COLLAGEN FIBRE PATTERNS IN MAMMALIAN BONE

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From its first appearance in the skeleton of the embryo until death occurs, mammalian bone is subject to two developmental processes. First there are those mechanisms taking place in relation to the periosteum, the endosteum and the epiphyseal cartilages by which the bone grows in length and girth. The greater part of this development is completed by the time the epiphyseal plates are ossified in late adolescence or early adult life, but, even after this time, minor intermittent changes in girth are frequently produced by reactivation of the periosteal and endosteal mechanisms. Associated with this growth process, but not necessarily contributing to it, is a continual change in the internal structure of the tissue. In this process of internal development, bone passes through a series of stages, each of which is characterized by a specific arrangement of the intra-osseous collagen fibres, both in relation to one another and in relation to the vascular spaces of the tissue. It is these differences in the pattern of the collagenous fibres that allows bone to be classified into a number of clearly defined types. The standard classification is that of Weidenreich (1930) which depends largely on the size of the collagen bundles and on the relationship which they bear to neighbouring bundles. In this investigation, however, a somewhat different classification has been found to be advantageous. This is based on three factors, namely, the relationship of neighbouring fibres to one another, their relationship to vascular channels, and the place occupied by the tissue in the developmental history of the skeleton as a whole. The types of bone recognized in this classification are enumerated below in the chronological order in which they appear in the development of mammalian bone: (1) woven-fibred bone; (2) primary osteones; (3) surface bone; (4) secondary osteones (Haversian systems); (5) interstitial bone.

The fibre patterns of secondary osteones, and of interstitial bone derived from secondary osteones, have been considered in a previous publication (Smith, 1959). The present paper is concerned mainly with the other types of bone.

METHODS

The investigation was carried out on the human tibia and femur and on long bones of the ox, horse, pig, sheep, dog and cat. Serial 5 μ paraffin sections were prepared in longitudinal and transverse planes and the majority of these were stained by Weidenreich's modification of Weigert's fibrin stain (Weidenreich, 1923). The interpretation of bone sections stained by this method has been discussed in a previous paper (Smith, 1959) in which it was demonstrated that bundles of collagen fibres running approximately parallel to the plane of section appeared as deep violet lines, whereas those running approximately at right angles to the plane of section appeared as circumscribed pink areas stippled by small violet spots (Pl. 3, fig. 1). The violet spots were interpreted as the fibres comprising the bundle and the enveloping pink area as an interfibrillar substance. In addition, ground transverse sections of whole bones were prepared and examined, after decalcification and clearing, by polarized light. This method was found useful for assessing the gross structure of large areas of bone but it was not used in the study of its fine structure.

OBSERVATIONS

Woven-fibred bone

Woven-fibred bone consists of a calcified matrix which is permeated by collagen fibres, and throughout it there are lacunae containing osteocytes. When it is first laid down it contains numerous large vascular spaces, but as its development proceeds these spaces become occupied by primary osteones.

The collagen fibres in woven-fibred bone are of two kinds which differ in appearance, and development. Thus the calcified matrix is always permeated by a meshwork of collagen bundles which bear no fixed relationship either to the lacunae or to the vascular spaces of the tissue. These bundles do not lie parallel to one another as is the tendency in all other types of bone; nevertheless, they usually show some degree of preferential orientation in a direction parallel to the long axis of the bone. In longitudinal sections (Pl. 1, fig. 1) the fibre bundles are therefore usually seen as interweaving fibrillar bands which stain violet purple in colour, whereas in transverse section (Pl. 1, fig. 2) they appear as polygonal areas which stain pink and are stippled by violet spots. The diameter of these bundles is not appreciably greater than that of the bundles found in other types of bone (Pl. 3, fig. 1), and it is considered that the alternative designations of *coarsely bundled bone* and *coarse-fibred bone* are unsuitable.

This type of collagen bundle is a constant feature of woven-fibred bone and the contained fibres will be referred to as the intrinsic fibres of the tissue. In many areas of woven-fibred bone, though not in all, other collagenous fibre bundles are also present. These are the elements commonly known as Sharpey fibres or perforating fibres. They are considerably larger than the intrinsic fibre bundles described above, a diameter of 10–12 μ being common, and they stain a deeper violet with the Weidenreich method. In longitudinal section (Pl. 1, fig. 3) the bundle consists of a variable number of fine, dark violet fibres interweaving with one another, whereas in transverse section (Pl. 1, fig. 4) they are seen as large pink areas stippled with deep violet spots. In many sections the bundles appear to have shrunk eccentrically from the surrounding tissue leaving a narrow peri-fibrillar space at one side. It is considered that these, like many spaces of similar appearance, are to be regarded as artefacts.

It is generally accepted that Sharpey fibres represent originally extra-osseous collagen bundles which have been included within the bone during its growth. This view is in conformity with the continuity which often exists between intra-osseous bundles and collagen bundles lying both outside the bone (Pl. 1, fig. 5) and in the vascular spaces within the bone (Pl. 1, fig. 6). Sharpey fibres in bone invariably stain deeply with the Weidenreich method, but their continuations both outside the bone and into its vascular spaces are unstained.

As might be expected from this mode of formation Sharpey fibres are often, though not invariably, arranged in groups running in parallel directions (Pl. 1, fig. 7), the direction varying from one group to another.

The vascular spaces which are included within woven-fibred bone as it is laid down form a continuous labyrinth throughout the tissue. In some regions this labyrinth is irregular and resembles the cavity within a sponge (Pl. 1, fig. 8), but in others the cavities of the labyrinth are preferentially orientated in one or two directions. Thus by examination of serial sections, it can be established that the vascular spaces in the posterior part of the femoral shaft in a 170 mm. human foetus (Pl. 1, fig. 9) are wide cylindrical canals which extend in a longitudinal direction and anastomose infrequently with one another. On the other hand, the vascular spaces in the lateral part of the same bone (Pl. 1, fig. 9) take the form of a series of parallel fenestrated clefts. The clefts extend longitudinally and circumferentially and have infrequent radial connexions with one another. The general form of these clefts can be appreciated from the reconstruction of the primary osteones which subsequently form within them (Pl. 2, fig. 3). Furthermore, it may be inferred from the form of certain primary osteones in the metacarpus of the ox (see below, Pl. 2, fig. 5) that at some stage in the development of that bone, vascular spaces exist in woven-fibred bone as a series of parallel, fenestrated clefts, similar to those described in the human femur, but extending in *radial* and longitudinal directions. Such spaces have not, however, been observed because of the difficulty of obtaining material of the correct age.

Primary osteones

Development and gross form

Primary osteones are invariably formed by the deposition of parallel-fibred bone on the walls of the vascular spaces which lie within woven-fibred bone. Just as those vascular spaces form a continuous labyrinth so the bone laid down within them is a continuum. It is therefore erroneous to regard primary osteones as individual entities or units: they are tracts of bone which have exact limits in the transverse plane but whose extent in a longitudinal direction cannot be exactly defined.

Two of the main features exhibited by primary osteones result from their mode of development. First, it is evident that the gross shape of a primary osteone is dictated by the shape of the vascular space in which it develops. Secondly, it is apparent that as long as it is not eroded by subsequent developmental processes, a primary osteone must always be completely surrounded by woven-fibred bone.

As has been previously noted, the vascular spaces within many regions of woven-fibred bone form a continuous and irregular labyrinth of intercommunicating spaces (Pl. 1, fig. 8). The initial stage in the formation of primary osteones in such a region may be the subdivision of the labyrinth by a number of bridges of pre-osseous tissue (Pl. 1, fig. 10). Parallel-fibred bone is then laid down on the walls of the vascular spaces as an extensive and convoluted layer (Pl. 1, fig. 11, *a*). Subsequently, further bridges of pre-osseous tissue form across the remains of the vascular spaces (Pl. 1, fig. 11, *b*). These bridges extend for some distance in a longitudinal direction dividing the original labyrinth into a variable number of wide longitudinal vascular channels. Thereafter the calibre of each channel is further diminished by the laying down of additional parallel-fibred bone on its walls (Pl. 1, fig. 11, *c*). Thus a fully developed primary osteone of this type is seen in transverse section as an irregular area of parallel-fibred bone embedded in a matrix of woven-fibred bone (Pl. 2, fig. 1). It contains a variable number of longitudinal vascular channels (three in the example illustrated) and these can be traced, in serial transverse sections, for considerable distances, establishing frequent communications with the channels of neighbouring osteones. This change in the vascular pattern from an extensive and irregular labyrinthine cavity in woven-fibred bone, to a series of narrow longitudinal channels in primary osteones is very striking and is associated with a considerable change in the physical properties of the tissue (Smith & Walmsley, 1959).

In those regions in which the vascular pattern of woven-fibred bone is preferentially orientated in one or two directions (see above), the process by which primary osteones are formed is similar to that described above, but their final gross form is different. Thus the primary osteones which are formed within the simple cylindrical cavities in the posterior part of the human femur (Pl. 1, fig. 9) are illustrated in Pl. 2, fig. 2, *a*. Here no division of the original cavities occurs and parallel-fibred bone is laid down in a continuously concentric fashion so that it eventually encloses a single longitudinal vascular channel.

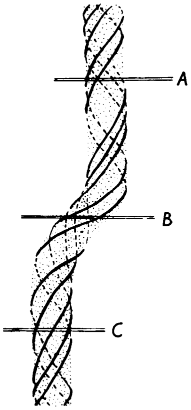
In those cleft-like spaces which are elongated in longitudinal and circumferential directions (Pl. 1, fig. 9) primary osteones develop through the same stages as those forming in an irregular labyrinth. Their definitive shape is illustrated by the wax-plate reconstruction in Pl. 2, fig. 3. They form a series of fenestrated walls, extending longitudinally and circumferentially. The walls are parallel to one another and to the endosteal and periosteal surfaces of the bone, and have infrequent radial connexions. Within the osteones numerous vascular canals (black) run longitudinally and these are connected to one another by occasional horizontal branches. In transverse section such osteones are seen as fusiform areas of parallel-fibred bone which are elongated in a circumferential direction (Pl. 2, fig. 4). They lie in a matrix of woven-fibred bone and contain a variable number of longitudinal vascular channels which are strictly aligned with one another. Lastly, there are those primary osteones which are presumed to develop in vascular clefts which are elongated in longitudinal and radial directions. These have a gross form very similar to that of the type just described, except that in transverse section, they are elongated in a radial rather than a circumferential direction (Pl. 2, fig. 5). It is thus convenient to classify primary osteones, according to their shape and orientation, into *irregular, cylindrical, circumferential* and *radial* types.

Primary osteones are by definition always formed within vascular spaces which have been included within woven-fibred bone in the process of its formation, and never in cavities created in pre-existing bone by erosion. It is because the formation of primary osteones is thus never associated with a change from a destructive to a formative process that no cement (reversal) lines ever demarcate them from the surrounding woven-fibred bone.

In the previous sections it was noted that the Sharpey fibres which are found in many regions of woven-fibred bone, are often continuous with collagen bundles lying within the intra-osseous vascular spaces (Pl. 1, fig. 6). Where they are present these collagen bundles become included within the primary osteones as the latter are formed, and simultaneously develop a staining reaction identical with that of the Sharpey fibres with which they were originally associated. The outer parts of many primary osteones are therefore penetrated by Sharpey fibres from the surrounding woven-fibred bone (Pl. 2, fig. 8).

The fibre pattern

The fibre pattern in primary osteones varies considerably. The simple cylindrical osteone is usually seen in transverse sections as an annular zone, surrounding a single vascular canal, and composed of pink areas which are stippled with violet spots. These are packed closely together and show no differentiation into lamellae (Pl. 2, fig. 2, *a*). From this appearance it may be inferred that the fibres of the osteone are all arranged parallel to one another in a predominantly longitudinal direction. However, within an area dominated by this type of osteone the appearance illustrated in Pl. 2, fig. 2, *b*, is occasionally seen. Here about two-thirds of the osteone is similar in appearance to the common form, but the rest of the annulus is composed of dark purple fibres running approximately in the plane of the section.



Text-fig. 1. Spiral arrangement of fibres in a cylindrical primary osteone.

It is considered that this pattern may be explained by certain features which are apparent in longitudinal sections of regions of bone containing similar osteones (Pl. 2, fig. 6). In such a section it is evident that although the vascular canals run for the greater part of their course parallel to the long axis of the bone, they are occasionally kinked; that is they undergo abrupt and temporary deviations. In Pl. 2, fig. 6, four deviations of this kind are indicated by arrows, and it will be noted that whereas the two on the left occur in the plane of the section, those on the right occur at right angles to that plane, so that in each case the osteone surrounding the canal is cut tangentially. Where such a tangential section occurs the collagen fibres are always seen running at an angle of about 20° to the long axis of the vascular canal (Pl. 2, fig. 7) and from this it may be argued that although the collagen fibres of these primary osteones are preferentially orientated in a longitudinal direction, in fact they form steep and continuous spirals, with a helix angle of about 70°, around the vascular canals as illustrated in Text-fig. 1. A transverse section through the strictly longitudinal parts of such a primary osteone (*A* and *C* in Text-fig. 1) would cut all the fibres at the same angle of 70°, giving the appearance shown in Pl. 2, fig. 2, *a*, whereas a transverse section which passed through one of the occasional deviations (*B* in Text-fig. 1) would cut the fibres on one side of the osteone at right angles and those on the other side almost longitudinally giving the appearance shown in Pl. 2, fig 2, *b*.

In the larger multi-channelled type of primary osteone (Pl. 2, figs. 1, 4, 5 and 8) a large part of the unit contains distinct lamellae of circumferential and longitudinal collagen fibre bundles. In transverse sections (Pl. 2, fig. 8) the circumferential lamellae are seen as dark fibrillar bands and the longitudinal lamellae as rows of discrete pink areas stippled with dark violet spots. Characteristically the inner lamellae encircle the individual vascular canals, whereas the outer lamellae envelop the whole osteone (Pl. 2, fig. 1).

This lamellated bone is often, though not always, associated with bone of two other fibre patterns. Thus in the most central part of primary osteones, the tissue frequently has an amorphous appearance, in which the collagen fibres cannot be distinguished (Pl. 2, figs. 5, 8). On the other hand, the outermost part of an osteone frequently contains only longitudinal collagen fibres which are not arranged in distinct lamellae (Pl. 2, figs. 2, 4 and 8).

Surface bone

Surface bone forms on the periosteal and endosteal aspects of mammalian diaphyses at various stages during their development. It is most commonly seen as thin layers of parallel-fibred bone clothing the surfaces of a bone shaft which has reached its definitive size (Pl. 4, fig. 3). In some bones, however, either the periosteal or the endosteal surface bone may form a layer of much greater thickness so that it comprises the greater part of the width of the diaphysis (Pl. 4, figs. 2, 7). In others a thin layer of periosteal surface bone may form during growth, and then become included (see below) within the diaphysis by superimposed woven-fibred bone (Pl. 3, figs. 4, 5).

In the most common form of surface bone, the collagen fibres are arranged in alternate lamellae of longitudinal and transverse bundles, running parallel to the surface of the bone (Pl. 2, fig. 9; Pl. 3, fig. 1). In some regions, however (Pl. 3, fig. 2), the longitudinal fibres predominate and the lamellae of transverse fibres are thin and fragmentary and are in places indistinguishable. It is evident that in such regions lamellation of the tissue is much less distinct or entirely absent.

When surface bone is formed in a region not previously ossified, Sharpey fibres, similar in all respects to those previously described in woven-fibred bone, are frequently included within it. In Pl. 3, fig. 3, Sharpey fibres traverse an area of surface bone at right angles to the plane of section, and the shrinkage of the fibres from the surrounding tissue (see above) accounts for its vesiculated appearance. In Pl. 3, fig. 6, on the other hand, Sharpey fibres can be seen traversing surface bone in the plane of the section. The blood vessels in surface bone are included within the tissue during its formation and their pattern varies with the width and position of the layer. In thin layers of either periosteal or endosteal surface bone, the tissue is traversed by only a few radially disposed vessels (Volkmann's canals) (Pl. 4, fig. 1). In a thick layer of endosteal surface bone (Pl. 4, fig. 7) the radial vessels are more numerous. Moreover, they give off longitudinal branches which are constantly aggregated along exact circumferential planes. On the other hand, in a thick layer of periosteal surface bone the radial vessels are less numerous while the longitudinal vessels are arranged in a random fashion (Pl. 3, fig. 3; Pl. 4, fig. 2). In lamellated surface bone the lamellae do not encircle these vascular channels as they do in secondary osteones. On the contrary they simply diverge on either side of them before regaining their original direction (Pl. 3, fig. 3).

Secondary osteones

The development of secondary osteones has been described by Petersen (1930). The first stage in their formation is the creation of tubular cavities within the bone, by the absorption of the tissue surrounding pre-existing vascular canals in primary osteones or in surface bone.

Subsequently, the absorption of bone ceases and appositional growth of new bone occurs upon the walls of the cavities, and progresses until a longitudinal vascular canal of definitive size is reformed. The reversal from an erosive process to a formative process, which is thus inherent in the development of these units, is indicated by their demarcation from the surrounding tissues by the cement or reversal line which is seen as an unstained peripheral zone in Pl. 3, figs. 6 and 10. The preliminary erosive process involves not only the perivascular bone but also any Sharpey fibres which are included within it, and consequently, these fibres are never present in secondary osteones. The erosive process usually proceeds eccentrically from the original vascular canal, whereas the subsequent appositional growth of new bone tends to proceed concentrically. As a result the formation of a secondary osteone usually involves a shift in the position of the vascular canal concerned (Smith & Walmsley, 1959), and such a unit never contains more than one vascular canal except in the region of an anastomosis.

The first secondary osteones to appear in an area of bone develop in one of two different environments. They may form in association with the vascular canals included within surface bone during its formation (see above) and are then entirely surrounded by that tissue (Pl. 3, fig. 6). It may be noted, however, that although surface bone contains both longitudinal and radial vessels, secondary osteones form only in relationship with the former type. Furthermore, it has been observed that secondary osteones form with much greater facility in periosteal surface bone than in similar tissue of endosteal origin. Secondly, similar units may develop in relation to the vascular canals within primary osteones, and then they abut against both the remains of these primary osteones and the neighbouring woven-fibred bone (Pl. 3, figs. 7, 8).

Subsequent generations of secondary osteones develop in relation to the vascular canals of similar pre-existing units. Such an osteone may be bordered by the remnants of primary and secondary osteones and by woven-fibred bone (Pl. 3, fig. 8, *c*), or by the remnants of secondary osteones and by surface bone (Pl. 3, fig. 9). However, as more and more generations of new units are formed the amount of woven-fibred bone, primary osteones and surface bone is progressively reduced and there is a corresponding tendency for secondary osteones to become completely surrounded by the remnants of similar units (Pl. 3, fig. 10).

The fibre patterns in human secondary osteones have been described previously (Smith, 1959). In the present study no new fibre pattern has been noted, but it has been observed that in bone from a species other than man there is little variation in the structure of the secondary osteones, one fibre pattern being characteristic for the species. Thus in the radius of the horse the characteristic fibre pattern is that designated Type I, whereas in the metacarpus of the ox it is Type II.

Interstitial bone

Interstitial bone is a by-product of the development of secondary osteones. As secondary osteones are formed within a region of bone, parts of the pre-existing tissue become separated both from the bone surface and from the adjacent vascular canals by the reversal lines surrounding these units. These isolated regions are termed interstitial bone. It is evident from a consideration of the process by which secondary osteones are formed that interstitial bone may be of three different kinds. It may consist of the remains of woven-fibred bone and primary osteones (Pl. 3, fig. 8); secondly, it may consist of surface bone (Pl. 3, fig. 9), and thirdly, it may consist of the remnants of secondary osteones (Pl. 3, fig. 10).

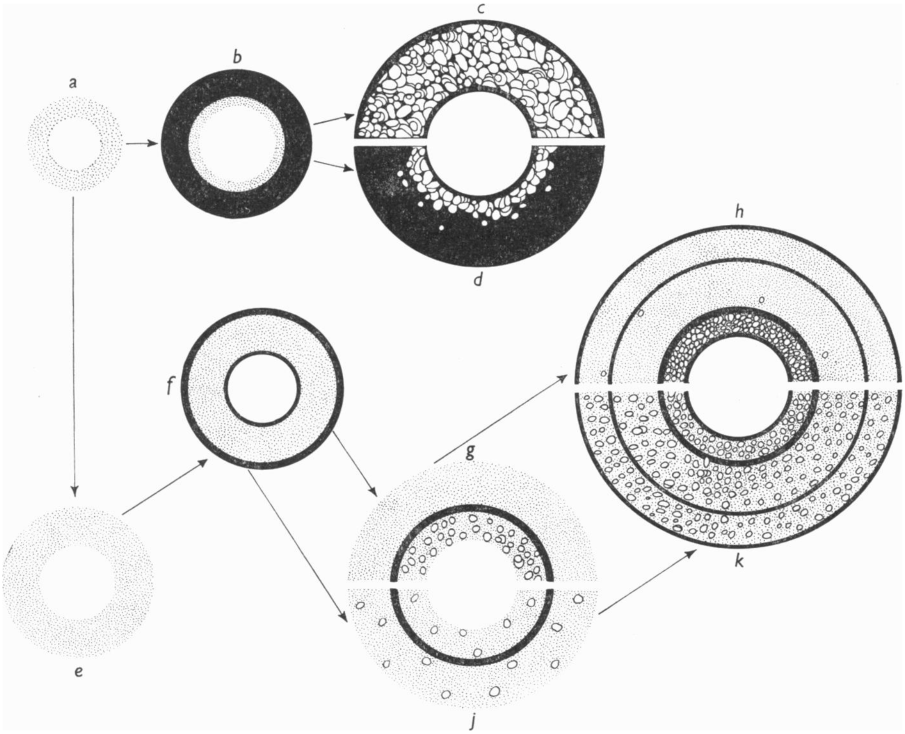
The relationship between the fibre pattern of a bone and its growth in girth

It is well known that, in general, the girth of the diaphysis of a long bone enlarges as a result of deposition of new bone on the periosteal surface and concurrent erosion of bone from the endosteal surface. The type of bone formed beneath the periosteum during growth varies in different species and at different stages of development, but always consists of either woven-fibred bone or surface bone.

After this subperiosteal bone has been formed, two changes occur in the internal architecture of the tissue—changes which, although they occur during growth, do not contribute in any way to that process. First, the vascular spaces in woven-fibred bone invariably become occupied by primary osteones soon after the tissue is formed. Secondly, secondary osteones are formed, by the process already described, in regions originally occupied by surface bone, or by woven-fibred bone and primary osteones. The time of onset of this change during development, and the rate at which it proceeds thereafter, varies in different species, in different bones of one species and even in different regions of one bone. The formation of secondary osteones usually begins long before growth is complete, but it does not cease when adult life is reached. On the contrary the process continues at a variable rate until death occurs.

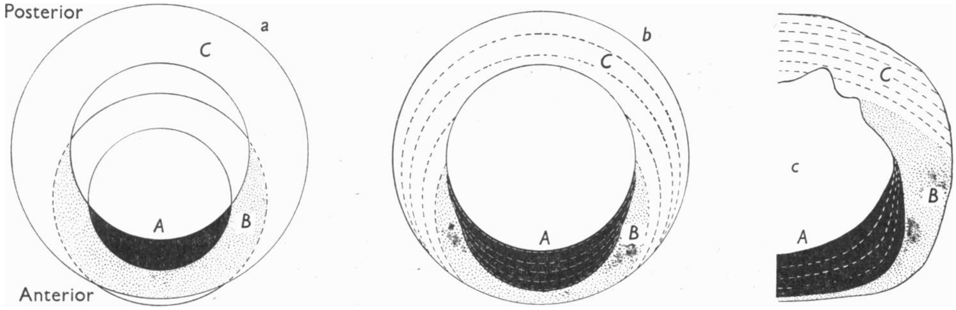
During life therefore a bone is affected by two distinct processes. The one is concerned with growth in the size of the bone and involves the production of woven-fibred bone and surface bone. The other does not contribute to growth in size: it is concerned with the internal architecture of the bone and involves the formation of primary and secondary osteones.

In the species examined during the present investigation, it has been observed that the maturation of long bones may proceed along two different lines of development and these are illustrated diagrammatically in Text-fig. 2. In the sequence *a*, *b*, *c*, *d*, the initial bone consists of woven-fibred bone in which primary osteones soon form (*a*). At an early stage of development, however, the nature of the subperiosteal deposition changes abruptly from woven-fibred bone to surface bone (*b*), and formation of this tissue continues thereafter until growth is complete. However, before the bone reaches its definitive size, endosteal erosion has removed all the original woven-fibred bone and primary osteones: moreover, secondary osteones have formed in relation to the longitudinal vascular canals within the surface bone (*c* and *d*). The adult bone thus consists of secondary osteones and surface bone together with interstitial bone which is derived from both of these tissues: the ultimate proportions of the various elements within the bone vary according to the rate of formation of secondary osteones. Where the rate is rapid (*c*) the bone may consist almost entirely of secondary osteones and interstitial bone except for thin marginal layers of surface bone on the periosteal and endosteal aspects. Such a pattern is exhibited by the transverse section of an adult cat femur in Pl. 4. fig. 1. On the other hand, when the rate is slow (*d*) secondary osteones may be confined to the innermost part of the bone, the greater part of the cortex consisting of unaltered surface bone. This structure is well illustrated in the transverse section through the tibia of a man of 68 years in Pl. 4, fig. 2. It was noted by Foote (1916) and has been confirmed by Amprino & Bairati (1936) that this mode of development is characteristic of human long bones.



Text-fig. 2. Stages in the development of mammalian long bones. Stipple represents woven-fibred bone and primary osteones; black represents surface bone; circles represent secondary osteones.

The other line of development is illustrated diagrammatically in Text-fig. 2 by the sequence *a*, *e*, *f*, *g*, *h*, *j*, *k*. The original model of woven-fibred bone continues to grow by deposition of woven-fibred bone and the formation within that tissue of primary osteones (*e*). Subsequently (*f*) the bone becomes coated on its periosteal and endosteal aspect by thin layers of surface bone. Thereafter, however (*g* and *j*) the endosteal layer becomes eroded as the marrow cavity enlarges, and simultaneously, the subperiosteal accretion reverts to woven-fibred bone. As a result a layer of surface bone becomes sandwiched between two regions of woven-fibred bone and primary osteones. The same process may be repeated so that additional layers of surface bone become similarly enclosed (*h* and *k*). The deposition of woven-fibred bone then continues until the adult size is reached, when thin final layers of surface bone are added to the endosteal and periosteal surfaces (*h* and *k*). Secondary osteones usually begin to develop while growth is in progress. In some situations these units form first in the older bone near the endosteal surface and spread outwards towards the periosteum (*g* and *h*) but in others they occur diffusely throughout the width of the bone (*j* and *k*). The number of secondary osteones varies considerably, even in different regions of the same bone. This mode of development is characteristic of horse, ox and dog. Thus Pl. 4, fig. 3, illustrates the posterior part of the radius of the adult horse. This region consists in large part of woven-fibred bone and primary osteones but also contains two included layers of surface bone and a few diffusely scattered secondary osteones. On the other hand, Pl. 4, fig. 4, shows the anterior part of the same bone in which secondary osteones are the predominant structural unit. They are evenly distributed throughout the bone and lie amongst the remains of the woven-fibred bone and primary osteones of which the region originally consisted.



Text-fig. 3. Eccentric diaphyseal growth. *a* and *b*, growth of rat femur (after Tomlin *et al.* 1953); *c*, tracing of transverse section of dog femur in Pl. 4, fig. 6. The interrupted lines in *b* and *c* indicate the orientation of collagenous formations.

The anterior part of the femur of a 13-year-old dog is illustrated in transverse section in Pl. 4, fig. 5. The outer part of the section consists of a periosteal layer of surface bone, two included layers of surface bone, circumferential primary osteones and woven-fibred bone. In the inner part, on the other hand, the original constitution of the tissue is now masked by numerous secondary osteones of the first and second generations.

Certain features additional to those already described may be found in those bones in which diaphyseal growth occurs eccentrically rather than concentrically. Thus Tomlin, Henry & Kon (1953) have demonstrated by auto-radiographic studies that increase in girth of the femoral diaphysis in the rat occurs in the manner illustrated in Text-fig. 3*a*. As the bone grows from the size indicated by the smaller annulus to that indicated by the larger, the posterior part of the bone extends by periosteal accretion and simultaneous endosteal erosion. The latter process eventually destroys the posterior part of the original bone. Anteriorly, on the other hand, the bone enlarges by endosteal accretion and periosteal erosion. The larger bone thus consists of three elements, namely an area of endosteal bone (black *A*), part of the original bone model (stippled *B*) and a large area of new periosteal bone (white *C*).

This mode of development accounts for certain features which are occasionally observed in mammalian long bones (Text-fig. 3*b*). Thus the area of endosteal bone (*A*) is always in the form of a crescent occupying the inner part of one side of the diaphysis, and in the material examined in the present investigation it has always consisted of surface bone. Moreover, as would be expected from its mode of formation the lamellae in the central part of the area lie parallel to the bone surfaces, whereas those on either side of the area tend to be directed obliquely from the endosteal towards the periosteal surface. The area of new periosteal bone (*C*) forms a larger crescent on the opposite side of the diaphysis and has a greater tendency than the endosteal crescent to occupy the whole width of the bone. Initially, it may consist either of surface bone or of woven-fibred bone in which primary osteones quickly form. But secondary osteones appear to develop in this area more rapidly than in the endosteal crescent so that the original character of the tissue may not be readily apparent. However, when the periosteal crescent consists of surface bone or of woven-fibred bone and circumferential primary osteones (p. 332), the lamellae, or the primary osteones as the case may be, lie parallel to the bone surfaces in the centre of the area, but again follow an oblique course from the endosteal to the periosteal surface on either side.

The area of original bone (*B*) consists of two wedge-shaped areas which intervene on either side between the periosteal and endosteal crescents and which are usually joined together behind the latter area. This is, of course, the oldest part of the definitive bone and is therefore the region most likely to be occupied by secondary osteones.

These three areas can be readily appreciated in the transverse section of the medial half of an adult dog's femur in Pl 4, fig. 6, and in the tracing of the section in Text-fig. 3*c*. The endosteal crescent (*A*) consists of surface bone and the inclination of the lamellae to the bone surface varies in the manner described above. The periosteal crescent (*C*) here consists of woven-fibred bone containing circumferential primary osteones and a few secondary osteones near the endosteal surface (see Pl. 4, fig. 5). And again the orientation of the primary osteones to the bone surfaces varies as they are traced from the centre to the side of the area. The area of original bone (*B*) extends in this case around the endosteal crescent and consists predominantly of secondary osteones.

In the transverse section of the femur of an adult cat (Pl. 4, fig. 8) the endosteal crescent of surface bone is readily apparent (see also Pl. 4, fig. 7) but because numerous secondary osteones have formed in the periosteal crescent the distinction between this area and that of original bone has been lost.

DISCUSSION

The terms which have been used in this paper to describe the various types of mammalian bone differ in some respects from those in common use. The simplest classification is the division of the tissue into primary and secondary bone, but unfortunately these terms are given different connotations by different authors. Thus for Lacroix (1951) the distinction between the two types lies in the time of their formation and their structure. Primary bone is found in the early stages of development and consists of what is described in this paper as woven-fibred bone, whereas secondary bone is formed during the later stages of development and consists essentially of the lamellated forms of the tissue. On the other hand, Fawcett (1954) regards primary bone as that formed in sites previously unossified and secondary bone as that formed in sites from which pre-existing bone has been absorbed. In this report Fawcett's definitions have been adopted. Another classification, which is derived from Weidenreich (1930), depends largely on the relationship which the collagen fibres of bone bear to one another. Thus bone is divided into woven-fibred bone in which the collagen fibres are arranged in a random fashion, parallel-fibred bone in which the fibres all run parallel to one another in the same direction, and lamellar bone in which the fibres are arranged in layers, the fibres of each layer having a specific orientation. The recognition of bone in which there is a random arrangement of the fibres and that in which there is an orderly arrangement is of value, but the distinction between parallel-fibred and lamellar bone, while academically correct, appears to serve no useful purpose, as it gives little indication of the developmental history of an area of bone.

This difficulty may be overcome, in part, by further subdividing parallel-fibred and lamellar bone into units or regions which are characterized by their developmental histories and the relationship of their collagen bundles to intra-osseous blood vessels. Thus osteones (Haversian systems) are those regions of bone in which the fibres are arranged in some concentric fashion around one or more vascular canals; whereas circumferential lamellar systems are those regions in which the fibres run parallel to the endosteal or periosteal surfaces of the bone and bear a tangential relationship to neighbouring vascular canals. It is evident, however, from the present investigation that there are two types of osteones—those forming *de novo* in the previously unossified vascular spaces of woven-fibred bone, and those whose formation is preceded by erosion of regions of pre-existing bone. Various terms have been employed to indicate this distinction. Thus osteones forming *de novo* have been designated primitive, simple, embryonal and atypical Haversian systems. Similarly, the first osteones to be formed in erosion cavities are regarded by some as the first generation of typical osteones and by others as the second generation of Haversian systems (Lacroix, 1951; Pritchard, 1956; Rouiller, 1956; Fawcett, 1954; Bloom, 1957).

Because the two types of osteones are distinct in both development and structure it seems reasonable to give definite recognition to this distinction in the terminology. The simplest way in which this can be done is to describe those osteones forming *de novo*, as primary osteones and to regard the units forming in erosion cavities as the first, second and third generation etc. of secondary osteones.

Again the term circumferential lamellar systems is inaccurate because the tissue concerned is by no means invariably lamellated and it is suggested that a more comprehensive term would be surface bone.

In this report, therefore, mammalian bone has been classified into four types, namely woven-fibred bone, primary osteones, secondary osteones and surface bone.

Interstitial bone consists of the remnants of the other four tissues. The main features of these tissue types are summarized in Table 1.

At the present time a large amount of experimental work is necessarily performed on the skeletal systems of lower mammals. Little regard is sometimes taken, however, of the different types of bone which are thereby being utilized, and very little is known of their particular properties or of their reaction to experimental procedures. It seems therefore of the greatest importance that the structure of the bones of an experimental animal should be clearly appreciated and that this structure should be taken into account when conclusions are drawn from experimental work.

The main stages through which the structure of a bone passes during its development are as much part of the inherent growth pattern as the shape of the definitive bone itself. On the other hand, it seems probable that further investigation may elucidate such factors as the incidence and rate of some of these changes. Thus it has been stressed by D'Arcy Thompson (1942) that in many mammals the rate of growth shows seasonal variations which are the results of changes in temperature and dietary conditions. Furthermore, it is well known that periosteal and endosteal layers of surface bone form when growth is slowing down towards its final completion. It may be, therefore, that the thin layers of periosteal surface bone which are periodically formed upon, and then included within, predominantly woven-fibred bones (Text-fig. 2) are associated with periods of diminished growth rate.

Table 1

	Woven-fibred bone	Primary osteones	Surface bone	Secondary osteones
Primary or secondary	Primary	Primary	Primary or Secondary	Secondary
Limitation by cement line	−	−	− +	+
Presence of Sharpey fibres	+	+	+ −	−
Arrangement of collagen bundles	Random	Orderly	Orderly	Orderly
Presence of lamellation	−	− +	− +	− +
Relationship of collagen bundles	Non-specific	Concentric	Tangential	Concentric

The rate of formation of secondary osteones in different parts of single bones is another problem which requires further investigation. The incidence of these units in the anterior and posterior parts of the radius of an adult horse of approximately twelve years (Pl. 4, figs. 3, 4), and in the human tibia and femur in old age (Pl. 3, figs. 9, 10) suggest that neither age of bone nor any hormonal influence is the predominant factor in stimulating their formation. Neither does the distribution of secondary osteones appear to be directly related to the attachments of muscles or ligaments. On the other hand, it is possible that the rate of formation of these units may be determined by the stress to which a given area of bone is normally subjected. The problem of stress distribution in individual bones is a difficult one which has received comparatively little attention, but the introduction of photo-elastic techniques (Milch, 1940; Jessop & Harris, 1949; Fessler, 1957) and the application of resistance strain gauges to the examination of fresh bone (Hirsch & Brodetti, 1957) may be expected to give more information on this important subject.

SUMMARY

1. The fibre patterns in bone from man, ox, horse, sheep, pig, dog and cat have been examined in sections stained by Weidenreich's method and in ground sections viewed by polarized light.

2. A classification of bone types is suggested which is based on the developmental history of the area, its fibre pattern and the relationship of the fibre pattern to vascular canals.

3. The fibre patterns in four types of bone are described, namely woven-fibred bone, primary osteones, surface bone and secondary osteones.

4. The relationship of these bone types to the mechanism of growth in girth is discussed.

I have to thank Prof. R. Walmsley for his advice throughout this investigation, and also Messrs J. Brown and R. Stuart of this Department for their technical assistance.

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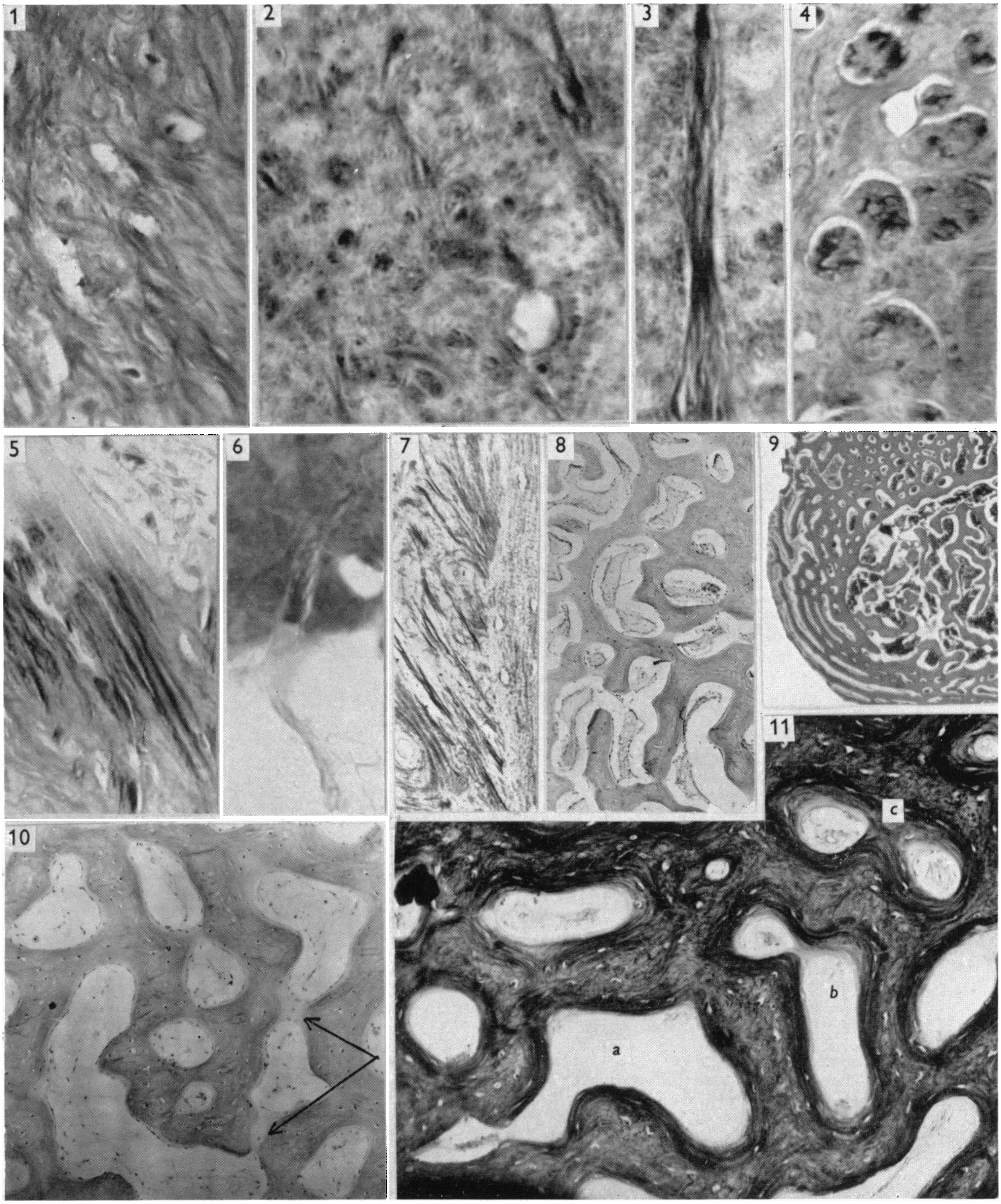

SMITH—Collagen fibre patterns in mammalion bone

(*Facing p.* 342)

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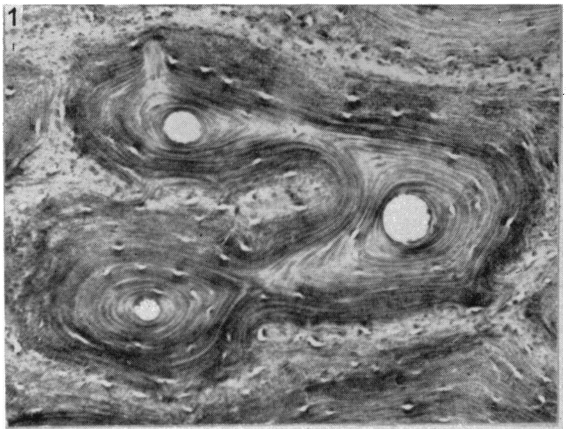

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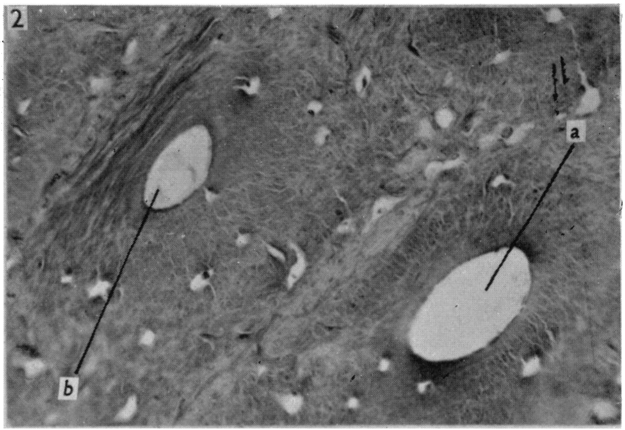

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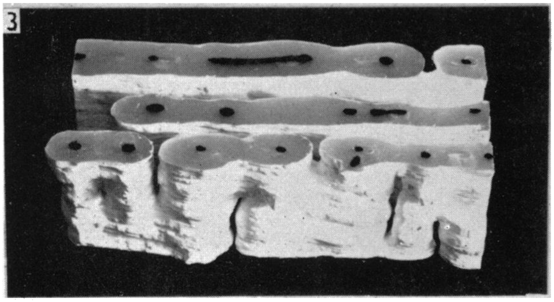

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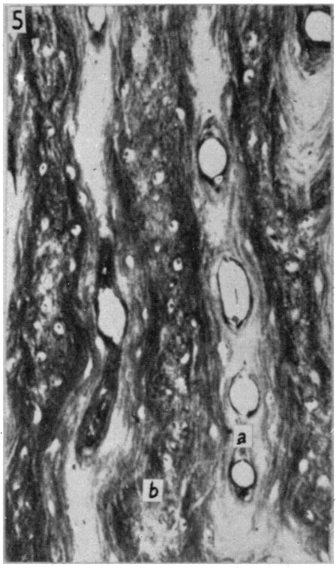

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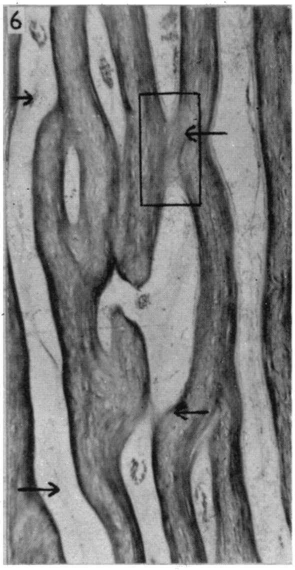

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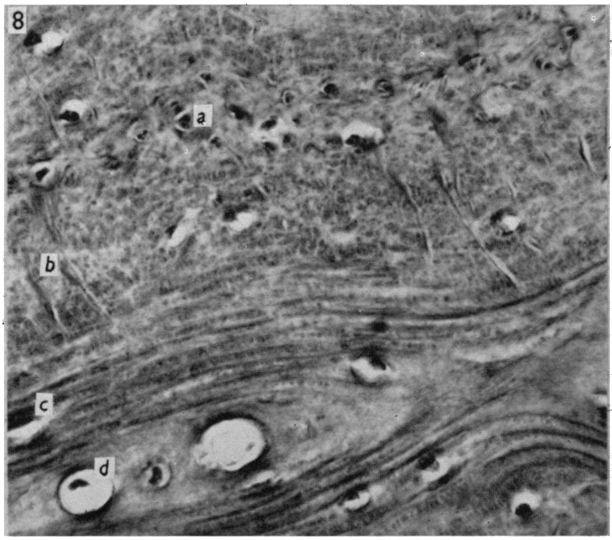

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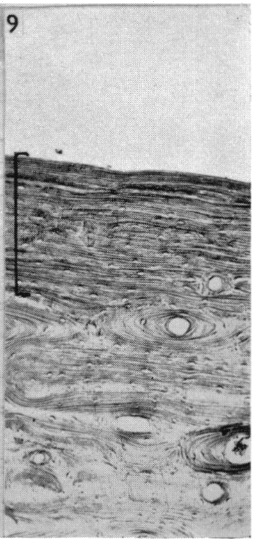
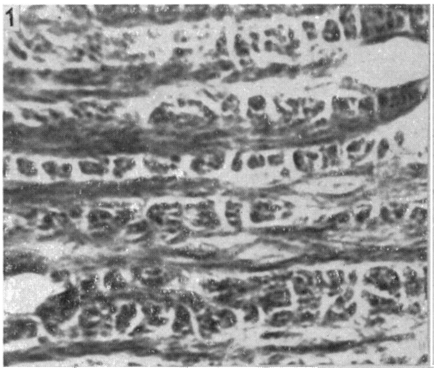
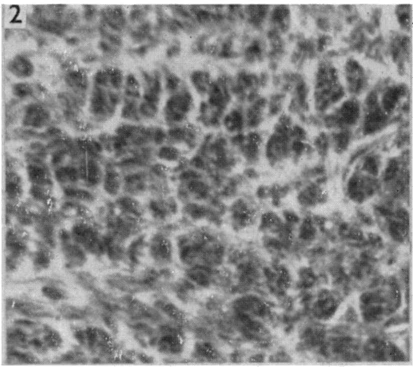
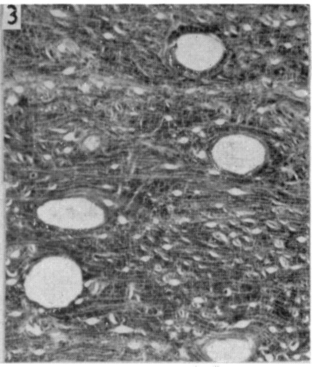
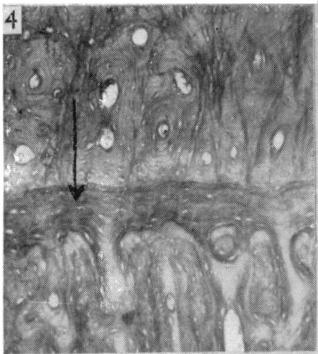


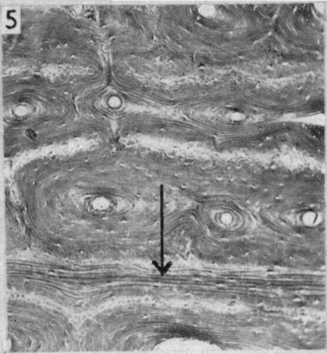
SMITH—Collagen fibre patterns in mammalian bone

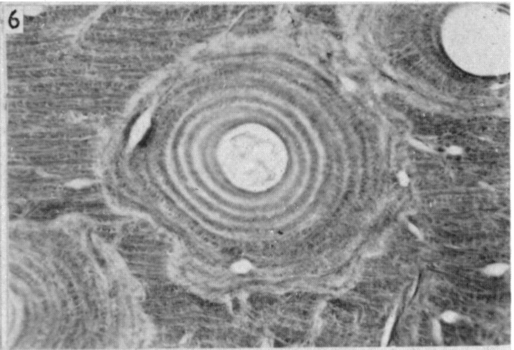


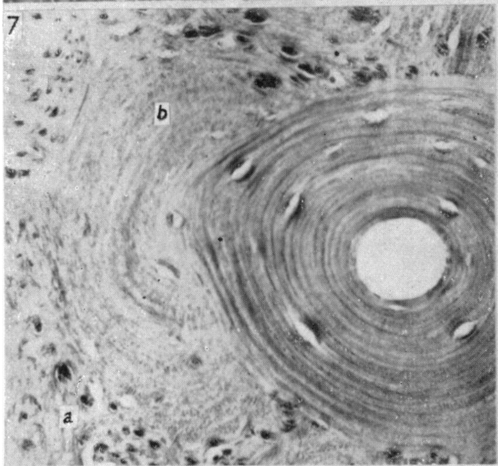


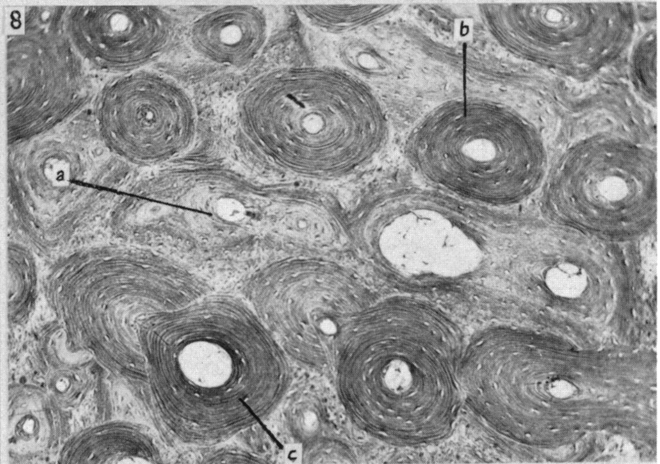


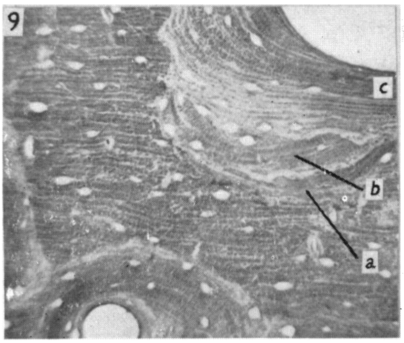


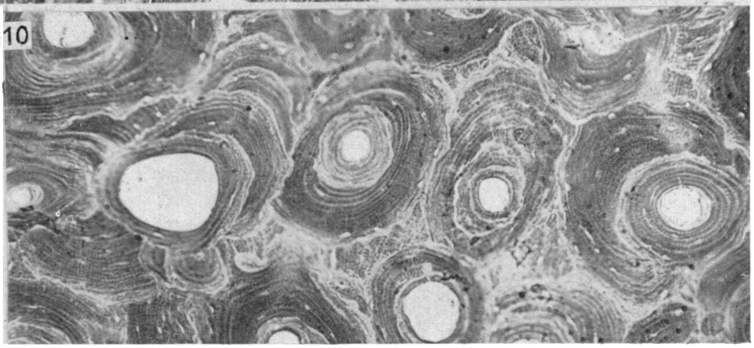












SMITH—COLLAGEN FIBRE PATTERNS IN MAMMALIAN BONE

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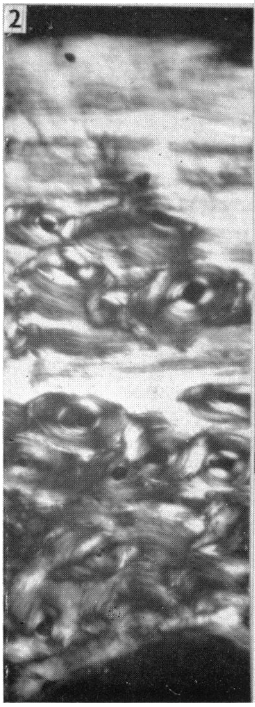

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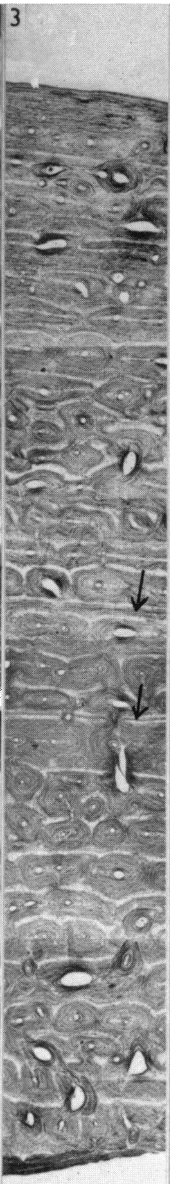

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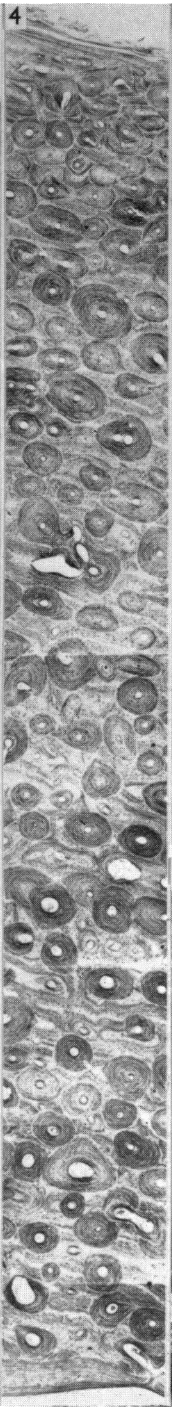

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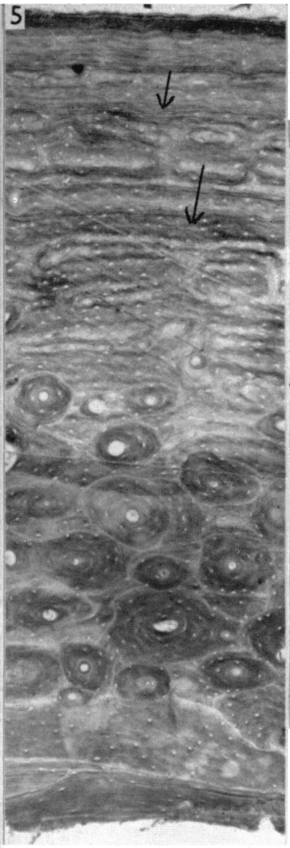

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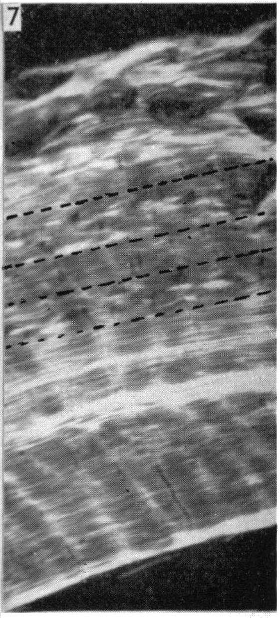

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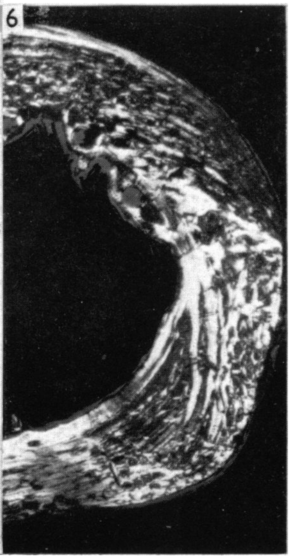

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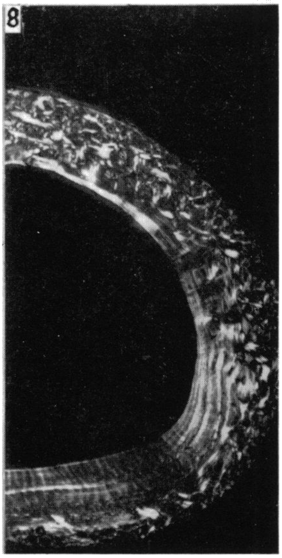

SMITH—COLLAGEN FIBRE PATTERNS IN MAMMALIAN BONE

EXPLANATION OF PLATES

PLATE 1

Fig. 1. L.S. human tibia at birth. Woven-fibred bone. Weidenreich, × 500.

Fig. 2. T.S. human tibia at birth. Woven-fibred bone. Weidenreich, × 500.

Fig. 3. T.S. metacarpus of ox at 2 years. Sharpey fibre. Weidenreich, × 900.

Fig. 4. T.S. femur of 170 mm. human foetus. Sharpey fibres. Weidenreich, × 900.

Fig. 5. T.S. periosteal surface of human tibia at birth. Bone below, soft tissues above. Weidenreich, × 150.

Fig. 6. T.S. metacarpus of 7 months ox foetus. Bone above, intra-osseous vascular space below. Weidenreich, × 600.

Fig. 7. L.S. radius of adult horse. Secondary osteone on right. Weidenreich, × 150.

Fig. 8. T.S. metacarpus of 7 months ox foetus. Weidenreich, × 70.

Fig. 9. T.S. femur of 170 mm. human foetus. Posterior aspect above. H. & E., × 17.

Fig. 10. T.S. metacarpus of 7 months ox foetus. Arrows indicate pre-osseous bridges. Weidenreich, × 120.

Fig. 11. T.S. metacarpus of ox at 2 months. Weidenreich, × 150.

PLATE 2

All sections stained by Weidenreich's method

Fig. 1. T.S. radius of adult horse. Irregular primary osteone surrounded by woven-fibred bone. × 150.

Fig. 2. T.S. human tibia at 5 months. *a* and *b*, cylindrical primary osteones surrounded by woven-fibred bone. × 250.

Fig. 3. Wax plate reconstruction of the primary osteones from the radius of the adult horse, seen in fig. 4.

Fig. 4. T.S. radius of adult horse. The upper and lower margins of the figure are parallel to the periosteal surface. *a*, woven-fibred bone; *b*, circumferential primary osteones. × 65.

Fig. 5. T.S. metacarpus of ox at 2 years. The upper and lower margins of the figure are parallel to the periosteal surface. *a*, radial primary osteone; *b*, woven-fibred bone.

Fig. 6. L.S. human tibia at 5 months. Arrows indicate sites of deflection on the predominantly longitudinal course of the vascular canals of cylindrical primary osteones. × 60.

Fig. 7. The area outlines in fig. 6. × 300.

Fig. 8. T.S. radius of adult horse. *a*, woven-fibred bone containing Sharpey fibres. *b*, *c*, *d*, circumferential primary osteone. *b*, non-lamellated zone; *c*, lamellated zone; *d*, amorphous zone.

Fig. 9. T.S. periosteal surface, radius of adult horse. Bracket indicates surface bone. × 65.

PLATE 3

All sections stained by Weidenreich's method

Fig. 1. T.S. adult human tibia. Lamellated surface bone. × 800.

Fig. 2. T.S. adult human femur. Non-lamellated surface bone. × 800.

Fig. 3. T.S. adult human tibia. Outer part of cortex. Lamellated surface bone, traversed by Sharpey fibres. × 80.

Fig. 4. T.S. metacarpus of ox at 7 years. The arrow indicates an included layer of non-lamellated surface bone. × 70.

Fig. 5. T.S. radius of adult horse. The arrow indicates an included layer of lamellated surface bone. × 65.

Fig. 6. T.S. adult human tibia. First-generation secondary osteone in surface bone containing Sharpey fibres. × 200.

Fig. 7. T.S. radius of adult horse. *a*, woven-fibred bone containing Sharpey fibres; *b*, cylindrical primary osteone; *c*, first-generation secondary osteone. × 360.

Fig. 8. T.S. radius of adult horse. *a*, circumferential primary osteone surrounded by woven-fibred bone; *b*, first-generation secondary osteone; *c*, second-generation secondary osteone. × 65.

Fig. 9. T.S. adult human tibia. *a*, *b* and *c*, first-, second- and third-generation secondary osteones in surface bone. × 200.

Fig. 10. T.S. adult human femur. Secondary osteones in interstitial bone derived from similar unit. × 110.

PLATE 4

Fig. 1. T.S. femur of adult cat. Periosteal surface above. Ground section. Polarized light, × 40.

Fig. 2. T.S. medial part of adult human tibia. Periosteal surface above. Ground section. Polarized light, × 30.

Fig. 3. T.S. posterior part of radius of adult horse. Periosteal surface above. Arrows indicate included layers of surface bone. Weidenreich, × 20.

Fig. 4. T.S. anterior part of radius of adult horse. Periosteal surface above. Weidenreich, × 20.

Fig. 5. T.S. anterior part of femur of adult dog. Periosteal surface above. Arrows indicate included layers of surface bone. Weidenreich, × 50.

Fig. 6. T.S. right half of femoral shaft of adult dog. Anterior aspect above. See text-fig. 3*c*. Ground section. Polarized light, × 8.

Fig. 7. T.S. posterior part of femur of adult cat. Periosteal surface above. The interrupted lines enclose the two circumferential zones of longitudinal vascular canals. Ground section. Polarized light, × 40.

Fig. 8. T.S. right half of femur of adult cat. Anterior aspect above. Ground section. Polarized light, × 8.