CARTILAGE CANALS

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INTRODUCTION

THE development of cartilage and bone in the primary centres of the skeleton has been the subject of a very large number of researches, and the morphological aspect of the various phases is now known in great detail. Ossification of the secondary centres in the epiphysial cartilages has on the other hand attracted less attention, although the history of the growth both of the cartilage and of the bone is quite different from that in the primary centres. For whereas the cartilage of the primary centre is avascular, and is ossified by a periosteal bud which erodes the calcified cartilage, the epiphysial cartilage contains during its later growth a rich series of large blood vessels which ramify in its interior, and when ossification occurs these supply the material for the formation of the centre. It is the arrangement, development and functions of these vessels that form the subject-matter of this paper.

The existence of vessels in the epiphyses has long been known. The earlier writers are not available to me, but are quoted by Bardeen in Keibel and Mall (1), where their work is summarised in the statement that "Blood-vessels, which spring from the periosteum and from the bone-marrow, penetrate into the epiphysial cartilage long before ossification begins.... In some cartilages the blood-vessels appear in the third foetal month. In the seventh all the larger cartilaginous areas show rich vascular plexuses."

These vessels do not lie in direct contact with the cartilage, nor do the arteries and veins run independently of each other. Stoss (10) and Stump (11) have shown that the artery carrying the blood into the cartilage, the vein bringing it out and the capillary plexus between them all lie in a matrix of connective tissue which serves as a bed for their passage. The whole structure, including both the vessels and the connective tissue, is known as a cartilage canal. These canals form conspicuous branching systems in the cartilage.

The nature of the canals was studied by Eckert-Möbius (3) in the petrous temporal. He showed that their primary function is that of nutrition of large cartilages, and that where this nutrition fails degeneration and calcification of the cartilage take place, so that the canals determine the position of the centre of ossification.

Hintzsche (5, 6), working on reconstructions of the lower end of the femur and of the calcis, gave the first accurate description of the forms taken by the canals. But he found no causal connection between their position and the site of the centre of ossification which he suggests is determined by mechanical forces, either in each individual embryo, or in the ancestors of the species. In this paper these findings are discussed in the light of studies on other bones and on other animals.

A number of special technical difficulties have to be met in the course of such a study. The canals are too small and delicate for macroscopic study, and the cartilage too opaque for study as a transparency. In cleared specimens the connective tissue of the canals is not differentiated from the cartilage, and even if the blood vessels be injected only a poor picture of the arrangement of the canals is obtained. Thus it is essential that a reconstruction model be made. The wax method was used by Hintzsche, but is unsuited to delicate branching structures. For this reason I have evolved a celluloid method which is well suited to the study, but which is so similar to that already described by Senior (6) that it is unnecessary to give a detailed description here. It may be noted that it gives accurate information about the distribution and branching of canals, but not about their thickness at any point. The drawings therefore are accurate on the first two points, but not on the third.

I have used Man as the type for this description, giving a series of reconstructions of bones in various developmental stages. Drawings from other animals have been used to illustrate certain aspects of the discussion. Under further headings are discussed the development of cartilage canals, their relation to epiphysial ossification, and their functions, while a separate section is added on the canals which pass from the epiphysial cartilage into the shaft, as the presence or absence of these has been a matter of interest in clinical studies.

CARTILAGE CANALS IN MAN

Fig. 1 shows a second phalanx from a five months' foetus, in which the cartilage canals have just formed and are in their earliest stage of development. The model is drawn so that the canals are seen at *A*, *A* as solid objects inside the transparent cartilage. Each forms a short unbranched stump. There are none at the distal end of the bone.

An examination of a section passing through one of the eight canals shows it to contain a core of loose young connective tissue continuous with that of the perichondrium. Embedded in this tissue is a small arteriole, continuous externally with the circulus vasculosus around the epiphysis.

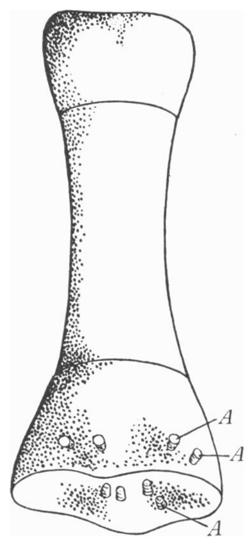

Fig. 1. Celluloid reconstruction of a second phalanx from a five months' human foetus.

Investigation of a first metatarsal bone from a six months' foetus was made. At each end is a series of canals, more advanced in development than those seen in fig. 1. The canals have assumed a simple branched form. These simple canals are characteristic of epiphyses at this early stage of development. The canals at the distal end of the same bone are of interest, for the cartilage there is ossified from the shaft and not from an epiphysial centre. As the bone of the shaft encroaches on the cartilage, reducing it to a thin articular plate, the canals disappear. Thus the presence of cartilage canals in cartilage is not necessarily connected with the processes of epiphysial ossification.

Fig. 2 shows the two halves of the head of a fibula from a six months' foetus. In this specimen the canals have already reached their greatest diversity of form, and it may be conveniently used as a type for their description.

At *A*, *A* are *simple unbranched canals*, similar to those of the preceding figure.

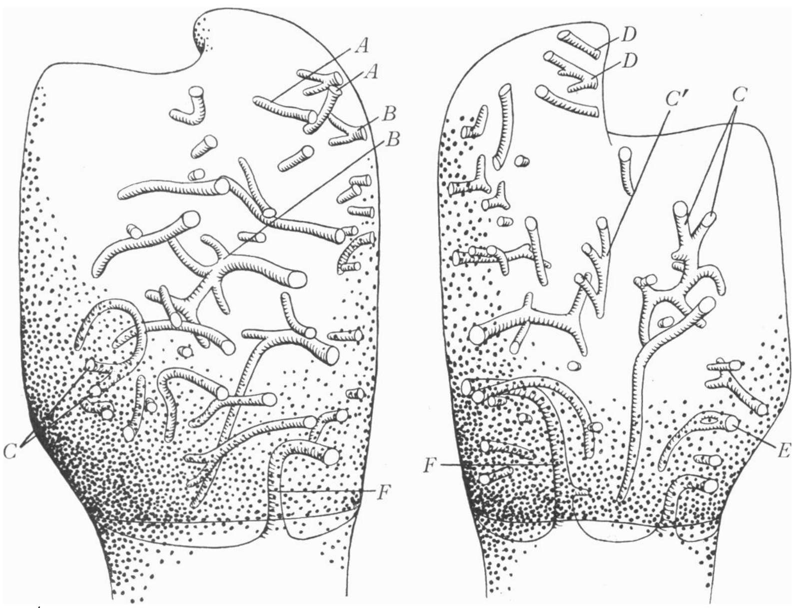

Fig. 2. Celluloid reconstruction of the upper end of the fibula of a six months' foetus.

At *B*, *B* are *simple branched canals*.

At *C*, *C* are canals either branched or unbranched which arise from the perichondrium by two separate roots, but these roots join soon after entering the cartilage. In no case does this union occur deeply within the cartilage. At *C′* there is a similar canal arising by three separate roots. These may be called *double and multiple rooted canals*.

At *D*, *D* are canals which pass directly through a projection of the cartilage from one side to the other. They occur only in those parts of the cartilage which are drawn out into projecting tongues. They may be termed *tunnel canals*.

At *E* is a canal which breaks into two divisions joining later to form again a single canal. Only one of this type occurs in this specimen. They are never common, but another is shown in fig. 4. I name these structures *divided canals*.

It may be noted in passing that these double-rooted, tunnel and subdivided canals are the only structures resembling anastomoses ever seen in epiphyses. There are no anastomoses between separate canals in the interior of the cartilage. Thus the rich vascular plexuses and the anastomoses spoken of by Bardeen (1) and Stump (11) have not been observed to occur. Their absence is demonstrated very clearly by complete reconstructions of the canal systems from serial sections. A study of separate sections gives a strong impression of rich anastomoses.

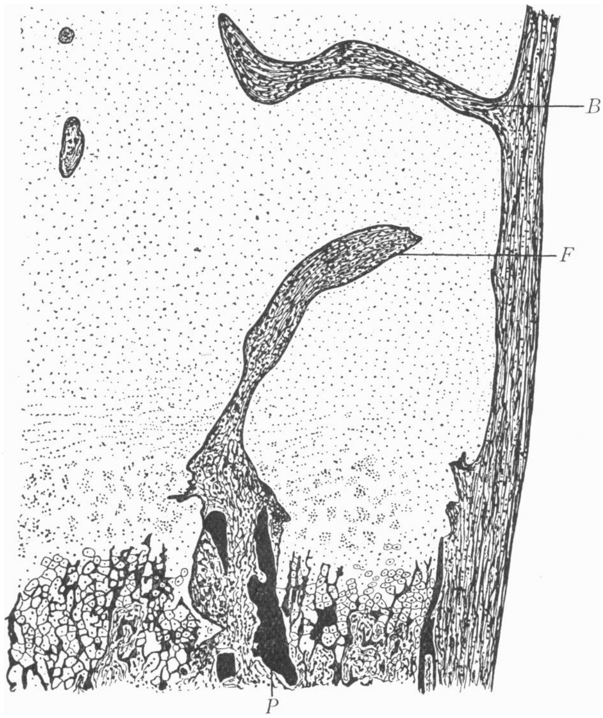

Fig. 3. Section from the fibula reconstructed in fig. 2, showing the entrance of a simple canal and the passage of a communicating canal into the shaft.

Finally at *F*, *F* are canals which, entering the epiphysis from the perichondrium, turn downwards and become continuous with the marrow spaces of the shaft. These may be called *communicating canals.*

Fig. 3 shows a section from the head of the fibula which has just been described. At *B* is seen the entry of a simple canal into the cartilage. At *F* a communicating canal passes into the shaft through the metaphysial plate of growth cartilage. The disturbance of the cartilage columns as the canal passes through is well seen. The connective tissue core of the canal is continuous from the perichondrium to the young marrow of the shaft. In the mouth of the canal is a mass of bone *P* which has ossified in the connective tissue. As this mass has ossified in membrane it differs in texture from the cartilage bone of the shaft around it.

Fig. 4 shows the upper part of a femur separated from the rest of the bone by a horizontal cut so that the upper part of the head and the great trochanter are seen from above.

The femur is in the same general stage of canal development as the fibula shown in fig. 2, and all the types of canal occurring there are found in the femur. This reconstruction showed the blood supply to the head of the femur in the developing human bone. A well-developed series of canals enter the carti-

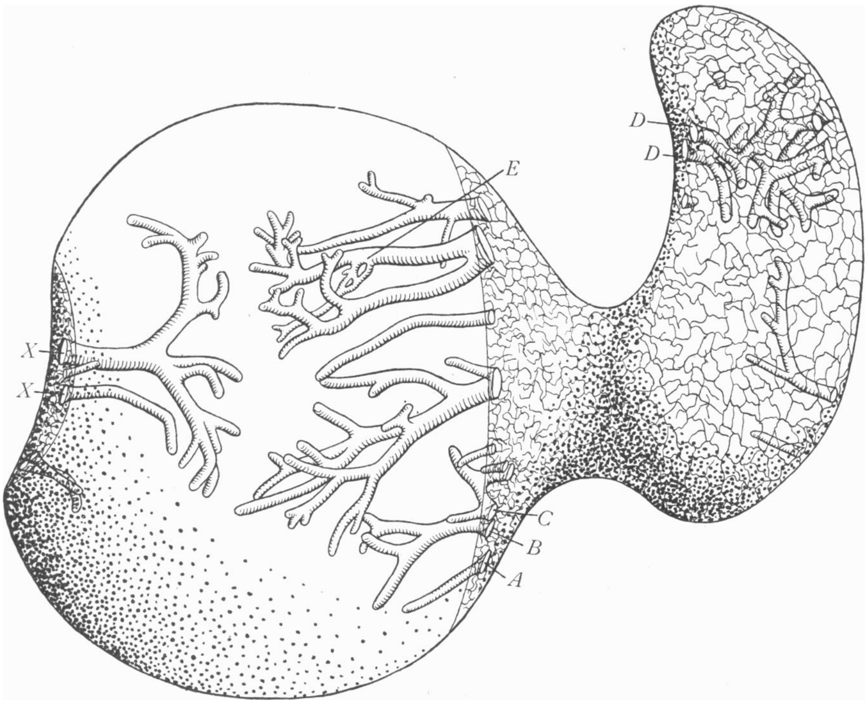

Fig. 4. Celluloid reconstruction of the uppermost part of the head and great trochanter of a femur from a six months' human foetus.

lage from the ligamentum teres. Thus at least at this stage in development the round ligament conveys a blood supply to the head of the femur. In the late foetus a considerable zone of the cartilage is supplied by blood carried by this route.

The clear figures given by Walmsley (13) bring out the fact that this supply from the ligamentum teres rapidly diminishes in extent, so that in his earliest specimen, from a child two years of age, it has become negligible, while in the adult it is confined to the connective tissue in the fossa for the ligament, and does not enter the bone. These findings are confirmed by my own study of the femur after ossification has taken place in the head, for though the group of canals from the ligamentum teres is still clearly recognisable in a child of eighteen months, it is much reduced in proportion to the other systems.

Investigation of the same specimen also brought out clearly the sharp separation of the teres group of canals from the remainder. There are no anastomoses between the teres group and the remainder, nor do they interdigitate, being separated by an avascular lamina of cartilage lying between the two groups. Such avascular laminae occur commonly in epiphyses and will be further considered in relation to centres of ossification.

Fig. 5 shows the cartilage canals in a navicular bone before ossification sets in. It is given as an example of a short bone possessing canals, to compare

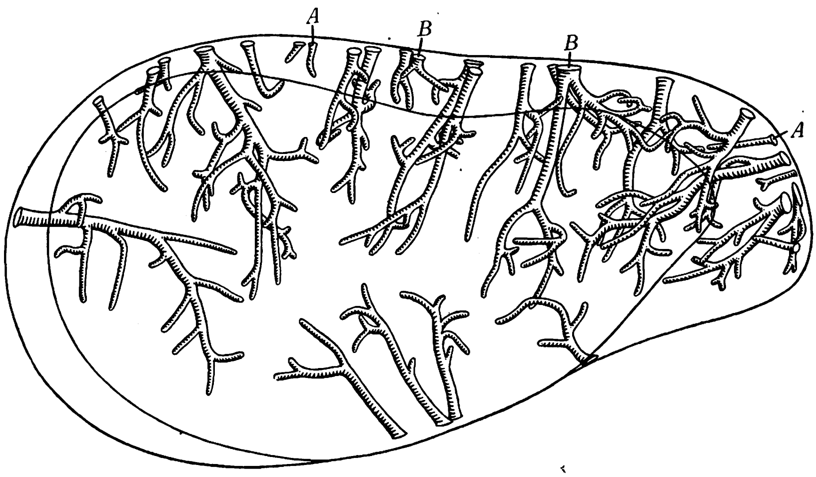

Fig. 5. Celluloid model of a navicular bone from a six months' human foetus.

with the epiphyses already described. The canals in the two cases are similar, but in this case only simple unbranched and branched types are present. A well-marked avascular lamina lies between the canals entering from the dorsal surface and those entering from the plantar surface.

Similar canals occur in other short bones. They have been reconstructed in the calcis by Hintzsche (6), and a series showing vascularisation of this bone and of the talus has been shown recently by Hurrell (7). A microphotograph of vessels in a cleared vertebra has been published by Todd (12).

All the types of cartilage canals that I have observed before the ossification centres appear have now been described and named.

In the earliest stages there are only simple unbranched stumps present, then the branched forms appear, and finally the more complex types. The problem of their development may now be considered.

THEORY OF THE FORMATION OF CARTILAGE CANALS

The generally accepted theory of the formation of cartilage canals was advanced by Stump (11). He emphasises the importance of the primitive connective tissue cells contained in the canals. These, he says, grow into the cartilage mass from the subperichondrial zone along channels which develop by solution of the chondromucin. This statement is based on the absence of chondromucin from the cartilage in the immediate vicinity of the canals, and on the presence within the canals of loose cells which he interprets as cartilage cells freed by solution of the cartilage matrix. This theory of the formation of cartilage canals by an active growth inwards may be called the *theory of invasion*. It is further supported by the work of Hintzsche (5).

The histological facts advanced by Stump are confirmed by a study of my series, but neither of the two pieces of evidence given can be taken as supporting the theory of invasion. For in the group of canals entering the femur from the ligamentum teres both the absence of chondromucin and the presence of the cells under discussion are found, although these canals are known to be undergoing regression in a child of eighteen months. Hence the two facts advanced are not evidence of active growth, and still less of invasion by cartilage canals.

Again, when cartilage is replaced by bone during growth, its cells undergo a preliminary multiplication and enlargement, and the matrix between the cells is calcified. Cartilage which has not undergone these preliminary changes is never eroded by the young connective tissue of the marrow spaces of the shaft or by the tissues of the perichondrium. When cartilage is destroyed directly, without multiplication, enlargement or calcification (as in the tadpole's tail at metamorphosis) the process is carried out by an army of leucocytes and not by young connective tissue. No such army of leucocytes is present around the young cartilage. So it is most unlikely that the theory of invasion is valid, and an alternative *theory of inclusion* is here suggested.

It is agreed that the cartilage of the epiphyses grows largely by change of the connective tissue cells of the perichondrium into cartilage cells, which add themselves to the periphery of the cartilage mass. Thus the perichondrium forms a zone of active growth around the epiphysis. In the process of change from connective tissue to cartilage the capillaries of the perichondrium are obliterated and their remains included in the cartilage.

But when the cartilage has attained a certain bulk all the blood vessels of the perichondrium are no longer destroyed. Some of the vascular loops, presumably the "strongest," persist, each surrounded by a zone of unchanged connective tissue derived from the perichondrium. By the formation of cartilage in the perichondrium around them these loops and their connective tissue matrix come to project into the mass of cartilage as short stumps—the beginnings of cartilage canals.

A continuation of these processes may lead to the inclusion within the cartilage of the arteriole and venule supplying several originally distinct cartilage canals, so that they now form offshoots of a single branched canal.

The phenomena noted by Stump may conveniently be considered here. The absence of chondromucin from the immediate vicinity of the canals is paralleled by its absence from the cartilage immediately underlying the perichondrium. It would appear that chondromucin depends for its formation on the absence of a vascular supply near by, so that it is not formed near the perichondrium or near the cartilage canals.

In a section from the navicular bone already described a canal was seen outlined by deeply staining boundaries, but containing nothing but ordinary cartilage cells similar to those outside it, except at one point where a few connective tissue cells are seen. Similar observations were made by Stump. These few cells, however, can hardly be held responsible for the formation of the whole cartilage canal by solution of the chondromucin. It is more probable that this structure is the remains of a canal whose vessels have become obliterated during growth, the connective tissue matrix being transformed into cartilage in just the same way as the connective tissue of the perichondrium is transformed. Thus, whereas Stump believes the presence of cartilage cells within a canal to be evidence of its active growth, I believe it to be evidence of its retrogression.

This obliteration of cartilage canals during growth is a phenomenon of common occurrence. It has already been described in the distal end of the first metatarsal, where there is a rich development of the canals in the young bone, but since there is no bony epiphysis for them to supply, they disappear in later development. In the femur again, the group supplying the head of the femur from the ligamentum teres is obliterated during development. The process will be noted again in the description, which follows, of the history of double-rooted, tunnel and communicating canals.

Fig. 6 shows the probable origin of several varieties of cartilage canal. Each depends on the pre-existing arrangement of the blood vessels in the perichondrium. Thus the double-rooted canal of diagram 1, A, B and C owes its origin to the inclusion of a capillary group supplied by an arteriole which is in turn derived from the point of anastomosis of two separate arterioles, both of which become included within the cartilage. By obliteration of one of these the canal becomes single rooted again before the two roots have sunk deep into the cartilage.

The tunnel canal of diagram 2 is developed by inclusion of vessels within a growing tip of cartilage. Here again the canal is obliterated at its weakest point, forming two simple canals.

The subdivided canal of diagram 3 is formed in a way similar to that of the double-rooted canal, but here the two separate arterioles are derived from a common trunk, which is eventually included to form the stem of the canal.

The development of communicating canals has attracted some attention owing to their supposed connection with the ossification of the epiphysial

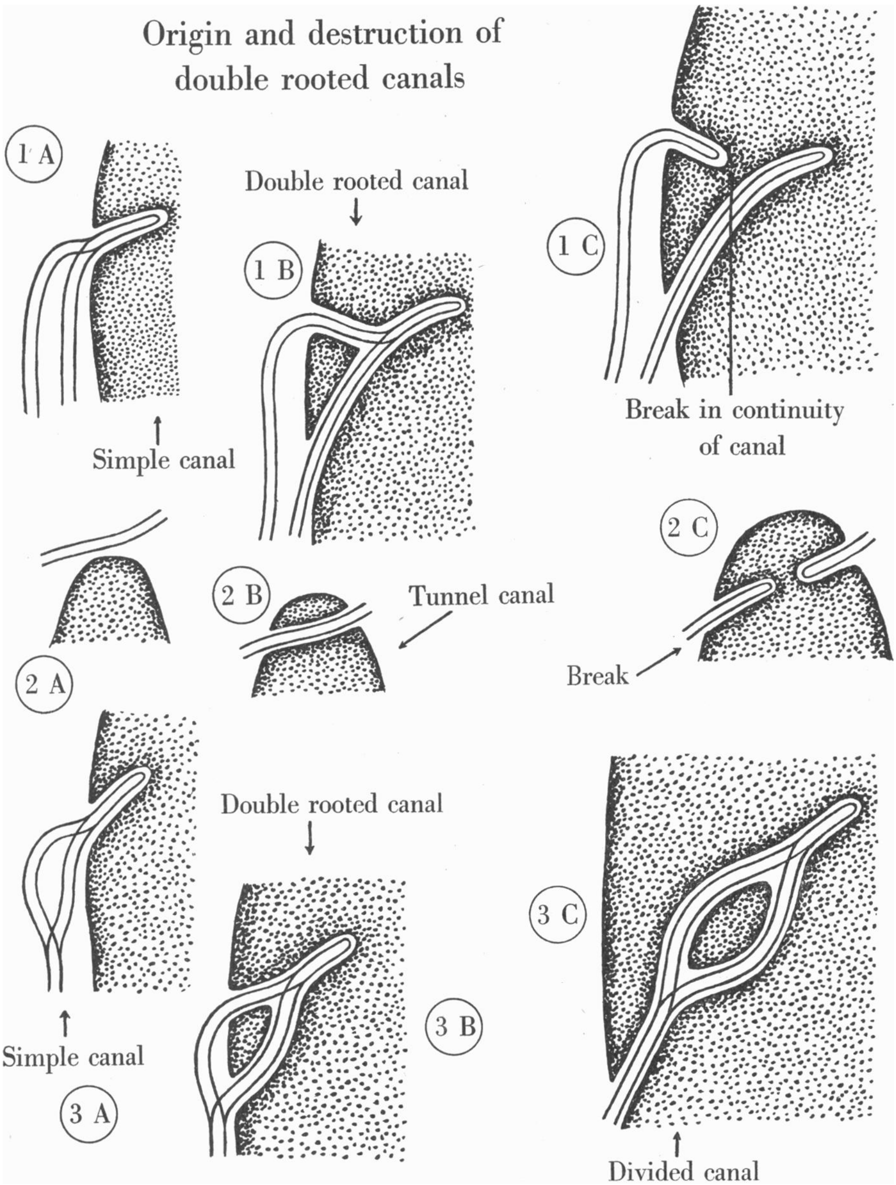

Fig. 6. Diagram showing the formation of varieties of cartilage canal.

centres. Parsons (8), who gives a good figure of these structures in the deerlet (*Tragulus*), describes them as growing up from the marrow of the shaft into the cartilage of the epiphysis to form the ossification centre.

If this theory of their development were true it should be possible to find canals springing from the bone marrow and ending blindly in the cartilage; I have not observed this to occur.

On the other hand numerous simple canals are present in the cartilage, at the stages before communicating canals are developed, and it is among these simple ones that the precursor of the communicating canals ought to be found. Now the cartilage lying nearest the shaft is undergoing changes preparatory to replacement by bone. It undergoes the processes of cell multiplication and enlargement, calcification and erosion by the young bone marrow as described in all text-books of histology. If the end of a simple canal should lie in the growing cartilage it may persist while the cartilage around it is calcified and then eroded, thus coming into secondary continuity with the young marrow of the shaft and forming a communicating canal.

This account agrees with that given by Hintzsche (6), but he describes processes which grow up from the shaft to meet the downwardly directed canals, which I would interpret as the remains of communicating canals which have become constricted and broken across.

CARTILAGE CANALS AND OSSIFICATION

The earlier work on the epiphyses was directed to the study of the bony centres rather than to that of the cartilages in which they grow. It is therefore not surprising to find that more attention was paid to the blood vessels in the epiphysial cartilages in connection with their ossification, e.g. Parsons (8) and Bardeen (1). Hintzsche (6) paid particular attention to this point in his reconstructions of the lower end of the femur, but did not extend his investigations to other bones.

Two specimens from Man will serve as types for this study.

Fig. 7 shows a thick section of the lower end of the femur of a full-time foetus, with a well-developed centre of ossification in the epiphysis.

At *A*, *B*, and *C* are seen unbranched, branched and double-rooted canals, similar to those already described. Any of these, if they impinge on the ossification centre, may form *nutrient canals* carrying blood vessels to it from the perichondrium, seen at *P*, *P*. These enter from both the dorsal and ventral surfaces of the epiphysis, the two groups being separated by the articular surface for the patella.

At *Q*, *Q* are very peculiar canals similar in structure to the others but arising from the centre of ossification, and not from the perichondrium as do all other canals. These may be called *centrifugal canals*.

Communicating canals stage completely absent in this specimen.

Fig. 8 shows the upper end of a femur in which the centre of ossification of the head is well formed, but the great trochanter is as yet unossified.

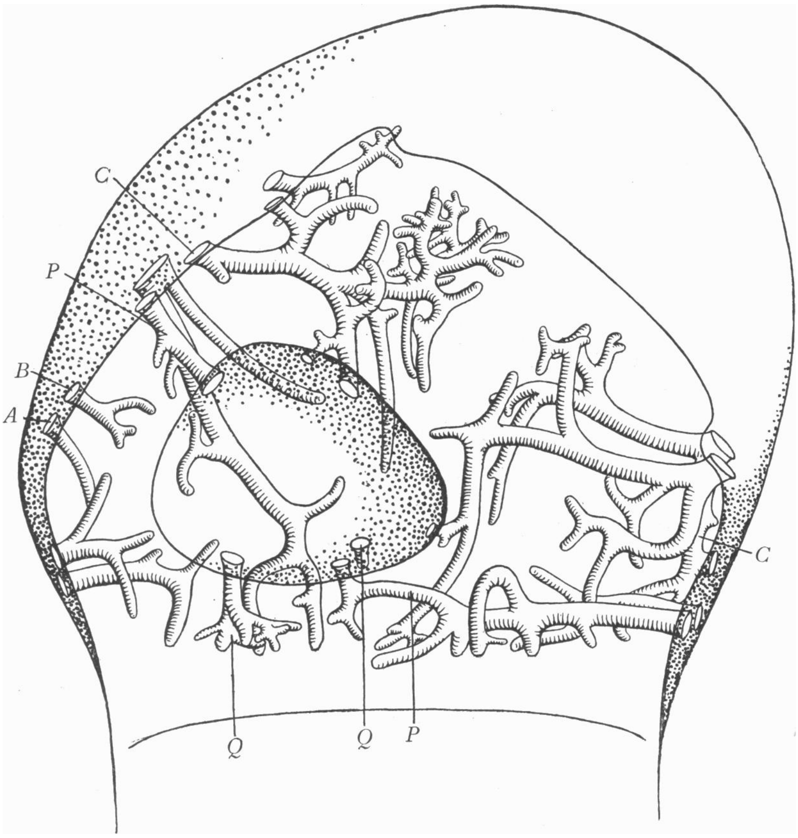

Fig. 7. Celluloid reconstruction of a thick section from the lower end of the femur of a full-time human foetus.

Fig. 8. Celluloid reconstruction of a thick section of the upper end of the femur from a child of eighteen months.

The bony centre lies between and is supplied by two groups of canals, the one entering from below the head and the other from the groove between the head and the great trochanter. This latter system, C', appears to consist of separate anastomosing canals, but I believe it to be a very complicated form of multiple rooted canal. No centrifugal canals spring from the centre.

At X a few canals are seen entering from the ligamentum teres. They penetrate only a small part of the cartilage, and they play no part in the supply of the bony centre.

From these two figures it will be seen that there can be no possibility of the osteoblasts of the epiphysis being derived from periosteal buds growing up from the bone marrow of the shaft, for at the time of ossification all communications between the shaft and the epiphysis have disappeared. It is highly probable that they are derived from the young connective tissue of the cartilage canals, just as the osteoblasts of the shaft are derived from the young connective tissue of the perichondrium. The connective tissues of the canals and the perichondrium are exactly similar and are continuous with one another.

THE POSITION OF THE OSSIFICATION CENTRE WITHIN THE CARTILAGE OF THE EPIPHYSIS

Here there are two sharply divided schools of thought. Parsons (8) working on epiphyses, Carey (2) on the primary centre of the femur in pig embryos, and Eckert-Möbius (3) on the cartilage canals of the temporal bone, support the older view that the degeneration of cartilage which precedes the formation of a centre of ossification is a result of a lack of nutrition of the cartilage. Hintzsche (6), however, in his reconstructions of the lower end of the femur, could find no difference between the nutrition of the site of ossification and that of many other parts of the cartilage. so that he could not consider lack of nutrition as a cause of degeneration. He suggests instead the mechanical effect of the patella as it glides over the femur, working either directly on the foetus itself or more probably through its ancestors. But it will now be shown that the ossification centre always appears in an avascular zone between two sets of canals, so that its position is probably dependent on that of the canals.

For this purpose it is necessary to study the arrangement of the cartilage canals in well-developed epiphyses. Man is an unsuitable subject for this, since the cartilages at the time of ossification are too large and the canals too complicated for extensive reconstruction. I have therefore used cats of suitable ages as a basis for the work, and the results are later confirmed for Man.

Figs. 9 and 10 show the major parts of the upper ends of the femora of two kittens aged four and ten days respectively, one before ossification takes place and one after. The simplicity of the arrangement of the canals and the convenient size of the specimens make them good material for study.

In fig. 9 the canals are divided into groups M, N and O, entering the femur from the underside of the neck, from the groove between the head and the

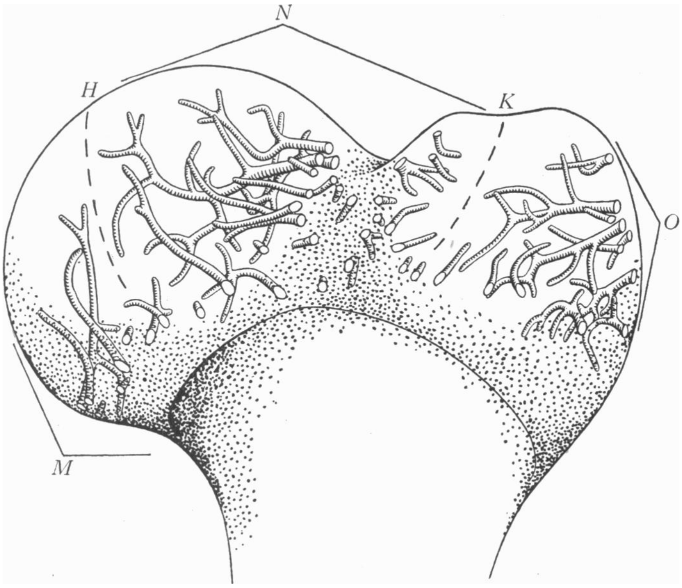

Fig. 9. Celluloid reconstruction of the major part of the femur of a four days old cat.

Fig. 10. Celluloid reconstruction of the major part of the upper end of the femur of a ten days old cat.

great trochanter, and from the lateral aspect of the great trochanter, respectively. Each of these groups supplies its own block of tissue and they are separated from each other by avascular laminae *H* and *K*. In the cat at this stage there are no canals springing from the ligamentum teres.

Fig. 10 shows the canals entering the ossification centre. From group *M* enter the canals *A* and *B*, from group *N* the canals *C* and *D*; that is the centre occupies the site of the former avascular lamina between the two groups and is supplied by canals from both groups. A comparison with Fig. 8 shows that in Man also the centre arises between and is supplied by the same two groups of canals, the group from the ligamentum teres playing no part in the supply. The centre for the great trochanter arises in the avascular lamina *K* between the canal groups *N* and *O*.

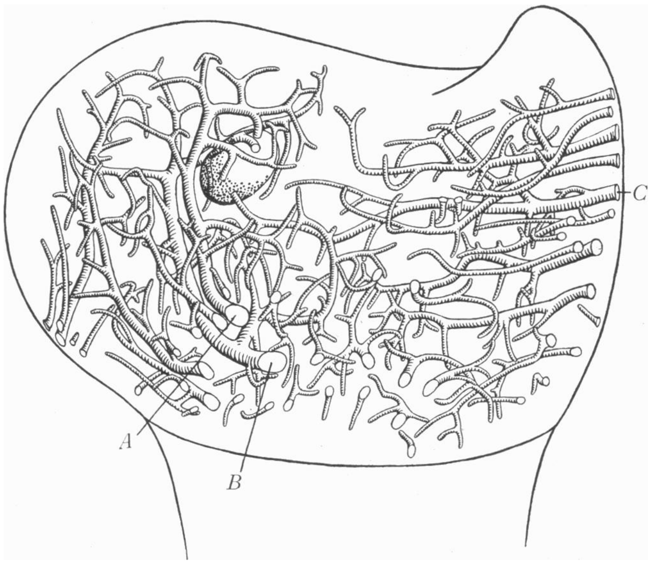

Fig. 11. Celluloid reconstruction of the major part of the upper end of the humerus of a four days old cat.

Fig. 11 shows the major part of a kitten's humerus with a young centre of ossification. I was guided in the choice of this specimen by Parsons' statement that a centre is present in a kitten of three days. In this bone the articular surface for the shoulder-joint comes as far laterally as the tendons inserted into the greater tuberosity, and the group roughly corresponding to the middle group *N* of the femur is much reduced. Their place is taken by a large group entering from the lateral aspect of the greater tuberosity, roughly corresponding to the group *O* of the femur.

The centre is supplied by two canals *A* and *B* entering from the lower part of the neck and by one canal *C* entering laterally. Here again the centre has arisen in the avascular lamina separating two groups of canals.

Finally in the lower end of the human femur already described the centre arises in a similar avascular lamina between two groups of canals separated at their entry by the articular surface for the patella.

Thus in all these cases the bony centre arises in an avascular lamina, and it is highly probable that it always does so. The next step is to show the nature of the avascular lamina itself.

Several stages in the development of an ossification centre for an epiphysis, and its relation to cartilage canals can be distinguished. In the beginning the cartilage exists before canals are present; next, the canals are developed on both sides of the cartilage leaving a clear space—the avascular lamina—between the two groups roughly corresponding in position with the cartilage mass before canals are present.

This is followed by calcification of the central part of the avascular lamina, which is at once the oldest and the least well nourished part of the cartilage.

Finally a bony centre supplied by nutrient canals from both sides of the original avascular lamina replaces the area of calcified cartilage. The severed ends of ordinary canals cut in two by the developing ossification centre may be the source of the centrifugal canals. The stems of these canals persist as nutrient canals, while their distal extremities now form centrifugal canals.

Thus the cartilage canals not only give origin to the osteoblasts and marrow of the epiphysial centre and carry the blood supply to and from the centre, but also determine by their distribution the position where the centre appears.

COMMUNICATING CANALS

The communicating canals were among the first structures in epiphyses to attract the attention of anatomists, and interest in them, rather than in the other types of canal, has persisted to the present day.

I have already mentioned that Parsons (8) described them as osteogenic buds growing up from the shaft to form the centre of the epiphysis. They are described in a similar way by Bardeen (1), but here canals passing into the cartilage from the perichondrium are also mentioned. It is now recognised that the perichondrium is the source of all the canals, so that Stump (11) for instance does not mention the communicating canals.

On the clinical side the communicating canals have attracted attention because they offer a possible path for injections passing from the shaft to the epiphysis or *vice versa*. Injection of the vessels in the canals has been carried out by certain authors whose work is not available to me but who are mentioned by Harris (4). Strangely enough Harris mentions the canals only to deny their very existence in any normal bone.

A good example of an early communicating canal has already been given in a human fibula from a six months' foetus. For comparison, I include here an example in a three weeks old dog.

Fig. 12 shows a section of a communicating canal from the femur of a three weeks' pup. It demonstrates the continuity of the connective tissue of the canal with the young marrow of the shaft, just as in the human fibula already described. Further, it shows the disturbance of the arrangement of the cells of the surrounding cartilage and the persistence of a sheath of hyaline cartilage around the canal projecting for a considerable distance into the shaft. If calcification of cartilage is dependent on a lack of nutrition, as suggested by Parsons (8), it would appear that the nutrition afforded by the canal has pre-

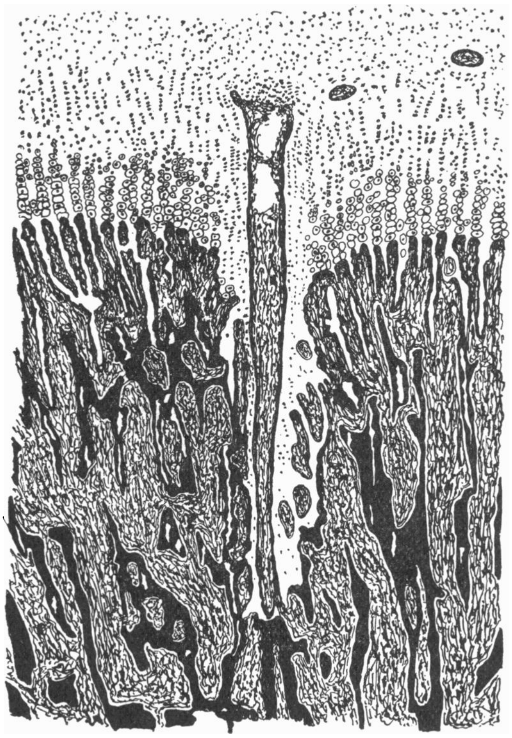

Fig. 12. Section from the lower end of the femur of a three weeks' pup, showing a communicating canal.

vented the calcification and destruction of a thin shell of cartilage around the canal, so that it hangs like a stalactite into the young bone.

This is the only well-formed communicating canal in the lower end of the femur of this pup, and there are none at all in the upper end of the tibia. It has already been mentioned that in Man the communicating canals disappear from the epiphysis soon after the centre becomes ossified, and no doubt this canal, the last of its kind in the pup's epiphysis, would soon have been obliterated had the animal lived.

The history of these communicating canals might be presented as follows. Following on an earlier phase when only simple canals are present, a later stage ensues when the ends of the simple canals become continuous with the marrow of the shaft as described in an earlier section.

When an ossification centre develops, the canals lose their communications with the shaft, so that they now behave as simple canals, forming nutrient and centrifugal canals as the ossification centre breaks them up. This is what occurs in Man.

If the communication with the shaft should fail to be broken before the canal is split into a nutrient and a centrifugal portion, the latter will form a *centrifugal communicating canal*, that is a canal passing directly from the bone marrow of the shaft to that of the epiphysial centre. That such connections can

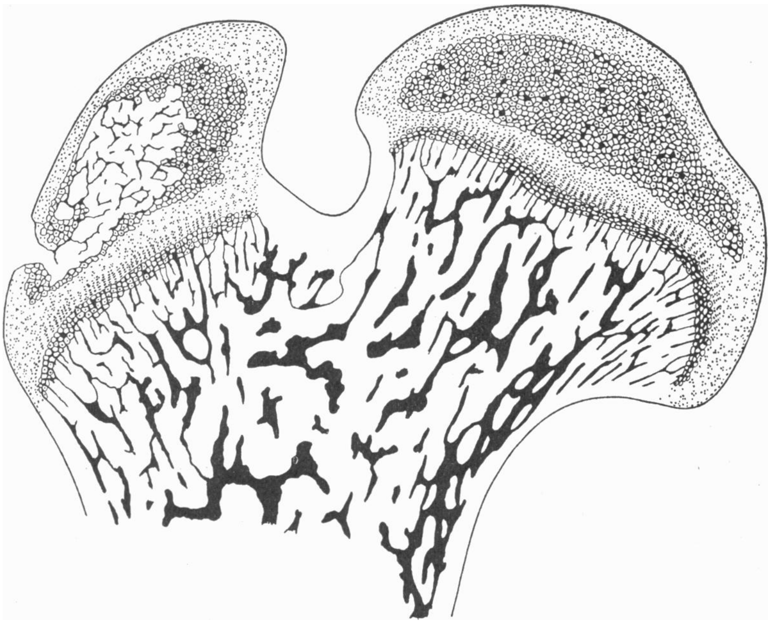

Fig. 13. Section of the upper end of the femur of a rat aged four weeks.

actually occur is shown by Parsons' figures of a deerlet in which numerous communicating canals are shown in an epiphysis in which there is already a well-developed centre of ossification. It is probably these structures which have given rise to the misconception that osteogenic buds grow up from the shaft into the epiphysis, giving rise to the centre of ossification.

EPIPHYSIAL OSSIFICATION WITHOUT CARTILAGE CANALS

This section deals with a type of epiphysial ossification which is fundamentally different from that already described. It is introduced into this paper because by its contrast with more familiar processes light is thrown on the functions of cartilage canals.

Fig. 13 shows the upper end of the femur of a young rat. The head is still completely cartilaginous, though the centre for the great trochanter has already appeared, a reversal of the sequence found in most Mammals.

In the head a large cap of calcified cartilage divides the hyaline cartilage into a covering of articular cartilage and a metaphysial plate of growing cartilage. The great trochanter also shows a mass of calcified cartilage, but in this case the mass is eroded by young bone marrow. This marrow communicates with the perichondrium at only one point, through which passes its whole vascular supply, indicating that ossification has been brought about by a single osteogenic bud from the perichondrium. There are no cartilage canals.

This kind of epiphysial ossification can best be compared to the ossification of the primary centres of the shafts of the long bones in other animals. In the large mass of calcified cartilage formed before ossification occurs, in the absence of cartilage canals, and in the activity of a single osteogenic bud, epiphysial ossification in the rat resembles primary ossification in the larger animals.

Having studied this example, which proves that an epiphysis can develop and ossify without the formation of cartilage canals, we may now proceed to discuss the functions of the canals where they do occur.

THE FUNCTIONS OF CARTILAGE CANALS

The earlier workers held that the function of the cartilage canals was the formation and nutrition of bony epiphysial centres, although it was well known that they are present in the cartilage long before ossification occurs. Todd (12) criticised this point of view by showing that ossification does not occur primarily along the course of the canals, but he suggests no other function for the canals.

I have already brought evidence to prove that there is no intimate connection between the formation of canals and ossification, quoting both the human first metatarsal, where the canals occur at the distal end but are not followed by ossification, and the rat where ossification occurs but is not preceded by the formation of canals. The primary function of cartilage canals must, I think, be studied in epiphyses which are still in the cartilaginous stage.

Every large block of cartilage has its cartilage canals: no small block has them. In Man, for example, all epiphyses are provided with cartilage canals; whereas in the rat there are no canals. In Man the thin cartilages of the larynx have no canals; whereas in the ox, whose larygngeal cartilages are thick, there is a rich canal system. The primary function of cartilage canals is therefore the nutrition of cartilages too large to be supplied by diffusion of nutriment through their substance.

As already mentioned, Parsons has suggested that lack of nutriment leads to calcification of cartilage. In supplying this nutriment the canals prevent the occurrence of premature calcification. Thus their presence retards rather than hastens the onset of ossification.

The structure of the contents and walls of the canals is exactly similar to that of the perichondrium and the cartilage underlying it, so that the two structures might be expected to have similar functions. Apart from nutrition the most important function of the perichondrium is the addition of new cartilage cells to the growing epiphysis. This has been shown to occur in the case of the canals, if my interpretation of the observations made by Stump, as given above, is correct. How important this contribution to new cartilage formation may be, I have no means of judging.

Thus the primary function of the canals is that of nutrition. They are not necessary to epiphysial ossification, for in the rat ossification takes place without them. Where they do occur the part they play in epiphysial ossification has already been described.

SUMMARY

The anatomy of cartilage canals as restored by reconstruction from serial sections is described in detail. The various types found before a centre of ossification appears in the epiphysis, are distinguished as:

1. *Simple canals, branched and unbranched,* which project into the cartilage and end blindly.
2. *Double and multiple rooted canals,* arising by two or more roots which join within the cartilage and thereafter behave as do the simple canals.
3. *Tunnel canals,* which pass straight through a projection of the cartilage, from one side to the other.
4. *Divided canals,* which break up into two or more branches, which then rejoin to form a single canal.
5. *Communicating canals,* which enter the cartilage from the perichondrium and end in the bone marrow of the shaft.

After the centre of ossification has appeared in the epiphysis, these canals are found:

6. *Nutrient canals,* which supply the epiphysis from the perichondrium, and
7. *Centrifugal canals,* which arise from the bony centre itself but otherwise behave as do simple canals.

These canals may be found in all large cartilages, but not in small cartilages such as the epiphyses of the rat.

The successive stages in the development of cartilage canals are described and a *theory of inclusion* advanced to account for the facts discovered. It is argued that the canals are portions of the perichondrial connective tissue, and blood vessels engulfed in the growing cartilage, rather than structures which have grown into the cartilage by solution of its matrix.

The functions of cartilage canals and the effects of their presence, deduced from the anatomical data, are:

1. They carry nutriment into the interior of blocks of cartilage too large to be supplied by diffusion through their substance, thereby allowing the cartilage to grow, and preventing early calcification or death. This is the primary function, other effects being secondary or incidental.

2. They are responsible for new cartilage cells being added to the epiphysis.

3. They determine when present the position of the centre of ossification within the cartilage. They provide the tissues for the formation of both the bone and the marrow of the epiphysial centre. They carry a blood supply to the epiphysial centre while it is still surrounded by cartilage.

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