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The patterns of cartilage canals

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INTRODUCTION

The presence of blood vessels in cartilage was first reported in the eighteenth century by William Hunter (1743). In his investigations of synovial joints in man, Hunter demonstrated 'the Vessels of the true cartilaginous Substance' by 'the Art of filling the vascular System with a [coloured] liquid Wax'. It was not possible to demonstrate the vessels in adult subjects, but 'In very young Subjects, after a subtle Injection, they are very obvious....The larger Vessels which compose the vascular Circle plunge in by a great Number of small Holes and disperse themselves into Branches between the Cartilage and Bone. From these again there arises a Crop of small short Twigs, that shoot towards the outer Surface; and whether they serve for nourishing only, or if they pour out a dewy Fluid, I shall not pretend to determine.'

Almost a century later, Weber (1827) reported the presence of blood vessels in human costal cartilages. He observed them in freehand sections of human newborn and adult costal cartilages, and noted that the blood vessels were rendered visible to the unaided eye by the red blood cells contained within them. The term 'cartilage canals' was first used to describe the vascular pathways in cartilage by Howship in 1815 (Watermann, 1961), although Bidder (1906) claimed that Miescher originated the term in 1836.

In practically every decade from Weber's time onwards several reports were published of investigations wholly or partly concerned with the cartilage canals, and a voluminous literature on the subject accumulated (see, for example, Schaffer, 1930, and the more critical review by Hintzsche, 1927). Despite this extensive literature, present-day textbooks of microscopic anatomy in the English language persist in describing cartilage as an avascular tissue (e.g. Copenhaver & Johnson, 1958) or as a tissue through which blood vessels may incidentally pass on their way to some other tissue or organ (e.g. Foster, 1962; Ham & Leeson, 1961; Bloom & Fawcett, 1962). However, the possession of blood vessels by some relatively large masses of cartilage for their own nutrition is categorically stated by Le Gros Clark (1958). It is also appropriate to recall Weber's words (1827): 'so scheinen viele Anatomen zu voreilig allen Knorpeln rothes Blut abgesprochen zu haben', a criticism that remains largely valid today, almost a century and a half later.

Descriptions of the overall pattern of the vascular canals in particular cartilages have been few and contradictory, and mainly confined to temporary cartilages in the human subject. The methods used to investigate overall pattern may be classified in four groups: (i) The blood vessels have been injected with a radio-opaque material and radiographs of the selected cartilage taken either during the injection or after its completion. This technique, already in use more than half a century ago by

Lexer, Kuliga & Turck (1904), has been used in recent years by Trueta (1957), Brookes (1958), Tilling (1958) and Haraldsson (1962). (ii) The blood vessels have been injected with a visually opaque material, the injected cartilage rendered transparent by fixation, dehydration and clearing, and examined with a stereoscopic microscope by transmitted light (Bertrand, 1923; Harris, 1929; Trueta, 1957). (iii) The cartilage has been fixed, embedded in paraffin wax and serially sectioned, and, from the sections, a three-dimensional model reconstructed (Hintzsche, 1927; Haines, 1933; Hurrell, 1934). (iv) Random sections have been examined histologically. This method is evidently inadequate and all descriptions of the overall pattern based on it may be dismissed as conjectural (e.g. Langer, 1876; Bidder, 1906; Stump, 1925). Only observations based on one or more of the first three methods are described below.

Lexer *et al.* (1904) described the blood vessels in human late foetal and postnatal temporary cartilages. These vessels ran parallel to the junction of epiphysis* and growth disc and turned at right-angles to traverse the growth disc and enter the metaphysis; others entered the growth disc from the metaphysis. Bertrand (1923) stated that the junctional area of epiphysis and growth disc in human late foetal long bones was particularly well vascularized, but no blood vessels were present in the disc itself. The region where the secondary centre of ossification was expected to develop was also well vascularized. The vascular canals did not anastomose with one another. Hintzsche (1927) described numerous blood vessels entering the human lower femoral epiphysis and directed at first towards a horse shoe-shaped region within the epiphysis that showed histological evidence of degenerative changes. The site of the future secondary centre was avascular, but avascular areas of similar size and larger were present elsewhere in the same epiphysis. Branching of the vessels was always dichotomous. Harris (1929) stated that, in healthy growing animals, the growth disc was avascular. Haines (1933), in a study of various human and animal cartilages, claimed that all blood vessels in the growth disc entered it from the epiphysis, none entering from the metaphysis. The site of the future secondary centre was evident as an avascular lamina between two or more groups of vascular canals.

Hurrell (1934) was unable to observe a constant canal pattern in any cartilage of the limbs in a series of human foetuses of different ages, or even in foetuses of similar age. Trueta (1957) described three groups of blood vessels in the cartilaginous human femoral head shortly after birth: an inferior, which took origin from the metaphysis and traversed the growth disc; a supero-lateral, from the lateral aspect of the neck; and a medial, from the ligamentum teres; shortly before the secondary centre of ossification was due to appear, a change was observed in the relative importance of these groups. Brookes (1958) described the vascular canals of cartilaginous human femoral and tibial epiphyses. In the femoral head there were upper and lower main groups, and a variable medial group along the ligamentum teres. In the lower femoral epiphysis there were medial, lateral, intercondylar and supra-patellar groups. In both the upper and the lower tibial epiphyses the vascular canals tended to converge centrally from many points on the circum-

* The term 'epiphysis' and other related terms, as used in this paper, are defined at the beginning of the section headed Observations.

ference. According to Brookes the growth disc was vascularized exclusively from the metaphysis. Tilling (1958) dealt mainly with bony epiphyses, but one of his radiographs showed the lower end of the femur of a bovine foetus following injection of radio-opaque material into the nutrient artery. None of this material was visible in the cartilaginous lower femoral epiphysis and growth disc. Haraldsson (1962) stated that in human postnatal upper limb epiphyses the vascular canals did not anastomose with one another; the site of the future secondary centre showed the richest vascularization, but the growth disc was avascular.

The literature thus contains a number of observations, not always in agreement with one another, on isolated details of canal pattern in various mainly human cartilaginous epiphyses. As regards overall canal pattern, and especially internal distribution, the information is meagre and essentially confined to the incomplete data of Trueta (1957) and Brookes (1958) in exclusively human material. No comparative studies have been reported.

It appeared desirable, therefore, that a detailed study be made of the overall pattern of the vascular canals in a selected cartilaginous element, with particular reference to internal distribution; that the development of the pattern be followed in a series of specimens of increasing age; and that the patterns be compared in the homologous cartilage of a number of different species.

The cartilaginous element selected was the unossified upper end of the developing tibia, and vascular canal patterns at this site were studied in the sheep, goat, cat, rabbit and man at the appropriate stages of development. In these species the vascular canals were present for a considerable period of time before the epiphysis developed its centre of ossification. Specimens were also examined from the rat, in which species the initial appearance of vascular canals in a cartilaginous epiphysis was accompanied or immediately followed by the changes leading to formation of a secondary centre of ossification. Specimens from goat and sheep foetuses received the most detailed study, partly because the foetuses were available in quantity in Jamaica all the year round, partly because their size facilitated the injection technique employed.

MATERIAL AND METHODS

The material consisted of over 40 sheep foetuses in the range 50–200 mm. C.R.; over 40 goat foetuses in the range 50–200 mm. C.R.; 20 foetal and neonatal cats in the range 70 mm. C.R. to 5 days postnatal; 15 foetal and neonatal rabbits in the range 70 mm. C.R. to 1 day postnatal; 14 human foetuses in the range 50–250 mm. C.R.; and 3 litters of rats, from each of which one rat was taken every day from the 5th to the 10th day postnatal inclusive, a total of 18 rats.

Most of the foetuses were injected by a method based on that described by Davies & Edwards (1948). The blood vessels were first washed through with physiological saline containing either 4% sodium citrate or heparin 1 i.u./ml. until the superficial veins of the lower limb appeared free of blood. In the smaller specimens the washing solution was injected via an umbilical artery, in the larger specimens via the descending aorta after incising the right atrium and/or inferior vena cava. The specimen was then covered with wet cotton wool and left overnight at room temperature, but if subsequent injection was likely to be delayed beyond the

following day the specimen was refrigerated until required and then allowed to warm slowly to room temperature. At the desired time 5–10% India ink was added to single or double strength plasma and, after filtering through cotton wool, the mixture was injected via the umbilical artery or the aorta or, in the larger specimens, via the common or external iliac artery. The pressure used varied from 10 cm. water in the youngest specimens to 15 cm. mercury in the oldest. The injection was allowed to run overnight, and just before it was discontinued the pressure was slowly raised 25–50% for up to 1 hr.

The postnatal animals were killed by a blow on the head or an overdose of nembutal, and the washing solution (see above) was injected into the left ventricle while the heart was still beating. Subsequent treatment was the same as for the foetal specimens. Other specimens, both foetal and postnatal, were injected with undiluted India ink or with a saturated aqueous solution of Prussian blue. These were usually injected from a syringe using moderate thumb pressure, and the injection rarely lasted more than ten minutes. A few attempts were made to inject coloured gelatine preparations, but they proved consistently unsuccessful and were therefore abandoned.

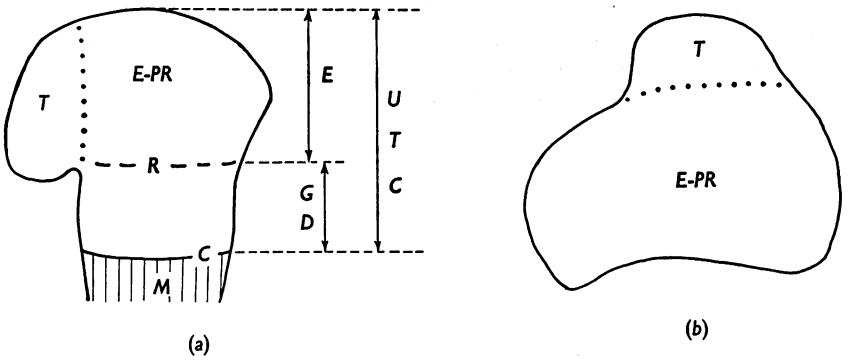
Following injection, the lower half of each animal was placed in 10% formalin or preferably 95% alcohol, and the skin was removed from the region of the knee. After fixation overnight the upper third of the tibia was dissected out and refixed for a further period, bleached in 25% aqueous or alcoholic hydrogen peroxide, dehydrated slowly through graded alcohols, cleared initially in benzene and then in a mixture of 5 parts methyl salicylate with 3 parts benzyl benzoate, and stored in the dark in the latter mixture.

Each specimen, immersed in the storage liquid, was dissected under a binocular dissecting microscope. After removal of muscle tags and ligaments the periosteum was gently peeled towards the cartilage in strips; by this method the perichondrium was removed without detaching pieces of cartilage with it. The specimen now appeared as a transparent white or yellow mass of cartilage continuous with a dense opaque cylinder of bone. The transparent cartilage was cut away from the opaque bone with one sweep of a razor blade at the junction of the two parts, if necessary with the aid of the microscope for the smaller specimens. The freed cartilage could now be stood upright on its flat cut surface, and turned to any desired angle for more detailed examination.

Camera lucida drawings were made of some of the injected sheep tibias. For this purpose each specimen, immersed in the storage fluid, stood unaided on its cut (inferior) surface while the drawing was made. In making the drawing the relative positions of the canals in depth, and their communications (if any) with others, could be checked throughout by suitably turning the whole specimen; the flat cut surface ensured that the initial orientation could always be regained.

OBSERVATIONS

Nomenclature. The nomenclature of the parts of a growing long bone is confusing, as different names have been given by different authors to one and the same part. It is necessary therefore to define some of the terms used in the description which follows (Text-fig. 1).



Text-fig. 1. Diagrams of the upper end of the developing tibia to illustrate the nomenclature employed; (*a*) sagittal section, (*b*) transverse section at the level of the tibial tubercle. *C*, Zone of calcified cartilage; *E*, epiphysis; *E–PR*, epiphysis proper; *GD*, growth disc; *M*, metaphysis; *R*, zone of reserve (mitotic) cells; *T*, tibial tubercle; *UTC*, upper tibial cartilage.

(1) The entire upper end of the tibia from the superior articular surface down to, but not including, the metaphysis is referred to as *the upper tibial cartilage*. It consists of two parts, *the epiphysis* forming the upper part and *the growth disc* forming the lower part (see below).

(2) *The epiphysis* is that part which extends from the superior articular surface as far as, but not including, the zone of reserve cells which give rise, by mitoses, to the cell-columns leading to the metaphysis.

(3) *The growth disc*, or more simply *the disc*, is that part which extends from the zone of reserve cells, described above, to the zone of hypertrophic cartilage cells and calcified cartilage matrix immediately adjacent to the metaphysis; and it includes both zones. This term is preferable to 'epiphysial disc' and 'epiphysial cartilage' since the part specified acts as a growth mechanism for the diaphysis, not for the epiphysis.

(4) Since the tibial tubercle forms a small part of the epiphysis, the remaining larger part of the epiphysis may be called *the epiphysis proper*.

(5) While the epiphysis remains entirely cartilaginous, it may be called *the cartilaginous epiphysis*. After the secondary centre of ossification appears, the term *bony epiphysis* is applicable.

(6) The terms *canalized* and *vascularized*, when they refer to the upper tibial cartilage, are used synonymously since only vascularized canals were demonstrated by the techniques employed.

Technical note. About one-third of all injections were unsuccessful, and these specimens were discarded. Rather less than one-third were fully injected. In the remainder, a partial injection was obtained; these specimens were useful for comparison of their well-injected regions with the relevant parts of the more successful specimens. In some, the course of poorly injected canals could be followed for a variable distance owing to their content of scattered particles of India ink, while in other specimens a line of altered refractility indicated the course of a non-injected canal.

Specimens fixed in formalin were more transparent and colourless and more pleasing to the eye than specimens fixed in 95% alcohol, but they were also much more easily damaged during manipulation. On the whole the mixture of India ink and plasma gave more complete filling of the vessels than either Prussian blue or undiluted India ink.

Goat

The central and greater part of the epiphysis was vascularized by a series of blood vessels that entered the epiphysis at intervals along a transverse line immediately above and behind the tibial tubercle deep to the patellar tendon (Pl. 1, fig. 1). They were distributed within the epiphysis proper in four to eight separate canals. In some specimens only a single group of blood vessels was present; at the middle of the transverse line mentioned above, the vessels entered a single canal which at once bifurcated into medial and lateral divisions, and from them four to eight separate canals were given off as before. The course of these canals was directed at first backwards and slightly downwards, then in the dorsal half of the epiphysis they curved sharply downwards towards or into the growth disc (Pl. 1, figs. 2, 5). Except in the smallest specimens one or two canals turned downwards almost at once in the ventral part of the epiphysis proper, and continued towards or into the disc. Those that did not enter the disc ended blindly within the epiphysis.

These vascular canals were distributed in approximately the central two-thirds of the epiphysis proper (Pl. 1, figs. 3, 4). The remaining peripheral parts were vascularized by smaller vessels that entered the epiphysis proper at numerous points on its medial, lateral and dorsal surfaces (Pl. 1, figs. 3, 4); and in addition a few branches entered its ventral surface from the main vascular canal of the tubercle, *q.v.* (Pl. 1, fig. 5). These peripheral vessels were generally directed towards the nearest branches of the central group described above. After a relatively short course within the epiphysis proper most of them ended blindly, a minority proceeded downwards to enter the growth disc.

Blood vessels entered the tubercle from about the centre of the transverse line of entry, and ran forwards and downwards in a canal that was distributed throughout the greater part of the tubercle (Pl. 1, fig. 5). In addition, several short marginal canals originated at the ventral surface of the tubercle and conveyed blood vessels inwards to a narrow region adjacent to the ventral perichondrium (Pl. 1, fig. 6). The short marginal canals ended blindly within the tubercle, as did most branches of the main canal; a few of the latter, however, ran backwards into the ventral part of the epiphysis proper, as described above, and either ended blindly there or continued downwards into the growth disc.

The growth disc derived its vascular canals exclusively from those of the epiphysis (Pl. 1, figs. 4, 5, 7). The great majority were branches of the canals that originated at the transverse line of entry, a few were branches of the peripheral canals (Pl. 1, fig. 9), and an occasional one was derived ultimately from the main canal of the tubercle via a branch given into the epiphysis proper (Pl. 1, fig. 5). From the epiphysis they entered the growth disc perpendicularly, i.e. parallel to its proximo-distal axis. In the younger specimens these vascular canals ended blindly in the growth disc; in the older specimens they made contact distally with the metaphysis

(Pl. 1, figs. 4, 5, 7, 9), but whether continuity was established between the blood vessels of the canals and those of the metaphysis could not be determined. No blood vessels entered the growth disc directly from its own perichondrial surface, nor did any enter its distal surface from the metaphysis and terminate blindly either in the disc itself or in the epiphysis after traversing the disc.* One specimen (Pl. 1, figs. 9, 10) was exceptional in the latter respect, it showed two vascular canals in contact distally with the metaphysis and extending proximally for a short distance before ending blindly in the growth disc.

From all but the shortest canals in the epiphysis branches were given off in various directions, and these divided and subdivided to produce a highly complicated pattern of vascular canals (Pl. 1, figs. 3, 4, 7–10). Branching occurred most frequently at or near the junction of epiphysis and growth disc, so that this junctional region was more richly vascularized than any other part of the cartilage (Pl. 1, figs. 4, 7). Apart from this, no other area was particularly well or poorly vascularized. The details of the pattern were extremely variable, no two specimens were exactly alike, nor even right and left sides of the same foetus. On the other hand, in all specimens the canals were arranged in well-defined groups, each with its own fairly constant area of distribution. Four canal-groups, central, peripheral, main tubercular and marginal tubercular, were distinguished (Text-fig. 2).

(i) The central group comprised those canals that originated at the transverse line of entry and ramified in the central and major portion of the epiphysis proper and in the corresponding part of the growth disc.

(ii) The peripheral group comprised those canals that originated at the lateral, medial, dorsal and ventral surfaces of the epiphysis proper and ramified in the peripheral parts of epiphysis proper and growth disc, i.e. the region between the outermost branches of the central group and the surface of epiphysis proper or growth disc respectively.

(iii) The main tubercular group, consisting of a single canal, originated at the transverse line of entry and ramified in the central and greater part of the tubercle.

(iv) The marginal tubercular group included those canals that originated at the ventral perichondrial surface of the tubercle, and sometimes at its dorsal surface also, and were distributed within the narrow areas between these surfaces of the tubercle and the nearest branches of the main tubercular group.

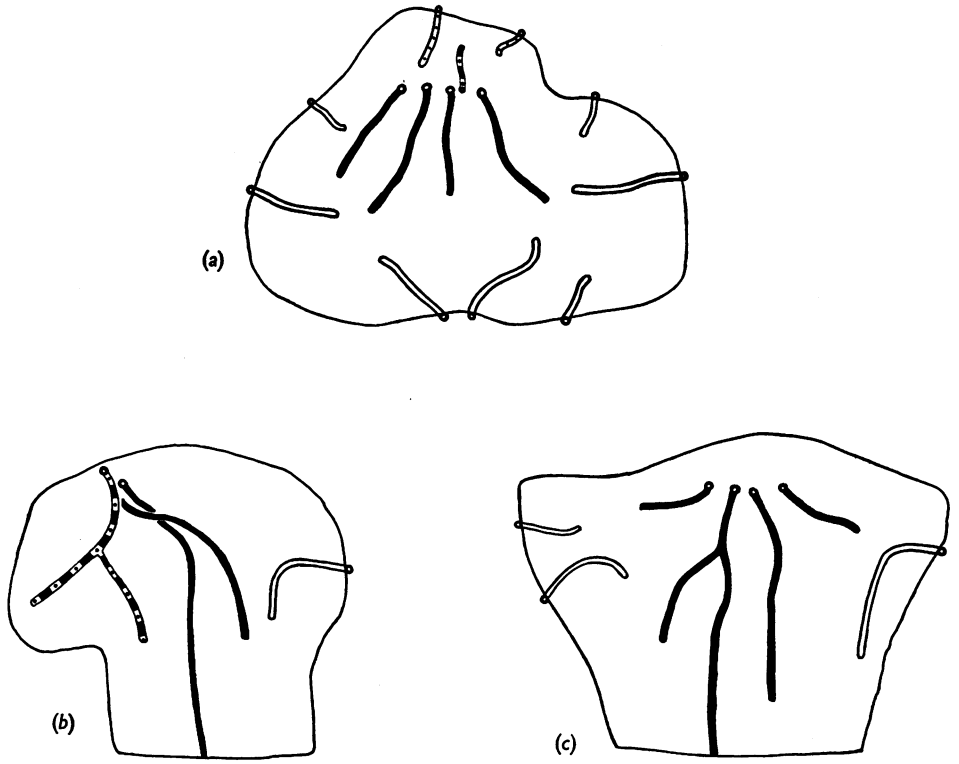
In the growth disc the canals were also observed to branch (Pl. 1, figs. 4, 8), but the branches were few and arranged in a regular manner. Diverging at first from the parent canal they soon turned parallel to it and continued towards the metaphysis. No branch ran a recurrent course, i.e. proximally towards or into the epiphysis.

The manner of branching of the canals varied (Pl. 1, figs. 7–10). In some instances it was dichotomous, in others monopodial, but in the majority of canals in all specimens it was irregular. Anastomoses were occasionally observed between two canals belonging to the central group in the epiphysis proper. They were never observed between the members of any other group, not between members of

* A canal that entered the growth disc from the metaphysis and did *not* end blindly, i.e. it anastomosed with a branch of an epiphysial canal, could not be distinguished from a canal that entered the growth disc from the epiphysis and reached the metaphysis.

two different groups. In the growth disc the canals did not anastomose with one another.

The pattern of canalization developed in a definite sequence. At first only the central group was represented (Pl. 1, fig. 1), as a single row of canals with few or no branches. Soon afterwards these canals were observed in two parallel rows, one behind the other (Pl. 1, fig. 2), and the branches were more numerous. At this stage representatives of the peripheral group were present, and the principal canal



Text-fig. 2. Scheme of basic canal-pattern in upper tibial cartilage of the goat, (*a*) from above, (*b*) from the side, and (*c*) from the front of the epiphysis proper. Solid black = central group, open = peripheral group, dot-and-dash = main tubercular group, dotted = marginal tubercular group.

to the tubercle began to develop. Of the peripheral group the canals situated dorsally appeared first, then those medially and laterally, and finally the ventral members. The marginal tubercular canals were the last to develop. Within the growth disc the canals first were observed in its central parts (Pl. 1, figs. 5, 7) and, as the number of canals in the disc progressively increased, the more central canals extended further towards the metaphysis than those situated more peripherally. The former also made contact with the metaphysis at an earlier stage.

Sheep

Most of the epiphysis was supplied by blood vessels which entered at a small circumscribed area immediately above the tibial tubercle deep to the patellar tendon (Text-fig. 4). This principal site of entry was single in the smaller specimens, single or double in the larger specimens. From this site the blood vessels were distributed within the epiphysis proper by three central canals, named dorsal central, ventro-lateral central, and ventro-medial central in accordance with the general areas in which they ramified.

The dorsal central canal proceeded straight backwards within the epiphysis proper, and just over half way to the dorsal surface of the epiphysis it bifurcated into widely diverging medial and lateral divisions, which ended blindly. When the principal site of entry was double (Text-fig. 4*e*) there was, in addition, an accessory central canal lying adjacent and parallel to the dorsal central canal on its lateral side. In some specimens these two canals communicated close to their origin. The accessory central canal turned laterally in front of the lateral division of the dorsal central canal and, like the latter, terminated blindly.

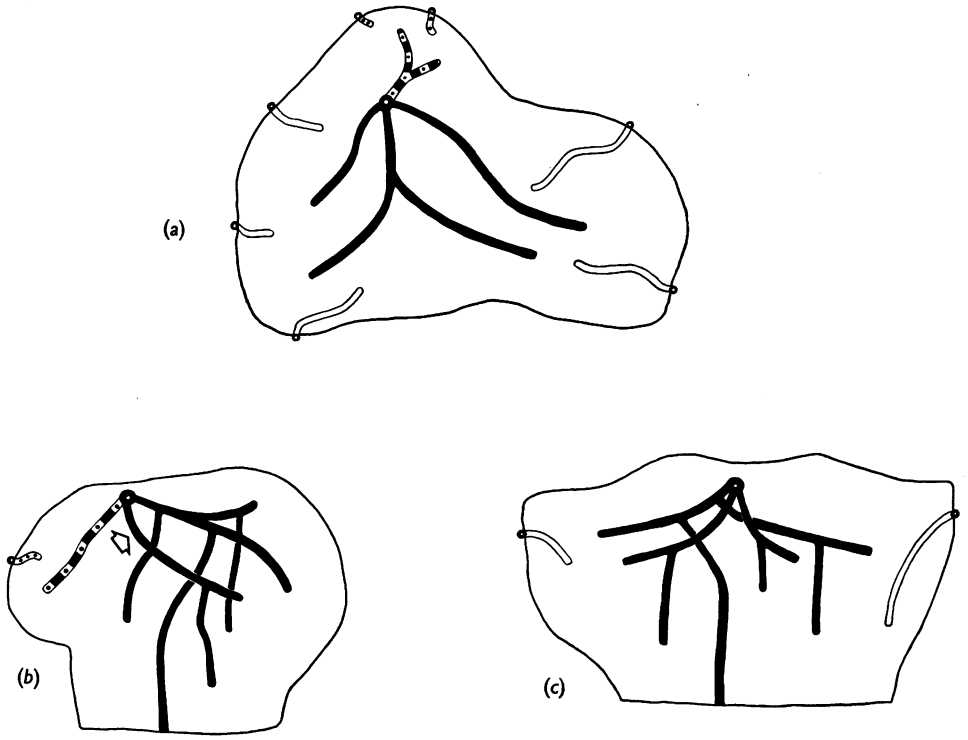
The ventro-medial and ventro-lateral central canals proceeded from the principal site of entry dorso-medially and dorso-laterally respectively. In contrast to the dorsal central canal they ran at first downwards and then turned parallel to the junction of epiphysis and growth disc, so that the greater part of their course lay on a deeper plane than the dorsal central canal. The exact plane could not be determined without histological examination, but it appeared to be at or near the junction of epiphysis and growth disc. These canals extended for half to two-thirds of the distance to the dorso-medial or dorso-lateral surface of the epiphysis before ending blindly.

In addition to the central canals, smaller peripheral canals penetrated the epiphysis proper from a number of sites at its circumference. The numerous circumferential sites were on the medial and lateral surfaces of the epiphysis proper and the immediately adjacent parts of the dorsal surface. None was observed on the central two-fourths of the dorsal surface, while ventrally the canal-system of the tubercle did not contribute any branches to the epiphysis proper. After a short course within the epiphysis, more or less at right-angles to the surface at their point of entry, most of the peripheral canals ended blindly, but a few continued down into the growth disc.

The tubercle was vascularized chiefly via a canal that originated independently at the principal site of entry and ran downwards and forwards into the tubercle. In some specimens it arose in common with the ventro-medial or the ventro-lateral central canal. In these cases the combined stem was very short and the two canals soon diverged. The canal to the tubercle was distributed throughout its extent, apart from a limited area subjacent to the perichondrium; the latter was vascularized through a small number of short marginal canals that arose at the ventral surface of the tubercle. The tubercle did not receive any branches from canals in the epiphysis proper.

The growth disc derived its vascular canals exclusively from those of the epiphysis (Pl. 2, fig. 11). None originated from the perichondrial surface of the growth disc

itself or from the metaphysis. From the epiphysis, branches of the central canals and some of the peripheral canals entered the proximal surface of the growth disc perpendicularly. In the younger specimens they ended blindly in the disc; in the older specimens they reached the metaphysis (Pl. 2, fig. 11), but it could not be determined whether continuity was established between their blood vessels and those of the metaphysis.



Text-fig. 3. Scheme of basic canal-pattern in upper tibial cartilage of the sheep, (*a*) from above, (*b*) from the side, (*c*) from the front of the epiphysis proper. Solid black = central group, open = peripheral group, dot-and-dash = main tubercular group, dotted = marginal tubercular group. For greater clarity in (*b*) the ventro-medial and ventro-lateral central canals were regarded as exactly superimposed and therefore represented as a single canal (open arrow).

All but the shortest canals in the epiphysis branched repeatedly in various directions to produce a highly complicated pattern. The junction of epiphysis and growth disc was particularly richly vascularized owing to the increased frequency of branching at that level. Other areas were vascularized to a similar extent. As in the goat, no two specimens were completely alike, but in all of them the canals were arranged in four well-defined groups: central, peripheral, main tubercular and marginal tubercular, each with its own fairly constant area (Text-fig. 3).

(i) The central group originated at the principal site of entry and ramified in the central and major part of the epiphysis proper and in the corresponding part of the growth disc.

(ii) The peripheral group comprised all those canals that originated at the medial, lateral and dorsal surfaces of the epiphysis proper and were distributed in the peripheral area between the outermost branches of the central group and the surfaces of epiphysis proper and growth disc.

(iii) The main tubercular group, consisting of a single canal, entered the tubercle from the principal site of entry and ramified throughout the tubercle except for a small area near the ventral surface.

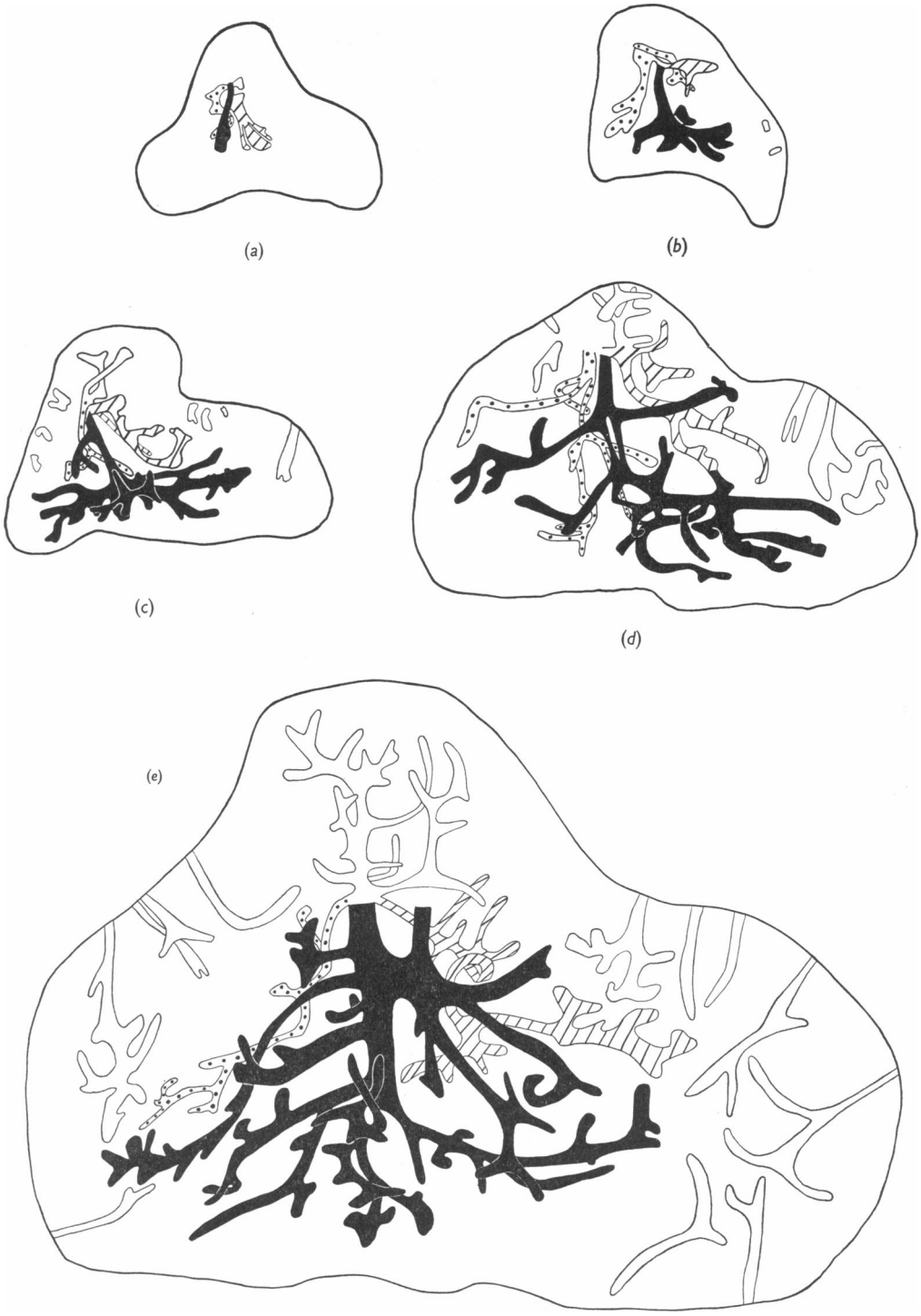
(iv) The marginal tubercular group consisted of several small canals that originated at the ventral surface of the tubercle and ramified in the narrow area between the ventral surface of the tubercle and the nearest branches of the main tubercular canal.

In the growth disc branching of canals was infrequent. The branches ran distally, at first diverging from the parent canal but then turning parallel to it. None of the branches ran a recurrent course into the epiphysis.

As in the goat, the manner of branching was irregular. Anastomoses were observed only in the epiphysis, and then only between two canals of the central group.

The canal pattern developed in a definite sequence (Text-fig. 4). At first a single short canal entered the epiphysis at the principal site of entry. Shortly afterwards the three canals forming the central group were observed, the dorsal central canal at this stage undivided (Text-fig. 4*a*). The peripheral group appeared next, first laterally and then medially, and at all subsequent stages the lateral canals were more numerous and on the average longer than the medial canals. The dorsal central canal showed terminal bifurcation (Text-fig. 4*b*). The main tubercular canal now developed (Text-fig. 4*c*), and branches of the central group reached the growth disc. The marginal canals of the tubercle were the last to appear (Text-fig. 4*d*). As in the goat, the more central parts of the growth disc received vascular canals at an earlier stage than its more lateral parts, and the central canals reached the metaphysis earlier than the lateral ones.

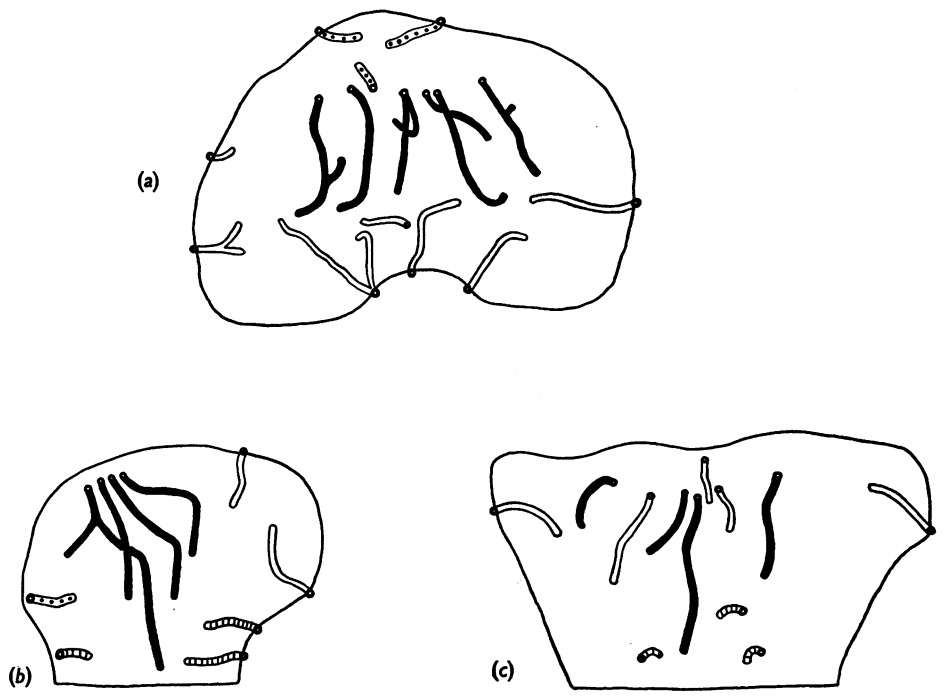
The above description was based on specimens of black-faced mountain sheep obtained in Northern Ireland. Specimens of grey-faced Suffolk sheep obtained in Jamaica showed the following minor but consistent differences: (i) The three central canals tended to lie in the same transverse plane. (ii) The dorsal central canal was the predominant member of the central group. One of the two other members of this group was frequently poorly developed, and sometimes both were so poorly developed, that the dorsal central canal was distributed over practically the entire central area. (iii) The principal site of entry often consisted of two or three adjacent sites of entry, each site giving origin to one or two members of the central group. (iv) The peripheral group included a number of canals which originated from the dorsal surface of the epiphysis in its central two-fourths as well as its marginal fourths. (v) The principal tubercular group consisted as a rule of two canals rather than a single canal, and frequently gave branches to the epiphysis proper and received branches from the canals in it. In all other respects the canal patterns were closely similar.



Text-fig. 4. Camera lucida drawings of injected-cleared upper tibial cartilage, viewed from above, in foetal sheep, showing the development of the vascular canal pattern. (*a*) 65 mm. C.R. length; (*b*) 85 mm. C.R. length; (*c*) 95 mm. C.R. length; (*d*) 125 mm. C.R. length; (*e*) 200 mm. C.R. length. (*a*)–(*d*) × 18, (*e*) × 14. Solid black = dorsal central canal, dotted = ventro-medial central canal, hatched = ventro-lateral central canal.

Cat

The central parts of the epiphysis were supplied by blood vessels that entered at a number of points along a transverse line immediately above the tibial tubercle deep to the patellar tendon (Pl. 2, fig. 12). The canals containing these vessels were arranged in two fairly well-defined sets, a smaller ventral and a larger dorsal, containing approximately equal numbers of canals. Both sets proceeded downwards and somewhat backwards in the ventral half of the epiphysis proper, and then downwards into the growth disc.



Text-fig. 5. Scheme of basic canal-pattern in upper tibial cartilage of the cat, (*a*) from above, (*b*) from the side, (*c*) from the front of the epiphysis proper. Solid black = central group, clear = peripheral group, dotted = tubercular group, hatched = direct canals of the disc.

The remainder of the epiphysis proper was vascularized via a number of canals that took origin from the medial, lateral and dorsal surfaces of the epiphysis in approximately equal numbers and ran inwards for varying distances (Pl. 2, fig. 12). In addition, one or two canals originated from the dorsal part of the superior intercondylar surface. Most of these canals ended blindly within the epiphysis proper, but some continued downwards into the growth disc.

The tubercle was vascularized through numerous short canals which arose at the perichondrial surface of the tubercle and the transverse line of entry. In a few specimens one large canal arose from the medial or lateral extremity of the perichondrial surface of the tubercle and ran transversely in it, the other canals being

correspondingly reduced. These canals generally ended blindly within the tubercle, although in some specimens branches extended into the adjacent part of the epiphysis proper.

The growth disc was vascularized chiefly from the vascular canals of the epiphysis proper (Pl. 2, figs. 13, 14), most of which continued downwards into the growth disc. In addition, a small number of canals carried blood vessels directly into the growth disc from its own perichondrial surface (Pl. 2, fig. 13). These direct canals ran more or less transversely in the disc at first, then turned distally towards the metaphysis. Occasionally one turned upwards towards the epiphysis (Pl. 2, fig. 13). All the vascular canals of the disc ended blindly within the disc itself; in only a single specimen did a vascular canal reach the metaphysis, although in several specimens ten or more canals were present in the disc.

All but the smallest canals in the epiphysis branched in various directions, but even so the pattern was much less complicated than in the ungulates. No region of the epiphysis was especially well or poorly vascularized. As in the ungulates, the details of the pattern varied from one specimen to another but, in all, the canals were arranged in four well-defined groups: central, peripheral, tubercular, direct disc, each with a fairly constant area of distribution (Text-fig. 5).

(i) The central group originated at the transverse line of entry and ramified in the ventral half or more of the epiphysis proper and in the corresponding part of the growth disc.

(ii) The peripheral group originated at the medial, lateral, dorsal, and sometimes also the ventral, surfaces of the epiphysis proper and the dorsal part of the superior intercondylar surface. This group ramified in the peripheral area between the surface of the epiphysis proper and the outermost branches of the central group, and in the corresponding area of the disc.

(iii) The tubercular group originated from the perichondrial surface of the tubercle and from the transverse line of entry, and ramified throughout the tubercle.

(iv) The direct group of the growth disc originated at the perichondrial surface of the disc itself and supplied limited areas of the disc adjacent to their sites of origin.

In the growth disc the manner of branching was similar to that observed in the ungulates, but unlike the latter many of the canals and their branches remained obliquely disposed to the proximo-distal axis of the disc (Pl. 2, fig. 14). The manner of branching of canals in the epiphysis was irregular. Anastomoses between canals were not observed in any specimen.

Rabbit

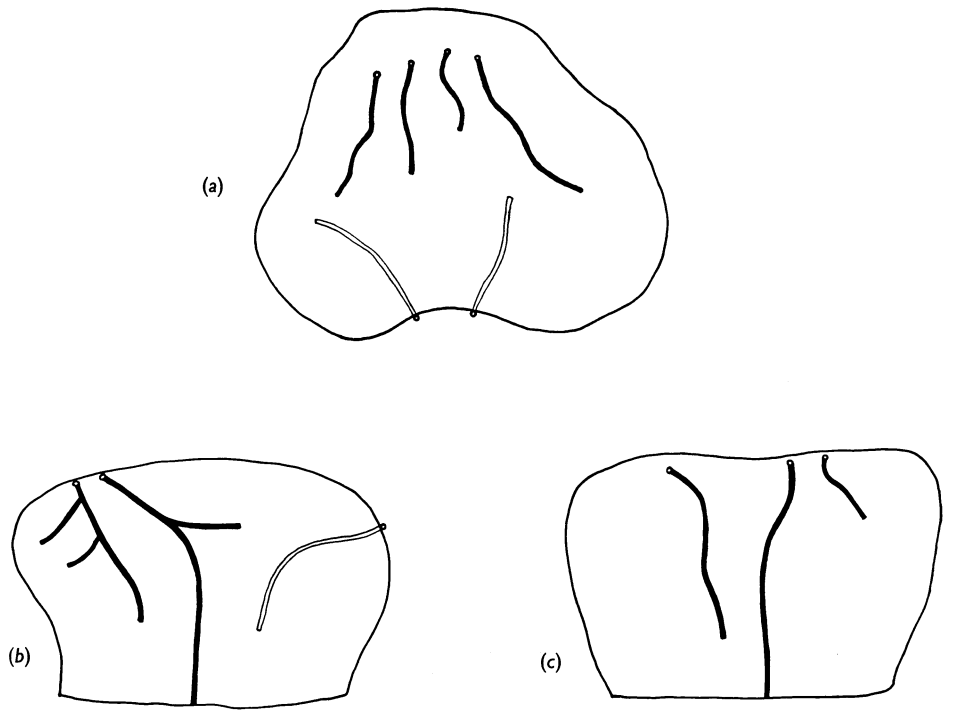
The main blood vessels to the epiphysis entered at intervals along a transverse line immediately above the tibial tubercle deep to the patellar tendon (Pl. 2, fig. 15). Three to six canals conducted them into the epiphysis proper. One or two canals ran straight down into the growth disc; the remainder at first ran dorsally, and about midway to the dorsal surface they turned downwards to enter the growth disc.

Additional canals originated from the middle two-fourths of the dorsal surface, and ended blindly in the dorsal third of the epiphysis or turned downwards into the disc.

There was usually no independent blood supply to the tubercle. Instead, the tubercle received two or three short branches from the more ventrally placed main canals.

The growth disc was vascularized exclusively from the vascular canals of the epiphysis. Most of the central and dorsal canals continued into the disc, and in the older specimens the majority reached the metaphysis.

Most of the canals in the epiphysis gave short branches in various directions, producing a simple pattern which, however, varied in its details from one specimen to the next. No region was especially well or poorly vascularized. In all specimens there were two groups of canals, central and dorsal, each with a fairly constant area of distribution (Text-fig. 6).



Text-fig. 6. Scheme of basic canal-pattern in upper tibial cartilage of the rabbit, (*a*) from above, (*b*) from the side, (*c*) from the front of the epiphysis proper. Solid black = central group, clear = dorsal group.

(i) The central group comprised the canals that originated from the transverse line of entry and ramified in the ventral half to two-thirds of the epiphysis, including the tubercle, and in the corresponding part of the growth disc.

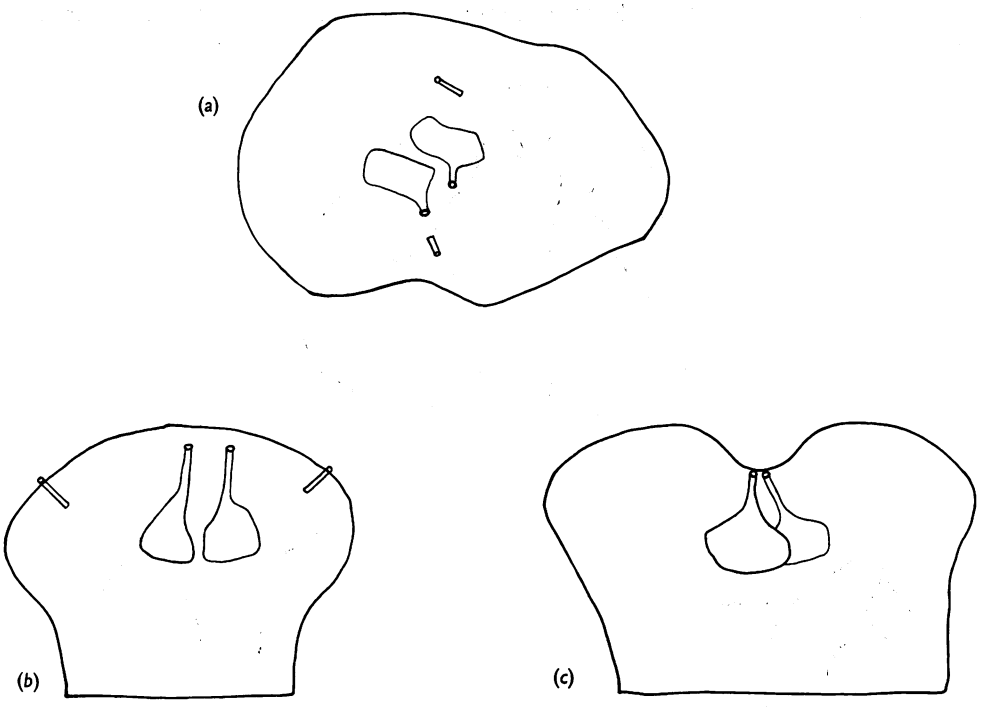
(ii) The dorsal group comprised the canals that originated from the dorsal surface of the epiphysis and ramified in the dorsal third approximately of the epiphysis and in the corresponding part of the growth disc.

Branching of canals in the disc was not observed. In the epiphysis, the manner of branching of the canals was irregular. With a single exception anastomoses between canals were not observed in any specimen.

Rat

Vascular canals were first observed in the epiphysis at the 5th or 6th postnatal day. They originated exclusively from the superior intercondylar surface, usually one to three canals from its ventral part, two larger ones from its middle, and another smaller canal dorsal to these (Pl. 2, fig. 16).

At first these separate canals ended blindly after a short course distally in the epiphysis (Text-fig. 7). About the 8th postnatal day when the two centrally placed



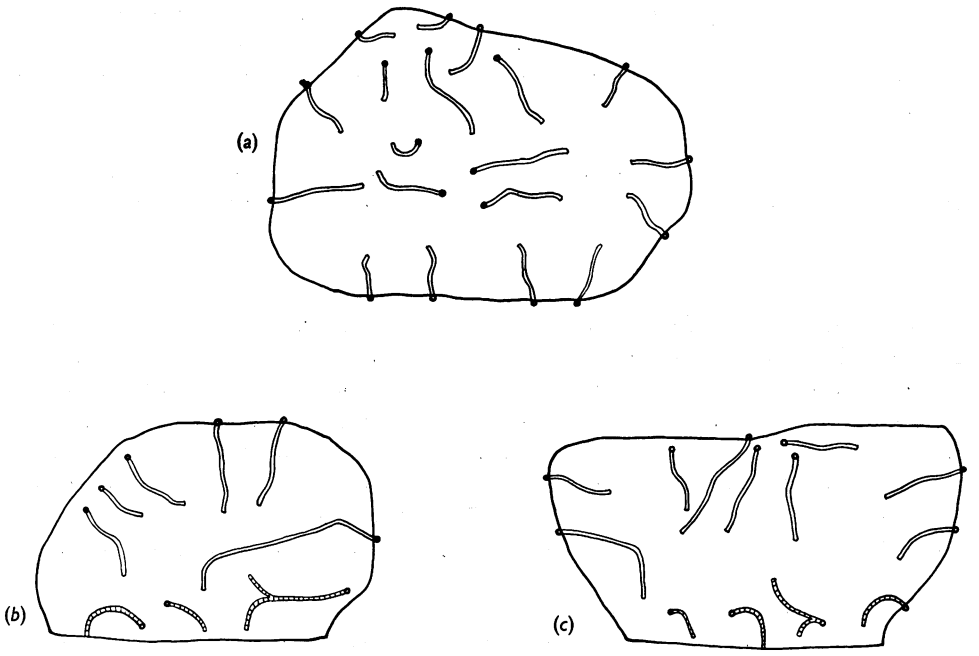
Text-fig. 7. Scheme of basic canal-pattern in upper tibial cartilage of the rat, (*a*) from above, (*b*) from the side, (*c*) from the front of the epiphysis proper.

canals had reached the middle of the epiphysis, their distal ends began to spread transversely each to its own side. By the following day they had also spread towards one another, and the two enlarged canals fused to form a single extensive vascularized region (Pl. 2, fig. 16). As the latter increased in size the smaller ventral and dorsal canals joined it, while additional canals developed from the superior intercondylar surface and also joined it.

No canals developed in the disc or the tubercle, and none originated from any site on the epiphysis other than the superior intercondylar surface. The canals did not anastomose with one another prior to their coalescence in the central region of the epiphysis. All the canals remained unbranched.

Man

The epiphysis including the tubercle was supplied by a large number of blood vessels which entered the medial, lateral, dorsal and ventral surfaces, the superior intercondylar surface, and a narrow strip just above the attachment of the patellar tendon and extending well beyond it on either side. In general the vascular canals tended to converge towards a central area situated in the lower half of the epiphysis, but marginally the ventral and dorsal canals tended to run towards one another (Pl. 2, figs. 17, 18, and Text-fig. 8). Most of the canals ended blindly within the epiphysis but some of those that originated close to the growth disc turned downwards into it.



Text-fig. 8. Scheme of basic canal-pattern in upper tibial cartilage of man, (*a*) from above, (*b*) from the side, (*c*) from the front of the epiphysis proper. Hatched = direct canals of the disc.

The disc was vascularized in part indirectly from the vascular canals of the epiphysis, as described above, but mainly by canals that originated directly from the perichondrial surface of the disc at various levels, some near the epiphysis, some very close to the metaphysis (Pl. 2, fig. 19). These direct canals ran more or less transversely at first, then turned obliquely towards the metaphysis. In the younger specimens the canals of the disc ended blindly within it, whereas in the older specimens they reached the metaphysis progressively from the central parts of the disc to its periphery. Some specimens showed direct perichondrial canals that, immediately on entering the disc, turned obliquely upwards (Pl. 2, fig. 19) and ran a recurrent course towards or into the epiphysis, and ended blindly.

Most canals in the epiphysis gave off a small number of branches which remained

close to the parent stem. They produced a simple pattern in which all the canals converged on a rectangular area, with its long axis transverse, occupying approximately the central one-fifth of the lower half of the epiphysis proper. Since the epiphysis as a whole was similarly rectangular, the pattern resulted in all canals being of the same order of length. No part of the epiphysis was especially well vascularized. The area towards which all the epiphysial canals tended to run was relatively poorly vascularized.

In the growth disc the canals were more branched than in the epiphysis and more variable in length. In marked contrast to the other species investigated, the canals of the human growth disc and their branches were not arranged uniformly parallel to the proximo-distal axis of the disc or at a moderately small angle to it. On the contrary, they coursed through the disc with all degrees of obliquity both distally towards the metaphysis and, though less often, proximally towards the epiphysis. Some of the former made contact with the metaphysis, none of the latter anastomosed with canals in the epiphysis. No canal entered the disc from the metaphysis.

The manner of branching of the canals was in some cases dichotomous, in others irregular. Anastomosis between adjacent canals was infrequent, both in the epiphysis and in the growth disc.

DISCUSSION

It was shown above in a number of mammalian species that the vascular canals in the cartilaginous upper end of the tibia were disposed in recognizable patterns. All members of a given species showed similar patterns, but different species presented different patterns. Although its complexity increased with age the pattern in each species persisted basically unchanged from its simplest expression, usually in early foetal life, at least until the epiphysis began to develop its centre of ossification. Even when vascular canals first appeared when the changes that led to ossification were almost due to begin, as in the rat, a characteristic pattern was evident during their brief intra-cartilaginous phase.

The existence of these definite patterns had not previously been reported, despite the many investigations that were made of the cartilage canals. This seems to have been due to two main factors, (i) the nature of the material studied, and (ii) the techniques employed. (i) In the large specimens which frequently were the only material studied, the complexity of the canal-system and its innumerable variations of detail would tend to obscure an underlying pattern. For example, Lexer *et al.* (1904), Harris (1929), Haines (1933), Trueta (1957) and Haraldsson (1962) confined their studies of the major human long bones to late foetal and postnatal stages, when the cartilaginous ends of the bones contained a large number of vascular canals with a profusion of branches. Examination of early foetal stages of man and other large animals in the present investigation, by reducing this complexity to a minimum, permitted the more simple underlying pattern to be appreciated in the younger specimens and its persistence recognized in the older ones despite its progressive elaboration. Of the authors cited above, only Haines and Trueta recognized that the elements of a pattern were present. Haines, however, was concerned principally with the avascular area of cartilage between

two or more separate groups of canals as the site at which the secondary centre of ossification developed. Trueta was mainly interested in the postnatal changes in the blood supply to the femoral head, particularly after the appearance of its centre of ossification. Neither author provided a description of the pattern of the vascular canals during the prenatal period, and the development of the pattern during this period was not investigated. (ii) For the study of a three-dimensional system such as cartilage canals, visual examination of a cleared specimen is preferable to radiographs, since the former method permits continuous viewing of the system while the specimen is rotated freely in various directions. The full length of every canal may then be followed, and its independence or anastomosis with other canals accurately determined. For this reason, although stereoscopic radiographs (Lexer *et al.* 1904; Tilling, 1958; Haraldsson, 1962) may reveal more of a three-dimensional pattern than single, i.e. non-stereoscopic, radiographs (Trueta, 1957; Brookes, 1958), only visual stereoscopic examination of cleared specimens provides the overall pattern by fully resolving its details. Even the standard methods of serial reconstruction, employed *inter alia* by Hurrell (1934), have been criticized in recent years, and the necessity for more accurate methods of orientation has been emphasized by Burston & Thurley (1957) and by Dixon & Howarth (1958). The imperfections pointed out by these authors might explain Hurrell's inability to observe, in his reconstruction models, any constant pattern of the vascular canals in homologous cartilages in human foetuses.

The differences in canal pattern shown by different species was an unexpected finding. These differences were observed between species belonging to different orders, such as rabbits and goats; between two species belonging to the same order, namely goats and sheep; and even between two different breeds of sheep. They were sufficiently evident that an unknown specimen could be assigned to its proper species with little difficulty. Yet the upper tibial cartilage in all the species examined was formed of the same three elements: epiphysis proper, tubercle and growth disc; and neither the minor differences in shape nor the greater differences in absolute and relative size of these elements appeared sufficient to account for the great differences in the overall patterns of the canals. For example, although specimens from human and sheep foetuses of the same C.R. length were similar in size and shape, in the sheep three long profusely branched internal canals diverging from a common stem ventro-superiorly were distributed through most of the specimen, whereas in man a large number of short independent canals with few branches radiated inwards from many points on the surface. Again, the growth disc in man possessed a number of canals originating directly from its own perichondrial surface, while the much smaller disc in the rabbit contained no canals of this type; size was not the decisive factor in producing this difference, as the growth disc in the cat possessed direct perichondrial canals while these were entirely absent from the much larger disc in the goat. It is evident, therefore, that differences in the pattern of the canals in homologous cartilages do not depend on differences in size and/or shape of the cartilages in which they lie.

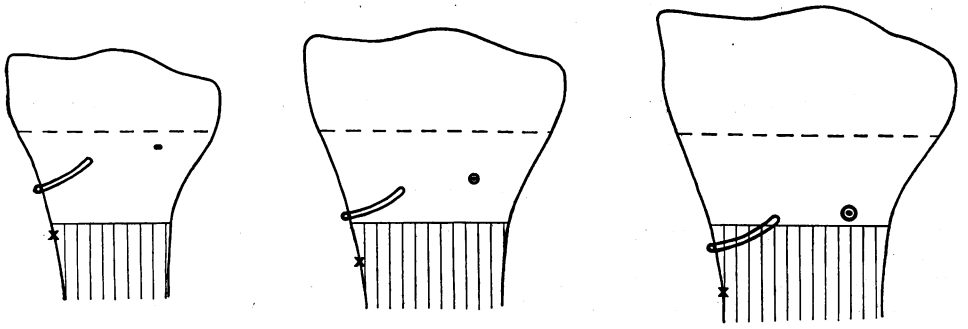
The observation of vascular canals in the growth disc in goat, sheep, cat, rabbit and man over a wide range of C.R. lengths conflicts with the observations of Bertrand (1923) and Haraldsson (1962), and with the statement of Harris (1929) that the

growth discs of actively growing healthy animals are avascular. Hurrell (1934) observed vascular canals in the growth discs in human foetal long bones, but was of the opinion on histological grounds that they were formed 'accidentally', lasted only a short time and were functionless. However, other studies of gross specimens have demonstrated their presence in certain growth discs in man (Lexer *et al.* 1904; Trueta, 1957; Brookes, 1958), in some cases persisting over a wide range of C.R. lengths (Brookes, 1958), and histological investigations have demonstrated their presence at some stage in the growth discs of many animals as well as man (see, for example, the reviews by Schaffer, 1930, and Hintzsche, 1927). The present study has revealed their presence over a wide range of C.R. lengths in a variety of animal as well as human upper tibial growth discs. Their persistence and widespread distribution strongly suggest that they are neither 'accidental' nor functionless, and disprove their alleged transitory nature.

The manner of distribution of the vascular canals raises a number of problems which will require further investigation. What are the factors that produce or modify the development of a particular pattern? What influence attracts blood vessels into the growth disc from its perichondrial surface in some species, but is absent or ineffective in others? By what process do the vascular canals extend in some species from the epiphysis into the growth disc and subsequently to the metaphysis? Perhaps the most interesting problem is posed by those canals that originated at the perichondrial surface of the growth disc and ran inwards and upwards towards the epiphysis (Pl. 2, figs. 13, 19), i.e. the direct recurrent canals of the disc. Theoretically, in the normal course of events in endochondral ossification (Text-fig. 9), any part of the growth disc except the reserve (mitotic) zone is displaced progressively away from the epiphysis by cells newly added at the reserve zone, and when it is finally 'overtaken' by the advancing metaphysis it comes to lie in the metaphysis. In a similar manner the site of origin of a direct recurrent canal in the growth disc ought, as growth proceeds, to come to lie in the metaphysis, so that in the isolated upper tibial cartilage the canal would appear to originate at the inferior (metaphysial) surface of the growth disc (Text-fig. 9). (Periosteal-perichondrial migration which accompanies elongation of the shaft would reinforce this apparent migration of the canal.) Despite these theoretical considerations no vascular canal was ever seen to enter the growth disc from the metaphysis and end blindly within the disc. It may therefore be conjectured (*a*) that as the metaphysis encroaches on the site of origin of such a canal the blood vessels of the latter are obliterated and the canal disappears, being replaced by a new formation nearer to the reserve zone; or (*b*) that the canal in some way maintains its distance relative to the reserve zone and so the advancing metaphysis never catches up with it. The latter might be accomplished by either of two methods: (i) the displaced cartilage 'flows round' the blood vessels of the canal but does not displace them, or (ii) the canal and its contents actively migrate towards the reserve zone at a rate that maintains them at a constant distance from it. No data are available from the present study on which a choice between these alternatives might be based.

When the development of the canal-pattern was examined in the sheep (Text-fig. 4) it was evident that, as the transverse diameter of the epiphysis increased, the peripheral canals on each side increased in length but not sufficiently to vascularize

the whole additional width of cartilage. Much of the additional width was vascularized by elongation of the medial and lateral terminal divisions of the dorsal central canal. Reference to Text-fig. 4 shows that this elongation could only have been brought about by their active growth. It was thereby demonstrated that vascularization of the epiphysis could not be brought about solely on the basis of a passive inclusion, within the growing cartilage, of blood vessels that lay in its perichondrium.



Text-fig. 9. Diagrams of three successive stages in the growth of the cartilaginous upper end of the tibia, illustrating the changes *anticipated* during growth in the relations of a direct recurrent canal in the growth disc. The reserve (mitotic) zone of the disc is represented by an interrupted line, and this zone is taken as a (stationary) reference level in all three diagrams. The metaphysis is vertically hatched. (i) A direct recurrent canal is shown in the growth disc. On the right a recently formed (flattened) cartilage cell lies close to the reserve zone. Below left, a cross acts as a metaphysial bone-marker. (ii) A little later, growth is indicated by the increased distance between the (enlarging) cartilage cell and the reserve zone, and between the bone-marker and the reserve zone. The direct recurrent canal is also situated further from the reserve zone. (iii) At a still later stage the direct recurrent canal first enters the metaphysis and then enters the growth disc from its inferior (metaphysial) aspect. (For further explanation, see text.)

In the sheep specimens also, it was shown that in the epiphysis proper there were two regions where groups of canals met, one region between the central group and the medial peripheral group, the other between the central group and the lateral peripheral group. According to Haines's postulate (1933) there should develop two centres of ossification for this epiphysis, one on each side, whereas there was only a single centre of ossification (Pl. 2, fig. 20) and it was situated in amongst the branches of the central group, not between this central group and one of the peripheral groups.

SUMMARY

1. The pattern of the vascular canals in the cartilaginous upper end of the developing tibia was investigated in the sheep, goat, rabbit, cat, rat and man. The blood vessels were injected with a visually opaque fluid, and the cartilage was fixed, dehydrated and cleared. Specimens immersed in their clearing fluid were examined visually in transmitted light with a stereoscopic microscope.

2. In each species the upper tibial cartilage showed a constant vascular canal pattern at all stages prior to development of the secondary centre of ossification.

The pattern was constant in broad outline only, and allowed great variation in individual details.

3. The canal pattern in any one species differed from the patterns of all the other species studied. The different patterns were not obviously related to differences in the size and/or shape of the homologous cartilage in the different species examined.

4. The course and distribution of the vascular canals indicated that the presence of these canals in cartilage cannot be explained solely as the result of passive inclusion of perichondrial vessels by growth of the sub-perichondrial cartilage around them.

I would like to record my gratitude to Prof. J. J. Pritchard for his long-continued encouragement and advice.

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EXPLANATION OF PLATES

All the figures in Plates 1 and 2 are photographs of gross specimens of injected-cleared upper tibial cartilage. The outline of each specimen, faintly shown in the original print, has been emphasised by drawing over it with ink.

PLATE 1

Fig. 1. Goat, 70 mm. C.R. length. Specimen viewed from above. All canals take origin from a transverse line *T*———*T* situated where the tubercle joins the epiphysis proper. The main canal to the tubercle runs forward into it from the centre of the transverse line. India ink/plasma × 15.

Fig. 2. Goat, 70 mm. C.R. length. Specimen viewed from the side. The transverse line of origin is shown in profile as a point, *T*. Canals of the epiphysis proper run backwards at first, then curve sharply down towards the growth disc in two sets; the latter are not clearly demarcated. The canal to the tubercle is double At this stage there are no canals in the growth disc. Prussian blue. × 15.

Fig. 3. Goat, 180 mm. C.R. length. Specimen viewed from above. The canals originating from the transverse line (cf. Fig. 1) vascularize the major part of the specimen. Peripheral canals, *P*, originate from the lateral and medial surfaces and from the dorsal surface; in the figure they appear to vascularize a greater area than in fact is the case. Prussian blue. × 5.

Fig. 4. Goat, 170 mm. C.R. length. Specimen viewed from the front. The central group of canals vascularized the major part of the epiphysis. Numerous canals derived exclusively from the epiphysis are present in the growth disc, for the most part parallel to the proximo-distal axis of the disc. Their branches at first run obliquely across the disc, but soon turn downwards towards the metaphysis. Several of the canals appear to reach the metaphysis. The junction of epiphysis and growth disc appears more richly vascularized than elsewhere. India ink/plasma. × 5.

Fig. 5. Goat, 130 mm. C.R. length. Specimens viewed from the side. The transverse line of entry is seen in profile at *T*. The canal to the tubercle gives off a branch, *B*, which runs backwards and downwards into the ventral part of the epiphysis proper and enters the growth disc. The canals of the epiphysis proper run at first backwards and downwards, then curve sharply downwards towards the growth disc. Canals in the growth disc are derived exclusively from the epiphysis, and the longest of them appears to contact the metaphysis. Prussian blue. × 8.

Fig. 6. Goat, 160 mm. C.R. length. Specimen viewed from the front. The outline of the tubercle has also been inked over. Numerous short marginal canals, *M*, are shown entering the tubercle on each side. The main tubercular canal is shown as a vertical line in the centre of the tubercle. India ink/plasma. × 5.

Fig. 7. Goat, 110 mm. C.R. length. Specimen viewed from the front. The canals of the growth disc are derived exclusively from the epiphysis. Those more centrally placed lie nearer the metaphysis; the middle canal appears to reach the metaphysis. The junction of epiphysis and growth disc appears more richly vascularized than any other region. India ink/plasma. × 7.

Fig. 8. Goat, 185 mm. C.R. length. Medial half of specimen, viewed from the ventro-medial aspect. Branching of the canals is irregular. In the growth disc, the canals are seen to branch. Prussian blue. × 8.

Fig. 9. Same specimen as fig. 3. Medial half of specimen, viewed from the dorso-lateral aspect. A recurrent canal, *R*, runs obliquely upwards from the metaphysis and, after dividing in two, ends blindly within the growth disc. At lower left, two canals from the epiphysis appear to reach the metaphysis. × 9.

Fig. 10. Same specimen as fig. 3. Lateral half of specimen, viewed from the dorso-medial aspect. A recurrent canal, R_1, runs obliquely upwards from the metaphysis into the growth disc and ends there blindly. This was observed in no other specimen of any species. × 9.

PLATE 2

Fig. 11. Sheep, 135 mm. C.R. length. Specimen viewed from the front. Canals in the growth disc are derived exclusively from those of the epiphysis. Branching of the canals in the disc is infrequent. Several of the canals appear to reach the metaphysis. India ink/plasma. × 7.

Fig. 12. Cat, 3 days postnatal. Specimen viewed from above. A number of canals run backwards from a transverse line *T*——*T* situated where the tubercle joins the epiphysis proper. Peripheral canals, *P*, run centrally from each side and from the dorsal surface. India ink/plasma. ×5.

Fig. 13. Cat, 90 mm. C.R. length. Specimen viewed from the dorso-medial aspect. Some canals enter the growth disc from the epiphysis above (broken arrow); others, *D*, originate at the periphery of the disc itself. One of the latter, D_1, runs a recurrent course towards the epiphysis. India ink/plasma. ×12.

Fig. 14. Cat, 1 day postnatal. Specimen viewed from the back. Most of the canals in the growth disc are derived from those in the epiphysis. Some of these canals run obliquely in the disc (arrows); cp. goat, fig. 4, and sheep, fig. 11. India ink/plasma. ×7.

Fig. 15. Rabbit, 45 mm. C.R. length. Specimen viewed from above. Most of the canals take origin ventrally from a transverse line, *T*——*T*, at the junction of the tubercle with the epiphysis proper. Two canals originate dorsally, a smaller one at lower left and a larger one at lower right; the origin of the larger appears to lie within the epiphysis, but this is due to its position at a lower level in the cartilage. India ink/plasma. ×12.

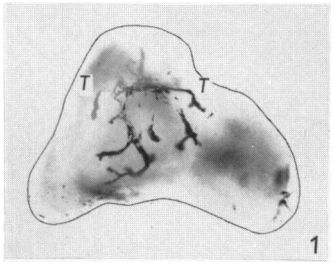
Fig. 16. Rat, 9th postnatal day. Specimen viewed from the side. The cartilage has been exposed but still lies in situ. Canals originate exclusively from the superior intercondylar area, and fuse within the epiphysis. The growth disc is devoid of canals. Undiluted India ink. ×9.

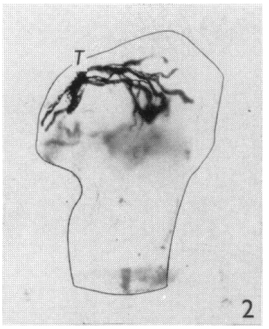
Fig. 17. Man, 110 mm. C.R. length. Specimen viwed from above. The dense mass in the centre is produced by the out-of-focus growth disc and its canals superimposed on the epiphysis. The canals of the epiphysis originate at many points all round the periphery and are all of the same order of length. There is no predominant canal or canal-group. At each side the ventral and dorsal canals tend to run obliquely towards one another, rather than centrally. India ink/plasma. ×8.

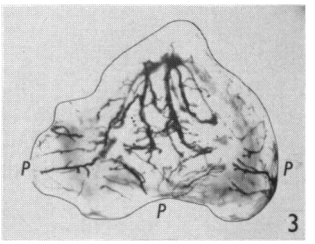
Fig. 18. Man, 160 mm. C.R. length. Specimen viewed from above. The canals of the epiphysis are numerous and short. They originate from every non-articular surface; those from the periphery of the epiphysis are shown by the open arrows, those from the superior intercondylar surface by broken squares. India ink/plasma. ×2·5.

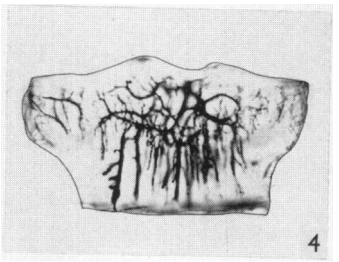
Fig. 19. Man, 125 mm. C.R. length. Specimen viewed from the front. Two short recurrent canals (open arrows) run upwards in the growth disc towards the epiphysis. A longer recurrent canal is marked by a succession of small closed arrows; the larger closed arrow marks the site of origin of this canal. India ink/plasma. ×3.

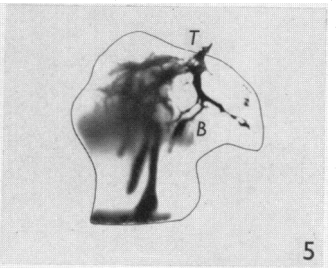
Fig. 20. Sheep, 260 mm. C.R. length. Specimen viewed from the back. The centre of ossification lies amongst the branches of the central group of canals (cf. Text-fig. 4), not between the central group and one of the peripheral groups. The canals on each side are only faintly visible, they lie for the most part in the nearly blank areas right and left. The growth disc contains an extremely large number of canals, most of which appear to reach the metaphysis. India ink/plasma. ×2.

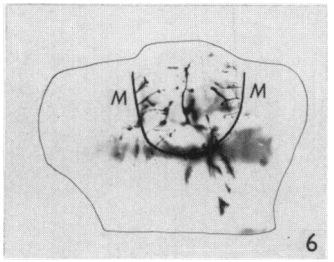


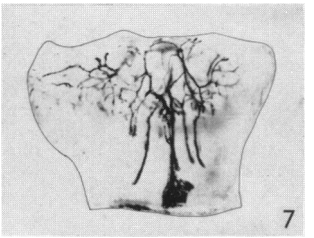


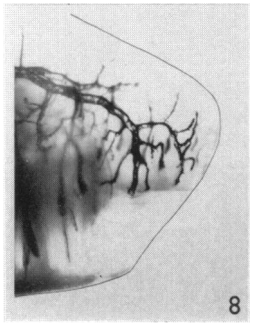


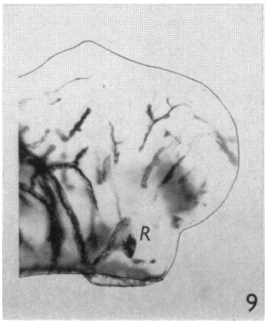


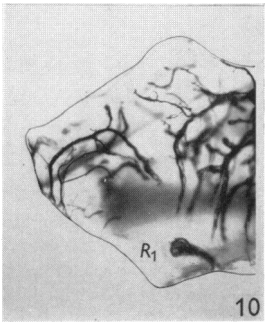












CYRIL LEVENE

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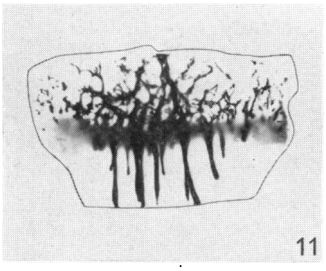
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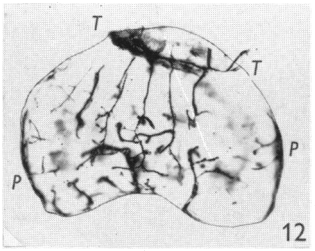

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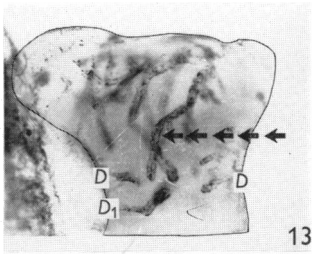

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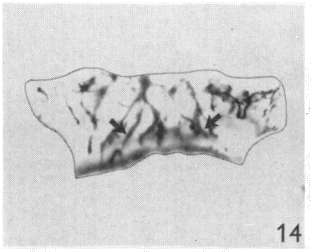
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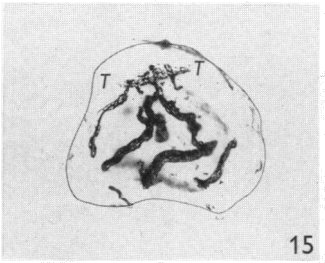

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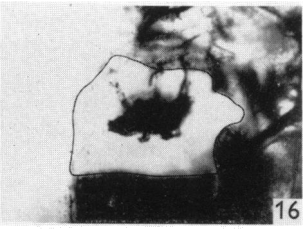
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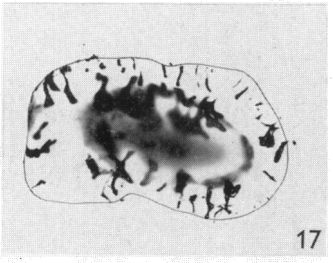
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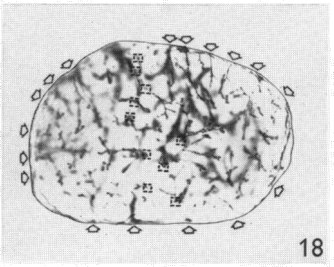
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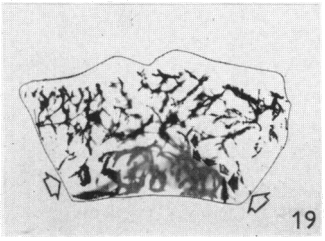
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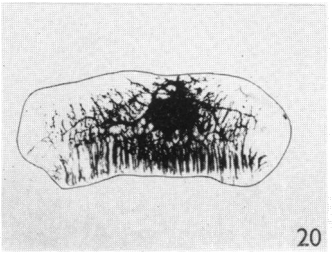
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