

THE CRANIAL MORPHOLOGY OF THE
LOWER LIASSIC LATIPINNATE
ICHTHYOSAURS OF ENGLAND

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By C. MCGOWAN

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SYNOPSIS

An account of the anatomy of the ichthyosaurian skull is given based upon several prepared and part-prepared specimens. It is shown that the temporal vacuity is bounded by the squamosal, postfrontal and parietal, the supratemporal being absent. As a result the Ichthyosauria can be removed from their phyletic isolation and placed with the plesiosaurs in the Subclass Euryapsida.

An attempt is made to reconstruct certain aspects of the soft anatomy including the membranous labyrinth, brain, and jaw musculature and the light this casts upon the ichthyosaurian way of life is examined. A detailed account of the individual elements of the skull is given.

INTRODUCTION

IN 1814 the discovery of a new group of fossil animals was heralded by Sir Everard Home with the publication of, 'Some account of the fossil remains of an animal more nearly allied to fishes than to any other classes of animals'. This paper figured and described a large skull¹ which had been collected on the beach at Lyme Regis, and is the first account of the cranial morphology of an ichthyosaur. There have been many other accounts of the cranial morphology since 1814, including two very detailed papers on *Ophthalmosaurus* (Andrews, 1910), and on *Ichthyosaurus* (Sollas, 1916), but even here there were shortcomings. Whereas the structure of the palate, lower jaw, and much of the dermal skull roof had been satisfactorily interpreted, there had been much confusion in the temporal and occipital regions, and the problem of the otic capsule remained largely unresolved. Furthermore, little progress was made in the reconstruction of the soft anatomy, and there have been inadequacies in the descriptions of individual cranial elements.

¹ This skull is now in the British Museum (Nat. Hist.) and an extensive search into the literature and the records of the Museum has revealed a weight of evidence to support the conclusion that this was Mary Anning's first ichthyosaur.

Most of the information in this present study has been obtained from material extracted from nodules by acetic acid, and the fine state of preservation has permitted an accurate reconstruction of the hind portion of the skull to be made. The successful interpretation of the skull has had a far reaching effect, for it clearly demonstrates the absence of a supratemporal, the temporal vacuity being in fact bounded by the squamosal, postfrontal and parietal. In consequence the Ichthyosauria can be removed from their phyletic isolation and placed with the plesiosaurs and protosauroids in the subclass Euryapsida. An attempt has been made to reconstruct certain aspects of the soft anatomy which gives some insight into the ichthyosaurian way of life. For the sake of completeness a detailed description of the individual cranial elements is given, but before turning to the morphological account a brief history of research on the cranial morphology will be outlined.

HISTORY OF CRANIAL RESEARCH

The first account of the ichthyosaurian skull was given by Sir Everard Home in 1814 in a paper which was also the first notification of the discovery of the new group of animals. Home was largely preoccupied with unravelling the problem of the affinities of this new find, although he did take note of certain cranial features. He observed that tooth replacement occurred, and compared it with the crocodilian condition, and noted the apparent presence of a retroarticular process. There was some confusion in the position of the external narial aperture, largely because it was partly occluded by a displaced sclerotic plate, and its true position was not established. Home published several more papers during the next few years, and in 1820 a paper appeared in which a second skull was figured (probably of *I. breviceps*), together with a section through the snout and lower jaw.

By 1821 a sufficient amount of cranial material had accumulated to permit a more exhaustive treatment, and in that year Conybeare published a joint paper with De la Beche dealing largely with the skull. The confusion in the position of the external naris was removed, and, notwithstanding certain anomalies in the terminology used, a very good account of the lower jaw was given, accompanied by a number of excellent figures including several transverse sections. The entire dorsal surface of the skull was figured, although some errors were made. The parietal and frontal were both described as unpaired elements, and it was believed that the prefrontal, postfrontal, and postorbital were not separate elements but processes of the frontal. It is interesting to note that only one element was shown in the temporal region, and this was described as, 'portions of the temporal bones'. The account of the palate was very much confused, and, in the absence of the hind skull, no account of the occiput could be given. Five years later, in 1824, Conybeare published a further account in which he discussed how, 'Mr De la Beche long since believed himself able, from the examination of the teeth, combined with some other characters, to establish three species, to which he has applied the names *communis*, *platyodon* and *tenuirostris*: and to these our joint observations have recently added a fourth, *Ichthyosaurus intermedius*.' A number of teeth are figured and described,

and the structure of the lower jaw is further discussed. Additional transverse sections through the jaw are given and the prearticular is figured for the first time (referred to as the 'crescent-shaped bone'). The temporal vacuity is discussed in further detail and compared with the upper temporal vacuity of the crocodile. Once more the paucity of occipital material prevented adequate account of the hind skull, but an admittedly conjectural reconstruction of the occiput was given, based upon a number of incomplete specimens.

Owen's Report to the British Association for 1839 includes an account of the cranial morphology of ichthyosaurs, but in the absence of figures and in the use of a confusing osteological nomenclature, his account is difficult to follow. The occipital region is discussed and although he recognized that the supraoccipital participated in the formation of the foramen magnum (Owen 1839 : 90), he refers on the next page to an element which, from its description, can only be the supraoccipital, but which is referred to as the interparietal. The basioccipital condyle is described but it is considered that the exoccipitals contribute to the articulation with the axial skeleton. The palate is described, but the true position of the internal narial aperture is not established, being confused with the interpterygoid vacuity. Owen discusses the robust nature of the quadrate and its firm bracing against the rest of the skull with reference to the powerful adduction of the lower jaw.

In 1880 Seeley figured and described the skull of a new species, *I. zetlandicus*. Of significance is the fact that the margin of the temporal vacuity is correctly shown to be formed by the parietal, postfrontal, and squamosal, but a second temporal element is shown lying between the squamosal and quadratojugal, and referred to as the supraquadrate.

Many excellent figures of skulls are included in Owen's (1881) Monograph on the Liassic Reptilia, accompanied by detailed descriptions. The problem of the palate is largely resolved, although the pterygoid is shown to overlap the palatine (Owen's ectopterygoid) dorsally, and the position of the internal naris is correctly established (Owen 1881 : plate 25). A good attempt is made to reconstruct the occiput (Owen 1881 : plate 24, fig. 1), and his previous error concerning the participation of the exoccipital in the articular condyle is corrected. The supraoccipital is correctly figured wedged in the notch formed by the two parietals, while the opisthotic (Owen's paroccipital) is shown as a strut between the basioccipital medially and the quadrate distally, although from Owen's figure it would seem that this element is in fact the stapes. It is recorded that the anterior portion of the basioccipital is notched or grooved in some species, 'as if for the outlet of the Eustachian canal.' The quadrate (tympanic) is shown in its correct relationship with the rest of the skull, and the foramen which it forms with the quadratojugal (zygomatic) is described as the auditory meatus. Referring to the neurocranium Owen writes, 'the side walls of the brain case proper seem to have been mainly cartilaginous.' A satisfactory description of the skull roof is given (Owen 1881 : 96, pl. 23, fig. 1), and in the temporal region the posterior and posterolateral margin of the vacuity is shown to be formed by the large triradiate squamosal (mastoid). A second temporal element, however, is figured lying immediately beneath the squamosal, referred to as the

prosquamosal, and beneath this is an element described as the zygomatic, (quadratojugal).

Fraas (1891) figures a number of skulls, both unprepared and prepared, and also some excellent sections through teeth. A lateral view of a skull of *I. zetlandicus* is given (Fraas 1891 : pl. 2, fig. 1), in which there is a satisfactory relationship between the individual elements, but here again a second element is figured lying between the squamosal dorsally and the quadratojugal ventrally. The misconception that there were two elements in the temporal region was by this time firmly established in the literature. In a reconstruction of the occiput of a specimen of *I. quadriscissus* the opisthotic is shown on the same horizontal level as the exoccipital, the proötic is oriented between the opisthotic and stapes, and the supraoccipital is shown lying outside the parietals. It is interesting to note that neither the opisthotic or the stapes are shown to have distal contact with the rest of the skull, and the present investigation has shown that there was almost certainly a cartilaginous intervention in both cases. An oblique view of the hind skull of a British Museum (Natural History) specimen from Lyme Regis is quite satisfactory but for the inversion of the epipterygoids. A number of individual elements are figured.

A very thorough description of the skull and post-cranial skeleton of *Ophthalmosaurus* was given in 1910 by C. W. Andrews. The individual skull elements are figured and described in detail, although their relationships are not always completely known. The squamosal is correctly shown to form the posterior and postero-lateral margin of the temporal vacuity, but in a restoration of the entire skull (Andrews 1910 : fig. 23), a second temporal element, the supratemporal, is shown immediately beneath it. The supratemporal is not figured as an individual element since it is said to have been missing or crushed beyond recognition in most cases, but reference is made to one specimen (R2740) in which this element can apparently be seen as a roughly triangular bone. The impressions of the membranous labyrinth in the proötic and opisthotic are described, but, since it was realised that the proötic did not have osseous contact with the rest of the skull, it was not oriented. In the lower jaw the articular is shown in its correct relationship with the other elements (Andrews 1910 : fig. 20a), and its facet for reception of the prearticular (described as the coronoid) is clearly demonstrated. A very satisfactory reconstruction of the occipital region is given.

In a discussion of the homologies of the bones in the temporal region in reptiles Watson (1914) concluded that the 'inner bone' of the temporal region in *Ichthyosaurus*, described by Andrews in *Ophthalmosaurus* as the supratemporal, was really the squamosal, but he went on to conclude that, 'this view has the great disadvantage of leaving unexplained the outer temporal element.'

The most extensive and informative cranial investigation was that of Sollas (1916), based on the study of serial sections. The squamosal is figured and described in its true light, but, although no supratemporal was present in the material sectioned, Sollas preferred to conclude that, 'This bone, as is commonly the case with *Ichthyosaurus* skulls, is missing.' The opisthotic was interpreted as resting with its paroccipital process in contact with the quadratojugal and pterygoid, while the

proötic was not oriented. The great value of this excellent study lies in the fact that the precise relationships existing between individual elements at the time of preservation can be determined, but it suffers from the unavoidable shortcoming that the individual elements could not be adequately figured and described.

Von Huene's monograph (1922) on the Liassis ichthyosaurs includes a number of figures of skulls and of some isolated elements, but little detail is given. Two elements are figured in the temporal region; that bordering the temporal vacuity is described as the supratemporal, the one below as the squamosal. Later, in 1949, von Huene figured the back of a skull of *P. acutirostris* showing a good relationship between the stapes, exoccipital and opisthotic, but the proötic is shown lying dorso-lateral to the exoccipital, and the basioccipital is inverted. An interparietal is figured, and, once again, two elements are shown in the temporal region.

Appleby (1956) in a paper on the osteology of *Ophthalmosaurus* describes the bone which forms the postero-lateral margin of the temporal vacuity as the supratemporal, and writes that, 'Between the bone in question (the supratemporal) and the quadrate on the external surface is a thin plate of bone which is rarely seen in *Ophthalmosaurus* but which meets the jugal, quadratojugal and postorbital and is therefore the true squamosal.' In a more recent paper Appleby (1961) gives an account of the cranial morphology of ichthyosaurs, and, as will be shown later, his interpretation of the otic region is at variance with the conclusions which have been drawn in the present investigation.

In the winter of this year Romer (1968) published a paper on, 'An ichthyosaur skull from the Cretaceous of Wyoming,' in which the whole problem of the supra-temporal and squamosal is looked into. Romer reaches the same conclusions as the present author, and includes some fine figures of material which D. M. S. Watson had worked upon.

CRANIAL MATERIAL EXAMINED DURING THE INVESTIGATION

Six prepared or partly prepared skulls were examined, together with some sixty compressed specimens.

A brief description of the six specimens, together with the state of their preservation, is given in Table I.

TABLE I

Museum No.	Description	State of Preservation
R8177	A moderately large partial skull not complete beyond the nares. The individual elements have been completely extracted from the matrix.	Most of the extracted elements are in a fine state of preservation and includes the palatal elements. Not all elements are present.
R6697	A small specimen similar to R8177 but far less complete.	Only part of the pterygoid is present and many of the elements of the left side are missing. Skull roof represented only by incomplete parietals.

TABLE I (*continued*)

Museum No.	Description	State of Preservation
Evans' nodule	Similar to specimen R6697 but includes the anterior portion of the axial skeleton.	The majority of the elements present are in a fine state of preservation.
R1168	A partial skull similar in size to R6697. The individual elements have been, in part, extracted from the matrix.	The preservation of the bone is poor and the presence of veins of insoluble substances in the matrix made preparation difficult.
R3375	A moderately large and near complete skull, dorso-ventrally compressed, lying embedded in a relatively soft and shaley matrix.	The dorsal surface is exposed, the ventral portion is hidden from view and much crushed.
49203	An in-the-round specimen similar in size to R3375. The lower jaw has been removed.	The bone is not as well preserved as in the ex-nodular material.

With the exception of specimen 49203 the six prepared skulls were in a condition which prevented identification to species level. However, from the evidence available, it would seem that all six were latipinnate, and therefore to be assigned to the genus *Ichthyosaurus*. Specimen 49203 could be referred to the species *I. communis*. [The systematics of the Lower Liassic ichthyosaurs are discussed in detail by the present author in a paper which is now in preparation.]

DESCRIPTION OF INDIVIDUAL ELEMENTS OF THE SKULL

With the exception of the nasal, maxilla and premaxilla the elements of the skull were complete and well preserved in the material examined. In the case of these three elements references to unprepared skulls and serial sections has contributed to their descriptions. The descriptions will be given in two main sections, the replacement bones, and the dermal bones.

REPLACEMENT BONES

A. Ossifications of the chondrocranium

The ossified chondrocranium is represented by six elements, the basisphenoid, basioccipital, supraoccipital and paired exoccipitals, opisthotics and proötics. The opisthotic and proötic together form the greater part of the ossified otic capsule, with a minor contribution from the supraoccipital.

1. *Basisphenoid* (fig. 1, plate 1a). The basisphenoid is a fairly stout dorso-ventrally compressed element which contributes to the floor of the cranium. Posteriorly it articulates with the basioccipital, and on either side ventro-laterally with the pterygoids.

The posterior surface faces obliquely backwards and upwards and is indented to receive the keeled anterior face of the basioccipital. This indentation continues rostrally as a fairly deep and narrow ascending fissure which bisects the dorsal

surface. Anteriorly the dorsal edges of the fissure are raised into a pair of pinnacles, and in one mature specimen (R8177) these processes have fused in the mid-line forming a bony buttress. It is thought that the fissure probably marks the position of a vestige of the upturned tip of the notochord, and this matter is referred to again when the reconstruction of the occiput is discussed (page 76).

Ventrally, on each side, the basisphenoid is drawn out into the winged basipterygoid process which slots into a corresponding depression in the pterygoid. The bone which borders the dorsal edge of the basipterygoid process has a spinous rugosity and in mature individuals the spines are quite prominent. The element is pierced by a wide channel which follows an oblique path, entering on the anterior face, and leaving from the posterior half of the ventral face. This channel, the carotid foramen, served to carry the two internal branches of the carotid artery to the brain.

The carotid foramen widens as it opens into the endocranial cavity, forming a rounded depression which is interpreted as the sella turcica. In life the sella turcica housed the pituitary gland and the bony arch above it, which is notched by the dorsal fissure (see fig. 1a) represents the ossified dorsum sellae. Immediately below the sella turcica is a pair of rounded depressions which are immediately underlain by the dermal parasphenoid. Similar paired depressions are found in the basisphenoid of *Sphenodon* where they have been interpreted as impressions of the paired trabeculae in the anterior portion of the ossified parachordal basal plate,

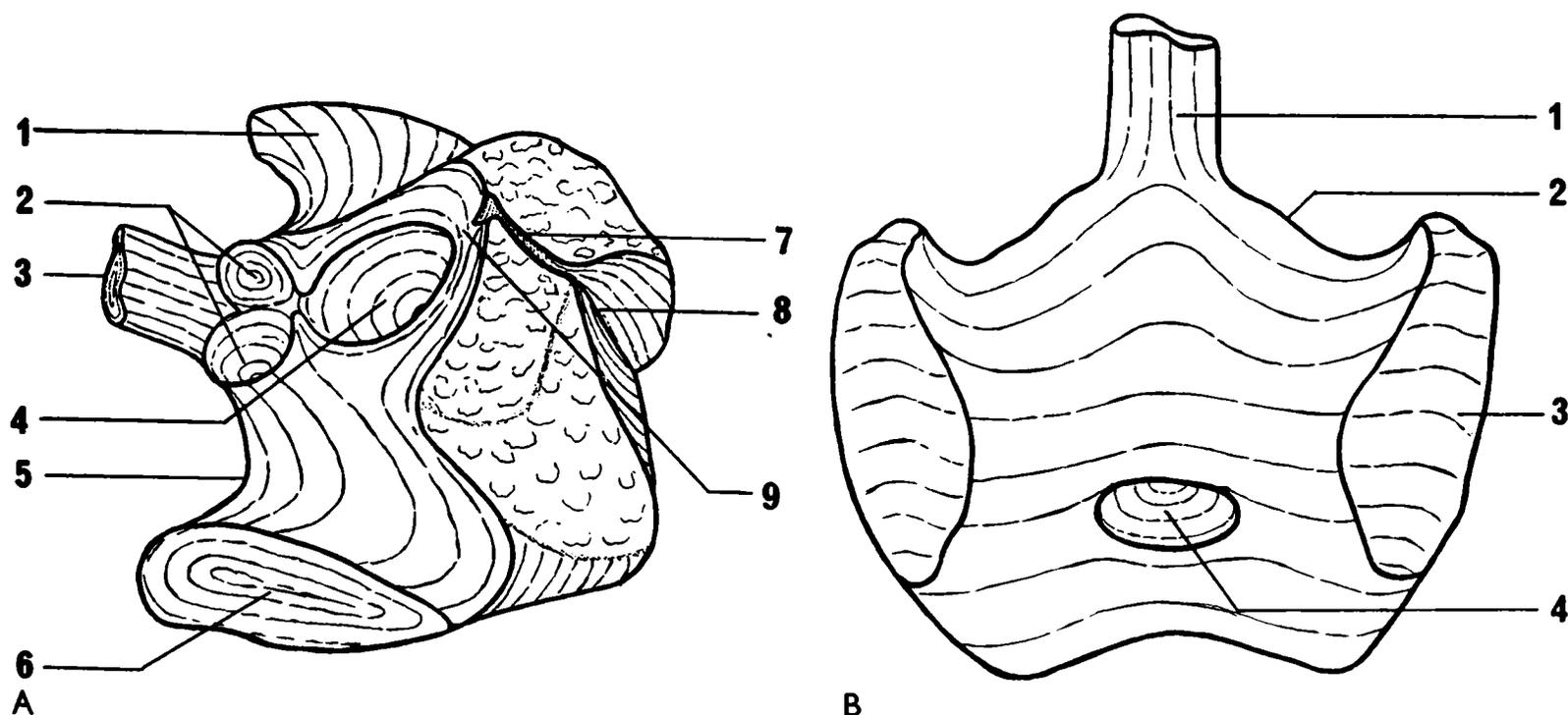


FIG. 1. (a). Basisphenoid, dorso-lateral view, $\times 2$, (Evans' nodule). 1, Basipterygoid process. 2, impressions of paired trabeculae. 3, parasphenoid. 4, sella turcica. 5, leading ventral edge which contributes to the interpterygoid vacuity. 6, distal articular facet of basipterygoid process. 7, dorsal fissure. 8, keeled posterior surface. 9, ossified dorsum sellae. (b). Basisphenoid, ventral view, $\times 2$, (Evans' nodule). 1, parasphenoid. 2, leading ventral edge. 3, ventral articular facet of basipterygoid process. 4, ventral opening of carotid foramen.

(Säve-Söderberg 1946). On either side of these depressions the leading ventral edge of the basisphenoid is emarginated, and is continuous with the curvature of the interpterygoid vacuity.

To the ventral surface of the basisphenoid is applied the dermal parasphenoid, and their relationship is so intimate that the actual extent of the latter is difficult, if not impossible, to determine. Sufficient remains of the parasphenoid to indicate that it was elevated at about 60 degrees to the horizontal.

2. *Basioccipital* (fig. 2, plate 1b). The basioccipital, the most posterior of the cranial series, is a stout and compact bone which bears the condyle for articulation with the vertebral column. Anteriorly and ventrally it articulates with the basisphenoid, dorsally with the exoccipitals. Postero-laterally it articulates with the opisthotic, and a little below this it makes touch contact with the proximal head of the stapes.

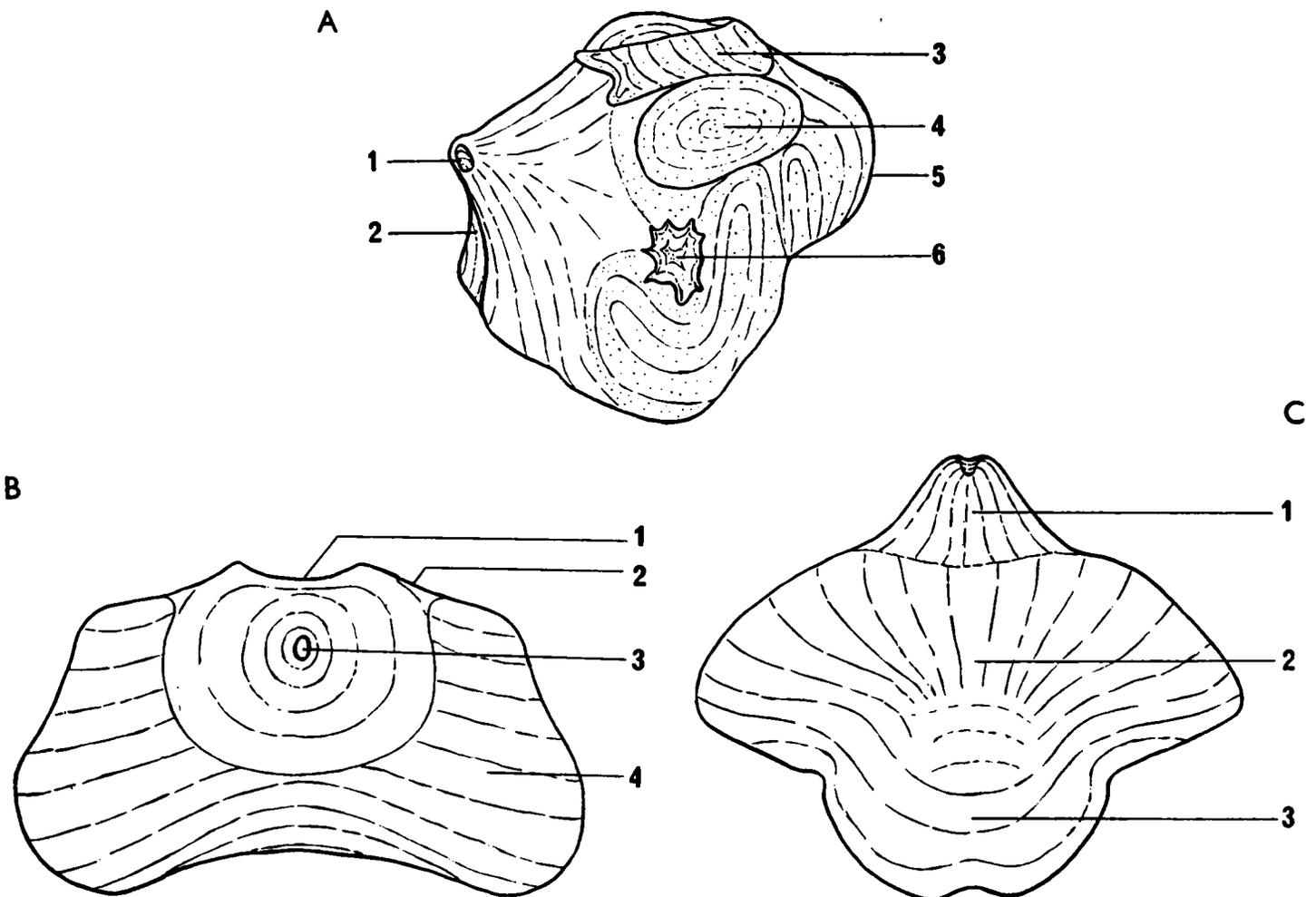


FIG. 2. (a). Basioccipital, antero-lateral view, $\times \frac{3}{2}$ (Evans' nodule). 1, notched tip of basioccipital peg. 2, keeled antero-ventral face. 3, floor of neurocranium. 4, exoccipital facet. 5, condyle. 6, stellate excavation probably marking position of lagena. (b). Basioccipital, posterior view, $\times \frac{3}{2}$ (Evans' nodule). 1, floor of foramen magnum. 2, exoccipital facet. 3, depression at centre of condyle. 4, posterior shield. (c). Basioccipital, ventral view, $\times \frac{3}{2}$ (Evans' nodule). 1, basioccipital peg. 2, ventral surface. 3, condyle.

The condyle is a spherical outpushing from the dorsal half of the posterior surface, and bears a small depression at its centre which has been interpreted by Andrews in *Ophthalmosaurus* (1910 : 6) as marking the position of the anteriormost remnant of the notochord. Since it is thought that the dorsal fissure in the basisphenoid marks the position of a vestige of the upturned notochordal tip, the depression in the condyle cannot represent the anterior most tip of the notochord. The true situation would seem to be that at least two vestiges of the notochord persisted in the skull and that the depression in the condyle marks the anterior tip of the second of these. When viewed from behind the rounded outline of the condyle is interrupted dorsally by the floor of the foramen magnum. Laterally and ventrally the posterior surface slopes away from the condyle, producing a curving shield of bone which continues, without interruption, with the ventral surface.

The dorsal surface is grooved in the midline by a shallow but wide excavation which bifurcates anteriorly into two tapering tongues, and which forms the floor of the cranial cavity. On either side is a large ovoid facet for the reception of the exoccipital. The dorsal surface is not horizontal, but slopes forward, and, just anterior to the median groove the slope becomes steeper. In addition to shelving, the dorsal surface is tapered, and because the lateral and ventral surfaces are similarly tapered, the bone is drawn out to a point, and this tapering process will be referred to as the basioccipital peg.

The ventral surface is of two parts; a posterior portion slopes upwards to become continuous with the posterior shield, and an anterior portion slopes upwards to become continuous with the basioccipital peg. In mid-ventral line the anterior portion is raised by a ridge and the keel thus formed corresponds closely with the postero-dorsal surface of the basisphenoid which is sculptured for its reception. Just beneath the tip of the basioccipital peg there is a small notch, and when the basioccipital and basisphenoid are placed in contact it is seen to align with the dorsal fissure in the basisphenoid. This notch is interpreted as marking the posterior end of the anterior notochordal vestige, a conclusion supported by the fact that the width of the dorsal fissure in the basisphenoid compares very closely with that of the notch in the peg, which in turn compares with the notch in the condyle. This matter is discussed in some detail in a later section (see page 76).

Sloping away from the tip of the basioccipital peg, on either side, is an antero-lateral surface, and this bears a stellate excavation at its centre which is thought to mark the position of the lagena.

3. *Exoccipital* (fig. 3, plate 1c). The vertically orientated exoccipital is a small element of some complexity which lies at the back of the skull on either side of the foramen magnum forming the postero-lateral wall of the neurocranium. Dorsally it articulates with the supraoccipital, whilst ventrally it rests in an oval depression on the dorsal surface of the basioccipital.

Essentially the exoccipital comprises a solid and ovoid base connected by a narrow waist to a somewhat swollen head. The entire dorsal surface is formed of a rounded articular surface for the supraoccipital and is relatively smooth, faces obliquely

forward and upward, and is inclined to the longitudinal axis so that the posterior edge lies medial to the anterior edge. The ventral surface is pitted and ridged, and is oval in outline, tapering anteriorly.

The element is pierced by three foramina which can be clearly seen in lateral view. Of these the most posterior is the largest, and is rounded rather than oval, whilst that adjacent to it is distinctly ovoid. Both foramina slope slightly antero-dorsally as

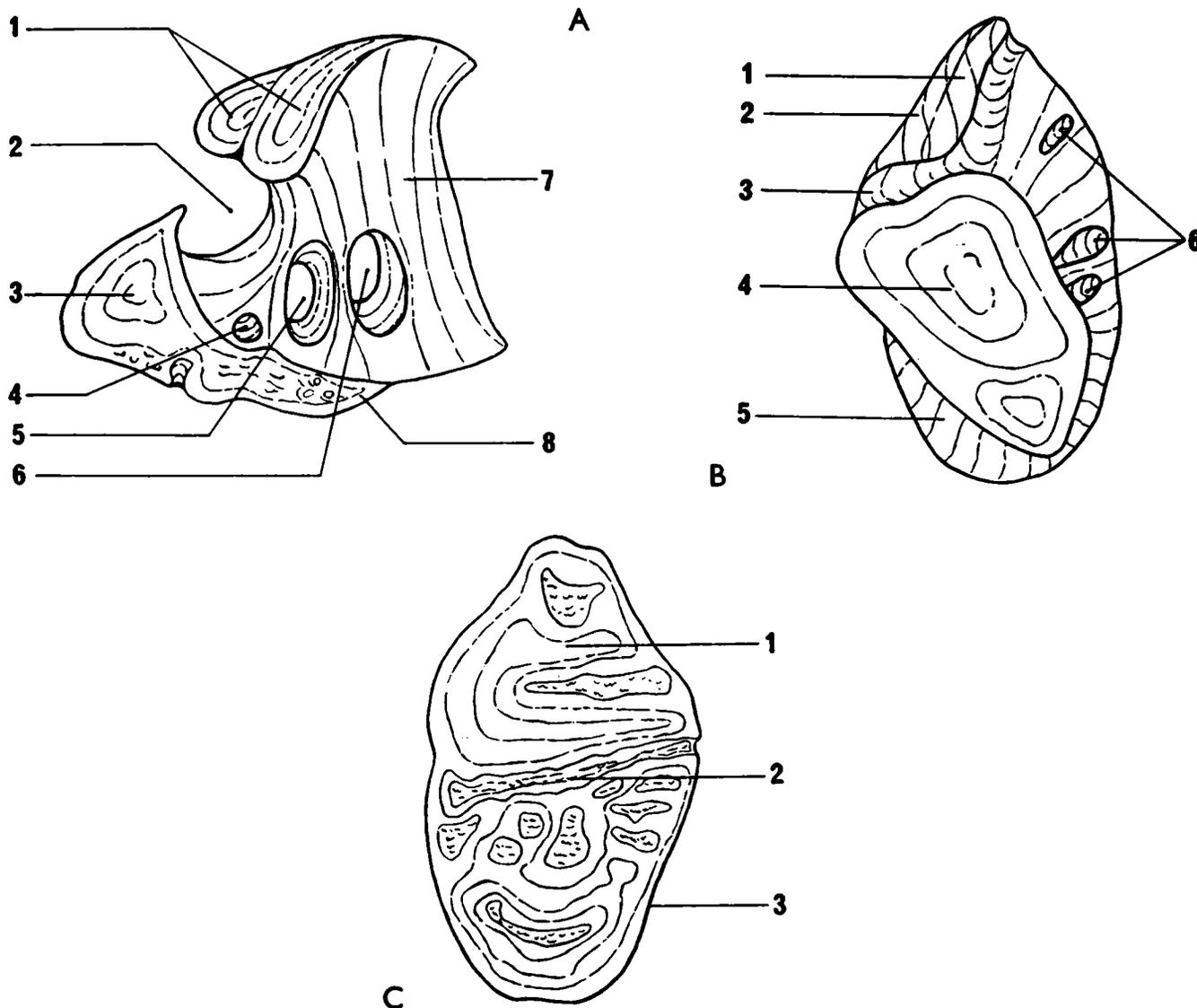


FIG. 3. (a). Exoccipital (left), external lateral view, $\times 3$ (Evans' nodule). 1, supraoccipital facet. 2, jugular foramen. 3, triangular process. 4, anterior nervous foramen, possibly for transmission of the spinal accessory nerve. 5, nervous foramen for transmission of anterior branch of the hypoglossal nerve. 6, nervous foramen for transmission of posterior branch of hypoglossal nerve. 7, external lateral surface. 8, ventral basioccipital facet. (b). Exoccipital (left), dorsal view, $\times 3$ (Evans' nodule). 1, medial edge of triangular process which was continuous with the cartilaginous wall of the otic capsule. 2, triangular process. 3, grooved floor of jugular foramen. 4, supraoccipital facet. 5, external lateral surface. 6, nervous foramina. (c). Exoccipital (left), ventral view, $\times 3$ (Evans' nodule). 1, anterior portion of basioccipital facet. 2, transverse groove, probably marking the course of a blood vessel. 3, external lateral edge of basioccipital facet.

they pass outwards, and are slightly divergent. Anteriorly there is a prominent emargination, the jugular foramen, and just beneath it is the third and smallest foramen, which can easily be overlooked. As in the other foramina, it follows an antero-dorsal passage through the bone. The posterior aspect of the exoccipital has a curved profile in both external and internal view.

The jugular foramen served to transmit the jugular vein, the vagus nerve, and perhaps also the glossopharyngeal. The two large foramina are believed to have transmitted two branches of the hypoglossal, while the smallest may have carried the spinal accessory. The foramina will be discussed in greater detail below.

In front of the jugular foramen is a bony process which is triangular in external view and which has a relatively smooth face. This process is inclined both forward and outward, and is inflected anteriorly to form a narrow and medial bony lip which was continuous with the cartilaginous wall of the otic capsule. Anteriorly the internal surface of the bone is smooth, and follows a curved path which slopes backwards and upwards as it passes outward and is continuous with the floor of the jugular foramen. Posteriorly the internal surface is much interrupted by the passage of the nerve foramina.

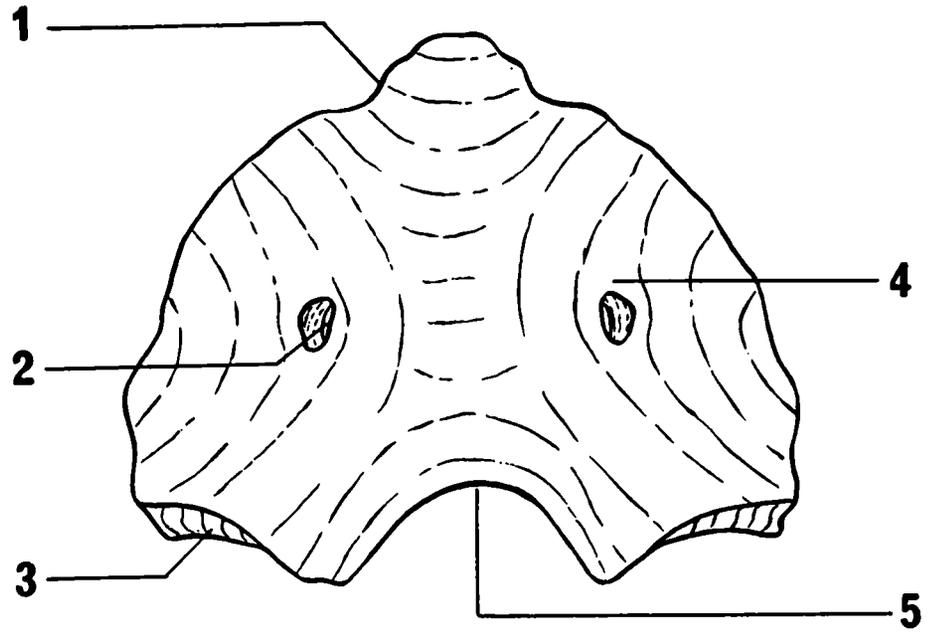
4. *Supraoccipital* (fig. 4, plate 1d). Resting on the paired exoccipitals the supraoccipital completes the occipital series, roofing the foramen magnum dorsally and forming the postero-dorsal wall of the neurocranium.

The posterior surface is convex from side to side and to a much lesser extent from top to bottom. The anterior surface is correspondingly concave from side to side giving it a strongly arched appearance when viewed from above. The bone is pierced by a pair of foramina which open out on the anterior and posterior surfaces of the bone. Due to divergence the foramina lie further apart on the posterior surface than they do anteriorly, and they are ovoid in shape rather than round. These openings may have served for the passage of the endolymphatic ducts, and the posterior surface of the supraoccipital is interrupted in the vicinity of each by a shallow triangular depression.

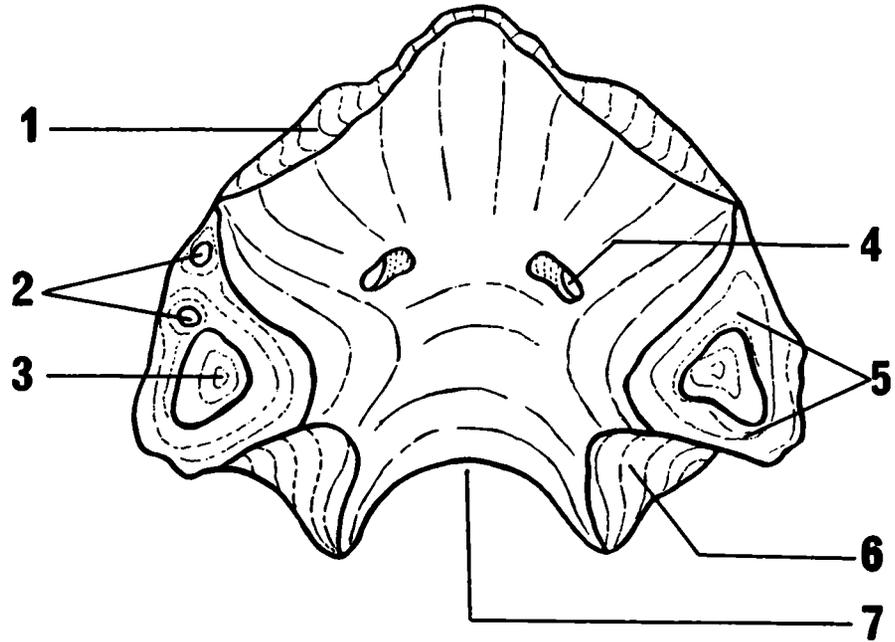
The dorsal edge is channeled by two shallow grooves on either side of the midline and also by a number of small depressions, and this marks the boundary between the ossified and cartilaginous portions of the neurocranium. Vento-laterally the sculptured dorsal margin is continuous with the triangular lateral surface. This is also marked by small indentations which embrace a small and triangular depression of cancellar bone which bears an impression of the membranous labyrinth.

The exoccipital facets are petaloid when viewed from beneath, and occupy the entire ventral surface on either side of the foramen magnum. The facets are hollowed, and because the internal margin is more strongly arched than the external margin, the smooth articular surface is inclined slightly inwards.

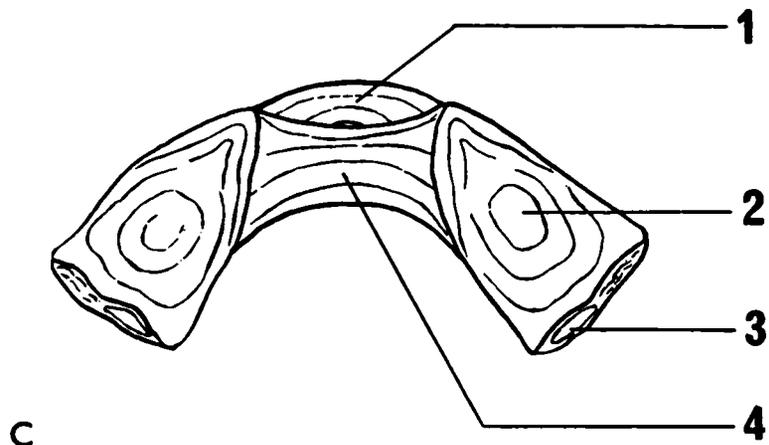
The dorsal arch of the foramen magnum is variable, and does not necessarily have a perfect bilateral symmetry. In some specimens the arch is wide, as in Evans' nodule, and the foramen has a rounded outline, whereas in others a narrow arch confers a distinctly ovoid foramen, as in R6697.



A



B



C

5. *Opisthotic* (fig. 5, plate 1e). The opisthotic is a compact bone which lies at the back of the skull lodged between the basioccipital proximally, the squamosal distally, and has contact with the head of the stapes ventrally. Being the posterior (and major) ossification of the cartilaginous otic capsule, it bears impression of the membranous labyrinth on its anterior surface.

Viewed from behind the opisthotic has a triangular outline with its apex represented by the rounded paroccipital process, directed laterally and dorsally. The medial surface is largely occupied by a shallow and crescentic articular facet which faces obliquely to make contact with the periphery of the basioccipital.

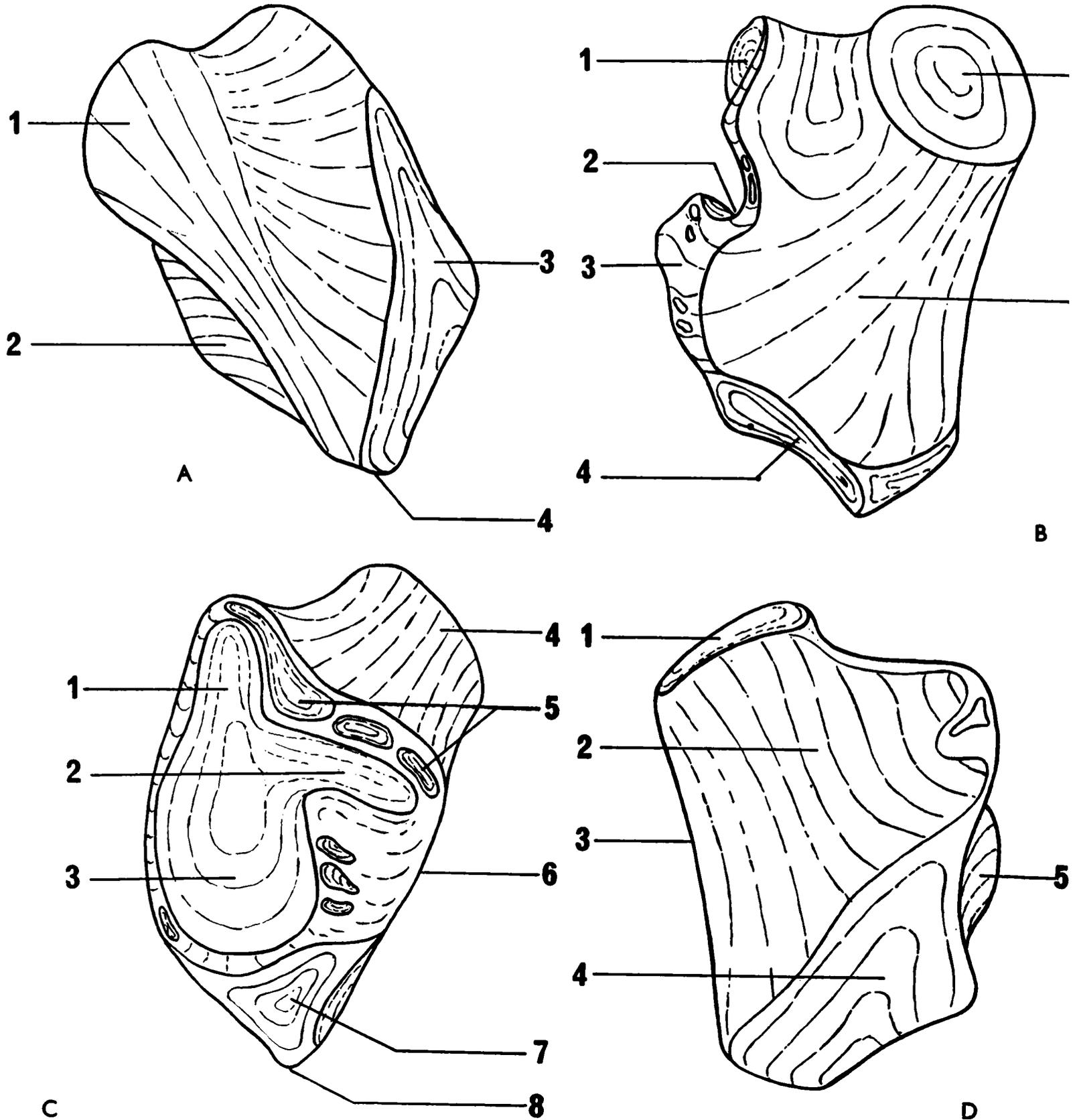
The membranous impression represents the posterior aspect of the utriculus and sacculus and the origin of the horizontal semicircular canal, possibly also the origin of the posterior vertical semicircular canal. The horizontal semicircular canal impression branches off from a pear-shaped depression and follows a curving path which passes externally and slightly ventrally. The bone of the depressed area is marked by fine striations which follow the contours like the shading lines of a drawing. Circumscribing the impression is a margin of bone which is excavated by shallow grooves and pockets, having the same grooved and pitted appearance as the dorsal edge of the supraoccipital. In life this margin was continuous with the cartilaginous wall of the otic capsule, and gives a good indication of its thickness. Lying outside and just ventral of saccular impression is a second and very much smaller depression which is oval in shape and lined with cancellar bone similar in appearance to that of the membranous impression in the supraoccipital. This is interpreted as probably being the impression of part of the lagena.

6. *Proötic* (fig. 6, plate 1f). The proötic is the third and last of the otic elements and, lacking contact with any other element, is the most difficult to interpret. Only after the membranous labyrinth had been partly reconstructed was it possible to arrive at a satisfactory orientation, and it is within the framework of this new relationship that the element will now be described.

The proötic is a small bone which forms the anterior wall of the otic capsule, and its posterior aspect thus bears an impression of the membranous labyrinth. Since its walls are relatively thin it has become partially moulded to the shape of the labyrinth, and has the appearance of a pyramidal seashell whose umbo lies at its centre. The membranous impression is pear-shaped, with a wide branch coming off at right angles about half way down its external side, and represents the union of two semicircular canals. One of these, the narrower, lies in the vertical plane, and is interpreted as being that of the anterior vertical semicircular canal. The

FIG. 4. (a). Supraoccipital, posterior view, $\times 2$ (Evans' nodule). 1, dorsal edge. 2, foramen, which probably transmitted endolymphatic duct. 3, exoccipital facet. 4, triangular depressed area surrounding foramen. 5, roof of foramen magnum. (b). Supraoccipital, anterior view, $\times 2$ (Evans' nodule). 1, grooved dorsal edge. 2, depressed areas of lateral surface. 3, impression of membranous labyrinth. 4, foramen. 5, grooved and pitted margin circumscribing membranous impression. 6, exoccipital facet. 7, roof of foramen magnum. (c). Supraoccipital, ventral view, $\times 2$ (Evans' nodule). 1, posterior surface. 2, exoccipital facet. 3, membranous impression. 4, roof of foramen magnum.

second is fairly wide, directed toward the outer edge of the bone, and lies in the horizontal plane marking the position of the horizontal semicircular canal. In some specimens there is the slightest indication of a depression at the point of union of the two canals, marking the position of the ampulla of the anterior vertical semicircular canal. The internal surface of the bone is marked by fine striations similar



to those seen in the opisthotic, but here they are not quite so prominent. The entire margin of the proötic is grooved and pitted and is thinner than that of the opisthotic.

B. Ossifications of the Mandibular and Hyoid Arches

The mandibular and hyoid arches have an origin and development separate from the chondrocranium, but certain parts become so intimately associated with it that they form an integral part of the skull.

The mandibular arch is of two parts, the palatoquadrate bar above, and the mandibular bar, or Meckel's cartilage, below. Meckel's cartilage has but a single ossification, the articular, and the lower jaw is formed largely from the dermal elements which become applied to it. For convenience the articular will be described together with the other lower jaw elements in a later and separate section. The palatoquadrate has two ossifications in tetrapods, an anterior epiptyerygoid, and a posterior quadrate, the latter articulates with the articular of the lower jaw. Both elements form an integral part of the skull, and are therefore described in the present section.

The hyoid arch has a number of ossifications. Dorsally there is a single element, the stapes, whilst ventrally are elements which constitute the hyoid apparatus. Since the latter structure, unlike the stapes, does not form part of the skull, it is dealt with elsewhere.

1. *Stapes* (fig. 7, plate 2a). The stapes is located at the back of the skull and forms a strut between the opisthotic and basioccipital proximally, and the quadrate distally. Essentially the element comprises of a rounded head which bears a facet for articulation with the opisthotic, and a shaft which has an angulate bend directed ventrally. Distally the shaft widens, and terminates in an oblique and elongate articular surface which faces forwards and outwards, and which corresponds with a facet on the quadrate which faces obliquely backwards and inwards.

FIG. 5. (a). Opisthotic (left), posterior view, $\times 3$ (Evans' nodule). 1, paroccipital process. 2, external lateral surface. 3, basioccipital facet. 4, ventral tip, part of which locates in a facet on the stapes. (b). Opisthotic (left), external view, $\times 3$ (Evans' nodule). 1, impression of the posterior portion of the utriculus (or possibly the origin of the posterior vertical semicircular canal). 2, impression of horizontal semicircular canal. 3, grooved and pitted margin circumscribing membranous impression. 4, ventral depression, probably marking the position of a lagena. 5, paroccipital process. 6, external lateral surface. (c). Opisthotic (left), anterior view, $\times 3$ (Evans' nodule). 1, impression of dorsal portion of the utriculus, or possibly of the posterior vertical semicircular canal. 2, impression of the horizontal semicircular canal. 3, impression of the sacculus. 4, paroccipital process. 5, grooves in margin circumscribing membranous impression. 6, external edge. 7, ventral depression probably marking the position of a lagena. 8, ventral tip. (d). Opisthotic (left), internal view, $\times 3$ (Evans' nodule). 1, paroccipital process. 2, internal surface. 3, posterior edge. 4, basioccipital facet. 5, impression of sacculus.

The head of the stapes is stout and moderately well rounded, although it does tend to become raised dorsally into a low ridge which appears more prominent in mature specimens (R8177). On the posterior aspect there is a groove which runs obliquely forward and upward and which in life carried forward the stapedia artery. The stapedia groove is not always a prominent feature, and is most clearly seen in R8177. Above the level of the stapedia groove the head is no longer rounded, and, as mentioned before, it tends to be drawn up into a low ridge. The greater part of this dorsal portion is occupied by a shallow and triangular depression for the reception of the ventral tip of the opisthotic. While there is a certain degree of demarcation between upper and lower portions of the head, at least in mature forms, and while the dorsal portion has articular contact with the opisthotic, whether or not it could be described as the dorsal process in the full sense is conjectural (compare with the structure of the stapes in *Ophiacodon*, Romer & Price 1940). There can be no doubt that the head of the stapes, being channelled by the stapedia groove, is the true footplate, and it seems reasonable to conclude that the portion lying above the groove and articulating with the opisthotic could represent the true dorsal process.

While the anterior aspect of the head in R8177 is virtually devoid of feature, in the smaller specimens it is occupied by a shallow concavity (fig. 7d, 4). When the stapes is articulated with the reconstructed skull this facet is observed to be directed towards, and lie very close to the position now thought to have been occupied by a lagena. Since this facet lies in such a position it is concluded to be that part of the footplate which in life attached to the fenestra ovalis.

Whilst the dorsal edge of the shaft follows a gentle curve, the ventral edge is sharply angulate and its apex, which is directed downwards, is roughened and may have been the origin of a muscle. Similar rugosities occur on the anterior surface of

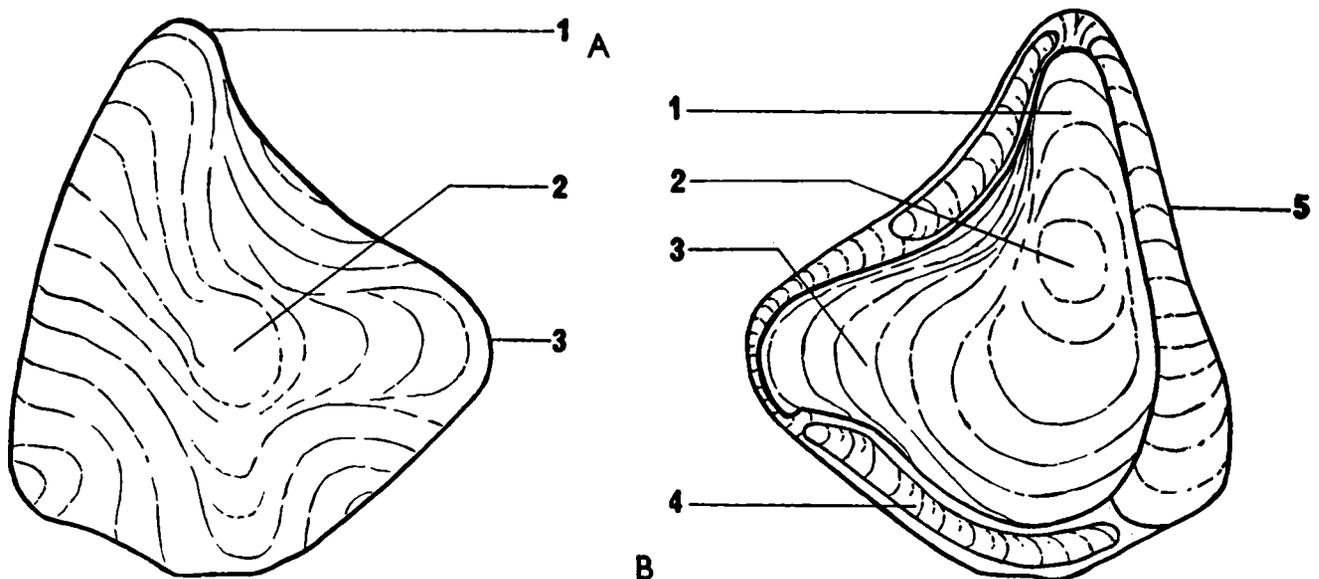


FIG. 6. (a). Proötic (left), anterior view, $\times 3$, (Evans' nodule). 1, dorsal tip. 2, 'umbo'. 3, outside edge. (b). Proötic (left), posterior view, $\times 3$ (Evans' nodule). 1, impression of anterior vertical semicircular canal. 2, probably the impression of an ampulla. 3, impression of the horizontal semicircular canal. 4, groove in margin of the bone which circumscribes the membranous impression. 5, internal edge.

the shaft, where it widens, and these are more prominent in some specimens than in others. The distal (quadrate) articular facet is slender and oval, and, facing forwards and outwards, its surface lies parallel with an oval depressed area on the posterior surface of the quadrate. It is quite smooth and sometimes slightly sunken so that the periphery is raised by a low lip. The quadrate depression is longer and wider than the facet of the stapes, and the two surfaces are separated by a gap so that it can safely be concluded that the stapes was continued distally in cartilage. The stapes must therefore have been an immobile strut between the quadrate distally and the otic capsule proximally.

2. *Epipterygoid* (fig. 8, plate 2b). Dorsally the epipterygoid enters into a complex and interdigitating suture with a descending process of the parietal, and has ventral contact with the pterygoid. The element therefore forms a strut between the skull roof and palate.

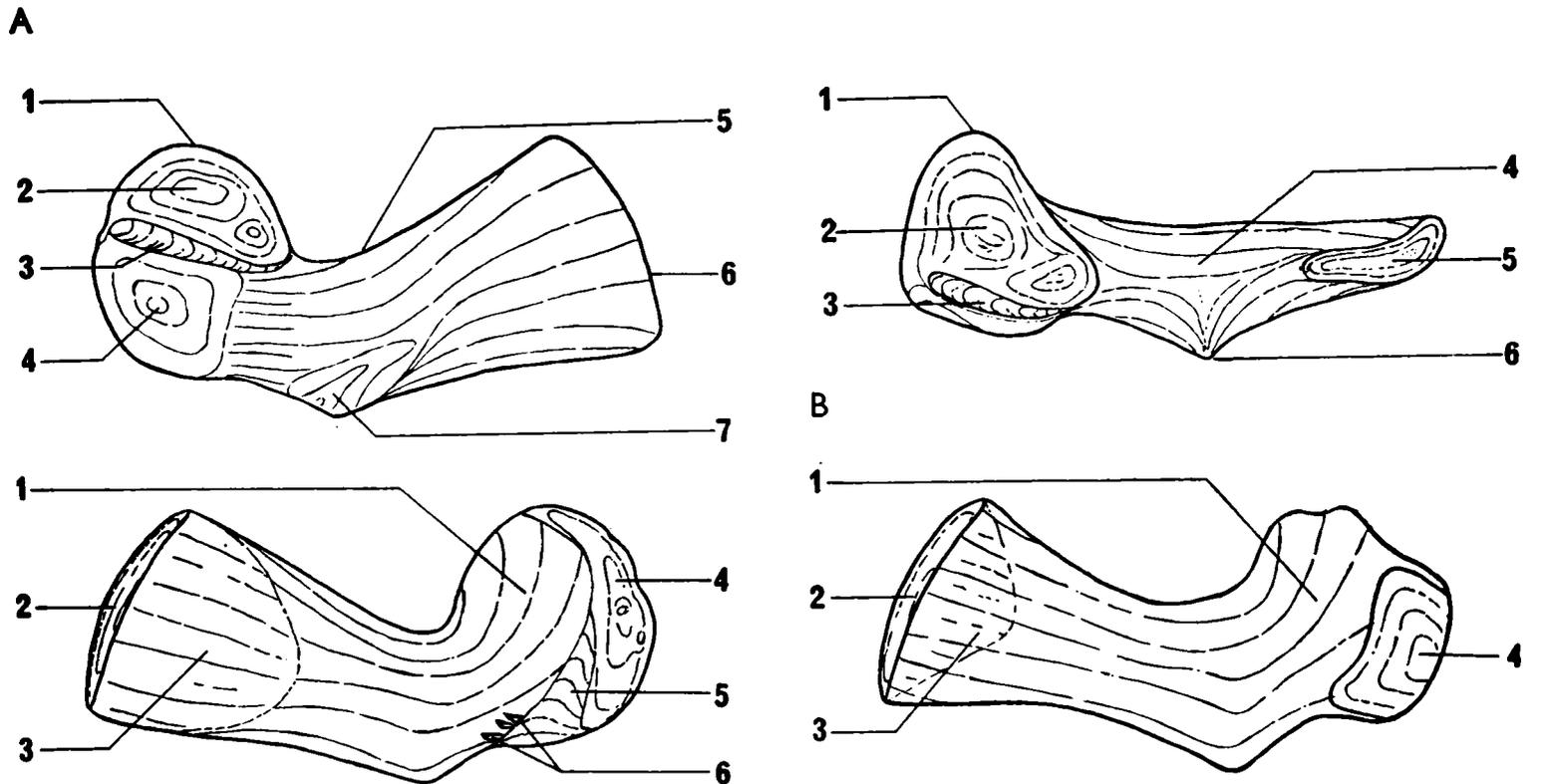


FIG. 7. (a). Stapes (right), posterior view, $\times 3/2$, (R8177). 1, raised dorsal ridge of head. 2, postero-dorsal facet for reception of opisthotic. 3, groove marking course of stapedia artery. 4, rounded posterior surface of head. 5, dorsal edge of shaft. 6, distal edge of shaft. 7, raised bony ridge which may have been an area of muscle origin. (b). Stapes (right), dorsal view, $\times 3/2$ (R8177). 1, raised dorsal ridge of head. 2, postero-dorsal facet for reception of opisthotic. 3, groove for stapedia artery. 4, dorsal edge of shaft. 5, distal facet of shaft which was in cartilaginous contact with the quadrate. 6, summit of raised bony ridge. (c). Stapes (right), anterior view, $\times 3/2$, (R8177). 1, laterally inclined anterior surface of head. 2, distal facet. 3, shallow depressed area of bone, somewhat rugose. 4, slight indentation. 5, shallow groove. 6, denticular rugosities. (d). Stapes (right), from a smaller individual, anterior view, $\times 2$, (based largely on R6697). 1, laterally inclined anterior surface of head. 2, distal facet. 3, area of rugose bone. 4, well marked facet on anterior aspect of head.

The epipterygoid bears superficial resemblance to a leg and foot, the toes of which rests in a shallow groove in the pterygoid, at the level of the basiptyergoid articulation. The shaft, or 'leg', lies approximately in the vertical plane, and its external surface is grooved for about half its length. This groove is not single, however, because it is invaded by bony flanges dividing it into a number of longitudinal compartments. The medial surface of the descending parietal process is correspondingly ridged and grooved, and the two elements come together in a rigid interdigitating suture. The internal surface of the shaft has a less complex appearance and widens dorsally into a flange of bone which locates in a shallow depression high up on the medial surface of the epipterygoid process of the parietal.

The foot of the epipterygoid is laterally compressed and has a hollowed external surface due to the fact that the 'heel' is turned out. The internal surface of the foot is consequently convex. Medially, at the place where the foot joins the shaft (i.e. at back of the 'ankle'), the surface of the bone is rugose, the extent of the roughening

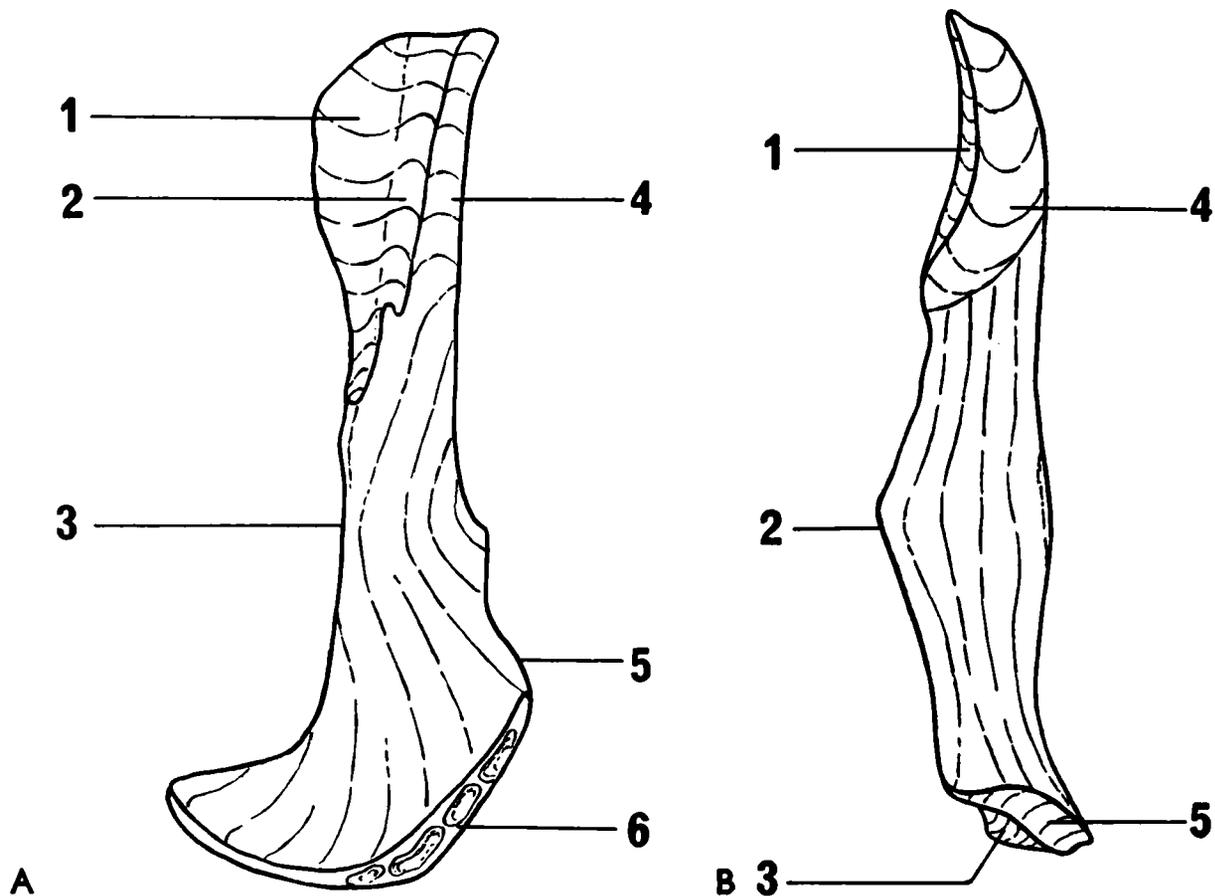


FIG. 8. (a). Epipterygoid (left), external lateral view, $\times 3/2$ (R1168). 1, bony flange which locates in an ovoid facet on the medial surface of the descending epipterygoid process of the parietal. 2, deep edge groove for reception of the medial edge of the descending epipterygoid process of the parietal. 3, leading edge of shaft. 4, shallow groove. 5, posterior edge of foot which is turned outwards. 6, grooved and pitted ventro-lateral trailing edge of foot. (b). Epipterygoid (left), anterior view, $\times 3/2$ (R1168). 1, medial surface of shaft produced into a smooth flange. 2, position of rugosity of the medial surface of the shaft. 3, medial surface of foot. 4, antero-medially inclined groove. 5, grooved and pitted ventral edge of foot.

varying from specimen to specimen. In some individuals (Evans' nodule) the rugosities are barely noticeable, whilst in others (R8177) they are very prominent, and the significance of this is discussed later (see *Kinesis*, below). The ventral trailing edge of the foot is grooved and depressed, indicative of cartilaginous continuity. The ventral portion of the leading edge of the quadrate has a similar

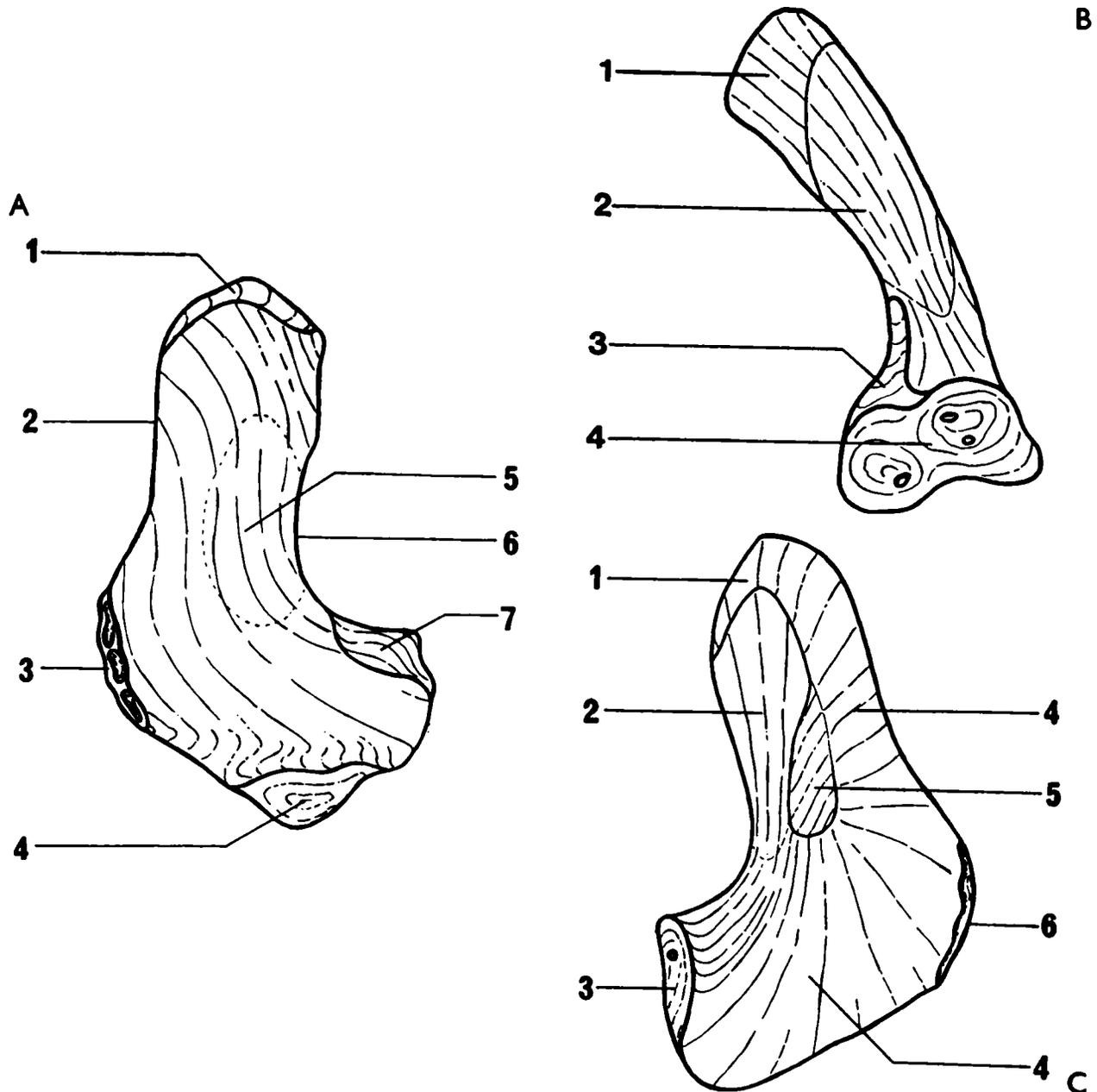
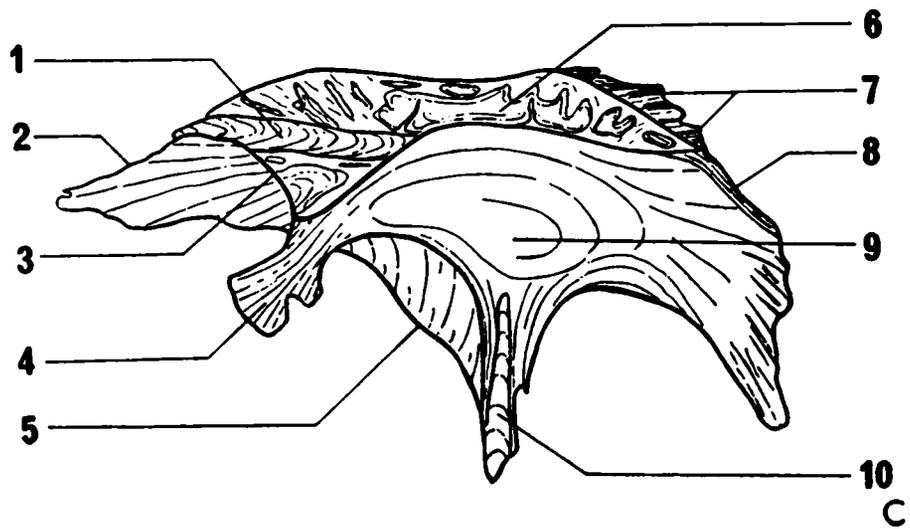
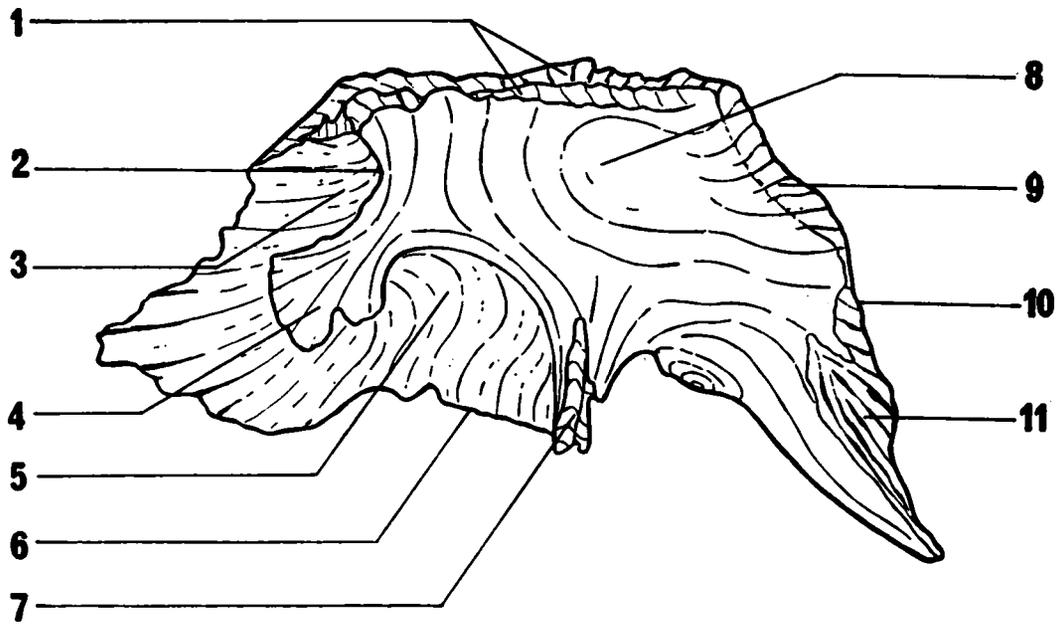
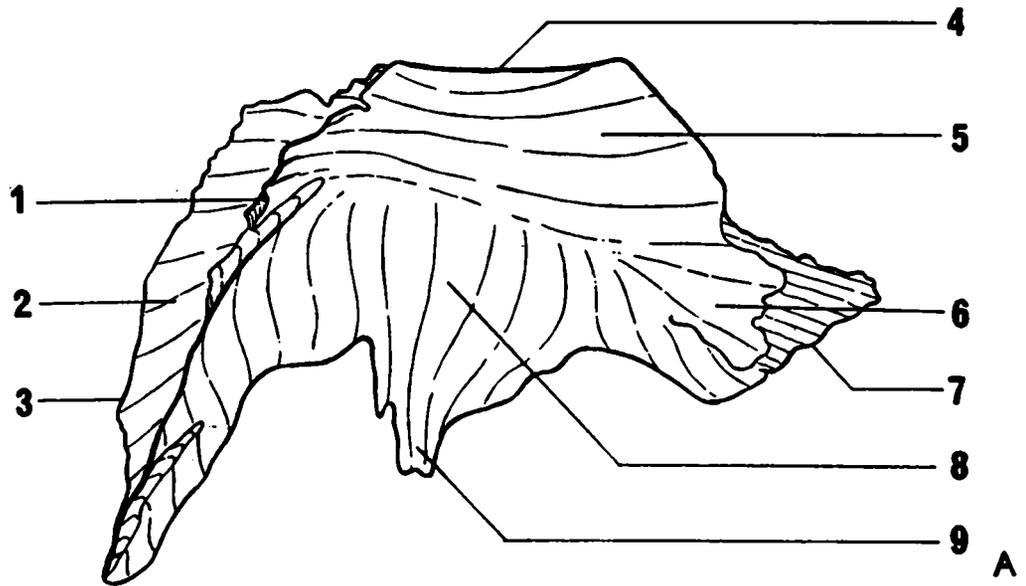


Fig. 9. (a). Quadrate (left), anterior view, just more than natural size (R6697). 1, grooved dorsal edge. 2, medial edge which slots into a groove in the squamosal. 3, pitted leading edge which was in cartilaginous continuity with the epipterygoid. 4, condyle. 5, area of origin of the *M. adductor mandibulae posterior*. 6, emarginated external edge. 7, quadratojugal facet. (b). Quadrate (left), external view, just more than natural size (R6697). 1, smooth facet of the external surface. 2, roughened area of the external surface. 3, quadratojugal facet. 4, condyle. (c). Quadrate (left), posterior view, just more than natural size (R6697). 1, smooth facet of external surface. 2, roughened area of external surface. 3, condyle. 4, posterior surface. 5, facet for reception of cartilaginous portion of stapes. 6, pitted leading edge.

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appearance, and lies close behind the epipterygoid, and it is concluded that the two elements were joined in life by cartilage.

The ventral edge of the foot is continued anteriorly where it ascends and becomes inflected forming a narrow shelf of bone (a 'toe-cap').

3. *Quadrate* (fig. 9, plate 2c). The quadrate is a relatively large element which has dorsal contact with the squamosal, medial contact with the pterygoid, and articulates with the lower jaw ventrally through the articular. Anteriorly it probably had cartilaginous continuity with the epipterygoid.

In anterior view the quadrate resembles an external ear flap, having a reniform outline, and being hollowed. In most specimens examined there is an oval area of bone (shown by a broken line in fig. 9a), where the surface is sculptured, and this probably marks the origin of the *M. adductor mandibulae posterior*. Since the bone is relatively thin the posterior surface tends to have a shape corresponding to the anterior surface, but is angulate rather than convex, forming two flat surfaces set at right angles to one another. For much of its length the dorsal portion therefore has an L-shaped section. The wider of these two faces is inclined backwards and inwards, and makes medial contact with the quadrate wing of the pterygoid. Contact does not involve the whole of this surface however, and posteriorly there is an oval and slightly depressed area which had cartilaginous continuity with the distal facet of the stapes.

The external edge is emarginated and contributes with the posterior edge of the quadratojugal in the formation of an elliptical foramen. On the external surface on some specimens a smooth dorsal facet is marked off from a roughened ventral portion, as shown in fig. 9b.

The quadrate thickens ventrally forming the articular condyle. In ventral view the condyle is triangular, tapering medially, and its anterior border which curves gently, continues the line of the intrapterygoid vacuity without interruption. The ventral surface of the condyle, which bears a triangular depression, curves upwards

FIG. 10. (a). Parietal (right), dorso-lateral view, just less than natural size (R8177). 1, parietal ridge. 2, bony shelf extending back from parietal ridge. 3, posterior edge. 4, dorsal edge. 5, depressed area of dorsal surface. 6, Bony lamella. 7, anterior edge. 8, descending lateral wall. 9, epipterygoid process. (b). Parietal, ventral view, just less than natural size (R8177). 1, bony lamellae of median dorsal edge. 2, transverse ledge forming the anterior margin of the optic lobe impression. 3, impression marking posterior portion of the cerebral hemisphere. 4, parietal flange. 5, extra-encephalic impression. 6, external lateral edge. 7, groove in epipterygoid process for reception of epipterygoid. 8, impression of optic lobe. 9, shallow depression marking position of cerebellum. 10, posterior edge. 11, rugosities. (c). Parietal (right), internal lateral view, just less than natural size R8177. 1, deep groove in median dorsal edge into which slots the postero-lateral edge of the frontal. 2, anterior edge. 3, impression marking posterior portion of the cerebral hemisphere. 4, parietal flange. 5, external lateral edge. 6, lamellate depression of median dorsal edge. 7, rugosities on median side of parietal ridge. 8, impression marking position of cerebellum. 9, impression of optic lobe. 10, groove in epipterygoid process.

externally and is continuous with the lateral surface, and it is only this portion which enters into articulation with the mandible. In external view, the articular surface of the condyle appears almost round. Just above the articular surface, at the anterior and external corner of the condyle, there is an oval bony protuberance circumscribed by a groove, and this receives the hollow articular facet of the quadratojugal.

DERMAL BONES

The dermal elements of the skull will be considered under four headings, those forming the skull roof and temporal arcade, the bones of the circumorbital series, the bones of the palate and upper jaw margin, and the sclerotic elements. The quadratojugal does not fall into any of these groups, but will be placed for convenience with the circumorbital elements, and the palatine, which is an element of mixed origin, is included with the dermal elements of the palate. Since the lower jaw is an integral structure which does not separate into individual elements, it is not possible to figure and describe the elements separately in the same way as those of the skull. The descriptions of the lower jaw will therefore be given in a separate section.

A. ELEMENTS OF THE SKULL ROOF AND TEMPORAL ARCADE

1. *Parietal* (fig. 10, plate 3a). The parietal is a massive element which forms the hind portion of the skull roof, and the medial margin of the temporal vacuity. That the mandibular muscles take direct or indirect origin from the parietal is reflected in the thickness of its walls, and in its various rugosities. Anteriorly it articulates with the frontal, and has contact with the prefrontal and with the postfrontal; posteriorly it articulates with the squamosal, and ventrally with the epipterygoid.

In dorsal view the parietal has the appearance of a trapezium, with its shorter side lying medially and its long side sloping steeply down forming the external lateral surface. The anterior edge is inclined to the longitudinal axis, being directed forwards, and terminates in an acute point. The posterior edge is also inclined, but faces backwards and inwards, and also curves ventrally. Running parallel with the posterior margin, and just anterior to it, is a very prominent and rugose crest which is referred to as the parietal ridge, and which articulates distally with the squamosal. The shelf of bone which extends back from the parietal ridge is relatively thin, and probably made contact with the dorsal margin of the supraoccipital.

The descending lateral wall is drawn out midway along its length into a tapering finger of bone which enters into a complex sutural union with the epipterygoid, and which is described as the epipterygoid process. In advance of the epipterygoid process the lateral margin slopes gently upward to meet the anterior margin, and behind it describes an arc, the leading edge of which runs approximately parallel with the parietal ridge. The parietal ridge thus marks the dorsal edge of a solid trigonid which curves downwards postero-laterally. The ventral surface of the parietal bears impressions of certain cerebral structures, and it is necessary to describe them in some detail, but the discussion of their significance is postponed till later.

The most prominent of the encephalic impressions lies at the level of the epipterygoid process, is ovoid, relatively deep, and has its longitudinal axis approximately

parallel with that of the skull. This impression is concluded to be that of the optic lobe of the brain. The anterior margin is formed by an almost straight and transverse ledge which is the ventral edge of a prominent buttress of bone formed by the thickening of the leading anterior edge of the parietal. Laterally the buttress is drawn out into a spatulate flange of bone which descends ventro-laterally with its flat ventral surface facing downwards and inwards. This flange, which probably gave support to the large optic lobe, is described as the parietal flange. The external lateral margin of the optic lobe impression is formed in part by the medial surface of the epipterygoid process. Caudally this is continued by a ridge which curves in towards the midline and which also forms the posterior margin. Rostrally the lateral margin is formed by a bony lip, which is also the medial margin of a deep and lateral extra-encephalic concavity, and which is continuous with the external edge of the descending parietal flange. The medial margin of the optic lobe impression is formed by the slightly raised ventro-medial edge of the parietal, and its posterior margin lies close to the posterior edge of the element, separated by a narrow ledge of bone which bears evidence of a second and far less well defined impression.

The second encephalic impression is very shallow and can easily be overlooked. It is slender, and approximates to a crescent, with the concave edge towards the posterior margin of the parietal. Caudally the impression tapers to a slender point. With its neighbour of the other side, and the ventral surface of the supraoccipital, it forms a single depression which embraced the cerebellum.

Immediately dorsal in position to the proximal portion of the parietal flange is an undercut which continues forward as a fairly shallow depression. This excavation contributes with a depression in the frontal element in the embrace of the cerebral hemisphere. The posterior medial corner of this excavation is much broken up by an area of pits and depressions of unknown significance. This third encephalic impression is narrower than that of the optic lobe but is perhaps just deeper.

The extra-encephalic depression is equally as deep as that of the optic lobe impression, but shallows anteriorly. The external lateral margin is formed by the internal lateral surface of the parietal and is bounded posteriorly by an almost vertical wall of bone which is continuous with the anterior surface of the epipterygoid process.

The medial edge of the parietal has a considerable depth and is relatively straight when viewed from above, but in ventral view is seen to follow an uneven path. The edge is not flat, but is broken up by a number of plates which interdigitate with those of the opposite edge when the parietals are articulated, thus forming a rigid suture.

2. *Frontal* (fig. 11, plate 3b). The frontal is a relatively small and delicate element which contributes to the skull roof, and which embraces the pineal foramen. For its greater part it is overlain by the nasal, and its postero-lateral edge slots into a recess in the leading dorsal edge of the parietal.

In dorsal view the frontal is somewhat crescentic. The external edge curves towards the mid-line both in front and behind, whilst the medial edge is straight for most of its length. Posteriorly, however, the medial edge bears an ovoid emargination which borders the pineal foramen. The dorsal surface is strongly arched from

side to side, corresponding to the encephalic excavations of the ventral surface. The anterior edge follows an S-shaped course, whilst the posterior edge follows a smooth convex curve.

The ventral surface bears two depressed areas; one circumscribes the pineal foramen and is the deepest, the other occupies the remainder of the surface and is shallow. The deep posterior depression is crescentic, and is interpreted as marking the position of the cerebral hemisphere. In the antero-medial corner of the cerebral hemisphere impression there is a prominent pitted area of unknown significance, similar to that seen in the parietal. The anterior excavation is separated from the one behind by a low ridge, and is concluded to be the impression of the olfactory lobe. This impression is shallow, and flattens out anteriorly.

3. *Nasal* (fig. 12, plate 3c). The nasal is a stout element which contributes to the skull roof posteriorly, and to the dorsal surface of the snout anteriorly. It has an overlapping contact with the frontal and prefrontal posteriorly, lateral contact with the lachrymal, and is overlapped anteriorly by the premaxilla. With the premaxilla and lachrymal it participates in the formation of the external narial aperture.

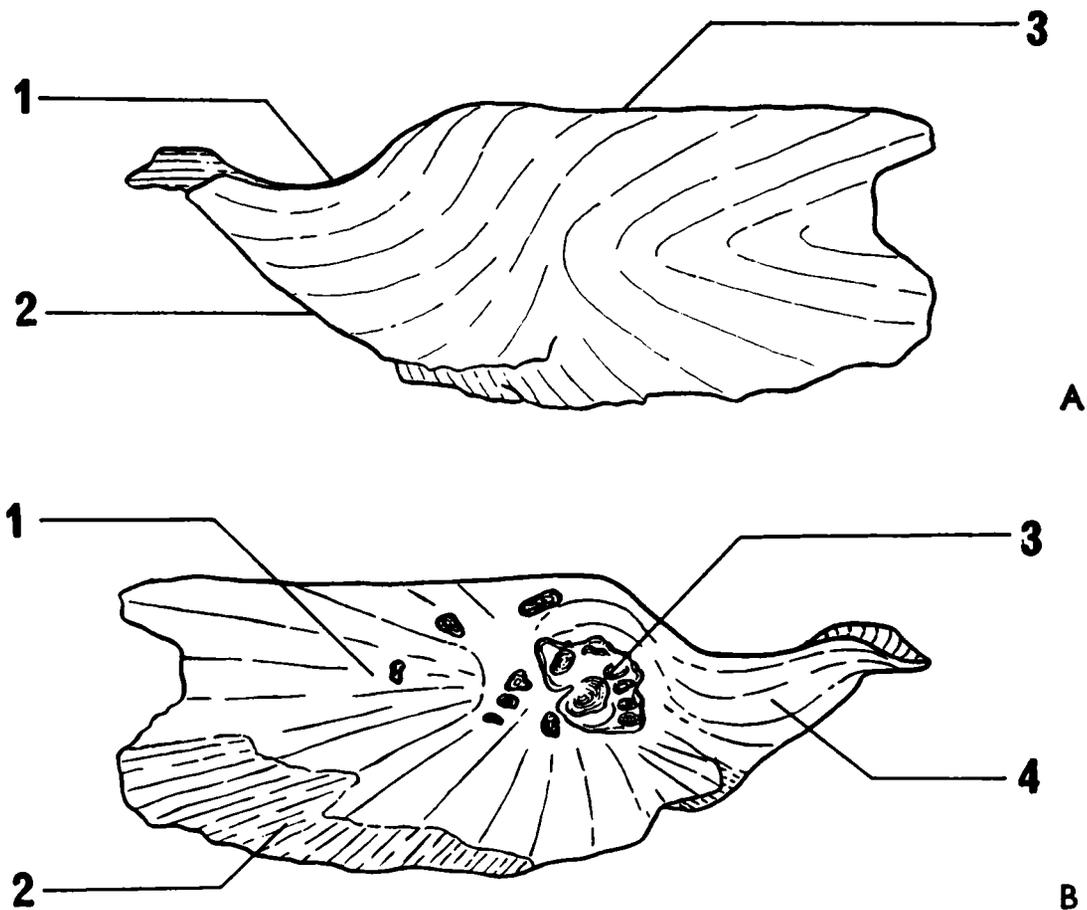


FIG. 11. (a). Frontal (right), dorsal view, $\times 4/3$ (R8177). 1, lateral margin of pineal foramen. 2, postero-lateral edge. 3, medial edge. (b). Frontal (right), ventral view, $\times 4/3$ (R8177). 1, shallow depressed area marking the position of the olfactory lobe. 2, roughened area of bone. 3, foraminous area. 4, deep crescentic depression marking the position of the cerebral hemisphere.

Since the nasal is preserved in the prepared material only up to the level of the external narial aperture, the rest of its structure must be inferred from the study of serial sections and unprepared skulls, and the present description is therefore somewhat incomplete.

The nasal is essentially a rectangular strip of bone, the external edge of which is turned down anteriorly, giving an L-shaped cross section. Before tapering posteriorly, the lateral surface is drawn out into a descending triangular process, which, being slightly outward-inclined, makes lateral contact with the medial surface of the prefrontal. Posterior to this level, the nasal is substantially flat, and tends to become splayed out. The divergent appearance is in part caused by a series of divergent ridges and striations which mark the dorsal surface of the bone. Furthermore there is a triangular depression in this posterior region which is flanked on either side by the divergent ridges. Up to this level the medial edge of the nasal is quite straight, and the two elements lie in flush contact on either side of the midline. Anteriorly,

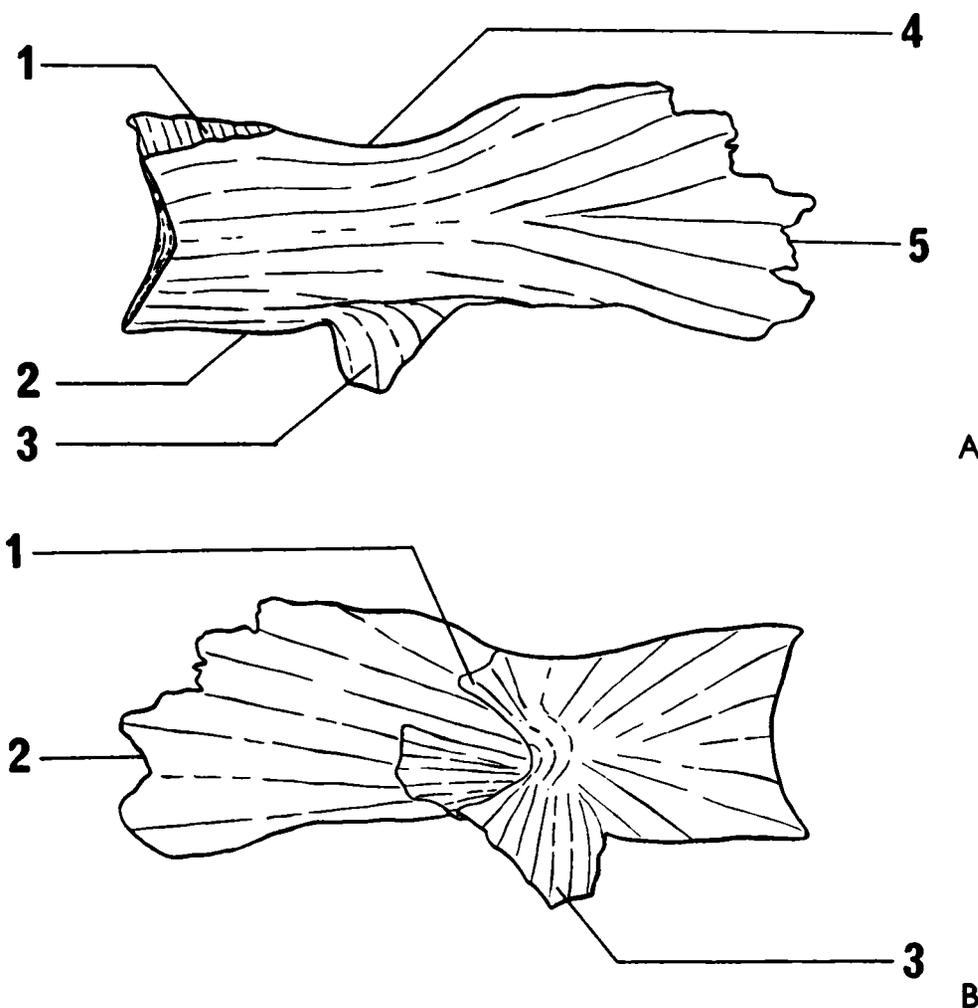
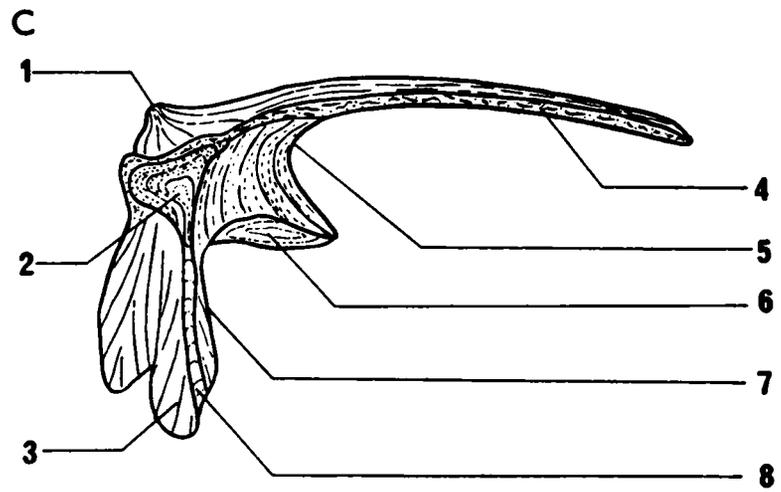
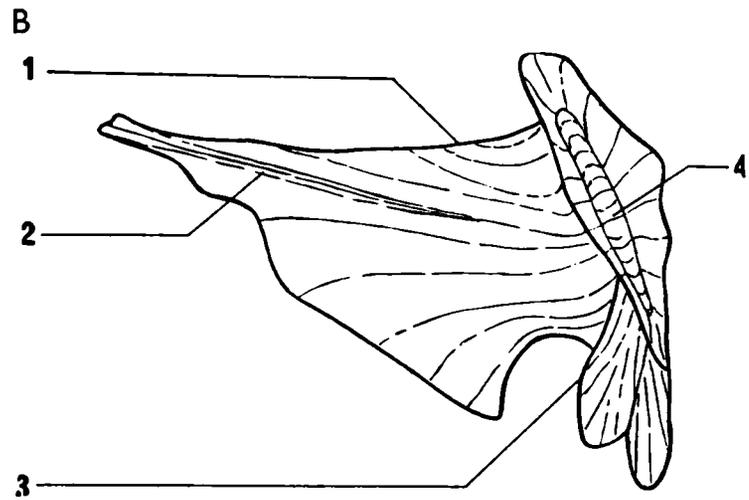
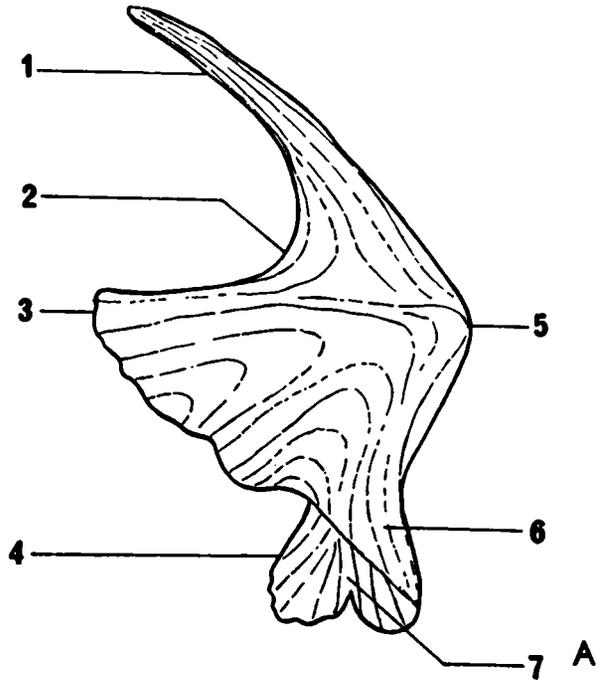


FIG. 12. (a). Nasal (left), dorsal view, slightly less than natural size (R8177). 1, articular facet for reception of the neighbouring nasal element. 2, external edge. 3, descending triangular process. 4, shallow emargination of medial edge which borders the internasal foramen. 5, posterior edge. (b). Nasal (left), ventral view, slightly less than natural size (R8177). 1, backwardly projecting bony spur. 2, posterior edge. 3, descending triangular process.

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however, the medial edge of each nasal has a shallow emargination, and the dorsal surface of the bone is depressed in this region. An internasal foramen is thus formed when the elements are articulated, and this is circumscribed by a shallow and elliptical depression. The bony edge of the emargination is thin, but thickening rostrally it becomes excavated, forming an articular facet for the reception of the corresponding edge of the other nasal bone.

The ventral surface is relatively smooth, but is roughened where it overlaps the frontal. Medially, just posterior to the emargination, there is a backwardly projecting bony spur. Into the angle of this spur slots part of the anterior edge of the frontal.

4. *Squamosal* (fig. 13, plate 6f). The squamosal is a tripartite element whose three rami lie approximately in the three planes of space. Forming the lateral and posterior margins of the temporal vacuity the squamosal has contact with the postfrontal anteriorly, the parietal posteriorly and medially, the quadrate postero-ventrally, and the postorbital and quadratojugal laterally.

From above the dorsal margin is J-shaped, the long arm being formed by the lateral ramus, the other by the much shorter medial ramus. Both rami increase in depth caudally, and thus have triangular profiles, and their external surfaces bear striations which converge upon a bony protuberance posteriorly. The protuberance is the most posterior point of the element, and lies just below the level of the rim of the vacuity. In addition to these striations, the external surface of the lateral ramus bears a number of low ridges which are also convergent upon the protuberance. Tapering anteriorly, the lateral ramus rests in a long and depressed facet on the postfrontal.

The medial ramus, being relatively short, is quite blunt, and has the appearance of an equilateral triangle when viewed from the side. The base of the triangle is directed obliquely forwards and downwards, and is furled out forming a semilunar hollow which embraces the distal portion of the parietal ridge.

The internal surface of the squamosal is hollow and relatively smooth, and its deepest portion corresponds with the protuberance of the outer surface. The internal surface of the lateral ramus is raised by a ridge, which, diminishing in its prominence posteriorly, disappears before reaching the centre of the depression.

The third ramus, the ventral ramus, is continuous with the medial one, and is directed downwards and inwards. It is a bifid flange of bone, which is set obliquely

FIG. 13. (a). Squamosal (right), postero-dorsal view, $\times 2/3$ (R8177). 1, lateral ramus. 2, rim of temporal vacuity. 3, medial ramus. 4, leading edge of ventral ramus. 5, bony protuberance. 6, ventral ramus. 7, medial surface of ventral ramus. (b). Squamosal (right), ventro-medial view, $\times 2/3$ (R8177). 1, dorsal rim of temporal vacuity. 2, ridge on internal surface of the lateral ramus. 3, leading edge of ventral ramus. 4, depression at distal end of medial ramus. (c). Squamosal (right), ventro-lateral view, $\times 2/3$ (R8177). 1, bony protuberance. 2, depression in angle between lateral and ventral rami. 3, external surface of ventral ramus. 4, ventral edge of lateral ramus. 5, dorsal rim of temporal vacuity. 6, depression at distal end of medial ramus. 7, leading edge of ventral ramus. 8, vertical groove.

to the longitudinal axis of the skull so that its external surface faces forwards as well as outwards. The external surface of the leading edge of the ventral ramus is grooved throughout its length and this groove slopes backward so that its distal end lies in advance of its proximal end. Dorsally this groove opens into a ventrally directed depression which is excavated in the angle between the lateral and ventral rami. Into this depression fits the dorsal edge of the quadrate, while much of its leading edge slots into the longitudinal groove of the ventral ramus. Both internal and external surfaces of the ventral ramus bear fine longitudinal striations which converge proximally.

B. THE CIRCUMORBITAL SERIES

The orbit is bounded by the prefrontal and postfrontal dorsally, the postorbital posteriorly, the jugal ventrally, and the lachrymal anteriorly. The postfrontal also

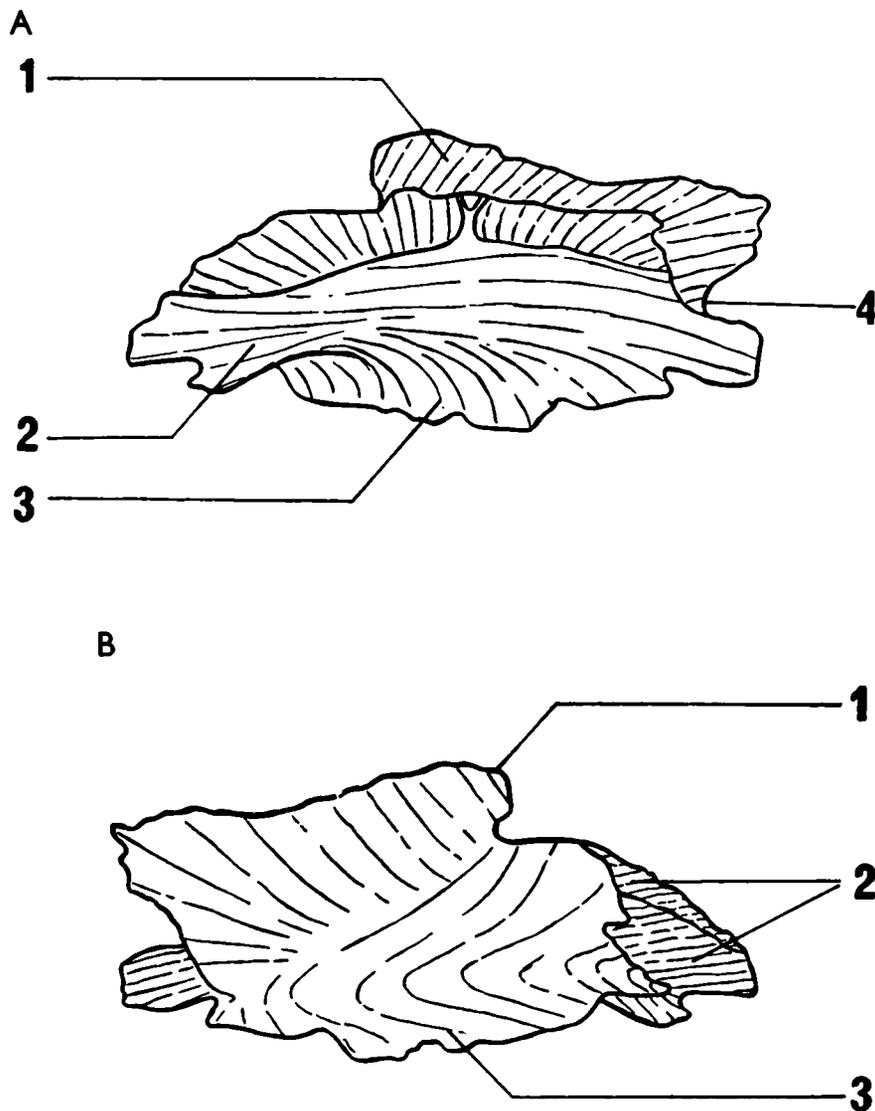


FIG. 14. (a). Prefrontal (right), ventral view, natural size (R8177). 1, medial flange. 2, midrib. 3, lateral flange. 4, posterior edge. (b). Prefrontal (right), dorsal view, natural size (R8177). 1, medial flange. 2, vertical bony lamellae ascending from anterior portion. 3, lateral flange.

participates in the formation of the temporal vacuity. The quadratojugal has no part in the formation of the orbit, but will for convenience be described here.

1. *Prefrontal* (fig. 14, plate 3e). The prefrontal is a narrow and curving element whose concave ventral surface contributes to the anterior dorsal margin of the orbit. Ventrally it articulates with the lachrymal, posteriorly with the parietal and postfrontal, and mesially with the nasal and frontal.

From below, the prefrontal comprises of a smooth and arched midrib, from which the bone tapers on either side forming a lateral and a medial flange. The midrib is rounded from side to side, and, with the smooth lateral flange, forms the anterior dorsal margin of the orbit. The medial flange is lamellate, and partly underlapped by the frontal and parietal, and makes a minor contribution to the skull roof. Anteriorly both lateral and medial flanges taper so that only the midrib makes ventral contact with the lachrymal. The two flanges also taper posteriorly.

The dorsal surface is very much roughened, and much of it is overlapped by the postfrontal. The lateral and medial margins of the prefrontal are both raised above the level of the midrib so that the dorsal surface is furrowed, and has a somewhat V-shaped cross section.

2. *Postfrontal* (fig. 15, plate 3d). The postfrontal is a dorso-ventrally compressed element which forms the posterior dorsal margin of the orbit. Medially it contributes

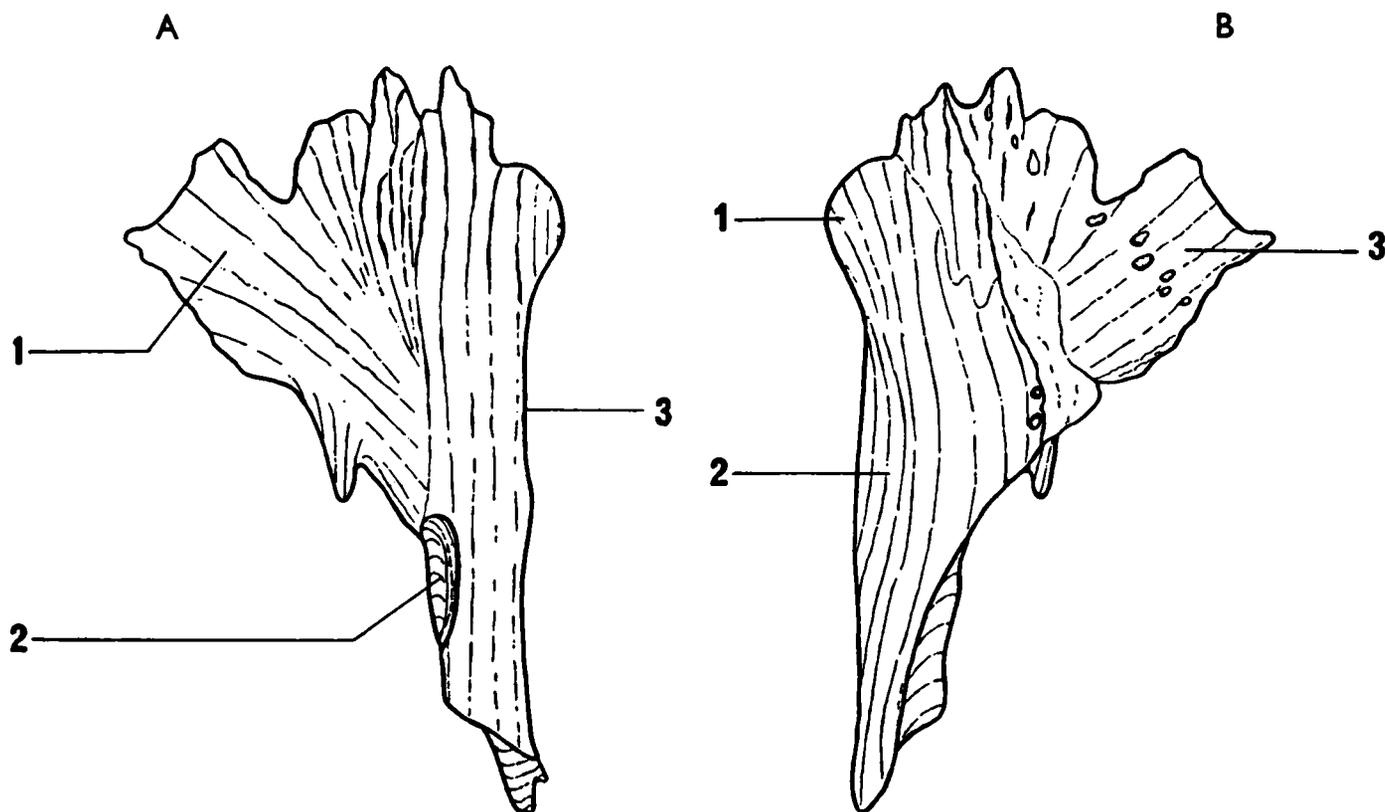


FIG. 15. (a). Postfrontal (right), dorsal view, just less than natural size (R8177). 1, medial limb. 2, squamosal facet. 3, dorso-lateral edge. (b). Postfrontal (right), ventral view, just less than natural size (R8177). 1, triangular area of smooth bone. 2, orbital margin. 3, medial limb.

to the temporal vacuity, and also forms part of the skull roof. It overlaps the prefrontal anteriorly, the nasal anteriorly and medially, and the parietal postero-medially. Posteriorly it articulates with the squamosal and also has contact with the postorbital.

Seen from above the postfrontal is Y-shaped, the two short limbs being directed rostrally. Of these, the medial one is narrowest, and set at an oblique angle to the other, which is continuous with the main limb, and which lies parallel with the longitudinal axis of the skull. While the dorsal surface of the medial limb is finely striated, that of the wide limb is thrown into prominent folds and is marked by coarse striations. The dorsal surface of the main limb is fairly smooth and is arched in correspondence with the line of the orbit. Furthermore it is twisted so that posteriorly it comes to lie almost in the vertical plane. Posteriorly and medially it is excavated by a long and oval facet for reception of the squamosal.

The ventral surface, save for a triangular area of smooth bone which borders the orbit, is rugose, and is applied to the similarly roughened dorsal surface of the prefrontal. The external margin of the orbital area is concave from side to side and becomes slightly convex medially, towards the apex of the triangle.

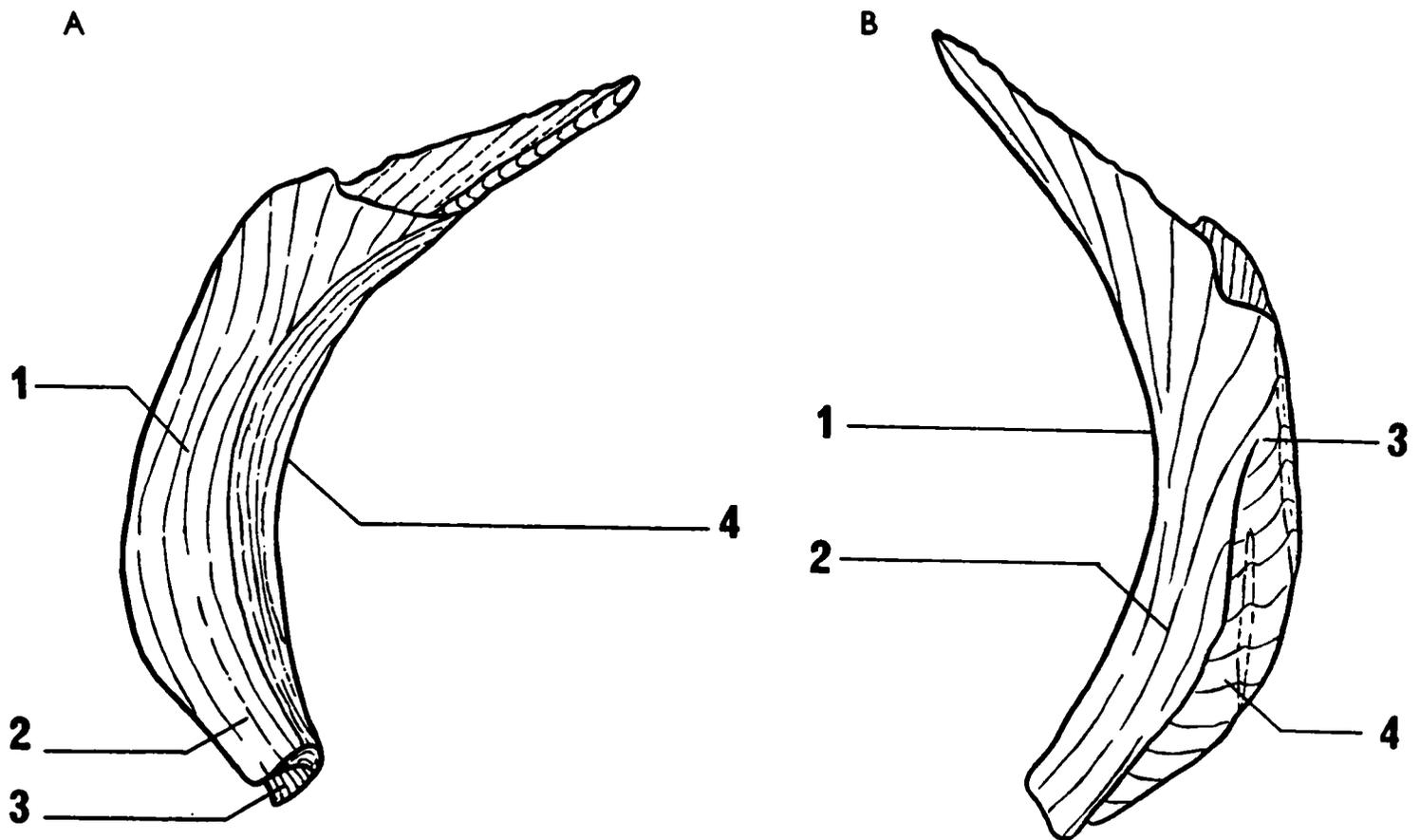


FIG. 16. (a). Postorbital (right), external lateral view, $\times 3/2$ (based on R6697 and R8177). 1, convex external surface. 2, external plate. 3, internal plate. 4, sharp anterior edge. (b). Postorbital (right), internal lateral view, $\times 3/2$ (based on R6697 and R8177). 1, sharp anterior edge. 2, internal plate. 3, commencement of fissure. 4, external plate.

Due to poor preservation posteriorly, the precise nature of its articulation with the postorbital cannot be ascertained. However sufficient information has been provided by specimen R8177 to show that a dorso-laterally inclined and roughened area of the postorbital made contact with, and was overlain by, a similarly roughened but ventro-lateral area of the postfrontal.

3. *Postorbital* (fig. 16, plate 4a). The postorbital is not well preserved in the material examined, and the following description is based upon two specimens, (R8177 and R6697), neither of which is complete. The bone is slender and sickle-shaped, its curving anterior edge forming the posterior border of the orbit. Posteriorly it articulates with the quadratojugal, ventrally with the jugal, while dorsally it has contact with the postorbital, presumably in an overlapping relationship.

The external surface is not flat, but is convex from before to behind. The anterior

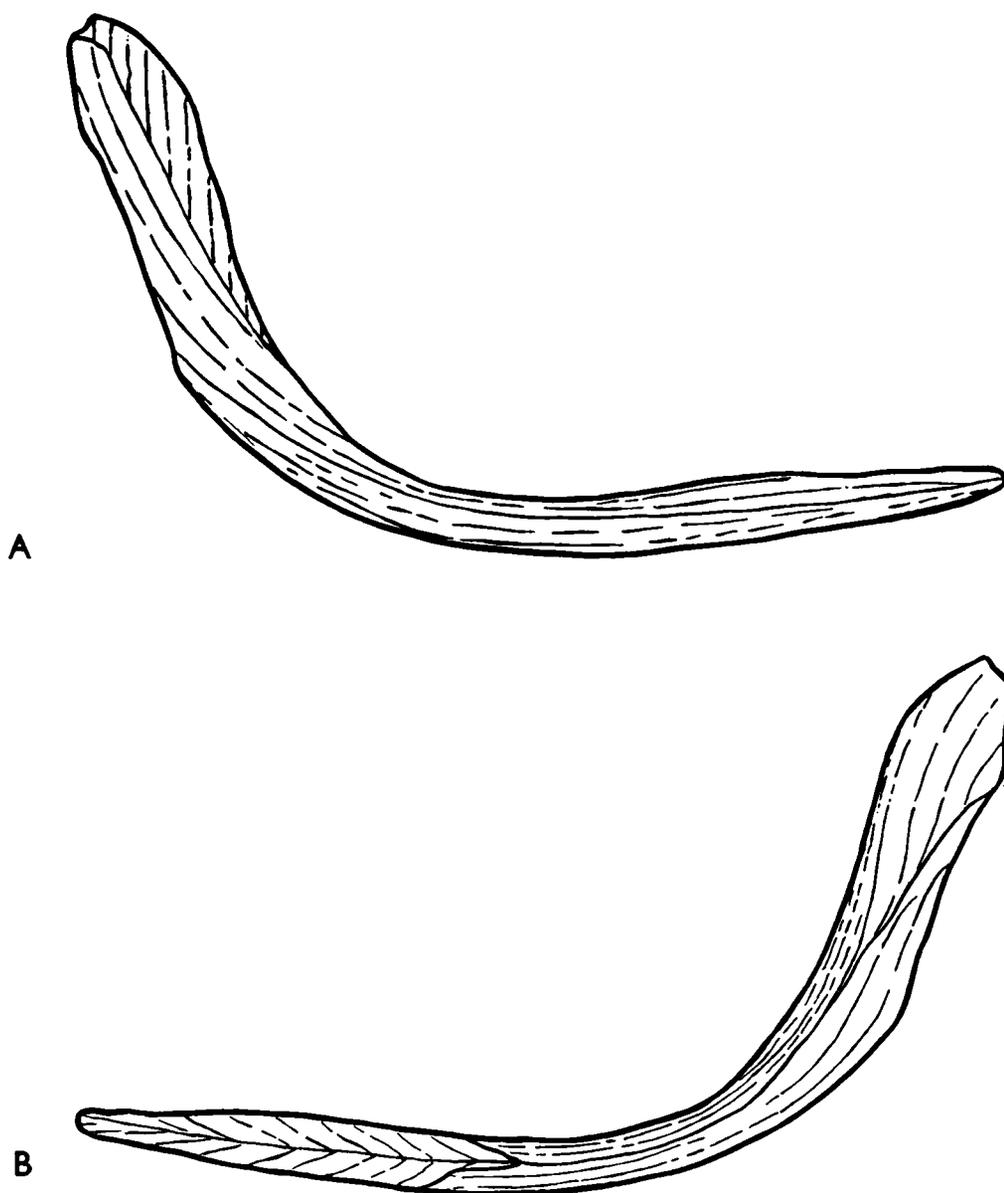


FIG. 17. (a). Jugal (right), external lateral view, slightly less than natural size (R8177).
(b). Jugal (right), internal lateral view, slightly less than natural size (R8177).

border follows a concave path, and the convexity of the external surface results in its having a sharp edge for much of its length. Dorsally and ventrally the sharpness is reduced, and gives way to rounded margins.

For much of its length the trailing edge of the element is divided by a fissure into two bony plates, one external, the other internal. The fissure commences high up on the medial surface of the element as a shallow groove, lying approximately midway between the anterior and posterior margins, and about one third of the way down from the dorsal edge. Widening as it deepens ventrally, the fissure separates the internal and external plates by a moderate gap. Most of the fissure is occupied by the leading edge of the quadratojugal, but ventrally it embraces the dorsal edge of the terminal portion of the jugal.

The internal surface of the postorbital is slightly concave from side to side, and therefore corresponds to the convexity of the external surface, but the portion forming the internal plate is quite flat.

4. *Jugal* (fig. 17, plate 4d). The jugal is a slender and gently curving element which forms the ventral, and part of the posterior border of the orbit. Posteriorly it articulates with the postorbital and it also has contact with the quadratojugal. Antero-medially it articulates with the maxilla, whilst its tip locates in a groove formed between the maxilla and lachrymal.

Although slender, the jugal is quite robust, and has an ovoid or triangular cross-section over much of its length. Sloping gently upwards anteriorly it becomes laterally compressed and finally tapers to a slender splint which locates in the groove above-mentioned.

Much of the anterior half is triangular in cross-section, with a fluted medial surface rising to the apex and articulating with a correspondingly sculptured area of bone on the posterior lateral surface of the maxilla. Caudally the cross-section becomes rounded, and dorso-ventrally compressed where the jugal forms the mid-portion of the orbital floor. As the jugal curves up to contribute to the posterior margin of the orbit it becomes laterally compressed and terminates in a moderately flat flange of bone which makes contact with the quadratojugal, and whose dorsal edge slots into the postorbital fissure.

5. *Lachrymal* (fig. 18, plate 4c). The lachrymal forms the anterior corner of the orbit, articulating dorsally with the prefrontal, and ventrally with the jugal and maxilla. The rectangularity of its sharp leading edge and the arcuation of its broad internal margin confers the appearance of the prow of Viking boat.

The internal orbital margin is relatively smooth, and its ascending dorsal limb is convex from side to side. Ventrally the orbital margin is concave and its width is increased by a flange of bone which arises from the external surface of the bone. Dorsally, at its widest point, this bony flange loses contact with the rest of the external surface and is produced as a biramous tongue.

The external surface, although ridged, is relatively flat, whereas the internal surface is much roughened and thrown into folds and ridges. A prominent ventro-

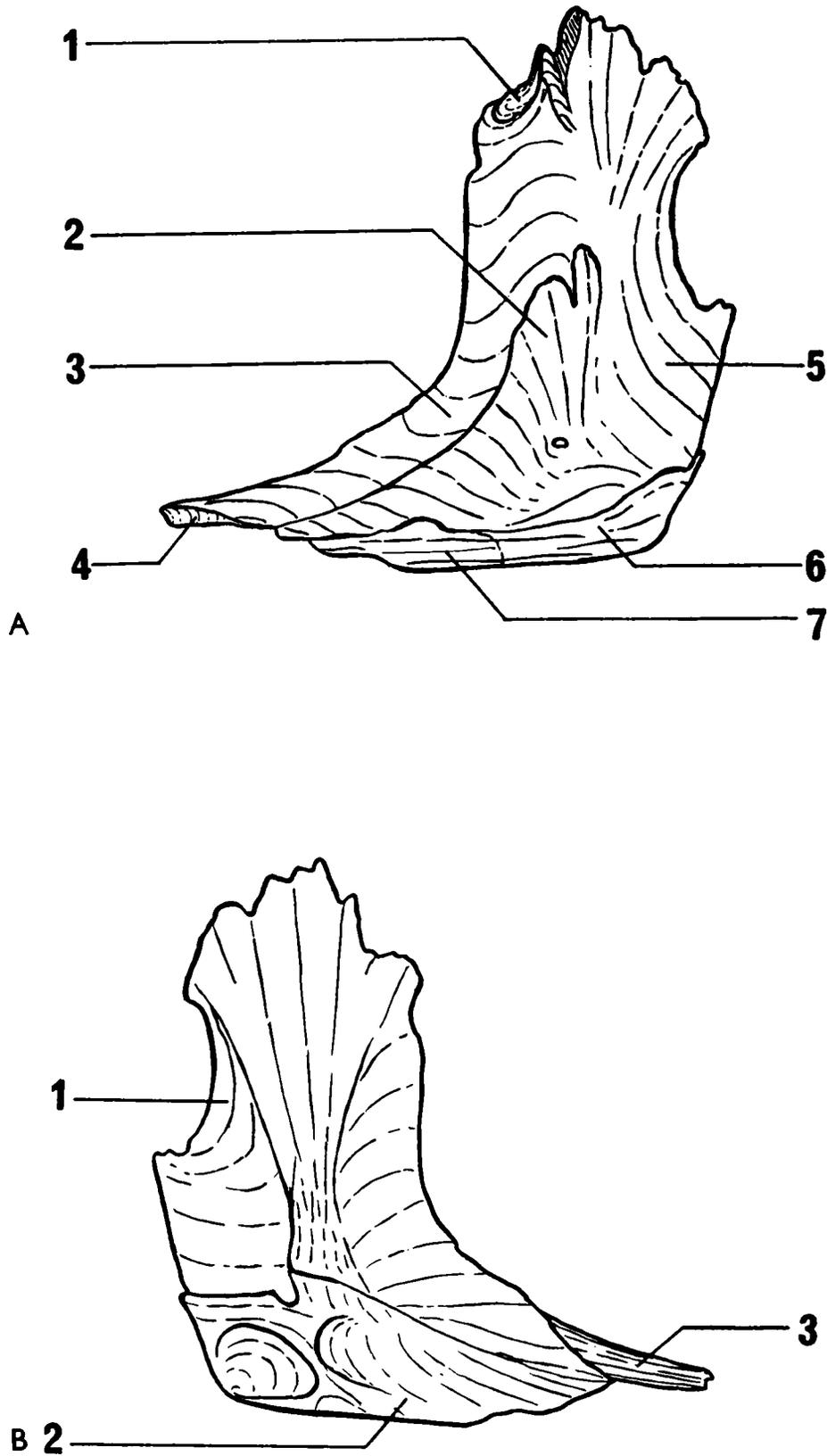


FIG. 18. (a). Lachrymal (right), external lateral view, slightly more than natural size (R8177). 1, prefrontal facet. 2, bony flange. 3, orbital margin. 4, posterior portion of ventro-lateral furrow. 5, anterior vertical plate. 6, ventral horizontal plate. 7, jugal facet. (b). Lachrymal (right), internal lateral view, slightly more than natural size (R8177). 1, anterior vertical plate. 2, ventral horizontal plate. 3, ventral portion of orbital margin.

lateral furrow articulates with a corresponding ridge on the dorsal surface of the maxilla.

Beyond the orbital margin the bone diminishes rapidly in its thickness, and is reduced to two thin plates, one anterior and vertical, the other ventral and horizontal. In the posterior corner of the ventral plate there is a small oval depression into which locates the anterior tip of the jugal.

The Quadratojugal (fig. 19, plate 4b). The quadratojugal is known from only three specimens, and is somewhat incomplete in each case so that this description suffers certain shortcomings.

Occupying a posterior and lateral position in the skull the quadratojugal articulates ventrally with the quadrate, and anteriorly with the postorbital and jugal. As mentioned above, part of its posterior margin contributes with the quadrate in the formation of a postero-lateral foramen of moderate size.

A thin and triangular element, the quadratojugal has something of the appearance of a mammalian scapula, its ventral quadrate articular facet corresponding with the glenoid fossa. The internal surface is smooth and hollow, whilst the external surface is convex and bears a prominent vertical ridge set a little way back from its anterior margin. This ridge curves over antero-laterally forming a groove into

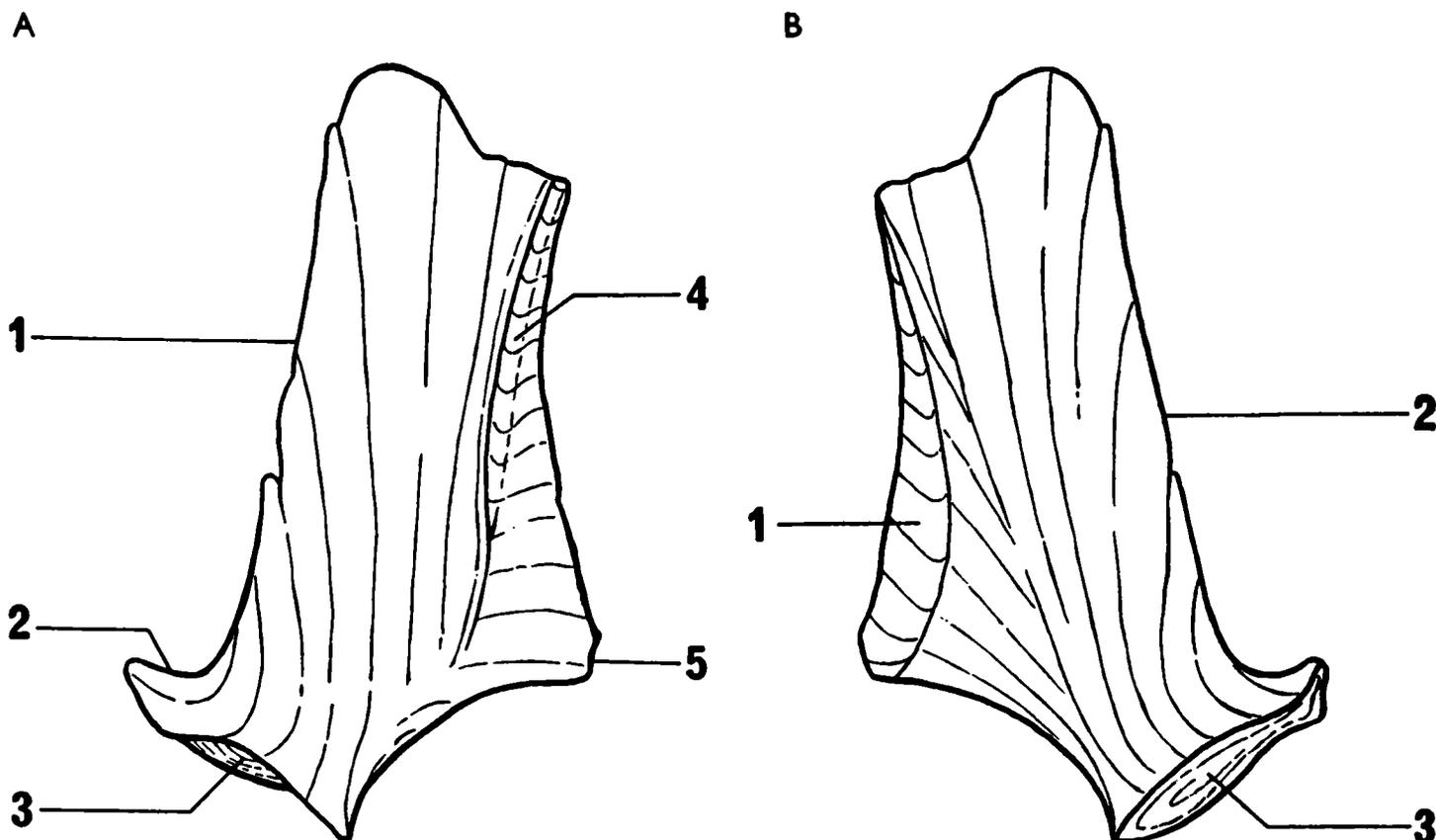


FIG. 19. (a). Quadratojugal (right), posterolateral view, $\times 2$, R6697. 1, posterior margin. 2, spur. 3, quadrate facet. 4, groove into which the postorbital slots. 5, apex of leading edge. (b). Quadratojugal (right), internal lateral view, $\times 2$, R6697. 1, postorbital facet. 2, posterior margin. 3, quadrate facet.

which slots the external posterior edge of the postorbital. A little way in front of this ridge is a second, though lesser one (in R8177), against which rests the posterior edge of the jugal. In specimen R6697 this ridge is not present.

Dorsally the quadratojugal widens out like a fan, while ventrally it becomes constricted, only to fan out once more to form an elliptical articular facet. Ventrally the facet is hollow, and articulates with a swelling on the quadrate which is shaped for its reception.

The leading edge of the quadratojugal is triangular and its longest side lies above the apex and slots into a deep fissure in the posterior region of the postorbital. The trailing edge is quite straight for most of its length, but ventrally it is produced into a slightly upturned and curved spur, which forms the floor of the oval foramen.

C. *ELEMENTS OF THE PALATE AND UPPER JAW MARGIN*

The palate is formed from the paired pterygoids, palatines, and vomers, with a minor contribution from the single and median parasphenoid. The upper jaw margin is formed largely from the premaxillae, the maxillae contributing to the posterior portion. Both maxilla and premaxilla are grooved and dentigerous. The descriptions of the palatal elements are based largely upon a single specimen, R8177.

1. *Pterygoid* (fig. 20, plate 5a). The pterygoid is an extensive element which makes a major contribution to the formation of the palate. Anteriorly it articulates with the vomer, posteriorly with the epipterygoid and quadrate, and medially with the basisphenoid, whilst much of its external margin is overlapped by the palatine.

Essentially the pterygoid is a tapering sheet of bone which is widest and thickest posteriorly where it is produced into three winged processes. Anteriorly the bone undergoes torsion so that the dorsal surface turns outwards finally becoming the external surface of a narrow terminal rod.

Two of the three triangular winged processes lie in approximately the same plane forming an extensive shelf which, facing obliquely upwards and outwards, makes contact over a wide area with the medial surface of the quadrate. This articular surface is referred to throughout as the quadrate wing of the pterygoid. The third wing is directed medially and somewhat ventrally, and rests with the dorsal aspect of its tip in touch contact with the ventral edge of the basioccipital. This process is referred to as the medial wing. For the most part the dorsal surface of the medial wing is rugose but becomes smooth anteriorly and forms the floor of an ovoid excavation, into which the basipterygoid process of the basisphenoid locates. Immediately anterior to this facet the internal edge of the pterygoid is emarginated and forms the interpterygoid vacuity (or internal palatal foramen), which is separated from its neighbour on the other side by the parasphenoid. Just posterior to this level there is a similar emargination of the external edge which constitutes the intrapterygoid vacuity (or external palatal foramen), and which, lying directly beneath the temporal vacuity, served for the passage of the mandibular adductor muscles. On the dorsal surface, at the anterior corner of the intrapterygoid vacuity, there is a small crescentic articular facet for the palatine.

On the dorsal surface, just medial in position to the intrapterygoid vacuity, there is a short longitudinal groove which receives the tip of the epipterygoid and which probably marks the position of the cartilaginous portion of the palato-quadrate bar, as noted by Appleby (1961, 339). In line but not in continuity with this groove, there is a shallow furrow extending almost the length of the element and which might also mark the position of the cartilaginous palatoquadrate.

Tapering gently from the level of the emarginations the pterygoid is produced

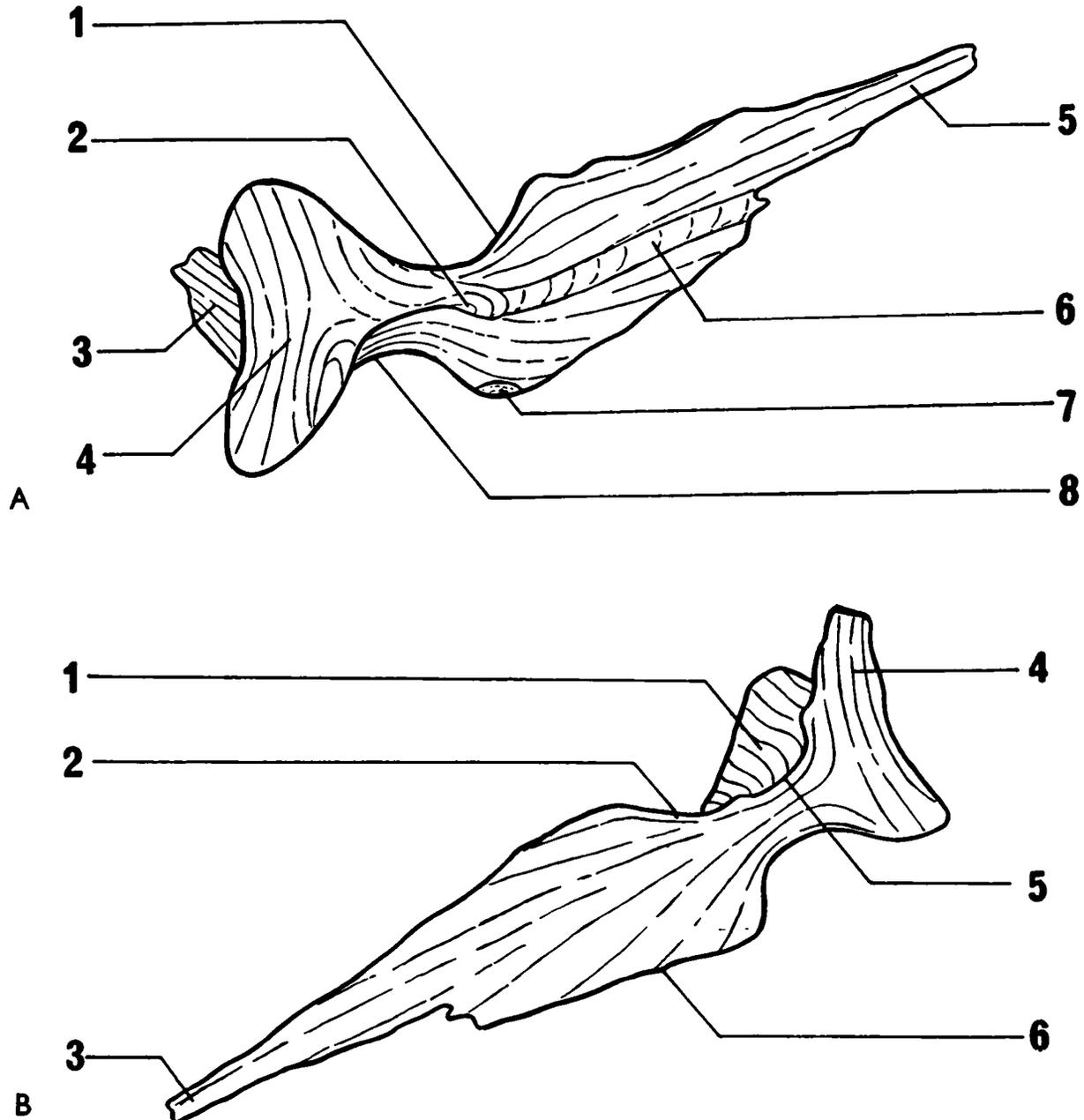


FIG. 20. (a). Pterygoid (right), external dorso-lateral view, $\times 1/2$ (R8177). 1, edge of interapterygoid vacuity. 2, epipterygoid facet. 3, dorsal surface of medial wing. 4, quadrate wing. 5, external surface of terminal rod. 6, shallow furrow. 7, palatine facet. 8, intrapterygoid vacuity. (b). Pterygoid (right), ventro-medial view, $\times 1/2$ (R8177). 1, medial surface of quadrate wing. 2, edge of interapterygoid vacuity. 3, longitudinal furrow. 4, ventral surface of medial wing. 5, ventral lip of basipterygoid facet. 6, external edge.

anteriorly into a narrow rod of bone. The medial and ventral surfaces of this rod are grooved and somewhat reticulate, though this may be due to damage, while the lateral surface is quite smooth and slightly furrowed, and has medial articular contact with the vomer.

The anterior portion of the dorsal surface of the pterygoid bears a low ridge which runs close to and approximately parallel with the lateral edge. This ridge has contact along its length with the medial edge of the palatine.

2. *Palatine* (fig. 21, plate 5b). The palatine is a relatively large and delicate bone which forms the outer margin of the palate, and has medial contact with the pterygoid throughout its entire length. Laterally it has contact with the maxilla for much of its length.

Rhombic in outline, the two long sides lie parallel with the longitudinal axis, and are raised above the level of the rest of the bone, producing a shallow basin. The posterior edge lies at almost 45° to the longitudinal axis, and slopes back so that the internal corner lies posterior to the external corner. The anterior edge lies very approximately parallel with the posterior edge, but tapers gradually to an oblique point.

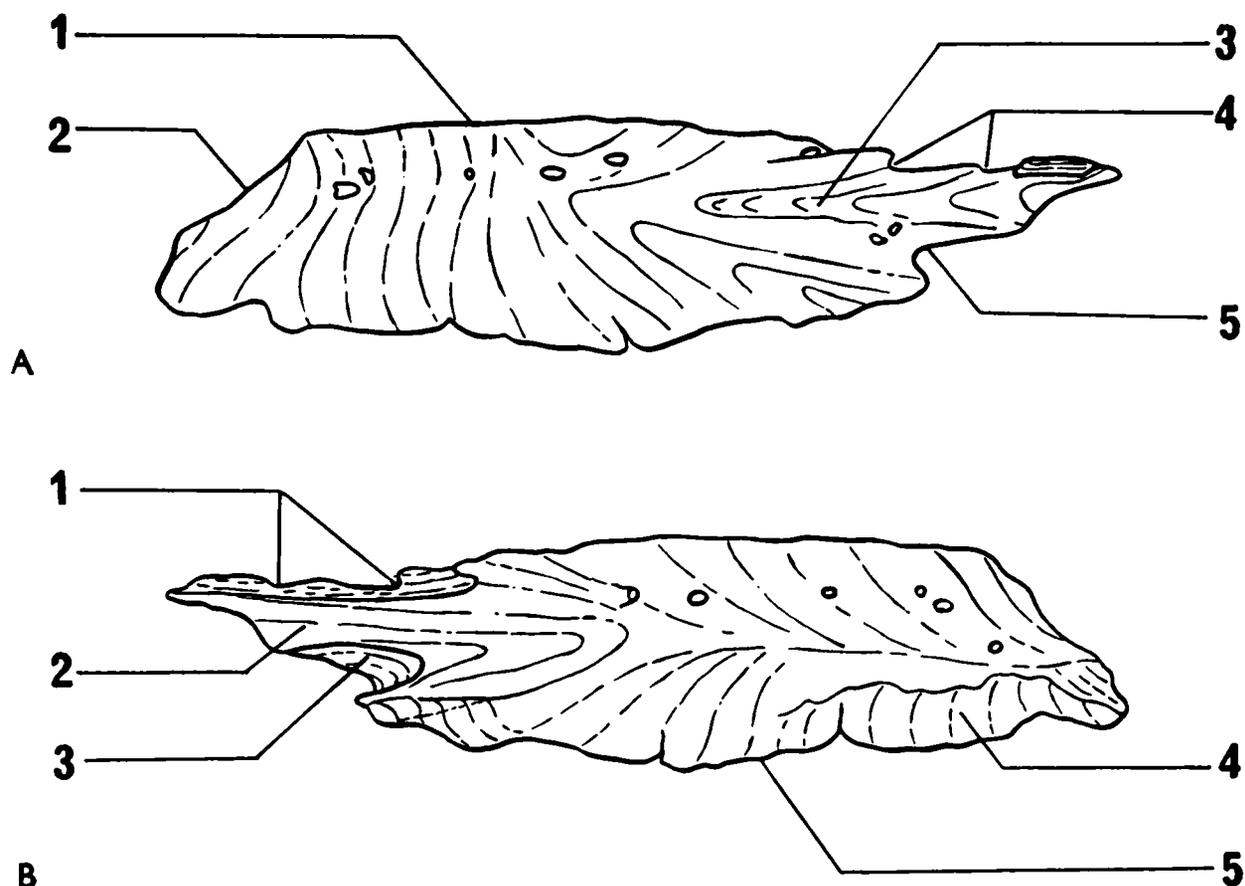


FIG. 21. (a). Palatine (left) dorsal view, $\times 3/4$, (R8177). 1, external edge. 2, posterior edge. 3, longitudinal furrow. 4, vascular foramina. 5, margin of internal narial aperture. (b). Palatine (left), ventral view, $\times 3/4$ (R8177). 1, vascular foramina. 2, medial surface of ventral keel. 3, margin of internal narial aperture. 4, pterygoid facet. 5, internal edge.

The dorsal surface is sculptured by various rugosities and striations and anteriorly is thrown into a prominent longitudinal furrow. Since the bone is so thin this furrow affects the ventral surface which is correspondingly produced into a keel. Anteriorly there is an ovoid excavation which is more prominent when viewed from beneath, and which contributes with the vomer in the formation of the internal narial aperture. Ventrally this excavation forms the medial boundary of the keel. The outer edge of the ventral keel has several fenestrations which correspond with similar fenestrations of the medial edge of the maxilla, with which articular contact is made. The foramina thus formed probably served to transmit blood vessels. For the most part the ventral surface is relatively smooth, but there is a posterior and medial area where the bone is lamellate, and applied to the dorsal surface of the pterygoid, but it is possible that this appearance is due to poor preservation.

A series of six foramina pierce the bone obliquely so that the dorsal aperture of each lies just posterior, though coincident, with the ventral aperture, and these probably transmitted blood vessels also.

3. *Vomer* (fig. 22, plate 5c). The vomer is the most anterior of the palatal elements and contributes with the palatine in the formation of the internal narial aperture. Externally, it has contact with the palatine, and for much of its length it is underlain by the pterygoid. Anteriorly the vomers of either side come into contact along their medial surfaces. Only the posterior portion of the element is adequately known from prepared material, but the remainder can be reconstructed by reference to part-prepared material and serial sections.

Posteriorly the vomer has a very pronounced ventral keel which is offset from the midline, lies towards the external margin, and makes medial contact with the pterygoid. The keel widens and becomes more shallow posteriorly so that it has the appearance of a raked stern of a ship. The dorsal surface in this region is concave, and the centre of its depression is towards the external margin which lies well below the level of the medial margin. The bone is thin, and for the most part is roughened and pitted.

The external lateral surface is quite smooth, convex from dorsal to ventral edges, and is gently incurved from before to behind. Anteriorly and dorsally there is an ovoid depression whose anterior margin is formed by an ascending bony spur and which is the medial margin of the internal narial aperture.

The medial lateral surface of the vomer is largely of cancellous bone, and is drawn out dorsally into a membranous overhang. Ventrally is a strip of relatively smooth bone which tapers posteriorly and which is the articular surface for contact with the pterygoid.

Anterior to the level of the internal narial aperture the dorsal aspect is produced into a thin vertical plate which reaches a maximum height then gradually tapers away. Anteriorly the vomer is reduced to a tenuous rod of bone which persists for a considerable distance, but it does not reach the tip of the snout.

4. *Parasphenoid* (fig. 1). As noted above, the parasphenoid is so intimately associated with the basisphenoid that its proximal limits are difficult to discern.

Anteriorly it is produced into a narrow strip of bone which lies in mid-ventral line between the pterygoids, making a minor contribution to the palate.

In the material so far examined the parasphenoid has been incompletely preserved and only the proximal portion is known.

5. *Maxilla* (fig. 23, plate 4e). The maxilla is known from only one prepared specimen (R8177), and only the posterior portion is preserved so that little can be said of its structure. Forming the posterior portion of the upper jaw margin, the maxilla has a dentigerous groove on its ventral surface. Contact with the palatine is made along the length of its medial margin, and the jugal rests in a groove on its external surface. Dorsally the maxilla has contact with the ventral surface of the lachrymal.

The dentigerous groove extends the full width of the ventral surface, and, diminishing in depth posteriorly, the element tapers to a blunt point. The medial margin of the dentigerous groove is perforated by a number of fenestrations which correspond with similar openings on the external margin of the palatine, as pointed out above. The dorsal surface is thrown into a number of prominent ridges which are separated by grooves. One of these ridges is particularly prominent and increases in width anteriorly forming a thin bony lamella against which the lachrymal abuts. The external surface gradually tapers to a point both before and behind, so that the element has the form of a slender wedge when the complete skull is viewed from the side.

6. *Premaxilla*. The premaxilla is an extensive element which forms the greater part of the snout and upper jaw margin. Since this element is not preserved in the prepared material at present available, its structure has been established by reference to unprepared skulls and serial sections.

The premaxilla commences at the level of the external narial aperture where it overlaps the anterior portions of the maxilla and lachrymal. Increasing in width rostrally, each premaxilla encroaches upon the nasal element of that side, and the nasals eventually disappear from view as the premaxillae meet above them in mid-dorsal line. The ventro-lateral edge of the premaxilla rapidly thickens rostrally forming the dentigerous upper jaw margin.

D. *THE SCLEROTIC RING* (fig. 24, plate 6e)

The sclerotic ring is composed of a variable number of individual plates, usually between 12 and 16, which come together in a complex sutural association. Each plate tapers towards its inner margin which is straight or slightly curved, whilst its outer margin, which is serrated, is invariably rounded. The sclerotic plate is not flat but is flexed at an angle of about 90° into an almost flat anterior surface, and a rounded lateral surface. The anterior surface contributes to the ring circumscribing the aperture, the lateral surface contributes to the lateral wall. The flat surface tends to be slightly hollow when viewed in profile, and its inner margin is somewhat raised. The elevation of the inner margin is accentuated by the inclination of the inner surface as it approaches the inner margin. The inner margin of the sclerotic ring is therefore

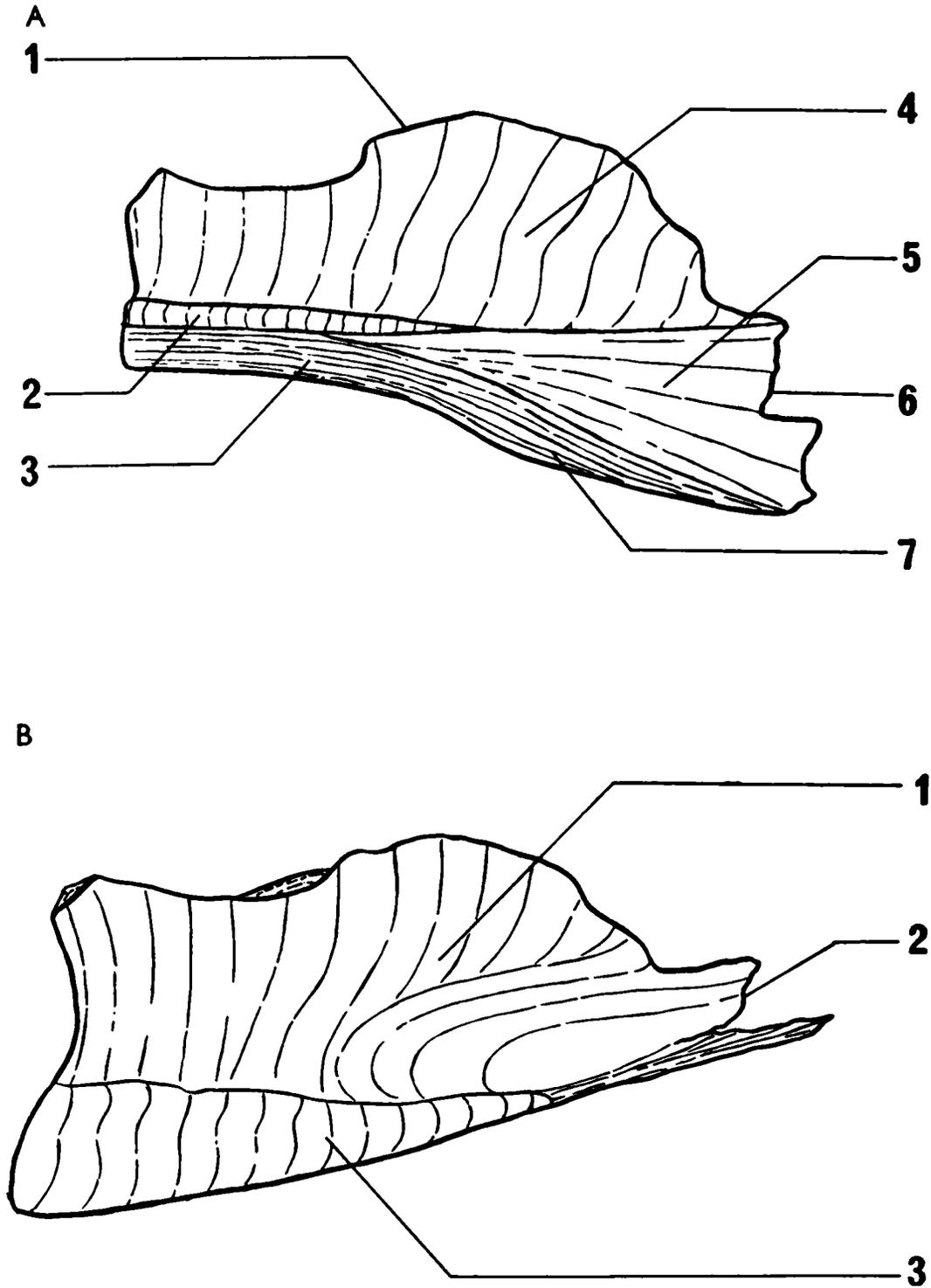
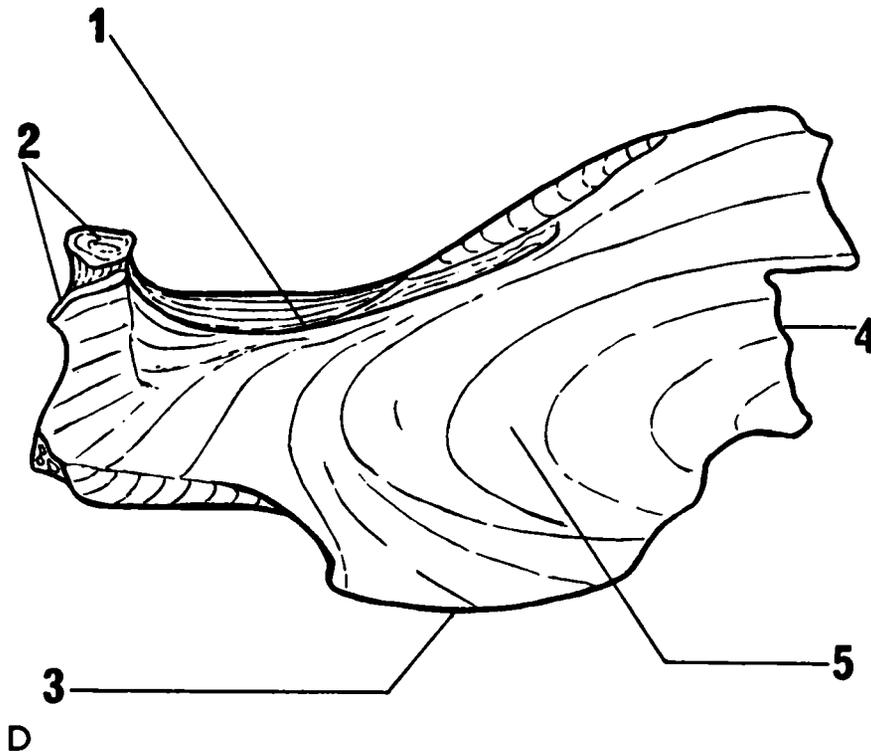
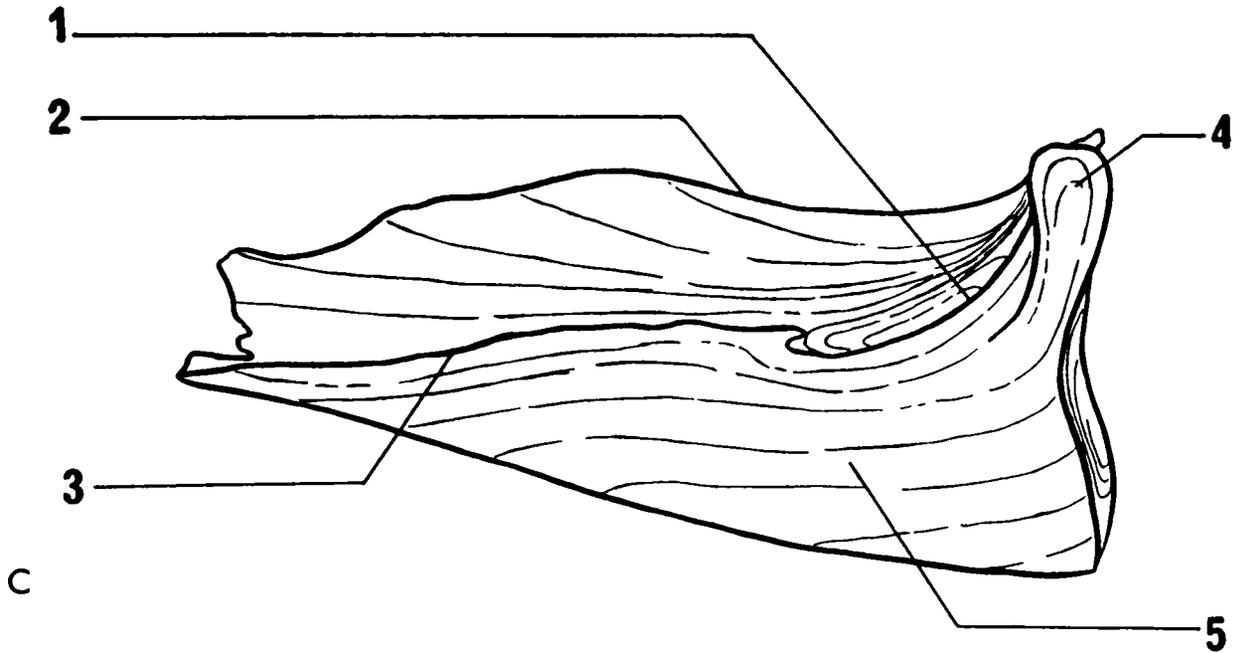


FIG. 22. (a). Vomer (right), ventral view, natural size (R8177). 1, medial edge. 2, pterygoid facet on medial surface of ventral keel. 3, external surface of ventral keel. 4, medial lateral surface. 5, ventral surface. 6, posterior edge. 7, external lateral surface. (b). Vomer (right), internal lateral view, natural size (R8177). 1, medial lateral surface. 2, posterior edge. 3, pterygoid facet of ventral keel. (c). Vomer.

raised very slightly, and thus circumscribed by a shallow suclus, the significance of which will be discussed later.

While the inner, (i.e. posterior), surface of the sclerotic plate is relatively smooth and flat, that of the outside is squamous and sculptured by fine and radiating striations.



(right), external dorso-lateral view, natural size (R8177). 1, medial margin of internal narial aperture. 2, medial edge. 3, external edge. 4, ascending bony spur. 5, external surface of ventral keel. (d). Vomer (right), dorsal view, natural size (R8177). 1, medial margin of internal narial aperture. 2, apex of ascending bony spur. 3, medial edge. 4, posterior edge. 5, hollowed dorsal surface.

Adjacent sclerotic plates come into contact at their lateral margins with little overlap but because of the interdigitation of the thin scales their simple arrangement is often obscured when the sclerotic ring is examined in its entirety. In specimen R8177, where the sclerotic ring has been well preserved, it can be seen that the plates

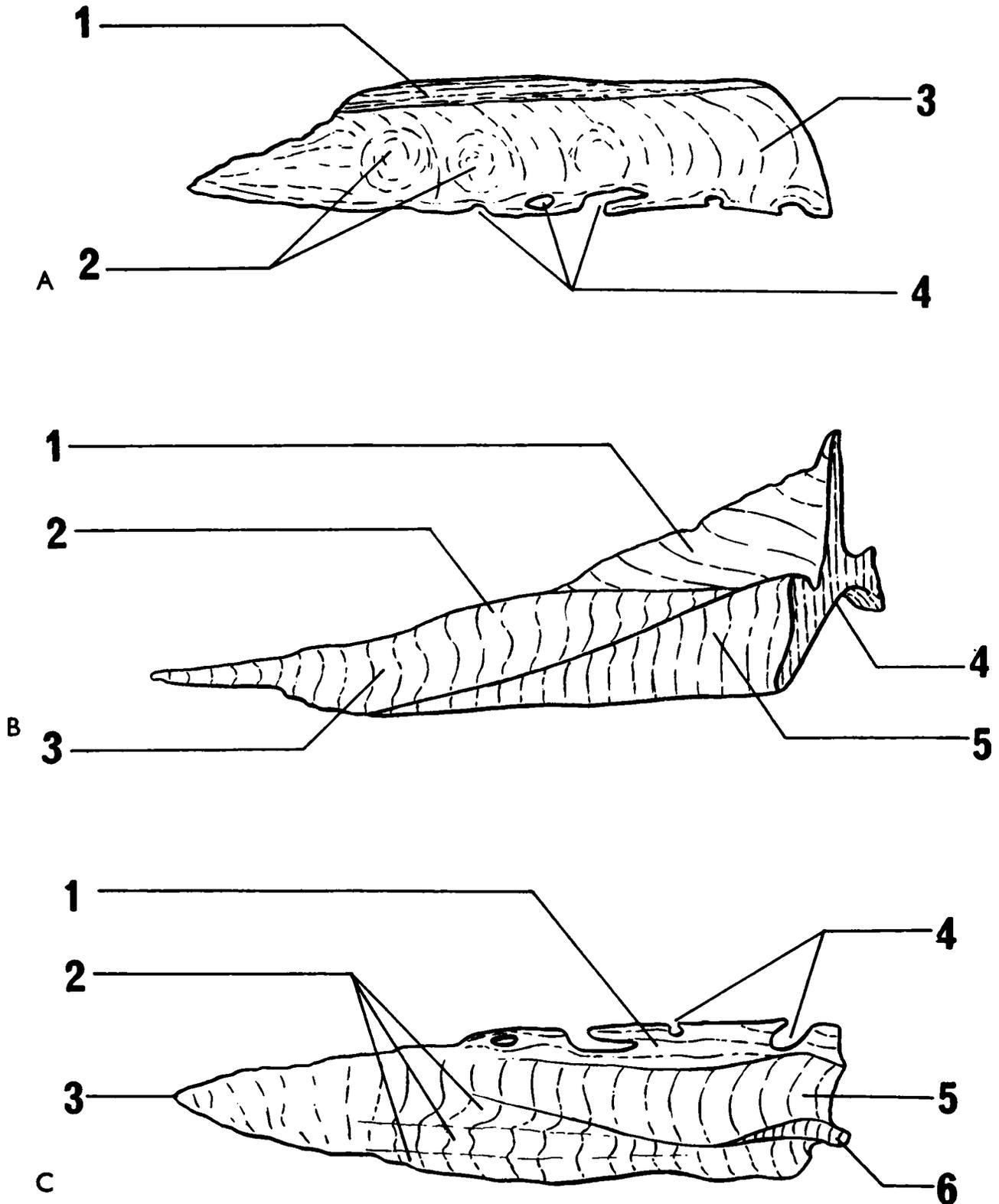


FIG. 23. (a). Maxilla (right), ventral view, $\times 3/2$ (R8177). 1, external surface. 2, shallow dental alveoli. 3, dentigerous groove. 4, vascular foramina perforating medial margin. (b). Maxilla (right), external dorso-lateral view, $\times 3/2$ (R8177). 1, bony lamella. 2, bony ridge which slots into a ventral groove in the lachrymal. 3, groove on dorsal surface. 4, dentigerous groove. 5, external surface. (c). Maxilla (right), dorsal view, $\times 3/2$ (R8177). 1, palatine facet. 2, grooves on dorsal surface. 3, posterior tip. 4, vascular foramina perforating medial margin. 5, wide groove. 6, dorsal margin of bony lamella.

are arranged so that one lateral margin tends to overlap that of an adjacent plate, whilst the other is itself overlapped.

In those latipinnates so far examined, the aperture of the sclerotic ring tends to be relatively large in comparison with the size of the whole structure, and is usually slightly oval, the long axis being almost coincident with the longitudinal axis of the skull.

DESCRIPTION OF THE LOWER JAW

(Fig. 25, plate 6a)

With the exception of the articular and coronoid, (an element hitherto undescribed in the Ichthyosauria), the elements of the lower jaw are firmly united, and their true relationships have long been known and well documented in the literature. Much of the information has been obtained by studying sections where the individual elements usually retain their original relationships. It will not be necessary there-

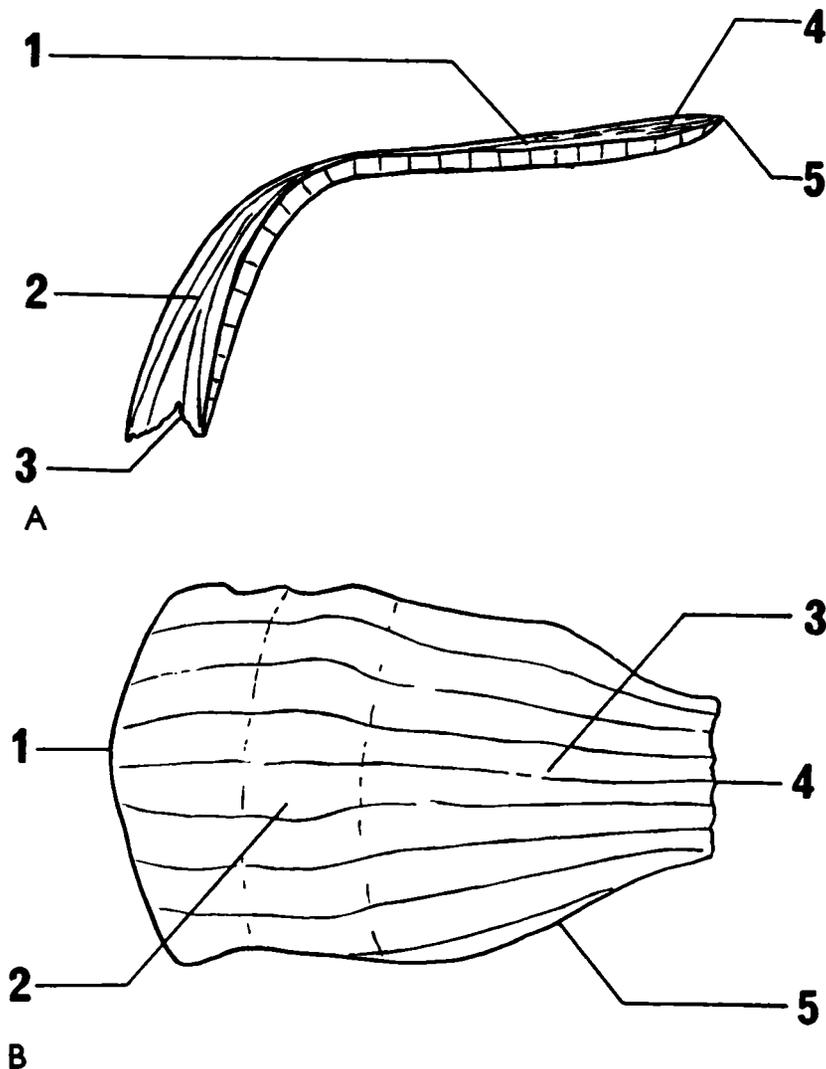
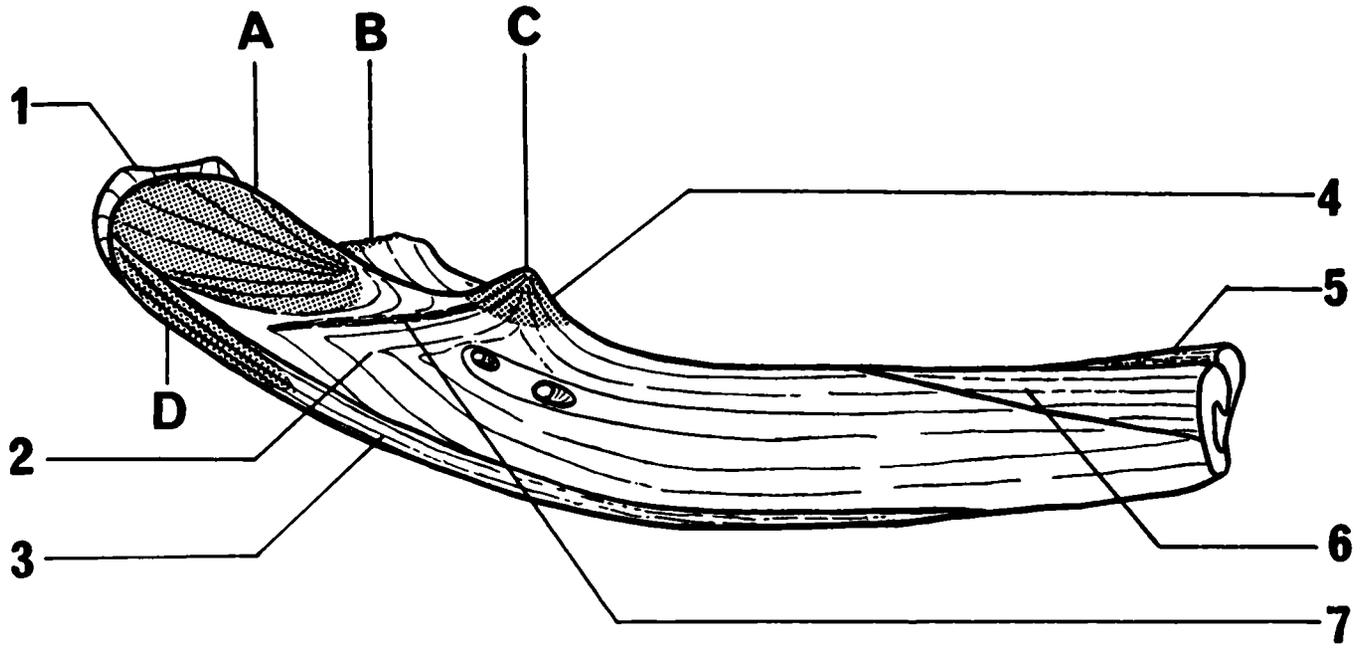
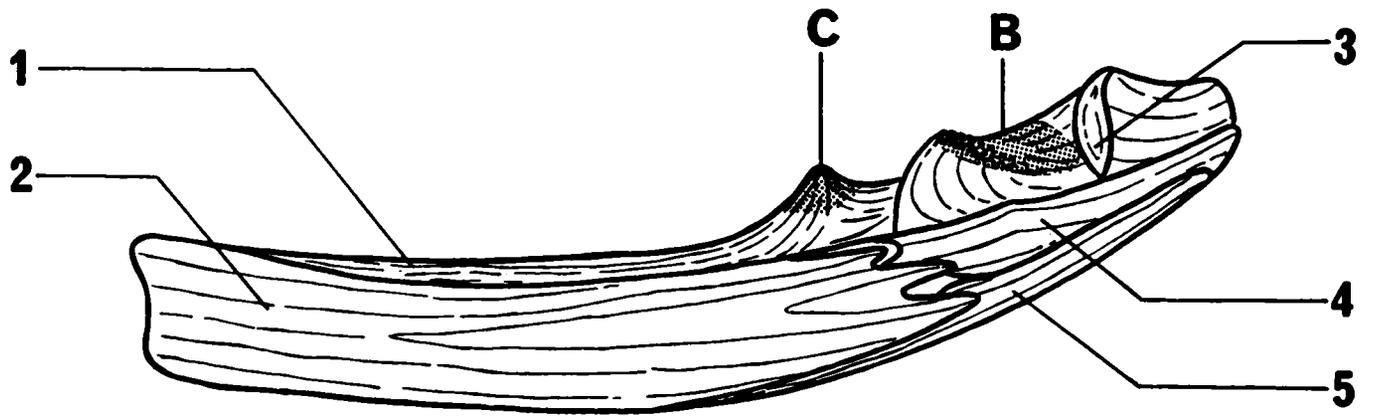


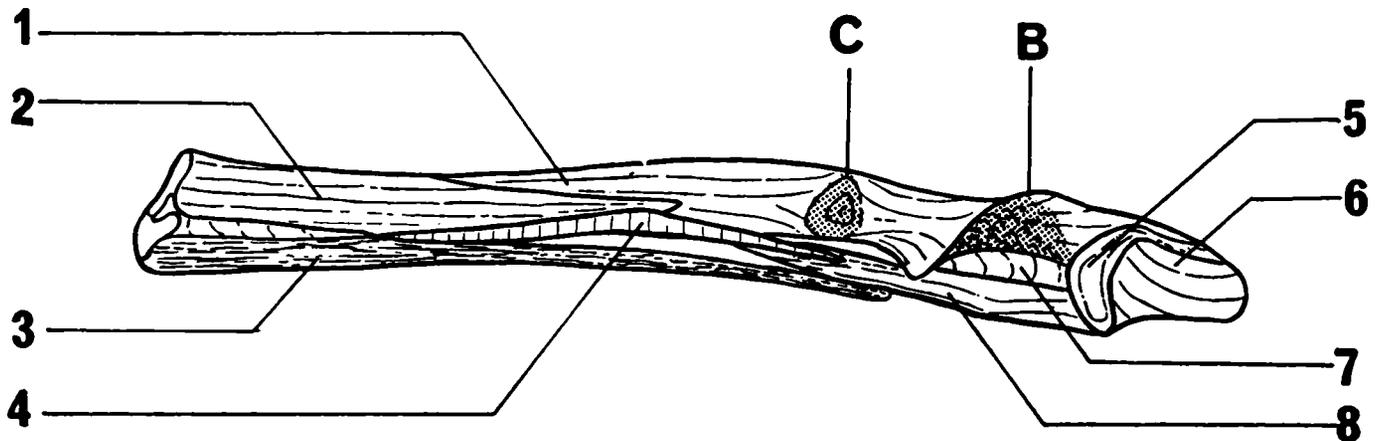
FIG. 24. (a). Sclerotic plate, side view, $\times 2$ (R6697). 1, anterior surface. 2, lateral surface. 3, outer margin. 4, shallow sulcus. 5, inner margin. (b). Sclerotic plate, anterior view, $\times 2$, (R6697). 1, outer margin. 2, lateral surface. 3, anterior surface. 4, inner margin. 5, lateral margin.



A



B



C

fore to deal in very much detail with those aspects which have already been satisfactorily discussed elsewhere, (the reader is referred in particular to the work of Sollas, 1916, for a very adequate account of the jaw).

The mandibular ramus is formed largely from the surangular, angular, splenial, and dentary. The prearticular makes a minor contribution to the medial jaw surface, while the role of the coronoid in its contribution to the dorsal surface is even smaller.

1. *Surangular* (fig. 25). The surangular forms the greater part of the external surface of the posterior region, and much of the dorsal aspect. Postero-ventrally it bears a deep and tapering recess into which the posterior portion of the angular locates. In the specimen sectioned by Sollas the relationship between these two elements is more intimate, due to interdigitation. Anteriorly the surangular is gradually overlain by the dentary, and therefore has a tapered appearance when viewed from the side. The surangular bears three prominent muscle insertion areas which have not been adequately described elsewhere, and these will now be considered.

Posteriorly and dorsally, on the external surface, there is an ovoid and slightly depressed area marked by numerous striations which tend to converge anteriorly and somewhat ventrally. This is the largest of the mandibular insertions, and, as will be seen later, is identified as that of the *M. depressor mandibulae*. The dorsal margin of the surangular is for the most part rounded from side to side, but the uniformity is interrupted caudally by a bony protuberance which has been described as the coronoid process. The coronoid process is pitted and marked by low rugosities and is interpreted as marking the insertion of the *M. adductor mandibulae pseudotemporalis*. The superficial sculpturing of the bone widens medially so that the area of insertion has a triangular dorsal aspect, the wide base of which lies medial and parallel with the longitudinal axis.

Some small distance behind the coronoid process the internal surface of the surangular is deflected outwards, exposing a demilunar and dorso-medially inclined

FIG. 25. (a). Lower jaw ramus (right side), external view, slightly more than 1/2 natural size (R8177). (Position of articular and terminal portion of jaw is part restored by reference to R6697 and Evans' nodule.) 1, articular. 2, surangular. 3, angular. 4, coronoid process of surangular. 5, splenial. 6, dentary. 7, raised lip which might have been part of the insertion area of the *M. adductor mandibulae externus*. (A) Insertion of the *M. depressor mandibulae* (the anteriormost portion of this shaded area may well mark the position of insertion of ligaments of the jaw joint capsule). (B) Insertion of the *M. adductor mandibulae externus*. (C) Insertion of the *M. adductor mandibulae internus pseudotemporalis*. (D) Insertion of the *M. adductor mandibulae internus pterygoideus*. (b). Lower jaw ramus (right side), internal view, slightly more than 1/2 natural size (R8177). 1, surangular. 2, splenial. 3, articular surface of articular. 4, prearticular. 5, angular. (B) Insertion of the *M. adductor mandibulae externus*. (c). Lower jaw ramus (right), dorsal view, slightly more than 1/2 natural size. 1, surangular. 2, dentary. 3, splenial. 4, coronoid. 5, articular surface of articular. 6, smooth dorso-medial surface of articular. 7, Meckelian fossa. 8, prearticular. (B & c) As for Figure 25 (b).

surface which is prominently roughened and marked by striations which converge antero-ventrally. This area is bounded laterally by the sharp dorsal edge of the surangular, which, curving towards the mid line anteriorly, is produced into a trench crest which faces obliquely inwards and forwards. Here the rugosities are most prominent and are dentiform. This very prominent insertion is interpreted as that of the three components of the *M. adductor mandibulae externus*.

The external surface of the surangular is excavated by a short but moderately deep groove which commences at the level of the coronoid process, and about half way down, and which is pierced by two oval foramina. These foramina open out medially into the Meckelian canal, and probably transmitted blood vessels from the Meckelian canal to the external surface of the jaw.

2. *Angular* (fig. 25). The angular contributes to the external surface of the jaw and lies ventral to, and is overlapped by, the surangular. Ventrally the angular is inflected and forms the ventral jaw margin for some distance, and much of the internal jaw surface posterior to the level of the coronoid process. Anteriorly the angular disappears from view beneath the ventral embrace of the splenial, but persists clandestinely for some considerable distance.

The terminal portion of the external surface is marked by a series of longitudinal striations which are interpreted as the insertion of the *M. adductor mandibulae internus pterygoideus*.

3. *Splenial* (fig. 25). The medial surface of the jaw is formed for almost its whole length by the splenial. Anteriorly the ventral splenial edge is outward turned and, embracing the angular from below, forms the ventral margin of the jaw. The splenial terminates posteriorly in a digitate edge just posterior to the level of the coronoid process.

4. *Dentary* (fig. 25). The dentary commences posteriorly, some distance in front of the coronoid process, as a slender splint of bone which is applied to the dorsal edge of the surangular. As the dentary increases in width anteriorly, it spreads over the external surface of the jaw and encroaches upon the surangular which it eventually covers completely. The dorsal margin of the dentary contributes with that of the splenial in the formation of a dentigerous groove.

5. *Prearticular* (fig. 26, plate 6b). The prearticular is a slender laterally compressed element which contributes, posteriorly, to the medial surface of the jaw. Ventrally it is overlapped by the angular and almost half of its depth is hidden from view. The area of contact with the angular is marked by a longitudinal articular facet. In the specimen sectioned by Sollas the prearticular (referred to by Sollas as the goniale) is shown to lie in the same vertical plane as the angular throughout its length. Furthermore it is shown to lie in articular contact with the splenial and in the same vertical plane for some distance (sections 457-462) before being overlapped, whereas in specimen R8177 the splenial always overlaps the prearticular.

The anterior half of the prearticular is quite straight but slightly twisted about a longitudinal axis so that the dorsal edge comes to lie just labial of the ventral edge.

Somewhat more than halfway along from its anterior end the bone is curved slightly inwards, and at this point the direction of torsion is reversed so that the dorsal edge comes to lie just medial of the ventral edge. Caudally the bone is gently upturned so that the entire element has the appearance of a complete jaw ramus when viewed from the side. For most of its length the cross-section is wedge-shaped, tapering gradually ventrally, and the depth and thickness decrease rostrally where the bone ends in a bifid tongue.

Posteriorly and ventrally the medial surface bears the longitudinal angular facet, and the ridge which forms its dorsal border is thickened anteriorly, forming a prominent lip. In advance of this facet the surface is relatively flat and unsculptured, while the external surface is slightly hollowed over most of its length.

The dorsal edge bears a long groove for reception of the coronoid, and this facet is tapered at either end and is inclined labially.

6. *Coronoid* (fig. 27, plate 6c). There has been some confusion in the literature over the use of the term *coronoid*. Conybeare (1821 and 1822) uses it synonymously with *surangular*, while Andrews (1910) uses it to describe the *prearticular*. The true coronoid has hitherto escaped notice in the Ichthyosauria, and full credit for its discovery is due to Rixon whose careful preparation of specimen R8177 revealed the presence of this frail and elusive element.

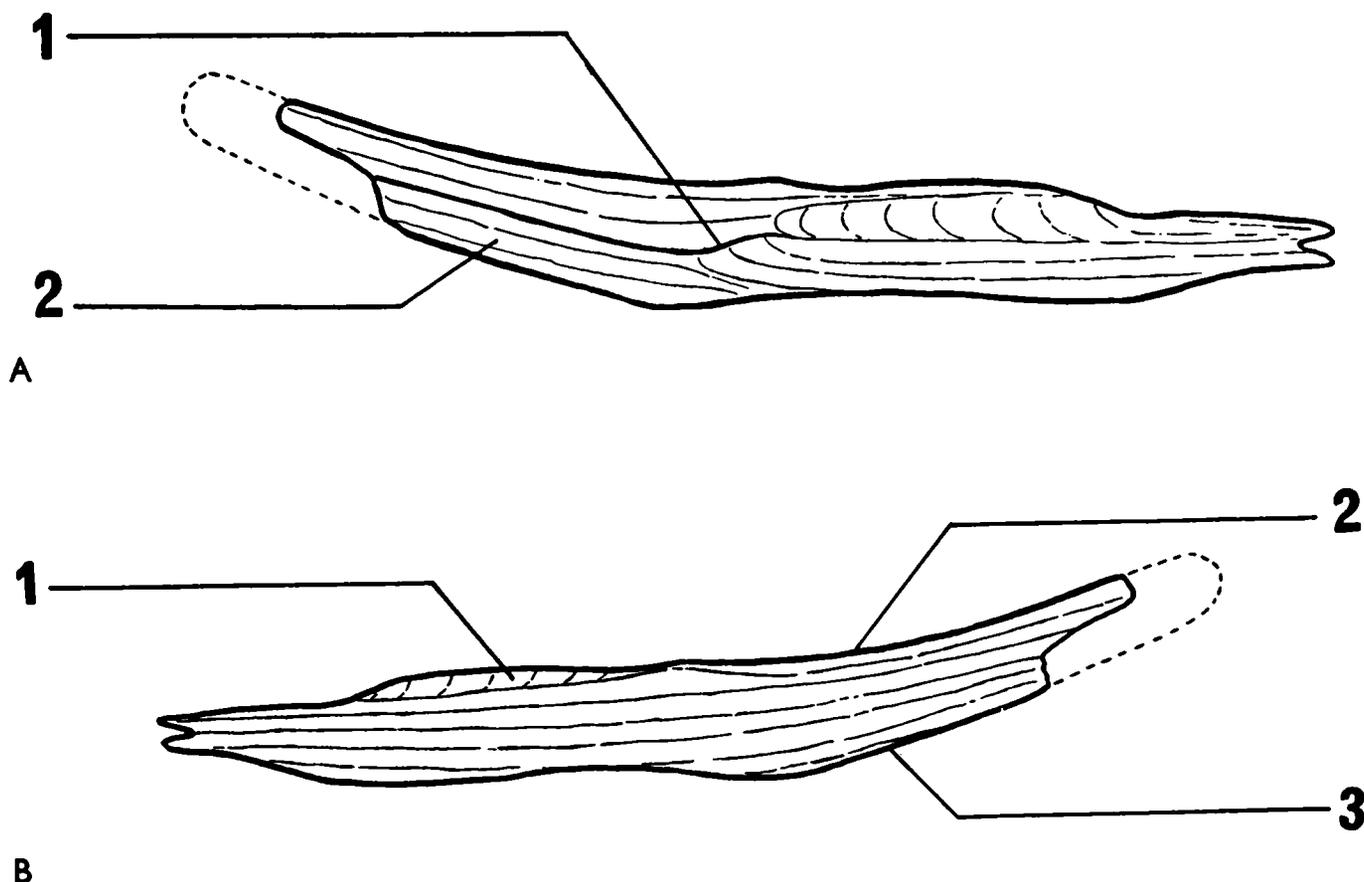


FIG. 26. (a). Prearticular (left), internal view, natural size (R8177). 1, dorsal border of angular facet. 2, angular facet. (b). Prearticular (left), external view, natural size (R8177). 1, coronoid facet. 2, dorsal edge. 3, ventral edge.

The coronoid is a very slender and fusiform element which lies in the dorsal dentigerous groove of the mandible, extending for some distance forward beyond the level of the coronoid process of the surangular. The dorsal surface therefore contributes to the dorsal aspect of the mandible, and it rests with its posterior third in the prearticular groove. In cross section it is triangular and the medial surface lies at right angles to the relatively flat and dorsal surface. The labial surface is therefore oblique and faces downwards and outwards. Viewed from above both internal and external dorsal edges describe arcs about centres which lie medially. Since the radius of curvature of the external edge is less than that of the internal edge, the bone widens towards its centre. The depth of the element is also greatest towards its centre. Because of the arcuation of its dorsal edges the coronoid does not make lateral contact with the rest of the jaw over its entire length. In the mid-portion of the element, where external lateral contact with the surangular and posterior portion of the dentary is made, the ventro-lateral surface bears a shallow articular facet for this purpose.

The widest part of the element is not coincident with its linear centre but lies caudally, so that the anterior process is longer than the posterior process, and is accordingly more slender. The anterior process also differs from the posterior in the possession of two small foramina which pass antero-ventrally through the bone.

7. *Articular* (fig. 28, plate 6d). The articular is a small laterally compressed element, which lies at the posterior end of the jaw ramus with the whole of its rounded external surface applied to the medial surface of the surangular. Ventrally its medial surface bears a triangular articular facet for the prearticular. This orientation

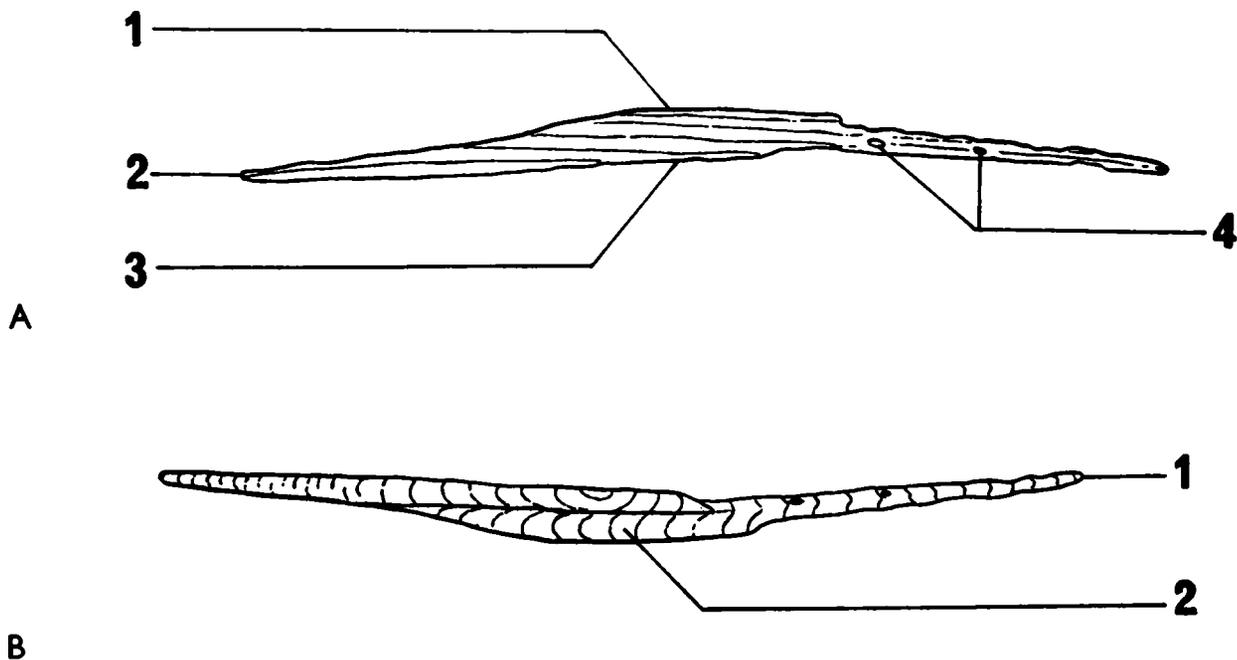


FIG. 27. (a). Coronoid (left), dorsal view, natural size (R8177). 1, external edge. 2, posterior end. 3, internal edge. 4, foramina. (b). Coronoid, (left), ventral and somewhat external view, natural size (R8177). 1, anterior tip. 2, articular facet for surangular and dentary.

has been unequivocally established, and, as will be seen later, gave rise to some difficulties in obtaining a satisfactory relationship with the quadrate.

The external surface is roughened and somewhat depressed, and has an oval outline, whereas the internal surface, is relatively smooth and almost rectangular in outline. From before to behind this surface is concave, while from top to bottom it is convex, conferring a superficial resemblance to a saddle.

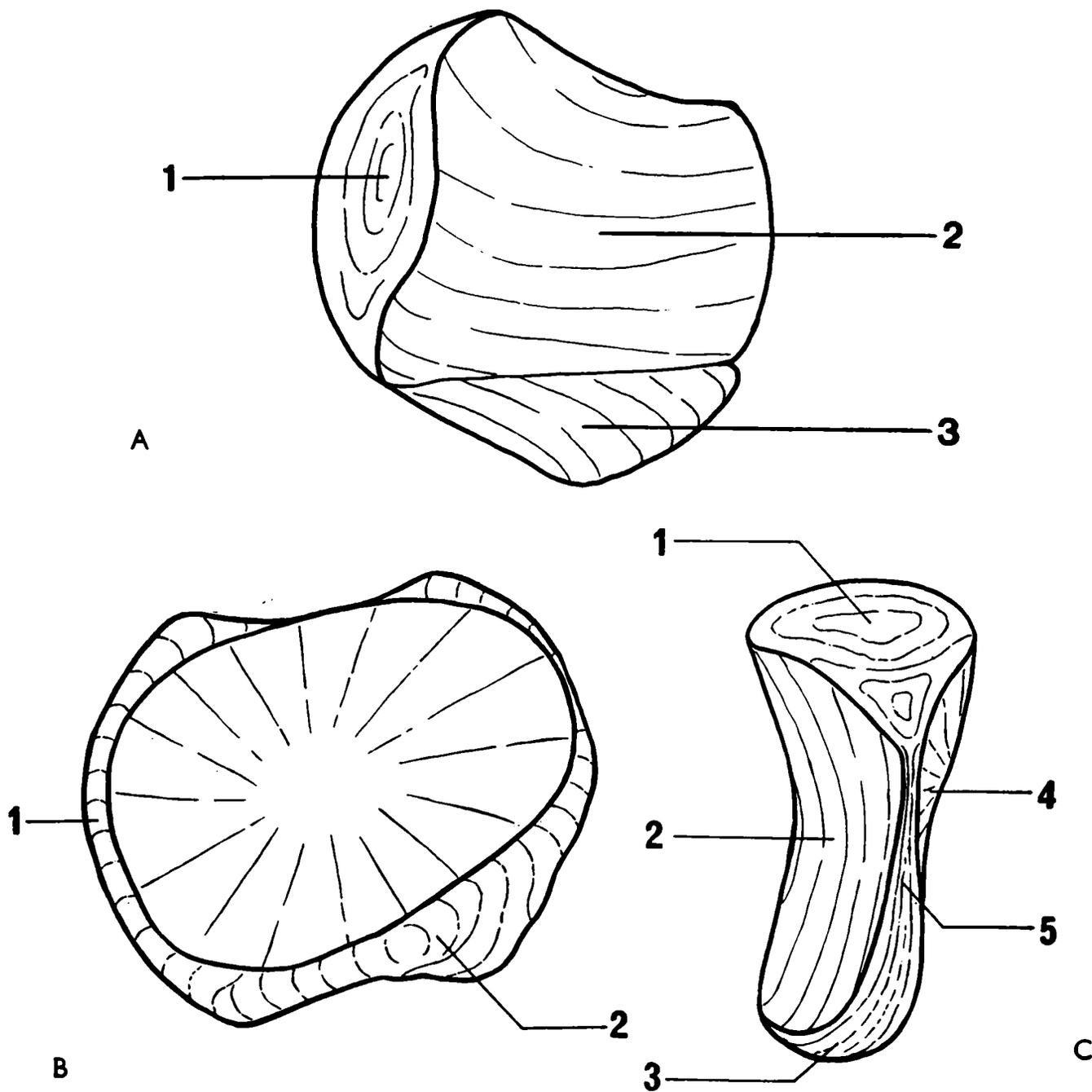


FIG. 28. (a). Articular (right), lingual view, $\times 3$ (R6697). 1, articular surface. 2, medial surface. 3, prearticular facet. (b). Articular (right), labial view, $\times 3$ (R6697). 1, posterior margin. 2, ventral surface. (c). Articular (right), dorsal view, $\times 3$ (R6697). 1, articular surface. 2, medial surface. 3, posterior margin. 4, external surface. 5, dorsal surface.

The articular is thinnest somewhere about its centre, and, thickening rapidly anteriorly, reaches its maximum thickness at its anterior face which has a relatively smooth surface, and is ellipsoid when viewed from in front. The posterior margin is relatively smooth and is narrow.

The ventral surface is narrow and triangulate, tapering caudally, and is coarsely corrugate. The dorsal surface is virtually non-existent, being the labially inclined dorsal portion of the internal surface.

In two specimens (R8177 and 49203) the articular has been preserved in approximately its natural position, and this provided the initial clue to its correct orientation. The articular lies with its rugose external surface firmly braced against the internal surface of the surangular, and the posterior edge faithfully follows the curvature of the surangular margin. Meso-ventrally contact with the prearticular is made in a well defined facet.

THE JAW ARTICULATION

The orientation of the quadrate, like that of the articular, has been established beyond all reasonable doubt, and the problem of the jaw articulation is that of determining their correct relationship with one another. Initially it was thought that the ventral surface of the quadrate condyle articulated with the saddle-shaped medial surface of the articular. However the only satisfactory relationship between these two surfaces could be obtained with the jaw in the vertical plane, at right angles to the longitudinal axis of the skull. Furthermore the medial surface of the articular is quite smooth and does not have the appearance of bone once invested in cartilage. The anterior surface of the articular, however, does have such an appearance, and when articulated with the postero-laterally inclined portion of the quadrate condyle a satisfactory relationship is obtained, their undulating surfaces corresponding moderately well (fig. 29). Thus oriented the articular lies entirely posterior to the level of the jaw joint and there is therefore a significant retroarticular process. The most convincing evidence that this is the correct relationship between the jaw and skull is furnished by two associated skulls, 49203 and R3375. The first is a complete in-the-round specimen, and from the way in which the upper and lower teeth mesh throughout, it is clear that the jaw is in its correct relationship with the skull. The quadrate condyle and the articular are both clearly visible on the right side, and the latter lies entirely posterior to the level of the former. In R3375, which has been dorso-ventrally compressed, only the dorsal half of the skull is exposed and it cannot be known for sure whether the jaw is in its correct position, but this does seem to be the case. Here again quadrate condyle and articular are clearly visible and the articular lies posterior to the quadrate.

THE HYOID APPARATUS

(fig. 30)

The hyoid arch is represented by a pair of stout rods which lie medial to, and parallel with, the jaw rami. These rods are gently curved, and extend from about

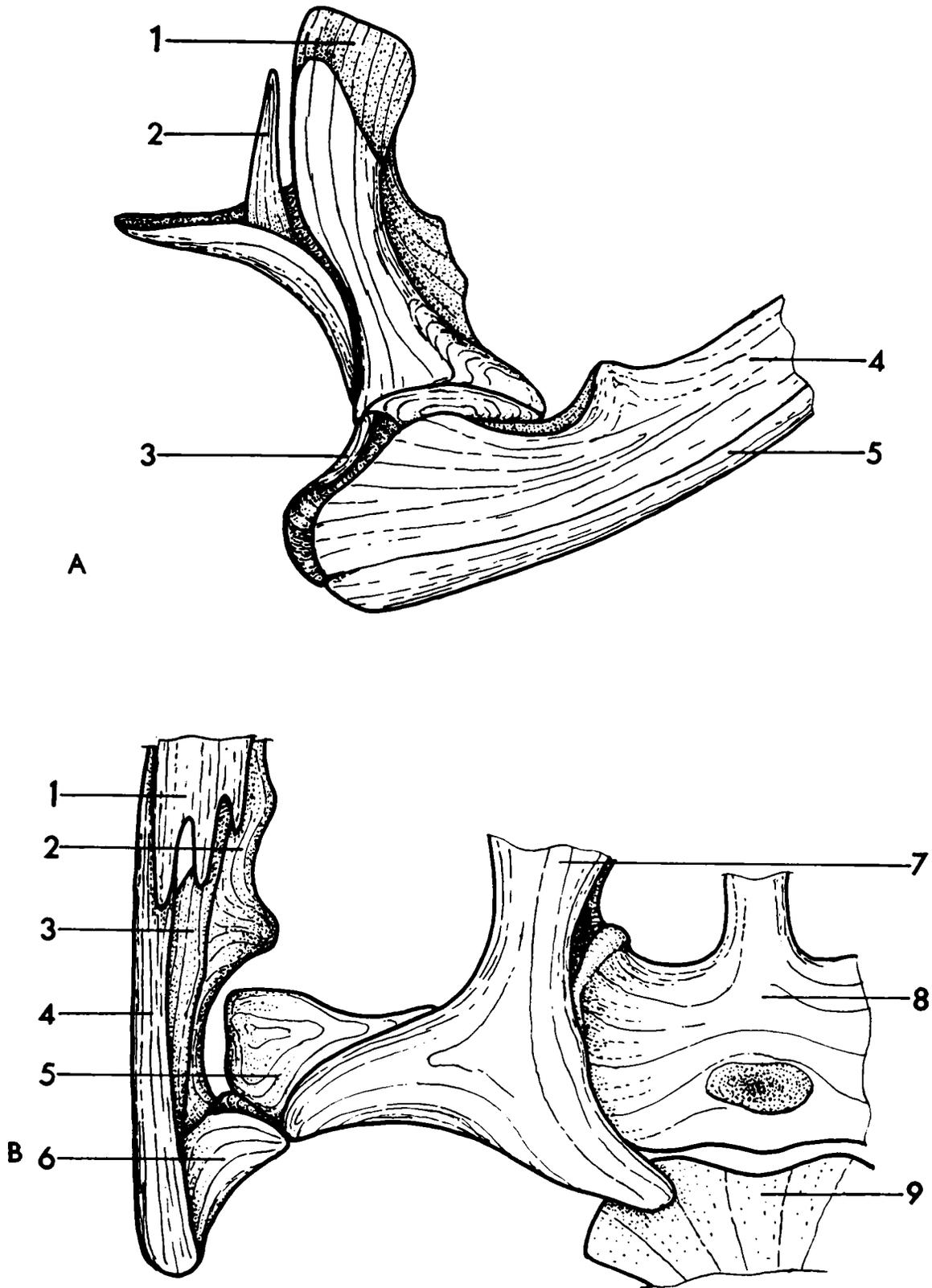


FIG. 29. (a). A reconstruction of the jaw joint (right side), postero-lateral view. 1, quadrate. 2, quadrate wing of pterygoid. 3, dorso-medial surface of articular. 4, surangular. 5, angular. (b). Reconstruction of the jaw joint (right side), ventral view. (In order to demonstrate the jaw joint more clearly the jaw has been rotated outwards somewhat and is shown in a ventro-lateral aspect.) 1, splenial. 2, surangular. 3, prearticular. 4, angular. 5, condyle of quadrate. 6, ventro-medial surface of articular. 7, pterygoid. 8, basisphenoid. 9, basioccipital.

the level of the quadrates almost as far as the anterior border of the orbit. They are often preserved in dorso-ventrally compressed specimens, and are figured by Owen, (1881, pl. 25, fig. 3). Sollas gives a very good account of the hyoid skeleton and also describes the elements of the first branchial arch, which, together with those of the hyoid, form a complex ventral skeleton (Sollas 1916, fig. 2, sections 425-507; fig. 15). For completeness Sollas' reconstruction of the hyoid and branchial skeleton is given below (fig. 30).

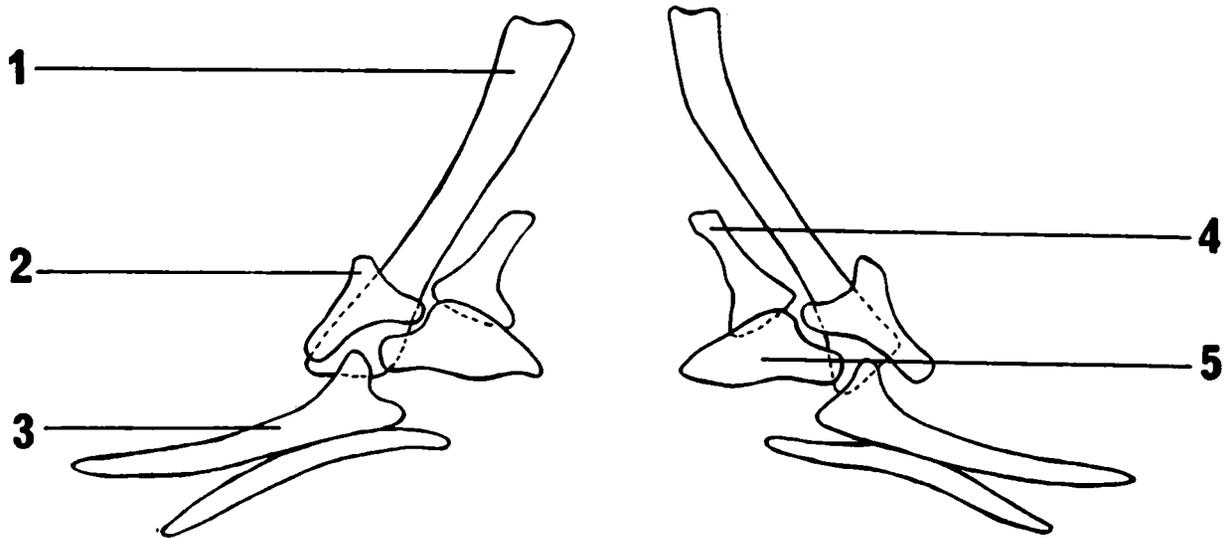


FIG. 30. Hyoid apparatus (ventral view), after Sollas. 1, hyoid rod. 2, first branchial arch. 3, second branchial arch. 4 & 5, third branchial arch.

THE TEETH

The teeth are somewhat variable in shape but generally have the form of fairly stout and curved cones. The crown, which has an enamel coating, forms but a small portion of the tooth, and though smoother than the root, it usually bears fine striations. The root is rough to the touch, is distinctly corrugate towards its base, and has a porous texture. The junction between the root and crown is marked by a raised annulation which may be smooth or ridged (fig. 31, plate 6g). The teeth have been very adequately figured and described by Fraas (1891 : pl. 1-2) who includes some excellent figures of sections.



FIG. 31. Tooth from 49203, $\times 2 \frac{1}{2}$.

THE RECONSTRUCTION OF THE SKULL

The skull reconstruction was carried out almost entirely with reference to ex-nodular material, and since the snout region is unrepresented there, the relevant information has been obtained by studying unprepared skulls, part-prepared skulls and sections. (The work of Sollas 1916 has been particularly useful.)

Sufficient material was available to permit the reconstruction of three hind skulls, and these were built up in parallel so that comparisons could be made between them at each stage, thus reducing the possibility of misinterpretation. Before commencing the reconstructions, however, it was necessary to take each bone and orientate it with respect to its adjacent elements until the precise relationship of each bone had been established, and recorded upon the bones themselves using keying-up marks. The three skulls were then reconstructed, fixing together component elements with water-soluble wax. In only one of the specimens, R8177, was it possible to reconstruct the skull roof and palate up to the external narial opening, though at least part of the temporal vacuity and parietal roof and part of the palate could be reconstructed in the other two specimens. Since the reconstruction proceeded in a number of distinct stages, the following account is subdivided.

1. *The reconstruction of the occiput* (fig. 32, plates 7b and 7c)

The occiput comprises the single median basioccipital, basisphenoid, and supra-occipital, and the paired exoccipitals, opisthotics, präotics, and the stapes. The first elements to be articulated were the basioccipital and basisphenoid, the foundation stones of the skull.

The postero-dorsal surface of the basisphenoid is deeply grooved for the reception of the keeled antero-ventral surface of the basioccipital, and it was found that the two elements fitted together with only a small degree of freedom enabling a good relationship to be obtained. As noted earlier when the structures of the basisphenoid and basioccipital were described, the small notch which lies just ventral on the basioccipital peg corresponds with the dorsal fissure of the basisphenoid marking between them the position of the upturned tip of the notochord. This relationship enables a very precise orientation to be made between the two elements. Since the basioccipital keel does not make flush mid-line contact with the deep basisphenoid groove a narrow channel is formed. This channel opens dorsally into the notochordal recess, and ventrally into a large elliptical aperture enclosed by the ventral edges of the two elements. This median ventral aperture corresponds closely in its position with the single Eustachian aperture of the crocodile, a fact which did not escape the attention of Owen (1881, 93) who wrote, "The fore part of the basioccipital presents, in some species, a slight notch or groove, as if for the outlet of an Eustachian canal." However, since the channel opens proximally into the cranial cavity it is inconceivable that it served an otic function and it seems most likely that it has no significance at all, merely arising out of the loss of mid-line contact between the basioccipital and basisphenoid. Indeed, since the channel is so narrow it is doubtful whether it did exist in life, being occluded by cartilage or periosteal membranes. In orientating the basisphenoid and the basioccipital, care

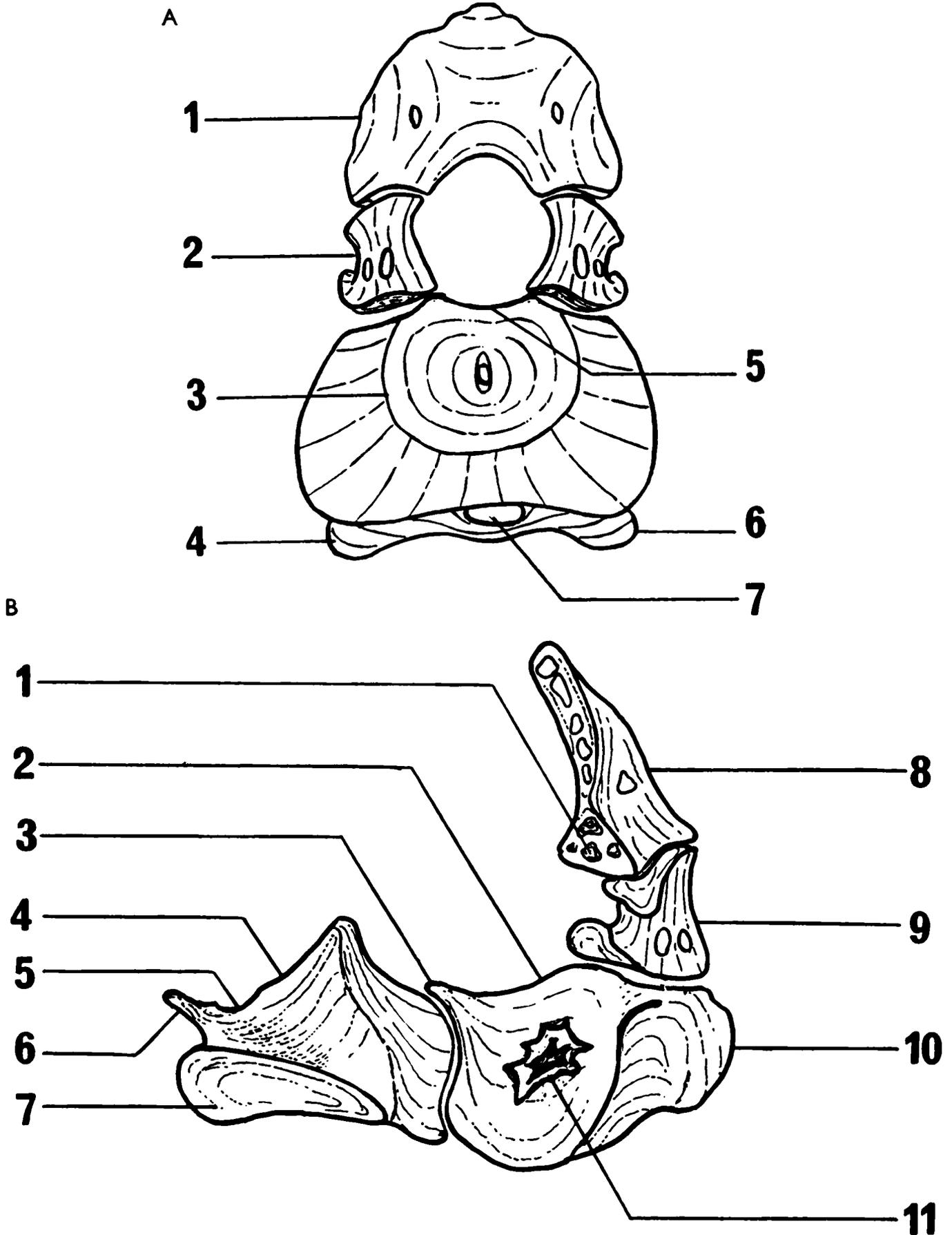


FIG. 32. (a). Reconstruction of occipital region of skull, posterior view, $\times 1$ (Evans' nodule). 1, supraoccipital. 2, exoccipital. 3, basioccipital condyle. 4, basisphenoid. 5, floor of foramen magnum. 6, basipterygoid process. 7, carotid foramen. (b). Reconstruction of occipital region of skull, lateral view, $\times 1$ (Evans' nodule). 1, membranous impression. 2, ascending dorsal surface of, $\times 1$. 3, basioccipital peg. 4, position of sella turcica. 5, position of paired trabeculae impressions. 6, parasphenoid. 7, basipterygoid process. 8, supraoccipital. 9, Exoccipital. 10, basioccipital condyle. 11, stellate excavation of basioccipital.

was taken to ensure that they laid symmetrically about a longitudinal axis, and, having obtained a satisfactory relationship, attention was turned to the supraoccipital and paired exoccipitals.¹

The articular facets for reception of the exoccipitals on the supraoccipital are deep and well defined, and it was found that the medial portion of the dorsal articular surface of the exoccipital located with precision, so that there was neither discontinuity in the cranial wall when viewed from within, or in the curvature of the foramen magnum when viewed from behind. The exoccipitals could thus be attached to the supraoccipital very accurately. The supraoccipital with its attached exoccipitals was lowered into position on the basioccipital. It was found that the exoccipitals fitted into the facets on the basioccipital so that the continuity of the foramen magnum was uninterrupted, and the medial ventral edge of each followed the contour of the basioccipital facet exactly. The paired exoccipital facets of the basioccipital are fairly shallow, and less well defined than those of the supraoccipital, and a flush contact between the respective articular surfaces does not occur at every point, indicating the intervention of a thin layer of cartilage between them (fig. 32).

Since the occipital elements fitted together so precisely it could confidently be concluded that the reconstruction was accurate. Before the otic elements could be oriented, however, it was necessary to reconstruct the rest of the skull and relate it to the occiput. The next stage was the reconstruction of the palate and the determination of its relationship with the rest of the skull.

2. *The reconstruction of the palate, and its relationship with the rest of the skull* (fig. 33, plate 7a)

The palate comprises of paired pterygoids, palatines, and vomers, and the median parasphenoid. The two halves of the palate form extensive shelves of bone which, narrowing rapidly, come into contact just anterior to the level of the internal nares. Posterior to this level the palate is formed largely from the pterygoids and palatines, and the vomers, which contribute with the palatines in the formation of the internal narial aperture, make but a minor contribution. Anterior to the nares the palate is formed entirely from the vomers, although the pterygoids do continue for some distance hidden from view.

The pterygoid and palatine were the first elements to be associated, and they were shown to have a very precise relationship with one another. Fusion does not seem to have occurred, except perhaps at the medial margin of the palatine, strength having been attained by overlapping. The palatine overlaps the pterygoid dorsally, and not ventrally, as figured by Owen (1881 : pl. 25, fig. 1). The posterior margin of the palatine slopes obliquely backwards towards the midline so that when placed in contact with the outer edge of the pterygoid the curvature of the intrapterygoid vacuity is continued without interruption (fig. 33, plate 7a). Furthermore, there is a small ovoid facet on the dorsal surface of the pterygoid, at the anterior corner of the intrapterygoid vacuity, which articulates with a corresponding facet on the

¹ In R8177 the exoccipitals are not preserved, but the problem was overcome by making a pair of plaster elements to scale, by reference to the small skulls.

posterior ventral surface of the palatine. Anteriorly there is a third point of reference, provided by a raised bony ridge on the dorsal surface of the pterygoid, against which abuts part of the internal palatine margin. Since both the palatine and pterygoid are curved from side to side, they form a basin when placed together.

The pterygoid narrows rostrally, and, due to torsion, the surface which posteriorly was dorsal, becomes turned outwards, forming an almost vertical surface which has articular contact with the medial surface of the vomerine keel. The latter surface bears a low longitudinal ridge which corresponds with a shallow groove in the pterygoid. Viewed from beneath, the outer edge of the pterygoid slopes gently forward towards the midline, and the keel of the vomer faithfully follows this line. Dorsally the vomer overlies the anterior portion of the pterygoid, obscuring it from

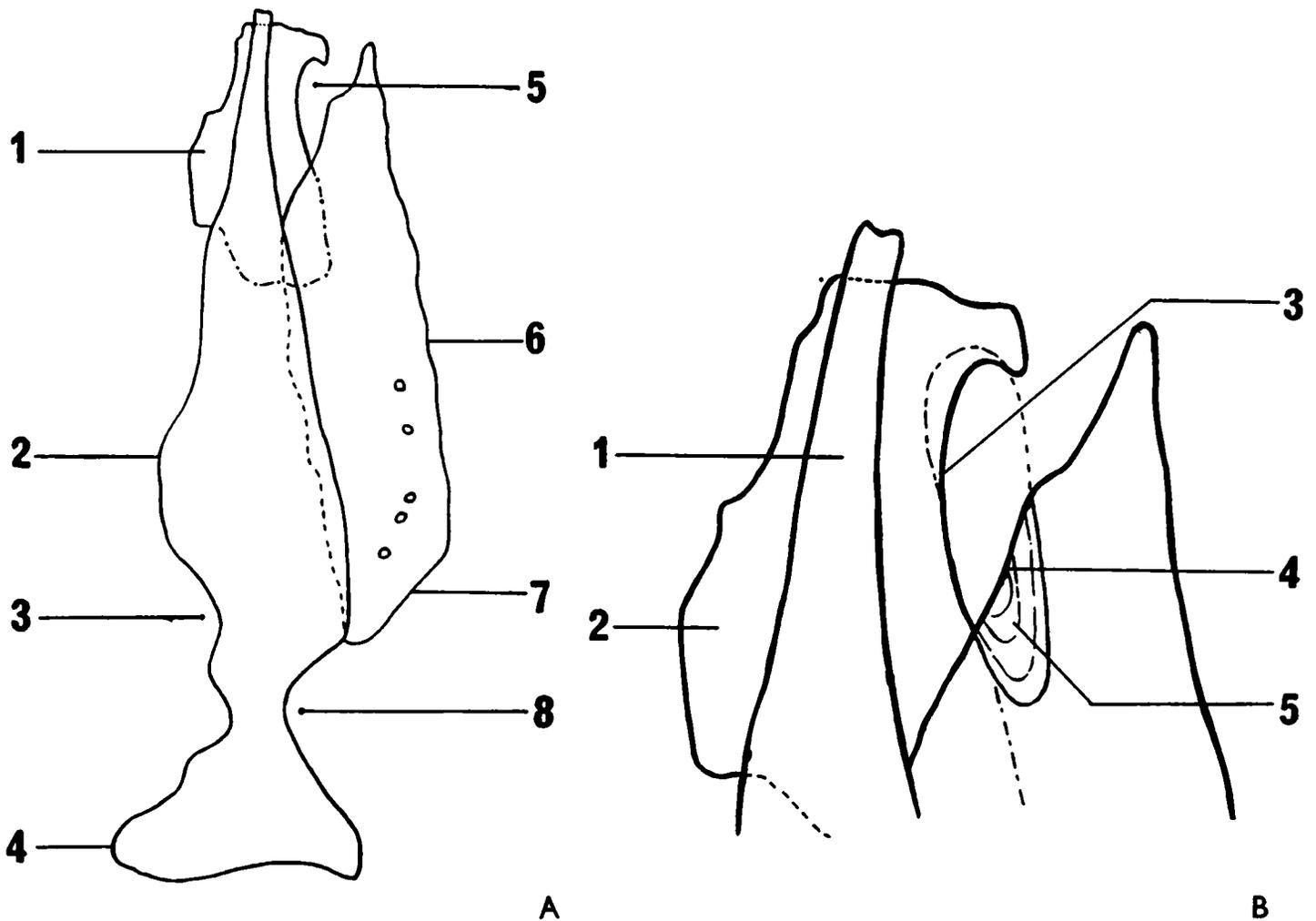


FIG. 33. (a). Reconstruction of palate (left side), ventral view, $\times 1/2$ (R8177). 1, vomer. 2, medial edge of pterygoid. 3, edge of interpterygoid vacuity. 4, medial wing of pterygoid. 5, internal narial aperture. 6, external edge of palatine. 7, posterior margin of palatine. 8, intrapterygoid vacuity. Note: Palatine lies dorsal to pterygoid and vomer lies dorsal to palatine. (b). Reconstruction of the internal narial aperture (left side), ventral view, slightly greater than natural size (R8177). 1, pterygoid. 2, vomer. 3, external edge of vomer. 4, medial edge of palatine. 5, depression.

dorsal view, (see Sollas 1916 : sections 334–359). Furthermore, since the pterygoids tend to curve upward toward their tip, and the vomers meet in midline beneath them, the pterygoids disappear from ventral view. An excavation of the outer edge of the vomer and of the medial edge of the palatine together form the internal narial aperture (fig. 33).

The parasphenoid is present in only one specimen, and is very incomplete, being represented for only a fraction of its entire length. As described above, the parasphenoid is fused with the basisphenoid so that its relationship with the rest of the palate could only be established after attachment of the palate to the occiput.

The relationship between the palate and occiput The only contact between the occiput and the palate is at the basisphenoid, which is drawn out on either side into the winged basiptyergoid processes which slot into a deep recess in the pterygoids. The basiptyergoid joint is quite definite, but possesses a certain degree of freedom, and two criteria have been used in arriving at a satisfactory relationship.

1. The distal facet of the basiptyergoid process is smooth and flat and faces outwards and upwards, and corresponds with an oblique medial facet in the pterygoid slot.

2. The curved edge of the internal pterygoid emargination is continued by the rounded leading ventral edge of the basisphenoid.

These criteria, however, do not unequivocally fix the position of the two halves of the palate, and since the palate has contact with the rest of the skull at three other points, it was necessary to reconstruct much of the skull before the true relationships of the palate could be established. These three points of contact are listed below.

1. With the quadrate, which in turn has contact with the temporal arcade.

2. With the maxilla which has contact with the circumorbital series and with the premaxilla.

3. With the eipterygoids which in turn articulate with the skull roof.

The relationship between the palate and quadrate. The relationship between the quadrate and palate can readily be obtained because the quadrate has a precise contact with the pterygoid over a relatively large area. The postero-lateral surface of the quadrate is somewhat convex, and the quadrate process of the pterygoid is hollowed to receive it in a fairly flush contact. The rounded ventral edge of the quadrate process conforms very closely to the curved edge of the quadrate, and the leading ventral edge of the quadrate fits into a shallow groove located just posterior and external to the eipterygoid groove, and continues the curvature of the intrapterygoid vacuity without interruption.

The relationship between the palate and maxilla. Anteriorly, and towards its external edge, the ventral surface of the palatine is carinate and the depth and width of this keel diminishes posteriorly. The dorsal surface of the maxilla possesses many grooves

and medially is a shallow groove which faces inwards and slightly upwards, narrowing posteriorly. The outer surface of the palatine keel locates in this groove and there is a pair of apertures towards the medial margin of the maxilla which corresponds with a pair of emarginations of the outer edge of the palatine. The two elements can be articulated with a good degree of accuracy. The apertures doubtlessly served for the transmission of blood vessels or nerves, and movement between the two elements could not have taken place, (see *Kinesis*, below).

Any further discussion of the palate will be postponed until the reconstruction of the rest of the skull has been dealt with.

3. *The reconstruction of the posterior skull roof and temporal vacuity*

The posterior skull roof comprises of paired parietals, frontals and nasals. Anteriorly the nasals are overlapped by the paired premaxillae which form the major part of the elongate snout. Laterally the nasals, frontals, and parietals have contact with the dorsal components of the circumorbital series. The pre- and post-frontals and the parietals have postero-lateral contact with the paired squamosals.

As mentioned above, the parietals come together in mid-dorsal line in a complex suture, but their union was not found to be without a degree of mobility, for the parietals could be rocked upon one another about an axis passing through the suture. They could therefore be articulated either with the dorsal edges of their sutural

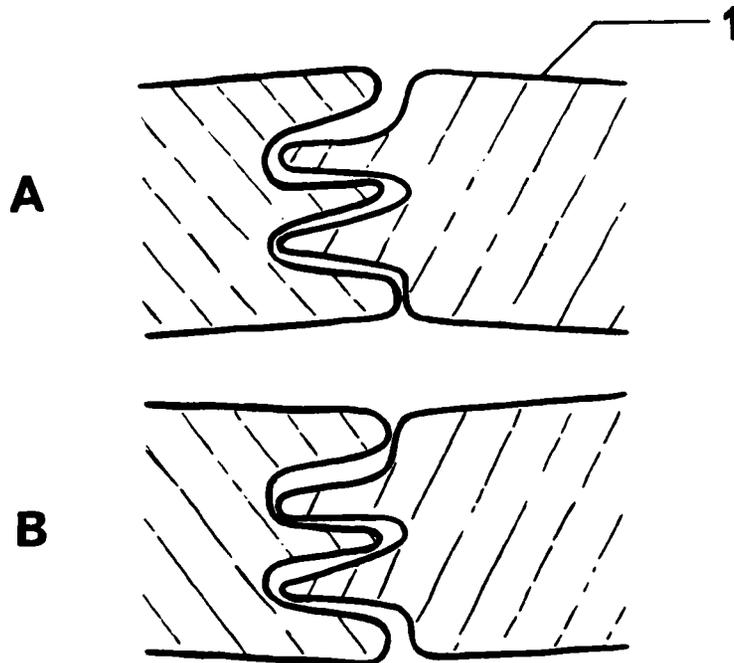


FIG. 34. Transverse section through the parietal suture. (A) Parietals articulated with their ventral edges in contact. (B) Parietals articulated with their dorsal edges in contact. 1, dorsal surface of parietal.

surfaces in contact, or, at the other extreme, with their ventral edges touching, (fig. 34). Whereas the dorsal edges are relatively straight, the ventral edges are jagged and correspond throughout their length, and the most satisfactory relationship seemed to be obtained when these ventral edges were placed into contact. With the parietals thus united their dorsal contact edges were widely separated, but it seemed reasonable that this gap would have been filled with cartilage in life. The relationship could be examined by attaching the epipterygoids and seeing if the distance between their distal facets approximated to the distance between the groove upon the pterygoids for their reception.

The relationship between the parietals and epipterygoids. The epipterygoid has an intimate relationship with the parietal, and the two elements can be articulated with precision. Dorsally the shaft of the epipterygoid is expanded forming a flange which locates in a shallow depression on the internal surface of the epipterygoid process of the parietal. A little further down this process enters into an oblique and interdigitating suture with the fluted external surface of the epipterygoid shaft, forming a rigid union. The epipterygoid could thus accurately be attached to the parietal.

Having attached both epipterygoids to the parietal canopy they were lowered into position upon the palate, but it was found that there was not a sufficient separation between them to permit location in the epipterygoid grooves. It was therefore necessary to adjust the parietal union until a satisfactory condition was reached, and this was found to be intermediate between the two extreme positions shown in fig. 34. When a satisfactory union between the parietals had been obtained the posterior skull roof could be completed.

The completion of the posterior skull roof (fig. 35, plate 8a). The leading edges of the parietals are raked so that rostrally they enclose a large V-shaped notch which is grooved for the reception of the posterior edges of the frontals, and a good relationship was obtained. Posteriorly the medial edge of each frontal is emarginated so that between them they enclose the pineal foramen. For the remainder the medial edges are straight, though down-curved due to the curvature of the element, and meet in mid-dorsal line in a flush contact. In only one specimen (R8177) are frontals and parietals complete, and there can be no doubt that in this instance the pineal foramen is formed entirely from the frontals with no parietal contribution. Skulls are often figured showing parietal participation in the pineal foramen, and this does not seem unreasonable. Anteriorly the frontals are overlapped for their greater part by the nasals.

On the ventral surface of each nasal is a curved ridge of bone which terminates towards the median line in a low projection which points obliquely backwards. The anterior edge of each frontal approximately corresponds with this ridge, and is embraced from below by the bony projection, so that the relationship between the nasals and the rest of the roofing bones can be accurately established. For the most part the medial edges of the nasals are in contact but at about the level of the anterior edge of the frontals they are slightly emarginated, and enclose between them

an elongate foramen, the internasal foramen. Medial contact is resumed once more in front of the foramen in a suture somewhat similar to that uniting the parietals, although far less complex. Posteriorly the nasals widen, and since their lateral and medial edges are somewhat raised, contact with the underlying frontals is made at only one point.

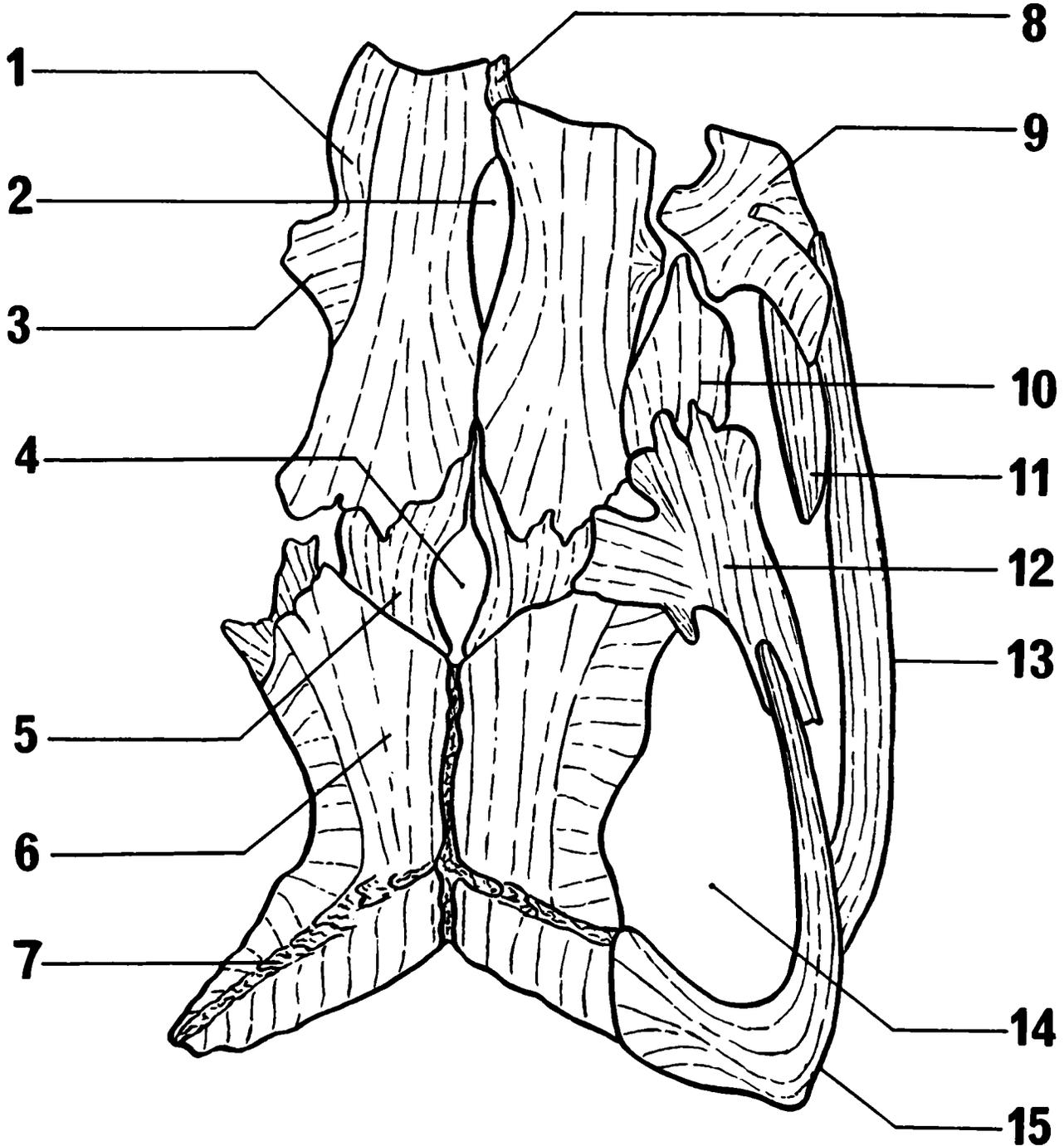


FIG. 35. Reconstruction of the skull roof (and circumorbital series), dorsal view, $\times 2/3$ (R8177). 1, lateral surface of left nasal. 2, internasal foramen. 3, descending triangular process of nasal. 4, pineal foramen. 5, frontal. 6, dorsal surface of parietal. 7, parietal ridge. 8, nasal facet excavated in medial margin of left nasal. 9, lachrymal. 10, prefrontal. 11, maxilla. 12, postfrontal. 13, jugal. 14, temporal vacuity. 15, squamosal.

The prefrontal is an element of the circumorbital series, but since it contributes to the skull roof it will be discussed here. The outer margin of the prefrontal has a smooth surface and contributes to the orbit, whilst medially it is drawn out into a narrow and roughened flange which is overlapped dorsally by the nasal. Ventrally, at its postero-medial corner it is underlapped by the parietal. Anteriorly the roughened medial flange is directed vertically as an ascending shelf of bone which makes contact internally with a descending process from the nasal.

The parietal makes a major contribution to the margin of the temporal vacuity, and the next stage in the reconstruction was the completion of the vacuity.

The completion of the temporal vacuity (fig. 35, plate 8a). The margin of the temporal vacuity is formed internally by the parietal, antero-laterally by the postfrontal, and is completed laterally and posteriorly by the squamosal. That there is squamosal and not supratemporal participation, as was previously supposed, is a matter of much taxonomic importance, and warrants closer examination.

In all the material so far examined there appears to be a single element forming the posterior margin of the temporal vacuity, whereas many other authors have figured and described two; Lydekker 1889 : fig. 2; von Huene 1922 : pl. 15, fig. 1; pl. 16, fig. 35; pl. 18, fig. 1; pl. 19, fig. 1; Watson 1914 : 95. When the temporal region of the reconstructed skulls are examined there is not found to be sufficient space to accommodate a second element, and, if there were one it would have to be ventral and medial to the other in its position, and considerably smaller. It is not altogether inconceivable that a second and very much smaller temporal element did exist and that it has always been lost, but it does seem rather unlikely. In those reptiles possessing both squamosal and supratemporal it is observed that the former is never subordinate in size to the latter, and if both elements existed in the Ichthyosauria, that bordering the vacuity, on *a priori* grounds, would be the squamosal and not the supratemporal. Romer (1968) reached the same conclusion and credits the present author for independently solving the problem.

The squamosal is a large element with two lateral and horizontal rami which embrace the vacuity, and a descending process which has contact with the quadrate (fig. 13, plate 6f). The free ventral margin of the medial ramus carries a deep and ellipsoidal depression which caps the distal portion of the oblique parietal ridge in a union which firmly anchors the squamosal to the parietal.

The postfrontal does not enter into such a definite union with the skull roof, but has an overlapping relationship which appears to be rather imprecise. Antero-medially the postfrontal is drawn out into a flat bony process which has a roughened ventral surface and which is applied to the dorsal surface of the prefrontal and parietal. Posteriorly, however, the postfrontal enters into a very precise union with the squamosal. The lateral ramus of the squamosal tapers to a rounded point and the postfrontal bears a dorsal groove for its reception, (fig. 15a). The lateral margin of the temporal vacuity, formed posteriorly by the lateral ramus of the squamosal, is thus continued without interruption by the postfrontal.

The descending process of the squamosal bifurcates into two spatulate flanges of bone which lie in the same plane, and which are set at an oblique angle to the

longitudinal axis of the skull. The leading and external edge of the anterior flange is grooved along its entire length, and this groove opens out dorsally into a prominent and horizontal recess. The leading edge of the quadrate slots into this vertical groove, and its dorsal edge locates in the horizontal recess.

It has been noted above that the true position of the two halves of the palate could not be ascertained until the skull reconstruction had been completed, and all that remains now is the completion of the circumorbital series. The stapes and otic elements must also be oriented, but these have no bearing on the relationships of the palate.

4. *The reconstruction of the circumorbital series, and the relationships of the quadrato-jugal (figs 36 and 37, plate 7e)*

The orbit is formed by the pre- and postfrontals dorsally, the lachrymal anteriorly, the jugal ventrally, and the postorbital posteriorly. The maxilla also participates,

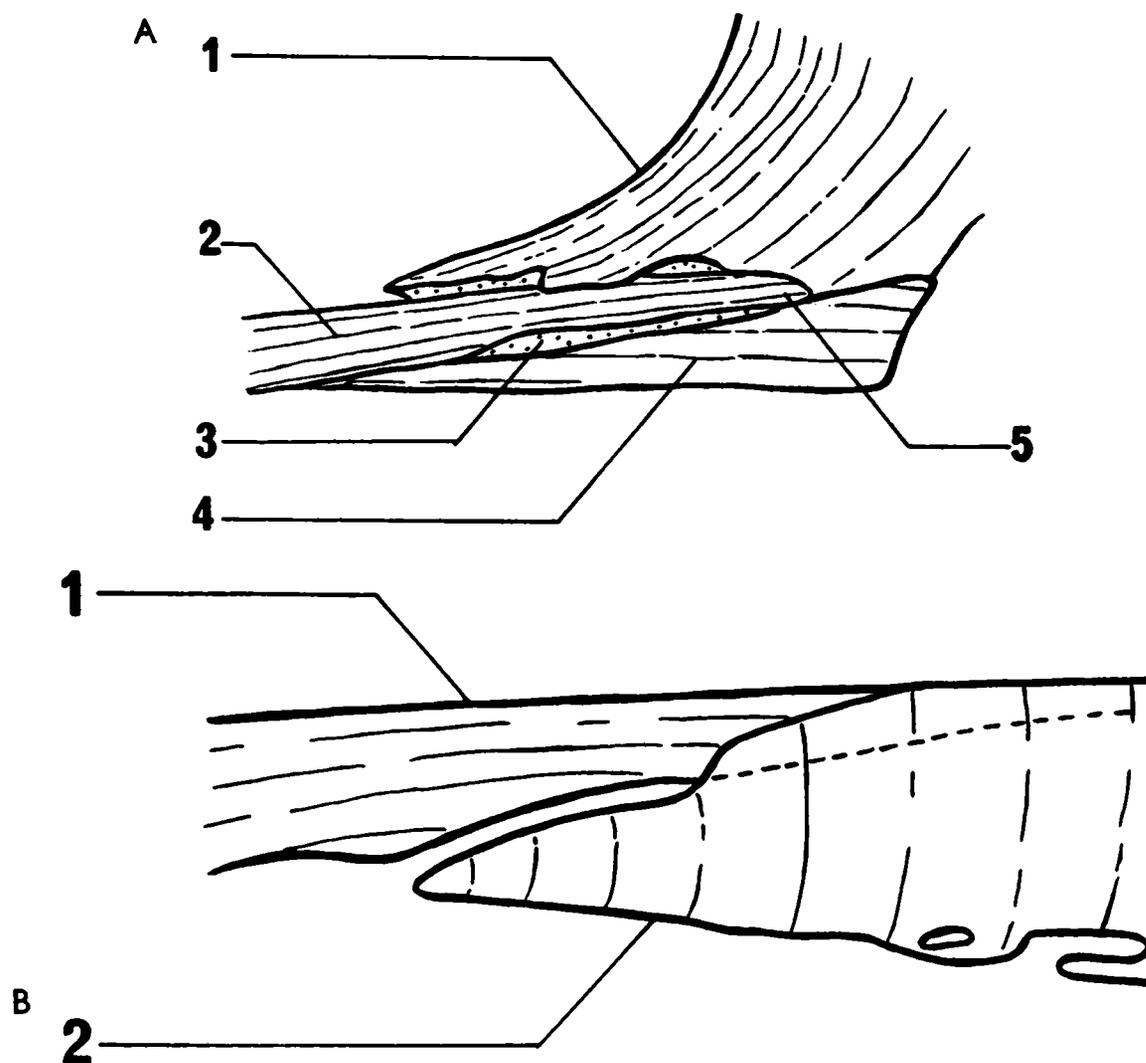


FIG. 36. (a). Antero-ventral corner of the orbit showing the relationship between the jugal, lachrymal and maxilla. External lateral view. 1, orbital margin of lachrymal. 2, jugal. 3, groove in maxilla for reception of the jugal. 4, external surface of maxilla. 5, anterior tip of jugal. (b). Antero-ventral corner of the orbit showing the relationship between the jugal, lachrymal and maxilla. Ventral view. 1, external margin of jugal. 2, medial margin of maxilla.

at its place of union with the jugal and lachrymal, but its contribution is very minor. The pre- and postfrontals are firmly united with the skull roof, the lachrymal is braced against the upper jaw margin, and the postorbital is braced against the quadrate through the quadratojugal.

The relationship between the lachrymal and the prefrontal cannot be known with absolute certainty because there is a degree of distortion in this region, and because it is not altogether clear whether the lachrymal is complete; the prefrontal is certainly incomplete. The lachrymal is an L-shaped bone whose inner margin is quite smooth and rounded, forming the anterior corner of the orbit. Anteriorly, and also ventrally, the thickness of the bone diminishes and two plates of bone are formed, one vertical the other horizontal. Dorsally the vertical plate overlaps a descending arm of the prefrontal, and the tessellate margin of the lachrymal interdigitates with the rugosities of its external surface. The circumorbital margins of the lachrymal and prefrontal meet in an oblique union which increases their area of contact giving greater strength. Ventrally the lachrymal enters into a complex union with the maxilla and jugal (Fig. 36a).

The dorsal surface of the maxilla is much fluted, with one particularly prominent bony lamella, which, diminishing in height posteriorly, is reduced to a low ridge. The ventral plate or keel of the lachrymal rests in the outermost groove of the dorsal maxillary surface, braced medially against the bony lamella. This lamella is S-shaped when viewed from above and the internal surface of the lachrymal follows its contours closely. Continuous with this same groove is a deep excavation which receives the anterior portion of the jugal. The lachrymal participates in the jugal articulation, for midway along its external ventral surface it bears a shallow depression for reception of the tip of the jugal, and posteriorly there is a ridge which forms the dorsal border of the maxillary groove. The anterior portion of the jugal has a triangular cross section, the apex being directed medially, and this internal surface is scored by longitudinal striae, and its contours conform closely with the maxillary excavation into which it fits. The jaw margin of the jugal meets the maxilla in an oblique union, (fig. 36b). Posteriorly the jugal articulates with the postorbital and appears also to have contact with the quadratojugal, though poor preservation makes interpretation a little difficult in this region.

The postorbital is a crescentic and laterally compressed element which is divided into two lamellae by a narrow but deep fissure which, commencing fairly high on the posterior margin, somewhat medially, traces a downward curving path to the ventral margin (fig. 16, plate 4a). Into the ventral portion of this fissure, where it is widest, slots the raised and tapered dorsal margin of the terminal portion of the jugal. The sharp leading edge of the quadratojugal slots into the posterior portion. Slotting greatly increases the area of contact conferring both strength and rigidity. Dorsally the postorbital makes contact with the postfrontal, completing the series, but since their areas of contact are badly damaged nothing can be said of their relationship.

Sloping postero-ventrally from its contact with the postorbital, the quadratojugal terminates in an elliptical cap which is applied to a low protuberance situated ventro-laterally on the quadrate, just above the articular surface. Enclosed by the

posterior edge of the quadratojugal and the external edge of the quadrate is a large oval foramen (see fig. 46). In the Lower Triassic thecodont, *Chasmatosaurus*, a similarly placed though much smaller foramen has been interpreted as marking the position of the tympanic membrane (Broili and Schroeder 1934). That this foramen may also have supported a tympanic membrane is rejected, largely on functional grounds (see p. 103).

5. *The adjustment of the palate and its true relationship with the rest of the skull* (figs 37 and 38, plates 7e and 8b)

Having completed the cranial reconstruction, save for the orientation of the otic elements, it should have been possible to adjust the position of the two halves of the palate satisfying all other points of contact between palate and the rest of the skull. Had there been no distortion in the cranial elements this would have been possible, but this was not the case and compromises had to be made, though these did not materially reduce the accuracy of the reconstruction.

The true position of the parasphenoid could not be established directly due to its incomplete nature but sufficient remained to allow a good approximation to be made by extrapolation. A short length of rod was attached to the ventral surface of

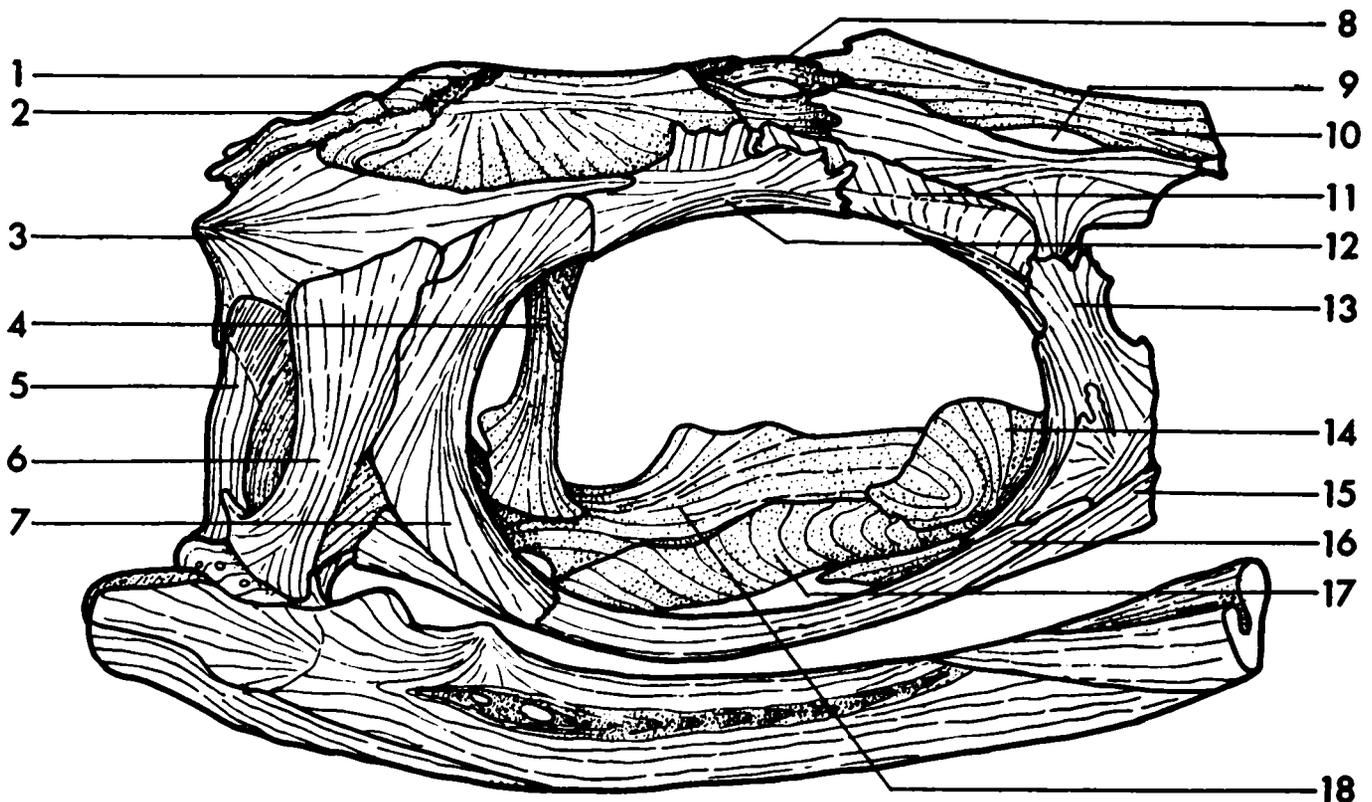


FIG. 37. Skull reconstruction, lateral view, $\times 1/2$ (R8177). 1, parietal ridge. 2, supra-occipital. 3, squamosal. 4, epipterygoid. 5, quadrate. 6, quadratojugal. 7, post-orbital. 8, frontal. 9, internasal foramen. 10, nasal. 11, prefrontal. 12, postfrontal. 13, lachrymal. 14, vomer. 15, maxilla. 16, jugal. 17, palatine. 18, pterygoid.

the parasphenoid, making sure that close contact was maintained along its length, and it was thus demonstrated that the element was situated just above the level of the medial edges of the pterygoids. This conclusion was confirmed by reference to Sollas' serial sections.

6. *The relationship between the otic elements and the rest of the skull*

The relationships between the otic elements and the hind end of the skull was a particularly problematic matter, and one which could only be resolved after the reconstruction of the membranous labyrinth. The main difficulty arises out of the fact that the otic capsule was incompletely ossified, and the three ossifications, (the opisthotic, proötic, and lateral margin of the supraoccipital) were united in cartilage

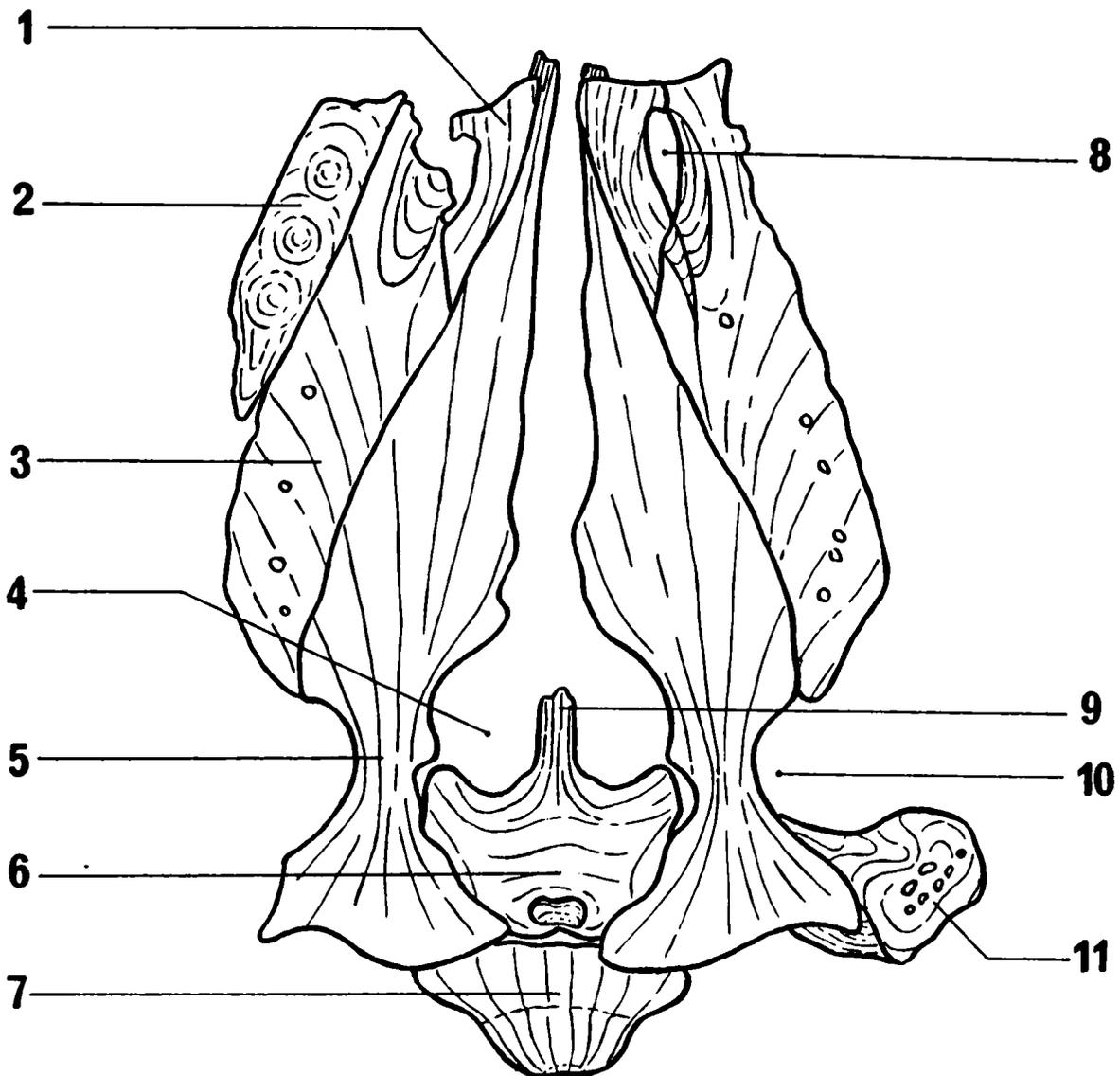


FIG. 38. Reconstruction of the palate, ventral view, articulated with the rest of the skull, $\times 1/2$ (R8177). 1, vomer. 2, maxilla. 3, palatine. 4, interpterygoid vacuity. 5, pterygoid. 6, basisphenoid. 7, basioccipital. 8, internal narial aperture. 9, parasphenoid. 10, intrapterygoid vacuity. 11, articular surface of quadrate.

with no direct contact between them. Fortunately the position of the supra-occipital is well known, so that at least one point on the otic capsule could be fixed. Furthermore the opisthotic has proximal contact with the basioccipital in a fairly well defined articular facet (though a pad of cartilage almost certainly intervened) and distally has a loose contact with the squamosal, providing a second point of reference. The proötic, however, has no contact with any other elements, and its position could only be established by reference to the reconstructed labyrinth.

Even though the stapes has contact with three other elements, the quadrate, opisthotic, and basioccipital, its interpretation has been made difficult by the imprecise nature of its articulations, and also by the intervention of cartilage.

Before postponing further discussion of the otic region until the labyrinth has been considered, it is necessary to consider further the relationships of the opisthotic.

The basioccipital facet of the opisthotic is a shallow triangular depression on the posterior surface, which faces postero-medially. Medial contact with the basioccipital is made, at about the level of the condyle, with the antero-lateral edge. The lateral margin of the basioccipital facet is curved, and slightly raised, and approximates to the curvature of the curved lateral edge of the basioccipital. The two edges do not come into direct contact and it is concluded that the opisthotic was separated from the basioccipital by a thin pad of cartilage. Dorso-ventrally the opisthotic terminates in a rounded paroccipital process which rests loosely in a depression in the squamosal. The surface of this process is quite smooth and has the appearance of an articular condyle (fig. 5).

The account of the cranial reconstruction would be incomplete without description of the snout and upper jaw, and in the absence of sufficient prepared material reference must be made to unprepared skulls and serial sections.

7. The reconstruction of the snout and upper jaw margin

The snout, in the context in which the term is used here, commences immediately in front of the orbit, and is formed from the paired nasals, lachrymals, maxillae and premaxillae, the last two mentioned forming the upper jaw margin.

The role of the maxilla in the formation of the upper jaw margin is subordinate to that of the premaxilla, which it meets anteriorly in an oblique suture. The free ventral margins of both elements are grooved for the reception of the teeth, and the groove is both wide and shallow. As the premaxilla encroaches upon the maxilla laterally, it also comes to overlies the nasal. Eventually the dorsal edges of the premaxillae meet in mid-dorsal line, closing over the top of the nasals and hiding them from view. The nasals, however, persist for a considerable distance beneath the premaxillae before finally tapering away.

The dorsal surface of the vomers and pterygoids, which posteriorly form the ventral floor of the snout cavity, are spongy, and each vomer is drawn out dorsally into a thin plate of bone, which, extending vertically into the cavity, bears resemblance to the mammalian turbinal bones.

The external narial aperture lies close to the anterior boundary of the orbit and is surrounded by the lachrymal, nasal, and premaxilla. In some individuals examined

the maxilla also participates, but is usually excluded by the union of the maxilla and premaxilla.

Attention will now be turned to the reconstruction of the soft anatomy. As mentioned above it was only after the membranous labyrinth had been reconstructed that the otic elements could be correctly oriented and the skull completed. Consequently the skull reconstruction will be referred to again after the description of the labyrinth.

A RECONSTRUCTION OF THE SOFT ANATOMY

1. *A reconstruction of the membranous labyrinth and its bearing on the orientation of the otic elements*

The correct interpretation of the ichthyosaurian otic region is a problem which has tormented authors past and present, and the key to its solution lies in the reconstruction of the membranous labyrinth.

That it is possible to reconstruct the membranous labyrinth is a reflection of its conservatism throughout the vertebrate series, and the following generalisations may be made.

1. The horizontal semicircular canal lies externally.
2. The ampulla of the horizontal semicircular canal lies in contact with, or close to, that of the anterior vertical semicircular canal.
3. The two vertical semicircular canals have a common origin, or originate close together and high up on the utriculus.
4. The origin of the horizontal semicircular canal lies below that of the two vertical semicircular canals.
5. The anterior and posterior vertical semicircular canals lie at right angles to one another.
6. The horizontal semicircular canal lies predominantly in the horizontal plane (De Beer; 1947).

By reference to these points a generalized labyrinth was modelled and used for comparison during the reconstruction of the ichthyosaurian labyrinth.

Latex casts were taken of the membranous labyrinth impressions of the proötic, opisthotic and supraoccipital and referred to the generalized labyrinth in order that they might be interpreted. The supraoccipital impression is relatively small, rather indeterminate, and also somewhat variable, so that the casts taken were of little value in the reconstruction. The most striking feature about the membranous impressions is that those of the semicircular canals are very wide so that there is barely any differentiation between them and the ampullae. When the otic elements of living reptiles are examined the semicircular canal impressions are found to be very narrow, and the impressions of the ampullae are very many times wider.

The interpretation of the membranous impressions. It is fortunate that the ossifications of the ichthyosaurian otic capsule occurred at points where the canals united with the utriculus, for each ossification conveys a maximum amount of information.

1. *Opisthotic.* In the discussion of the relationships of the otic elements it was pointed out that the relative position of the opisthotic is quite well known, and it lies with its membranous impression directed anteriorly, and therefore represents the hind-most portion of the otic capsule. The cast obtained is pear-shaped, with a side arm which curves outwards and downwards coming off about half way down its outer margin (fig. 39). There can be little doubt that this arm represents the horizontal semicircular canal, and it would seem that the apical portion represents the origin of the posterior semicircular canal, though it is quite possible that it merely represents the apical portion of the utriculus. Similar conclusions have been drawn elsewhere (Andrews 1910 Appleby 1956 for *Ophthalmosaurus*; Sollas 1918 for *Ichthyosaurus*).

2. *Proötic.* The proötic is invariably preserved with its longitudinal axis lying in the horizontal plane and the membranous impression facing inwards, a fact recorded for *Ophthalmosaurus* (Appleby, 1956) and also observed by the present author. Often it lodges between the ascending quadrate wing of the pterygoid and the basisphenoid. These observations have lead everyone to conclude this to be the natural position of the element, and Appleby 1956: 413, comments that while the proötic (of *Ophthalmosaurus*) may have been displaced after death, it is unlikely that it could have turned through an angle as great as a right angle.

The membranous impression of the proötic is ovoid, and has two channels set at right angles. Orientating the element according to Appleby, the horizontal channel is narrower than the vertical, (fig. 40), and is interpreted by Appleby as the horizontal semicircular canal, while the other is concluded to be that of the anterior vertical semicircular canal. Since there are two channels meeting in a right angle,

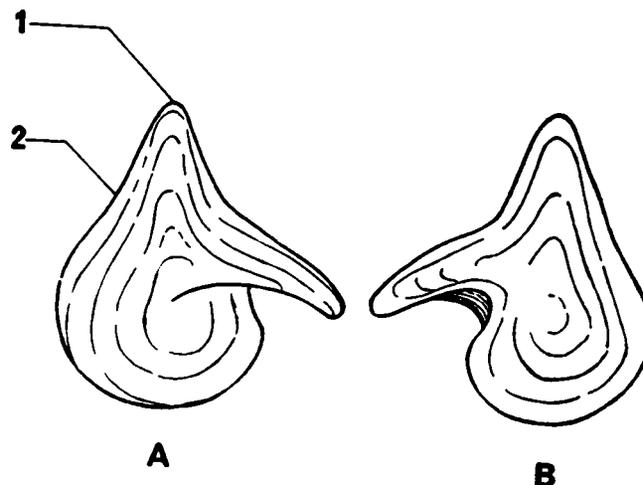


FIG. 39. Latex cast of the membranous impression of the opisthotic (right), $\times 2$ R1168. (A) Posterior view. (B) Anterior view. 1, apex. 2, medial margin.

and since some of the casts show evidence of an ampulla, it seems quite certain that the proötic does indeed mark the point at which the horizontal and the anterior vertical semicircular canals returned to the utriculus, but it was necessary to test the validity of Appleby's orientation.

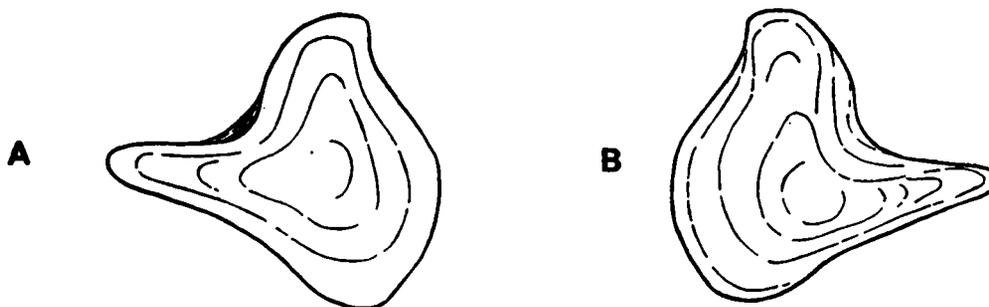


FIG. 40. Latex cast of the membranous impression of the proötic (right), $\times 2$ R1168. Oriented according to Appleby (1956). a, external view. b, internal view.

When a cast of the proötic impression is related with this orientation to the generalized labyrinth, it is found that there is no point of concurrency, and it is not difficult to see the reason why. The horizontal semicircular canal, arising from the utriculus caudally, passes in an external arc to meet the utriculus again anteriorly. Given that the proötic impression represents the anterior point of union of the horizontal semicircular canal with the utriculus, it *must* be orientated with one of its channels pointing caudally to receive it. Rotating the proötic through 90° satisfies this requirement, as shown in fig. 41. Nor is it even necessary to rotate the proötic through as large an angle as 90° , for it is quite probable that the horizontal canal joined the utriculus somewhat obliquely. Furthermore the argument that the proötic could not have rotated through as much as a right angle is really without

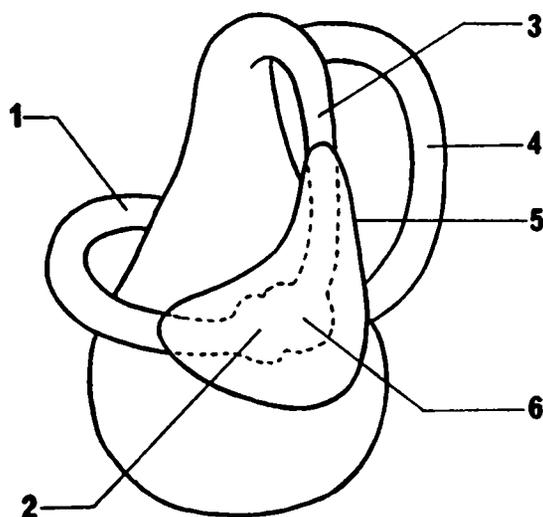


FIG. 41. Anterior view of a generalized membranous labyrinth (right), with the orientation of the proötic set at right angles to that proposed by Appleby. 1, horizontal semicircular canal. 2, ampulla of horizontal semicircular canal. 3, anterior vertical semicircular canal. 4, posterior vertical semicircular canal. 5, proötic. 6, ampulla of anterior vertical semicircular canal.

foundation. The shape of the proötic is such that it can rest on a flat surface in any of several positions, one of which approximates to that in which it is found. If a proötic element is orientated as described here, with the narrowest canal directed vertically, and attached with water-soluble wax to the inside of a beaker which is then filled with water, it will be observed to rotate as it sinks to the bottom. It is therefore concluded that the proötic impression represents the most anterior portion of the membranous labyrinth. The widest canal is that of the horizontal canal, the narrowest that of the anterior vertical semicircular canal.

The reconstruction of the labyrinth. Since the true shape of the membranous labyrinth can be deduced from only two impressions, the reconstruction of the whole organ is inherently speculative and inferences drawn from its structure correspondingly so. Inasmuch as the reconstructed labyrinth is used here primarily to establish the relationships between the three otic elements, where the relationships of two are already quite well defined, the degree of uncertainty is probably small.

Taking the latex casts of the proötic and opisthotic impressions, the remaining parts of the labyrinth were reconstructed in modelling wax by reference to the generalized pattern. Wax was used because it is one of the few materials to which latex adheres. The thickness of the three canals is known from their impressions in the bone, and some indication of the size of the utriculus is given by the opisthotic impression. Having produced a labyrinth conforming to these requirements, (fig. 42) the opisthotic and proötic were attached, and the whole structure was tentatively

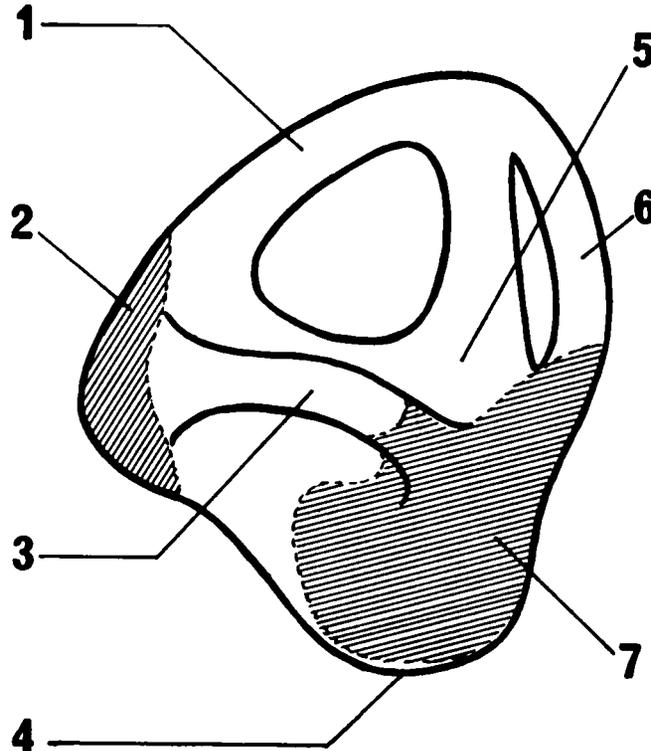


FIG. 42. Reconstruction of the membranous labyrinth, (left), external lateral view, $\times 2$ (based largely on Evans' nodule). Shaded areas represent latex impressions. 1, anterior vertical semicircular canal. 2, proötic impression. 3, horizontal semicircular canal. 4, saccular portion of labyrinth. 5, utricular portion of labyrinth. 6, posterior vertical semicircular canal. 7, opisthotic impression.

positioned at the back of the skull. The amount of space available for accommodation of the otic capsule is limited, and the nascent labyrinth had to be reduced in size in order that the capsule might fit. From the position of the supraoccipital relative to the rest of the otic capsule it was apparent that it must have roofed the labyrinth.

The otic impression in the supraoccipital is somewhat triangular, with its long side lying almost horizontally, and from its position it seems reasonable to conclude that it represents the point at which the two vertical canals took origin from the apex of the utriculus (fig. 43). In the largest ex-nodular specimen, R8177, the impression is relatively small and deep, and probably embraced the apical tip of the utriculus, the two vertical canals taking origin below this level. However, in R3375, a specimen of comparable size, the impression is like that of the smaller skulls. After a number of trials and modifications a satisfactory reconstruction was obtained (fig. 44).

The impression of the labyrinth in the opisthotic shows no indication of a constriction between a saccular and utricular portion, and the sacculus is apparently represented by the rounded ventral portion of the labyrinth. Ventrally this saccular portion lies above the stellate excavation of the basioccipital and it seems probable that this marks the position of a small lagena. A small depression lying just beneath the level of the main depression of the opisthotic probably also contributed.

2. *A reconstruction of the cartilaginous walls of the otic capsule*

The bone circumscribing the otic impressions of the three otic elements has the familiar indentation pattern indicative of a cartilage junction where it was continuous with the cartilaginous wall of the otic capsule, and the thickness of this wall can readily be determined. The wall was thickest in the supraoccipital region, and, reducing anteriorly and ventrally, was thinnest in the proötic. By joining the bony edges with thin sheets of Plasticine the cartilaginous walls were reconstructed, and the three otic elements were united with the exoccipital in a most satisfactory relationship (fig. 45). The longitudinal ridge of the leading edge of the exoccipital was clearly demonstrated to be continuous with the cartilaginous otic wall. Furthermore, the smooth dorsal surface which lies outside articular contact with the supraoccipital bears some evidence of a depression which corresponds to the course of the posterior vertical semicircular canal (fig. 44a). The internal curvature of the supraoccipital arch is continued by the internal wall of the otic capsule and forms the lateral wall of the chondrocranium. A cartilaginous pad of moderate thickness must have intervened between the opisthotic and basioccipital, and this was probably continuous with the cartilaginous posterior margin of the otic capsule, and perhaps also with the pad between the exoccipital and basioccipital. The successful reconstruction of the otic capsule is reciprocal confirmation of the validity of the labyrinth, and now that the otic elements had been oriented, the stapes could be put into position completing the cranial reconstruction.

The orientation of the stapes. The stapes is a fairly stout element which forms a strut between the otic capsule proximally and the quadrate distally. The opisthotic

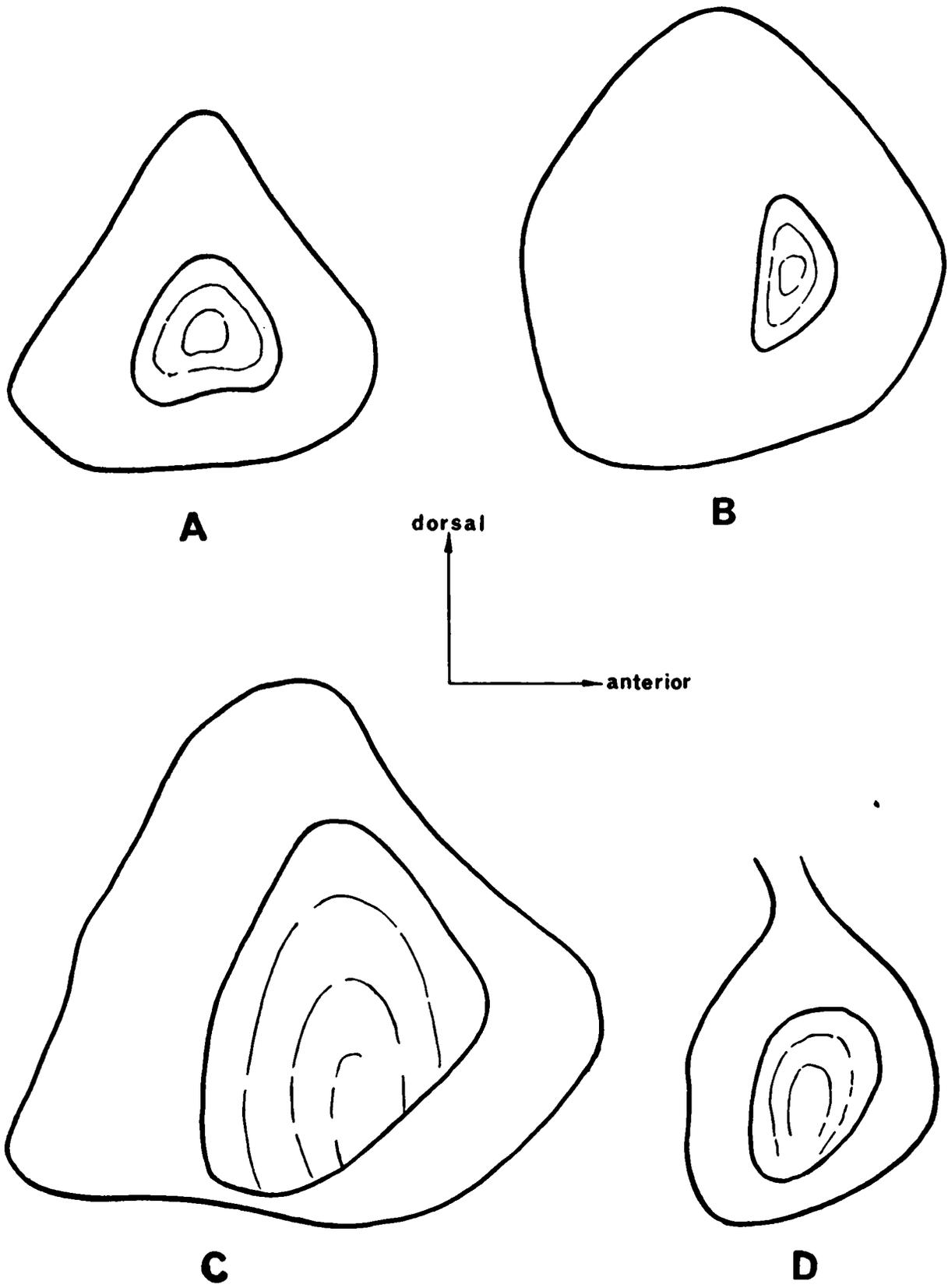


FIG. 43. Membranous impression of the supraoccipital in different specimens (external view, right side), all to same scale $\times 3$. a, Evans' nodule. b, R8177. c, R3375. d, R6697.

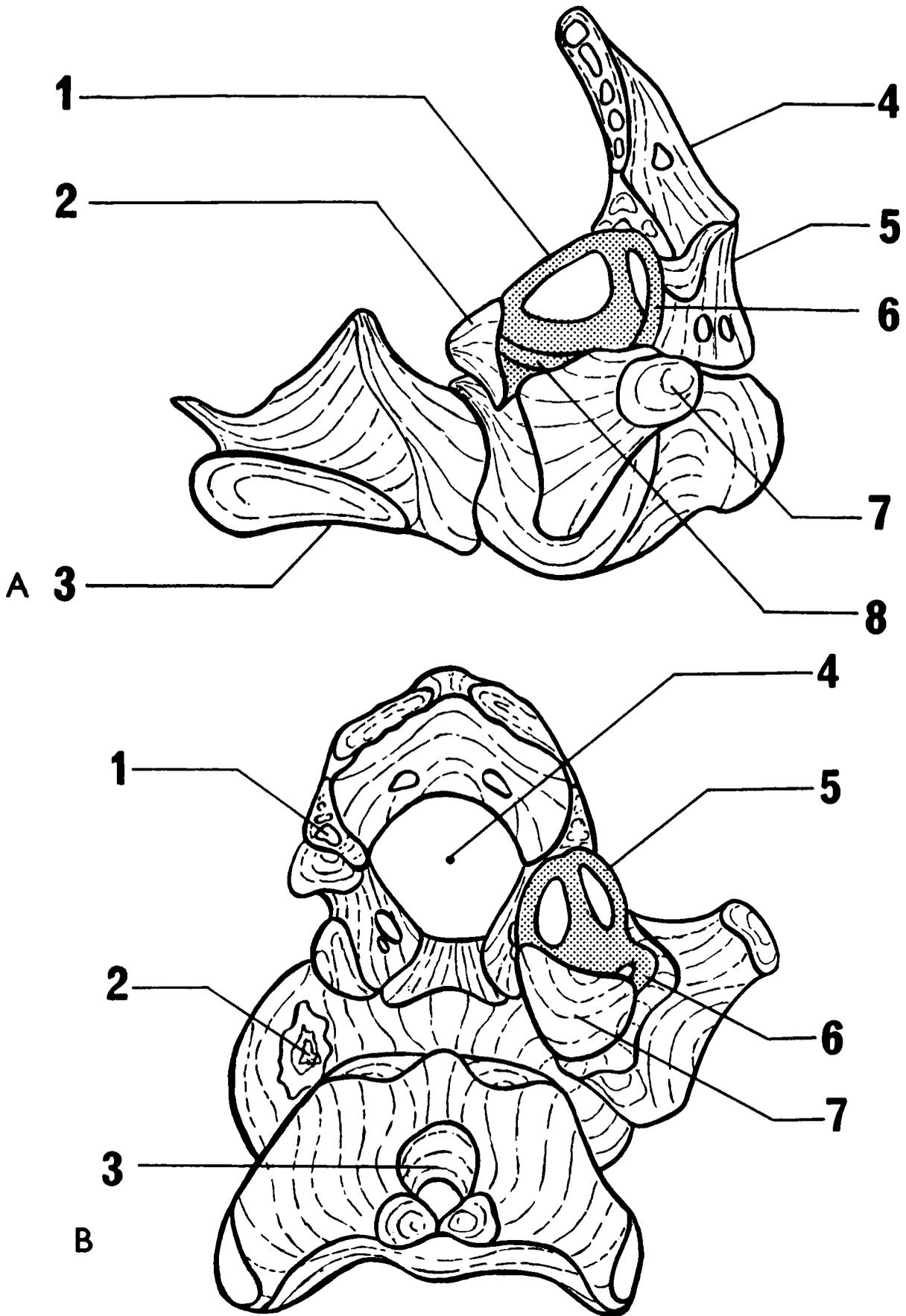


FIG. 44. (a). Reconstructed occiput with a reconstruction of the membranous labyrinth (left side), external lateral view $\times 1$ (Evans' nodule). 1, anterior vertical semicircular canal. 2, proötic. 3, basisphenoid. 4, supraoccipital. 5, exoccipital. 6, posterior vertical semicircular canal. 7, paroccipital process of opisthotic. 8, horizontal semicircular canal. (b). Reconstructed occiput with a reconstruction of the membranous labyrinth (left side), anterior view $\times 1$ (Evans' nodule). 1, membranous impression of supraoccipital. 2, stellate excavation of basioccipital. 3, carotid foramen. 4, foramen magnum. 5, posterior vertical semicircular canal. 6, horizontal semicircular

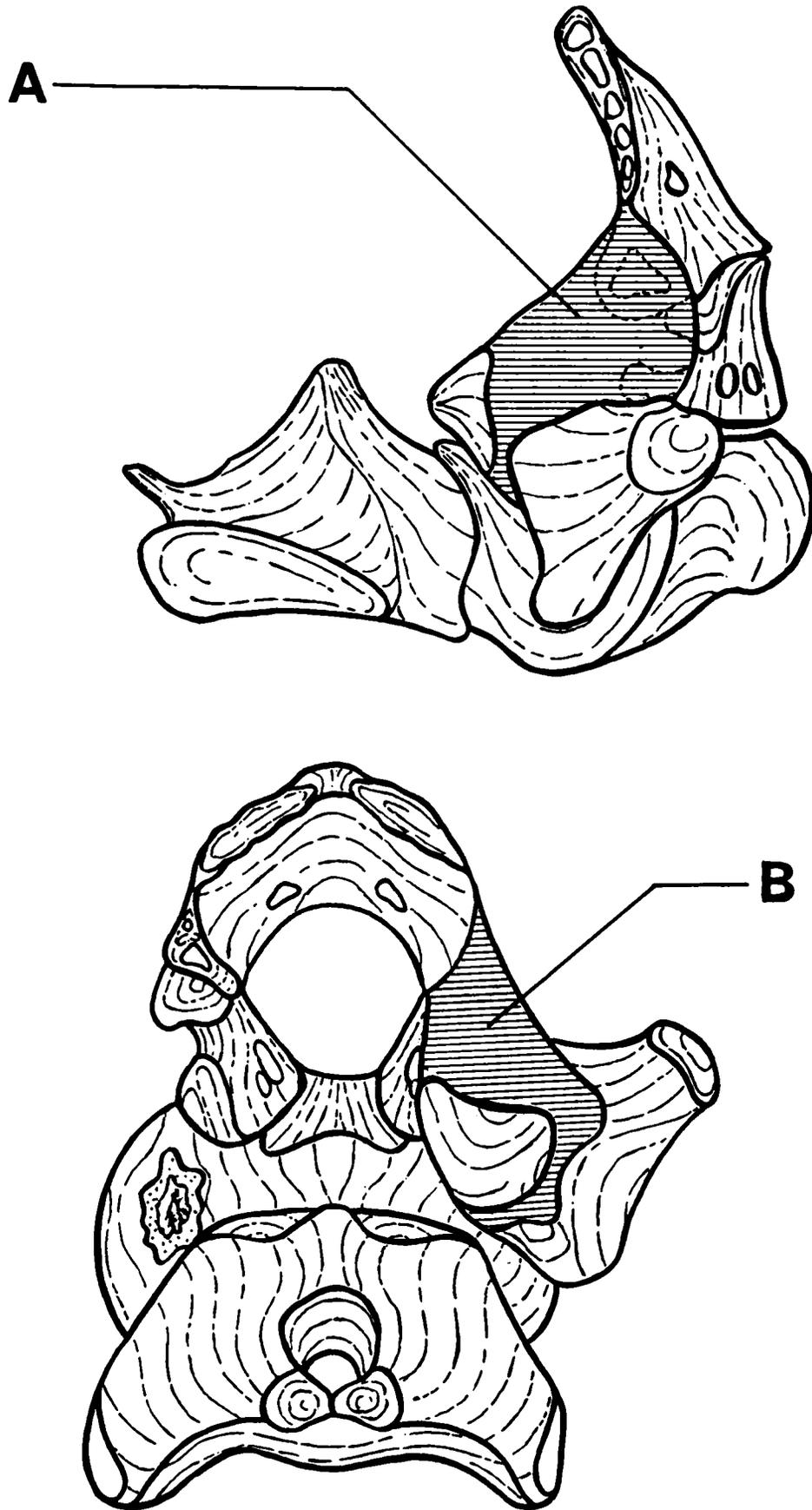


FIG. 45. (a). Reconstructed occiput with a reconstruction of the cartilaginous otic capsule (left side), external lateral view $\times 1$ (Evans' nodule). (A) Cartilaginous otic capsule. (b). Reconstructed occiput with a reconstruction of the cartilaginous otic capsule anterior view, $\times 1$ (Evans' nodule). (B) Cartilaginous otic capsule.

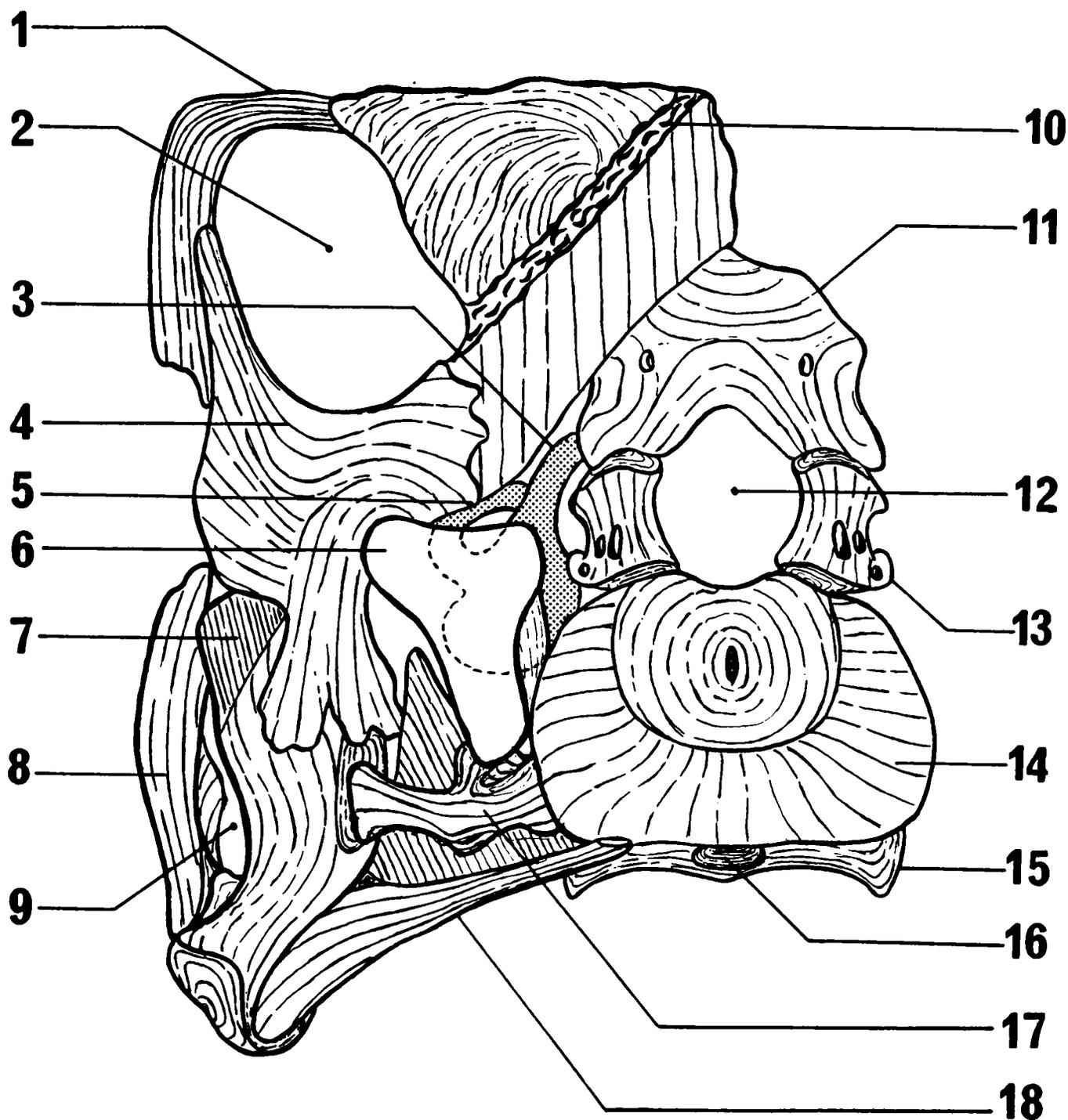


FIG. 46. Skull reconstruction, posterior view, with reconstructed membranous labyrinth, $\times 4/3$, based largely on R6697. 1, postfrontal. 2, temporal vacuity. 3, posterior vertical semicircular canal. 4, squamosal. 5, horizontal semicircular canal. 6, opisthotic. 7, quadrate. 8, quadratojugal. 9, oval foramen. 10, parietal ridge. 11, supraoccipital. 12, foramen magnum. 13, exoccipital. 14, basioccipital. 15, basisphenoid. 16, carotid foramen. 17, stapes. 18, medial wing of pterygoid.

facet on the postero-dorsal aspect of the head is but a shallow depression and it is therefore not possible to obtain a positive relationship between these two elements. There is a similar degree of freedom existing between the stapes and quadrate, and a pad of cartilage almost certainly intervened. No information is forthcoming from the relationship between the basioccipital and stapes because they make only touch contact, no evidence of articular surfaces being apparent. However, in most of the material examined there is a well marked groove for the stapedia artery and this has been a particularly important factor in arriving at a solution to the problem.

The stapedia artery is a branch of the carotid and passes through a notch or groove in the head of the stapes before gaining access to the endocranial cavity. The stapes therefore had to be oriented with the groove directed obliquely forward and inward. On the anterior face of the head, just below the level of the stapedia artery groove, there is, in smaller specimens, a concave facet which has been interpreted as that part of the footplate which inserted into the fenestra ovalis. This facet therefore has to be directed towards the saccular region of the reconstructed labyrinth thus offering another point of reference. There is no direct evidence of a fenestra ovalis since the otic capsule is not ossified in this region. Five reference points are therefore available for the orientation of the stapes, and although in each there is an amount of freedom, considered together they establish the position of the stapes with a good degree of confidence thus completing the skull (Fig. 46, plate 7d.)

Distally the stapedia shaft widens and terminates in an oval facet whose oblique face lies parallel with a depressed area on the postero-medial surface of the quadrate. As previously mentioned, direct contact with the quadrate does not seem to have been made and it seems quite certain that the stapedia shaft was continued in cartilage. The stapedia facet on the quadrate is wider than the distal facet of the stapes and the cartilaginous extension of the stapes was probably expanded to fill it.

Having completed the account of the membranous labyrinth and its implications, attention can be turned to a reconstruction of the brain and cranial nerves.

3. *A reconstruction of the brain and cranial nerves*

The brain

The fact that the reptilian brain (fig. 47) lies loosely within the cranium, not filling it to nearly the same extent as in the mammal, is well established and requires no further amplification here. It was therefore with caution, tempered with a degree of scepticism, that the possibility of reconstructing the brain was examined. Since the ichthyosaurian skull contained so much cartilage that the sides and much of the cranial floor cannot be reconstructed, it would not have been altogether unreasonable to dismiss the matter, but the fact remains that the skull roof bears four distinct encephalic impressions and these had to be interpreted (fig. 48).

There are a number of points of reference on the skull which permit the positions of the lobes of the brain to be established, hence the encephalic impressions of the skull roof could be interpreted. These points are listed below.

1. The posterior limit of the brain is marked dorsally by the supraoccipital arch,

laterally by the exoccipital foramen for the hypglossal nerve, and ventrally by the diverging portion of the median basioccipital excavation.

2. The position of the ventral flexure of the hindbrain is marked by the descending basioccipital peg and the ascending dorsal surface of the basisphenoid (fig. 44a, plate 7b).

3. The position of the junction between the fore- and midbrain is approximated dorsally by the pineal foramen, and ventrally by the sella turcica.

4. The proötic, being the most anterior part of the otic capsule, indicates the approximate level of the facial nerve (the otic capsule lies between facial and glosso-pharyngeal in all craniates), and hence the anterior limit of the hindbrain (fig. 44a).

5. The trigeminal nerve arises at a level which is posterior to that of the epipterygoid (the epipterygoid separates the profundus from the maxillary branch of the trigeminal), and, since the trigeminal takes origin from the anterior portion of the hind brain, it follows that the hindbrain must lie wholly behind the level of the epipterygoids.

6. The level of the external narial aperture approximately indicates the anterior limit of the brain.

The four encephalic impressions in the skull roof were clearly demonstrated by making a latex cast (fig. 49). The most prominent of these is formed by the parietals at the level of the epipterygoid process. This is not a single impression but is paired, and the two halves are formed by the two parietals, separated by a low ridge in the midline. The two impressions are ovoid, their longitudinal axes lying approximately parallel with that of the skull, and are deepest in front, becoming shallow caudally. The external lateral margin is formed in part by the medial surface of the epipterygoid process, and is continued posteriorly by a ridge which

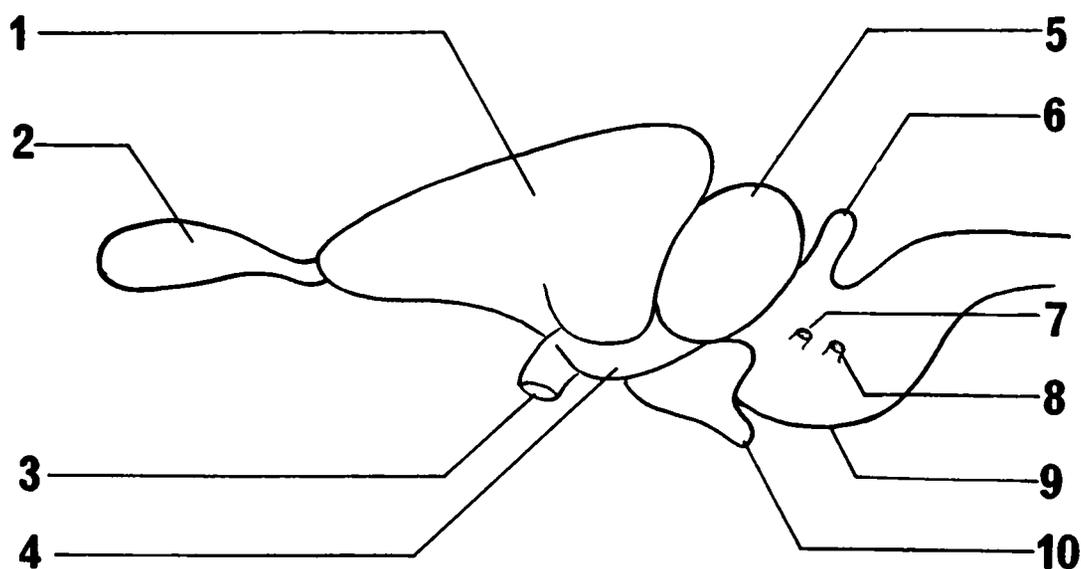


FIG. 47. Brain of *Lacerta* (left side), external lateral view. 1, cerebral hemisphere. 2, olfactory lobe. 3, optic nerve. 4, optic tracts. 5, optic lobe. 6, cerebellum. 7, 5th cranial nerve. 8, 7th cranial nerve. 9, medulla oblongata. 10, pituitary. (After Parker).

CRANIAL MORPHOLOGY OF

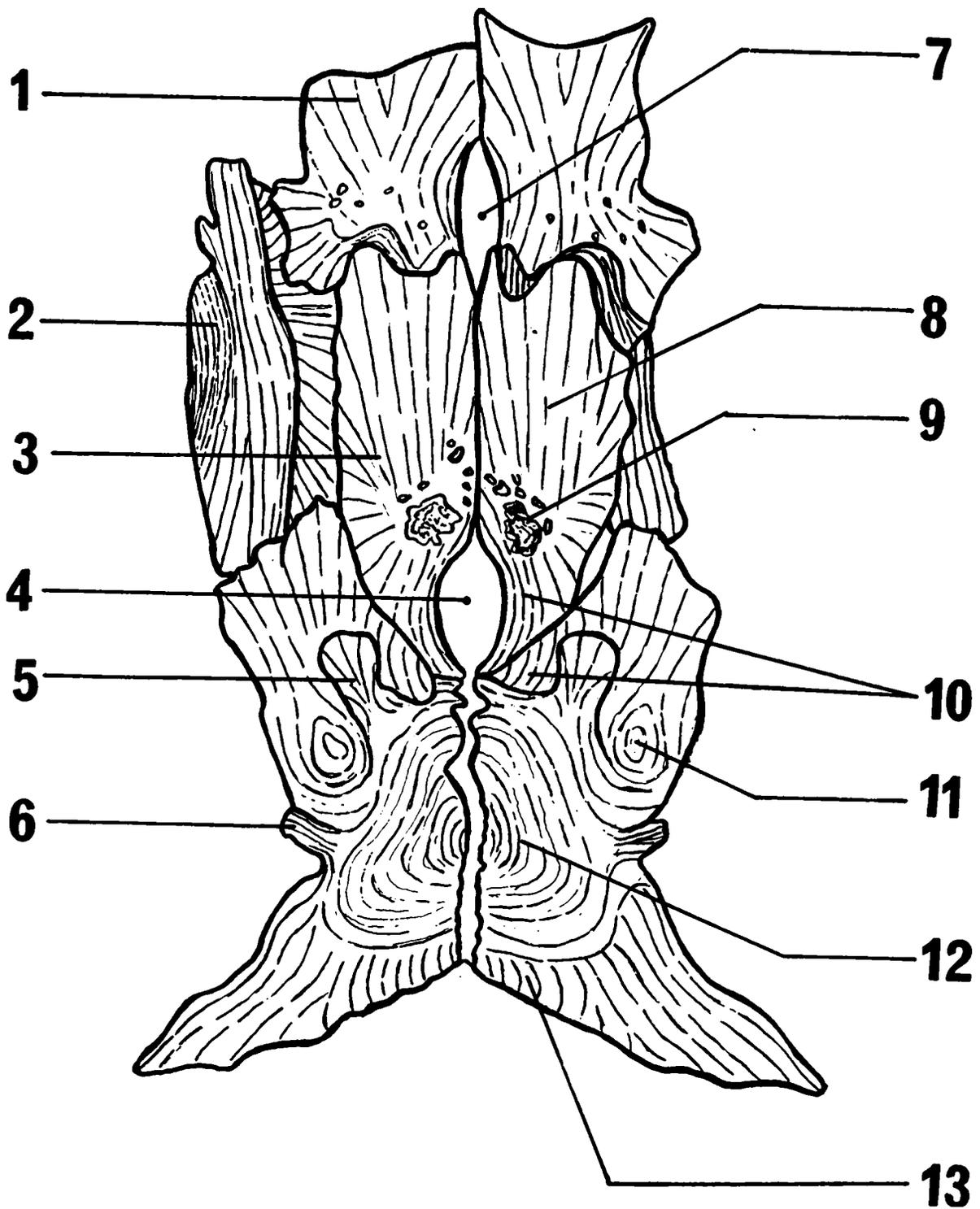


FIG. 48. Skull roof, ventral view, showing encephalic impressions, $\times 3/4$ (R8177).
 1, nasal. 2, prefrontal. 3, frontal. 4, pineal foramen. 5, descending parietal flange.
 6, epipterygoid process. 7, internasal foramen. 8, impression of olfactory lobe.
 9, foraminous area. 10, impression of cerebral hemisphere in frontal and parietal.
 11, extraencephalic depression. 12, impression of optic lobe. 13, impression of cerebellum.

then curves towards the midline to form the posterior margin. In front of the epipterygoid process the lateral margin is formed by a bony lip, which is also the external margin of a lateral extra-encephalic depression, and which is continuous with the external edge of the descending parietal flange. The anterior margin is marked by an almost straight and transverse ledge which is the ventral edge of a prominent bony buttress formed by the thickened leading edge of the parietals. The posterior margin lies close to the posterior edge of the parietals, but is separated by a narrow ledge of bone which bears evidence of a second and unpaired depression.

The second encephalic impression is very shallow and indistinct, but its presence was confirmed by the latex cast. When compared with a cast taken of the internal

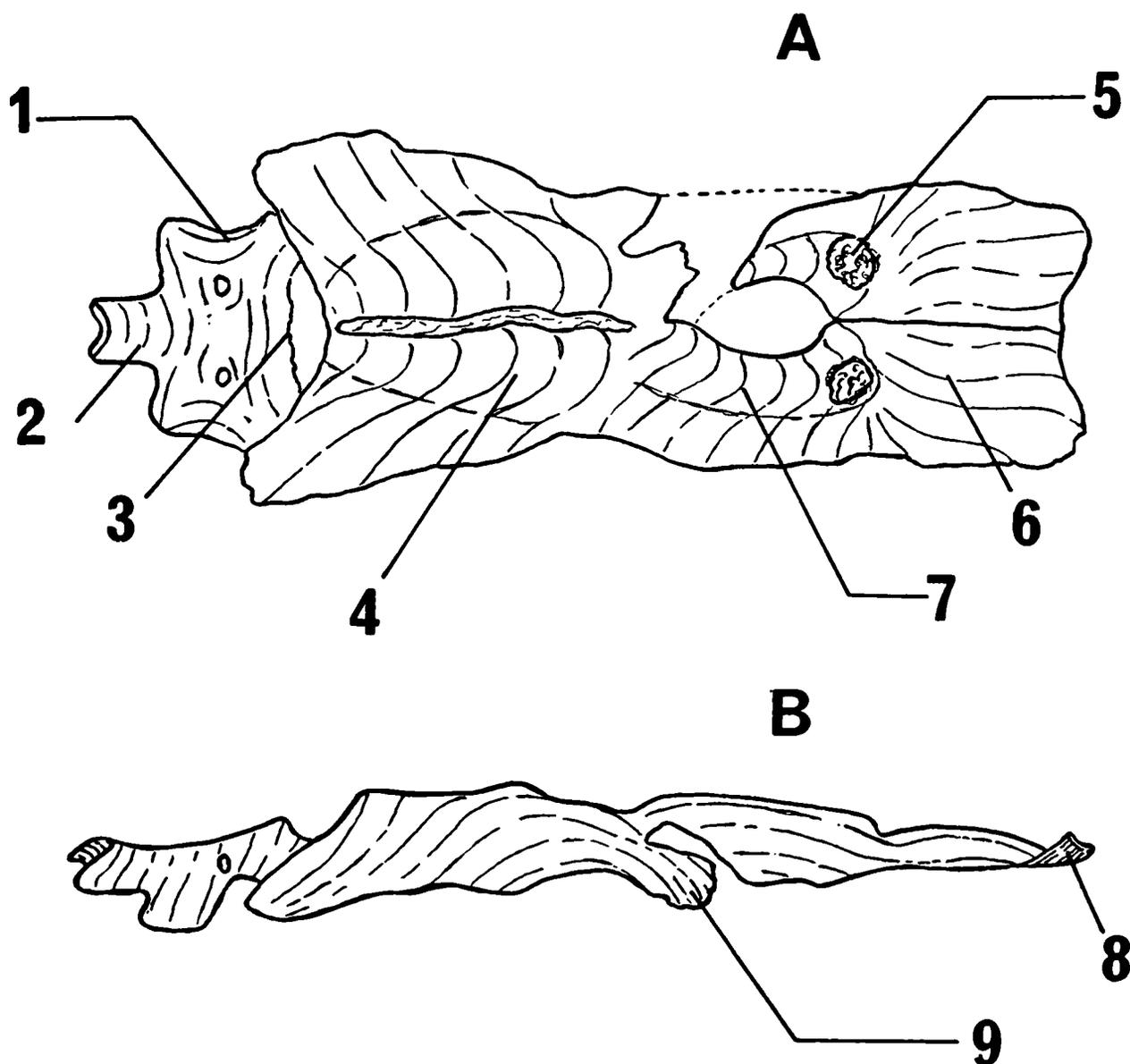


FIG. 49. Latex encephalic cast, $\times 3/4$ R8177. (A) Dorsal view. (B) Lateral view (right side). 1, cast of supraoccipital impression. 2, spinal cord. 3, cerebellum. 4, optic lobe. 5, foraminous area. 6, olfactory lobe. 7, cerebral hemisphere. 8, upturned thin leading edge of cast. 9, cast of descending parietal flange.

surface of the supraoccipital, similarities were found both in the overall width, and in the radius of curvature, and it was concluded that the two impressions embraced the same encephalic structure. Because of its posterior position, its continuity with the spinal cord, and its unpaired nature, there can be no doubt that this impression embraced the dorsal surface of the hindbrain, and from its position it must represent the cerebellum. By reptilian standards this was very large. However, it would be expected that the ichthyosaur, so highly adapted to the aquatic environment, would have a well developed cerebellum, and in this respect they compare with the cetaceans where the cerebellum is better developed than in other mammals (Slijper 1962). The ventral portion of the hindbrain rests in the depression formed by the descending basioccipital peg and the ascending dorsal surface of the basisphenoid (fig. 44). Caudally this depression is continuous with the median longitudinal channel of the dorsal basioccipital surface, which supported the spinal cord.

Having unequivocally established the position of the hindbrain it was concluded that the paired parietal depressions, which lie immediately anterior to that of the cerebellum, embraced the optic lobes of the midbrain. That these depressions might have embraced the cerebral hemisphere can be immediately dismissed because they lie too far back, and because there is anyway a second pair of depressions directly anterior to them (these lie largely in the frontals), which are interpreted as the cerebral hemisphere impressions. The optic lobes are the most prominent of the cerebral structures, a reflection of the large size of the eyes, and confirmation of the conclusion already reached that vision was the predominant sense. The descending parietal flanges no doubt gave mechanical support to the large optic lobes. The paired impressions of the cerebral hemispheres are jointly formed by the parietals and frontals, and between these two impressions is the pineal foramen.

The impression of the cerebral hemisphere is oval and of comparable length to that of the optic lobe, though narrower and more strongly arched. At the apex of each there is a rounded foraminous area of unknown significance. A similar area is found posteriorly, and is underlain ventrally by the proximal portion of the descending parietal flange. The pineal organ in ichthyosaurs is atypical in its posterior position, being flanked on either side by the cerebral hemispheres, and, judging by the large size of the foramen, it was probably photosensitive. The last of the cerebral impressions are a pair of shallow depressions which lie in the anterior half of the frontals and which are interpreted as roofing the olfactory lobes.

From the shallow nature of their impressions in the bone, it would seem a reasonable inference that the olfactory lobes were not extensive. Somewhat rectangular in outline, the impressions become shallower rostrally, finally flattening at a level just posterior to the external narial aperture (fig. 49b).

By reptilian standards the brain was extensive, and in specimen R8177 the brain had a length of about 13 cm which is about one-third of the skull length. The cerebral architecture was overshadowed by the prominence of the optic lobes, which probably accounted for almost half of the total volume. The cerebellum was very large, a condition which is indicative of a high level of locomotor integration. The cerebral hemispheres were relatively large and swollen, somewhat similar to the avian condition where the enlarged corpora striata are responsible for their rotundity.

The corpus striatum is the seat of innate behavioural activity and it seems reasonable to conclude that the ichthyosaur possessed a wide spectrum of instinctive behavioural patterns.

From observations of specimens in which the remains of unborn offspring are preserved it is clear that few were born at any one time and these were delivered from the cloaca tail first. The birth would certainly have been attended by a considerable degree of parental care, and may also have been accompanied by displays of social co-operation by other individuals. It is very probable that ichthyosaurs were gregarious and some evidence for this is available from Germany where aggregations of specimens have been found in some quarries. The gregarious habit is associated with co-operative behaviour which is further evidence of cerebral activity at a high centre.

The olfactory lobes were relatively small and the significance of this is discussed below (see section titled—*Olfaction*).

The cranial nerves. Little is known of the cranial nerves since only four nerve foramina are preserved in bone, all of which pierce the exoccipital (fig. 3, plate 1c).

Since the exoccipital is the most posterior portion of the cranial wall its posterior foramen is concluded to be that for the exit of the hypoglossal nerve. Immediately anterior to this is a second foramen of comparable size which was for the exit of a second branch of the hypoglossal, or for the exit of the spinal accessory, or a branch of the vagus nerve. Since the spinal accessory is usually a relatively small nerve and usually passes out with the vagus by way of the jugular foramen (Romer 1956), the first possibility is the least likely. Furthermore, since the bone passages of the two posterior foramina tend to converge medially it seems reasonable that they conducted a pair of nerves whose origins were in close proximity, and it is therefore concluded that the second foramen conducted another branch of the hypoglossal.

The largest of the foramina, the jugular foramen, is not completely circumscribed in bone. In addition to transmitting the internal jugular vein, the jugular foramen served for the passage of the vagus nerve, probably the glossopharyngeal, and perhaps also the spinal accessory. Just beneath the jugular foramen is the last and smallest of the nerve foramina which might well have conducted the spinal accessory nerve.

4. *A reconstruction of the mandibular musculature*

The mandibular muscles have been classified by Luther (1914) according to their function and position relative to the trigeminal nerve. Three groups of mandibular muscles have been recognized; the adductor mandibulae group which serve to close the jaws, the constrictor dorsalis group which is developed in kinetic skulls for the purpose of elevating and moving the maxillary segment relative to the occipital segment, and the constrictor ventralis group which, passing between the mandibular rami, aids swallowing and respiratory movements (see also Edgeworth, 1935). The reptilian abductor muscle, the *M. depressor mandibularis*, which opens the jaws is innervated by cranial nerve 7 and belongs to the hyoidean branchial muscle division, but for convenience it will be discussed here.

The reconstruction of the mandibular musculature in fossil forms is beset with problems because of the difficulties in recognizing muscle attachment areas and

because of the variations from one species to another. The problem is further aggravated in the Ichthyosauria by the complete absence of knowledge of the trigeminal nerve. Since the adductor muscles are identified according to their positions relative to this nerve, the present reconstruction cannot claim to be anything more than a tentative solution of the problem.

The mandibular rami do not bear any obvious muscle scars of the constrictor ventralis group, nor is there evidence of muscles of the constrictor dorsalis division, so that the present account is restricted to the adductor mandibulae group.

The adductor mandibulae group. The adductor mandibulae group is divisible into three parts according to position relative to the trigeminal nerve.

1. The *M. adductor mandibulae externus* division which lies between the maxillary and mandibular branches of the trigeminal, and which is in turn subdivided into three:

- a. *M. adductor mandibulae externus superficialis*
- b. *M. adductor mandibulae externus medialis*
- c. *M. adductor mandibulae externus profundus*

2. The *M. adductor mandibulae internus* division lies medial to the maxillary branch of the trigeminal nerve, and has two components:

- a. *M. adductor mandibulae internus pseudotemporalis*
- b. *M. adductor mandibulae internus pterygoideus*

3. The *M. adductor mandibulae posterior* division which lies medial and posterior to the mandibular branch of the trigeminal nerve, and which is usually not subdivided.

While the mandibular insertions of the adductor muscles are usually prominent and well delimited, their cranial origins are less well defined and individual identities cannot be established.

The mandibular muscle insertion areas (fig. 25). Four insertion areas for the mandibular muscles can be discerned in the lower jaw. Anteriorly there is the coronoid process, a low swelling of the dorsal margin of the surangular which is finely marked by small pits and which has a triangular outline when viewed from above. Posteriorly and still on the surangular is the 2nd insertion, a triangular, dorso-medially inclined area, which is coarsely marked by denticulate processes, and which is produced rostrally into an antero-medially inclined and sharp crest. The third insertion is a depressed area on the external surangular surface which lies, for the most part, just posterior to the last mentioned insertion, and is largely retro-articular in position. Superficially it is sculptured by fine longitudinal striae which have a tendency to converge antero-ventrally. The fourth is the least well defined area and lies on the retroarticular surface of the angular and perhaps also on the terminal portion of the surangular where its boundaries with the previous mentioned insertion become indefinable. It is marked superficially by fine striations which become indistinct anteriorly. The floor of the Meckelian canal bears little evidence

of any muscle scars, but this is frequently the case for this particular insertion area and it was almost certainly a place of muscle attachment.

The identities of the muscle insertions outlined above were investigated by a comparison with extant reptiles, and the origins and insertions of the mandibular muscles in various reptiles is contained in Table 2.

TABLE 2
CRANIAL MUSCULATURE

A. MANDIBULAR MUSCULATURE

Three groups of mandibular muscles can be recognized:

Adductor Mandibulae Group *Constrictor Dorsalis Group* *Constrictor Ventralis Group*

Adductor Mandibulae Group

This group is divisible into three parts:

M. adductor mandibulae externus *M. adductor mandibulae internus* *M. adductor mandibulae posterior*

M. adductor mandibulae externus

This muscle is divisible into three parts:

<i>M. adductor mandibulae externus superficialis</i>	<i>M. adductor mandibulae externus medialis</i>	<i>M. adductor mandibulae externus profundus</i>
Typically originates from the inner surface of the ventral boundary of the upper temporal vacuity in diapsids, and passes ventrally, inserting on the lower jaw posterior to the level of the coronoid process.	Originates from and inserts into a similar place to that of the <i>superficialis</i> . In <i>Sphenodon</i> the origin is reduced and the major area of attachment is on the dorso-lateral surface of the braincase.	Originates from the lateral wall of the cranium on the squamosal. This is the deepest portion of the <i>externus</i> and fills much of the upper temporal vacuity and usually has a common area of insertion with the other parts.

M. adductor mandibulae internus

This muscle is divisible into two parts:

M. adductor mandibulae internus pseudotemporalis
This is frequently the largest of the temporal muscles in living reptiles and originates from the lateral surface of the cranium in the anterior portion of the upper temporal vacuity. Its area of insertion usually lies on the coronoid process.

M. adductor mandibulae internus pterygoideus
This muscle may have a double origin being divisible into a *pterygoideus dorsalis* and a *pterygoideus ventralis*. The *pterygoideus ventralis* takes origin from the posterior surface of the pterygoid ventral to the basipterygoid process, while the *pterygoideus dorsalis* originates from the maxilla. The insertion of the *pterygoideus* is quite constant in living reptiles and lies on the lateral and medial surfaces of the retroarticular process so that part of the muscle wraps around beneath the jaw ramus.

TABLE 2 (contd.)

M. adductor mandibulae posterior

This is a single muscle which typically originates from the anterior surface of the quadrate and inserts in the intramandibular fenestra.

Constrictor Dorsalis Group

This group is largely concerned with raising and moving the palatal region relative to the rest of the skull and is found in kinetic forms. Three divisions have been described, *M. protractor pterygoidei*, the *M. levator pterygoidei*, and the *M. levator bulbi*. The first two muscles are concerned with kinetic movements and are developed only in kinetic forms.

M. levator pterygoidei

In *Sphenodon* this muscle takes origin from the ventrolateral wall of the orbito-sphenoid, medial to the dorsal extremity of the epipterygoid. This is a narrow muscle which lies medial to, and runs parallel with, the epipterygoid shaft, inserting on the dorsal and medial part of the pterygoid and on the lower part of the medial surface of the epipterygoid.

M. protractor pterygoidei

In *Sphenodon* this muscle originates from the ventrolateral surface of the proötic and passes posteroventrally as a broad sheet which inserts on the dorsal margin of the quadrate process of the pterygoid. Ostrom (1962), has shown that the development of the *levator* and *protractor* muscles in *Sphenodon* varies from individual to individual.

M. levator bulbi

This is a very problematic muscle which is well developed in most living reptiles and which takes origin from the lateral cranial wall.

Constrictor Ventralis Group

This group is represented by the *M. mylohyoideus* which generally has the form of a superficial sheet of muscle between the lower jaw rami. The *M. mylohyoideus* is present in all living forms and is developed to a variable extent. In the crocodile it is a single sheet of muscle which extends from the posterior portion of the jaw to the symphysis, while in *Sphenodon* and certain lizards it is divided into two sheets, one anterior to the other.

B. BRANCHIAL MUSCULATURE

Included in this group is the abductor muscle which closes the jaws, *M. depressor mandibulae*. This is a conservative muscle which usually has its origin in the dorsal occipital region and inserts upon the rectoarticular process of the lower jaw.

From this it is concluded that the coronoid process is the insertion area of the *M. adductor internus pseudotemporalis*, and that the dorso-medially inclined insertion area was for the three parts of the *M. adductor mandibulae externus*.

The extensive retroarticular area on the external surface of the surangular was for the insertion of the depressor muscle, while the *M. adductor mandibulae internus pterygoideus* inserted on the retroarticular portion of the angular.

The slightly sunken insertion area of the depressor muscle is continued forward by a tapering furrow which extends to the posterior level of the coronoid process, and its ventral boundary is raised forming an oblique bony ledge (fig. 25a7). It is possible that part of the *M. adductor mandibulae externus* inserted into this ledge, though nothing more definite than this can be said at the present time. Having as far as possible interpreted the mandibular insertions it was necessary to establish the origins of the muscles.

The mandibular muscle origins (fig. 50)

1. *M. adductor mandibulae externus* (fig. 51a, b and c)

The outer rim of the temporal vacuity is formed by the lateral limb of the squamosal. On its inside surface is a low ridge which, commencing at the anterior tip, slopes slightly ventrally as it passes back almost to the posterior margin of the vacuity. Because of the convexity of the squamosal wall the dorsal lip of the vacuity lies medial to this ridge. It is thought that this ridge was the origin of the *superficialis* division, whilst the *medialis* division took origin from the dorsal lip of the vacuity. These two almost vertical sheets of muscle probably filled the lateral sector of the temporal vacuity, converging ventrally to insert on the surangular.

The *profundus* division is the deepest part of the *M. adductor mandibulae externus*, and typically lies medially, filling the posterior portion of the vacuity. The rugosity of the parietal ridge, which is continued on the squamosal, is taken to mark the origin of this muscle, (fig. 52c).

2. *M. adductor mandibulae internus* (fig. 51d and e)

The *pseudotemporalis* division is frequently the largest of the temporal muscles and fills the anterior portion of the vacuity. The dorsal surface of the parietal bears a shallow depression, which, commencing just in front of the parietal ridge, is continued forward up to the anterior edge. This is interpreted as the origin of the *pseudotemporalis* muscle. The antero-lateral corner of the parietal is roughened but it cannot be established whether this is due to poor preservation or whether this too formed part of the origin. The *M. adductor mandibulae internus pterygoideus* took its origin somewhere on the pterygoid, probably anterior to the basipterygoid region, but in the absence of very obvious muscle scars any further discussion would be speculative. In living reptiles the pterygoideus wraps around beneath the mandible to insert upon the external surface of the retroarticular process, and there seems no reason to doubt a similar course for this muscle in ichthyosaurs (fig. 51e).

3. *M. adductor mandibulae posterior* (fig. 5If)

In the typical reptilian condition this muscle originates from the anterior surface of the quadrate and inserts in the Meckelian canal, and this position is assumed for the ichthyosaurs. The anterior surface of the quadrate is hollowed and in some speci-

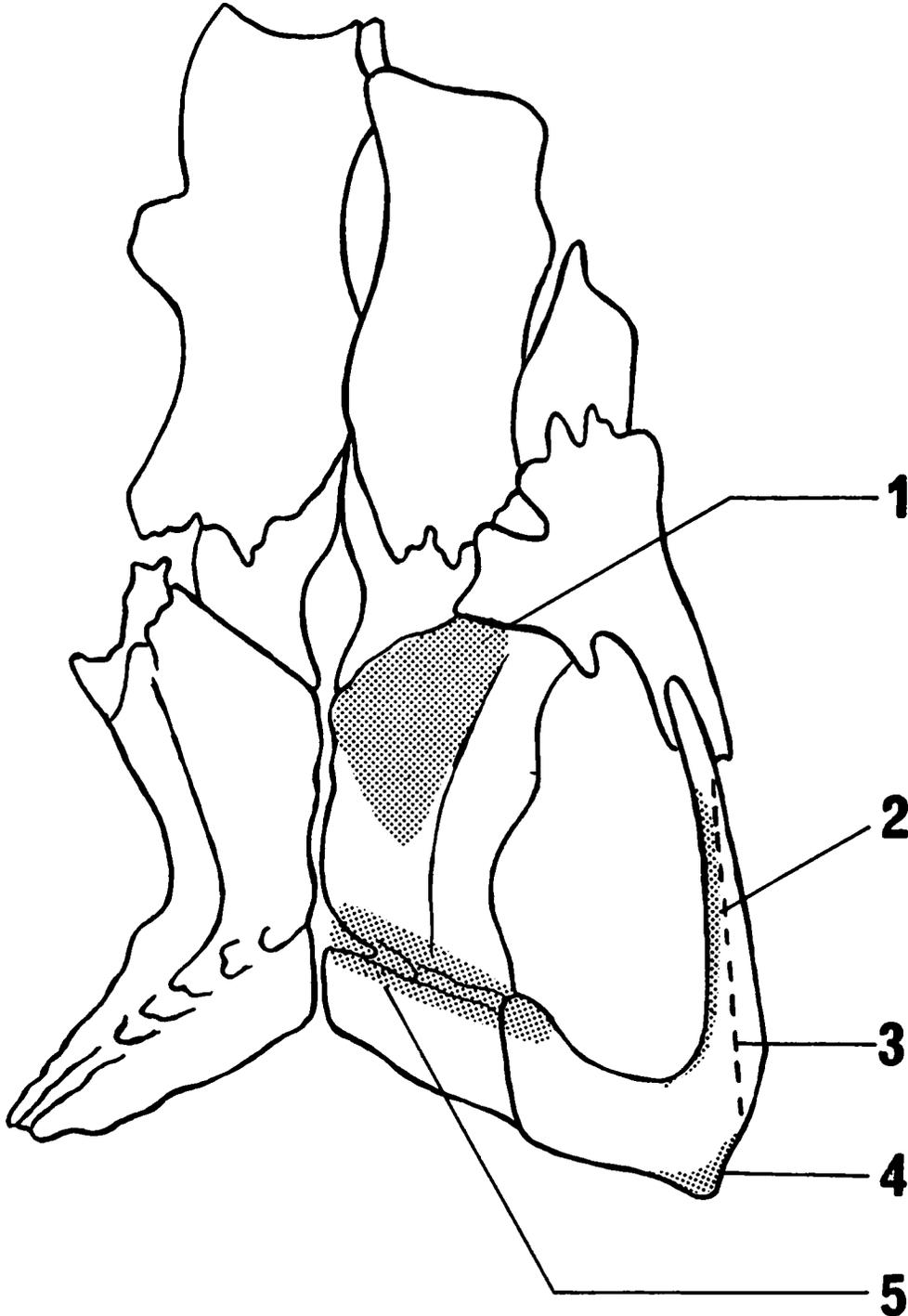


FIG. 50. Skull roof, dorsal view, showing approximate positions of the origins of the mandibular muscles, $\times 2/3$ (R8177). 1, origin of the *M. adductor mandibulae internus pseudotemporalis*. 2, origin of the *M. adductor mandibulae externus medialis*. 3, position of the origin of the *M. adductor mandibulae externus superficialis*. 4, origin of the *M. depressor mandibulae*. 5, origin of the *M. adductor mandibulae externus profundus*.

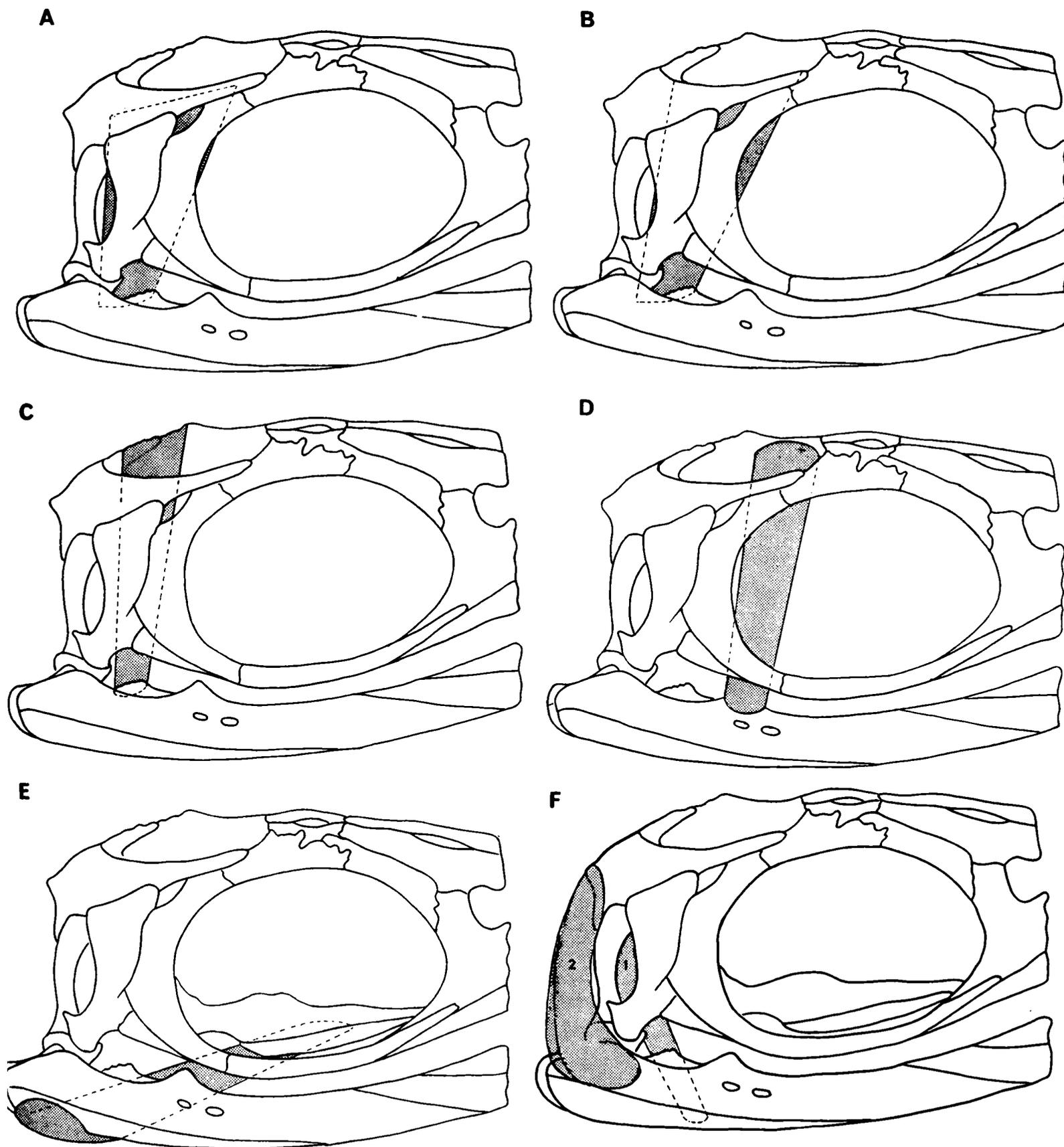


FIG. 51. (a). Lateral view of skull (R8177) with a reconstruction of the *M. adductor mandibulae externus superficialis* $\times 1/3$. (b). Lateral view of skull (R8177) with a reconstruction of the *M. adductor mandibulae externus medialis* $\times 1/3$. (c). Lateral view of skull (R8177) with a reconstruction of the *M. adductor mandibulae externus profundus* $\times 1/3$. (d). Lateral view of skull (R8177) with a reconstruction of the *M. adductor mandibulae internus pseudotemporalis* $\times 1/3$. (e). Lateral view of skull (R8177) with a reconstruction of the *M. adductor mandibulae internus pterygoideus* $\times 1/3$. (f). Lateral view of skull (R8177) with a reconstruction of 1, the *M. adductor mandibulae posterior*. 2, *M. depressor mandibulae*.

mens (R6697, R8177, Evans' nodule), there is a reticular area in the middle region towards the outer edge which may be the origin of the muscle (fig. 9a).

The abductor muscle (fig. 51f). The reptilian abductor muscle, the *M. depressor mandibulae*, belongs to the branchial group and usually takes origin from the dorsal occipital region to insert on the retroarticular process. The posterior surface of the squamosal is marked by striations which converge upon a backwardly directed bony protuberance, and this is believed to be the origin of the depressor muscle.

When the structure of the jaw was discussed it was noted that the largest muscle insertion area was on the external surface of the surangular (see fig. 25a) and that this has been interpreted as being that for the depressor muscle. When the jaw is articulated this insertion area is largely retroarticular in position. Quite frequently a backward prolongation of the angular is encountered which increases the extent of the retroarticular insertion area but unfortunately the terminal portion of the mandible is often damaged, as in the case of the available prepared material, and it cannot be known with certainty whether it is a constant feature.

FUNCTIONAL MORPHOLOGY AND PHYSIOLOGY

Jaw function

Before discussing jaw function it is necessary to define some mechanical terms in the context in which they are used here.

Moment arm = Perpendicular distance from the pivot to the line of action of the muscle.

$$\begin{aligned} \text{Mechanical advantage} &= \frac{\text{Distance from pivot to effort}}{\text{Distance from pivot to load}} \\ &= \frac{\text{Moment arm of muscle}}{\text{Distance from pivot to load}} \end{aligned}$$

$$\text{Velocity ratio} = \frac{\text{Distance through which load moves}}{\text{Distance through which effort moves}}$$

The load arbitrarily will be considered to be acting upon the jaw midway along the dental row, a procedure often followed in discussions of jaw function.

The ichthyosaurian jaw is relatively long and the adductor muscle insertion areas lie very close to the joint. The insertion of the *M. adductor mandibularis externus* lies closer to the pivot than that of the *M. adductor mandibularis internus pseudo-temporalis*, and the former muscle therefore has the smaller moment arm and mechanical advantage, but larger velocity ratio. The different mechanical characteristics of these two muscles may be evaluated. In specimen 49203 the jaw has a length of 48.5 cm and the distance from the centre of the articular surface of the articular to the middle of the dental row is 28.5 cm. Measuring between perpendiculars, the distance from the articular to the centre of the dorso-medial insertion area

of the *externus*, and to the centre of the coronoid insertion area of the *pseudotemporalis*, are 2.5 and 5.5 cm respectively, (fig. 52a). From this information the following may be evaluated:

$$\text{Moment arm of } \textit{externus} = 2.5$$

$$\text{Moment arm of } \textit{pseudotemporalis} = 5.5$$

$$\text{Mechanical advantage of } \textit{externus} = \frac{2.5}{28.5} = .088$$

$$\text{Mechanical advantage of } \textit{pseudotemporalis} = \frac{5.5}{28.5} = .193$$

$$\text{Velocity ratio of } \textit{externus} = \frac{L}{x} \text{ (Fig. 52b)}$$

$$\text{Velocity ratio of } \textit{pseudotemporalis} = \frac{L}{y}$$

$$x : y : L = 2.5 : 5.5 : 28.5$$

$$\frac{y}{x} = \frac{5.5}{2.5}, \frac{L}{x} = \frac{28.5}{2.5}$$

$$\text{If } x = 1, y = \frac{5.5}{2.5} = 2.2, L = \frac{28.5}{2.5} = 11.4$$

$$\text{Velocity ratio of } \textit{externus} = \frac{L}{x} = \frac{11.4}{1} = 11.4$$

$$\text{Velocity ratio of } \textit{pseudotemporalis} = \frac{L}{y} = \frac{11.4}{2.2} = 5.2$$

From this it can be seen that the mechanical advantage of the *externus* is about half that of the *pseudotemporalis*, while its velocity ratio is approximately double. It may be inferred that while the *externus* provided for rapid adduction, the *pseudotemporalis* contributed much of the power.

During contraction a muscle generally shortens by something like 1/5 to 1/3 of its length (see Smith & Savage, 1956). The lengths of the *externus* and *pseudotemporalis* muscles were similar, and in specimen 49203 were in the order of 9 cm. If these muscles shortened by, say, 1/5 of their length during contraction, the vertical movement brought about in the jaw at the level of the insertion would be about 2 cm. A movement of 2 cm in the *pseudotemporalis* would bring about a movement at the tip of the jaws of about 17 cm. When the abductor muscle is considered it will be seen that it could produce a gape at the tip in excess of 20 cm, and this estimate, like that for the *pseudotemporalis*, is conservative. Bearing in mind the short time taken for a muscle to contract it can be seen that the jaws could be snapped tight upon a suitable prey with great speed.

The line of action of the *M. adductor mandibularis posterior* laid at about 45° to the perpendicular and its insertion was not very far in front of the jaw joint, (fig. 52c). The mechanical advantage was therefore small and it is thought that this muscle contributed a relatively slow but powerful adductor force. This muscle may well have been extensive, filling much of the Meckelian fossa.

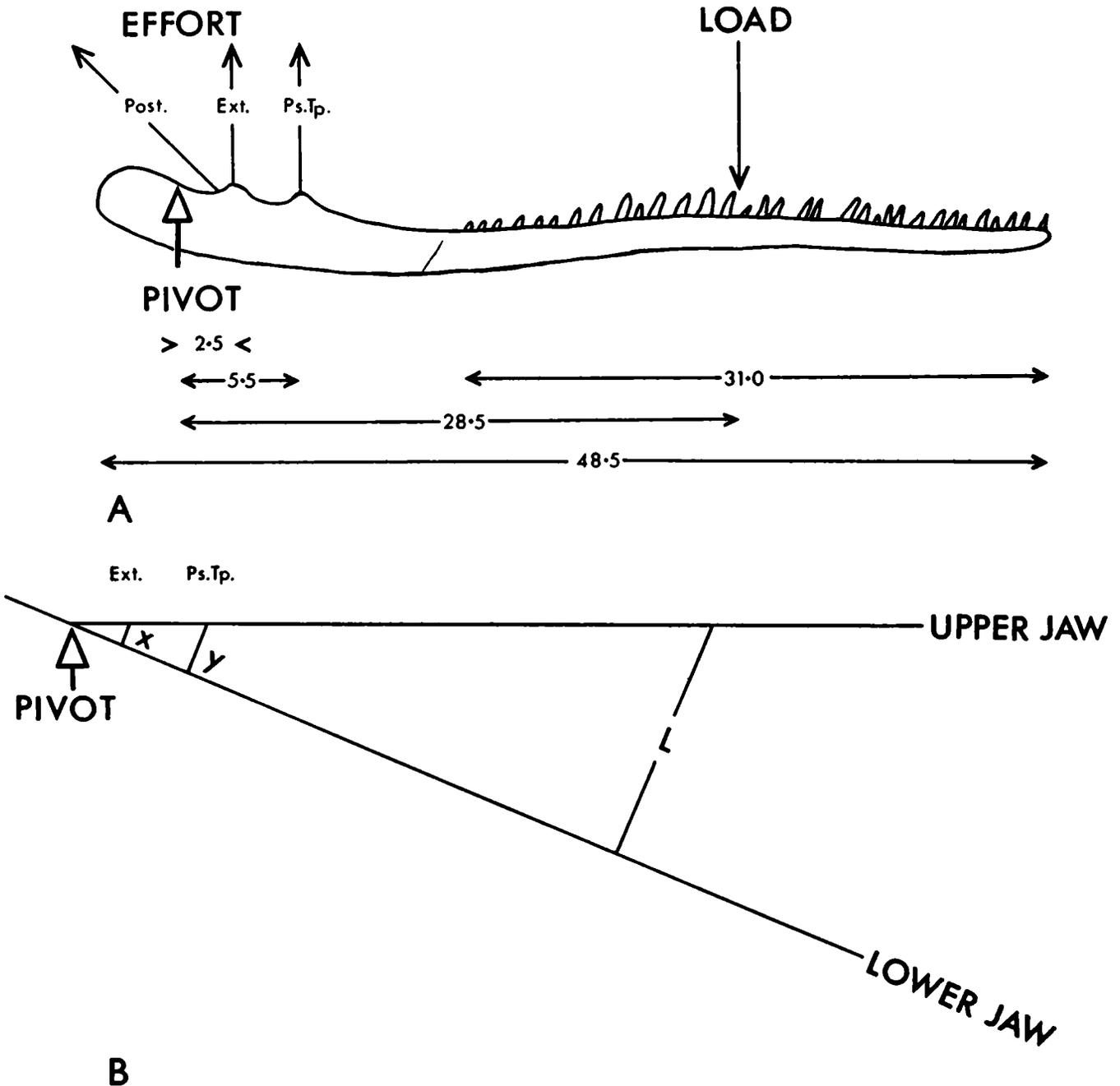


FIG. 52. Jaw mechanics, based upon data from specimen 49203. (a). Lower jaw (right side), lateral view, $\times \frac{1}{4}$. Post., effort produced by the *M. adductor mandibularis posterior*. Ext., effort produced by the *M. adductor mandibularis externus*. Ps. Tp., effort produced by the *M. adductor mandibularis internus pseudotemporalis*. (b). Diagram to show relationship between the distances moved through by the *externus* and *pseudotemporalis* muscles, and by the load. Ext., effort produced by the *M. adductor mandibularis externus*. Ps. Tp., effort produced by the *M. adductor mandibularis internus pseudotemporalis*. (c). Diagram to show the relative small size of the moment arm of the *M. adductor mandibularis posterior*. post., line of action of the *M. adductor mandibularis posterior*. M., moment arm of same. (d). Diagram to show the relative small size of the moment arm of the *pterygoideus* muscle. ptgys., line of action of the *M. adductor mandibularis internus pterygoideus*. M., moment arm of same. (e). Diagram to show the gape produced at the tip of the jaws when the retroarticular process is moved through a distance of 2 cm by the abductor muscle. Abd., line of action of the *M. depressor mandibularis*.

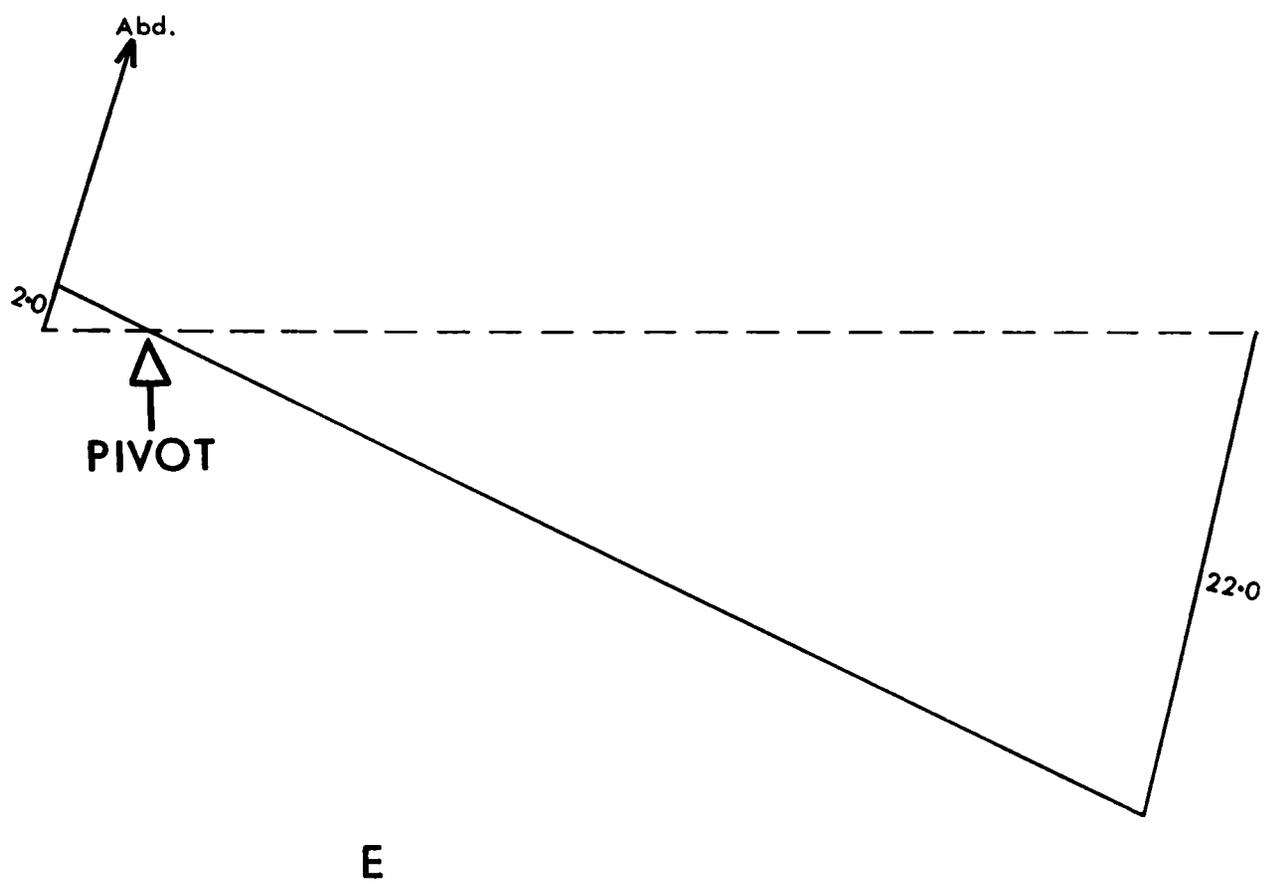
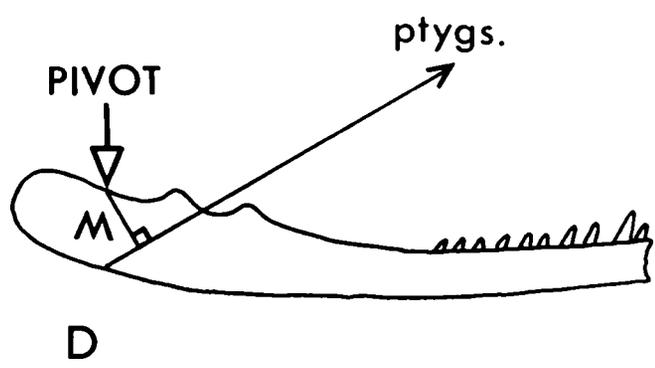
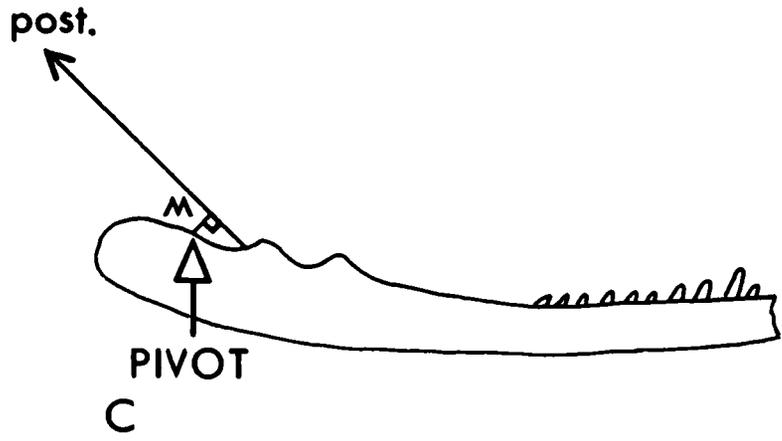


FIG. 52

The abductor muscle is somewhat longer than the adductors and in specimen 49203 was in the order of 12 cm. Again, if it is assumed that this muscle shortened by 1/5 its length during contraction, it can be seen that the vertical distance through which the retroarticular process would be moved would be about 2 cm. A movement of this magnitude would produce a gape at the tip of a little more than 22 cm., (fig. 52e).

The upper and lower jaw teeth interdigitate throughout the length of the jaw, as in the Crocodilia and Delphinoidea, and it is essential that there should be no lateral or anteroposterior jaw movements during adduction. Jaw freedom is eliminated in the crocodiles by the descending ectopterygoids, which function as jaw guides, while in the Delphinoidea it is accomplished by the presence of an extensive fibro-connective capsule (Purves, pers. comm.). There are no jaw guides in the ichthyosaurian skull, but the jaw joint is such that the forward and inward facing articular surface of the articular is braced anteriorly against the postero-laterally inclined articular surface of the quadrate. The only displacement permissible is therefore that of an oblique backward shift of the jaw, and this is prevented by the action of the *M. adductor mandibularis internus pterygoideus*. The origin of the *M. adductor mandibularis internus pterygoideus* lies well anterior to its insertion (see fig. 51e), and its line of action subtends an angle of about 30° to the long axis of the jaw. The moment arm of this muscle is therefore short (fig. 52d) and it follows that its mechanical advantage is small. The main function of this muscle was one of pulling the jaw tightly inwards and forwards against the articular surface of the quadrate and it probably contributed but little to the adduction of the jaw. Since the origins of the other adductor muscles were medial and anterior to their insertions, it follows that they also tended to pull the jaw forwards and inwards during adduction assisting the *pterygoideus* in its action. This relationship between the adductor muscles and the jaw joint, together, no doubt, with the presence of an extensive fibrous capsule, served to restrict jaw freedom to the biting plane.

The force exerted by the lower jaw when biting against the upper jaw decreases with distance from the joint, and most of the teeth in the ichthyosaur would have been ineffectual in biting and crushing. This is reflected in the generally slender and pointed form of the teeth, and in the lower jaw's lack of depth. During jaw adduction, which was very rapid, the velocity of the acuminate teeth would enable them to penetrate flesh with ease, especially towards the tip of the snout where the velocity of the teeth was highest. The ichthyosaurian jaw apparatus was therefore an efficient snapping mechanism for the apprehension of fish and other rapid-moving marine organisms.

PHYSIOLOGY

Feeding mechanism

The form of the lower jaw, its musculature, and its dentition, have all the attributes of an animal which fed upon active prey. While the teeth of the upper jaw margin slope posteriorly, those of the lower jaw are inclined forwards, and, when occluded, they interdigitate forming an efficient fish trap. The dentition and jaw proportions

are so much like those of *Delphinus* that a similar feeding mechanism is envisaged, but it cannot be concluded that fish alone were taken, and it will be shown below that cephalopods formed a large part of their diet.

In ichthyosaurs and dolphins the buccal cavity is narrow for much of its length, but widens posteriorly. The dolphin feeds by taking one fish at a time which is grasped by the head and swallowed lengthways. Fish of larger size than can be accommodated lengthways in the mouth are probably not taken, maximum size being determined by whether they can be swallowed whole. The teeth therefore serve in the first instance to grasp the fish, then to prevent its escape once within the buccal cavity, they are in no way masticatory. There is no indication of muscle scars on the medial surfaces of the jaw rami marking the position of the muscles of the *constrictor ventralis* group, but this does not necessarily mean that the muscle was not well developed. In many odontocetes these muscles are not well developed and swallowing is probably brought about largely by the tongue. The well developed hyoid arch of the ichthyosaurian skull indicates the possession of a well developed tongue important in swallowing and perhaps also in the manipulation of food.

A preliminary investigation by Pollard (1968) into ichthyosaurian gastric contents has revealed the presence of numerous dibranchiate cephalopod hooklets in a number of specimens, and the remains of fish of the genus *Pholidophorus* in certain others. Pollard examined about twenty specimens in all (pers. comm.), about fifteen of which had recognizable gastric contents. Of these, two possessed remains of *Pholidophorus* (J 13587 and J 13593, both in the Oxford University Museum; the latter also possesses a very sparse scattering of hooklets), while the others had dibranchiate hooklets only.

In addition to examining gastric contents Pollard has made an examination of Lower Liassic coprolites which on faunal, lithological, and chemical grounds he concludes to be identical to the ichthyosaurian gastric contents described by Buckland (1836). Fifty well preserved coprolites were examined from Buckland's Collection in the Oxford University Museum, and forty-five were found to contain recognizable fish remains, largely scales, fin rays, and spines of *Pholidophorus*, less commonly of *Lepidotus* and *Dapedium*. Two more contained reptilian bones, but none contained any visible remains of dibranchiate hooklets. Since hooklets are invariably present in ichthyosaurian gastric contents but absent in (presumed) ichthyosaurian coprolites, it must be concluded that either: (1) Ichthyosaurs had a mixed diet of fishes and cephalopods and that the undigested hooklets were retained in the stomach, or, (2) Some ichthyosaurs lived mainly on fish whilst others lived mainly on cephalopods and only the faeces of the piscivorous forms have been preserved. The latter alternative is most unlikely since there is no reason to suppose that faeces predominating in hooklets are less readily fossilised than those containing only fish remains. Furthermore the presence of hooklets in gastric contents are not restricted to any one species but have been identified in three of the four latipinnate species, *I. conybeari*, *I. breviceps*, and *I. communis* (specimens 38523, 43006 and 36256 respectively). Specimen J13587, one of the two which have fish remains in the gastric contents, is identified as belonging to the

species *I. communis*, and it is therefore almost certain that latipinnate ichthyosaurs had a mixed diet comprising of both fishes and cephalopods. While fish scales and spines were egested, cephalopod hooklets were retained in the stomach. A similar circumstance is observed in living sperm whales where squid beaks and other hard parts are retained in the stomach, presumably to avoid damage to the more delicate lining of the intestine. The majority of piscine remains found in coprolites and gastric contents belong, as already noted, to *Pholidophorus*, which was of the order of size of a herring and one of the swiftest of Liassic fishes.

Fish and cephalopods were almost certainly located by sight, but the lack of a binocular vision would have made the judgement of distances difficult. Many of the Osteichthyes have large eyes and correspondingly large optic lobes, but very few have a binocular vision. To what extent a fish uses its eyes in the location of food is not known, but the olfactory organ and the lateral line system are of much significance, (Greenwood, pers. comm.). Perhaps olfaction was important to the ichthyosaur when closing in on its prey, and it has already been noted that olfaction was probably of some importance in the life of the individual. The ear may be dismissed as an organ of location (a discussion of the evidence is given below). Having closed in upon a suitable animal the body was sufficiently agile, and its reactions sufficiently swift, to follow any evasive movements and effect capture. Of cervical vertebrae only the axis and atlas were fused and the cervical count generally exceeds that of the Cetacea. In *I. communis* the mean cervical count is 10 and some individuals possess as many as 12 (specimen R12 in the B.M.N.H.). There were fewer cervicals in the short-snouted species *I. breviceps*, a count of 6 having been made for specimen R216 (B.M.N.H.). Although the 7 cervicals of the dolphin are fused, the head is capable of some degree of movement relative to the body and this is probably of some significance to them during apprehension, and in the manipulation of fish prior to swallowing. From this it may be concluded that the ichthyosaur certainly possessed a greater degree of head mobility than that seen in the dolphin. When the great length of the ichthyosaur's snout is considered it can be appreciated that a relatively small lateral movement of the head would cause the tip of the snout to swing through a considerable arc. In *Xiphias* the great lateral sweeps of the rostrum during hunting are effected, not by movements of the head relative to the body, but by movements of the whole body (Scott, pers. comm.), and there is no reason to suppose that the agile ichthyosaurian body could not similarly implement wide sweeps of the head. The ability to move the head rapidly from side to side has obvious advantages in the seizure of prey. Furthermore some degree of head mobility enables a fish which has been impaled on the teeth to be tossed into a suitable position for swallowing. While an ichthyosaur might have taken most of its fish lengthways so that they could immediately be swallowed, there would have been times when some manipulation would have been necessary. Cephalopods presumably would have needed a good deal of manipulation.

Kinesis

The skulls of many reptiles possess a degree of intra-cranial mobility which assists in the manipulation of captured prey, and in the reduction of stresses on the neuro-

cranium during jaw adduction. Intra-cranial mobility is best exemplified in the Lacertilia (see Robinson, 1967), where the general reduction in ossification has probably been a contributory factor, and at least four forms of mobility have been recognized.

The term kinesis has generally been applied to the mobility of the occipital segment (the cranium) with respect to the maxillary segment (the remainder of the skull). The axis of rotation of the occipital about the maxillary segment is termed the metakinetic axis and lies transversely, passing through the paroccipital process of the opisthotic on either side. The maxillary segment may be divided into two subunits which are moveable upon each other about a second axis, the mesokinetic axis, which is a transverse hinge between the frontals and parietals.

A third form of mobility is that of the quadrate relative to the rest of the skull, termed streptostyl. Skulls may be metakinetic without being streptostylic and vice versa. Lastly, each half of the palate may be capable of movement relative to the rest of the skull by its movement about the basipterygoid-pterygoid joint. Such movements enable the two halves of the palate to be raised and moved forward by the action of muscles of the constrictor dorsalis group (*M. levator pterygoidei* and *M. protractor pterygoidei* respectively), assisting in the retention of a struggling prey. An interesting condition is found in *Sphenodon* (Ostrom, 1962), where in some individuals both the *M. levator pterygoidei* and the *M. protractor pterygoidei* muscles are developed, while in others the muscles are not represented, and this is no doubt correlated with variations in diet.

The ichthyosaurian quadrate could not have been streptostylic because of the firm embrace of its head and much of its leading edge by the squamosal. The oblique slotting union between the parietals and the frontals also removes any possibility of there having been a hinge joint between these two elements. However, the possibility of the existence of mobility between the maxillary and occipital segments, and of mobility of the two halves of the palate relative to the rest of the skull cannot be so readily dismissed. The occipital segment has contact with the maxillary segment at four points:

1. Postero-dorsally between the supraoccipital and the parietal.
2. Postero-laterally between the paroccipital process of the opisthotic and the squamosal.
3. Postero-laterally between the distal facet of the stapes and the stapedia facet of the quadrate.
4. Vento-medially between the basipterygoid process of the basisphenoid and the articular facet of the pterygoid.

At none of these points is there fusion, but there is very good indication that the free margin of the supraoccipital was continued in cartilage which was in turn continuous with the dermal skull roof, and also that the stapes terminated in a pad of cartilage which lodged in the oval depression of the quadrate. The basipterygoid-pterygoid joint possesses a certain degree of freedom, however, and it is conceivable

that movement between the occipital and maxillary segments could have occurred at this point, but, in the light of the above, this now seems unlikely.

Since there is a degree of freedom in the articulation between the pterygoids and the occiput it is possible that the two halves of the palate were capable of movement relative to the rest of the skull. However in order that this could occur it would be necessary that fusion did not occur at any of the points of contact of the palate with the rest of the maxillary segment, and of these there are three:

1. Postero-medially between the quadrate wing of the pterygoid and the quadrate.
2. Laterally between the labial margin of the palatine and the medial margin of the maxilla.
3. Postero-dorsally between the foot of the epipterygoid and the groove for its reception on the pterygoid.

The contact surfaces of the quadrate and quadrate wing of the pterygoid are both quite smooth, but it is difficult to see how the pterygoid could have moved relative to the quadrate since its freedom is restricted by its contacts with the basisphenoid, basioccipital and with the squamosal. The palatine meets the maxilla in a well defined and carinate articulation which on initial inspection appears to be modified for movement. However the free edges of the two elements are emarginated, and these emarginations correspond with one another and almost certainly transmitted blood vessels. Clearly no movement between the two elements was permissible. The foot of the epipterygoid rests loosely within the groove on the pterygoid, and movement at this point would seem possible, but it is almost certain that the groove was filled with the cartilaginous vestiges of the palatoquadrate.

That there is no evidence of the origins of muscles of the constrictor dorsalis group is a reflection of the lack of ossification in the otic region, and not necessarily of their absence. The bony pterygoid flange which overhangs the basiptyergoid fossa has a rugose margin and could conceivably mark the insertion of the *M. levator pterygoidei*.

From the evidence available at present it is concluded that the ichthyosaurian skull was probably akinetic. While it is recognized that kinesis might have assisted in the manipulation of fish within the buccal cavity, it is noted that no such mechanism exists in dolphins.

External respiration

Before discussing external respiration it is necessary to consider very briefly the habits of ichthyosaurs since this has an important bearing upon the interpretation of the morphological evidence. Were they very active animals which spent most of their time submerged, like cetaceans, surfacing for only brief periods to respire, or were they more akin to their reptilian class in spending most of their time in relative inactivity, diving only periodically for food? This question cannot be answered until an extensive investigation of the post-cranial skeleton has been carried out, but at this stage it would seem that the latter possibility is probably closest to the truth. The main reason for arriving at this conclusion is that reptiles do not

possess a diaphragm and it seems unlikely that the ichthyosaurs were capable of the rapid ventilation seen in the Cetacea, or that they possessed comparable physiological adaptations. Furthermore, sustained activity is not a typically reptilian attribute.

From the general body proportions, (plate 9b), it seems likely that an ichthyosaur would float with much of its head beneath the surface. The external narial aperture is not placed very high on the skull, lying approximately at the level of the sclerotic aperture, and would probably not have been clear of the water. Even if the head were held largely above the surface, the turbulence caused by its forward progression would have resulted in the nares being awash for much of the time and they would almost certainly have been guarded by sphincters. The internal nares lie just posterior to the externals, and are more ventral in position, though above the level of the jaw margins. Whether the jaw margins formed a water-tight seal when the mouth was closed is not known, but there would certainly have been a pharyngeal valve at the back of the throat, as in the crocodiles, so that water could not pass from the buccal cavity to the lungs. It seems quite probable that the buccal cavity was water-tight and respiratory exchange could then be effected simply by raising the head and opening the narial sphincter and pharyngeal valve. If on the other hand the buccal cavity were awash while swimming on the surface, it would be necessary to allow the water to drain prior to ventilation. This procedure would be necessary anyway when returning to the surface after diving.

It is rather surprising to find that there was no development of a secondary palate, or any evolutionary tendency for the external nares to migrate to the top of the head, and it is tempting to assign a respiratory function to the median dorsal internasal vacuity which was described above [see footnote]. This aperture is surrounded by a depressed area of bone which could have housed a sphincter, and being high on the head it would always have been kept clear of the water. There may have been a direct air passage connecting this aperture with the pharynx. In life the intrapterygoid vacuity (fig. 38), would have been occupied by the mandibular muscles, but it is just conceivable that the interapterygoid vacuity, even if partly closed by membranes, could have functioned as an internal respiratory aperture (fig. 53). By raising the buccal floor against the buccal roof just in front of these openings, an air passage would be formed enabling respiration to occur with the mouth flooded. However, this is all quite speculative and it may be pointed out that if the internasal aperture were respiratory in function it would provide an unprecedented case of an old structure persisting side by side with a new structure of similar function.

It would be useful to establish the incidence of the internasal foramen in the Lower Liassic latipinnates, but this is not an easy matter. In the first place, because of its median dorsal position, it cannot be demonstrated in laterally exposed specimens and these constitute the majority of ichthyosaurian material. Furthermore, since the foramen lies at the bottom of a shallow depression it cannot be seen if there is any matrix in this region, so that it is almost always necessary to do some preparation on the specimen, which is often not possible. Of the skulls examined during this investigation (see Table 1), the internasal foramen was definitely observed in R8177 and R1168 and seems to have been present in 49203. The other three skulls were incomplete beyond the parietal region. The internasal foramen was present in the skull sectioned by Sollas, and is clearly seen in his sections numbered 359-349 (Sollas 1916 : Fig. 2 (9)).

It is concluded that ventilation probably occurred with the mouth closed and with the head momentarily raised so that the external nares cleared the water. The mouth may well have been water-tight so that ventilation would not always have to be preceded by draining water from the buccal cavity, though this would have been necessary when returning to the surface after a dive.

Olfaction

The olfactory organ of a marine animal is functional only in the detection of water-borne chemostimuli. The external narial aperture of crocodiles and cetaceans has direct communication with the lungs via the nasal canals, and must therefore be closed on submergence, under which conditions the olfactory sense is then lost. In the ichthyosaur, however, in the absence of a secondary palate, the external nares communicated directly with the buccal cavity, and there would be no premium placed upon keeping the external nares closed on diving. It is quite possible therefore that the nares opened on occasion in order to sample the water. Indeed the external nares may have remained open for much of the time so that the water could be continuously sampled.

It has already been noted in the descriptive section that the vomers were produced dorsally into thin bony lamellae which extended into the nasal passage like mammalian turbinal bones. Since the air over the sea is virtually devoid of particulate matter it is doubtful whether the lamellae supported a mucous-secreting epithelium for filtration, and it seems reasonable that a fairly extensive olfactory epithelium was present. The olfactory lobes of the brain were not particularly large, but were moderately well differentiated, and it would appear that olfaction, although very much subordinate to sight may have been of some significance in the life of the individual.

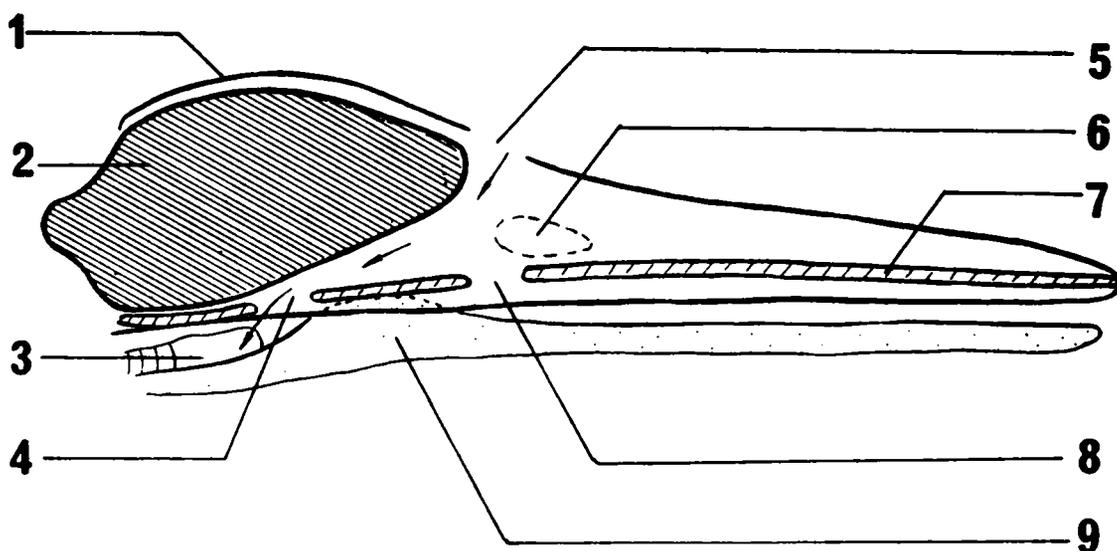


FIG. 53. Longitudinal section through skull showing hypothetical air passage connecting the internasal foramen with the larynx. 1, dermal roof. 2, neurocranium. 3, larynx. 4, interpterygoid vacuity. 5, internasal foramen. 6, external narial aperture. 7, palate. 8, internal narial aperture. 9, tongue.

Hearing

The whole problem of a directional hearing underwater is perplexing and one on which specialists are a long way from reaching agreement. The following discussion, therefore, cannot claim to be on a particularly firm footing. However, it is hoped that it will demonstrate that the possession of directional hearing by the ichthyosaurs is extremely doubtful.

The detection by a terrestrial animal of the direction of a sound source depends partly upon the arrival of vibrations at the two receptor organs at slightly different times. The density of animal tissue differs so much from that of the surrounding air that very little absorption occurs, and the sound waves impinging on the head are largely reflected. Only those vibrations falling upon the pinna reach the inner ear, and conduction through bone does not occur to any extent. In aquatic animals, however, the situation is reversed because the density of the water does not differ very much from that of the body tissues. Incident vibrations are conducted through the body, largely through bone, rather than being reflected. Since the velocity of sound in bone is high, and the distance between the two inner ear structures is relatively small, sound waves reaching the receptor farther from the source, by conduction through bone, arrive at virtually the same instant as those reaching the other receptor, and great difficulty is experienced in locating the sound source.

The cetacean ear, however, is a very sensitive apparatus which can accurately determine the direction of a sound source, and it is able to do this partly because each otic capsule is insulated from the rest of the skull by adipose and vascular tissue. Only those vibrations passing down the external auditory meatus reach the cochlea, and there is consequently a significant time lag in the arrival of vibrations at the two receptors (Slijper 1962).

There is evidence to suggest that seals are able to locate sound sources underwater, in spite of the fact that the otic capsule of the seal is firmly attached to the skull. However, it has been pointed out by Reppening (pers. comm.) that the petrosal is fused firmly only with the mastoid, and while the mastoid is fused to the squamosal and bulla, the entire temporal system of ossification is more or less detached or unfused with other bones of the skull. There is thus some measure of bony discontinuity, most conspicuous in the basioccipital region. Sound entering the head from one side has to pass across several bone/flesh reflective surfaces before reaching the cochlea of the other side. There would, then, seem to be some measure of isolation of the otic capsules in the seal. Furthermore, the high density of the bone of the bulla is probably of great significance in reflecting much of the sound falling upon it.

A further problem facing aquatic animals is that of the hydrostatic pressure upon the tympanic membrane. The cetaceans have evolved a compensatory mechanism whereby the pressure within the tympanic cavity is increased on diving; this equalises the pressure on either side of the membrane, thus preventing its rupture and permitting it to oscillate freely. The oscillations of the tympanic membrane are conducted to the fenestra ovalis by the otic ossicles which, therefore, must clearly be free to vibrate.

The remarkable accuracy of the cetacean location system is inherent in the use of high-frequency emissions which give a better resolution than low frequencies. Clearly the ability to perceive high-frequency sounds is dependent upon the possession of a fairly sophisticated sensory receptor.

At this point it would be useful to list the apparent requirements for directional hearing underwater:

1. Some measure of isolation of the otic capsule.
2. A mechanism for equalising the pressure on either side of the tympanic membrane.
3. Freely oscillating otic ossicles.
4. Sensory receptors which are sensitive to high frequencies.

The ichthyosaurian otic capsule is firmly braced against the squamosal, basioccipital and stapes, and there could be no flesh-bone interfaces at any of these points. There was, however, some cartilage in the otic region, and at least at the basioccipital contact there was an intervening pad of cartilage. It would therefore appear that the two capsules had a good degree of direct bony contact with one another.

The stapes is firmly wedged between the basioccipital and opisthotic proximally, and the quadrate distally, so that any oscillation of the stapes must be denied. If the stapes were not free to oscillate it could not have served to transmit vibrations from the tympanic membrane to the fenestra ovalis. Furthermore the evolution of some pressure equalisation system for the tympanum, comparable to that seen in the Cetacea, does seem a little unlikely. In the absence of evidence to the contrary it is concluded that the tympanic membrane had probably been lost altogether.

The last piece of evidence to support the absence of direction location in the ichthyosaurs is the nature of the sensory receptor. It has already been noted (p. 75) that the lagena was probably a small structure, and this evidence, slender as it might be, is not suggestive of an acute sense of hearing. Furthermore, as far as the author is aware, high-frequency response is not an attribute of the reptilian ear. It is therefore concluded that the possession of directional hearing capabilities in the ichthyosaurs is extremely doubtful.

Sight

That ichthyosaurs lived in neritic waters is evident from the associated fauna which contains some terrestrial organisms. Since the silt deposited was very fine it is apparent that these were still waters, where light intensities were probably relatively high. The large size of the orbit, sclerotic ring, and optic lobe of the brain corroborates the importance of sight in ichthyosaurs. In those latipinnates which have been examined, the aperture of the sclerotic ring is relatively large and circumscribed by a shallow sulcus. In terrestrial reptiles the cornea is an important refracting body, and its outer convexity is maintained by a prominent sclerotic sulcus (fig. 54). In aquatic animals the difference in refractive index between the corneal

tissue, with its underlying aqueous humour, and the surrounding water is so small that the cornea is no longer functional as a refracting body and is very much reduced. In consequence the sclerotic ring of an animal which uses its eyes primarily underwater has little or no development of a sulcus, and intermediate conditions are found in those forms which use their eyes partly above water, (Underwood, pers. comm.). The inference from the material examined is that the ichthyosaurian sclerotic ring did not support a very prominent cornea, and the eye was primarily adapted for underwater vision. This conclusion is supported by the relatively large size of the sclerotic aperture, which is indicative of an eye adapted to operating in dull light.

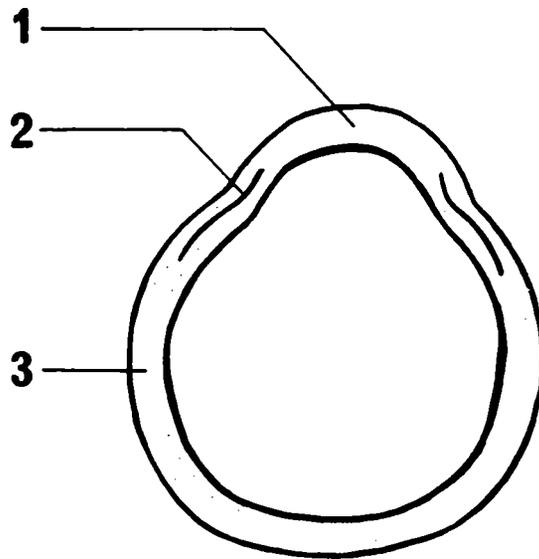


FIG. 54. Sagittal section through the eye of a terrestrial reptile. 1, cornea. 2, sulcus of sclerotic plate. 3, sclerotic layer.

CONCLUSION

The present investigation, it is hoped, will clear up some of the anomalies which have been associated with ichthyosaurian cranial anatomy, and also demonstrate the affinity of the ichthyosaurs with the euryapsid reptiles. It is regretted that so much of this work had to be devoted to straightforward description, which is not absorbing reading, but a detailed account of the skull has been long overdue. The morphological treatment, however, has permitted certain conclusions to be drawn concerning the way these animals lived, and any information which adds to a picture of Mesozoic life justifies the efforts involved.

The ichthyosaur may be visualized as a highly successful animal whose adaptations to a life at sea have been surpassed only by the Cetacea, then only after the passage of some considerable interval of time. Some measure of their success is reflected in the wealth of material which they have left behind. Their heyday came during the early part of the Jurassic when they thronged the shallow seas which covered so much of the globe. Well before the close of the Jurassic, however, their numbers began to dwindle, and relatively few survived into the Cretaceous. While the last

chapters of the Age of Reptiles were being written on the land, the last of the ichthyosaurs slipped quietly and unpretentiously into oblivion. Perhaps one day we shall understand why.

TECHNIQUES

The use of 'Carbowax'. 'Carbowax', the water-soluble wax used to cement the elements, is available with a number of different melting points, and that used here, 'Carbowax 4000', melts at about 60°C. If the wax is kept in a boiling water bath it remains mobile, and when applied to the point of contact between two bones it spreads rapidly forming a firm union within seconds. If a less permanent join is required the wax is allowed to cool before application, so that spreading does not occur, and the wax then forms a bead which can subsequently be removed quite easily. This method of cementation was used during the early stages of the reconstruction so that readjustments in orientation could be effected with little difficulty. After a particular section had been completed the joints were made more permanent by remelting the wax with a hot seeker and allowing it to spread between the contact edges. Excess wax may be removed from the surface of bones by using a hot seeker and paper tissue. It must be remembered that skulls which have been reconstructed using wax cannot be left in direct rays of the sun, or anywhere where the wax might soften. Furthermore it has been found that the wax becomes brittle after a month or two and this must be borne in mind when handling a reconstruction which has been stored. The properties of the old wax can be restored by remelting with a hot seeker and allowing it to set, and it is best to do this for each joint before handling stored material. Presumably a slow change in the crystal structure of the wax takes place which reduces its mechanical strength, and this is reversed by remelting.

Sometimes it is necessary to join elements whose area of contact is very small, and this cannot be done in the ordinary way. A technique which has proved very useful is to construct bridging splints of wax and tissue. A piece of tissue is cut to the required size and laid across the gap between the elements to be joined. A drop of hot wax is then applied at either end, and in between. When this is cool, more wax is added, and if greater strength is required more pieces of tissue are

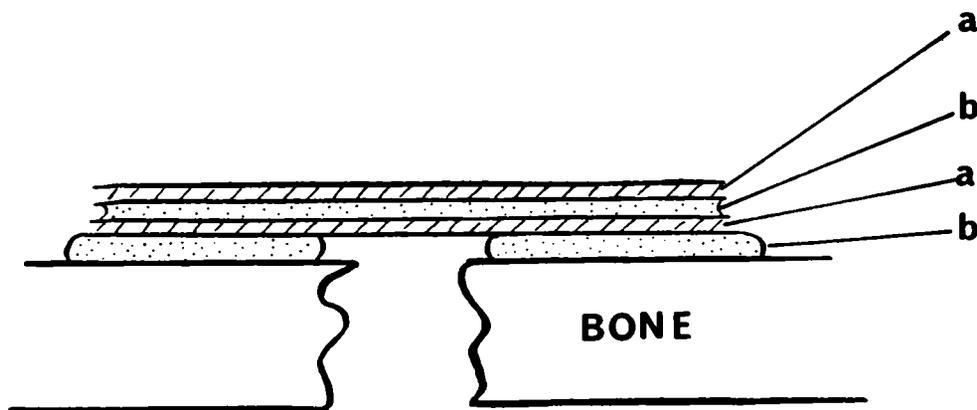


FIG. 55. Section through two bones being temporarily held together by Carbowax tissue bridge. a, tissue. b, Carbowax.

added thus forming a laminated strut (fig. 55). The strut possesses much strength and can readily be removed when it is no longer required. The position of two bones thus joined can be adjusted as desired by warming the strut which becomes plastic and remains pliable for several seconds before cooling to its former rigidity.

A plastic hypodermic syringe was used to deliver the hot wax to the bone, and with a little practice this could be operated orally, leaving both hands free for manipulation.

The most satisfactory method of separating elements affixed with wax is by means of steam delivered in a fine jet. Since some difficulty was initially experienced in obtaining a suitable jet the matter will be discussed here.

The generation of a steam jet. Steam is usually generated in the laboratory by using a steam can. The can is fitted with two exits, one for the delivery of steam, the other serving as a safety valve. The safety outlet comprises a short length of glass tubing which reaches the bottom of the can and extends for several centimetres above the bung. When the pressure within the can exceeds atmospheric pressure a column of water ascends the tube. The effusion of a jet of steam through a fine aperture requires a steam pressure much in excess of atmospheric pressure, and under normal conditions this drives a column of water through the exhaust valve. The apparatus is modified by attaching a long length of rubber tubing to the exhaust and this is held vertically. As the pressure increases water is forced up the tube, but, provided the nozzle aperture is not much less than 2 mm in diameter, the hydrostatic pressure does not exceed about 1 metre. A water-trap is inserted between the steam delivery pipe and the nozzle in order to collect the water carried over with the steam. The steam jet is not required all the time but it is best to keep the water boiling steadily and the steam given off is condensed in the bath in which the wax is kept hot.

In addition to its use in separating wax joints the steam jet is very useful for cleaning bones and has also on many occasions been used for the separation of bones which have been fused together by veins of acid-resistant material. No bone damage has been recorded which is attributable to steaming, and this is mainly because it is localized and does not go on for long periods. Indeed, if pyritic decomposition of fossil bone is brought about by bacterial activity, this technique might have some beneficial effect.

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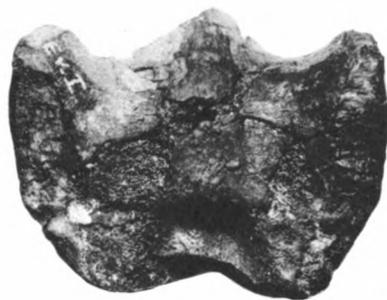
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PLATES

Note: Centimetre scale throughout. All specimens referred to are in the collection of the British Museum (Natural History)

PLATE I

- a. Basisphenoid (Evans' nodule), dorsolateral, dorsal and ventral views.
- b. Basioccipital (Evans' nodule), dorsolateral, posterior and ventral views.
- c. Exoccipital left and right (Evans' nodule), internal, external and dorsal views.
- d. Supraoccipital (Evans' nodule), anterior, posterior and ventral views.
- e. Opisthotic left (R6697), anterior and posterior views.
- f. Proötic, left (Evans' nodule), anterior and posterior views.



a



b



c



d



e



f

PLATE 2

- a. Stapes, right (R8177), posterior, dorsal, and anterior views.
- b. Epipterygoid, left (R1168), lateral and medial views.
- c. Quadrate, left (R6697), anterior, lateral and posterior views.



a



b



c

PLATE 3

- a. Parietal, right (R8177), dorsolateral and ventral views.
- b. Frontal, right (R8177), dorsal and ventral views.
- c. Nasal, left (incomplete, posterior portion, R8177), dorsolateral and ventral views.
- d. Postfrontal, right (R8177), dorsal and ventral views.
- e. Prefrontal, right (R8177), dorsal and ventral views.

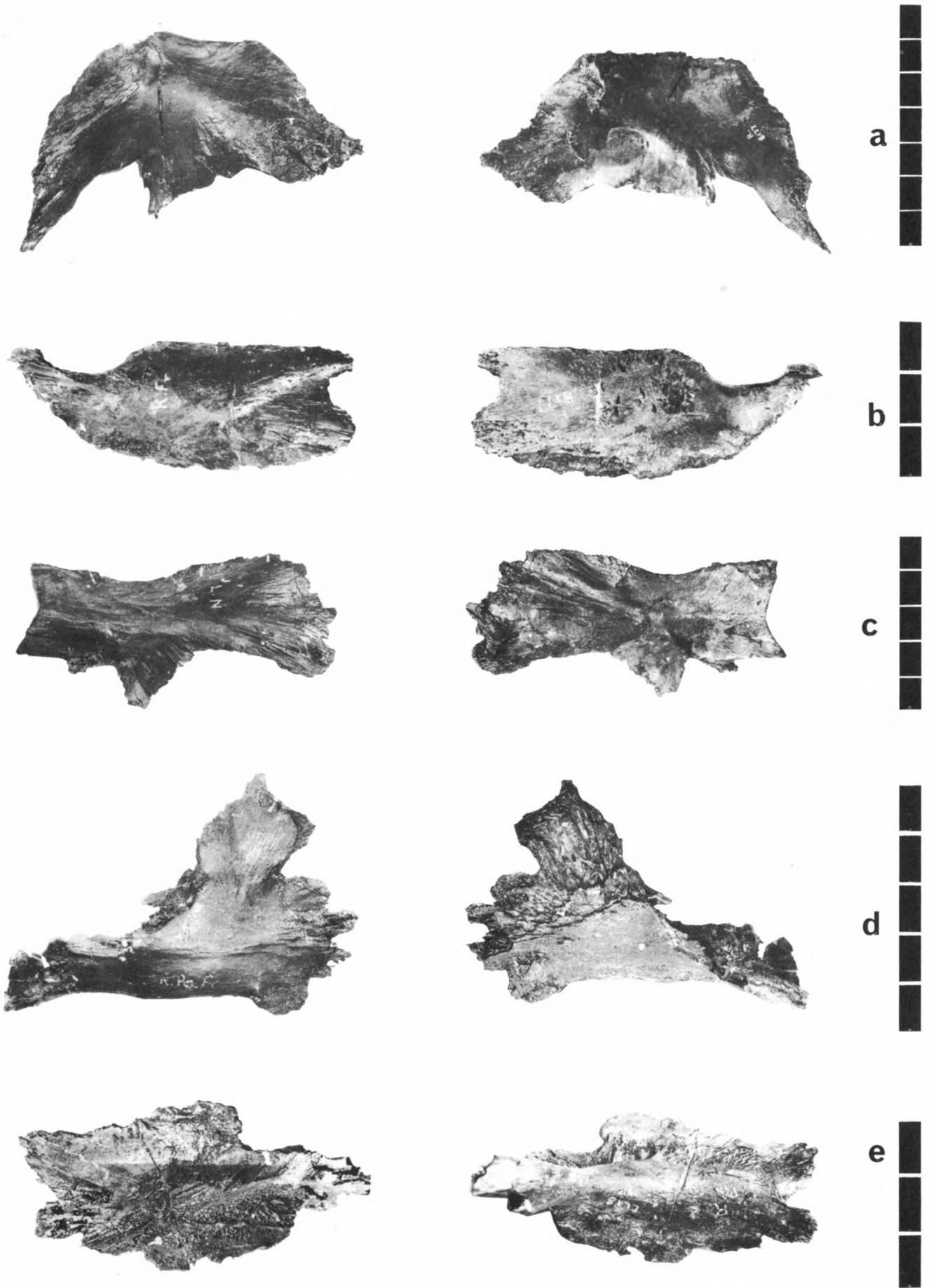


PLATE 4

- a. Postorbital, left (R6697), lateral and medial views.
- b. Quadratojugal, right (R6697), posterolateral and internal lateral views.
- c. Lachrymal, right (R8177), lateral and medial views.
- d. Jugal, right (R8177), lateral and medial views.
- e. Maxilla, right (R8177), ventral and dorsal views (incomplete).



a



b



c



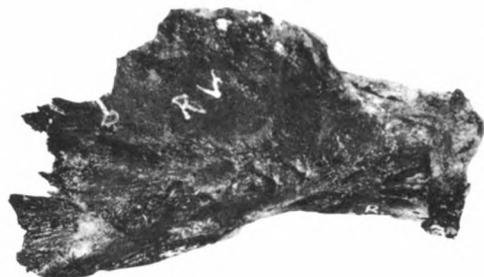
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PLATE 5

- a. Pterygoid, right (R8177), dorsolateral and ventromedial views.
- b. Palatine, left (R8177), dorsal and ventral views.
- c. Vomer, right (R8177), dorsolateral, dorsal and ventral views (incomplete).



a



c



b



PLATE 6

- a. Lower jaw ramus, right (R8177), lateral, medial, and dorsal views.
- b. Prearticular, right (R8177), external and internal views.
- c. Coronoid, left (R8177), ventral and dorsal views.
- d. Articular, right (R8177), lingual, dorsomedial and labial views.
- e. Sclerotic ring, right (half of complete ring, R8177), lateral and medial views.
- f. Squamosal, right (R8177), posteromedial and somewhat dorsal, and dorsal views.
- g. Teeth in different stages of development (49203).

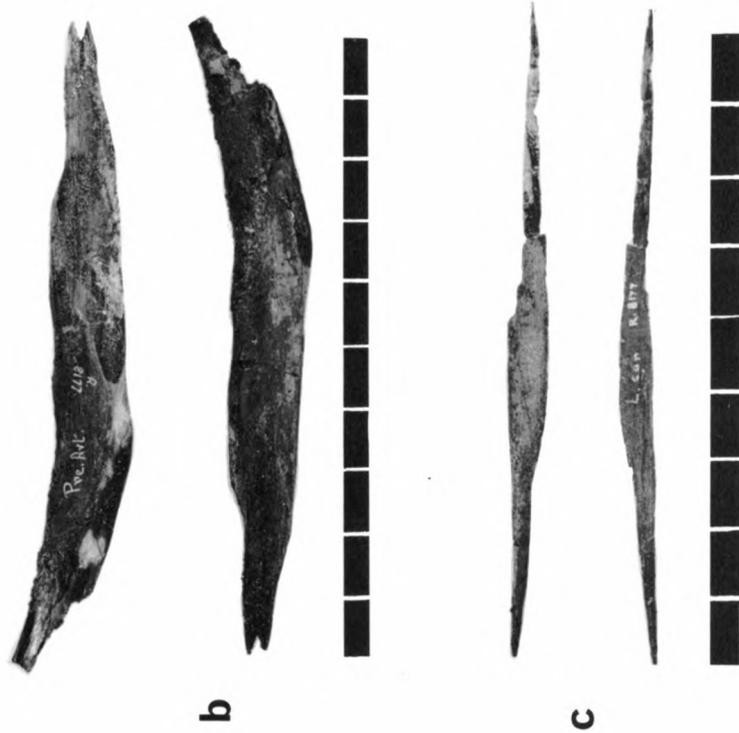
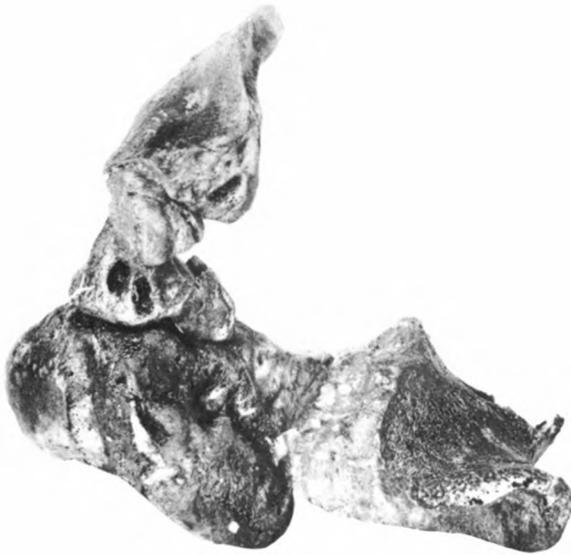


PLATE 7

- a. Reconstruction of left half of palate (R8177), dorsal view.
- b & c. Partial reconstruction of occiput (Evans' nodule), lateral and anterolateral views.
- d. Partial skull reconstruction (R6697), posterior view.
- e. Partial skull reconstruction (R8177), complete up to level of external narial aperture, anterolateral and somewhat dorsal view.



a



b



c



d

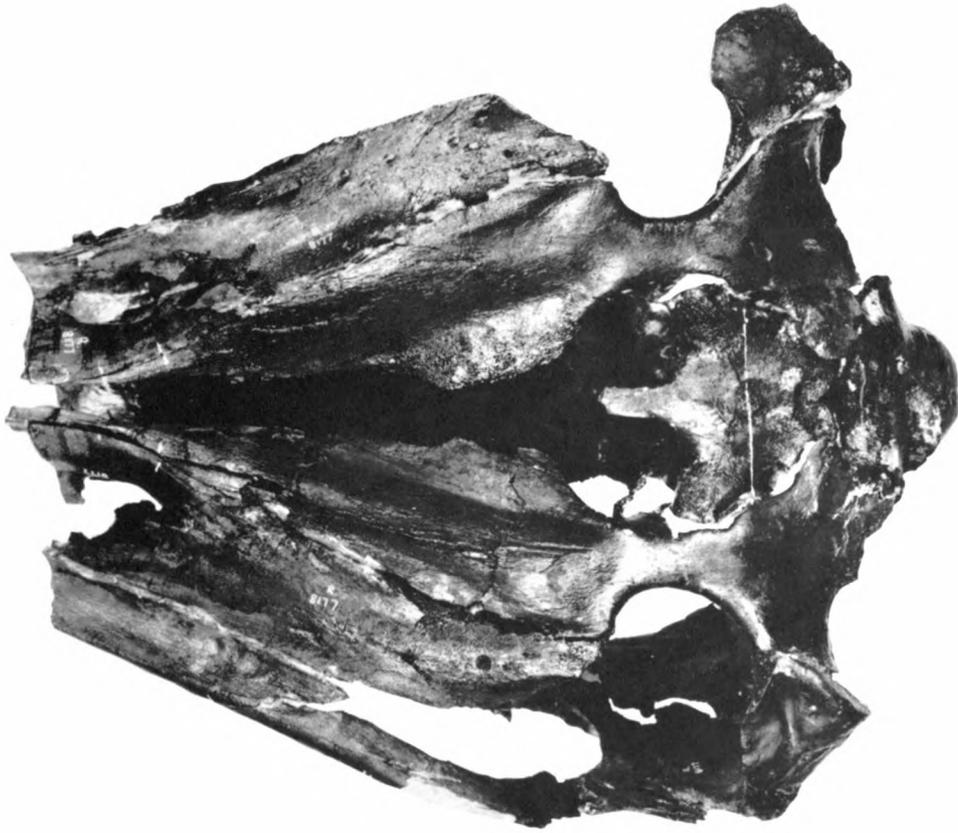


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PLATE 8

a & b. Partial skull reconstruction (R8177), complete up to level of external narial aperture, dorsal and ventral views.



b



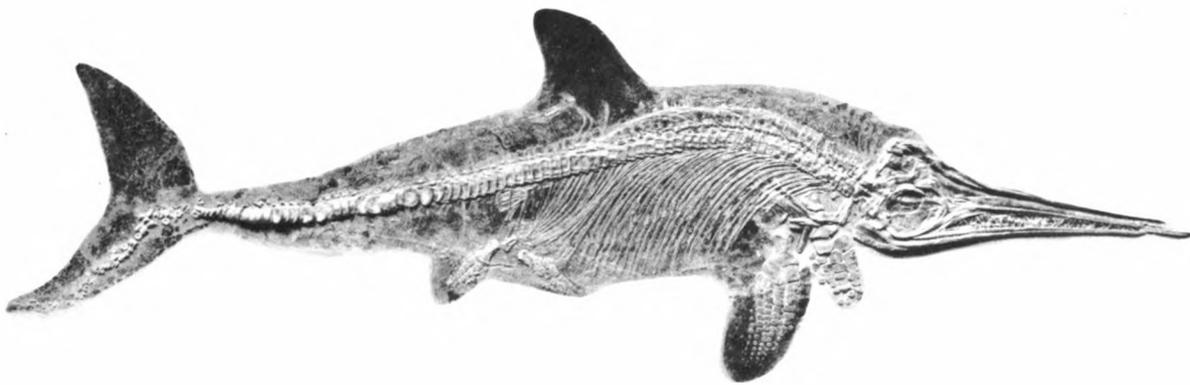
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PLATE 9

- a. Skull of a well preserved and complete specimen (2013), from the Lower Lias of Street, Somersetshire, dorso-lateral view, about one quarter natural size.
- b. Complete skeleton (R4086), showing body outline preserved as a carbonaceous film, from the Upper Lias of Holzmaden, Germany, about one-eleventh natural size.



a



b