is neutral in reaction, tasteless and colourless, and by the action of caustic alkalies or superheated steam may be decomposed into its respective fatty acid and glycerin. The fatty acids are capable of crystallising.

The solid fat of the body is composed principally of stearin, such as is found in the ox and sheep ; the more liquid fat, such as is found in the horse and carnivora, predominates in palmatin, but in all cases a mixture of the three fats is obtained.

The amount of fat in the body must depend upon the feeding of the animal, and will obviously vary within extreme limits. In individual tissues marrow has the largest amount ; nerve, brain, milk, muscle, liver, bone, bile, and blood, have proportions which decrease in the order given.

The change which the fats undergo in the alimentary canal is discussed in the chapter on the pancreas (p. 207), whilst the origin of fat in the body and its function is dealt with under nutrition (p. 283).

Butyric Acid is found in the intestines, and in milk it exists in union with glycerine as a neutral fat, which gives the odour to rancid

butter. It may also be produced by the second stage of lactic fermentation in the stomach and alimentary canal, being derived from the carbo-hydrate matter ingested.

Glycerine is a viscid, colourless, sweet fluid, soluble in all proportions in water and alcohol, but insoluble in ether. When heated strongly it yields *acrolein*, a substance which gives the pungent odour to burned fat.

Soaps are formed when neutral fats are heated with lime or caustic alkalies, salts (called soaps) being formed by the union of the metal with the alkali, while the glycerine is left in solution.

Pancreatic fluid has a similar decomposing effect on fat, the fatty acids uniting with the alkali of the juice to form soaps. The emulsifying effect of a mixture of bile, free fatty acids, and soap is considerable, and largely determines the absorption of fat.

Lactic Acid exists in two forms in the body ; ethylidene-lactic acid is the chief product of the lactic fermentation of sugars, and is found in the stomach and intestines especially after a diet containing carbo-hydrate ; sarco-lactic acid occurs in muscles, and is the cause of their acidity after activity.

Cholesterine is a peculiar substance extracted originally from gall-stones. It can be obtained in sparkling crystals which are soapy to the touch, and of characteristic microscopical shape. Cholesterine is the only alcohol which occurs free in the body ; it has been called a non-saponifiable fat, but it is not a fat, though, as a matter of convenience, it is generally dealt with in speaking of fats.

Cholesterine is found in the nervous system, and is especially common in the pia mater of the cerebellum and plexus choroides of the horse where it may give rise to tumours, the nature of the growth being readily recognised from its silvery fish-scale-like appearance. It is also found in lanoline or wool fat and in dandruff, where it replaces the glycerine in the fat.

Carbo-hydrates.—This important class is of the greatest interest to the physiologist, inasmuch as the bulk of material consumed as food, especially in the herbivora, consists of carbo-hydrate matter. It is an extensive group of bodies consisting of such substances as starch and its derivatives, the various forms of sugar, and cellulose. Though so much carbo-hydrate material enters the body but little can be found in the tissues. An animal starch may be found in the liver and other organs, minute amounts of sugar may be found in the blood, and a sugar exists in milk ; but very much less carbo-hydrate is recovered from the body than enters it as food, for the reason that the bulk of it becomes oxidised to carbonic acid and water.

The carbo-hydrates may be divided into the starch group, the dextrose group, and the cane-sugar group.

THE STARCH GROUP.

Starch.—The formula for starch is unknown, it is considered to be $(C_6H_{10}O_5)n$, where n is not less than 5 or 6, and probably much larger.

Starch exists in plants in the form of grains, the shape of which depends upon the group from which it is derived, thus potato, bean, wheat, and other starch grains have each a distinctive shape. The grain is composed of two parts, an envelope known as cellulose, and an interior called granulose. The granulose is the starch ; the cellulose is not, however, identical with the ordinary cellulose of plants.

Starch is insoluble in cold water, but when boiled the grains burst,

and a viscid, opaque, pasty mass results, which is not, however, a true solution of starch. A solution of starch can be obtained from this mass by digestion with an enzyme, such, for instance, as human saliva, or by the action of dilute acid ; when this takes place the material becomes watery, perfectly transparent, and filters readily, while previously this was impossible. To this limpid fluid the term soluble starch has been given.

The characteristic test for starch is the blue colour produced on the addition of iodine ; starch has no reducing action on Fehling's solution.

Dextrin.—When starch paste is acted upon by dilute mineral acid, or the enzymes found in the saliva and pancreatic juice, soluble starch is first formed as above described ; but if the process be allowed to continue, further changes rapidly occur, leading to the production of dextrin and finally of sugar. There are probably several dextrins, though two are generally described, viz., erythro- and achroo-dextrin. These are distinguished from starch and from each other by their colour reactions with iodine, erythro-dextrin giving a reddish colour, while achroo-dextrin gives no colour. Much the same change which can be brought about by acting upon starch out of the body takes place in a more perfect and complete form within the body.

The conversion of starch into dextrin and finally into sugar under the influence of certain enzymes, performs a most important physiological function ; neither starch nor dextrin is capable of being absorbed as such, whereas the sugar which results from this conversion is readily soluble.

Glycogen closely resembles starch ; it is found in several of the tissues of the body, and its origin and use in the economy have been previously discussed (see p. 198). It may be obtained as an amorphous white powder, readily soluble in water, and gives with iodine a port-wine colour instead of blue. By the action of acids or enzymes it is readily converted into dextrin, and finally into sugar. The sugar resulting from the action of acid is dextrose, whereas that produced by the enzyme is maltose ; in the liver the sugar produced is dextrose and not maltose, and the method by which this conversion is obtained has been previously dealt with (p. 200).

Cellulose, though not found in the animal body, is of great interest to the physiologist from its intimate relation to the feeding of the herbivora. The food substance in plants is locked up in a cellulose envelope, and until this envelope is broken down the material within cannot be acted upon by the digestive juices. This breaking down is accomplished by laceration during the process of mastication, but also by a digestion of the covering, by which means it is removed and the food substance exposed.

The digestion of cellulose is a question which has given rise to great discussion, inasmuch as no animal is known to secrete a cellulose enzyme, although many, such as the herbivora, are known to digest cellulose. Bunge states that sheep are capable of digesting 30 per cent. to 40 per cent. of the cellulose of sawdust and paper when mixed with hay.

The two views most generally held at the present time with reference to the digestion of cellulose are that it is either due to putrefactive organisms or to a specific enzyme.

Cellulose may be digested outside the body under the influence of putrefactive organisms, with the evolution of marsh gas and carbonic acid. Every condition necessary for this change exists within the

body ; for example, in the rumen of the ox, and the large intestines of the horse ; but it would appear to be more than probable that a cellulose-dissolving enzyme exists. Young cellulose is better digested than old ; it is certain that the older parts of the plant are converted into lignin, and this to the majority of animals must be insoluble.

Cellulose when treated with strong sulphuric acid is converted into a dextrin-like product, and is finally converted into dextrose.

THE SUGAR GROUP.

Dextrose, *Glucose*, or *Grape Sugar* has the formula $C_6H_{12}O_6$; it is probably the form in which all the carbo-hydrates are absorbed from the alimentary canal. Dextrose undergoes three fermentations, viz., alcoholic, lactic, and butyric ; the two latter are probably always present in the intestinal canals of animals, especially after a carbo-hydrate diet.

Levulose.—This occurs in fruits and honey mixed with glucose ; it may also be prepared by acting upon cane-sugar with sulphuric acid, by which means the cane-sugar is converted into equal parts of dextrose and levulose.

Saccharose, or cane-sugar, is not found as part of the animal body, but exists largely in plants, and forms a well-known supply of carbo-hydrate to the system. Cane-sugar does not give some of the characteristic sugar reactions, among others it has no reducing action upon salts of copper, but by boiling with dilute mineral acids it is converted into equal parts of glucose and levulose, and the same change may be effected by enzymes in the stomach and small intestines. The conversion of cane-sugar is recognised by its action on polarized light, by which the ray is turned from right to left, viz., inverted ; hence the name invert sugar.

If cane-sugar be injected into the circulation it passes out unaltered ; it is certain that before this sugar can be assimilated it must be converted into dextrose.

Maltose is formed by the action of malt extract (diastase) on starch paste, also by the action of saliva and pancreatic juice upon starch paste or glycogen. In its tests it corresponds closely to dextrose, but it has a less reducing action upon Fehling's solution, and it does not reduce Barfoed's reagent,* which dextrose is capable of doing.

In all probability maltose is non-assimilable, like cane-sugar, for if injected into the circulation it is excreted unchanged, and it is probable that before absorption it has to be converted into dextrose.

Lactose, or milk-sugar, is found solely in milk. It reduces Fehling's solution, and has the same rotatory power as dextrose, but it does not reduce Barfoed's reagent, nor does it undergo direct alcoholic fermentation with yeast. If boiled with dilute mineral acids it is converted into equal parts of dextrose and galactose.

Lactose readily undergoes lactic fermentation, as, for instance, in souring milk. The cause of this is a micro-organism ; but there are reasons for believing that an enzyme may also bring it about.

In spite of the fact noted above, that isolated lactose is unable to ferment in the presence of yeast, yet an alcoholic fermentation is capable of occurring in milk, such, for instance, as the kumys and kephyr from mare's milk. It is probable that the changes which bring this about are very complex, and due to several organisms.

Lactose, like saccharose and maltose, is non-assimilable, and it is pro-

* A solution of cupric acetate to which is added acetic acid.

bable that it is changed into dextrose before absorption, not necessarily as the result of any digestive secretion, but during its passage through the intestinal wall.

TESTS FOR SUGAR.

1. *Trommer's.*—An excess of caustic potash and a small amount of dilute solution of copper sulphate is added to the fluid and the whole heated. The copper is reduced to suboxide by the sugar and a red precipitate falls. Fehling's solution, which is used as a quantitative test for sugar, consists of hydrated cupric oxide in caustic soda, and the double tartrate of sodium and potassium. The principle of this test is the same, viz., the reducing action of the sugar, which robs the cupric compound of its oxygen.

2. *Moore's.*—A solution of sugar boiled with caustic potash turns brown.

3. *Böttcher's.*—Bismuth oxide and excess of caustic potash are added to the fluid containing sugar and heated ; the solution becomes gray and then black, from the deposition of metallic bismuth.

4. *Picric Acid Test.*—Heat the solution of sugar with a little picric acid ; add caustic soda in small quantities, and a brown-red coloration is obtained.

5. *Fermentation Test.*—The fluid containing a piece of yeast is placed in a tube and inverted over mercury ; if sugar be present it undergoes fermentation, and carbonic acid is given off, which collects in the tube.

INORGANIC CONSTITUENTS.

The inorganic substances found in the body are water, gases, and salts. *Water* forms about 60 per cent. of the whole body ; it is taken in with the food and drink, and a small quantity may be formed within the system.

The amount of water consumed by animals depends upon the nature of their food and the class of animal. Horses fed on dry food consume more water than cattle, the food of which contains as a rule a considerable amount of water.

An excess of water leads to body waste by carrying off the solids through the kidneys, whilst reduction in the amount of water produces thirst and loss of nutrition.

The *Gases* found in the body are oxygen, nitrogen, hydrogen, carbonic acid, sulphuretted hydrogen and marsh gas. The two former are taken in with the inspired air, carbonic acid is formed in the tissues, while hydrogen and its compounds are formed in the intestinal canal as the result of cellulose and other decompositions.

The largest portion of the inorganic matter consists of the various *Salts* of sodium, potassium, calcium, magnesium, and iron, in the form of chlorides, sulphates, phosphates, and carbonates. The distribution of these salts throughout the tissues is very variable, some, like bone, are excessively rich, whilst others are remarkably poor in them. Certain tissues and fluids have a preponderance of some salts to the exclusion of others.

The amount of the salts existing in the body depends upon the age of the animal, and their nature is modified by the character of the food. The daily quantity ingested and stored up is largely affected by the rate of growth, young growing animals storing up material which the adult rejects.

The diet of the herbivora furnishes considerably more potassium

than sodium salts to the system, with the result that in the excretions salts of potassium are in excess over those of sodium.

Sodium and *Potassium.*—Owing to the poorness of vegetable food in sodium salts, Bunge believes that the administration of common salt with the food of herbivora is a necessity. As this view is open to question his arguments in the matter should be known.

Bunge says in spite of the many inorganic salts found in the food, one only, viz., sodium chloride, is taken separately by the human subject in addition to that already existing in the food. But carnivora avoid salted food, as sufficient sodium chloride exists in the blood and tissues in the raw state in which these are consumed by them. Herbivora, on the other hand, have been known to travel considerable distances to obtain salt.

According to Bunge the explanation of the desire shown by herbivora for common salt lies in the large amount of potassium consumed in their diet, the effect of potassium salts in the blood being to withdraw sodium salts from the system.

Here are some tables given by him to show the proportion potassium bears to sodium in various articles of diet.

In every 1,000 parts of dried material :

	Potassium.	*Sodium.*
Rice	1 ...	·03
Bullock's blood	2 ...	19·0
Oats, Wheat, Rye, Barley	5 to 6 ...	·1 to ·4
Dog's milk	5 to 6 ...	2 to 3
Peas	12 ...	·2
Milk of herbivora	9 to 17 ...	1·0 to 10·0
Hay	6 to 18 ...	·3 to 1·5
Beef	19 ...	3·0
Beans	21 ...	·1
Clover	23 ...	·1

For one equivalent of sodium the equivalents of potassium are :

	Equivalent K_2O.
Mangel-wurzel	2·0
Milk of herbivora	·8 to 6·0
Beef	4·0
Wheat	12·0 to 23·0
Barley	14 to 21
Oats	15 to 21
Rice	24
Rye	9 to 57
Hay	3 to 57
Peas	44 to 50
Clover	90
Beans	110

The preponderance of potassium over sodium salts is here most marked, and Bunge considers that when a relation of from 4 to 6 equivalents of potassium to one equivalent of sodium is obtained in a diet no addition of sodium chloride is necessary ; but where the proportion of potassium is higher than this the animal instinctively seeks for sodium, for the reason previously given.

We do not deny the stimulant to the palate which common salt may afford the herbivora, but so far as horses are concerned, and we think the same argument must apply to cattle, it is quite certain that no addition of common salt to the ordinary diet is necessary, and that the food furnishes ample sodium for the purposes of the body.

Calcium forms the largest mineral deposit in the body ; it is taken in by means of the food. Bunge states that it is probable that the lime salts required for the growth of bone in young animals are contained in some organic compound, and that the administration of inorganic compounds of lime in rickets is irrational and useless.

Lime exists largely in clover and hay, but only in small quantities in the cereal grains ; it is principally by the hay that the amount excreted by horses through the kidneys is supplied. In the urine it passes from the body in such quantities that it cannot be held in solution by the alkaline fluid, and the urine is therefore always turbid in the horse. In the body calcium exists in the form of phosphate, sulphate, and carbonate, in the urine principally as carbonate and oxalate.

Magnesium salts occur in the body principally as phosphates, and in this form they enter largely into certain foods, such as oats. The amount of magnesium passing away from horses through the kidneys is small, but considerable quantities derived from the food pass out with the fæces, as they cannot be utilised in the body. By collecting in the bowels this salt produces the ammonio-magnesium phosphate calculi so common in horses.

Phosphates are united with soda, potash, lime, and magnesia. They are principally taken in with the food, but may also be formed in the body from the metabolism of phosphorus-containing compounds. The foods richest in phosphoric acid are oil-cake and bran, whilst hay and straw are poorest in this substance. Phosphoric acid is principally excreted by herbivora with the fæces, only small quantities passing away with the urine.

Carbonates are found in several of the secretions of the body, notably in the urine where they cause the most intense evolution of gas on the addition of an acid. The carbonates in the system of the herbivora result from the carbonates of the food, and the combustion of organic acids, malic, citric, tartaric, etc. ; these enter the body as salts of sodium and potassium, and the bases being set free unite with carbonic acid to form carbonates.

The *Sulphur* in the body is derived from the albumin of the food, in the system it is converted into sulphuric acid, and in this form 80 per cent. of the ingested sulphur appears in the urine. Sulphur exists in horn, hair, and epidermis.

The importance of the sulphates in the urine is considerable as they afford a passage out of the body for the products of proteid decomposition. Phenol and allied compounds are in this way got rid of in the form of phenol sulphate of potassium.

Iron is an important constituent of the complicated substance hæmoglobin. It is also found in the hair, skin, bile, lymph, most body fluids and tissues, and a small quantity in the fæces. Bunge considers that the iron which enters the system can only be absorbed when in the from of an organic compound. Inorganic iron, though largely used in the treatment of certain diseases, is not absorbed from the intestinal canal ; food contains only organic and not inorganic iron, and the hæmoglobin of the blood is formed from the complex organic compounds of iron which are produced by the vital process of the plant.

INDEX.

Aberration. *See* Sight
Abomasum, digestion in, 155
Absorbents. *See* Lymph
Absorption, 211
  from cellular tissue, 229
  from conjunctiva, 229
  of fats, 232
  from intestines, 230
  from peritoneum, 230
  from the pleura, 230
  of proteids, 234
  from respiratory passages, 228
  by the skin, 229
  from the stomach, 157
  of sugar, 234
Accommodation of the eye, 400
Achroodextrin, 122
Acid, amido, 256
  aspartic, 552
  benzoic, 261, 553
  bile, 194
  butyric, 554
  carbonic. *See* Carbonic acid
  carbolic, 182, 553
  cholalic, 194
  fatty, 207, 554
  glycocholic, 194
  glycuronic, 273
  hippuric, 258, 553
  hydrochloric, in stomach, 142
  lactic, 142, 322, 555
  lactic, conversion of starch into, 555
  lactic ferment, 148, 557
  lactic, in gastric juice, 142
  oxalic, 262
  phosphoric, 265, 560
  stomach, 142
  sulphuric, 261, 547, 554. *See* Urine
  sulphuric conjugate, 204, 261, 553
  taurocholic, 194
  uric, 258, 553
Age, old, 545
Air, changes in, during respiration 86
  composition of, 86
  expired, composition of, 101
  inspired, composition of, 101
  quantity breathed, 100, 102
Albumen. *See* Proteid
  conversion into peptones, 148, 206
Albumin, circulating, 282
  tissue, 282
Albuminoids, 550
Albumose, 148, 549
Allantoic fluid, 524
Allantoin, 553
Allantois, formation of, 520
Amble, the, 458
Amides and amido acids, 552
Ammonia in urine. *See* Urine
Amnion, 520
Amœboid movement, 11
Amylolytic action of saliva, 122
  action in stomach, 149
Amylopsin, 206
Anabolism, 278
Anelectrotonus, 331
Animal body, composition of, 276, 547
  expenditure and income of, 277
Animal heat. *See* Temperature
Animal starch. *See* Glycogen
Anti-albumose, 149
Aorta, elastic recoil of, 33
Apnœa, 94
Arterial pressure, 56
Arteries, 49
  pulse in, 60
  tension in, 63
Asphyxia, 94, 98
Astigmatism, 402
Auditory canal, 428
  centre, 374
  nerve, 381
Automatic action, 357
Automatism in nerve centres, 357

Basal ganglia, 362

Benzoic acid, 261, 553
Bile, 190
Bile acids, 194
  action on food, 196
  analysis of, 191
  fate of, 198
  pigments, 192
  quantity of, 196
  reaction of, 190
  salts of, 194
  secretion of, 195
  use of, 196
Bilirubin, 192
Biliverdin, 192
Birth, 531
Bladder, urinary, 274
  gall, 195
Blastodermic vesicle, 516
Blind spot, 398
Blood, 1
  analysis of, 23
  arterial and venous, 19
  bilirubin in, 19, 193
  buffy coat, 14
  carbonic acid in, 19, 22, 92
  changes in, during respiration, 89
  circulation of, 26, 59
  coagulation of, 13
  coagulation, theories of, 15
  compared with lymph, 217, 219
  composition of, 2, 23
  corpuscles, 4, 11. *See* Corpuscles
  corpuscles, destruction of, 6, 12, 75
  distribution of, 21
  effect on respiratory centre, 98
  extractives of, 18
  fibrin in, 13
  ferment, 13, 16
  gases of, 21
  globin in, 10
  glucose destroying ferment in, 202, 210
  hæmoglobin in, 7
  laky, 6
  liquor sanguinis, 2
  methæmoglobin in, 9
  opacity of, 6
  oxygen in, 22
  physical characters of, 1
  plasma, 2
  plasma, carbonic acid in, 92
  plates, 13
  pressure, 38, 54, 55, 58, 67, 71, 83
  pressure, stimulation of depressor on, 71
  proteids of, 3
  quantity of, 20
  salts of, 19
  serum, 2
Blood, sugar in, 19, 199
  temperature of, 20
  velocity of, 64
  venous, 19
Bloodvessels, 49
  constrictor fibres, 69
  dilator fibres, 70
  pressor fibres, 72
  influence of nerves on, 66, 96, 70, 72
  mechanism of circulation, 52
  tension in, 63
  tortuosity of, 74
  See Circulation
Body, composition of, 276, 547
  metabolic processes in, 278
Bowels. *See* Digestion and Intestines
Brain, circulation in, 73, 375
  coverings of, 375
  function of. *See* Cerebrum, Cerebellum, etc.
  pulsation of, 73
  ventricles of, 376
Breathing. *See* Respiration
Bulb. *See* Medulla
Butter, formation of, 536
Butyric acid, 554

Cæcum, 171, 173
  digestion in, 172
Calcium in urine, 263
  in blood, 15
  salts, 560
Calories, heat, 304
Canter, physiology of, 458
Capillaries, 50, 59, 223
Capsules, renal, 77
Carbo-hydrates, 283, 555
  formation of fat from, 284
  source of energy, 201, 287, 288, 322
Carbolic acid, 182, 261, 553
Carbon in the body, 547
Carbonates in body, 560
Carbonic acid in the air, 86
  absorption of, 92
  blood plasma, 92
  during rest and work, 101
  in expired air, 101
  partial pressure of, 92
  production of, 92
  removal at lungs, 92
Carbonic oxide hæmoglobin, 9
Cardiograph, 36
Cartilago nictitans, 410
Casein, action of rennin upon, 150
Cellulose, 556
  digestion of, 150, 172, 175, 556
Cell globulin, 17
Centre ano-spinal, 358

Centre, auditory, 374
cardio-accelerator, 39
cardio-inhibitory, 39
cilio-spinal, 358
diabetic, 202
for coughing, 360
for defæcation, 358
for erection, 358
genito-spinal, 358
for heat, 363, 374
micturition, 274
parturition, 358
respiratory, 94
swallowing, 361
for sweating, 359
vaso-motor, 66
vesico-spinal, 358
visual, 372
for vomiting, 361
Cerebellum, 364
Cerebral fluid, 73
Cerebrum, 365
functions of, 365
motor areas in, 371
removal of, 371
ventricles of, 376
Chlorides in urine, 265
Chlorine in body, 548
Cholesterine, 555
Chorda tympani, 70, 124, 379, 380
Chorion, 522
Chyle, 225
analysis of, 226
comparison with lymph, 227
Chyme passage through small intestines, 169, 171
passage of, from stomach, 132
physical characters of, 169
Circle of Willis, 72
Circulation, aids to, 66
arterial, 49
of blood, 26
capillary, 50, 59, 229
duration of, 66
embryonic, 526
fœtal, 527
in brain, 73, 375
in foot, 501
in living tissues, 59
influence of nervous system on, 66
influence of respiration on, 58, 83
mechanics of, 52
peculiarities in, 72
pulse, 60
venous, 51
Clipping, influence on sweating, 238
influence on temperature, 301
Coagulation of blood, 13
Cochlea, 430
Colon, 173, 176
Colon, absorption from, 176
condition of ingesta in, 174
description of, 173
digestion in, 175
fermentation in, 182
single, 176
Colostrum, 536, 538
Condition, 98, 324
Conjunctiva, absorption from, 229
Constrictor fibres in bloodvessels, 69
Contraction of muscle, 317, 319, 321
Co-ordination in nerve centres, 357
Copulation, act of, 506
Cord, umbilical, 523
spinal. *See* Spinal cord
Cords, vocal, 105, 107
Cornea, 393
Corpora nigra, 395
quadrigemina, 362
striata, 362
Corpus cavernosum, 73, 506
Corpuscles in blood, 4
alterations in shape, 19
colostrum, 538
destruction of, 6, 12, 75
number of, in blood, 5
third, 13
red, 4
white, 11
Cotyledons, 522
Coughing, 110
Cranial nerves, 377
Creatin, 256, 552
Creatinin, 261
Cresol, 553
Crura cerebri, 362
Currents in muscle, 315
in nerve, 330
Curves, Traube-Hering, 68
Cycle, cardiac, 29

Dandruff, 244
Death, 539, 545
Decay, 539, 544
Decidua, 522
Defæcation, 188
centre for, 358
Deglutition, 116
influence of saliva on, 118
nervous mechanism of, 118
Dentition, 542
Depressor nerve, 44, 47, 71
Dextrin, 122, 556
Dextrose, 557. *See* Sugar
Diaphragm, during rumination, 164
movements during respiration, 79, 83
spasm of, 110
tetanus of, 96
Diastole of heart, 29

Diabetic puncture, 202
Diabetes, pancreatic, 210
Diapedesis, 12
Diet. *See* Food.
Diffusion in air of lung, 88
  laws of, 88
Digestibility of food, 294
Digestion, 111
  of cellulose, 150, 172, 175
  in cæcum, 172
  in colon, 175
  comparison of peptic and pancreatic, 206
  of hay, 135
  intestinal, 167, 177
    small intestines, 167
    large intestines, 171
  movements of stomach during, 165
  of oats, 137
  palate, soft, use of, 117
  pancreatic, 206
  post-mortem of stomach, 158
  stomach, 131
  stomach of dog, 156
  stomach of pig, 155
  stomach of ruminants, 152
Dissociation of gases, 93
Draught, force exercised during, 464
  physiology of, 464
Drinking, 113
Duct, thoracic, 225
Ductus arteriosus, 530
  venosus, 529
Duodenum, effect of pressure upon, 134
  pyloric curve of, 134
Dyspnœa, 94

Ear, cochlea of, 430
  external, 428
  internal, 429
  labyrinth of, 429
  lymph of, 430
  middle, 429
  nerve, auditory, 432
  organs of Corti, 431
  semicircular canals, 429
  tympanum, 429
Ejaculation, mechanism of, 507
Electrotonus, 331
Elements of the body, 547
Embryo, development of, 515
  circulation of, 526
Emmetropia, 401
Energy yielded by food, 288
  foot tons of, 289
Enzymes, 551
Epidermis, 237
Epiglottis in deglutition, 117
Erection, phenomena of, 505
Erythrodextrin, 122
Eustachian tube, uses of, 429
Excretion, definition of, 247
Exercise. *See* Muscles
  on respiration, 82
  on production of heat, 297
  on production of carbonic acid, 101
Expiration, 80
Eye. *See* Sight
Eyeball, movements of, 404
  muscles of, 405
Eyelashes, 411
Eyelids, 411

Facial sinuses, 85
Fæces, 185
  analysis, 185
  amount of, 187
  colour of, 186
  composition of, 186
  expulsion of, 188
  meconium, 189
  odour, 188
Fallopian tube, 510
Fat, 554
  absorption of, 232, 555
  in chyle, 225
  emulsion of, 207, 555
  formation of, 284
  saponification of, 207, 555
Fatigue, muscle, 318, 323
Fatty acids, 554
  nitrogenous matters, 552
Fattening diet, 292
Ferments, 551
  amylolytic, development of from food, 149
  butyric, 557
  blood, 13, 16
  cellulose, 151, 557
  cyto-hydrolytic, 151
  gastric, 147
  glucose-destroying, 202, 210
  lactic acid, 148, 555
  liver, 200
  pancreatic, 206
  of succus entericus, 168
Fibrin, 549
  in blood, 15
  ferment, 13, 16
Fibrinogen, 15
Fibriny tissue, 16
Fœtal circulation, 527
Fœtal lung, 81
Fœtal membranes, 523
Food, absorption of. *See* Absorption
  amount required by animals, 289, 294

Food, digestibility of, 294
energy yielded by, 288
inorganic, 284
nitrogenous, 280
non-nitrogenous, 283
prehension of, 111
time occupied in consumption of, 115
Foot, anti-concussion mechanism, 495
age of, 487
bars of, 476, 493
bones of, 468
composition of, 485
corium of, 471
coronary substance, 472
cushion plantar, 470
evaporation from, 483
expansion of, 497
the frog, 479, 494
sweat glands of, 483
hoof of, 474
horn formation of, 481, 492
horn structure of, 480
joint, 467
laminæ of, 477, 488, 491
lateral cartilages of, 470, 489, 495
moisture in, 483, 484
movements of, 498
navicular bursa of, 468
pad, 479, 494
pedal bone, descent of, 560
physiological shoeing, 502
sole of, 472, 478, 493
structure of, 467
surface it affords, 491
vascular mechanism of, 501
supply, 473
wall, 471
the wall, 475, 486
weight, how carried by, 488
See Horn
Foramen ovale, 529

Gall bladder, 195
Ganglia, 329
basal, 362
cardiac, 45
Gasserian, 378
spinal, 337, 346
structure of, 329
sympathetic, 329, 386
trophic influences of, 334, 386
Ganglion submaxillary, 379
Gallop, physiology of, 459
Gases of body, 558
absorption of, by fluids, 87
dissociation of, 93
in blood, 21
intestinal, 183
partial pressure of, 88
Gases of respiration, 86
of stomach, 159
Gastric juice, 143, 146
acids of, 142
action of, 148
colour of, 147
composition of, 146
effect upon food of, 148
glands, 143
pepsin in, 147
rennin in, 148
secretion of, 143
Generation, 504
Germinal epithelium, 509
Germinal vesicles, 511
Gestation, period of, 530
Glands, gastric, 143
gastric changes in, during digestion, 144
of foot, 483
fundus, 144
mammary, 534
meibomian, 411
thymus, 75
pineal, 77
pituitary, 77
pyloric, 145
salivary, 119
sebaceous, 244
small intestines, 167, 215
sweat, 241
thyroid, 75
vascular, 75
Globin, 10
Globulin, 10, 549, 550
cell, 17
Glottis, movements of, 84
Glucose. *See* Sugar
destroying ferment, 202, 210
Glycerine, 555
Glycin and glycocoll, 194, 198, 552
Glycogen, 198, 556
conversion into sugar, 302
in muscle, 200, 313
source of, 201
use of, 201
Graafian follicles, 511
Growth, 539
Gustation. *See* Taste
Guttural pouches, 108, 435

Hæmatin, 10
Hæmatoblasts, 13
Hæmatoidin, 10
Hæmatoporphyrin, 10
Hæmin, 10
Hæmochromogen, 10
Hæmoglobin, amount of in body, 7
in blood, 7
carbonic oxide, 9

Hæmoglobin, compounds of, 9
nitric oxide, 10
reduction of, 8, 90
spectrum of, 8
union with oxygen, 8, 89
Hair, 237
shedding of, 237
Hay, digestion of, 135
Hearing, 427
Heart, 25
bony tissue in, 28
capacity of, 36
changes in shape of, 32
contraction, nature of, 44
daily work of, 37
depressor nerve of, 44, 47, 71
diastole of, 29
during work, 99
effect of drugs on, 47
ganglia of, 45
muscle of, 27, 44
nervous mechanism of, 39
pause of, 31
position of, 27
pressure within, 34
revolution of, 29
sensory nerves of, 39
sounds of, 34
systole of, 29
valves of, 26-28, 32, 33
Heat, animal, 297
amount of, 304
calories, 304
centre, 363
formation, seat of, 297
loss of, 298
regulation of, 303
sources of, 297
unit, 288, 297, 304
See Temperature
Hemi-albumose, 149
Hemi-peptone, 149
Hiccough, 110
Hippomanes, 526
Hippuric acid, 258
Hoof, 474
Horn, formation of, 481
composition of, 485
evaporation from, 483
structure of, 480
Hunger, 427
Hybernation, 307
Hydrochloric acid in stomach, 142
Hydrogen in body, 547
Hypermetropia, 402

Images, retinal, 417
Impregnation, 514
Income and expenditure of body, 277
Indican, 554
Indigo, 554
in urine, 262
Indol, 182, 188, 554
Indoxyl-sulphuric acid, 554
Inflammation, 59
Infusoria in intestines, 183
Inhibition, 327
Inhibition of heart, 39, 42
Inhibitory nerve of heart, 39
Inogen, 322
Inspiration, 78
Intelligence in animals, 366
Intercourse, sexual, 506
Intestines, 167
absorption from, 230
cæcum, 171
colon, 173, 176
digestion in, 167
in ruminants, 177
in other animals, 177
duration of digestion in, 171-173, 177
gases of, 183
glands of, 167
ileum, function of, 170
infusoria in, 183
juice of, 167
large, 171
movements of, 174
nervous mechanism of, 179
putrefactive processes in, 181
reaction of contents, 169
small, 167
Iron in body, 560
Iris, 394

Jacobson, organ of, 421
Joint, elbow, 443
fetlock, 444
foot, 467
hip, 443
hock, 439
knee, 443
shoulder, 443
stifle, 442
Joints, synovia of, 439
Jump, the, 460

Katabolism, 278
Kathelectrotonus, 331
Keratin, 486
Kicking, physiology of, 461
Kidney, function of, 247
nerve supply of, 254
structure of, 248
tubules of, 250
vessels of, 248, 251
Kreatin, 256, 552

Lacteals, 231
Lactic acid in stomach, 142
Lactose, 557
Lameness and locomotion, 447
Laminæ of foot, 477, 488, 491
Lanolin, 244
Larynx, 103
  during deglutition, 105
  during respiration, 105
  muscles of, 104
  nerve supply of, 105
  ventricles of, 108, 109
  vocal cords of, 105, 107
Lecithin, 12, 548
Lens, convex, passage of light through, 415
  crystalline, 393
Leucin, 203, 552
Leucocytes, 11
Levers, theory of, 436
Levulose, 557
Ligaments, check, 445
  sprain of, 450
  suspensory, 444
Lime salts, 560
Lips. *See* Prehension
Liver, 190
  conversion of substances into urea in, 203
  ferment in, 200
  glycogen in, 198
  summary of changes in, 204
  uses of, 196, 203
  See Bile
Locomotion, 436
  amble, 458
  anti-concussion mechanisms, 449
  co-operative antagonism, 438
  the canter, 458
  centre of gravity, 446
  check ligament, use of, 445
  daily work of horses, 461
  draught, physiology of, 464
  the gallop, 459
  joints, 438
  the jump, 460
  kicking, 461
  lying down, 452
  lameness, 447
  muscles, action of, 438
  rearing, 460
  a reflex act, 355
  rising, 453
  standing, act of, 452
  suspensory ligament, use of, 444
  the trot, 457
  velocity of paces, 462
  the walk, 453
  the weight carried, 463
  weight on the limbs, 446
Locomotion, weight of limbs, 437
Legs, weight of, 437
Lung. *See* Respiration
Lying down, act of, 452
Lymph, 211, 217
  analysis of, 218
  analysis of, compared with that of blood, 217, 219
  capillary, 212
  cells, 217
  comparison of, with chyle, 227
  extractives of, 217
  fibrin in, 217
  gases of, 217
  movements of, 223, 224
  quantity of, 219
  salts of, 217
  secretion of, 220
  spaces, 211
  vessels, 212
Lymphagogues, 221
Lymphatic glands, 215

Magnesium salts, 560
  in urine, 264
Malpighian bodies, 248
Maltose. *See* Sugar
Mammary gland, 534
Marsh gas, 159, 175, 182, 183, 558
Mastication, 113
  time occupied in, 115
Meconium, 189
Medulla, 359
  centres in, 39, 66, 94, 202, 360
  cerebellar tract in, 359
  columns of, 359
  decussation of fibres in, 360
  formation of, 359
  function of, 362
  grey matter of, 360
  pyramidal tract in, 359
  respiratory centre in, 94
  tracts in, 359, 360
  vaso motor, centre in, 94
Membranes, fœtal, 523
Metabolism, 278
Methæmoglobin, 9
Micturition, 274
Milk, action of stomach juice upon, 150
  colostrum, 536, 538
  composition of, 535
  fat of, 536
  proteids of, 536
  salts of, 536
  secretion of, 534
  uterine, 531
Movement, co-ordination of, 364
Mucus, secretion of, by stomach, 133, 146

Mucus, in urine, 268
Muscle, acid of, 322, 323
changes in active and resting, 312
chemical composition of, 312
'condition' of, 324
contraction of, 289, 317, 322
contraction, effect of cold on, 319
contraction, cause of, 321
co-operative antagonism, 438
currents, 315
curves, 318
elasticity of, 322
excitability of, 315
fatigue, 320, 323
glycogen in, 312, 313
heart, 27, 44
heat in, 314
latent period in, 318
nerve supply of, 308, 314
refractory period in, 45
respiration of, 90
rigor mortis of, 322, 324
seat of heat production, 297
skeletal, proportion in body, 308
structure of, 309
tetanus of, 319
urea in, 256
wave, 317
work of, 320
Muscular system, 308
Myopia, 401
Myosin, 312

Nasal chambers, 84
Navicular bursa, 468
Negative variation, 331
Neighing, 109
Nerve, axis cylinder of, 328
cells, 329
centres. *See* Centres
current in, 330
endings, 336
impulses, 333
terminations, 329, 336
Nerves, 326
afferent, 326
bladder, 274
bloodvessel, 66, 69, 70
cardiac, 39
chorda tympani, 70, 124, 379, 380
classification of, 326
conductivity of, 330, 334
cranial, 377
first pair, 420
second pair, 390
third pair, 377
fourth pair, 377
fifth pair, 97, 377
sixth pair, 380
seventh pair, 100, 380
Nerves, cranial, eighth pair, 381
ninth pair, 381, 423
tenth pair, 39, 44, 95, 166, 179, 382, 385
eleventh pair, 385
twelfth pair, 386, 424
depressor, 44, 47, 71
degeneration of, 334
efferent, 226
elasticity of, 329
electric phenomena of, 330
electrotonic state of, 331
excitability of, 330
ganglia on, 45, 329. *See* also Ganglia
intestinal, 179
kidney, 254
laryngeal, 97, 106, 107, 382
lingual, 386, 424
masticatory, 113
motor, 326
negative variation of, 331
nutrition of, 334, 335
œsophageal, 119, 384
of muscles, 308, 314
olfactory, 420
optic, 390
pharyngeal, 382
phrenic, 99, 164
pilo-motor, 238, 389
pneumogastric. *See* Nerves, Cranial, Tenth
branches to intestines, 179
branches to stomach, 166, 385
heart, 39, 44
respiration, 94, 96, 97, 382, 385
ramus communicans, 338, 345, 387
sensory, 326
spinal, 337, 344
splanchnic, 67, 72, 180, 388
stomach of, 166
structure of, 328
suture of, 335
sympathetic, 386
of taste, 381, 423
tongue of, 112
trophic, 336, 380, 388
vaso motor, 66, 69, 70, 388
velocity of impulse, 334
Nervous mechanism of heart, 39
of heat production, 303
of intestines, 179
of larynx, 105
of respiration, 90
of rumination, 164
of salivary secretion, 124
of stomach, 166
of swallowing, 118
of sweating, 240

Nervous system, 326
cerebrum, 365
corpora quadrigemina, 362
corpora striata, 362
crura cerebri, 362
medulla oblongata, 359
pons varolii, 362
spinal cord, 337
sympathetic system, 386
thalami optici, 362
Nitrogen in body, 547
no measure of muscular work, 289
Nitrogenous bodies, 548
equilibrium, 280
fats, 552
food, 280
Non-nitrogenous food, 283
Nostrils, 84
Nuclein, 12, 548
Nucleo-albumin, 17
Nutrition, 276
amount of food required for, 289
cause of body waste, 287
composition of body, 276
effect of nitrogenous food upon, 280
effect of inorganic food upon, 284
effect of muscular exertion upon, 287
effect of non-nitrogenous food upon, 283
effect of starvation upon, 285
income and expenditure, 277
See Food

Oats, digestion of, 137
Odour, 421
Œdema, cause of, 222
Œsophageal groove in rumination, 163
Œsophagus during deglutition, 162
during rumination, 165
nerve supply of, 119, 384
structure of, 118
wave in, 119
Oil. *See* Fat
Old age, 544
Olfactory nerves, 420
sensations, 421
Omasum, 154
Ophthalmoscope, 398
Optic nerve, 390
Orbit, 390
Organ of Jacobson, 421
Organism, constituents of, 547
Ovum, 510
development of, 514
impregnation of, 514
Ovary, 509
Oxygen in the tissues. 90
absorption of, 89
Oxygen, amount required, 101
in air, 86, 93
in body, 547
in expired air, 86, 101
in muscle, 90
inhalation of, 93
partial pressure of, 88
union with hæmoglobin, 8, 89
uses of, in tissues, 91

Painful sensations, 425
Palate, 113, 117
Pancreas, 204
changes in cells of, 208
nervous mechanism of, 210
Pancreatic diabetes, 210
digestion compared with that of stomach, 206
juice, 204
action on proteids, 206
action on fats, 207
action on starch, 206
amount of, 209
analysis of, 205
emulsifying action of, 207
ferments of, 206, 210
salts of, 205
secretion of, 209
uses of, 205
Papillæ of tongue, 423
Parotid gland, 119
Parturition, 531
Penis, circulation in, 70, 73
erection of, 70, 506
Pepsin, 147
Peptone, 148, 550
Peritoneum, absorption from, 230
Perspiration. *See* Sweat
Pharynx during deglutition, 116, 118
Phenol, 182, 553
Phonation, 107
Phosphorus in body, 548, 560
Pig stomach, digestion in, 155
Pigments, 551
bile, 192
urinary, 262
Pilo-motor nerves, 238, 389
Pineal gland, 77
Pituitary body, 77
Placenta, 522
Pleura. *See* Serous cavities
Pneumogastric. *See* Nerves
Polar bodies, 511
Pons varolii, 362
Portal vein, 234, 527
Potassium salts, 559
in urine, 264
Pouches, guttural, 108, 435
Pregnancy, duration of, 530
Prehension of food, 111

Prostatic fluid, 505
Proteids, 548
absorption of, 234
classification of, 549
decomposition of, 182, 204, 549
food, 280
gastric digestion of, 147
intestinal digestion of, 206
reaction of, 550
sulphur in, 547
Ptyalin in saliva, 122
Puberty, period of, 507
Pulse, 60
tension, 63
tracings, 61
wave, 61
Pupil of the eye, 394
Putrefaction in intestines, 181
Pylorus, duodenal curve of, 134
Pyramidal tracts, 265
Pyrocatechin, 554

Rearing, 460
Reason in animals, 366
Rectum, absorption from, 176
contents of, 176
innervation of, 180
Reflex action, 353
Reflexes, tendon, 356
Refraction, 403
Renal capsules, 77
Rennin, 148
Respiration, 78
apnœa, 94
asphyxia, 94, 98
amount of air required, 100, 102
carbonic acid of, 101, 102
centre for, 94, 98
changes in air and blood, 86
changes in tissue, 89, 90
diaphragm, movements of, 79
dyspnœa, 94
effect of muscular exertion on, 82
effect on circulation, 83
expiration, 80
facial nerves in, 100
facial sinuses in, 85
gases of, 86
inspiration, 78, 82, 84, 85
movements of diaphragm in, 79
movements of nostrils during, 84
muscles employed in, 81
of muscle, 90
nasal chambers, 84
nervous mechanism of, 94
nostrils and glottis, 84, 105
number of, 82
oxygen in, 86, 93, 101
phrenic nerves in, 99
pressure in trachea during, 82
Respiration, quantity of air breathed, 100, 101, 102
self-adjusting mechanism, 96
Respiratory exchange, 101
function of skin, 245
Respiratory passages, absorption from, 228
Respiratory quotient, 87, 102
Reticulum, 154
Retina, the, 397, 408, 417
Rigor mortis, 322, 324
Rising, act of, 453
Roaring, cause of sound, 107
Rumen, digestion in, 152
Rumination, 162
nervous mechanism of, 164
œsophageal groove in, 163
respirations during, 82
salivary secretion during, 164

Saccharose, 557
Saliva, 119
action on starch, 122
amount of, 120
amylolytic action of, 122, 149
analysis of, 120
characters and properties of, 120
during deglutition, 118
effect of fasting on secretion of, 121
gases of, 121
glands producing, 119
nervous mechanism concerned in secretion of, 124
physical properties of, 121
ptyalin in, 122
secretion of, 124
unilateral secretion of, 121
use of, 121
Salivary glands, mucous and serous, 119
changes in cells of, 127
Salts of body, 284, 558
Sebaceous secretion, 244
Secretion, definition of, 247
Segmentation of ovum, 514
Semen, 504
Semicircular canals, use of, 381, 429
Sensations, auditory, 432
olfactory, 420
of taste, 422
painful, 425
temperature, 424
touch, 425
Senses, 390
Sensibility, recurrent, 345
Serous cavities, 212
Serum. *See* Proteids
Sexual desire, 507
intercourse, 506

Shoeing, physiological, 502
Sight, 390
accommodation, 400
astigmatism, 402
blind spot, 398
cartilago nictitans, 410
choroid, 396
chromatic aberration, 419
ciliary zone, 397
ciliary muscle, 397, 401
cornea, 393
corpora nigra of iris, 395
crystalline lens, 393
dioptrics, 414
emmetropia, 401
eye, cardinal points of, 412
reduced, 412, 415
schematic, 412
structure of, 391
fundus, appearance of, 399
humours of eye, 392
hypermetropia, 402
the iris, 394
katoptric test, 403
lens, passage of light through, 415
ligamentum pectinatum, 396
movements of eyeball, 404
muscles of eyeball, 405
myopia, 401
nerve of, 390
ophthalmoscope, 398
optic axis of the eye, 398
optics, 411
refraction, 403
the retina, 397
formation of image on, 417
retina, corresponding points of, 408
secretion of tears, 411
spherical aberration, 418
tapetum lucidium, 396
vision, binocular, 407
vision, monocular, 407
visual angle, 418
visual centre, 372
Silica, 548
Sinuses, facial, 85
lymph, 216
venous, 73, 526
Skatol, 554
Skin, 236
absorption by, 229
dandruff of, 244
hair of, 237
respiratory function of, 245
sebum of, 244
secretion of, 238
Smegma, 245
Smell, 419
seat of, 420
Soaps, 555
Sodium salts, 559
glycocholate and taurocholate, 194
in urine, 265
Solar plexus, 179
Solitary follicle, 215
Sound, 427
Spermatic fluid, 504
Spermatozoa, 508
Sphygmograph, 61
Spinal cord, 337
acts, reflex, in, 353
afferent and efferent paths in, 350
arrangement of, 338
automatism in, 357
centres in, 358
conducting paths in, 350
connection with sympathetic system, 338
co-ordinate movement in, 357
distribution of nerves in, 341
functions of, 359
ganglia on superior roots, 337, 346
nerves, 337, 344
structure of, 338
superior and inferior roots of, 341, 342
tracts in, 347
Wallerian, degeneration in, 345
white and grey matter in, 340
Splanchnic nerves, 67, 72, 180, 388
Spleen, 75
Sprains, 450
Standing, act of, 452
Starch, 122, 555
action of pancreatic juice on, 207
action of saliva on, 122
conversion in small intestines, 168, 207
conversion in stomach, 149
Starvation, 285
Steapsin, 206
Stearin, 554
Stercobilin, 186
Stomach, absorption from, 157
acids, 142
amylolitic changes in, 149
appearance of food in, 141
arrangement of food in, 138
capacity of, 132
cellulose fermentation in, 151
digestion compared with pancreatic, 206
digestion in, 131
digestion in dog, 156
digestion in pig, 155
digestion in ruminants, 152
digestion of hay in, 135
digestion of milk in, 150
digestion of oats in, 137

Stomach, gases of, 159
gastric juice, 143, 146
glands of, 143
horse's, points in structure of, 134
lactic ferment in, 148
movements of, 165
mucin in, 133, 146
mucous membrane of, in horse, 132
nervous mechanism of, 166
of the dog, 156
of the pig, 155
of ruminants, 152
openings of, 133
passage of food from, 131
passage of water to cæcum, 140
pepsin in, 147
peptone in, 148
periods of digestion in, 151
rennin in, 148
secretion of mucin by, 133, 146
self-digestion of, 158
starch conversion in, 149
vomition, 159
Succus entericus, 167
Sucking, 113
Sugar, 122, 150, 153, 168, 198, 200, 557
absorption of, 234, 557
course taken by, during absorption, 198
destroying ferment, 202, 210
in the blood, 18, 199
in urine and glycogen, 199, 201
tests for, 558
used by muscle, 201
Suint, 245
Sulphur in body, 547, 560
in urine, 261, 552, 560
Suspensory ligament, use of, 444
Swallowing, 116
Sweat, 239
glands, 241
influence of drugs on, 242
Sweating, effect on condition, 240
nervous mechanism of, 240
Sympathetic system, 386. *See* Nerves
Synovia, 439
Systole of heart, 29

Tactile sensations, 425
Tapetum lucidum, 396
Taste, 422
goblets, 423
nerves of, 423
Taurin, 198, 552
Tears, secretion of, 411
Teeth, 112
Temperature, body, 305
heat production, centre for, 363
Temperature, normal, of animals, 305
post-mortem, 307
regulation of, in the body, 298
seat of heat formation, 297
sense of, 424
topography, 306
See Heat
Tendon reflexes, 356
Testicles, 512
Tetanus of muscle, 319
Thalami optici, 362
Thermotaxic mechanism, 303
Thoracic duct, 225
Thirst, 427
Thymus gland, 75
Thyroid gland, 75
Tongue of horse, 112
nerves of, 112
of ox, 112
papillæ of, 423
Touch, 424
Tracts in cord, 347
medulla, 359, 360
Transudation, 220
Trophic nerves, 336, 380, 388
Trot, physiology of, 457
Trypsin, 206
Tympanum of ear, 429
Tyrosin, 203, 553

Umbilical cord, 523
Urea, 256, 283, 552
amount of, 257, 273
formation of, 256
Uric acid, 258, 553
formation of, 258
Urine, 247
of the calf, 271
colouring matter of, 262
composition of, 255
creatinin in, 261
influence of diet on, 270, 272
discharge of, 273
of dog, 272
of horse, 267
mucin in, 268
odour of, 268
organic matter of, 255
of the ox, 270
of the pig, 272
quantity of, 267
reaction of, 266
of rest and work, 269
salts of, 255, 263, 269
secretion of, 248, 253
sheep, 271
solids of, 268
specific gravity, 267, 270
ammonia in, 265
benzoic acid in, 261, 553

Urine, calcium in, 263, 560
chlorine in, 265
creatinin in, 261
glycuronic acid in, 273
hippuric acid in, 258, 553
indican in, 262
magnesium in, 264
oxalic acid in, 262
phosphoric acid in, 265
potassium in, 264
sodium in, 265
sulphuric acid in, 261, 552, 560
urea in, 256
uric acid in, 258
Uriniferous tubes, 250
Urobilin, 262
Uterine milk, 531

Vagus. *See* Nerves, Pneumogastric
Valves of heart, 26, 28, 32, 33
of lacteals, 227
of lymphatics, 212, 223, 225
veins, 51
Vaso-motor nerves, 66, 69, 70, 388
Veins. *See* Circulation
of foot, 474, 501
Velocity of paces, 462
Ventricles of brain, 376
of heart, 26, 30
Vestibule of ear, 429
Villi, 213, 231
lacteals of, 233
Vision. *See* Sight
Vocal cords, 105, 107
Voice, 107
coughing, 110
hiccough, 110
neighing, 109
sneezing, 110
production of, 107
yawning, 110
Vomiting, 159

Walk, physiology of, 453
Water in body, 276, 558
passage of, to cæcum, 170
after feeding, effect of, 140
Ellenberger's view upon, 141
Weight carried by horses, 463
increase during growth, 540
Work of horses, 461

Yawning, 110
Yelk, segmentation of, 514

THE END.

Baillière, Tindall and Cox, King William Street, Strand.

ERRATA.

Page 109, 4 para. A region in the brain of the dog has recently been described by Russell, stimulation of which leads to abduction of the cords; it is situated in front of the adductor centre.

Page 168, 5 para. The action of the succus entericus on cane sugar should be read in conjunction with para. 5, p. 557. Cane sugar is converted by the succus into equal parts of glucose and levulose.

Page 314, 4 para. *For* 'Heidenham' *read* 'Heidenhain.'

E/18