

Observations on the structure and development of bone / by John Tomes and Campbell de Morgan.

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IV. *Observations on the Structure and Development of Bone.* By JOHN TOMES, F.R.S.,
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THE structure and development of bone is a subject which has occupied the attention of physiologists both of present and past times, and holds a prominent place in their writings. From the time of CLOPTON HAVERS, who was the first to point out the vascular canals in bone, and whose name they have since borne, to the year 1850, when M. KÖLLIKER's elaborate work on Structural Anatomy appeared, physiological writers have dwelt at considerable length on this branch of their subject. All have, however, concluded with the admission that more remained to be learned before this important structure could be regarded as fully understood*.

It is the purpose of the authors in this communication, to lay before the Royal Society the results of an extended series of observations on the structure and development of bone. Such of these results as are novel might, perhaps, be described without reference to those points which are already well known. It will, however, be seen, in the subsequent pages, that they are in themselves, and in their relations to osseous tissue and its development, as well as to structural anatomy generally, of such a nature, as would hardly admit of an intelligible description apart from some consideration of the whole subject. Hence it will be necessary to point out the relations between that which is already known, and that which it is the special purpose of this paper to communicate, and it is proposed to consider the details of the subject as they present themselves in the progress of investigation with but little reference to authorities, adding in the form of notes, those statements which require acknowledgement, either as agreeing with, or as being opposed to, the views advanced in this paper.

In treating of the structure of bone, it is convenient to commence by describing the appearances which a thin transverse section from the shaft of an adult long bone presents when placed in the field of a microscope having a magnifying power of from 200 to 300 linear. In addition to the large central space which corresponds to the medullary cavity of the bone, the section is seen to be perforated by numerous small apertures, each of which is surrounded by a series of laminæ of osseous tissue concentrically arranged. Lying amongst the laminæ are many small cavities, from which minute tubes radiate. These were called bone-corpuscles by PURKINJE, who

* Mikroskopische Anatomie, von Dr. A. KÖLLIKER. Leipzig, 1850.

first described them ; but latterly, with a more correct appreciation of their nature, the name of lacunæ has been substituted at the suggestion of Dr. TODD and Mr. BOWMAN*, who have also described the Haversian canals, their surrounding laminæ, and their lacunæ, under the inclusive term of Haversian systems. The whole substance of the bone is made up of Haversian systems, connected by irregularly-shaped patches of short laminæ which occupy the spaces between the systems (Plate VI. fig. 1 *b*). These have received the name of interstitial laminæ from KÖLLIKER. In addition to the Haversian and interstitial laminæ, we have in most instances others that surround, or partly surround the whole, and form the outer surface of the bone. These, from the position they occupy, are called the circumferential laminæ. A similar series more or less perfect is found to form the wall of the medullary cavity.

If the section be taken from near the end instead of from the middle of the shaft of a long bone, the Haversian canals will appear much larger, and in the place of one great central opening we shall see numerous lesser ones, corresponding to the cancellous part of the bone. From whatever bone, or part of a bone, the section be taken, the arrangement of laminæ and lacunæ is substantially the same ; the differences between the compact and cancellous portions consisting in variations in the relative quantities of the bone tissue and the size and number of the canals, and not in any real difference in the structure.

The elongated bones of some of the vertebrata, when cut transversely through their centres, are seen to be composed, at that part, of a single Haversian system. The rib of a Boa may be cited as an example.

Having drawn attention to the several parts which are recognised as entering into the composition of bone, the authors will now proceed to describe the results of their investigations under the subjoined heads:—

- 1st. The Haversian canals and other spaces.
- 2nd. The laminæ.
- 3rd. The lacunæ and canaliculi.
- 4th. The Haversian systems.
- 5th. Ossified cartilage of joints.
- 6th. Ossified cells.
- 7th. Bone tissue.
- 8th. Development of bone.
- 9th. Growth of bone.

Haversian and other Canals of Bone.—The Haversian canals have been described by all recent writers on the subject of bone ; their variable size and not unfrequent anastomoses have been pointed out ; and the fact of the larger apertures in the spongy parts of bone being similar in the structure of their parietes to the smaller ones in the denser parts of the osseous tissue has not failed to be recognized. It may be remarked, that whether the canals are large or small, their section presents an

* The Physiological Anatomy and Physiology of Man, by Dr. TODD and Mr. BOWMAN, vol. i. p. 109.

oval or circular outline, and that the walls of such canals have a tolerably uniform surface. When examining sections of bone it is necessary to bear this fact in mind, for on a close inspection it will be seen that there are other spaces which possess a different character, although up to the present time, so far as the authors know, this difference has not been recognized.

These spaces are irregular in shape, and have an irregular, festooned and often jagged outline, similar to that found on the surface of bone which has been removed by exfoliation, similar also to the surface left upon the fang of a tooth after a part has been absorbed. Such spaces correspond in shape to the peripheral outline of one or more of the Haversian systems, and are in fact subservient to the development of those systems, and necessarily precede their formation (Plate VI. figs. 2 a, 3 a, 4 a). It is proposed to call these spaces which are produced by absorption, *Haversian spaces*, as this name is indicative of their ultimate connection with the Haversian systems. In the Haversian canals we have surrounding laminæ, but in the spaces the boundaries are formed by portions of several systems, each of which has been in part removed in the formation of the spaces, as shown in figures 2 and 3, and Plate V., which, on being compared with figure 1, will illustrate the difference between the spaces and canals; allowance must, however, be made for the difference of size, as in figure 1 the parts are less magnified than in the other illustrations. In newly-formed bone situated near ossifying cartilage, the Haversian spaces are exceedingly numerous and large, frequently affording room for the development of two or more systems (fig. 5, Plate VI. fig. 24, Plate VIII.), while in older bone they are far less numerous, and generally less in size. In no case, however, are they wholly absent. They are found even in the bones of old subjects, and in connection with them newly developed systems.

This is a very important fact, as it demonstrates that the old tissue is removed in masses, and a new one developed in its place. It has long been taught that the older particles of an internal tissue are removed by absorption and new ones substituted, and this throughout the life of the individual. But the authors believe that they have demonstrated it for the first time.

On examining with care a series of sections, the Haversian spaces will be found in various conditions. In one place the space will have attained a large size, while in another part of the same section its commencement will be seen extending from one side of an Haversian canal. In a third instance, its occupation will have commenced, and its festooned margin will be lined by the peripheral lamina of an Haversian system. Then, again, examples may be found where one side of a space is becoming the seat of a new system, while the opposite one is undergoing further enlargement. In no case is there any difficulty in distinguishing between an enlarging Haversian space and a developing Haversian system. The authors have preparations which show that these conditions of absorption and reproduction take place in old as well as in young or middle-aged subjects; but it would appear that the frequency dimi-

nishes with the increasing age of the individual. It may however be observed in the bones of those who have passed the sixtieth year. The more recently formed systems differ from those of older date in the somewhat larger size of their lacunæ and canaliculi, and in the greater abundance of the latter, as shown in fig. 6, Plate VI.

Laminae of Bone.—Lamination is a tolerably constant character of mammalian bone, although the degree of its distinctness is subject to considerable variation. In the bones of young subjects it is less pronounced than in those of mature animals (fig. 4, Plate VI.); it is also much less observable in the cancellous than in the compact tissue. When lamination reaches its highest degree of development, each lamina is seen to be made up of two parts, an outer, which is highly granular, composed oftentimes of a single line of large granules or cells*, as shown in Plate VI. fig. 8; and an inner portion, which is singularly clear and transparent, and to all appearance without granulation or any recognizable structure.

KÖLLIKER has described and figured a somewhat similar appearance from a specimen treated with turpentine, but he does not seem to regard it as very readily discoverable in ordinary preparations†; there is, however, no difficulty in exhibiting this arrangement of structure in well-made sections, either simply polished or (which is better) put up in hard Canada balsam.

Very favourable views of lamination may be seen in transverse sections from the shafts of long bones; some of the most striking illustrations in the possession of the authors were obtained from the tibia of a subject the whole of whose bones were slightly hypertrophied, and from the femur of a limb which had from infancy been atrophied and useless.

Strongly marked laminae, with their transparent and granular portions, are however not always met with; yet in their absence the observer will seldom fail to find laminae of more uniform granularity surrounding the Haversian canals in well-marked concentric rings.

On examining the Haversian systems, it will be seen that the peripheral lamina has its internal surface marked by an even line, while the external is subject to slight bulgings, which correspond with and accurately fit into the indentations that form the margin of a pre-existing Haversian space (Plate VI. fig. 1). Hence the outer lamina of a system will present on its external surface a certain number of alternating dilatations and contractions; a peculiarity possessed by none of the more internal of the series. We may, however, find the whole of the laminae of a system presenting different degrees of thickness on the opposite sides of a canal, from the latter being a little eccentric in its position. But when the eccentricity is considerable, as in the case illustrated in Plate VI. fig. 7, the laminae are not all continued round the canal‡. Hence,

* The nature of these bodies will be more fully considered under the head of development and growth of bone.

† KÖLLIKER, *oper. cit.* page 284. In 'The Microscopic Anatomy of the Human Body,' by A. H. HASSALL, this appearance is indistinctly figured, but no description of it can be found in the letterpress.

‡ KÖLLIKER, *oper. cit.* at page 283, states that in the eccentric systems the whole of the laminae generally

in such a system, there are more laminæ on one side than on the other, and those on the side occupied by the greatest number are thicker in their centres than at their extremities, where they become gradually thinner, and are ultimately lost. The inner lamina, whether the systems are eccentric or not, forms, when the development is completed, a perfect ring, and not unfrequently presents a second peculiarity. The tissue of which it is composed is transparent, and affords, with our present means of investigation, little evidence of structure (Plate VI. figs. 6 and 7). It is transparent and glass-like, resembling that tissue which lines the Haversian canals in the antlers of the Cervidæ before they are cast (Plate VII. fig. 9).

The interstitial laminæ are abundant, and strongly marked in transverse sections of long bones, or in any sections of bone in which the Haversian systems are cut transversely. The laminæ vary both as to their number and length, and are usually more or less curved. They are arranged throughout the bone in well-defined isolated groups, in each of which the constituent laminæ are parallel (Plate VI. fig. 1*b*). Professor KÖLLIKER*, when treating of this subject, observes that it is difficult to account for the presence of the interstitial laminæ, and suggests that the appearance may perhaps be produced by the Haversian systems being cut obliquely, but at the same time admits that this explanation is not satisfactory. M. KÖLLIKER had not recognized the presence of the Haversian spaces and the manner of their production and subsequent occupation, otherwise he would have seen that the interstitial laminæ are the remaining parts of Haversian systems, the larger portions of which had been removed by absorption. But that the term *interstitial laminæ* is already in use and has a definite meaning, the authors would have proposed the substitution of *partial Haversian systems*, as being more descriptive of these parts.

In addition to the laminæ of the perfect and imperfect Haversian systems, others that surround several linearly arranged systems are not uncommon, producing the appearance illustrated in Plate VI. fig. 5. In these instances a large oval system of laminæ has become occupied by several lesser ones. The occurrence of one system within another is by no means rare. We may then see the characteristic emarginated outline of the older system, and within this a second similar outline marking the periphery of the younger system, as shown in Plate VI. fig. 6, in which the lamination of each is delineated †.

The circumferential laminæ are the most external, and where they exist form the surface of the bone. Their occurrence, however, is by no means so constant as is generally described, and even when present they seldom extend perfectly round the bone. The authors have scarcely seen an example in which the laminæ have been continued without interruption around the shaft of a long bone, and in flat bones encircle the canal, but that they are individually thicker on the one than on the other side. Although this may be the case in some instances it has been but rarely seen by the authors.

* KÖLLIKER, page 289, *oper. cit.*

† This appearance is figured by M. KÖLLIKER, but no reference is made to the peculiarity in the letterpress.

they are even less constant. When present they appear to indicate that the bone is nearly stationary in its growth as regards thickness, for in the fast-growing bones of young animals these laminæ are entirely absent, while in the bones of adults they are usually well-developed in some parts. In number they seem subject to considerable variation, and not unfrequently are arranged in different concentric series with three or four laminæ in each division, separated from the adjacent series by a broad and transparent lamina, suggesting the idea of periods of greater activity of growth, alternating with others of less activity. Like those of the Haversian systems, the circumferential laminæ are perforated by Haversian spaces and systems (Plate VII. fig. 10), and in many examples to such an extent that they are recognized only as interstitial laminæ; but their uniform direction parallel with the surface of the bone will satisfactorily indicate their previous existence as continuous circumferential laminæ. In this part of a bone we may sometimes discover a peculiarity of character, in the presence of Haversian systems, consisting of two or three laminæ, or of even a single lamina only, so small has been the preceding Haversian space.

In the progress of development canals are sometimes formed which proceed from the surface of the bone into its substance, and around these the circumferential laminæ are inflected, thereby forming systems, the laminæ of which are continuous with those of the surface of the bone. On the other hand, Haversian spaces not unfrequently occur which are continued from the surface towards the centre of the bone, cutting the circumferential laminæ abruptly across; systems are subsequently developed in these spaces; but in such instances the laminæ of the systems are not continuous with those of the surface (the latter appearance is shown in Plate VII. fig. 10).

In young rapidly growing bone the circumferential laminæ are replaced by a series, which, from the character of their course, might be termed the undulating laminæ. The bone in its growth sends off outrunning processes between those vessels of the periosteum which lie nearest the surface of the bone. These processes are formed of reduplicated laminæ which are continued from process to process, following the undulating surface of the bone for a considerable distance before they are lost. The growing processes as they increase in size and length arch over towards each other by the dilatation or bifurcation of the outer extremities. The salient points so formed come into contact and unite, thereby enclosing the vessels. The spaces enclosed in the manner described become the seat of Haversian systems. Hence we have at this period of growth, bone composed of Haversian systems with intervening undulating laminæ, a character by which the observer cannot fail to recognise young growing bone as differing from that of adult animals. Over the points where the processes have met and united, laminæ are extended which are continued outwards to form similar and more external processes; these in their turn become united and inclose spaces. This mode of increase by the development of outgrowing processes is repeated again and again until the rate of growth becomes

arrested, when the formation of ordinary circumferential laminæ is assumed in some cases to be again replaced by the development of undulating laminæ. It must however be remembered that in the rapidly growing bone of young subjects lamination is much less strongly pronounced than in the bones of the adult (Plate VI. fig. 4), and that in many cases it is indicated more distinctly by the arrangement of the lacunæ than by the presence of well-marked outlines in the laminæ themselves.

In addition to laminated tissue we sometimes find portions of superficial bone run in, as it were, between two or three Haversian systems, and without any appearance of lamination, but with a general transparency, and with lacunæ scattered through it of indefinite form, and wanting in that arrangement which prevails in laminated bone*.

Lacunæ of Bone.—In a transverse section of the Haversian systems the lacunæ are seen as elongated oval spaces, lying amongst, and with their long axes in the direction of, the laminæ; numerous canaliculi proceed from them, the bulk of which in this view pass off towards either the Haversian canals or the outer surface of the systems. The lacunæ are however somewhat different in appearance at different ages of the systems and of the subject. In youth they are large, numerous, and richly supplied with canaliculi; on the other hand, in an old subject they are less numerous and have fewer canaliculi. Moreover, they vary a little in character in different parts of the same preparation, according to the age of the particular spot in which they are examined (Plate VI. fig. 6). Then, again, they frequently exist without canaliculi; while in other cases they may be found, together with the canaliculi, in great part filled up with solid matter, leaving only a small round open space in their centre. This state of consolidation has not, so far as the authors are aware, been previously observed. It is however present to a considerable extent in the long bones of adults who have in infancy suffered from rickets, and whose bones have remained permanently distorted (Plate VII. fig. 12 *a* and *b*). More rarely a similar condition may be seen in the bones of those who have passed the middle period of life without having suffered from rickets in childhood. Hence consolidation must be regarded as a normal condition of the lacunæ, of occasional occurrence, rather than as the result of disease.

In favourable sections it may be shown that both the lacunæ and canaliculi have parietes, which are manifested by appearances similar to those observed in the dental tubes †. In lacunæ which have no canaliculi the walls are well-marked, and in

* KÖLLIKER, *oper. cit.* p. 288, objects to the opinion of ARNOLD that the interstitial laminæ have a different origin from the external and internal circumferential laminæ, the former of which he believes to originate in the cartilage, the latter in the external and internal periosteum.

KÖLLIKER'S views are inserted in the text, but it is seen above that the observations of the authors do not coincide with those of either ARNOLD or KÖLLIKER.

† This point will receive additional confirmation in a subsequent part of the paper, when the development of the lacunæ and canaliculi is described.

a transverse section of the latter the parietes are readily recognized, as shown in figure 11, Plate VII.

In a longitudinal section of Haversian systems we have the laminae on either side of the canals cut at right angles, or nearly so, while immediately over the canals they are exposed in their breadth; in the one instance we look upon the cut edges, in the other upon the surface of the laminae. The lacunae in the two parts present differences in outline. In the former part they resemble those seen in the Haversian systems divided transversely, in the latter they approach a circular, or slightly oval figure, and send out canaliculi indifferently from all parts of their circumference. After examining the lacunae from these three different points of view, it will be manifest to the observer that the normal form is that of a greatly compressed hollow sphere or oval, from which numerous minute tubes are continued. To this prevailing form we find numerous exceptions, which, although of not unfrequent occurrence, form but a small part of the whole number that may be seen in an ordinary preparation. The outlines assumed by the exceptional lacunae are too varied and too irregular to admit of such a description as would embrace every departure from the ordinary form. It is however worthy of mention, that lacunae may sometimes be met with, normal in form, but of three times the usual dimensions.

What has been said of the lacunae of the Haversian systems will of course apply also to those occupying parts of systems known under the name of interstitial laminae. In the circumferential laminae the lacunae are for the most part similar to those already described. But we have in this situation what may perhaps be regarded as modified lacunae, presenting themselves in the form of elongated tubes arranged in bundles, or occurring singly, and passing more or less obliquely from the surface towards the interior of the bone (Plate VII. fig. 13). When these tubes attain a considerable length they are commonly bent at a sharp angle once or twice in their course, and at each flexure change their direction, presenting sometimes a loose resemblance to the letter *z*. When these tubules are divided transversely they exhibit parietes. On tracing them in parts abounding with lacunae, it will be seen that they form lateral connections with the canaliculi, at the same time that they cross these as well as the lacunae and laminae obliquely. The presence of the oblique tubes is not however constant. In one part of the circumferential laminae they will be abundant, while in another they will be sparingly present or altogether absent. Then, again, they may be seen in one series of laminae, while in the contiguous set they are absent, but may reappear in a third and more deeply-seated series. They are, however, we believe, strictly confined to the limits of the circumferential laminae, and are seldom present unless these are tolerably abundant.

The lacunae situated in the transparent non-laminated bone, which is sometimes found on or near the surface, and to which we have before alluded, are less compressed in form than those hitherto described. They are subject to great irregularities of outline, and send off canaliculi equally from all parts of their circumference, thereby

imparting a peculiarity to the tissue which cannot fail to be remarked. The presence of persistent nuclei in the lacunæ has been questioned by recent authors; some state that they may be detected at times, while others regard their presence as very problematical. Mr. GOODSIR* describes the lacunæ as containing a little mass of nucleated cells.

M. KÖLLIKER†, after citing SCHWANN, KRAUSE, KOHLRAUSCH, HEISCHMANN, GÜNTHER and DONDEERS, all of whom believe in the persistence of the nuclei in the lacunæ, goes on to say that he has paid great attention to the subject. In the bones of an individual eighteen years old he found them after the sections had been treated with acid. The authors have had no difficulty in finding the nuclei in recent bone without the aid of chemical treatment. If a small fragment be taken from the spongy portion of a fresh bone and freed from adherent fat, the nuclei may be seen as small rounded bodies attached to the walls of the lacunæ; their appearance is shown in Plate IX. figs. 27 and 29. In dry sections of bone the nuclei are less readily recognized, although we may find them here and there. The authors have sections of a fossil bone from the Wealden (supposed to be Pterodactyle) in which all the lacunæ have well-defined nuclei (Plate VII. fig. 14).

Haversian Systems.—Having described the several parts entering into the formation of Haversian systems, it now remains to say a few words on the relations of these to each other, and to the other parts of bone which are not included under that term. The union of the Haversian and other systems of laminæ is seen, in a transverse section of a long bone, to be effected by the interposition of a layer of transparent tissue. In a recently-formed system the canaliculi do not appear to pass through this layer, but in older ones they are seen to pass across from the external lacunæ and to anastomose with those from the interstitial or circumferential laminæ, or with those of adjoining Haversian systems (Plate VII. fig. 10). After these intercommunications have been fully established, the connecting layer loses something of its original transparency, but not the whole, for in the bones of aged subjects it may still be distinguished.

In Dr. TODD and Mr. BOWMAN'S 'Physiological Anatomy,' it is stated, on the authority of Mr. TOMES, that the canaliculi of adjoining systems anastomose but scantily. A more extended examination into the subject has shown this to be true of the more recently developed systems, but not of those of greater age. In addition to the connection of systems of laminæ by the juxtaposition of their external members, instances not unfrequently occur where several Haversian systems, linearly arranged, are encircled by a series of laminæ common to the whole. This is shown in Plate VI. fig. 5. But although we may find groups of systems thus bound together by enclosing laminæ, in addition to the general or partial investment by circumferential laminæ, such binding together is clearly not necessary to ensure the strength of the bone, as we see many

* Anatomical and Pathological Observations, by JOHN GOODSIR and HENRY D. S. GOODSIR, 1845.

† KÖLLIKER, *oper. cit.* p. 296.

bones altogether destitute of circumferential laminæ, and very few with these laminæ complete; while the encircling of several Haversian systems with laminæ common to the whole is the exception rather than the rule.

In the progress of their investigations the authors have failed to discover any instances in which pre-existing laminæ, partially absorbed, have become continuous with newly-developed ones, end to end; indeed there seems good reason for supposing that such seldom, if ever occurs, otherwise the Haversian systems would not be so strongly marked, neither should we have the festooned outline to the systems lying against the cut ends of the laminæ, in the manner shown in Plates VI. and VII. figs. 1 and 10.

In examining Haversian systems divided transversely, one will be occasionally found in which the canal has been completely obliterated by the development of a lacunal cell in its centre. This condition is illustrated in fig. 1 c.

Ossified Cartilage of Joints.—Dr. SHARPEY has shown that beneath the articular cartilage lies a layer of bone produced by the gradual ossification of this tissue*. Professor KÖLLIKER† has observed this form of bone to be present in all the articulations, excepting that of the jaw and the hyoid bone, in which situations he has failed to detect it. The authors have numerous sections from the articular process of the lower jaw, in all of which it is present, and although in smaller amount than is usually found in corresponding parts of other bones, still it is sufficiently distinct. The peculiarity of the articular bone consists in the maintenance of the same arrangement of parts as existed in the cartilage prior to its conversion into bone. The cells for the most part are arranged in groups or in lines parallel with the long axis of the bone, each cell presenting a roundish mass surrounded by granules, and rendered rather indefinite in outline. Not uncommonly several cells become connected end to end, thus producing an elongated form. It is when in this condition that the cells and basement tissue may be restored to the appearance of cartilage by the use of hydrochloric acid. Occasionally, however, a cell becomes converted into a well-developed lacuna, and near the ordinary bone the cells may be seen in more or less advanced stages towards their conversion (Plate VII. fig. 17).

In the ossified cartilage, when the tissue attains a considerable thickness, broad and ill-defined lines or bands of opacity may generally be found running parallel with the articular surface, and giving a stratified character to the part in which they are situated, as shown in fig. 17 b. When seen by transmitted light, these lines appear of

* Dr. QUAIN'S Anatomy, fifth edition, by Mr. QUAIN and Dr. SHARPEY, part ii. page 158. "In the slow growth of bone which encroaches on the attached surface of articular cartilage, the ossification would almost seem to be produced merely by the impregnation of the cartilaginous matrix with earthy matter (corresponding with the first step of the ordinary process); and in this case, the cells and clusters of cells being surrounded by calcified matrix, may remain as little vacuities or lacunæ in the bone; but this as well as the formation of lacunæ in the crista petrosa of the teeth, and the production of adventitious bony deposits in different textures, requires further investigation."

† KÖLLIKER, page 318, *oper. cit.*

a deep rich brown colour, and as if possessed of a much higher degree of granularity than the surrounding parts. The cells of the tissue are not uncommonly surrounded by a similar granular condition of the matrix. This state of granularity is most conspicuous near the bone, and less so near the cartilage, where the tissue becomes clear and transparent. The ossified cartilage is generally separated by a well-marked line from the subjacent bone. Exceptions to this, however, are not wanting, where the two pass, the one into the other, by insensible gradations. The bone at the line of junction is usually advanced into the ossified cartilage by rounded projections of variable size; some of which reach nearly to the surface, while others are situated at some little depth. From this arrangement the articular bone is necessarily irregular in quantity. In one part it will dip to a considerable depth into the bone, while at another and perhaps contiguous part it will form but a thin layer. The external or articular surface is but slightly affected by the irregularities of the surface attached to the bone; on the contrary, it presents an even surface, on which the articular cartilage is placed in a uniform layer.

The absence of Haversian canals, and the unfrequency of lacunæ with canaliculi in the articular bone, renders this tissue much less porous than ordinary bone, a condition which probably contributes to its strength, and to the strength of the part in which it occurs.

In the presence of this peculiar form of tissue at the articular extremities of bones we may perceive a striking instance of design.

It would appear that the articular cartilage must rest upon a firm and uniform surface, otherwise it would, under pressure, yield unequally, and the joint would probably be but imperfect in its action. Circumferential laminae are developed only on free surfaces, and do not present there a very level outer surface. A surface formed by Haversian systems would be irregularly fluted or nodulated, like that beneath the calcified cartilage. Neither of those forms of development, then, would effect a condition of surface similar to that attained by the ossified cartilage. A careful consideration of the foregoing facts will, we think, lead to the conviction, that the presence of ossified cartilage as a basis for articular cartilage must not be regarded simply as the result of a slowly progressing ossification of a tissue prone to ossify; neither must it be regarded as an imperfectly developed tissue in which the formative process was arrested before the part had been perfected*; but it must be regarded as a constant element in the osseous system, having its special use, and necessary to the perfect organization of the skeleton in the higher forms of Vertebrata.

Ossified Lacunal Cells.—In addition to the parts already described, the authors have found a condition of bone which has hitherto escaped observation, or if seen, has not been recognized as a form of osseous tissue. The bones of aged people not unfrequently become extremely light and spongy, readily break, and from the diminished amount of compact tissue, may in the case of the flat bones, such as

* KÖLLIKER, *oper. cit.* page 318, speaks of this tissue as imperfectly formed bone-substance.

those of the pelvis, be indented by firm pressure with the finger. Such bones, after maceration, contain within the spaces enclosed by the cancelli, a white powder, which readily falls out if the bone be broken. If a little of this powder be mounted in Canada balsam, and placed in the field of the microscope, the observer will see that it is mainly composed of large nucleated cells, some of which are detached, others united into masses.

The isolated cells have a spherical or oval form, and appear to consist of a granular nucleus surrounded by a very thick cell-wall, external to which we commonly find an aggregation of granular matter, indefinite in amount and presenting a ragged outline (Plate VII. fig. 15). The cells which are united into masses are connected by this granular matter, or ossified blastema, as it might perhaps be called. The cells themselves are similar to the loose ones, excepting that in some cases their character is rendered more apparent by the nucleus assuming the form of a lacuna. If a section of the bone be examined, similar cells will be found adherent to the walls of the Haversian canals, with the canaliculi of contiguous lacunæ advancing into them, while the nuclei of the adherent cells are assuming the form of lacunæ and throwing out canaliculi.

Again, in the substance of the bone, the outline of the formative cells, similar in size and shape to the loose ones, may be in places recognized, having lacunæ and canaliculi as their centres. The recognition of these ossified cells in their isolated state will be followed by the observation of similar cells occupying the Haversian canals and cancellar spaces in the majority of microscopic preparations of adult bone (Plate VI. fig. 5 *a*); and the same may sometimes be seen on the outer surface of bone (Plate VII. fig. 18). The appearance of the cells is, however, liable to be modified by the various circumstances which operate upon growing bone, such as the presence of a tendon, or of a large pulsating vessel, or in fact, by pressure from any cause. Thus if situated in the immediate neighbourhood of a tendon, they assume an elongated form; while on the other hand they may be flattened by pressure.

It has been thought desirable to describe the ossified lacunal cells at this place, on account of their frequent occurrence in adult bone (Plate VI. fig. 5 *a*, and Plate VII. figs. 16 and 18).

Bone Tissue.—Hitherto we have confined our description to the forms in which the bone substance is arranged, as into laminæ, Haversian systems, &c. We have now to consider the ultimate structure of the tissue itself. But little has been said upon this point until within the last ten years. In the ‘Physiological Anatomy’ of Dr. TODD and Mr. BOWMAN*, it is stated that bone is made up of an aggregation of granules in a scarcely distinguishable matrix. Latterly, other views have been proposed. Dr. SHARPEY has advanced the hypothesis, that although the bone developed in cartilage is at one period granular†, a reticulate fibrous arrangement of the elements

* Dr. TODD and Mr. BOWMAN, *Physiological Anatomy*, page 108.

† Dr. QUAIN’s *Anatomy*, edited by Mr. QUAIN and Dr. SHARPEY, page 157. “The primary osseous matter forming the original thin walls of the areolæ is, as Mr. TOMES observes, decidedly granular, and has a

of the tissue takes its place, and must be regarded as the general condition of bone*. Dr. SHARPEY, when he formed this opinion, had directed his attention principally to thin fragments torn from the surface of bone macerated in hydrochloric acid. The authors have seen the appearance both in decalcified bone, and in sections which have not been chemically treated; but they believe the fibrous appearance to be an optical effect produced by the canaliculi and granules when the light is unequally distributed, or the object-glass in bad adjustment. It will be shown in the subsequent details, that the appearance can be produced and dispelled at pleasure by alterations in the direction of the transmitted light. If thin sections of bone are seen by transmitted light (passing through in the axis of the microscope,) the tissue will appear either granular or structureless, and in the laminae alternations of granular and structureless parts will be seen. But if the light be allowed to pass in one direction only, and with considerable obliquity through the specimen, then the appearance of extremely minute fibres will present itself; and this not only in adult bone, but in the isolated cells of old and in developing young bone. They are most strongly marked over the lacunæ; to which, and to the canaliculi, a confused and broken outline is given. The fibres appear as though arranged in series of short and broken lengths, parallel, and without plaiting. If the specimen be a little out of focus there will be an appearance of reticulated fibres marked by

dark appearance; the subsequent or secondary deposit, on the other hand, is quite transparent, and of a uniform and homogeneous aspect, without obvious granules. This begins to cover the granular bone a very short distance (about the $\frac{1}{80}$ th of an inch) below the surface of ossification, and, as already stated, increases further down. The lacunæ first appear in this deposit; there are none in the primary granular bone. In what further regards the nature and formation of the secondary deposit, my own observations lead me to differ considerably from the views of Mr. TOMES. He supposes that it is formed of cells which become impregnated with earthy matter,—the cartilage cells in the first instance, and afterwards the cells newly formed in the blastema. Now although certain appearances render it not improbable that there may be a layer of flattened and calcified cells next to the surface of the granular bone, I am nevertheless disposed to think that the subsequent and chief part of the deposit results from the calcification of successive layers of fibres generated in the blastema, and possibly derived from the granular cells, some cells being perhaps also involved along with the fibres, as in the ossification of the flat bones of the cranium: in short, it appears to me that the deposit in question is formed after the manner of intramembranous ossification already described (page 150). I infer that such is the process from the structure of the layers, for they are made up of fine reticulated fibres like the lamellæ of perfect bone shown at page 143."

* On this point KÖLLIKER, *oper. cit.* p. 289, observes, "Die Grundsubstanz der Knochen besteht nach SHARPEY und HASSALL aus einem Netzwerk feiner Fasern mit rhombischen Maschen, von welchen Fasern ich weder an frischen, noch an mit Reagentien behandelten Knochen eine Spur habe entdecken können. Was ARNOLD neulich Primitiv-fasern der Knochen nennt, sind, wie seine Abbildungen lehren, nur die Granula der Grundsubstanz, an denen er eine lineare Aneinanderreihung zu erkennen glaubt, und seine Querstreifen auf Flächenschnitten, und radiären Linien auf Querschliffen, wenigstens die letzteren sicher, nichts als die Ausläufer der Knochenhöhlen. Sollten durch irgend ein Reagens in dem Knochengewebe deutliche Fibrillen nachgewiesen werden können, was mir aber noch nicht gelungen ist, so könnten dieselben wohl keine anderen sein, als diejenigen, welche in ossificirenden Knorpel das streifige Ansehen bewirken und die von SHARPEY und mir bei der Knochenbildung aus dem Periost beschriebenen."

nebulous outlines. On the other hand, if we have light passing from all sides obliquely through the preparation, that is, if the object be illuminated by a hollow cone of light, in the manner obtainable by Mr. GILLETT'S arrangement of achromatic condenser, or by rendering opaque the centre of the lower lens of the ordinary achromatic condenser, the fibres disappear, and we see in their place a granular tissue, with a tendency here and there to a linear arrangement of the granules, and the lacunæ and canaliculi clear and distinct, when well in focus, but with a fibre-like nebulosity when slightly out of focus, especially in those parts where the latter run obliquely through the specimen. This is more especially the case where the canaliculi are filled with fluid, or where they have become solid, a condition very common in the bones of old subjects. Indeed, in many specimens where the bone is not highly developed, a fibrous appearance at once strikes the eye, and it is only on careful examination of the surface of the section that the illusion is dispelled by the orifices of the canaliculi appearing at the termination of the apparent fibres. Amongst a great many examples the authors have not seen an instance in which the fibrous appearance could not be traced to canaliculi, this effect being often increased by the presence of granules. If parallel dentinal tubes be viewed by a side light, in the manner we have described, each tube will throw two or three strong nebulous lines, which might be mistaken for fibres; and if tubes cut transversely be inspected in a similar manner, each will appear to have several concentric lines extending half round it on the side opposite to that from which the light proceeds.

That the presence of granules imbedded in a less refractive tissue may, when viewed by a side light, give an appearance of fibres, is shown on an examination of pus-globules under similar circumstances, when each globule will seem to have a striated surface; and that slightly rounded prominences will produce a like effect is shown in the case of some species of *Navicula*. The surface of these latter objects is marked by rows of slight prominences, which, when the light is oblique and passes through the specimen from one point only, appear as lines or fibres, the direction of which will change with alteration in the direction of the light; that is to say, shadows will extend from one eminence to another in the opposite direction to that from which the light enters. If we examine the projecting spiculæ of bone forming in temporary cartilage under corresponding conditions as regards light, a similar fibrous appearance will be developed.

Under these circumstances the authors are forced to the conclusion that bone substance, instead of being made up of minute reticulate fibres, is composed of granules or granular cells, imbedded in a more or less clear homogeneous or subgranular matrix. This subject will receive further elucidation under the head of development. These views are supported by the appearances presented not only in developing bone of young subjects, but also in the bone of adults.

Thus as regards the basement homogeneous tissue, it will be found that where lamination is highly developed, the laminæ have a transparent and structureless, and

a more opaque and granular part, to which the former appears to be the matrix. The peripheral lamina of the Haversian systems is generally clear and free from granularity, and the internal lamina sometimes presents a similar structureless appearance. The matter which fills up the Haversian systems in the full-grown antlers of the Cervidæ, affords another and a very striking example of transparent structureless osseous tissue, which in this instance is the more distinct from the absence of canaliculi in its substance. Then, again, we have another instance in the clear tissue which is sometimes found between the superficial Haversian systems of ordinary bone. It has already been described as a non-laminated element found on the *surface* of certain bones. In the instances already cited, and no doubt in many others which may be found in the skeletons of the lower vertebrata, we have bone tissue without obvious granularity and without obvious structure, and although it forms but a small part of the general mass, yet from its constant presence at all ages and in all subjects, it must be regarded as an integral and normal part of mammalian bone. The granular condition of bone tissue is tolerably obvious in all preparations, though it is much more strongly marked in some specimens than in others. The amount of the component granules varies in different parts of the same specimen, and in specimens taken from different parts of the skeleton. Thus in one situation we may see laminae with a highly granular part gradually merging into a transparent tissue, while in another the laminae may be granular throughout. Again in young bone developed in cartilage, the part between the cells becomes highly granular; fragments of which may be found in certain adult bones, as in the petrous portion of the temporal bone (Plate VII. fig. 16 *b*). Bone near the articular surface frequently presents a well-marked granularity. Whether the granular and the transparent parts of bone contain different relative amounts of phosphate of lime is a question yet to be decided.

Development of Bone.—Temporary cartilage, when it first appears in the embryo, consists of an aggregation of closely packed nucleated cells, which in the process of growth become separated by the development of a tissue external to them, usually designated the hyaline tissue of cartilage. At this stage of growth we have a granular cell occupying a cavity in the hyaline tissue; at a previous period the granular cell was inclosed by an outer cell-wall, to which it formed the nucleus, but now the cell-wall has merged into the hyaline tissue, from which it can no longer be distinguished, while the granular cell contains itself one or more nuclei. In making sections of cartilage many of these granular cells escape from their cavities in the hyaline tissue, and may be seen detached and floating about in the field of the microscope. Some little confusion of terms has arisen in connexion with this part of the subject. The granular cells are not unfrequently described under the name of cartilage-nuclei containing nucleoli, while in fact they are cells capable of separation from the matrix, and are at one period the only recognisable cartilage cells. They occur singly or in groups, more frequently however two or three are extended in a line. It is proposed in the present communication to call

these bodies *granular cartilage cells*, as distinguished from a form which the cells assume previous to ossification. Cartilage previous to its conversion into bone undergoes a rapid growth, which takes place principally in the direction of the long axis of the future bone. Each granular cell becomes divided into two by segmentation transverse to the line of ossific advance. These are again divided, and the process repeated from time to time, till in the place of a single granular cell we have a long line of cells extending from the unchanged cartilage to the point where ossification has taken place. Contemporaneously with this development of lines of cells, other changes are going on in the individual cells composing them. If we examine those situated near the advancing bone, it will be observed that the granular cells have enlarged, have become separated from each other by wide intervals, and that each has become invested with a thick pellucid cell-wall (Plate VIII. figs. 19 and 20). The increase in the size of the cells has occurred at the expense of the hyaline tissue, which, at those points where the rounded cells approach each other, is reduced to a thin film, although in the intervals left by the packing of the uncompressed cells it exists to a considerable amount. Here then we have a matrix containing cartilage cells composed of an outer pellucid coat, within which is a granular cell containing central nuclei, a cell consisting of three distinct parts. The nucleus existed previous to the segmentation of the granular cell, but the outer wall is the product of a subsequent development. It will be observed that growth is effected by two modes; first, by the increase of the number of the cells; and, secondly, by the increase of their size individually.

While these changes are going on for lengthening the shaft of a long bone, cells are being added by a somewhat similar process of division to the surface, so as to increase the diameter of the cartilage. For the development of the epiphysis the cells become multiplied on a similar principle, but instead of occurring in lines they are accumulated in oval or rounded groups*.

From this general view of the subject we will now proceed to consider in detail those conditions of cartilage which precede and prepare for its conversion into bone. These phenomena may be conveniently examined in the cartilage which connects the diaphysis and epiphysis of long bones, and we may take those of a lamb or calf, as they present the same conditions as are found in the human subject, and have the advantage over those of other domestic animals of being readily obtainable at all times without the necessity of destroying the animal for the sole purpose of physiological investigation.

At that point in the cartilage where the linear arrangement of cells commences, several of these bodies lie side by side in the same column, but by following the line downwards towards the advancing bone, it will be seen that the column usually divides, forming two or three distinct lines, in each of which the cells are arranged

* Previous to the ossification of the epiphysis the cartilage at the heads of the bone is increased in its bulk from additions to the surface, by a process somewhat similar to that through which the growth of bone is effected. This process will be described when the latter subject is considered.

in single file. It does not appear that the number of cells entering into the formation of a series is at all limited; hence the lines or columns vary in length. Neither does it appear that the consecutive lines are placed, as a rule, end to end, so as to form one long continuous straight line by the junction of several shorter ones. On the contrary, each series is complete in itself, and is generally placed a little to the one or other side of those above and below it. We have in fact interrupted lines of cells, each line the offspring of a single cell, the outer walls of which have merged into the intercellular or hyaline tissue.

When the destined number of cells forming a linear series has been developed, each cell becomes itself a centre of growth. The granular cell enlarges, together with its nucleus, and becomes invested with a cell-wall. In examining a line of these bodies extending from the forming bone of the diaphysis, we shall see them in various degrees of forwardness. Thus, if attention be directed to the end of the line furthest from the bone, the cells will be found small in size, granular, and with a perceptible nucleus, but without an outer wall, distinguishable from the hyaline substance, which is abundant between the contiguous lines, but small in quantity between the cells composing the lines. But if the other end of the line be examined, very different conditions will be observed. The granular cells will be seen to have become rounded in form, to have increased to three times their original bulk, and to possess well-marked circular nuclei; in addition to which each granular cell will have acquired a thick pellucid outer wall, while the hyaline tissue between contiguous lines of cells will have dwindled down to a thin film, excepting in those parts where spaces are necessarily left in the approximation of spherical bodies (Plate VI. figs. 19, 20). The abundance of the hyaline tissue in the earlier condition of cartilage, affords space for the development of the cells in the breadth of the bone, but in the direction of the length of the bone we find but little of that tissue, yet each component cell of the almost innumerable lines of cells that exist, even in a bone of small size, is itself a centre of growth. At the osseous end of a line, a single cell occupies more space than four or five at the opposite extremity; and as in each situation the cells are imbedded in hyaline tissue, it is evident that there is a concurrent growth of the latter throughout each line of cells, and also of the cells and hyaline tissue in the breadth of the cartilage. But for this provision of nature, cells would grow at the cost of those in their neighbourhood, a condition which obtains wherever space for a secondary development of bone is required, a description of which will follow in the subsequent pages of this paper. Then, again, had we concurrent growth in each cell of a series without a similar growth in all the other series, throughout the breadth of the bone, the growing series would encroach upon the cartilage in which the linear arrangement had not commenced, and ultimately unite by osseous tissue the epiphysis and diaphysis before the bone had acquired its normal length. And supposing concurrent growth to take place over the one-half of the breadth of a bone and not in the other, the bone would become curved and the limb distorted.

We have traced in temporary cartilage those changes which occur preparatory to its conversion into bone: it now remains for the authors to describe the results of their researches on the mode in which that conversion is effected, and concerning which there hitherto has been a great diversity of opinion.

Preceding ossific deposit, the intercolumnar tissue, which may not only be seen between the columns of cells, but also passing more or less perfectly between the individual cells, becomes in some cases slightly fibrous in appearance, and of a light brown colour; this condition speedily gives way to a highly granular state; in fact it has become bone, and encloses, in osseous cavities or crypts, the cartilage cells. For reasons which will hereafter be sufficiently obvious, we shall in future call these lacunal cells. If thin sections be made with a very sharp knife through ossifying cartilage, and placed in water or albumen under the quarter or eighth object-glass, we shall occasionally find lacunal cells which have escaped from their osseous crypts, floating loose in the fluid, and offering a favourable opportunity for the examination of their characters. It may then be seen that the thick pellucid outer investment has become granular, and that the enclosed granular cell has lost its regular outline, and become angular or ragged, while the nucleus has become obscured by the changes in the more external parts of the cell, an early stage of which is seen in Plate VIII. fig. 19 and 22 *a*. Such are the appearances presented in some of the detached lacunal cells, but they may be seen in both earlier and later stages of development than that described. Thus instances may be found where the outer coat has only a few granules on the surface, in which case the granular cell may be seen more distinctly, and minute elongated processes traced, extending from its surface (Plate VIII. figs. 19 and 20). In a favourable section we sometimes find such a cell with its outer coat torn, exposing to full view the granular cell, with numerous and well-marked processes extending from it. Dr. SHARPEY kindly placed at the disposal of the authors the rickety bone of a child who died during the active condition of the disease. In this specimen granular cells with radiating processes can with great readiness be detached by tearing a thin section, for in this case cartilage assumed the arrangement of bone without the impregnation of earthy ingredients (Plate VIII. fig. 23)*.

The third condition, in which we may find isolated lacunal cells detached from the osseous crypts of the intercellular tissue, differs from those already described in their greater solidity. The whole mass has become highly granular, and the granular cell with its processes has united to the outer coat, so that the two can no longer be

* KÖLLIKER, *oper. cit.* at p. 360, describes accurately the formation of lacunæ from cartilage cells in a rickety bone, and although he has not observed the changes with equal distinctness in normal bone, appears to have satisfied himself that in the ossification of cartilage the cells of the latter become converted into lacunæ. M. KÖLLIKER does not however seem to have recognized the relation of the lacunal cells as such to the intercellular tissue, neither does he mention the fact that the granular cells with their long stellated processes can be separated from the investing cell-wall in the manner described in the text.

separated the one from the other, and are no longer to be recognized as distinct parts. If accidentally broken across, we see that they have a hollow centre, in fact, a lacuna; but when loose and entire, they appear as rounded dense masses, projecting from the surface of which we may not unfrequently detect a few short needle-like processes. Lacunal cells of the latter kind are not, however, very easily detached, for when they have advanced thus far in development, their union with ossified intercolumnar tissue is too strong to admit of ready separation; indeed, after this period their separation is impossible. It has been stated that the granular cells of cartilage previous to the formation of lacunal cells send out processes. There are, however, a certain number of granular cells that do not appear to undergo this change, but preserve their state of granulation and their external figure, and show the round nucleus even after they are surrounded by and imbedded in ossified tissue. Indeed, we may find perfectly ossified crypts of intercolumnar tissue at some little depth within the forming bone, containing several of these granular cells in an unaltered condition, and this without the cavities having been enlarged by absorption of their walls (Plate VIII. fig. 19 *d*). It is important to bear this point in mind, as it will subsequently be shown that similar granular cells lie loose in the large cavities formed by absorption, and that they are concerned in the formation of bone when that tissue is not preceded by ordinary cartilage.

If a section of developing bone, including a little of the cartilage, be dried, and mounted in Canada balsam, we shall be able to recognize, first the cartilage with the cells greatly contracted, then the ossified intercolumnar tissue full of little crypts, from which, in the process of drying, the lacunal cells have disappeared (Plate VIII. fig. 24 *a*); and lastly, we shall see bone in which ossified lacunal cells run in lines corresponding to the preceding lines of cartilage cells (fig. 24 *b*). The latter appearance is, however, interrupted by the presence of numerous large spaces produced by the absorption of both the intercolumnar tissue and the lacunal cells (fig. 24 *c*), the process for the removal of which commences concurrently with the impregnation of the lacunal cells with the earthy salt.

These conditions can be also very favourably observed in sections of the long bones of a foetal lamb, taken previous to the commencement of ossification of the epiphysis, and examined in the liquor amnii; water will not answer as a substitute for this fluid, as the cartilage cells are speedily altered in character by its presence. And we may here observe that the examination of developing bone should be conducted on perfectly fresh subjects, and that care should be taken to keep the knives, glass, &c., which are used in preparing the sections, perfectly free from extraneous matter; otherwise the results will be unsatisfactory. Thus a small quantity of spirits of wine or of acid will produce changes of character in the specimen, and thereby lead the observer into an erroneous conception of the normal characters of the tissue.

Hitherto the authors of this communication have spoken principally of those appearances which are presented in sections made parallel with the advancing bone;

attention must now be directed to sections made across the bone, so as to cut transversely the lines of cartilage cells.

If, then, we take a thin section through the cartilage where ossification of the intercellular tissue is advancing, the following appearances will be seen. The intercellular tissue will present itself in the form of more or less perfect septa lying between and enclosing the lacunal cells, in such a manner as to produce a uniform pattern over the surface of the section (Plate VIII. fig. 20). On close inspection it will be seen that the intercellular tissue is granular, and that in each enclosure it encircles one or two lacunal cells, which in the latter case lie in contact, with the contiguous sides flattened, while the peripheral surface of the two form together a tolerably perfect circle in close contact with the intercellular tissue.

The lacunal cells are beautifully shown in the kind of section under consideration. Their circumference is becoming granular, and frequently may be seen as a perfect ring of granules in close contact with the intercellular tissue, while in the centre we see the granular cell with a well-defined nucleus, and with numerous rudimentary canaliculi, extending from the circumference of the inner cell towards the surface of the outer cell-wall. Where two cells lie in contact, the rudimentary canaliculi may sometimes be found running across from the one cell to the other. If after examining such sections as may be made with a knife, we take one through the bone immediately below the partially ossified cartilage, rendered thin by grinding, and mount it in Canada balsam, the various points described as existing in ossifying cartilage will be seen in that which has been converted into bone. Thus we shall see the intercellular tissue preserving its original form, and highly granular, and that while the outer walls of the lacunal cells have become calcified, the granular cells will have assumed the form of perfect lacunæ and canaliculi, the latter freely intercommunicating where the surface of the lacunal cells is in contact, but seldom extending into the ossified intercellular tissue. These conditions are shown in Plate VII. fig. 25.

The ossified lacunal cells, and the intercellular tissue which have existed in the temporary cartilage, and have there served their part in forming the skeleton of the fœtus, are destined to have but a short existence, for we find that no sooner is the bone formed than large spaces are produced by absorption. Whole lines of ossified lacunal cells with the enclosing intercellular tissue disappear, to be replaced by more or less perfectly developed Haversian systems, which also last but for a time, when they by a similar process are removed to give place to others, or to contribute to the formation of permanent cavities. It has been well stated by Dr. SHARPEY, that the long bones of the fœtus are not equal in size to the medullary cavities of the corresponding bones of the adult. Hence as growth takes place, gradually comes the necessity for the removal of parts to make way for the development of others upon an enlarged scale.

It has been shown that primary bone, if we except two or three of the cranial bones, is merely calcified cartilage which has previously assumed the structural

arrangement of bone. It is proposed to restrict the term primary bone to tissue so formed, as it will be subsequently shown that the development of Haversian systems in the spaces formed in primary bone, is effected by processes similar to those which are concerned in the growth of bone generally, and in the extension of the flat cranial bones. Age and situation no doubt modify the conditions of growth, or development of secondary bone, as it may be called, but the processes in either case are alike.

Hence, in describing the manner in which a long bone increases in diameter, we shall in fact be describing the process by which a flat cranial bone is extended. Before however going to this point the authors will state the results of their observations on the subject of the absorption of bone, on that interesting and important process by which the Haversian spaces are formed out of the solid tissue of bone.

During the present winter it became necessary to remove a portion of the femur which protruded from a stump six weeks after the removal of the limb. From the medullary cavity a granulating mass projected and covered the surface of the bone left by the saw, and as the bone was rapidly wasting from the inner or medullary surface, we had in this specimen a favourable opportunity of examining the tissue which lay in immediate contact with the surface of the wasting bone. On cutting through this piece of femur in its length with a very fine jeweller's saw, it was found that a dense pale pink tissue lay in contact with the inner surface of the bone, which was hollowed with numerous minute cavities, into which the soft tissue accurately fitted, but from which it could be detached without tearing. The outer surface of the bone had been deprived of membrane many days before its removal from the limb.

The examination of the tissue thus closely applied to the fast wasting bone, offered as favourable an opportunity for learning something of the means by which absorption is effected as we could reasonably expect to obtain, the more so since the outer surface having been for some time exposed and covered only by dried periosteum, the actions had been confined to the inner surface of the bone. A careful examination showed that the surface of this tissue was composed of minutely granular nucleated cells, which lay in close and immediate contact with the bone, and increased in an exact ratio with its diminution. What the bone lost in bulk the cells gained, the cellular mass presenting a perfect cast of the surface of the bone, suggesting to the mind that the soft was growing at the cost of the hard tissue, or at all events that the former was instrumental in the removal of the latter. The cellular mass was tolerably vascular, but the vessels did not reach the surface in contact with the bone; hence they could not be regarded as having any immediate action in the process of absorption. Section of the bone showed that the medullary cavity had been greatly enlarged by absorption, and no doubt had sufficient time been allowed the femur at that part would have been reduced to a thin scale. A transverse section showed that in many, though not in all instances, the Haversian canals had been enlarged and rendered irregular in shape, but it was evident that the process of removal had been less active in this situation than on the medullary surface of the bone.

If we examine the fangs of temporary teeth when they are undergoing removal, similar states to those described as existing in the portion of femur will be found to obtain. A similar cellular mass will be seen to be closely applied to that surface of the tooth which is in process of removal, and the surface itself will present the characteristic emargination observed in the bone. When we connect these conditions with the fact that the nucleated cells which form the embryo have the power of appropriating the material which lies about them to the purpose of their own growth and their conversion into the various animal tissues, it is difficult to resist the belief that the cells which lie in contact with wasting bone and dentine, take up those tissues and use all or part of their element for the purposes of their own increase or multiplication, or else form a medium through which they are passed into the circulation. But as the process of absorption with concurrent development of cells is most active in primary bone where but few vessels exist, the former hypothesis seems the more probable. An objection may be raised to the supposition, that the bone is absorbed by the cells, on the ground of the density of the former; but it must be borne in mind, that as the density is gradually imparted to the bone through the agency of the adjoining soft parts, there seems no good reason for disbelieving that they may also be instrumental in its removal.

Growth of Bone.—Under this head will be described the extension of flat bones, the increase in the diameter of cylindrical bones, and the development of Haversian systems.

If the advancing edge of a parietal bone be taken either from a human fœtus or a fœtal lamb, and the pericranium and dura mater be carefully removed from their respective surfaces, we shall find the growing bone still invested with soft tissue both on the outer and inner surface, which is prolonged from the free edge. When examined under a favourable light this tissue will show differences of character in different parts, varying with the distance from the bone at which the observations are made. Thus, if attention be directed to the part furthest removed from the bone, it will be seen that the membrane-like mass is composed of oval cells with slight prolongations from the extremities, which are frequently arranged in the form of bands of fibrous tissue (Plate VIII. fig. 26). Dr. SHARPEY has observed that the membrane into which the bone extends is like fibrous tissue in an early stage of development*, and this observation is strictly true when confined to the part indicated, but the analogy

* Mr. QUAIN and Dr. SHARPEY, *oper. cit.* cxlix. and page clix. Dr. SHARPEY says, "When further examined with a higher magnifying power, the tissue or membrane in which ossification is proceeding, appears to be made up of fibres and granular corpuscles, with a soft amorphous or faintly granular uniting matter. The fibres have the character of the white fibres, or rather fasciculi of the cellular or fibrous tissue, and are similarly affected by acetic acid. The corpuscles are for the most part true cells with an envelope and granular contents; some about the size of blood-particles, but many of them two or three times larger. In certain parts the fibres, but in most the corpuscles predominate, and on the whole the structure may be said to be not unlike that of fibrous tissue in an early stage of development." KÖLLIKER, *oper. cit.* p. 289, confirms Dr. SHARPEY's statement, but denies that a fibrous arrangement can be traced in formed bone.

ceases as we extend our examination towards the bone. Here in the place of cells with elongated processes, or cells arranged in fibre-like lines, we find cells aggregated into a mass, and so closely packed as to leave little room for intermediate tissue. The cells appear to have increased in size at the cost of the processes which existed at an earlier stage of development, and formed a bond of union between them. Everywhere about growing bone a careful examination will reveal cells attached to its surface, while the surface of the bone itself will present a series of similar bodies ossified (Plate IX. figs. 27, 28 and 29). To these we propose to give the name of *osteal cells*, as distinguished from lacunal and other cells.

In microscopic characters the osteal cells closely resemble the granular cells of temporary cartilage, so closely indeed, that the latter when detached from the cartilage could not well be distinguished from them. They are for the most part spherical or oval in form, and lie on the surface of the growing bone in a crowded mass, held together by an intervening and apparently structureless matrix (Plate IX. fig. 27 *b*). Here and there we find a cell which has accumulated about itself an outer investment of transparent tissue, and has in fact become developed into a lacunal cell destined to become a lacuna*. These points are illustrated in fig. 29 *b*.

The process of growth may be thus described. In the meshes of the fibrous tissue

* The various views which have been entertained regarding the formation of the lacunæ and canaliculi have been concisely stated by Dr. SHARPEY, *oper. cit.* p. 158. He observes, that "they are generally supposed to be derived from the cells of the soft tissue involved in the ossification by some sort of metamorphosis which has been variously conceived. Some suppose that the cells become the lacuna and send out branches (like the pigment cells) to form the canaliculi (SCHWANN¹). Others think that it is not the cell but its nucleus that undergoes this change, and that the substance of the nucleus is afterwards absorbed, leaving the lacuna (TODD and BOWMAN²)." The nucleus described by TODD and BOWMAN is identical with that which in this communication is called the granular cell, and from which the authors have shown the lacuna is formed. "HENLE³ thinks that the lacuna is a cavity left in the centre of a cell which has been partially filled up by calcification, and that the canaliculi are branched passages, also left in consequence of the unequal deposition of the hard matter, as in the instance of the pore cells of plants." "It rather appears to me as if the lacunæ and canaliculi were little varieties left in the tissue during the deposition of the reticular fibres, as open figures are left out in the weaving of some artificial fabrics (but not within a cell, as HENLE imagined), and that thus the apposition of the minute apertures existing between the reticulations of the lamellæ gives rise to the canaliculi." "At the same time it seems not unlikely that a cell or a cell-nucleus may originally lie in the lacuna or central cavity, and may perhaps determine the place of its formation." HASSALL⁴ agrees with SCHWANN, while GERBER⁵ and BRUNS⁵ appear to hold the views of TODD and BOWMAN. With the exception of Dr. SHARPEY, the above-named authorities may perhaps differ more in the use of terms than in matter of fact. The appearances represented in figs. 14 and 27 would at first view seem to justify the opinion expressed by Dr. SHARPEY, but a careful examination of the tissue during its development, the unquestionable fact that in the development from cartilage the granular cell becomes converted into a lacuna, together with the circumstance that lacunal cells are frequently found in the Haversian canals and cancellated structure, especially in the bones of old subjects, and at times imbedded in the structure of the bone, have left no room for doubt in the authors' minds that the lacunæ are formed from special nucleated cells, in the manner described in the text.

¹ Mikroskopische Untersuchungen.

² Physiological Anatomy.

³ Anatomie Générale.

⁴ Microscopic Anatomy of the Human Body, p. 310.

⁵ Allgemeine Anatomie.

on the surface of the bone *osteal cells* are developed and gradually take its place; a few cells become developed into lacunal cells; the earthy salts are added, and concurrently lacunæ and canaliculi are formed; we then have bone presenting the usual characters of that tissue*. In bone developed in the foregoing manner, we find the canaliculi not merely extending to the surface of the cell-wall, or anastomosing with the canaliculi of lacunal cells lying in contact with it, but extending freely in all directions and passing through or amongst the ossified cells, and establishing rich plexuses of anastomosis. Indeed we see the boundary of the original lacunal cells only in those cases where the lacunæ have but few, or are entirely devoid of canaliculi. It would appear to be a law, to which there are few if any exceptions, that when anastomosis is established between adjoining lacunæ, the lacunal cells blend with the contiguous parts, and are no longer recognisable as distinct bodies. The process by which the cylindrical bones are increased in diameter is in all essential points similar to that described as pertaining to the growth of flat bones. Similar osteal and lacunal cells are present, but the relative amount of the matrix is greater; moreover the osteal cells have a disposition to assume a linear arrangement corresponding to the direction of the laminæ of the contiguous bone. In these lines the cells are placed so close to each other as to leave but little room for intervening tissue, but between the lines an appreciable amount may be recognized (Plate IX. fig. 31). This appearance however varies in different specimens. In one the cells predominate, in another the transparent tissue is the more abundant. Generally the younger the animal the greater will be the amount of the intervening transparent tissue, and the smaller the number of the osteal cells. But in all cases, whatever the age of the subject, or from whatever part of the skeleton the specimen be taken, the cells and the intermediate tissue become blended in the process of ossification, and the whole presents a uniform granular appearance, excepting in the instances in which lamination is strongly developed, or in those which have been noticed in the previous part of the paper. We frequently find portions of bone where the osteal cells, lacunal cells, and intermediate tissue are so perfectly fused together that neither can be recognized, but in their place we have a minutely granular mass, divisible only into lacunæ and canaliculi and the tissue in which they lie imbedded. In Plate IX. fig. 32, taken from the tibia of a foetal lamb, the osteal and lacunal cells have become blended to a considerable extent, but without the

* When speaking of the growth of cartilage, it was stated that the bulk of that tissue at the epiphysis increased laterally by the division of the cells, but the fact that it also increased on the free surface of the greatly enlarged cartilaginous epiphysis of the fœtus by a process similar to that by which the diameter of bones is increased, was reserved to be described in connection with the latter subject. If a longitudinal section be taken from the epiphysis of a foetal long bone, including some portion of the perichondrium, it will be seen that the cartilage passes gradually into a more or less fibrous tissue, which forms the exterior of the part. Amongst the fibres will be found numerous elongated cells, which on tracing the specimen inwards will be seen to be similar to the cartilage cells at and near the surface of the tissue, while the fibres will be seen to give way to or become converted into hyaline tissue, as shown in Plate IX. fig. 30, in which the cartilage is indicated at *a*, and the cells included in the fibrous tissue at *b*.

occurrence of lamination. The lamina which is represented at the margin is composed of still uncalcified cells. It shows the mode in which the undulating laminae are formed. Fig. 33 also, taken from the fibula of a calf, shows ossified lacunal and osteal cells without any tendency to lamination.

The manner in which the Haversian spaces become gradually occupied by Haversian systems is peculiarly interesting. To obtain a good view of the process, it is necessary to make a transverse section of the developing systems. It may then be seen that osteal cells arrange themselves in single file within the Haversian space with intermediate lines of transparent tissue, and here and there a lacunal cell; the process commencing at the surface of the Haversian space, and extending gradually inwards till the system is completed. In fact the soft tissue takes the permanent form previous to the addition of the salts of bone, much in the same manner and to the same degree as occurs in temporary cartilage before the earthy ingredients are deposited. Lamination is nothing more than a definite linear arrangement of the osteal cells with their outlines permanently retained in the perfected bone; a character much more strongly marked in the bones of adult than in those of young animals.

In pursuing their inquiries into the growth of bone, the authors found it necessary to take sections of perfectly fresh bone and to examine them in albuminous fluid; spirits of wine, whether diluted or not, obscures the normal appearances, and water is not more favourable as a medium.

Sections permanently mounted in dilute spirit lose a good deal of their character; still the appearances are preserved with more or less of their original distinctness. Sections mounted in Canada balsam show some of the points remarkably well. For instance, the partially ossified osteal and lacunal cells are tolerably well preserved, but unfortunately those cells which have not received any of the indurating salts are represented only by a transparent mass, in which but little structure can be recognized; thus, the part *b* in fig. 32 would have appeared but as a transparent line had the specimen been mounted in Canada balsam. In addition to the necessity for care in the examination of osseous structures, under the most favourable circumstances, as regards the selection of specimens and the fluid used in their preparation, it is equally necessary to have the more recent appliances for the illumination of the objects.

Mr. GILLETT's achromatic condenser, with what is called the white cloud illuminator, renders it very easy to demonstrate points which with the ordinary microscopic apparatus are shown with difficulty. It need not however be urged, that it is desirable in pursuing structural anatomy to avail ourselves of the most perfect instruments that can be obtained. It is proper that the authors should, before leaving this part of the subject, draw some comparison between the development of bone in cartilage and in the softer tissues.

Temporary cartilage, previous to the development of bone, affords a mechanical support and protection to the surrounding or enclosed softer tissues. These offices

could not be rendered by a mere aggregation of soft cells, but are efficiently performed by the dense intercellular substance, which forms so characteristic a feature of the cartilage. Hence in the mechanical function of cartilage the intercellular element of the tissue must be regarded as the most important.

A second, and scarcely less important purpose effected by temporary cartilage, is that of affording a medium for which a more solid tissue may be substituted, without the mechanical support being withdrawn from the adjoining parts during the process of change. It affords also a means by which the long bones are gradually increased in length, without any interference with the functions of the limb. These changes are brought about by the gradual increase in the number of the cartilage cells, at those parts only where ossification is about to commence, and by the conversion of the cells into lacunal cells, at the cost of the intercellular tissue, which, whilst its bulk is diminishing, becomes impregnated with the earthy salts; so that although the quantity is lessened, the strength of that which remains is increased. Now, in examining the process by which growing bones are enlarged, it must be borne in mind that the mechanical function of the cartilage is performed by the bone which has replaced it, and that no such office is required of the new tissue which is gradually adding to the bulk of the bone. The necessity for a dense intercellular tissue no longer exists. Hence we have an aggregation of osteal cells with so much only of intercellular tissue as will serve to connect them into a mass. A certain number of these cells, by additions to their exterior, become lacunal cells. We have then in the place of lacunal cells and dense intercolumnar tissue, lacunal and osteal cells united by a small and almost imperceptible amount of a semifluid intercellular medium; the relative proportions of these several parts varying a little with differences of age. Thus in aged subjects aggregations of lacunal cells may here and there be found with but few osteal cells and but little intercellular tissue, while in a young subject osteal cells will preponderate.

In all cases a direction may be given to the cells of a growing part, by their being in relation with the insertion of a tendon.

A consideration of the foregoing facts will, we think, lead to a conviction that the two different forms in which bone is developed, are designed to meet the requirements of the animal at different periods of life, and that bone developed by means of osteal and lacunal cells is the higher form of the tissue. In early embryonic life a soft cartilaginous skeleton is laid down, which is hard as compared with the surrounding parts, and capable of affording them the required amount of mechanical support. As the various tissues advance in development the cartilage increases in density by the elaboration of its hyaline tissue, and after awhile those changes occur which precede its conversion into bone. But in the bone so formed, it has been shown that the canaliculi anastomose only at those points where the lacunal cells come into contact (Plate VIII. fig. 25). In bone formed from osteal and lacunal cells, the anastomosis of the canaliculi prevails throughout the tissue, while the outline of the

formative cells is almost entirely lost in the general blending of the whole into a subgranular mass subject to lamination, in the manner already described.

It will therefore be in accordance with the preceding views, to regard the intercolumnar tissue present in primary bone, rather as an accessory element calculated to give support during the ossification of the lacunal cells, than as an integral and necessary element of osseous tissue; for it has been shown that it offers an obstruction to the anastomosis of the canaliculi, and that the lacunal cells preserve their outline so long as they are enclosed within it, instead of becoming lost in the surrounding tissue, as occurs in secondary bone. It must not, however, be forgotten that small patches of ossified intercolumnar tissue may here and there be found between the Haversian systems, even in the bone of old subjects (Plate VII. fig. 16); so that its presence in a small amount, (as accidentally left when the Haversian spaces are forming), is not incompatible with the normal condition of perfect bone.

It may also be stated in this place, that the undulating laminæ formed on the surface of growing bone, although for the most part removed to make way for Haversian systems, are also found here and there in small patches in the bones of adults.

The subject of absorption, as it relates to the removal of bone, has already been partly discussed, but something more remains to be said. Although the process of absorption has not, and probably cannot be seen in actual operation, yet a consideration of the relative position of the increasing and wasting parts, and of their conditions, will, in the authors' opinion, justify the conclusion that the bone is removed through the agency of cells.

In seeking to find the circumstances under which the absorption of bone takes place most rapidly, and to the greatest extent, the authors have been led to examine bones which had been placed in various conditions, both of health and disease. It has been already stated that bone developed in cartilage is speedily removed; but it does not seem that bone formed by osteal and lacunal cells is absorbed with equal rapidity, although in the course of a short time it not less surely disappears. This difference in the rate of absorption is probably the result of the vascularity and higher state of development of the latter tissue. In bone developed in cartilage Haversian spaces have to be formed before it can be permeated by vessels; hence in this tissue absorption proceeds rapidly, the process being established as soon as the bone is formed. In adult bone, when in a normal condition, we find here and there an Haversian space; but if a bone around which the soft parts are in a state of inflammation be examined, numerous Haversian spaces will be seen. If we examine the same bone in the neighbourhood of that part where the inflamed is merging into the healthy investing texture, we shall find new osseous matter in the process of deposition on the surface of the pre-existing bone. Examples of this may frequently be found in the vicinity of diseased joints.

We have here an instance of the development of new tissue, and the removal of a pre-existing one being set in operation, by what would appear to be a different degree

only of the same action. Hence a more particular examination of the cellular mass, by which bone appears to be absorbed in the one case and deposited in the other, naturally suggests itself, and attention has been directed to this point as frequently as favourable opportunities for observation have presented themselves. The differences, however, in microscopic characters between the two tissues, have not been so strongly marked, as to admit of any definite description being given, by which the one may, in all instances, be distinguished from the other, when removed from their natural positions, as is almost necessarily the case with regard to the absorbent cells, from the readiness with which they separate from the wasting bone (Plate IX. figs. 27 and 34).

Lacunal cells moreover will not be found in the absorbing tissue; but it is not easy to recognize them, even in the tissue from which bone is developing, as they are frequently obscured by the osteal cells; so that their presence, although a good ground of distinction, cannot in all instances be demonstrated. When, however, developmental cells are seen *in situ*, their character is readily distinguished. They are closely applied to the surface of the increasing bone, which loses the festooned and assumes an even outline, to which the osteal cells adhere.

The source from which the cells destined for effecting absorption arise is at present unknown to the authors, any further than that they arise in connection with soft tissues, the three situations in which they occur being beneath the periosteum or medullary membrane, or within an Haversian canal. These are no doubt the points from which the development of the cells starts, but the law which regulates their occurrence at one part rather than another, and gives to them their peculiar function, is at present unexplained. Neither is it more easy to understand why, at a particular period, the process of absorption is arrested and development of new tissue commences; the new bone may, for anything we have seen to the contrary, be formed from the same cells that have been concerned in the removal of the old. The organ by which the fangs of teeth are absorbed offers a very favourable object for examination.

This we find to commence within or beneath the periosteum which covers the fang of the tooth, and increases with the wasting of the tooth, until it comes in contact with the pulp, which then assumes a similar function and becomes an absorbing organ, increasing gradually in size, till, if the tooth be left undisturbed, but little of the crown remains excepting the enamel. If, when in this condition, the crown of the tooth be carefully removed, we shall see the absorbent papillæ projecting a little above the gum, firm in substance, and not disposed to bleed unless rudely handled. Within two or three days it becomes covered with epithelium, either by the extension of the epithelial membrane from the surrounding parts, or from a change in character in the superficial cells of the part itself*. Gradually the papilla loses its

* In the 26th volume of the Medico-Chirurgical Transactions, there is a short paper by Mr. DALRYMPLE, in which he describes a small tumour from the eyelid, consisting essentially of epithelial cells, in which the ordinary contents had been replaced by ossific matter.

distinctness of outline and merges into the surrounding gum, from which it can no longer be distinguished. Here then we have a second instance in which an absorbent tissue has its function finally suspended, and a new one substituted. In the place of increasing at the cost of pre-existing tissue, growth is suspended, and it unites with and assumes a similar office to that of the surrounding gum.

In conclusion, the authors may allude to an interesting fact, with reference to the subject of absorption, which has been recently observed by Mr. STANLEY and subsequently by Mr. BOWMAN. In the treatment of ununited fracture, the practice has of late been successfully adopted of drilling cylindrical holes into the bone in the neighbourhood of the injury, and of driving in pegs of ivory, accurately fitted to the perforations, for the purpose of setting up action in their vicinity. These pegs, after remaining in the bone several weeks, have been removed, and have been found on inspection to present erosions similar to those which are seen on absorbing bone or tooth. In fact, they closely resemble the fangs of temporary teeth recently attacked by absorption. Mr. BOWMAN kindly placed at the disposal of the authors one of the pegs which had been used for this purpose, a section of which presents, at the parts eroded, in its microscopic characters, the usual emarginated outline so frequently alluded to in the foregoing pages. They have not however had the opportunity of investigating the condition of the tissues around the pegs; but it is exceedingly probable that absorption has in these cases been effected by processes similar to those which occur in the formation of Haversian spaces.

EXPLANATION OF THE PLATES.

PLATE VI.

- Fig. 1. Transverse section of compact bone, showing the ordinary appearances. *a.* Haversian system. *b.* Interstitial laminæ. *c.* A new Haversian system within an older one, the Haversian canal obliterated by the development of a lacunal cell.
- Fig. 2. Transverse section of compact bone, showing an Haversian space, with its characteristic emarginated outline.
- Fig. 3. The same, from a less compact part of the bone, from a man aged fifty-six.
- Fig. 4. Transverse section from the fibula of a child two years old, showing the general characters of bone in young subjects. *a.* Haversian space.
- Fig. 5. Section of compact bone, showing several Haversian systems enclosed within a single series of laminæ. *a.* A lacunal cell attached to the surface of an Haversian canal.
- Fig. 6. Section showing the characters of a new Haversian system, developed within an older one.

- Fig. 7. An excentric Haversian system, illustrating the arrangement of the laminae.
 Fig. 8. *a.* Lamination of bone, as it appears under a low power. *b.* The same highly magnified, showing the lines of osteal cells and the intermediate transparent tissue.

PLATE VII.

- Fig. 9. Transverse section of a stag's antler, after shedding, showing the transparent tissue which lines the Haversian canals.
 Fig. 10. Section showing the circumferential laminae, perforated by an Haversian system.
 Fig. 11. Section showing the orifices of the canaliculi, with their parietes.
 Fig. 12. Sections from rickety bone. *a.* Consolidated lacunae. *b.* Lacunal cells, from which no canaliculi have proceeded.
 Fig. 13. Section showing circumferential laminae, with elongated canals passing amongst the lacunae and canaliculi.
 Fig. 14. Section of fossil bone, from the Wealden, supposed to be Pterodactyle, in which the nuclei have been preserved by fossilization.
 Fig. 15. Ossified lacunal cells, from the spongy portion of a bone of an old subject.
 Fig. 16. Section from the petrous portion of a temporal bone of an adult. *a.* Lacunal cells, containing lacunae and canaliculi. *b.* Intercellular granular tissue, similar to that found in bone developed in cartilage.
 Fig. 17. Section showing ossified articular cartilage. *a.* Lacuna developed from a cartilage cell. *b.* Lines of granules.
 Fig. 18. Section from an incus in a subject aged seventy-five, showing osteal and lacunal cells on the surface.

PLATE VIII.

- Fig. 19. Longitudinal section of ossifying temporary cartilage, showing—*a.* Ossified intercolumnar tissue. *b.* Lacunal cells. *c.* Granular cells in process of conversion into lacunae. *d.* Lacunal cells imbedded in ossified intercolumnar tissue, without conversion into lacunae.
 Fig. 20. Transverse section of ossifying cartilage from femur of a child, fourteen days old. *a.* Intercolumnar tissue. *b.* Lacunal cell. *c.* Similar cell, with granular cell in process of conversion into a lacuna.
 Fig. 21. Section from femur of same subject, taken a little way below the ossifying cartilage.
 Fig. 22. A longitudinal section of new bone, a little further advanced than in fig. 19. *a.* A detached lacunal cell, showing the three parts of which these bodies are composed.

- Fig. 23. From rickety bone. *a.* Lacunal cells. *b.* A detached granular cell in process of conversion into a lacuna.
- Fig. 24. Longitudinal section of developing bone from the tibia of a calf, mounted in Canada balsam. *a.* Intercolumnar tissue, from which the lacunal cells have disappeared. *b.* Ossified intercolumnar tissue and lacunal cells. *c.* Space produced by absorption. *d.* Haversian system in process of formation.
- Fig. 25. Transverse section of same, taken at level of *b* in fig. 24. *a.* Intercolumnar tissue. *b.* Ossified lacunal cell. *c.* Secondary bone.
- Fig. 26. Arrangement of cells and fibres in the neighbourhood of developing parietal bone.

PLATE IX.

- Fig. 27. Advancing spicula of bone, from parietal bone of fœtal lamb. *a.* Developed bone, showing its cellular character. *b.* Osteal cells arranged around the bone previous to their calcification.
- Fig. 28. From the epiphysis of the long bone of a calf, showing osteal and lacunal cells.
- Fig. 29. From the parietal of a human fœtus, showing osteal and lacunal cells, occupying the space betwixt two advancing spiculæ of bone.
- Fig. 30. Longitudinal section of cartilage with epichondrium attached. *a.* The developed cartilage. *b.* Fibres of perichondrium, with cells of a similar character to those of the cartilage.
- Fig. 31. Circumferential laminæ of human tibia, showing the manner in which the laminæ are developed from osteal cells. *b.* A compound cell, the origin? of the osteal cells.
- Fig. 32. From the tibia of a fœtal lamb. *a.* Developed bone, showing the cellular character. *b.* Undulating lamina in process of development, and containing lacunal cells. *c.* Osteal cells, not yet arranged. At *d* is shown an Haversian space, enclosed in the advancing ossification, while at *e* the laminæ are approaching towards one another to enclose a space.
- Fig. 33. From the fibula of a calf, showing growth on the external surface.
- Fig. 34. From an inflamed femur, showing absorption, with the cells contained in the Haversian space.

Fig. 20. From the left, a lateral view of the head of a female pupa in the process of ecdysis into a female.

Fig. 21. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 22. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 23. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 24. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 25. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

PLATE III

Fig. 26. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 27. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 28. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 29. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 30. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 31. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 32. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 33. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 34. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 35. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 36. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 37. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 38. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 39. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 40. Lateral view of the head of a female pupa from the time of ecdysis into a female. A, dorsal view of the head of the pupa.

Fig. 1.

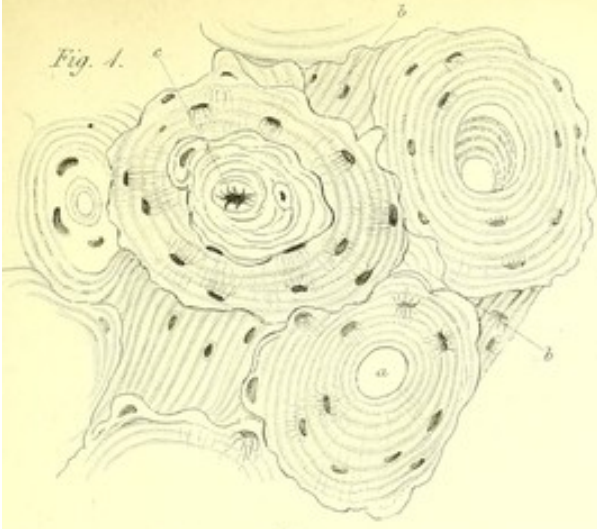


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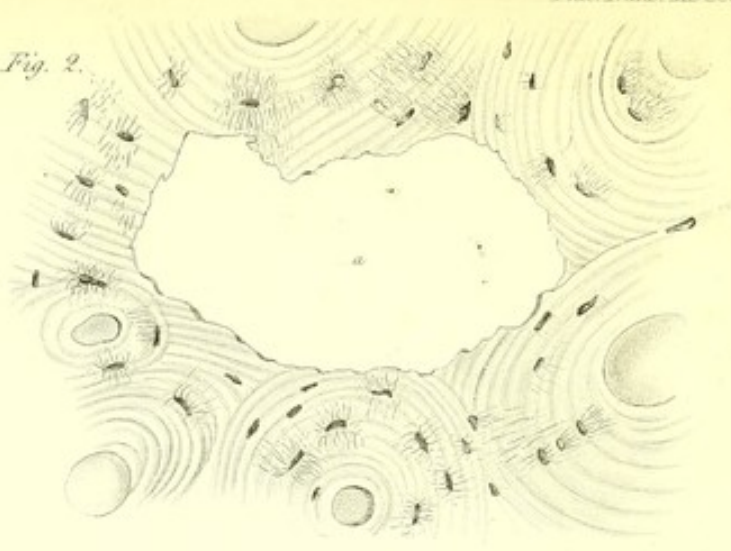


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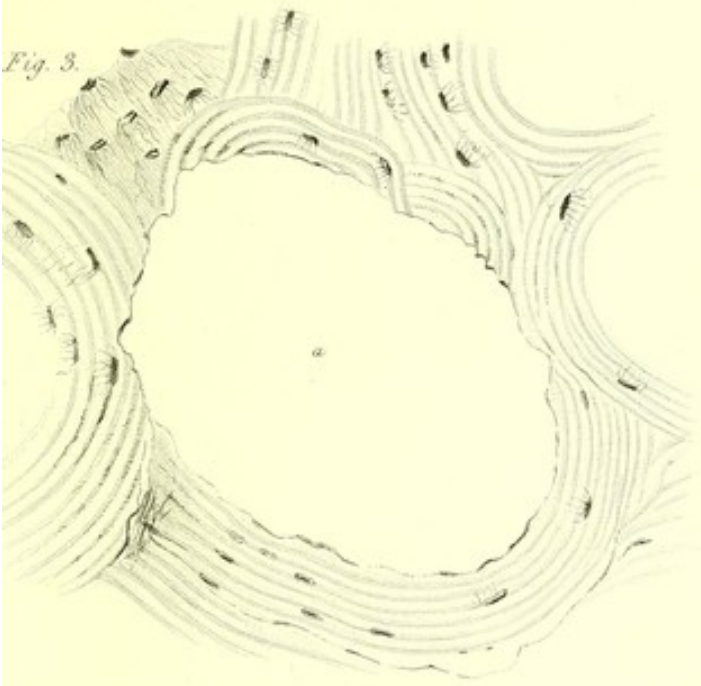


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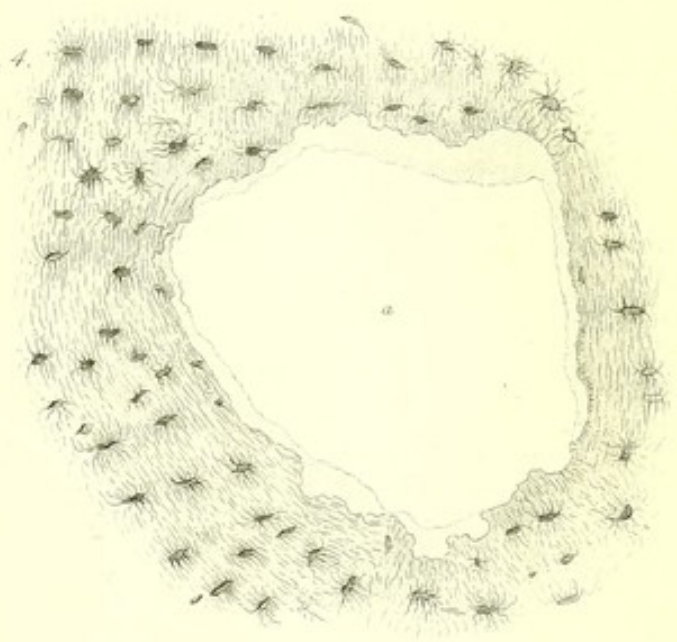


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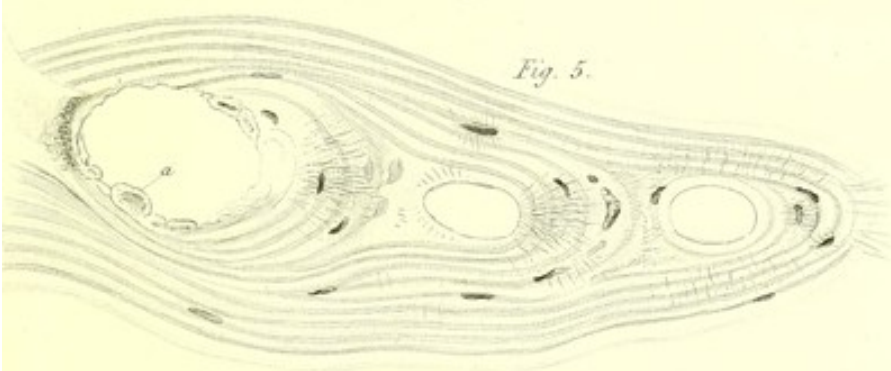


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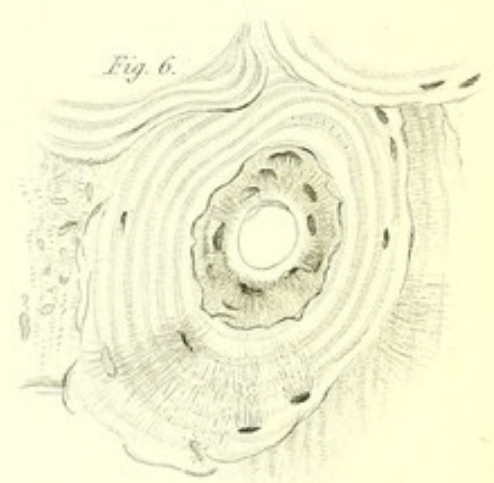


Fig. 7.

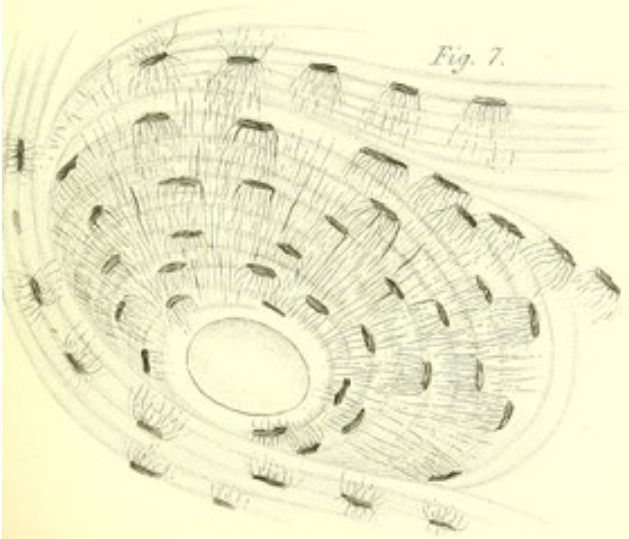


Fig. 8.

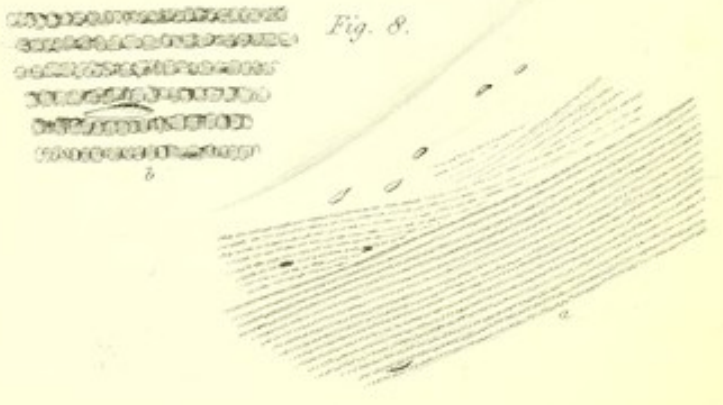




Fig. 9.

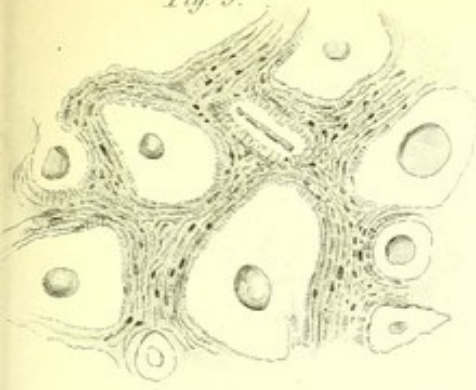


Fig. 10.

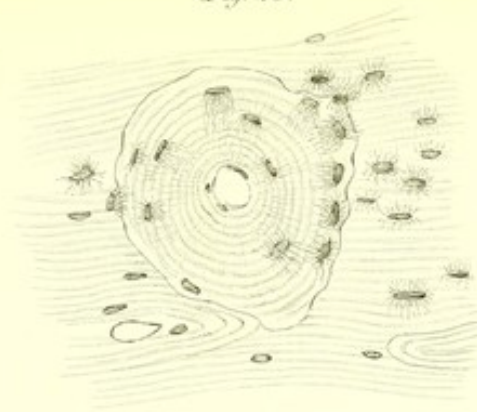


Fig. 11.



Fig. 13.



Fig. 12.

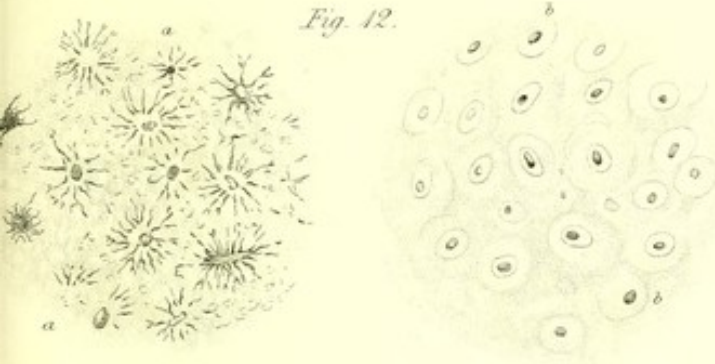


Fig. 14.



Fig. 15.

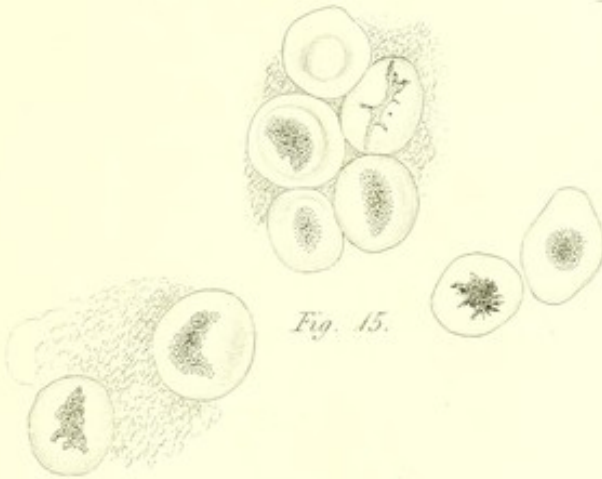


Fig. 16.



Fig. 17.

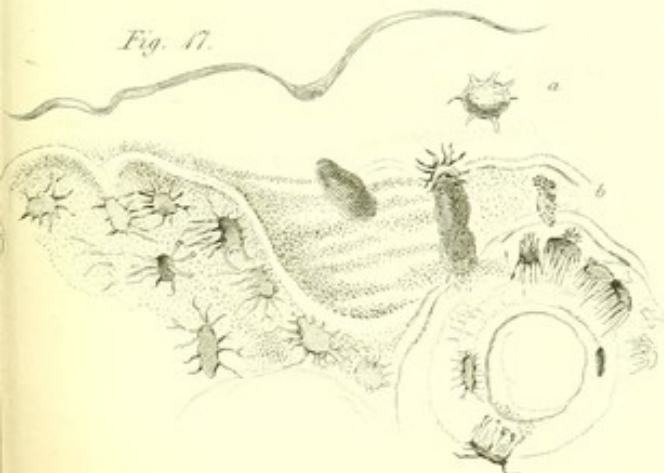


Fig. 18.





Fig. 19.



Fig. 20.



Fig. 21.

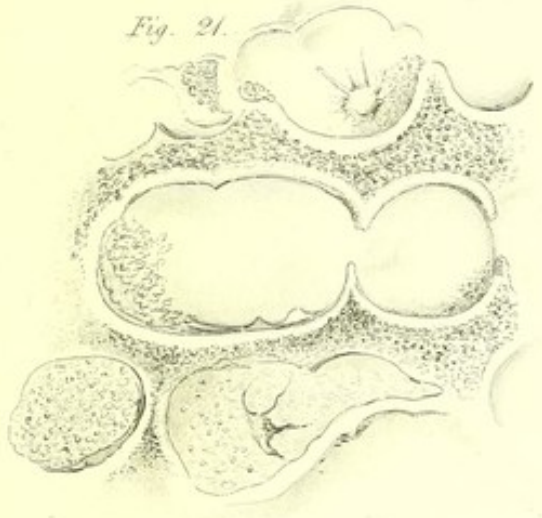


Fig. 22.



Fig. 23.

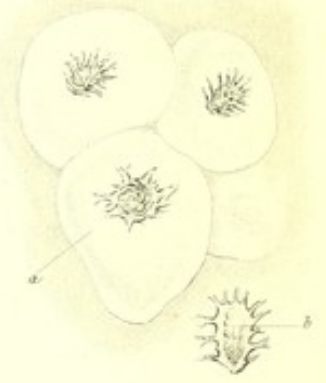


Fig. 24.

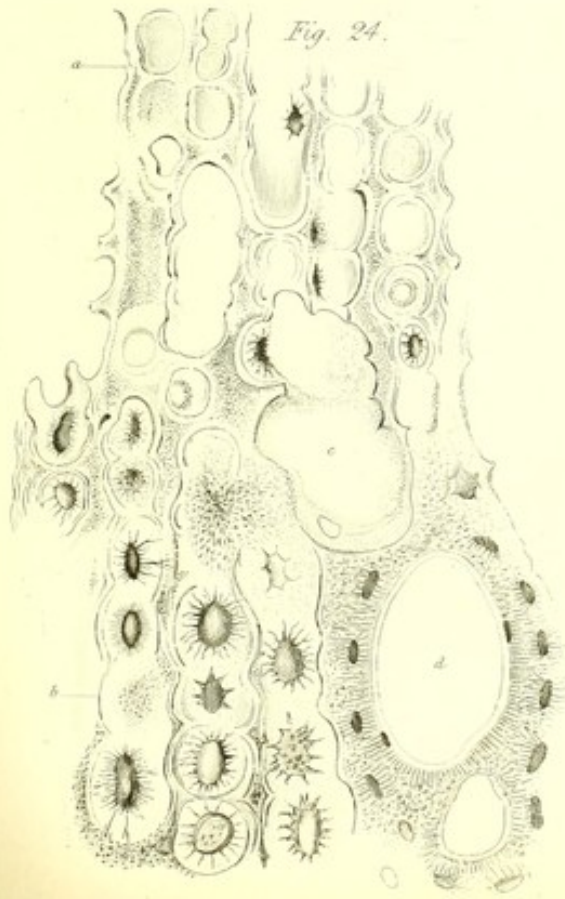


Fig. 25.



Fig. 26.





Fig. 27.

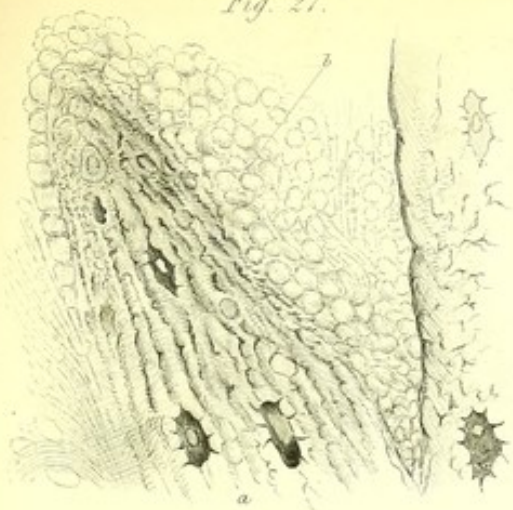


Fig. 30.



Fig. 28.



Fig. 31.

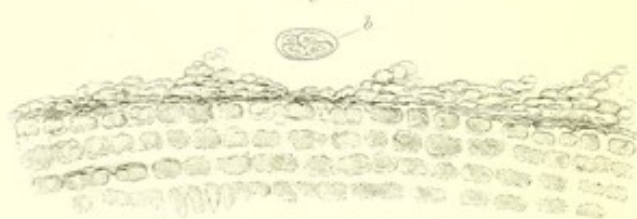


Fig. 29.



Fig. 32.

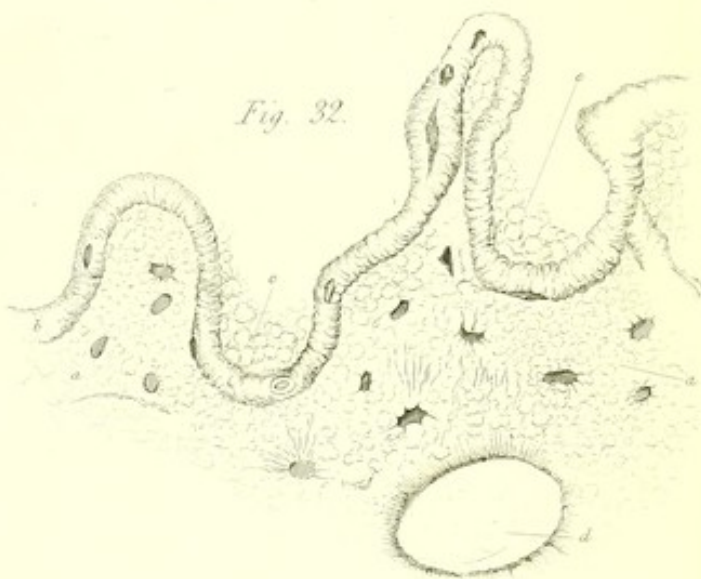


Fig. 33.



Fig. 34.

