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The Foramen Ovale and Sphenoidal Angle in Man

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Summary. The structure of the greater wing of the sphenoid in the region of the foramen ovale and sphenoidal angle is described in both the adult human and in two partly ossified human embryos. It is shown that the foramen ovale of man is enclosed by membrane bone, derived from a medial process associated with the scaphoid fossa, and a lateral tongue, the most dorsal part of which is present in many adults as a process on the lateral margin of the foramen. These structures are parts of an extensive membrane bone which forms the larger part of the greater wing of the sphenoid. It is shown that the foramen of Vesalius represents the site of fusion between this membrane bone and the more medial, cartilaginous, ala temporalis. Various inconstant patterns of grooves and foramina in the vicinity of the foramen ovale can be interpreted as arising from the interplay of the various parts of the membrane bone and the emissary venous plexus from the middle meningeal veins to the pterygoid plexus. The embryonic anlagen of the pterygo-sphenoidal and pterygo-spinous ligaments are described, and the association of these structures with the parts of the membrane bone are discussed.

Key words: Sphenoid bone – Greater wing – Membrane bone – Human – Osteology.

Introduction

It is now more than a decade since one of us (F.L.D.S.) observed that the outline of the foramen ovale in the human skull is as often as not interrupted by a small spicule of bone which grows posterolaterally into its lumen from the anterior border (Fig. 1 a). In the small series examined at that time it appeared that this process was to be found in those specimens where traces of the spheno-

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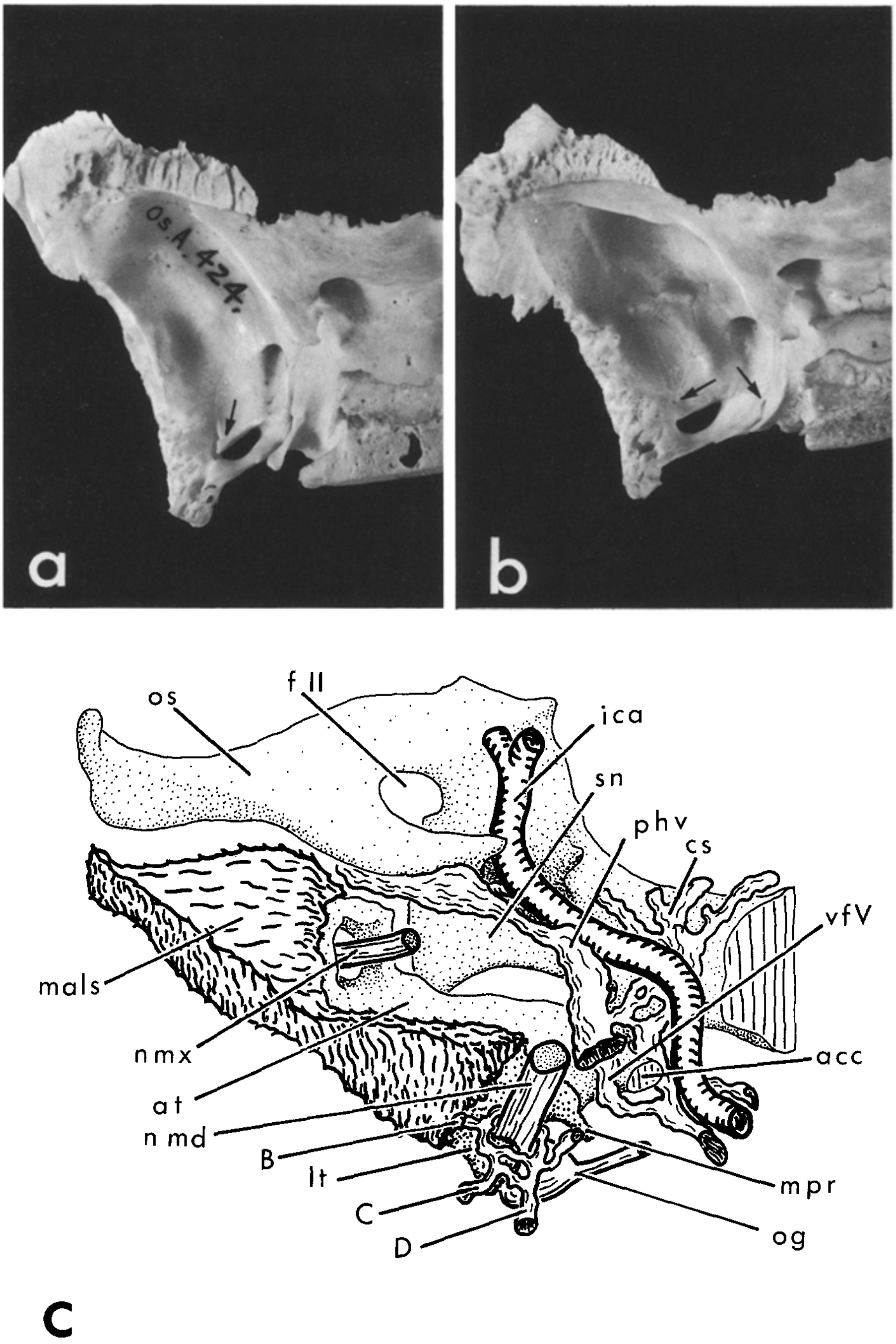

Fig. 1. a shows adult human left greater wing with process *(arrow)* and groove lateral to it. **b** shows an accessory emissary foramen *(arrow)* and no process; foramen Vesalii (arrow) is present and its position should be compared with that of the deep cleft between angle and lingula in (a). **c** is a graphic reconstruction of the developing left greater wing region in an 81 mm human embryo viewed postero-laterally. The membranous alisphenoid and the cartilaginous ala temporalis are only connected by ossification at the lateral margin of the foramen rotundum. The medial process and the lateral tongue are drawn in heavy stipple as they are only present as condensed mesenchyme flanking the mandibular nerve. Vein A of the emissaries is not distinct in this specimen. Magnifications (a), (b), natural size; (c) ca. ×15

occipital synchondrosis were still present. Although it seemed that its presence was characteristic of the younger skull, its development was not understood and no cogent reason for expanding the literature was recognised.

Descriptions of the base of the skull, even in the older literature, do not refer to the structure, although it is figured in its less well-developed state in Graf Spee's account of the development of the sphenoid bone (Spee 1896) and the groove which separates it from the more lateral region is referred to in the text. Some other texts include the process in drawings of the cranial base from the superior aspect.

In this paper we establish that the spicule and grooves are not, in their presence or absence, a useful guide to the age or sex of the specimen. Our examination of embryological material confirms the observation of Fawcett (1910) that beyond the limits of the relatively small cartilaginous ala temporalis the greater wing of the sphenoid developes in membrane bone. It is possible to interpret the various inconstant grooves and foramina, and the spicule found in this region of the human skull, by recognising the complex development of the greater wing: the inconstant details may reflect the junctions between distinct embryonic components.

Materials and Methods

To establish whether or not the presence of the process or groove bore any relationship to the age or sex of the subject a random sample of 50 skulls from the repository of identified skeletons at St. Bride's Church, Fleet Street, London (Steel 1962) and 38 dissecting-room specimens in the Department of Anatomy, University College, Cardiff were examined. Because the process and groove proved difficult to see with certainty using indirect vision in the intact skull, only those specimens were used whose calvaria were not intact. In 11 of the St. Bride's series and 26 of the dissecting-room series only one side of the cranial base was available for inspection. It was therefore decided to treat the individual sides independently and not as pairs occurring in the same skull. This is justified since in those specimens with both sides available neither the process nor the groove were necessarily present on both sides of the same skull.

To investigate the development of the region, reconstructions were made from serial sections of human embryos cut transversely to the naso-sellar axis. In each case sections were of 10 µm thickness: one embryo was of 81 mm. C-R length and stained with Masson's Trichrome, and the other was of 120 mm. C-R length and stained with Weigert's Haematoxylin and Eosin.

The findings were considered in the light of the examination of whole skulls and disarticulated sphenoid bones, including some non-human primate material in the osteological collection of this department.

Figs. 1–3. *Abbreviations A, B, C, D:* emissary meningeal veins so categorized in text; *acc* alicochlear commissure; *at* ala temporalis; *atp* pterygoid process of ala temporalis; *cs* cavernous sinus; *ds* dorsum sellae; *eut* pharyngo-tympanic tube; *fi* foramen innominatum; *fo* foramen ovale; *fr* foramen rotundum; *fV* foramen Vesalii; *fII* optic foramen; *ica* internal carotid artery; *lC* pterygo-spinous ligament (Civinini); *lH* pterygo-sphenoidal ligament (Hyrtl); *lt* lateral tongue of membrane bone; *mals* membranous alisphenoid; *mda* mandibular nerve (anterior division); *mdp* mandibular nerve (posterior division); *mlpt* lateral pterygoid muscle; *mmpt* medial pterygoid muscle; *mpr* medial process of membrane bone; *nmd* trunk of mandibular nerve; *og* otic ganglion; *os* orbitosphenoid cartilage; *phv* primary head vein; *px* pharynx; *sn* septum nasi; *tg* trigeminal ganglion; *ts* tentorial sinus; *tvp* tensor veli palatini muscle; *vFV* vein of foramen Vesalii; *vpt* pterygoid venous plexus

Results

Adult Subjects

The observations on adult specimens were analysed to test the initial hypothesis that the process and its flanking groove (Fig. 1 a) at the lateral margin of the foramen ovale represented incomplete fusion between developmental elements of the greater wing. Tables 1, 2, and 3 present the data (each side separated), so grouped as to test for association respectively with age, sex and co-appearance.

There is no statistical evidence of any association. It was concluded that the two features were independently and randomly assorted, the groove being present in somewhat under half the specimens and the process in about a third. It follows that any developmental explanation of these features must be more complicated than the mere failure to obliterate a single "suture".

Table 1. Correlation with age

Age (yrs)	0–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99
Groove present	4	0	4	5	6	5	11	12	10	0
Groove absent	0	4	14	14	7	5	12	14	5	2
Process present	4	0	3	6	2	3	11	15	9	1
Process absent	0	4	15	13	11	7	12	11	6	1

Table 2. Correlation with sex

	Male	Female
Groove present	34	24
Groove absent	38	43
Process present	29	26
Process absent	43	41
Total	144	134

Table 3. Correlation of groove with process

Present together	39
Absent together	65
Present independently	35

81 mm and 120 mm Human Embryos (Figs. 1c, 2a and b)

Each specimen shows an extensive membrane bone contributing to the greater wing lateral to the ala temporalis, which in the younger specimen is almost entirely cartilaginous. The maxillary nerve passes through a complete foramen rotundum in the ala, but the mandibular nerve leaves the middle cranial fossa well laterally to and behind the cartilage. The margins of the foramen ovale are represented by a lateral tongue and a medial process, mesenchymatous in the younger specimen, but bony parts of the membranous alisphenoid in the older. Completion of the foramen by the meeting of the extensions of these processes, behind the mandibular nerve, is late. In some skulls it may never take place (Edinger and Kitts 1954).

The venous pattern corresponds closely with the detailed description of Padgett (1957). Even in the 120 mm embryo the substance of the brain and the leptomeninges are drained by tributaries of the embryonic tentorial sinus which, though it passes through the region over the lateral surface of the trigeminal ganglion, does not at this time communicate substantially with the neighbouring veins and thus will not be further considered. The tissues of the orbit and the tissues within the anterior cranial fossa drain into the primary head vein (Padgett's pro-otic sinus, 1957). This communicates with the dorsal pharyngeal plexus both medial and lateral to the alicochlear commissure, and with the developing cavernous sinus and its distributaries at the level of the posterior part of the sella turcica.

In both specimens the principal drainage of the primary head vein is into the pro-otic sinus. In the 81 mm specimen the venous plexus, which will become the middle meningeal sinus system, is represented by small vessels lateral to the mandibular nerve and posterior to the membrane bone of the greater wing. These vessels communicate with the pterygoid plexus through fine vessels parallel to but at various distances from the mandibular nerve. The pterygoid plexus is distinct from the pharyngeal and joins the external jugular system anterior to the level of the pharyngeal plexus. The latter drains largely backwards parallel to the internal carotid artery to join the internal jugular system.

The lesser superficial petrosal nerve runs directly from the tympanic plexus upon the cochlear promontory to the otic ganglion, which is applied to the postero-medial aspect of the mandibular nerve just below its emergence from the plane of the chondrocranium. The line of the nerve is well ventral to the plane of the endocranial aspect of the developing bones so that any concomitant vessels are not favourably placed to contribute to the definitive venous drainage of the endocranium.

In the 120 mm specimen the bone has developed sufficiently around the veins to give a reliable guide to the interpretation of the grooves and foramina in the adult skull. The cavernous sinus drains laterally into a segment of the primary head vein, which has emissaries medial to the alicochlear commissure draining into the venae comitantes of the internal carotid artery posteriorly and, to a small extent, laterally into the pterygoid plexus. But the most lateral of these emissaries lies lateral to the alicochlear commissure, between its cartilage

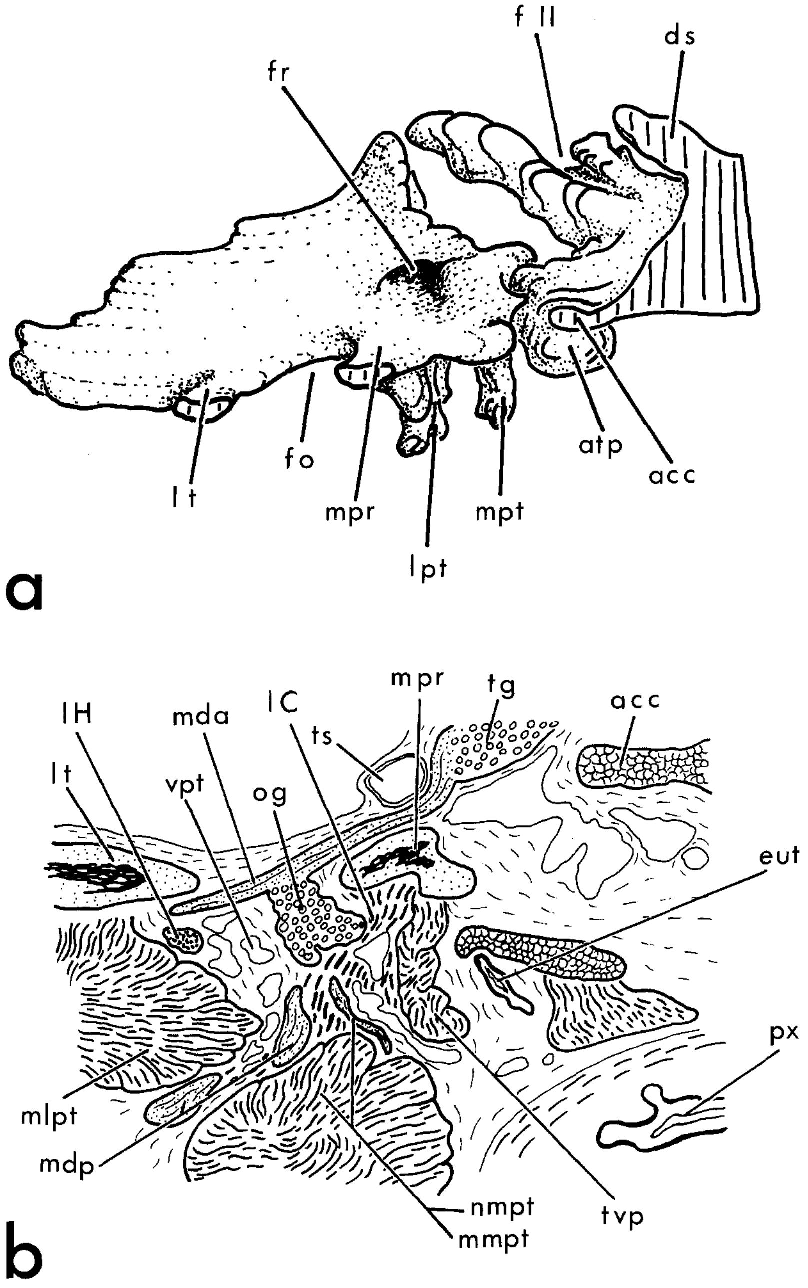

Fig. 2. **a** is a drawing of a wax-plate reconstruction of the left greater wing of a 120 mm human embryo viewed postero-laterally. Co-ossification of the membranous alisphenoid and ala temporalis extends medially beyond the foramen rotundum. The pterygoid process, body and alicochlear cartilage of the ala temporalis are of unmodified hyaline cartilage, against the perichondrium of which rests the membranous alisphenoid. Note especially the lateral tongue and the much broader, notched medial process which lies between foramen ovale and the ala temporalis. **b** is a camera lucida drawing of one section from the specimen of (2a) in a plane just anterior to the back of the model. Note the relationships of the pterygo-spinous (Civinini) and pterygo-sphenoidal (Hyrtl) ligaments to the lateral tongue, medial process and soft tissues. For clarity, the pterygo-spinous ligament has been drawn with emphasis relative to adjacent fascia: no histological differentiation is present in the specimen. Magnifications: (a) ×4, (b) ×10

and the most medial process of the membrane bone of the greater wing, which is notched in the position of the future scaphoid fossa. This emissary joins the pterygoid plexus in the medial part of the scaphoid fossa; its retention and closure by bone will form the vein of the foramen Vesalii.

Much more laterally in the 120 mm specimen the developing middle meningeal veins pass to the pterygoid plexus by several emissaries which converge towards the mandibular nerve over the endocranial aspect of the tongue of membrane bone which forms the lateral margin of the notch representing the future foramen ovale. It is the tip of this tongue of bone which is at this stage projected most prominently of all the parts of the greater wing toward the cavity of the middle cranial fossa: the more medial process of membrane bone, forming the medial margin of the notch for the mandibular nerve, slopes, as it passes back, further ventrally from the plane of the dura mater.

The meningeal venous emissaries can be classified for analysis as: –

(A) One which runs forward and medially with the meningeal branches of the maxillary nerve to the level of the anterior border of the mandibular nerve, which border it then follows to reach the pterygoid plexus.

(B) One which runs directly to the lateral surface of the mandibular nerve, there subdividing into an emissary plexus. This vein crosses the endocranial aspect of the lateral tongue of the membrane bone.

(C) One which runs parallel to the lateral border of the tongue, then turns under its tip to emerge upon the posterior aspect of the mandibular nerve.

(D) More posterior veins which converge from postero-lateral to join the concomitant veins of the middle meningeal artery. At this stage neither artery nor veins are enclosed by bone, but emerge together at a position just medial to the tip of the lateral tongue.

The pattern of these emissaries is illustrated in schematic form in Fig. 3.

The soft tissues ventral to the membrane bone throw light on the origins of the pterygo-spinous ligament (ligamentum crotaphitico-buccinatorium of Hyrtl: von Brunn 1891, Grosse 1893). Dorso-medial to the inferior head of the lateral pterygoid muscle lies a distinct fascicle, fibrous at origin and insertion, but with a small muscular belly. The origin is from the lateral aspect of the caudal edge of the lateral pterygoid plate and the insertion into the periosteum of the base of the lateral tongue of the membrane bone. It passes ventral to the buccal and temporal nerves, and corresponds exactly to the anomalous belly of lateral pterygoid described by Eisler (1912). The muscle fibres stain more darkly than those of adjacent muscles, and the nuclei look pyknotic: its appearance suggests reduction to a ligament. This structure therefore corresponds to ligamentum pterygo-sphenoideum.

Medial and dorsal to this a more extensive tract of looser fibrous connective tissue interspersed by large irregular venous channels of the pterygoid plexus can be seen. This tissue lies dorsal to the medial pterygoid muscle and therefore runs from the medial aspect of the lateral pterygoid plate medial to the sensory branches of the mandibular nerve. It is penetrated by the internal pterygoid nerve, and at about the level of the otic ganglion becomes bound to the periosteum of the under-surface of the medial process of membrane bone, immediately lateral to the area of origin of the tensor veli palatini muscle, and well medial

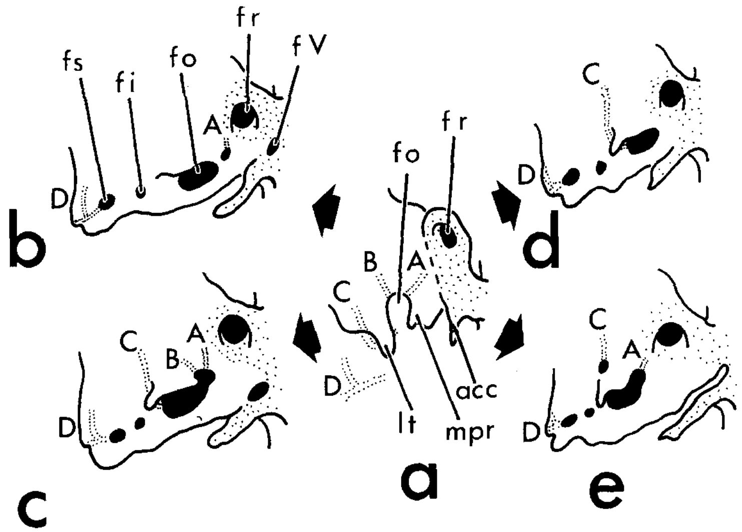

Fig. 3a–e. Schematic drawings of left greater wings. **a** during early development, showing emissary veins A–D. **b** an adult specimen with the commonly-encountered foramina and an accessory emissary foramen for vein A. **c** an adult specimen with retention of veins A-D and a process lateral to the foramen ovale. **d** retention of veins C and D, and a lateral process. **e** retention of A, C and D with an accessory foramen for C and retention of the lateral process. In all drawings the ala temporalis or its derivatives are stippled. Note that many other possible variants can be encountered

to the middle meningeal artery. Such a position corresponds to that of the pterygo-spinous ligament, although at this stage it is not histologically differentiated as true ligament.

Discussion

Comparison of the developmental features described above with the structure of disarticulated adult sphenoid bones reveals the complexity of growth in this region. It is not possible to state with certainty where bone hays been deposited and where resorbed in the transition from the 120 mm stage to adult size, in the absence of studies using markers such as tetracycline lines. But it seems reasonable to suppose that enlargement of the middle cranial fossa leads to the resorption of most of the bone which is present on the endocranial aspect of the 120 mm specimen, while if any of its more ventral bone survives it is likely to be deep within layers of subsequently apposed bone in the adult. This remodelling may be expected to obliterate most lines of junction between the component parts of the embryonic bone once synostosis has occurred between them. From this it is likely that if the adult retains signs of the junctions between such elements this may well be because the retention of a soft tissue structure which follows the line has affected the remodelling. It will be argued that the meningeal venous plexus does have such an effect, and the pleomorphism of this region may be better understood by recognising the various possibilities.

The bony components to be considered here are: the endocranial bone of the ala temporalis, the medial process, and the lateral tongue, of the membrane bone of the greater wing. The detection of these components is not original: they may be seen in Starck (1975, Fig. 544). Two of us (Presley and Steel 1976) have argued elsewhere that the membrane bone which extends the greater wing may be of great morphological significance in the understanding of the evolution of the mammalian cavum epiptericum. The classical view (de Beer 1937, Goodrich 1930) has not placed much emphasis on this membrane bone, which is responsible for bringing about relationships between the greater wing and the maxillary and mandibular nerves which complicate the view that the alisphenoid is the homologue of the epipterygoid or columella cranii of other vertebrates. The interpretation of this region is still being discussed (Kuhn 1971, Starck 1978) and much depends on the interpretation of the value for homology of extensions of cartilaginous bone by membrane bone apposed to the perichondrium. In German usage a clear distinction is made between "Deckknochen" and "Zuwachsknochen", and our "membrane bone" would fall in the latter category, in the case of the greater wing of the sphenoid. Patterson (1977) has discussed this problem, and drawn attention to the possibility that membrane bone extensions of cartilage bones may need more careful morphological consideration than has been accorded them in the past.

In this paper it is not necessary to resolve these difficult problems of comparative anatomy. That there is a cartilaginous ala temporalis, extended by a more lateral portion ossifying in membrane, seems universally agreed. Our descriptions are fully compatible with previously published work, and we claim originality only for the interpretation of the detailed pattern of development of the subdivisions of the developing greater wing.

The junction between cartilage (ala temporalis) and membrane bone is easy to recognise in its posterior part in the adult. In the embryonic specimens synostosis is established at the level of the foramen rotundum by the spread of ossification from the membrane bone into the cartilage, but in both cases there is no endochondral ossification from the level of the anterior margin of foramen ovale backwards: the membrane bone, where it abuts on the ala, does so against unmodified hyaline cartilage. The most posterior portion of the cartilage of the ala temporalis is the alicochlear commissure, which in both our specimens abuts against the cochlear capsule without fusion. We concur with the generally accepted view that the lingula sphenoidale is the adult derivative of the alicochlear commissure (de Beer 1937). In the adult there is often a deep sulcus between this and the greater wing, visible from both dorsal and ventral aspects. The sulcus slopes laterally as it is followed ventrally, as does the canal leading to foramen Vesalii, when present. In the embryo the emissary vein here emerges in association with the origin of the tensor veli palatini muscle (that part arising from the ventral aspect of the medial process of membrane bone). If this association persists, then the obliquity of the sulcus or canal may reflect the pattern of appositional growth in this region, from an early stage, which leads to the divergence of the medial pterygoid plates (followed ventrally) in the adult. The case for recognising the sulcus as the line of fusion is thus reasonable: the foramen Vesalii may be regarded as a special case where the vein has become completely enclosed within the line of fusion.

The medial, slightly notched process of membrane bone has part of the insertion of the tensor veli palatini muscle upon its ventral surface; but the lateral tongue in the embryo has no such association. If it be assumed that these relationships are conserved in further development, then it follows that the contribution to the adult sphenoid derived from the medial process includes the relatively slender bar of bone seen from dorsally as the postero-medial margin of the foramen ovale, and from ventrally as the postero-lateral extension of the scaphoid fossa from the bases of the pterygoid plates to the sphenoidal spine. Since at 120 mm the lateral tongue is already in contact with the middle meningeal artery and its concomitant veins and tributaries (D), any contribution from the medial process to the sphenoidal spine must probably be confined to the very slender medial rim of the foramen spinosum: at 120 mm the medial process is well separated from these vessels.

The development of the lateral tongue, and that part of the membrane bone more lateral still seems both to be more complex and more variable. The lateral tongue is very prominent in the endocranial plane at 120 mm, but it is clear that during further development it must, at a slightly more ventral level, be overtaken in growth by the more lateral part. This follows from the observation that at 120 mm the middle meningeal artery lies in contact with the tip of the tongue, posterior to the exit of the mandibular nerve, but caudal to this level the posterior margin of the more lateral part of the membrane bone runs sharply laterally away from the tongue. Thus in this embryo the tongue has already attained the anatomy of the antero-lateral margin of the foramen ovale, but the very robust postero-lateral margin and the bulk of the sphenoidal spine are not represented in bone. It seems most probable that this bone is formed by apposition just below the tip of the tongue to carry the middle meningeal artery posterolaterally away from foramen ovale, buttressed by a very substantial contribution growing in a posterior and medial direction from the more lateral part of the greater wing. Retention of vein C (Fig. 3c, d) will lead to the retention of the lateral process dorsal to the vein, whose groove will indicate the line of early separation of the tongue from the more lateral part. That this may indeed be regarded as a suture is indicated by the occasional presence of an unnamed emissary foramen leading through the greater wing from the groove, lateral to the foramen ovale (Fig. 1a, 3e). Rentention of vein B will emphasise the medial aspect of the root of the tongue by producing a notch (Fig. 3c), while retention of vein A will produce a venous groove leading from the direction of the foramen rotundum to the anterior margin of the foramen ovale (Fig. 3c, e): this groove does not represent a suture.

The subtle distinction between the most endocranial bone of the lateral tongue, represented by the lateral process of the foramen ovale in the adult, and the slightly deeper but related bone which grows so much more substantially to produce the sphenoidal spine and angle, is emphasised by the behaviour of the latter with respect to the lesser superficial petrosal nerve. This is slightly deeper in the embryo, thus avoiding involvement in the superficial emissary vein system, and where in the adult it runs over the sphenoidal angle to reach the foramen ovale, it is underlain by the derivatives of the deeper bone, but in a plane slightly beneath that of the tip of the lateral process. Where the nerve is enclosed by bone to produce a canaliculus innominatus, inspection shows that the tip of the lateral process, if present, stands slightly proud of the endocranial wall of the canaliculus.

It is of interest that in the 120 mm specimen the pterygo-sphenoidal ligament is clearly represented by muscle originating from the vicinity of the base of the lateral pterygoid plate and inserting into the ventral aspect of the lateral tongue, which will become the base of the sphenoidal spine anterior to the foramen spinosum. The relatively early appearance of this structure confirms the view of Grosse that a tract in this position is a fundamental feature of mammalian morphology (Grosse 1893). The pterygo-spinous ligament is less clearly differentiated at this stage although it seems reasonable to recognise its precursor in the extensive fascia running from the lateral pterygoid plate to the medial process of the membrane bone which will form the postero-lateral part of the scaphoid fossa. It is perhaps not reasonable to expect the pterygo-spinous ligament to have attained its adult form by 120 mm. Both the lateral pterygoid plate and the angle of the sphenoid must subsequently undergo very great transformation: the former with much elongation while the latter and the spine of the sphenoid are not present as bone at this stage. But the variable and irregular fenestration of the ligament in the adult may well reflect the passage through the fibrous tract of a number of subdivisions of the perygoid venous plexus.

No clear explanation can be offered for the observation (Eisler 1912) that muscle may be present in the adult in both these ligaments: each unites parts of one bone from the earliest stages. Each ligament can have ossified derivatives in Man (von Brunn 1891; Grosse 1893), and such ossifications are usual in some lower primates (see Hershkowitz 1977 for recent discussion). That man can have muscle here may lend some support to the hypothesis that both the lateral pterygoid plate-sphenoidal spine complex, and the fascicles of the pterygoid muscles may have been more extensive at some point in human ancestry than is presently the case in Man. It seems clear that the membrane bone in this region requires more detailed descriptive and functional analysis throughout mammals than has previously been the case.

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References

Beer GR de (1937) The development of the vertebrate skull. Oxford University Press, Oxford
Brunn A von (1891) Das Foramen pterygo-spinosum (Civinini) und der Porus crotaphiticobuccinatorius (Hyrtl). Anat Anz 7:96–104
Edinger T, Kitts DB (1954) The foramen ovale. Evolution, Lancaster, Pa. 8:389–404
Eisler P (1912) Die Muskeln des Stammes, in Bardeleben: Handbuch der Anatomie des Menschen Bd 2 Abt 2 Teil 1. Gustav Fischer, Jena
Fawcett E (1910) Notes on the development of the sphenoid. J Anat 44:207–222

Goodrich ES (1930) Studies on the structure and development of vertebrates. Macmillan, London

Grosse U (1893) Über das Foramen pterygo-spinosum (Civinini) und das Foramen crotaphitico-buccinatorium (Hyrtl). Anat Anz 8:321–348

Hershkowitz P (1977) Living new world monkeys, Vol 1. University of Chicago Press Chicago

Kuhn HJ (1971) Die Entwicklung und Morphologie des Schädels von *Tachyglossus aculeatus*. Abh Senckenb Naturforsch Ges 528:1–224

Padgett DH (1957) The development of the cranial venous system in man from the viewpoint of comparative anatomy. Contr Embryol 36:81–140

Patterson C (1977) Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton, In: Andrews, Miles and Walker: Problems in Vertebrate Evolution, 77–121. Academic Press, London

Presley R, Steel FLD (1976) On the homology of the alisphenoid. J Anat 121:441–459

Spee F Graf von (1896) Skeletlehre: Kopf, In: Bardeleben: Handbuch der Anatomie des Menschen Bd 1 Abt 2. Gustav Fischer, Jena

Starck D (1975) Embryologie. 3rd edn. Georg Thieme, Stuttgart

Starck D (1978) Das evolutive Plateau Säugetier. Sonderbd Naturwiss Hamburg 3:7–33

Steel FLD (1962) The sexing of long bones, with reference to the St. Bride's series of identified skeletons. Jl R Anthrop Inst 92:212–222

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