THE STRUCTURE AND DEVELOPMENT OF CRANIAL AND FACIAL SUTURES

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It is surprising, in view of the controversy which has long raged about the functional role of the sutures in the growth of the skull, that so little attention has been paid to their histological structure and development. The most comprehensive study is that of Sitsen (1933), who describes the development of the lambdoid suture in man between the 8th month of foetal life and 12 years. Mair (1926), Petersen (1930), Troitsky (1932), Bernstein (1933), Weinman & Sicher (1947), Moss (1954), and Scott (1954) have made more limited contributions to the literature.

As it was evident that much more detailed and accurate information was required in order to provide the necessary basis for experimental work on the morphogenesis and functions of the sutures, it was decided to investigate the development and structure of a variety of sutures in available foetal, young and adult material.

MATERIALS AND METHODS

Serial sections through the heads, or parts of the heads, of several stages in the development of six species were used. These comprised: nine human specimens, ranging from 45 mm. C.R. to full term; seventeen sheep from 48 mm. C.R. to 18 months; six pigs from 30 mm. C.R. to 5 months post-natal; five cats from 40 mm. C.R. to 57 days post-natal; four rabbits from 35 mm. C.R. to full term and an adult; and a series of ninety-three rats ranging in age from the 15th day of foetal life to 1 year.

More than one half of the total number of specimens were cut coronally, the remainder were chiefly cut in the sagittal plane but a few were transverse. Most of the series were stained by Masson's or Mallory's methods, or with Weigert's haematoxylin and van Gieson. Some sections were impregnated with silver by Wilder's method, and a few were stained with Harris's haematoxylin and eosin or safranin. Some alcohol-fixed rat heads were also cut and stained for alkaline phosphatase by Gomori's method and for glycogen by the periodic-acid-Schiff method.

The Masson and Mallory stained sections were most useful for determining the patterns of relatively coarse collagenous fibres. Wilder's silver method gave more precise information about the finest collagen fibres. Weigert's haematoxylin and van Gieson was especially useful in the correlation of cellular with fibrous patterns. Sites where active osteogenesis was in progress were clearly demonstrated in sections stained for alkaline phosphatase and glycogen.

METHODS

All the sutures examined went through essentially similar stages in their development. It will be more convenient, therefore, and less repetitive, to describe the observations stage by stage, rather than to attempt to give the chronological history of each suture separately.

(1) *Stage of approaching bone territories.* (i) It is to be noted that the term '*bone territory*' includes the definitive bone, the preosseous cambial layer and the fibrous periosteum. (ii) A '*suture*' is to be regarded as the entire complex of cellular and fibrous tissues intervening between, and surrounding, the definitive bone edges.

(2) *Stage of meeting of the bone territories.*

(3) *Early growing stage.*

(4) *Late growing stage.*

(5) *Adult stage.*

(1) *Stage of approaching bone territories*

Two main types may be distinguished, viz. (*a*) that in which the bones approach one another through loose mesenchymatous tissue, as in the face (Pl. 1, fig. 1); and (*b*) that in which the bones approach within a preformed fibrous membrane, as in the cranial vault (Pl. 1, figs. 2, 4).

(*a*) *The facial skeleton*

Each approaching 'bone territory' shows three well-marked zones: (1) an outer periosteal fibrous capsule, (2) a periosteal cambial layer, (3) an inner plate of woven membrane bone (Pl. 1, figs. 1, 9).

The *periosteal fibrous capsule* shows an essentially tangential arrangement of collagenous fibres interspersed with similarly orientated elongated fibroblasts (Pl. 1, fig. 9). At the advancing edge of the bone territory these fibres run at right angles to the plane of the bone: elsewhere they are parallel to it.

The *cambial layer* shows fine collagen bundles running in a radial direction from the bone to the fibrous capsule. These are the osteogenetic fibres, some of which will later develop into stout Sharpey's perforating fibres. The cambial layer is very cellular, showing an outer zone of small rounded proliferating elements (pro-osteoblasts) and an inner zone next to the bone of larger cells, pyriform or polygonal in shape (definitive osteoblasts) (Pl. 1, fig. 9).

In a previous paper (Pritchard, 1952) the cytology of these cells has been considered in detail. Suffice it to state here that the pro-osteoblasts show numerous mitotic figures, and are rich in glycogen (Pl. 2, fig. 16), and alkaline phosphatase, while the definitive osteoblasts do not show mitotic figures, contain no glycogen, somewhat less phosphatase than the pro-osteoblasts, intense cytoplasmic basophilia, a very large Golgi apparatus and numerous elongated mitochondria.

The cambial layer is evidently the site of very active osteogenesis, the new bone being of the woven variety. It is evident also that the fibrous periosteal capsule must be expanding to keep pace with the growing bone.

In the loose cellular mesenchyme between the bone territories the future location of the definitive suture is not indicated by any special differentiation of cells or fibres

(Pl. 1, fig. 1), although in the palate a very thin strand of condensed mesenchyme runs between the approaching bone territories. This may possibly serve to guide the bones towards each other (Pl. 1, fig. 1).

(*b*) *The cranial vault*

Unlike the bones of the facial skeleton, those of the cranial vault approach each other within an already differentiated fibrous membrane, the ectomeninx, desmocranium, or fibrous brain capsule (Pl. 1, figs. 2, 4). Each bone is surrounded by a cambial layer of osteogenetic cells and fibres similar to that described for the facial skeleton, outside which the fibrous periosteal layers, represented by the pericranium and dura mater, are well differentiated. These two membranes, however, do not encapsulate the cambium at the extreme edge of the bone with fibres running at right angles to the plane of the bone, as in the face. Instead, they join in front of the advancing cambium and run across the region of the presumptive suture parallel to the plane of the bones. The approaching bones with their cambial layers therefore appear to be delaminating the ectomeninx into pericranial and dural strata.

The presumptive suture is thus chiefly composed of parallel fibres continuous with the pericranium and dura mater of the approaching bone territories. The eventual meeting place of the bones is as yet unmarked by any special arrangement of cells or fibres, although in the case of the presumptive sagittal suture the position of the definitive suture can be inferred from the position of the sagittal venous sinus (Pl. 1, fig. 2).

(2) *Stage of meeting of the bone territories*

Because of the differences between the face and cranial vault in respect of the composition of the bone territories and the structure of the tissue lying between them, sutural junction is effected in two different ways. In the face the fibrous capsules of the bone territories become united by means of two fibrous laminae, an external and an internal, which make their appearance as the territories come close together (Pl. 2, figs. 3, 5). These will be referred to as the *uniting layers*. The rounded extremities of the fibrous capsules, however, retain their separate identities, for a remnant of the loose cellular mesenchymal tissue, which previously lay between the approaching bone territories, intervenes.

The suture at this stage therefore presents *five distinct layers* as one passes from the edge of one bone to the edge of the other, namely the first cambial layer, the first fibrous capsule, the loose cellular middle zone, the second fibrous capsule and the second cambial layer. These will be referred to as the *intervening layers* of a suture as opposed to the aforementioned uniting layers.

The cambial and capsular layers on each side retain the general appearance they had before the bone territories met. They are, therefore, identical in structure, and directly continuous with, the cambial and fibrous layers of the periosteum on the non-sutural surfaces of the bone (Pl. 1, figs. 3, 5).

The meeting of the cranial vault bones is different in that the approaching bone territories are not separated by loose mesenchyme, but are united by the fibrous ectomeninx which is continuous with the periosteal layers of each bone (Pl. 1, figs. 2, 4). Moreover, there are no preformed fibrous capsules as in the facial skeleton. These, however, rapidly appear on each side as the edges of the bones approach closely.

The width of undelaminated ectomeninx between the bones progressively decreases until the cambial layers on either side are almost in contact, when the remnant begins to split into relatively dense outer and inner uniting layers leaving a looser layer between them (Pl. 1, fig. 4). The way might now seem clear for the cambial layers to fuse across this loose region, but the rapid appearance of a pair of encapsulating fibrous strata prevents this (Pl. 1, fig. 8). These capsules consist of relatively coarse parallel fibres running at right angles to the uniting layers, covering the cambial layers on each side and separated from each other by the loose middle tissue (Pl. 2, fig. 14). The origin of the capsular fibres is difficult to determine with certainty, but the appearances suggest that the more peripheral cambial cells become transformed into fibroblasts around which collagen fibres are laid down.

In this way the sutures of the cranial vault come to possess five intervening and two uniting layers as in the facial skeleton (Pl. 1, fig. 8; Pl. 2, fig. 14).

(3) *Early growing stage*

For some time after the meeting of the bony territories and formation of the suture, all the layers mentioned continue to be well marked and easily differentiated (Pl. 1, figs. 7, 10; Pl. 2, fig. 11). The edges of the bones pass from a unilaminar to a bilaminar or a multilaminar state (Pl. 2, fig. 11) as they increase in thickness by surface accretion on both external and internal surfaces. Diploic spaces are formed, partly by enclosure of the spaces between the laminae of bone, partly by osteoclastic resorption. The cambial layer shows clearly defined pro-osteoblastic and osteoblastic zones; and cellular proliferation, indicated by the frequency of mitotic figures in the pro-osteoblastic zone, is evidently very active. In the cambial zone, also, bundles of osteogenetic fibres emerge from the bone and run radially between the osteogenetic cells to join the tangentially running fibres of the capsular zone. The cambial zone shows intense alkaline phosphatase activity and conspicuous glycogen storage, similar in distribution to that previously described, but the fibrous capsular zone and the loose middle zone are practically devoid of both these substances (Pl. 3, figs. 18, 19). The suture at this stage is evidently the site of rapid marginal extension of the adjoining bones, two growth centres being apparent, viz. the pair of cambial zones surrounding the edges of the bones. The fibrous capsular zones and the middle zone, however, show little evidence of active cellular proliferation, although the capsular tissue must in fact be growing in order to accommodate the ever increasing volume of the contained osseous tissue.

(4) *Late growing stage*

The bone edges are now thicker and more compact (Pl. 1, fig. 6; Pl. 2, fig. 12) and have a smoother surface. Instead of pointed trabeculae of woven bone projecting radially towards the suture, as in the early growing period, compact lamellar bone is now being added tangentially. Much of the earlier formed woven bone has been removed and replaced with lamellar bone containing simple Haversian systems. The cement lines near the suture edge, moreover, are mostly evenly curved and parallel, indicating a more or less continuous process of surface accretion. Reversal lines, and Howship's lacunae with osteoclasts, are occasionally seen, indicating local areas of past and present resorption, probably associated with internal remodelling. There is little evidence that extensive surface resorption plays an important role in suturogenesis, even in squamous over-lapping sutures. The sutural connective tissue still shows the five intervening zones already described, but their proportions have altered. The cambial layer is reduced to a single layer of osteoblasts, and in places these are represented only by inconspicuous cells flattened against inactive bone surfaces. The two fibrous capsular layers are denser, but the direction of the fibres remains tangential to the sutural faces of the bones (Pl. 2, fig. 12). Some strong bundles of radially directed fibres emerge from the bone surfaces and end in the capsular layers (Pl. 1, fig. 6). These should now be interpreted as Sharpey's fibres, binding the bone to the capsule, and not as osteogenetic fibres, the term more appropriate in the early growing stage. Very similar, but weaker, Sharpey's fibres, are found in the remnant of the cambial layer of the non-sutural periosteum.

The fibrous periosteum covering the non-sutural surfaces of the bones now has the appearance of splitting into two layers as the suture is reached, the outer of which runs straight across the external boundary of the suture from one bone to the other to form one of the uniting layers of the suture; while the inner turns into the suture to form one of the fibrous capsules, which in turn joins the inner layer of the periosteum on the other side.

The middle zone is now very vascular, exhibiting large thin-walled sinusoidal vessels which join the diploic vessels, the dural sinuses and the pericranial veins. Its fibres are in the form of independent bundles which course between the blood vessels from one fibrous capsule to the other. Their predominant direction is at right angles to the capsular fibres, but some are oblique. On the whole the middle zone is much less densely fibrous than the capsular zones on either side of it. In parts of some sutures, however, where the vessels are scanty, the middle zone is inconspicuous, for the two capsular zones are very close together and partly fused.

At this stage growth of the bones at the suture is evidently very slow and chiefly directed towards rounding and smoothing the bone edges.

(5) *Adult stage*

The bone edges now show no signs of growth activity, and the cambial layer is reduced to a single layer of inconspicuous flattened cells (Pl. 2, figs. 13, 17). The potential osteogenetic nature of these cells, nevertheless, is proved by their rapid re-awakening to activity in the presence of a fracture in a distant part of the bone. The fibrous capsules, on the other hand, are still distinct (Pl. 2, fig. 13), and are separated from one another by a middle zone which is even more vascular than before (Pl. 3, fig. 22).

The general direction of the fibres is the same as in the growing stages, but now numbers of Sharpey's fibres can be traced in continuity from one bone to the other (Pl. 2, fig. 15). Despite these the strongest bond of union is through the uniting layers at the external and internal boundaries of the suture.

CARTILAGE

In several sutures cartilage has been found at the margins of the bones or in the sutural tissues proper. It was most common in the sagittal and mid-palatal sutures at the end of the period of rapid growth, and was of two types.

The first type occurred as irregular islands or areas of large-celled cartilage with scanty matrix, interspersed with, or capping the trabeculae of woven bone at or near the sutural edges. In one specimen such cartilage ran from one parietal to the other across the sagittal suture (Pl. 3, fig. 21).

The second type presented a more orderly appearance. In the palate of the rat, for example, both cambial layers of the suture were temporarily transformed into expanded epiphysis-like masses covering the margins of the bones. Each mass showed a regular gradation from pro-cartilage near the middle of the suture, through definitive hyaline cartilage, to hypertrophic cartilage adjacent to the bone (Pl. 3, fig. 20). The two cartilage masses were separated in the middle of the suture by a narrow band of compressed fibrous tissue representing the fused capsular and middle zones.

In the rat a sagittal rod of cartilage was found transiently just above the sagittal venous sinus (Pl. 1, fig. 2), but it disappeared soon after birth, and as it lay beneath that part of the ectomeninx in which the definitive suture was destined to form, it evidently plays no part in suture formation. This cartilage appeared to be a forward extension from the tectal region of the chondro-cranium.

SYNOSTOSIS

In several specimens localized areas of synostotis across the suture were found. This was not uncommon in the sagittal suture of the rat at any time after the third week from birth. Other examples were found in the mid-palatal suture. In one such specimen the connecting bone contained hypertrophic cartilage cells (Pl. 2, fig. 22), suggesting that bony union had been preceded by cartilaginous union as in the example previously mentioned. In the sagittal suture *partial* synostosis was sometimes found (Pl. 3, fig. 24), the bones being united on the dural but not on the pericranial side.

GROSS SUTURAL MORPHOLOGY

This paper is not concerned with the detailed description of adult sutural patterns. It is to be noted, however, that a similar five-layered arrangement of cells and fibres was found in simple harmonic sutures, in complicated denticulate sutures (Pl. 1, fig. 10) as well as in squamous overlapping sutures, and the general observations reported apply equally well to all these varieties.

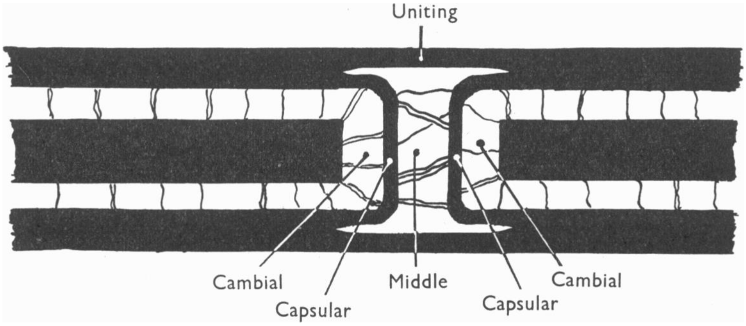
CHRONOLOGY

The absolute time-course of suture differentiation varied considerably in different sutures, in different animals and even in different parts of the same suture, but all went through essentially similar stages in their development. This study was not competent to determine absolute, or even relative, growth rates at different sutural margins, nor was interest especially directed to the widely different times at which suture margins cease growing. It was apparent, however, that the mode of growth, if not its rate, conformed to a common pattern in all cases.

CONCLUSIONS AND DISCUSSION

Fundamental structure of cranial and facial sutures

In the animals studied, the sutures throughout their development exhibited *five* distinct layers of cells and fibres *between* the edges of the adjoining bones. In addition, the outer and inner boundaries of the suture were marked by fibrous strata which ran without interruption from the fibrous periosteum of one bone to that of the other. Thus we have *five* intervening layers and two *uniting* layers comprising the basic structure of a suture (Text-fig. 1).



Text-fig. 1. Diagram to show the general construction of a suture.

All these layers have, at one time or another, been described by previous workers, but no single worker seems to have recognized them all. Thus Sitsen (1933), in the human lambdoid suture, describes three intervening layers in the newborn, which seem to correspond to the cambial layers and the middle layer of our description, but he fails to recognize the capsular layers. At a later stage he describes only one layer, apparently the combined capsular and middle layers. Troitsky (1932) describes the uniting as well as the cambial layers. He also mentions a 'non-osteogenic' middle layer, but he does not differentiate this into capsular and middle zones. Bernstein (1933) mentions a loose middle layer and the perforating fibres of the cambial layer. Weinman & Sicher (1947) mention three layers, the cambial layers not being described. Moss (1954) describes a suture as possessing three layers at an early stage of development, corresponding to our capsular and middle layers, but in the adult he recognizes only a single (fibrous) layer. Scott (1954) describes four layers, the cambial and the capsular on each side, but does not mention the middle layer.

It is probable that the authors mentioned missed some of the layers because selective fibre stains were not always employed. Both Scott and Troitsky stress the continuity of the cambial and capsular layers with the corresponding cambial and fibrous layers of the periosteum. This important fact for the understanding of bone growth at sutures seems to have been overlooked by other investigators.

Initial development of sutures

This investigation has shown two differing modes of suture formation in the foetus. In the formation of the facial sutures the cambial and capsular layers are present around the advancing edges of the bones well before they meet, but the uniting layers are not differentiated until the sutural junction is about to be effected. In the skull vault, on the other hand, the edges of the bones are provided with a cambial layer, but no capsular layer, and the uniting layers are already present (as the undivided ectomeninx), although not yet delaminated from each other. In the skull vault it is the capsules which appear as the bones meet. The middle layer in each case arises from the mesenchyme or ectomeninx which lies between the bone territories.

Each bone territory thus contributes cambial and capsular layers to the suture. The middle layer and the uniting layers, on the other hand, are provided by the inter-territorial tissues. Of previous workers only Scott (1954) seems to have appreciated that a suture is constructed from the periosteal layers of a pair of osseous territories, though he failed to recognize the contribution from the tissue between the territories.

At this point it is of interest to compare and contrast suture development with that of a diarthrodial joint. The three-layered *interzone* of diarthrodial joints described by Haines (1947) is paralleled by our five-layered *intervening* zone; his chondrogenous layer corresponding to our combined cambial and capsular layers, while his intermediate loose layer and our middle layer are evidently homologous. But Haines describes the disappearance of the chondrogenous layer as it is transformed into articular cartilage, while the corresponding layers in sutures persist. Haines's loose intermediate layer breaks down to form part of the synovial cavity but the middle layer in a suture persists and becomes very vascular, besides containing fibres which run from one bone to the other.

The fibrous capsule of a diarthrodial joint appears homologous with the uniting layers of a suture, but, just as Haines distinguishes two kinds of capsular development, viz. that arising from non-blastemal mesenchyme (the usual method) from that arising from the skeletal blastema (in fish, mammalian hyoid), so in our study we find the uniting layers of facial sutures originate from non-blastemal mesenchyme but in the cranial vault from the blastemal ectomeninx.

No special differentiation or orientation of cells or fibres marks the future site of meeting of the bone territories before the sutures have been established. This suggests that the position of the sutures is determined by, and is not determined until, the meeting of the bones, a conclusion which is supported by experimental work on the rat in which the skull has been damaged *in utero* leading to abnormal sutural patterns after birth (Girgis & Pritchard, 1955). Troitsky's (1932) finding of normal sutural patterns following damage to the neonatal skull is attributable to the sutures having been already established at the time of experimental interference.

Changes in suture structure during development

As development proceeds profound changes take place in the structure of a suture. The cambial layers, which originally were thick and exhibited several strata of proliferating and differentiating osteogenetic cells, become progressively thinner until eventually only a single layer of cells, flattened against the surface of the bone, remains. The finer bundles of osteogenetic fibres which ran between the osteoblasts of the earlier active cambium are gradually replaced by stout Sharpey's fibres, some of which pass directly from one bone to the other. The capsular layers become increasingly dense until they form the main bulk of the suture. The middle zone, on the other hand, becomes increasingly vascular.

Nevertheless, in spite of these changing appearances, the original five-layered structure of the suture is always discernible. Sitsen (1933) and Moss (1954), who have described a simplification of the sutural structure down to a single 'sutural membrane' in the adult, have failed to appreciate the remnant of the cambial layers, and, unaccountably, have not apparently noticed the very vascular middle layer.

The changes in sutural histology just described are paralleled by changes in the appearance of the sutural faces of the bones. At an early stage pointed trabeculae of woven bone project into the thick cellular cambial layers. The trabeculae are covered with large active osteoblasts and the classical appearance of rapid bone formation is found. Later the bone margin presents a smoother, rounded face to the suture and a single epithelioid layer of active osteoblasts covers its surface. The superficial layers of the bone consist now of circumferential lamellae containing here and there simple Haversian systems. In places osteoclasts in Howship's lacunae witness to the remodelling which is taking place, whereby the earlier woven bone is removed and replaced by lamellar bone. Later still the bone edge is quite smooth and the osteogenetic layer is inactive. These changes in the structure of the bone (but not of the cambium) are described in detail by Bernstein (1933) and Sitsen (1933).

The mode of origin of the interlocking of the bone margins in complex sutures has not been specially investigated here, so that a firm opinion cannot be expressed as to whether the denticulations arise by differential accretion only or by combined accretion and resorption. The surprising infrequency of signs of osteoclastic erosion at sutural margins of the bones, however, would lead us to suspect that differential accretion is the more probable, a conclusion also reached by Mair (1926), Bernstein (1933), Massler & Schour (1951), and Baer (1954).

Functional significance of sutural morphology

The histology of the suture suggests that it has two main functions, viz. that it is a site of active bone growth, and that it is at the same time a firm bond of union between the neighbouring bones, which nevertheless allows a little movement.

That sutures have this dual function has been expressly stated by Bernstein (1933), Giblin & Alley (1944), Massler & Schour (1951), Moss (1954), Baer (1954), and Scott (1954).

That active bone formation takes place at sutures is rendered very probable from the fact that the cambial layers show the classical histological picture of new bone formation in an even more marked degree than the cambial layers of the periosteum on the non-sutural surfaces of the bones. The intense phosphatase activity and glycogen storage of the sutural cambial layers further reinforces this view. Moreover, direct measurement of the rate and amount of bone growth at sutures is possible by the employment of markers. Thus, von Gudden (1874) showed that holes drilled in the parietal and frontal bones of young rabbits moved apart in subsequent growth. Troitsky (1932), using silver wires placed in the skull vault of puppies, Giblin & Alley (1942), using trephine holes filled with lamp-black, and Massler & Schour (1951) and Baer (1954), employing alizarin staining, have confirmed this separating growth at sutures. Baer made an extensive series of measurements which demonstrated the over-riding importance of bone formation at sutures in the enlargement of the skull; and also the vital role of differential growth at different sutural margins in determining the changing form of the skull during ontogeny. The failure of von Mijsberg (1932) and Brash (1934) to demonstrate such growth is probably accounted for, as Moss (1954) argues, by their using animals of an age at which cranial expansion had virtually ceased.

Despite this majority view that bones grow at their sutural margins, the sutural element responsible for growth is in doubt. Bones cannot grow interstitially, and it is generally recognized that soft-tissue growth must take place at sutures to provide the substratum for bone formation, but while Weidenreich (1930), Bernstein (1933), Giblin & Alley (1944), and Weinman & Sicher (1947) think that the middle layer of loose cellular connective tissue is the important proliferating tissue, Troitsky (1932), Massler & Schour (1951), Moss (1954), and Scott (1954), correctly, we believe, attribute this role to the cambial layers. These certainly have the histological appearance of rapidly proliferating tissues, including numerous mitotic figures, but the middle zone has not. The latter has, in fact, the character of a neutral zone between two growth zones. Troitsky (1932) has also stressed the non-osteogenetic nature of the central part of the suture as a means of *limiting* bone growth and thus preventing synostosis. Perhaps of more importance is the fact that the provision of two sutural growth zones, separated by indifferent tissue, should enable growth at each bony margin to be independent of the other as regards rate, direction and duration, so allowing for changes in the shape and proportions of the growing skull (Moss, 1954).

The factors controlling osteogenesis at sutures have often been the subject of speculation. The most generally favoured view is that the expanding brain and continuing intracranial pressure lead to tension in the sutural soft tissues, and bone growth is a direct response to such tension (Weinnold, 1922; Loeschke & Weinnold, 1922; Massler & Schour, 1951; Moss, 1954). The experimentally-determined fact that opposing bony margins may have very different growth rates (Giblin & Alley, 1942; Moss, 1954; Baer, 1954), however, suggests that individual differences in inherent growth potential are also involved. Giblin & Alley (1944) and Moss (1954) stress the plasticity of suture growth whereby activity at one suture can compensate for inactivity at another, without the form of the skull as a whole being affected. Scott (1954), besides brain expansion, invokes the cartilages of the cranial base, nasal septum and lower jaw (Meckel's cartilage and the condyloid secondary cartilage) as 'pacemakers' governing sutural bone growth from a distance. Muscle activity associated with mastication may also profoundly affect the shape of the skull (Washburn, 1947), and thus, by inference, sutural activity.

Considered as articulations, the sutures possess the means for resisting gross separation of the bones, while at the same time permitting slight relative movement. The uniting layers are the strongest bond of union between the bones, and are evidently homologous with the fibrous capsule of diarthroses. The central zone, however, with its weak fibre bundles running in all directions and its sinusoidal blood vessels, could well allow some slight movement of one bone against the other, and so could be regarded as analogous to a synovial joint cavity. In most diarthroses the growth zones of the articulating bones are separated from the joint surfaces, and hence protected from undue mechanical stress (in particular, shearing stress), by the cartilaginous epiphyses. In sutures a similar protective role may well be a function of the fibrous capsules surrounding the cambial zones, cartilage being generally unnecessary because the major stresses are likely to be tensile ones.

The middle zone, in addition to separating the growing regions, and permitting momentary adjustments of one bone relative to the other, probably also enables slow progressive angulation to take place between the bones as the skull alters in shape during growth, thus saving the need for very extensive remodelling (cf. von Mijsberg, 1932). The great vascularity of the middle zone is more difficult to explain. It might simply be a means of filling the unwanted spaces between the fibre bundles without embarrassing movement; it might be a part of the emissary system of veins; on the other hand, it might serve as a hydrostatic cushion between the ends of the bone reinforcing the other protective measures against undue mechanical stresses.

Cartilage in sutures

Cartilage was found for a limited period in some post-natal sutures, especially the sagittal and mid-palatal. The appearance of secondary cartilage in the course of membrane bone development has often been described (de Beer, 1937; Symons, 1952; Dixon, 1953). It is evidently an alternative to bone formation among proliferating osteogenetic cells, and as such it is prominent in fracture repair of long bones (Pritchard & Ruzicka, 1950), and even in parietal fractures cartilage is occasionally formed (Pritchard, 1946). Similar tissue appears in cultures of bone *in vitro* (Fell, 1933). In membrane bones it may function as a growth cartilage (Symons, 1952) for long periods (e.g. mandibular condyle, ends of clavicle) or it may rapidly disappear, either by resorption with or without endochondral replacement, or by direct conversion to bone (Pritchard & Ruzicka, 1950).

The significance of sutural cartilage is debated. Sitsen (1933), who found it in infants under 6 months of age in the lambdoid suture, regards it as the result of particularly strong pressure and shearing stresses between the bones associated with recumbency at this stage of life, for it is well known that fibrous tissues may become cartilaginous when subject to such stresses. The effect of masticatory forces ought perhaps also to be considered in relation to the development of sutural cartilage.

A protective function for such cartilage is also a possibility, for, as is well known, growing bone is intolerant of pressure and shearing stresses. That cartilage is not present at all stages in suture development accords with the view that normally sutural tissues are under tension.

There remains the possibility that cartilage formation is the result of temporary ischaemic conditions associated with rapid growth (cf. Ham, 1930). In this connexion it is of interest that much greater amounts of cartilage appear in fractures of the skull vault when the blood supply to the area is deliberately reduced than under normal conditions of repair (Girgis, 1955, unpublished observation).

Closure of sutures

Obliteration of sutures and synostosis of the adjoining bones, if it happens at all, occurs usually after all growth has ceased. Different sutures and different animals vary greatly in this respect. In the great apes synostosis of all sutures occurs immediately growth has ceased, but in man and most laboratory animals sutures may never completely close (Bolk, 1915). These differences have been attributed to the differences in the degree of development of the masticatory apparatus. In this investigation local areas of synostosis were found in the adult rat sagittal and palatal sutures, and even as early as 3 weeks after birth partial bony union had occurred at some sites in these sutures. Such synostoses are probably without special significance as, in any case, growth at these sutures ceases very early (10–20 days, Massler & Schour, 1951), while compensatory overgrowth at other sutures, as already mentioned, readily occurs.

SUMMARY

1. The structure and development of cranial and facial sutures has been studied histologically in the rat, sheep, pig, cat, rabbit and man.

2. At all stages from their first development up to and including the adult, sutures show *five intervening* layers of cells and fibres between the adjoining bones as well as *two uniting* layers bounding the suture externally and internally.

3. The intervening layers comprise pairs of cambial and capsular layers continuous with the cambial and deeper fibrous strata respectively of the periosteum covering the non-sutural surfaces of the bones, and a middle looser zone. The uniting layers run directly between the outer fibrous layers of the periostea on each side.

4. Sutures arise somewhat differently in the face and cranium. In the face the cambial and capsular layers are already present before the suture is formed, while the middle and uniting layers are derived from the mesenchyme between the approaching bone territories. In the cranium the capsular layers are not formed until the cambial layers have almost met, while the uniting and middle zones are derived from the delamination of the fibrous ectomeninx between the bones.

5. As a suture matures its cambial layers are gradually reduced to a single layer of flattened osteoblasts, the capsular layers thicken but their predominant fibre direction continues to be parallel to the sutural faces of the bones, while the middle layer becomes increasingly vascular. The uniting layers form the strongest bond of union between the bones.

6. Cartilage, either of the hypertrophic or the hyaline variety, is found at the margins of the bones in some sutures during the neonatal period. Cartilage union across the suture is occasionally found.

7. Areas of partial synostosis were found in some palatal and sagittal sutures both during, and after the completion of, skull growth.

8. It may be deduced from their mode of development and their histological organization, that sutures form a strong bond of union between adjacent bones while permitting slight movements, and at the same time allowance is made for marginal expansion of the bones during the growing period.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. 75 mm. C.R. sheep foetus. Presumptive palatal suture. Weigert's haematoxylin and Van Gieson. × 32.

Fig. 2. 20-day rat foetus. Presumptive sagittal suture. Shows tectal cartilage. Haematoxylin and safranin. × 100.

Fig. 3. 90 mm. C.R. sheep foetus. Palatal suture. Shows meeting of bone territories. Weigert's haematoxylin and Van Gieson. × 25.

Fig. 4. 90 mm. C.R. sheep foetus. Presumptive sagittal suture. Shows beginning of delamination of ectomeninx at the site of the future suture. Wilder. × 25.

Fig. 5. 110 mm. C.R. sheep foetus. Palatal suture. Shows formation of uniting layers. Mallory. × 25.

Fig. 6. 9 months' postnatal sheep. Nasal suture. Shows Sharpey's fibres. Mallory. × 43.

Fig. 7. 125 mm. C.R. pig foetus. Nasal suture. Shows capsular and uniting layers. Masson. × 25.

Fig. 8. 110 mm. sheep foetus. Sagittal suture. Shows early formation of capsular layers. Wilder. × 25.

Fig. 9. 75 mm. C.R. sheep foetus. Edge of bone territory in palate showing cellular lamination. Weigert's haematoxylin and Van Gieson. × 420.

Fig. 10. Newborn pig. Nasal suture. Masson. × 25.

PLATE 2

Fig. 11. 250 mm. C.R. sheep foetus. Palatal suture. Early growing stage. Masson. × 43.

Fig. 12. Newborn sheep. Part of sagittal suture. Late growing stage. Wilder. × 43.

Fig. 13. 57-day-old cat. Nasal suture. Adult stage. Mallory. × 43.

Fig. 14. 110 mm. C.R. sheep foetus. Sagittal suture. Higher power view of part of Fig. 8. Shows arrangement of fibres in capsular, middle and uniting layers. Wilder. × 150.

Fig. 15. Adult rabbit. Nasal suture. Shows capsular and middle layer fibre pattern. Mallory. × 420.

Fig. 16. Newborn rat. Palato-maxillary suture. Glycogen shown by periodic-acid-Schiff method. × 43.

Fig. 17. Adult rat. Part of sagittal suture showing cellular structure. Haematoxylin and eosin. × 150.

PLATE 3

Fig. 18. Newborn rat. Palatal suture. Alkaline phosphatase shown by Gomori's method. × 100.

Fig. 19. Newborn rat. Palatal suture. Glycogen shown by periodic-acid-Schiff method. × 100.

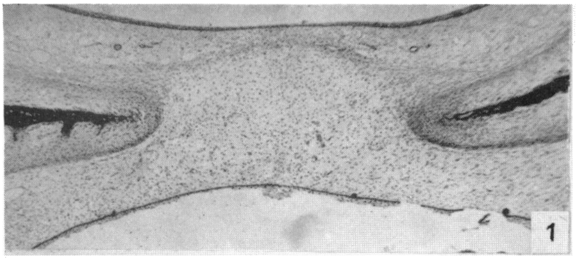
Fig. 20. 6-day-old rat. Palatal suture. Cambial layers replaced by cartilage. Haematoxylin and eosin. × 110.

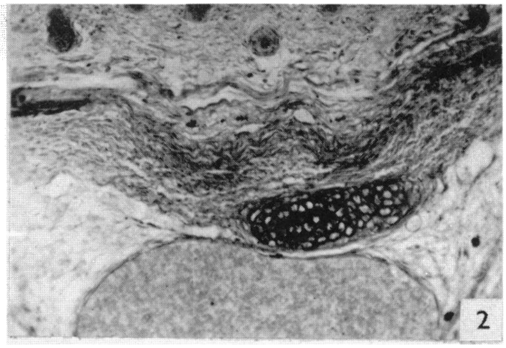
Fig. 21. 14-day-old rat. Sagittal suture. Shows cartilage uniting bones across suture. Weigert's haematoxylin and Van Gieson. × 150.

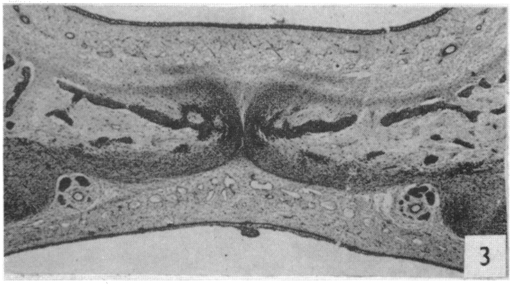
Fig. 22. 3-day-old rat. Palatal suture. Shows synostosis with islands of hypertrophic cartilage. Masson. × 170.

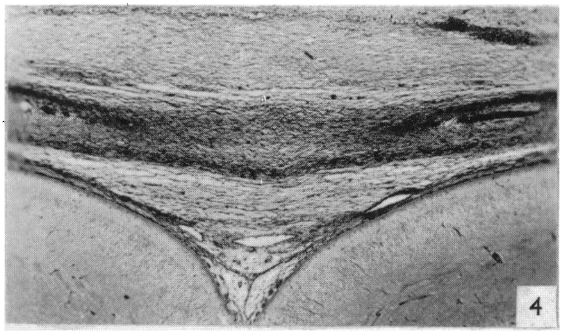
Fig. 23. Adult rat. Temporo-parietal suture. Shows great vascularity of middle layer. Haematoxylin and eosin. × 100.

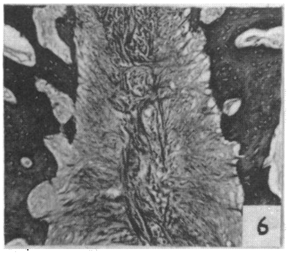
Fig. 24. 3-week-old rat. Sagittal suture. Shows partial synostosis. Weigert's haematoxylin and Van Gieson. × 150.

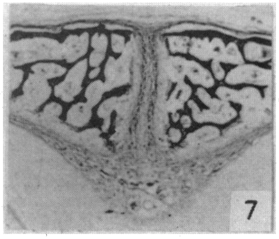


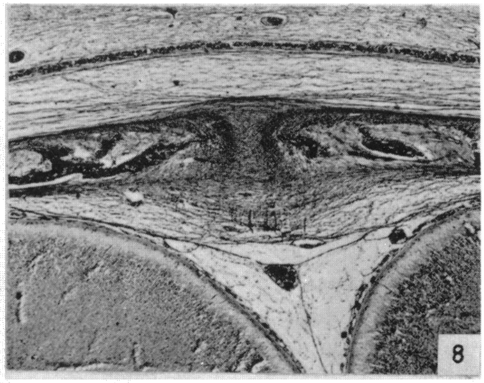


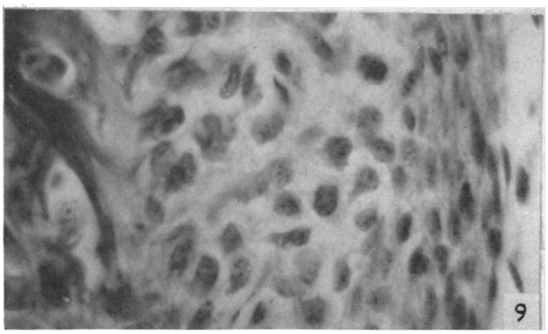


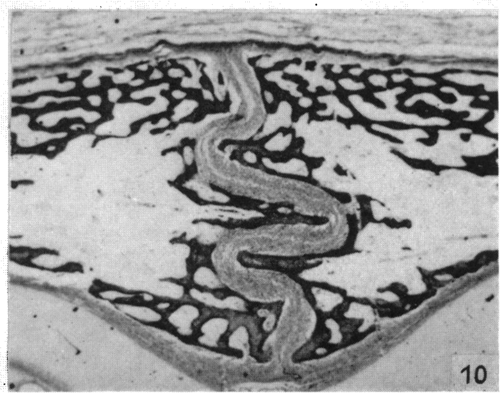








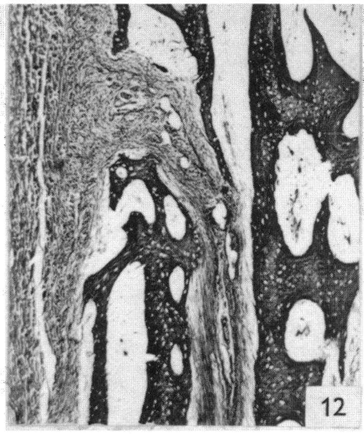




PRITCHARD, SCOTT AND GIRGIS—THE STRUCTURE AND DEVELOPMENT OF CRANIAL AND FACIAL SUTURES

(*Facing p.* 86)


11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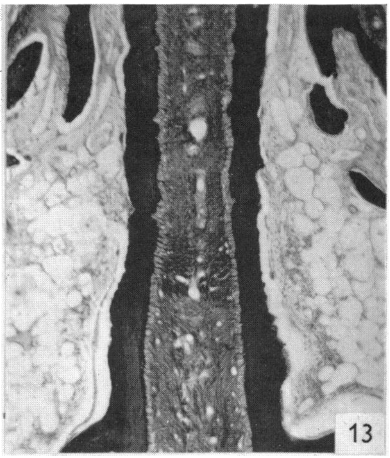
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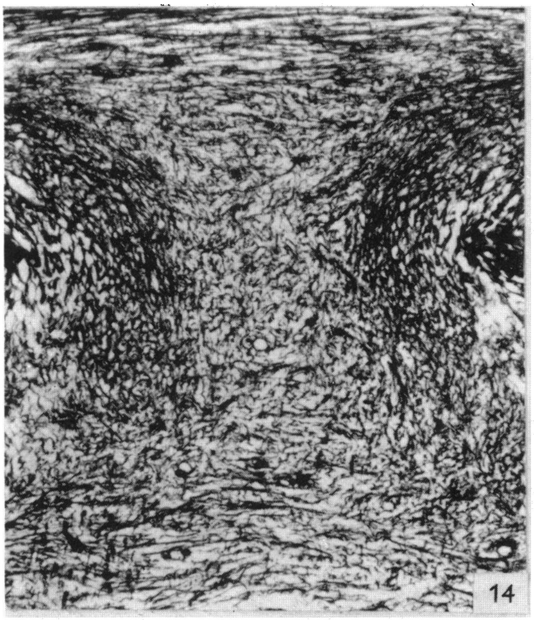
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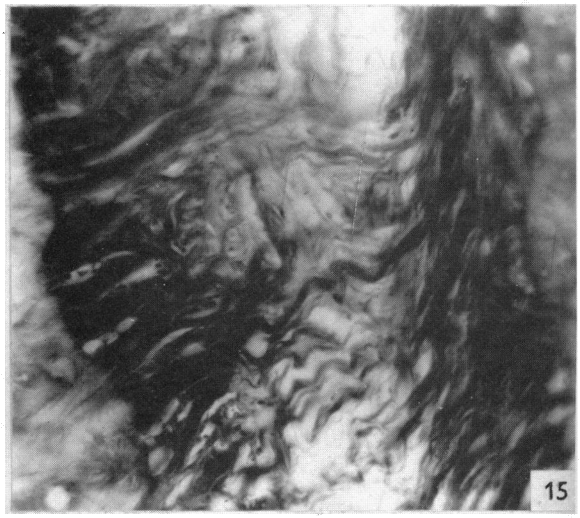
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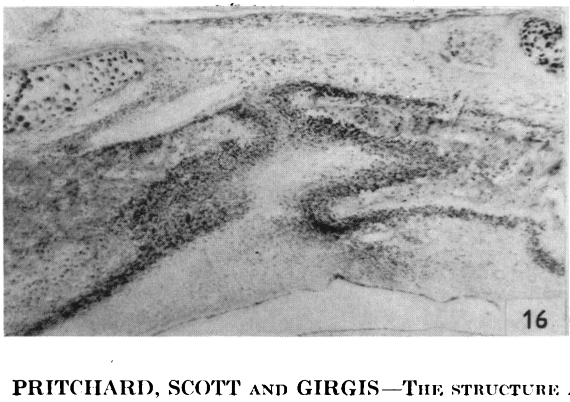
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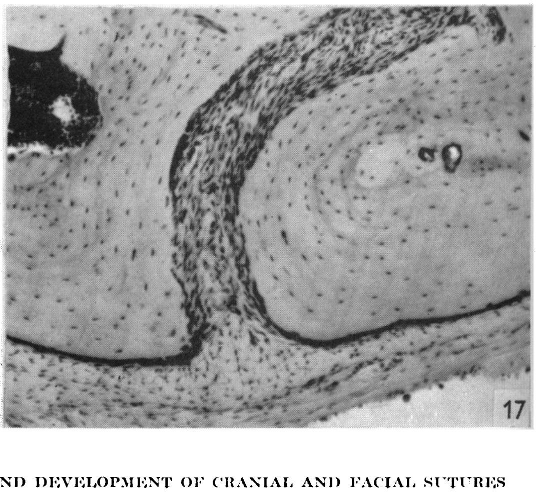
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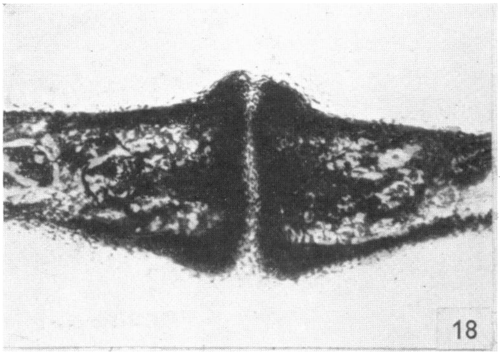
PRITCHARD, SCOTT AND **GIRGIS**—THE STRUCTURE AND DEVELOPMENT OF CRANIAL AND FACIAL SUTURES



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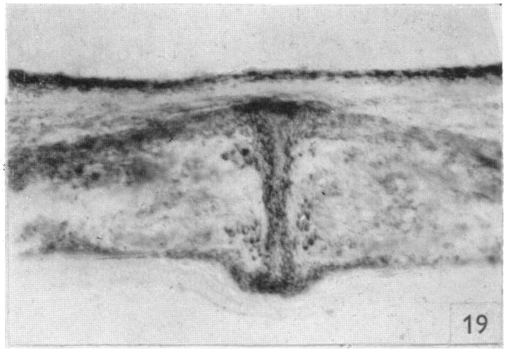

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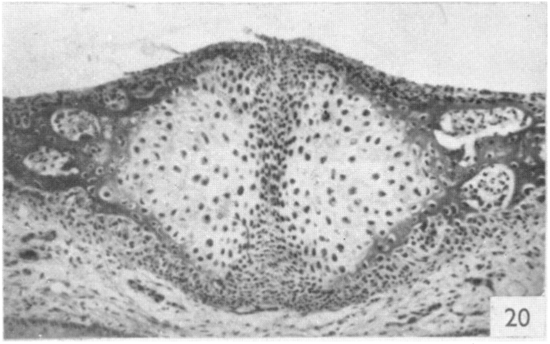

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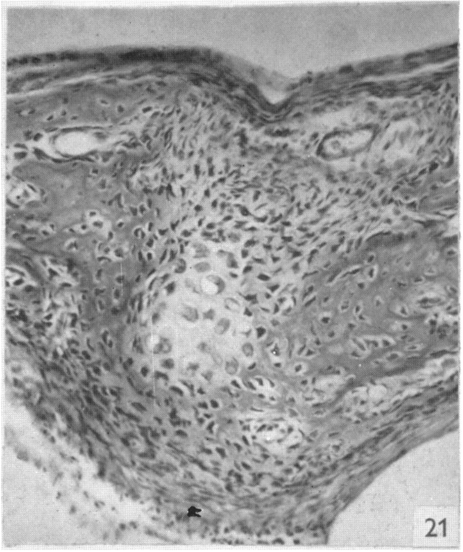

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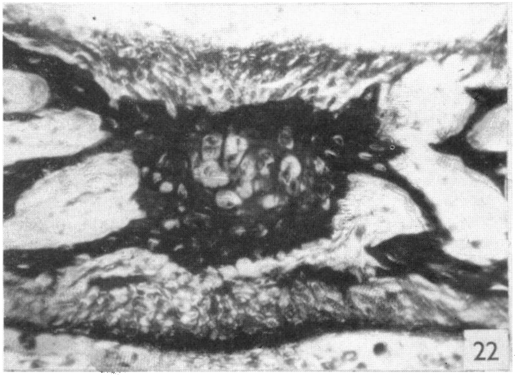

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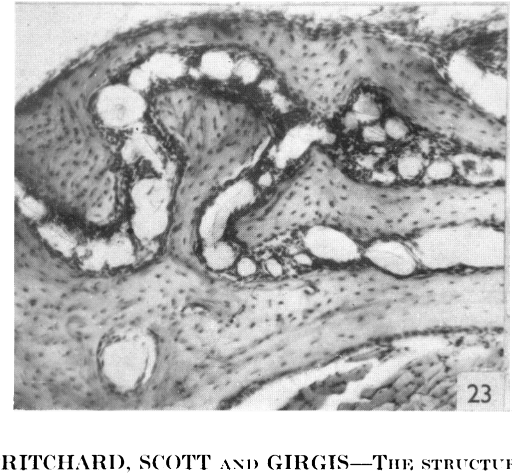

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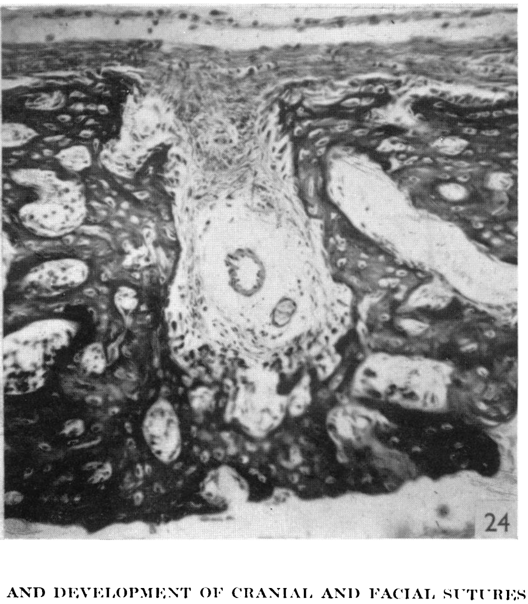

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