A REVIEW OF BRITISH UPPER JURASSIC ICHTHYOSAURS

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ABSTRACT

The introduction to the thesis presents a synopsis of British Jurassic stratigraphy, and a brief account of the occurrence of British Upper Jurassic ichthyosaur remains which highlights the importance of the Leeds Collection of ichthyosaurs. A historical review of the publications concerning British Upper Jurassic ichthyosaurs (members of the order Ichthyopterygia) is presented.

The British Upper Jurassic ichthyosaur taxa are reviewed. Of the five genera and fourteen species erected, only four generic and four specific names are found to be valid. The rejected names are listed with reasons for their rejection. After a listing and discussion of the synonymy of each valid species, a diagnosis and list of referable material is presented, then each species is described in detail.

New reconstructions of the skull in dorsal and lateral views, the palate, the lower jaw and the complete skeleton of *Ophthalmosaurus icenicus* are presented. A reinterpretation of the forepaddle of *O. icenicus* proposes that previous interpretations have presented the forepaddle laterally inverted.

The discovery that a bone of uncertain homology, designated element B, is present in the temporal region of the skull of *O. icenicus*, has important implications in the problem of the phylogeny and affinities of the Ichthyopterygia, and this is discussed. The presence of element B in the skull, which has been denied by previous authors, leads to the proposal of two alternative hypotheses concerning the relationships of the Ichthyopterygia to other reptiles. The preferred hypothesis is one that states that element B is a neomorph, and that the Ichthyopterygia are diapsid derivatives.

A critique of previous schemes of classification of the Ichthyopterygia is presented, and a new classification is proposed. The validity of the division of the Ichthyopterygia into two groups, the latipinnates and longipinnates, is questioned.

Finally, a discussion of functional aspects of the anatomy of O. icenicus is presented.

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Characters employed:-

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Ophthalmosaurus icenicus

Grendelius mordax

Nannopterygius enthekiodon

Brachypterygius extremus

CHAPTER 1 : INTRODUCTORY CHAPTER

SECTION 1: INTRODUCTION

The ichthyosaurs, members of the order Ichthyopterygia, were a group of highly specialised marine reptiles which flourished throughout the seas of the Mesozoic era. The earliest known members already showed evidence of marked aquatic specialisation, and in their morphological adaptations, as well as their probable ecological role, the group as a whole can be compared with the cetaceans.

As a result of an apparently rapid adaptation to a marine existence, the known ichthyosaurs form a relatively homogeneous group whose relationship to other reptile groups remains uncertain.

The ichthyosaurs of the Jurassic and Cretaceous show the most extreme adaptations to a marine existence. These include a streamlined, fusiform body, limbs adapted as hydroplanes, and a shark-like tailfin and dorsal fin (as revealed by preserved skin impressions). These features are less well developed in the Triassic members of the order. All ichthyosaurs, however, possess neural arches that remain unfused to the amphicoelous centra in adults, infolding of the tooth-base dentine, caudal vertebrae specialised for the support of a tailfin, and a relatively large eye. These unique derived characters can be taken to define the order.

The ichthyosaur skull possesses a single superior temporal opening which has previously been considered to be uniquely derived from an anapsid condition, and as such it was a character used to define the order. Recent studies, however, have revealed the possibility that the temporal opening is derived from a diapsid condition, and under this interpretation it is seen as a character shared with the Sauropterygia (plesiosaurs and nothosaurs) and the Placodontia.

The fossil remains of ichthyosaurs first became known in the late 17th century from British localities (Howe et al, 1981), but it was not until the early 19th century that they were recognised as a new group of extinct reptiles by Sir Everard Home (1814), who published the first anatomical descriptions based on specimens collected from the Lower Liassic locality of Lyme Regis. The group became known by the generic name Ichthyosaurus which was proposed by König in 1818 in recognition of their many fish-like characteristics.

Ichthyosaurs make their first appearance in the fossil record in beds of Spathian age (Lower Triassic) of Spitzbergen (Mazin, 1980). They are then found in most major marine deposits throughout the Mesozoic until the last traces of the group appear in the Maastrichtian of New Jersey (McGowan, 1978).

In terms of geographical distribution, ichthyosaurs have been found almost worldwide. British localities have yielded particularly large amounts of valuable material. The oldest remains in Britain are found in the Rhaetic deposits of Gloucestershire, but these are largely fragmentary. Numerous well-preserved and articulated skeletons have been obtained, however, from Lower Liassic deposits, in particular of Dorset and Somerset. Ichthyosaur remains are uncommon in Middle Jurassic strata, but once more become abundant in the British Upper Jurassic strata of the Oxford and Kimmeridge Clays. The Oxford Clay specimens are particularly well-preserved with little crushing, though they are largely disarticulated.

The majority of existing descriptions of Upper Jurassic taxa were produced around the turn of the century, at the time when most of the known material was originally collected; since then, very little redescription has been attempted. McGowan (1976) reviewed the taxonomy of the Upper Jurassic ichthyosaur taxa, exclusive of the Oxford Clay forms, but a comprehensive redescription and taxonomic review of all Upper Jurassic ichthyosaur material was still needed. The present study aims to fulfil this need.

SECTION 2: BRITISH UPPER JURASSIC STRATIGRAPHY

Throughout the Jurassic period, much of Britain was submerged beneath a shallow epicontinental sea, continuous with the Tethys (Rayner 1971, Wills 1962). Upland areas remained in Devon and Cornwall, Wales and much of Scotland, whilst a major area of uplift in the east formed the London Platform. In the submerged areas, relative shallows centred on the Mendips, Oxfordshire and the Market Weighton upwarp. Between these shallows were regions of subsidence characterised by thicker deposits: these are the basins of the Wessex and the Weald, the Severn and Cotswolds region, and Lincolnshire and Yorkshire.

Following a general shallowing of the sea which characterised the Middle Jurassic period, there developed, in late Bathonian times, a general transgression which resulted in the deposition of the Cornbrash beds. The Upper Cornbrash marks the beginning of the Upper Jurassic.

In southern and central England there then followed a brief phase of deposition of clays and sands of the Kellaways beds. A long period of deposition from muddy seas then developed, laying down the beds of the Oxford Clay, the first of the two great clay strata that dominate the Upper Jurassic. The major part of British Upper Jurassic ichthyosaur material derives from this horizon. At the end of Oxfordian times, the sea became shallow and clear enough in places to produce the coral reef limestones of the Corallian beds, though in some areas marine clays were deposited as the Ampthill clays.

A second major transgression then developed, marking the beginning of the Kimmeridgian stage. The resulting deposits of marine clays form the Kimmeridge Clay, another important source of fossils of marine reptiles.

At the end of the Kimmeridgian, a general uplift of land excluded the

TABLE 1: BRITISH UPPER JURASSIC LITHOLOGY

(from Rayner, 1971)

SYSTEM	LITHOLOGY	STAGE
Upper Jurassic	Purbeck Beds (in part)	Portlandian
	Portland Beds	
	Kimmeridge Clay	Kimmeridgian
	Corallian Beds	Upper Oxfordian
	Oxford Clay	Middle Oxfordian Lower Oxfordian Upper Callovian
	Kellaways Beds	Lower Callovian
	Upper Cornbrash	

sea from the whole of the British Isles with the exception of a gulf in the south reaching as far north as Oxfordshire. In this gulf the Portlandian formations of the Portland Sand and Portland Stone were laid down.

Further retreat of the sea towards the close of the Jurassic resulted in the development of predominantly deltaic conditions in the south, with intermittent transgressions and emergences. During this period, the Purbeck beds were deposited. The Jurassic/Cretaceous boundary is usually taken as the Cinder Bed of the Middle Purbeck.

Upper Jurassic rocks now outcrop in a belt stretching north-eastwards across central and eastern England from Dorset in the south to Yorkshire in the north. Smaller outcrops remain on the Kent coast between Dover and Folkestone, in north-east Scotland near Brora and on the shores of Cromarty, and on Raasay, Skye, Eigg and Mull of the Inner Hebrides.

SECTION 3: OCCURRENCE OF ICHTHYOSAUR MATERIAL: A NOTE ON THE LEEDS COLLECTION

Ichthyosaur remains have been recovered from most beds in the Upper Jurassic. Isolated centra (now in the British Museum (Natural History) and in the Yorkshire Museum) are known from the earliest beds of the Cornbrash and the Kellaways Beds.

By far the greatest quantity of British Upper Jurassic ichthyosaur material derives from the Oxford Clay. Of this material the major part was collected from brick pits in the Oxford Clay of the Peterborough area. Almost all the ichthyosaur specimens obtained from this area form part of the fossil collection made by the Leeds brothers of Eyebury, near Huntingdon, Cambridge, between the years 1865 and 1917. It is a result of the Leeds brothers' efforts that this British locality has yielded one of the most important assemblages of ichthyosaurs of this age in the world. Most of the Leeds Collection fossils are thought to have been retrieved from the Jason, Coronatum and Athleta zones (after Calloman 1968) of the Lower Oxford Clay (Callovian stage). The clay is still quarried today for brick-making purposes, but mechanisation of the pits has made the collection of good fossil material virtually impossible. The story of the Leeds Collection was recorded by E.T. Leeds in a book published in 1956. The collection was initiated by Charles E. Leeds in 1865, but was continued by his brother Alfred N. Leeds in 1887 following Charles' emigration. Alfred continued collecting until his death in 1917, and during these years collected the major part of the whole collection.

The greater part of the Leeds Collection was sold to the British Museum (Natural History) in two main consignments, one in 1890 and the second following Alfred Leeds' death. Most of what remained was sold to the Hunterian Museum, Glasgow. Smaller amounts went to the National Museum of Wales, Cardiff, to the Kendal Museum, Cumbria, and to Liverpool Museum (the specimens of which are now in the British Museum (Natural History)).

Part of the Leeds Collection is now also in the Manchester Museum. A certain amount of material was sold abroad during Alfred Leeds' lifetime, in particular to the University of Tübingen, Germany, but also to various other museums in France and Germany. Some material is now also located in Austria and the U.S.A.

Oxford Clay ichthyosaur material is known from localities other than in the Peterborough area, but the remains are rarely associated and most often consist of isolated centra or limb bones. My own research has shown that quantities of Oxford Clay material from the counties of Dorset, Bedfordshire, Northamptonshire, Norfolk and Oxfordshire are now to be found in local authority and university museums in these counties and in the British Museum (Natural History).

Ichthyosaur remains are rare in Corallian beds, but fragments are known from the Corallian of Malton, North Yorkshire (now in Hull Museum), from the Ampthill Clay of Cambridgeshire (in the Sedgwick Museum, Cambridge) and from the Coral Rag of Dorset (Dorchester Museum).

In comparison with Oxford Clay finds, probably a greater number of individual discoveries have been made from the Kimmeridge Clay, but the material is by no means as complete or as well-preserved as that from the Oxford Clay. As a consequence of this, the Kimmeridgian taxa are osteologically less well understood. Remains have been found in the Kimmeridge Clay of the counties of Dorset, Somerset, Wiltshire, Buckinghamshire, Oxfordshire, Cambridgeshire, Norfolk and Suffolk. These remains are held in local authority and university museums of these counties, and in the British Museum (Natural History).

Ichthyosaur finds once more become rare in the Portland and Purbeck. Delair (1959, 1969) reported isolated finds from the Portland and Purbeck beds of Dorset.

SECTION 4: BRITISH UPPER JURASSIC ICHTHYOSAURS - A HISTORY OF PUBLICATIONS

The first published record of the occurrence of ichthyosaur remains in British Upper Jurassic deposits is to be found in Owen's (1839) Report on British Fossil Reptiles. He erected the new species Ichthyosaurus trigonus, the type of which was a single centrum from the Kimmeridge Clay of Wiltshire. Owen regarded this as distinctive in possessing triangular contours of its articular faces, the ventral border forming the apex.

In the same publication Owen erected the species I. thyreospondylus for five centra in the Bristol Museum which he described as having distinctive raised areas in the normally concave articular faces. Owen did not state their horizon or locality, but Philips (1871) applied this specific name to numerous vertebral centra from both the Oxford and Kimmeridge Clays of Dorset, Buckinghamshire and Oxfordshire.

In 1869 Seeley described a partial skeleton in the Cambridge University Museum which he named I. megalodeirus, and which was derived from the Oxford Clay of the Peterborough area. He did not point out any distinguishing features, but merely stated that the species was new. In the same publication Seeley referred to the remains of two more individuals, both represented only by the "unankylosed axis vertebra", and both from the Kimmeridge Clay of Cambridgeshire. He named them I. chalarodeirus and I. hygrodeirus, but did not state their specific characteristics, nor did he describe them.

Three new species were erected by Philips in 1871, once again based solely on vertebrae derived from the Kimmeridge Clay of Dorset, Wiltshire and Oxfordshire. The species were I. dilatatus, I. ovalis and I. aequalis. The centra of I. dilatatus were said to be distinctive in their great proportional breadth. Similarly he described the centra of I. ovalis as being distinctively oval along their ventro-dorsal axis, whilst the single caudal centrum representing I. aequalis was thought by Philips to be unique in having rib facets exactly halfway down the sides of the centrum.

In the same year, Hulke (1871) described a new species, I. enthekiodon, from the Kimmeridge Clay of Dorset. The type specimen was a near complete, though poorly preserved, skeleton which was distinct in having extremely reduced paddles and elongate coracoids.

It was during this period in the latter half of the nineteenth century that Mr. Charles Leeds began to build up his fossil collection from the brick pits around Peterborough. When its existence became known to them, the anatomists of the time soon realised the valuable contribution to their knowledge that the well-preserved skeletal elements could make. Unlike the marine reptile remains from the English and Continental Lias, these fossils were preserved in three dimensions, and were relatively free of matrix. Seeley (1874) described ichthyosaur remains forming part of the Leeds Collection and recognised that they represented a new species and genus which he named Ophthalmosaurus icenicus. The character he took to warrant the generic distinction was the nature of union of the clavicles by a loose interdigitating suture.

Owen's (1881) monograph included figures of vertebral centra which he named I. brachyspondylus, but he failed to describe or define the species and did not state its horizon. Lydekker (1889a) suggested the species was probably synonymous with I. thyreospondylus, of Kimmeridgian age.

In 1890 a new species of Ophthalmosaurus was erected by Lydekker (Mansell-Pleydell 1890). O. pleydelli was erected to accommodate an isolated humerus from the Kimmeridge Clay of Dorset. There were said to be some differences from the Oxford Clay O. icenicus humeri, but the three unequal distal humeral facets, characteristic of the genus, were present.

In 1904 an unusual ichthyosaur paddle was discovered in the Kimmeridge Clay of Weymouth. Notice of its discovery was given by Boulenger (1904 a,b) who described the humerus as having articulation distally with three bones. He realised, however, that the humerus of this new ichthyosaur, which he named I. extremus, articulated with the radius, ulna and intermedium,in marked contrast to the humerus of Ophthalmosaurus which articulated with radius, ulna and "pisiform".

During the last years of the nineteenth century, a debate developed in the literature concerning the relationship of Ophthalmosaurus to the North American ichthyosaur genus Baptanodon, and many publications on both sides of the Atlantic dealt with this problem. The European view (Lydekker 1888, Woodward 1898, Baur 1887, Fraas 1904) held that the two genera were synonymous, but American workers (notably Gilmore 1905, Knight 1903) argued to maintain the generic distinction between the two forms. The European view was upheld by Andrews (1907) in a preliminary note on the osteology of Ophthalmosaurus, written whilst he was engaged in a detailed study of part of the Leeds Collection. In 1910 and 1913, Andrews published a catalogue of the Leeds Collection, then housed in the British Museum (Natural History). In it he produced a detailed account of the osteology of Ophthalmosaurus, and on the basis of this knowledge expanded more fully on his reasons for synonymising Baptanodon with Ophthalmosaurus.

The debate then rested and the majority of subsequent writers have accepted Andrews' interpretation (Von Huene 1922, Kuhn 1934, Romer 1968, McGowan 1976, 1978). However, Appleby (1956), in an account of the osteology of the Oxford Clay ophthalmosaurs housed in the Leicester and Peterborough Museums, resurrected the generic status of Baptanodon. He used evidence from a comparison of reconstructions of the occiput of the two forms. In the same paper, Appleby recognised a second species of Ophthalmosaurus amongst the material, and he published the new species name O. monocharactus.

The most recent new taxon to be described from the British Upper Jurassic is Grendelius mordax, represented by an almost complete skull with the associated remains of vertebral centra, ribs and poorly preserved pectoral girdle elements. The skeleton was unearthed in 1958 during the excavation of a drainage channel in the Kimmeridge Clay near Stowbridge, Norfolk. McGowan (1976) described and named the specimen and, in an attempt to establish its taxonomic status, undertook a review of Upper and Middle Jurassic ichthyosaurs exclusive of Ophthalmosaurus. He concluded that of twenty-two species erected worldwide, only two were valid - G. mordax and I. enthekiodon (Nannopterygius enthekiodon, Von Huene 1922). He made no mention, however, of the English Kimmeridgian species I. extremus.

Summary of Taxa Erected (alphabetical order of species name)

Ichthyosaurus aequalis	Philips, 1871	Kimmeridge Clay
I. chalarodeirus	Seeley, 1869	Kimmeridge Clay
I. dilatatus	Philips, 1871	Kimmeridge Clay
I. enthekiodon	Hulke, 1871	Kimmeridge Clay
I. extremus	Boulenger, 1904	Kimmeridge Clay
I. hygrodeirus	Seeley, 1869	Kimmeridge Clay
Ophthalmosaurus icenicus	Seeley, 1874	Oxford Clay
I. megalodeirus	Seeley, 1869	Oxford Clay
O. monocharactus	Appleby, 1956	Oxford Clay
Grendelius mordax	McGowan, 1976	Kimmeridge Clay
I. ovalis	Philips, 1871	Kimmeridge Clay
O. pleydelli	Lydekker, 1890	Kimmeridge Clay
I. thyreospondylus	Owen, 1839	Kimmeridge Clay
I. trigonus	Owen, 1839	Kimmeridge Clay

Three new genera were established to receive some of these species by Von Huene (1922). These are Macropterygius, for I. trigonus, Nannopterygius, for I. enthekiodon, and Brachypterygius for I. extremus.

CHAPTER 2 : REVIEW OF BRITISH UPPER JURASSIC ICHTHYOSAURS

SECTION 1 : DESCRIPTION OF VALID SPECIES

Genus Ophthalmosaurus Seeley, 1874

Sauranodon Marsh, 1879 (preoccupied name)

Baptanodon Marsh, 1880

Microdontosaurus Gilmore, 1902

Apatodonosaurus Mehl, 1927

Ancanamunia Rusconi, 1940

Type species:

O. icenicus Seeley, 1874

Additional British species:

None

Diagnosis: As for monotypic species below

Ophthalmosaurus icenicus Seeley, 1874

Ichthyosaurus megalodeirus Seeley, 1869

O. icenicus Seeley, 1874

O. pleydelli Mansell-Pleydell, 1890

O. monocharactus Appleby, 1956

Discussion of synonymy; genus name:

In 1874 Seeley separated some Oxford Clay ichthyosaur remains from the genus Ichthyosaurus on the basis of differences in the union between bones in the shoulder girdle. He named the new material, which was then in the possession of Mr. Alfred Leeds, Ophthalmosaurus icenicus.

In 1879 Marsh published a description of reptilian remains from the Upper Jurassic, Sundance formation, of North America. He placed the reptilian remains in a new order which he named the Sauranodonta, and applied to them the generic name Sauranodon. A year later, after realising Sauranodon was preoccupied, Marsh (1880), by now recognising the remains as ichthyopterygian, renamed the taxon Baptanodon. In 1902 one specimen of Baptanodon was found by Gilmore to possess teeth. Because no other specimen of Baptanodon had been found to possess teeth, Gilmore separated this specimen as a new genus Microdontosaurus. However, in 1903, teeth were discovered in the type of Baptanodon, and so the new generic name was withdrawn.

During the next thirty years a debate between American and English authors was maintained over whether Baptanodon and Ophthalmosaurus were synonymous (Lydekker 1888, Woodward and Sherborn 1890, Knight 1903, Fraas 1904, Gilmore 1905).

Andrews (1910) upheld the European view that the two forms were congeneric, and he demonstrated that the supposed generic differences proposed by Gilmore (1905) were either unfounded, or accountable for as the consequence of individual variation. Since then most authors have agreed (e.g. Kuhn 1934, Romer 1968, McGowan 1978) with the one exception of Appleby (1956) who maintained their generic separation. He based this decision on differences in form of the back of the skull between Baptanodon and Ophthalmosaurus, as judged from reconstructions made by Gilmore (1905) and Appleby (1956). He found six points of difference; I consider all these to be minor differences which are the result of inaccuracies in the reconstructions of the occiputs.

My own reconstruction (figure 6) shows similarities to and differences from both Gilmore's and Appleby's reconstructions. It is therefore my opinion that *Baptanodon* is a junior synonym of *Ophthalmosaurus*.

In 1927, Mehl erected the new genus *Apatodonosaurus* to accommodate Upper Jurassic ichthyosaur remains from Wyoming. In 1928 he described the remains which included part of a skull and jaws, limbs, vertebrae and ribs. The specimen was very incomplete, but Mehl outlined a number of unique features which apparently separated it from *Ophthalmosaurus*. Among these was an anteriorly placed naris, wide postorbital bar, small orbit, a unique arrangement of bones in the orbito-narial region, and apparently functionless, inwardly-directed premaxillary teeth. The latter feature inspired the name *Apatodonosaurus*. A forepaddle preserved with the remains shows the characteristic generic features of *Ophthalmosaurus*. It is my opinion (also held by Romer 1956) that *Apatodonosaurus* is a junior synonym of *Ophthalmosaurus*. The apparently unique features are almost certainly the result of gross misinterpretation of the fragmentary material.

Upper Jurassic ichthyosaur remains from Argentina were described by Rusconi in 1940 and 1942. He placed them in the genus *Myobradypterygius* under the specific name *mendozanus*, but in the later paper he removed them from that genus and erected the new genus *Ancanamunia*. In 1948 he produced a more complete description of the remains which showed that the forelimb was diagnostic of the genus *Ophthalmosaurus*. I suggest that *Ancanamunia* is a junior synonym of *Ophthalmosaurus*.

Species name synonymy:

In 1869 Seeley catalogued and briefly described the remains of a skeleton, found in the Oxford Clay of the Peterborough district, under the new name *Ichthyosaurus megalodeirus*. When, five years later, Seeley named and described the new genus and species *Ophthalmosaurus icenicus* he made no reference to *I. megalodeirus*.

The type of I. megalodeirus consists of trunk and caudal vertebrae, coracoids, scapulae, a humerus, femora, and some skull bones. I can find no significant difference between the specimen and other specimens of O. icenicus. I. megalodeirus preceded O. icenicus in time, but need not take priority following Article 23(a-b) of the International Code of Zoological Nomenclature; for the sake of stability, a long-established name should not be replaced by its senior synonym.

In 1890 Mansell-Pleydell erected the new species O. pleydelli, to accommodate a humerus with three distal facets, diagnostic of the genus Ophthalmosaurus. Snout fragments and two vertebral centra were also presumed to be associated with the humerus by Mansell-Pleydell. These remains were derived from the Kimmeridge Clay of Dorset.

Features which Mansell-Pleydell believed distinguished the remains from O. icenicus were: in the humerus, a relatively larger pre-axial distal facet (Mansell-Pleydell's post-axial facet), a relatively shorter total humeral length and an ulnar ("radial") facet terminating in a blunt and rounded, instead of a pointed, extremity. The two vertebrae were said to possess a distinct longitudinal ventral groove, supposedly not present in O. icenicus.

The characters of the humerus I find to be within the range of individual variation of the Oxford Clay specimens, and a ventral groove is, in fact, present (associated with two lateral keels) in the mid-trunk vertebrae of O. icenicus (see descriptive section). I would then agree with Appleby (1956) who synonymised O. pleydelli with O. icenicus.

When Seeley (1874) first described O. icenicus, he designated as holotype a specimen which is now in the British Museum (N.H.) catalogued as R.2133. Seeley figured what he interpreted as the right coracoid (ventral view) of the specimen which showed the usual (for Ichthyopterygia) notch in its lateral border, just anterior to the facet for the scapula; however, the coracoid also displayed a second, posterior notch in its lateral border immediately behind the glenoid. This notch was not seen in any other specimen of Ophthalmosaurus in the Leeds collection.

Although Seeley (1874) did not mention it, the left coracoid of R2133 was grossly and abnormally thickened, whilst the left scapula was similarly greatly thickened and deformed, and has the distal portion of the left clavicle completely fused to its diseased bone substance. The abnormality of the coracoids, in fact, led Seeley to misorientate the figured bone so that he interpreted the glenoid surface as the intercoracoidal, and vice versa. He also reversed the figured coracoid antero-posteriorly, interpreting the wide anterior notch as the posterior notch. In 1893 he decided the figured bone must be a left coracoid, with the result that the lateral inversion of the bone was corrected.

This abnormality has also led other authors to misinterpret the bones (Andrews 1910, Appleby 1956). My own interpretation of the type coracoids is that Seeley's (1874) figured coracoid, which is from the less diseased, right side of the pectoral girdle, is a right coracoid seen in ventral view, and that the anterior notch is wider than the posterior notch. It is possible to determine correctly the anterior edge of the bone by the fact that the antero-medial edge of the coracoid bears a facet, described in the descriptive section below, for articulation with the interclavicle.

Andrews (1910) took the double-notched nature of the type coracoids to be deformation as a result of the injury or disease afflicting the left-hand side of the pectoral girdle.

Appleby (1956), however, decided that this was not the case, and that the posterior notch could be taken as a valid taxonomic character. This decision was based on his discovery of an isolated pair of coracoids, from the Oxford Clay, which are housed in the Leicester Museum (L.M. 100'1949/20) (plate 3). These coracoids both displayed a posterior notch. Appleby believed that because neither coracoid showed abnormal thickenings or other evidence of disease, the notch must be a normal feature, and was therefore evidence that there were two ichthyosaur taxa in the Oxford Clay. He therefore maintained O. icenicus for BMNH R2133 and LM 100'1949/20, whilst erecting the new species O. monocharactus for all the remaining single-notched specimens, some forty-one individuals in the British Museum (N.H.), the Leicester, Peterborough and Hunterian museums.

Appleby's decision rests on the assumption that the remaining elements of the pectoral girdle of LM 100'1949/20 were free from disease and of normal form. Since only the coracoids of this specimen are preserved, I find this assumption rather bold.

A number of ichthyosaur taxa from the Lias display double-notched coracoids, for example species of Ichthyosaurus (McGowan 1974b). Within the Upper Liassic genus Stenopterygius, the presence of a posterior notch in addition to the anterior notch varies between individuals (McGowan 1979). The notch in the postero-lateral border of the coracoids of these taxa is always a widely open embayment which would, in life, have formed the ossified portion of the postero-lateral edge of the coracoidal plate.

The posterior coracoid notch in the two Ophthalmosaurus specimens, however, (plate 3; figure 34) differs considerably in form from this. In these specimens the notch is a deep invagination, with a narrow opening, which lies on the posterior, rather than the postero-lateral border. The left coracoid of LM 100'1949/20 shows that the opening may have been closed off by cartilage. The notch bites deeply into the coracoidal plate, partially severing the glenoid from the rest of the plate. This posterior notch, then, has more the appearance of a fenestration, or an incision in the coracoidal plate, rather than being merely an indentation of the postero-lateral border. No other ichthyosaur taxon possesses such a notch and I consider it most likely that the notch in both specimens is a result of rearrangement of muscle insertions and their adaptation to a pathological abnormality in the remainder of the shoulder girdle, as was assumed by Andrews (1910) and

Seeley (1874) for BMNH R2133. I therefore consider O. monocharactus to be a junior synonym for O. icenicus.

Holotype:

BMNH R2133, an incomplete skeleton of a large, well-ossified individual, lacking in parts of the skull, caudal vertebrae, some ribs, pectoral limbs, pelvic girdle and limbs. Collected by Mr. Alfred Leeds, and described by Seeley (1874), who based the new genus on the nature of the union of the bones of the pectoral girdle.

Figured	Seeley (1874, plates XLV, XLVI)
Figured	Andrews (1910, text figs. 9, 26, 33c; plate 1, figs. 11-15)
Figured	Appleby (1956, figs. 19, 20)

Syntype:

Seeley (1874) figured and described a left humerus and partial fore-paddle of an individual other than R2133. He did not identify the specimen, but Andrews (1910) recognised it to be BMNH R2134.

Figured	Seeley (1874, plate XLVI, fig. 3)
Figured	Andrews (1910, text fig. 36 A,B, C)

Type locality:

The holotype specimen is part of the collection of fossil reptiles made by Mr. Alfred N. Leeds, and as such was collected from one of the brick pits in the vicinity of the city of Peterborough, though the precise locality is not recorded. The brick pits are named in E.T. Leeds' (1956) book, and all lie south and east of the city, near the villages of Farcet, Yaxley, Fletton and Whittlesea.

Type horizon:

Upper Jurassic, Callovian Stage. Andrews (1910) states that the fossils in the Leeds collection were obtained from the lowest deposits of the Oxford Clay, from the Jason, Coronatum and Athleta zones (see Callomon, 1968), with the majority of fossils being derived from the Jason zone.

Diagnosis:

Member of the family Ichthyosauridae (order Ichthyopterygia, suborder Ichthyosauria, infra-order Ichthyosauri) possessing:

(1) Humerus with three distal facets, the anteriormost facet for articulation with a pre-axial accessory ossicle which supports a pre-axial accessory digit.

(2) Extremely large eye and narrow postorbital region. Quadratojugal reduced to splint which is barely visible on side of skull. (McGowan's (1974a) orbital ratio (diameter of orbit/jaw length) is 0.28 for largest known specimen, BMNH R3013. There is not enough material for calculation of standard deviation, but this value is large when compared to McGowan's (1974 a,b, 1976) figures for other taxa.)

(3) Clavicles meet in midline by means of an interdigitating suture with no overlap. (In the genera Stenopterygius (Johnson 1979) and Ichthyosaurus (McGowan 1974b), clavicles do not interdigitate, but overlap.)

Distribution:

Diagnostic material is known from the Oxford Clay of the Peterborough district, and also from the Kimmeridge Clay of the Oxford district, Wiltshire and Dorset.

Range:

Upper Jurassic, Callovian to Kimmeridgian Stages.

Referred specimens:

See Appendix for catalogue of referred specimens.

Description

THE BRAINCASE

Basioccipital (Figure 1)

The basioccipital is a massive bone forming the whole of the articular condyle. The condylar surface is circular in occipital aspect, with a slight embayment dorsally for the foramen magnum. Two further embayments, for the exoccipital facets, are developed to a variable degree on either side of the foramen magnum. The condyle itself is convex, with a small central notochordal pit, and its bone surface is irregular, indicating the presence, in life, of articular cartilage. On either side of the condyle are two elongate, slightly concave regions of smooth periosteal bone which are broadly visible in occipital view. Ventrally these surfaces are prevented from meeting by a roughened surface to which cartilage was applied. In some specimens this ventral surface is raised above the level of the smooth surfaces flanking it.

At the lateral extremities of the smooth surfaces are developed facets for the opisthotic and the head of the stapes. The facet for the stapes is ventral to and larger than that for the opisthotic; its bone surface is deeply pitted indicating that a relatively thick pad of cartilage intervened between the two bones. The facet for the opisthotic is in two parts - a postero-dorsal deeply pitted portion, and a circular raised area of smoother bone ventral and anterior to this. When the basioccipital and opisthotic are articulated it can be seen that the cartilage between them becomes thinner in this antero-ventral region, indicating a thinning of the walls of the otic capsule. Just anterior to the surface for articulation with the opisthotic the basioccipital bears a small depression which is interpreted as part of the cochlear recess which housed the cochlear duct and associated portions of the periotic labyrinth (Baird 1970). McGowan (1973a) identified a similar depression on the basioccipital of Ichthyosaurus as the lagenar recess, the most antero-ventral portion of the cochlear recess.

The whole of the anterior face of the basioccipital is deeply pitted indicating a relatively thick covering of cartilage. The surface for contact with the basisphenoid is in the form of two oval bosses separated by a median groove of variable depth. When well developed, this groove causes a notch in the anterior edge of the ventral surface of the basioccipital, as shown by BMNH R4522 (figure 1). Above the basisphenoid facet is a diamond-shaped area which bears a small central pit. The bone here is occasionally drawn out anteriorly into a peg-like structure which bears the central pit at its anterior extremity. The peg is variably developed but is well-shown in HM V1070. It corresponds to the basioccipital peg of Ichthyosaurus (McGowan 1973a). but in this genus the peg has a more constant expression and is more completely ossified. The pitted, or notched tip of the peg marks the posterior limit of a vestige of the notochord which extended forwards in the floor of the cavum cranii to end on the posterior surface of the dorsum sellae.

The dorsal surface of the basioccipital bears two oval concavities, one on either side of the foramen magnum. The surfaces are irregularly pitted and had contact, via cartilage, with the exoccipitals. The floor of the foramen magnum is seen as a smooth, elongate, slightly concave raised area of bone lying between the exoccipital facets.

Basisphenoid (Figure 2)

The basisphenoid is fused ventrally to the base of the parasphenoid, and the division between the two bones is almost indistinguishable.

The surface on the basisphenoid for contact with the basioccipital is deeply and irregularly pitted indicating that a thick layer of cartilage intervened. Running dorso-ventrally across the whole of the posterior surface of the bone is a median groove (gr, figure 2d) which may be an indication of its original ossification from two lateral centres. The groove ends dorsally in a notch (no, figure 2) in the dorsal edge of the dorsum sellae, which may mark the anterior extremity of an upturned vestige of the notochord, as concluded by Andrews (1910) and McGowan (1973a)

The basisphenoid is pierced ventrally by the single, large carotid foramen which lies approximately in the centre of the ventral surface. On the lateral edges of the foramen, in some individuals, a trace of the suture with the parasphenoid is visible, showing that this element did not extend far posterior to the carotid foramen.

Laterally, the basisphenoid is drawn out into a pair of basipterygoid processes which bear laterally facing, deeply pitted surfaces. These processes were received in sockets on the pterygoid, and the presence of intervening cartilage might suggest that some movement was possible between the palate and braincase. The posterior ventral edge of each basipterygoid process bears a groove which appears to represent the path of a blood vessel or nerve which would seem to descend from the sidewall of the braincase to continue a course anteriorly, ventral to the basipterygoid process. Because of its close association with that process, and its relatively medial course ventral to it, the groove is interpreted as marking the path of the palatine ramus of the facial (VII) nerve.

Posterior to the basipterygoid process, the pitted lateral surface of the basisphenoid was in contact, via a thick pad of cartilage, with the anterior part of the head of the stapes. A contact with the stapes has not been previously recognised in Ophthalmosaurus.

The anterior face of the basisphenoid is largely of smooth periosteal bone. Two smooth, antero-dorsally facing surfaces continue from the main body of the bone onto the dorsal surfaces of the basipterygoid processes.

These surfaces are interrupted in the midline by the dorsum sellae and the sella turcica. The smooth surfaces line an extracranial space which is equivalent to the anterior part of the cranio-quadrate passage (Goodrich 1930), and which carried major blood vessels, serving the head, and the more posterior cranial nerves. It is possible that muscle slips of the extrinsic eye muscle group also extended onto these surfaces as in living crocodiles (Underwood 1970), but there is no evidence of scarring. In some specimens the surfaces are pierced by small nutrient foramina (figure 2).

The dorsum sellae rises as a vertical wall posterior to the sella turcica. Its dorsal edge is developed into two processes, separated by a notch, which are interpreted as ossifications in the base of the pilae antoticae. Opening at the base of the dorsum sellae is the foramen for the paired internal carotid arteries. The region between the carotid foramen and the dorsum sellae is usually termed the sella turcica, or pituitary fossa. As in living reptiles, the pituitary body would probably have been positioned well above the floor of the fossa (Hopson 1979), and arteries, venous sinuses and possibly extrinsic eye muscles would have occupied the actual floor.

Ventral to the pituitary fossa, on either side of the midline, are two ovoid depressions which mark the posterior limit of the paired trabecular cartilages. Just above these impressions, on each side of the carotid foramen, is a small pit which may be the point of origin of an eye muscle.

Parasphenoid (Figure 9)

The base of the parasphenoid is almost indistinguishably fused to the basisphenoid, so that its actual extent over the ventral surface of the basisphenoid cannot be determined. The anterior portion of the bone projects forwards as the slender cultriform process. In cross-section, the process is horizontally ovoid at its base, but it becomes deeper and narrower more anteriorly. Along the ventral surface of the posterior half of the cultriform process is developed a fine median ridge which fades by its midpoint. Just anterior to this point the sides of the process become pinched-in ventrally by facets for the pterygoids, and in this region the process assumes a diamond-shaped cross-section. The posterior half of the dorsal surface of the cultriform process is slightly concave and roughened, and along this surface would have lain the fused trabecular cartilages from which the septal cartilage develops. The trabecular cartilage impression narrows anteriorly and disappears at around the posterior limit of the pterygoid facets. The process itself narrows anteriorly as it passes between the pterygoids in the palate. No specimen of _Ophthalmosaurus_ known to me has a parasphenoid complete in its anterior section, but evidence from serial sectioning of _Ichthyosaurus_ (Sollas 1916) suggests that the process would have persisted for a short distance dorsal to the pterygoids after they had come together in the midline, and in _Ichthyosaurus_ the process ended at the level of the anterior edge of the internal narial opening.

Opisthotic (Figure 3a-e; Figure 7)

The opisthotic consists of a massive base, which takes part in the walls of the otic capsule, and a slender paroccipital process, which reaches towards and articulates with the skull roof. The whole of the ventral surface of the base of the opisthotic is roughened, and three distinct articular surfaces can be distinguished. The postero-medial corner of the ventral surface is deflected upwards to form a surface for articulation, via cartilage, with the basioccipital. When the opisthotic is articulated in the braincase, this surface faces medially and ventrally and also slightly posteriorly. The surface for articulation with the stapes is divided into two unequal parts by a groove which runs across the ventral surface of the bone. The function of the groove will be discussed in a later section.

Immediately above the basioccipital facet the medial edge of the opisthotic bears a notch which forms the lateral wall of the vagus foramen. The vagus foramen carried nerves X, XI and possibly also branches of nerve XII and the posterior cerebral vein. Above and below the vagus foramen the opisthotic had contact with the exoccipital; however, only in well-ossified individuals was this contact a close one, and only in these specimens does the opisthotic develop distinct facets for the articulation. The dorsal exoccipital facet, when present (e.g. BMNH R2161) is borne on a bony projection from the dorso-medial corner of the bone. The ventral facet is developed only rarely, but Appleby (1956) described a specimen (L.M. 100'1949/64) in which it can be seen.

The antero-medial face of the opisthotic displays impressions of the posterior components of the membraneous labyrinth of the inner ear. These take the form of two smooth-floored channels which become confluent antero-ventrally to form a V-shape. The more posterior channel is interpreted as the impression for the posterior vertical semicircular canal. The anterior channel curves slightly in its course through the bone, and when the opisthotic is articulated in the braincase it can be seen that the curve brings the channel into a horizontal plane (see figure 7). The channel is interpreted as the impression for the horizontal semicircular canal. The posterior vertical canal impression widens as it reaches the point of confluence of the two channels, and this widening is interpreted as the impression of the posterior ampulla. At this point the horizontal canal would probably have passed internally to the posterior ampulla. The opisthotic bone becomes thinner in this region of the posterior ampulla, indicating a thinning of the walls of the otic capsule. Just anterior to the ampullary recess the ventral internal edge of the bone is notched by the groove across its ventral surface. Surrounding the smooth-floored impressions of the labyrinth, the bone surface is irregularly pitted, indicating the walls of the otic capsule were continued in cartilage.

Laterally, the opisthotic bone is drawn out to form a slender paroccipital process, the dorsal surface of which formed the floor of the post-temporal fossa. Its ventral surface was also of finished bone and contributed to the roof of the cranioquadrate passage. The distal end of the process is roughened for the application of cartilage which intervened at its junction with the squamosal . In the majority of individuals, ossification of the tip of the paroccipital process is not extensive and the tip has a simple blunt ovoid form. In these individuals there is no distinct, well-ossified facet on the squamosal for the reception of the process. However, in well-ossified individuals, such as BMNH R2133, and LM 100'1949/64, the distal end of the process is more complex, and takes the form of two distinct articular surfaces which articulate with a corresponding bipartite facet on the squamosal. Even in these well-ossified individuals, a thin layer of cartilage intervened between the two bones, and it is possible that a certain amount of movement took place between them.

The anterior surface of the opisthotic is roughened and raised into a series of ridges extending along the paroccipital process. Small nutrient foramina pierce the bone surface in this region, suggesting that muscle slips, possibly of the M. adductor mandibulae externus group, took their origin here. In living reptiles this muscle may originate from the otic capsule (Haas 1973).

Prootic (Figure 4c,d)

The prootic is a small, roughly rectangular bone whose edges were continued all round by the cartilage of the walls of the otic capsule. Because of this lack of bony contact with the rest of the braincase, and, furthermore, because of the dissociated nature of the material, it is not at first obvious to which side of the skull any one prootic bone belongs. Until the sidedness of the prootic is known, neither its correct orientation in relation to the rest of the braincase can be decided, nor can the two semicircular canal impressions on the internal surface of the bone be interpreted.

In determining the sidedness of the prootic I have referred to an acid-prepared Liassic skull which was embedded in a limestone nodule - Hancock Museum No. G.44.19. In this skull both prootics were preserved relatively undisturbed from their position in life. From comparisons with these prootics it was possible to conclude that the prootic in figure 4 (B.M.N.H. R4522) must be a right prootic. This decision allows an interpretation of the semicircular canal impressions to be made.

The canal impressions take the form of a V-shaped, smooth-floored excavation on the internal surface of the bone. The prootic is ossified in the antero-lateral region of the otic capsule, and it follows that one of the limbs of the V should have accommodated the anterior vertical canal, whilst the other limb enclosed the horizontal canal. In living forms the horizontal canal passes externally from its posterior utricular source to its anterior terminal ampulla which lies adjacent to the terminal ampulla of the anterior vertical canal (see Hamilton 1964, for a description of the inner ear of lizards). It follows, then, that the prootic must be orientated so that one of its canal impressions is directed posteriorly and externally to receive the horizontal semicircular canal. There is thus only one possible interpretation. The wider of the two channels on the prootic must have accommodated the horizontal canal, whilst the narrower canal, which swells ventrally to accommodate a terminal ampulla, must be for the anterior vertical canal. This agrees with McGowan's (1973a) interpretation of the prootic of Ichthyosaurus, and, as McGowan pointed out, it disagrees with

Appleby's (1956, figure 4) interpretation of the prootic of Ophthalmosaurus. Appleby had reversed the names of the two canals and the sidedness of the bone, so that, under his interpretation, the horizontal canal would have been directed posteriorly, but internally to the rest of the otic capsule.

At the point of confluence of the two canal impressions, near the ventral edge of the bone, there is a widening of the impression which may represent the position of the sacculus of the otic labyrinth. Appleby (1956) figures a division into two parts of this ventral saccular impression. The additional impression appears to be a continuation of the horizontal canal impression, after it has apparently passed internally to the ampulla of the anterior vertical canal. I interpret it as part of the utriculus - I think it more unlikely that it is, as Appleby has suggested, part of the foramen for the auditory (VIII) nerve.

The edges of the prootic are irregularly pitted and represent cross-sections of the walls of the otic capsule which were continued in cartilage. The walls can be seen to be thickest in the most ventral corner of the bone. This point corresponds to the ventralmost point of a low ridge on the external surface of the prootic. The ridge runs parallel to the most medial edge of the bone, and its surface is roughened and pierced by small nutrient foramina which spread over much of the surrounding bone surface. These features are taken as an indication that muscle slips took origin from the external surface of the prootic. The muscles in question may have been either part of the M. adductor mandibulae externus, or the M. protractor pterygoidei, both of which may take origin from the prootic bone in living reptiles (Haas 1973). McGowan (1973a) did not find any evidence of muscle origins from the prootic bone of Ichthyosaurus.

Supraoccipital (Figures 6 and 7)

The supraoccipital forms an arch above the foramen magnum and also takes part laterally in the walls of the otic capsule. It contacts the exoccipitals ventrally and underlaps the parietal dorsally, but, because of incomplete ossification of the otic capsule, it does not contact either the opisthotic or prootic.

The ventral facets on the supraoccipital for contact with the exoccipitals are roughly triangular in shape, with their apexes directed anteriorly. These facets are concave, fitting closely the convex dorsal surfaces of the exoccipitals, and it is apparent that only a thin layer of connective tissue intervened. The posterior face of the supraoccipital is of smooth, finished bone, but its smooth relief is interrupted on either side of the foramen magnum by two large foramina which lie in shallow depressions. Lateral to these depressions the edge of the supraoccipital is notched at a point immediately above the capsular portion of the bone. The foramina pierce the bone forming intraosseous canals which diverge outwards from the endocranial cavity: their possible function will be discussed below.

The broad dorsal edge of the supraoccipital faces anteriorly and dorsally; it is hollowed and pitted indicating that it was continued in cartilage which extended forwards below the parietal bones of the dermal skull roof for a short distance. Laterally, the dorsal edge of the bone curves downwards and lies in the same plane as the laterally facing capsular portion, but is separated from it by the lateral notches mentioned above. The capsular portion of the supraoccipital faces ventro-laterally and also anteriorly, and bears impressions of the internal and dorsal parts of the membraneous labyrinth of the inner ear. The impression takes the form of a T-shape, with its stem directed antero-ventrally. These impressions are interpreted as having accommodated the posterior vertical and anterior vertical semicircular canals at their point of common origin from the common crus, which has moulded the stem of the T.

The internal surface of the arch above the foramen magnum is variable in form, as was pointed out by Appleby (1956) and Andrews (1910); in some individuals, for example, BMNH R2161, a blunt median process projects into the opening of the foramen: its significance will be discussed below. In the majority of specimens the supraoccipital arch opening is constricted ventrally by an ingrowth of the sides of the arch, just above the junction with the exoccipitals. These ingrowths are the lateral processes of Andrews and Appleby. The projecting bone surfaces are roughened, suggesting that cartilage or ligaments may have been present reaching across the archway, thus cutting off the supraoccipital arch-opening from the rest of the foramen magnum below it. Andrews (1910) similarly suggested that the actual neural canal was restricted to that part of the foramen magnum lying ventral to the lateral processes. This would seem reasonable in view of the fact that the complete archway formed by both supraoccipital and exoccipital looks rather too vertically elongate to have functioned solely as an opening for the nerve cord.

It seems reasonable to suppose that the supraoccipital part of the archway transmitted structures other than the nerve cord. I would suggest that the paired posterior cerebral veins may have exited from the braincase here, after having left the longitudinal venous sinus which lay beneath the roof of the cranium. The bipartite form of the roof of the arch seen in some individuals would support this interpretation. In living reptiles, the posterior cerebral veins may exit through the foramen magnum, or the vagus foramen, which is a remnant of the fissura metotica, or both.

It is possible that the pair of foramina piercing the supraoccipital could serve as an additional exit for the veins from the longitudinal venous sinus, and in this way they would carry out a similar function to the vagus foramen of living forms. The Liassic genus Ichthyosaurus (McGowan 1973a) does not have a deeply excavated supraoccipital and it is possible that in this genus only the lateral exit was used. A second possible interpretation of the function of the supraoccipital foramina is that they allowed passage into the cranial cavity of the vena capitis dorsalis. This vein drains the tissues of the occiput and primitively ran through the post-temporal fenestrae along the side of the braincase for a distance before entering the transverse sinus within the endocranial cavity (Romer 1956). In other reptiles the point of entry into the braincase is anterior to the supraoccipital ossification. It is possible that in Ophthalmosaurus and Ichthyosaurus the vein entrance has moved posteriorly and has become "trapped" in the lateral edge of the supraoccipital.

McGowan (1973a), following the interpretation of Andrews (1910), suggests that the foramina carried extensions of the endolymphatic sac. Such extensions are known among living lizards in members of the Ascalabota, Iguanidae and Gekkonidae. Here the enlarged sac protrudes from the braincase between the parietal and supraoccipital bones or through the vagus foramen, and lies in the tissues of the neck. The functions of the sac and the significance of its enlargement are poorly understood (Kluge 1967). Until a better understanding is reached in living forms, the possibility that ichthyosaurs had acquired similar specialisations remains, however speculative this interpretation may be.

Exoccipital (Figure 5e,f)

The exoccipitals form two short pillars on either side of the foramen magnum. They contact the basioccipital ventrally via oval facets which are drawn out anteriorly into tongue-like projections. The pitted surfaces of these facets indicate that cartilage intervened. Dorsally each bone has a much closer bony contact with the supraoccipital. This articular surface is smoother, and slopes downwards anteriorly to follow the contour of the ventral surface of the supraoccipital. Lateral to the supraoccipital facet the dorsal surface of the exoccipital slopes downwards and makes contact with the opisthotic. Below this union the two bones diverge, to enclose between them the vagus foramen, before again making contact along their ventral edges. Close bony contact between the exoccipital and opisthotic only took place in well-ossified individuals: in most cases cartilage intervened. The medial face of each exoccipital bone is pierced anteriorly by a pair of foramina which are interpreted as points of exit for branches of the hypoglossal (XII) nerve. Each branch follows a course running postero-laterally through the bone before emerging - the larger branch onto the posterior face of the bone, whilst the smaller branch exits via a more lateral foramen which opens into the vagus foramen. The posterior face of each exoccipital bears a low ridge extending obliquely downwards from the dorsal medial edge of the bone. The ridge has a roughened summit and it may be interpreted as a site for the insertion of occipital muscles.

Stapes (Figures 5a-d and 6)

Although embryologically a hyoid arch derivative, the stapes forms an integral part of the braincase, and it is convenient to treat it here. The stapes is a massive bone consisting of a large head, which articulates with the braincase, and a slender shaft reaching ventro-laterally to contact the quadrate. There is no stapedial foramen.

The head of the stapes does not fit into a conventional fenestra ovalis, but, instead, abuts against broad surfaces on the basioccipital and basisphenoid. The articular surfaces on these bones and on the corresponding proximal surface of the stapes head are irregularly pitted, and it is clear that pads of cartilage intervened. Only a small area of the stapes head could have come into close association with the perilymphatic cistern; the greater part of the bone surface of the head was applied to the basioccipital and basisphenoid.

Dorsally the head of the stapes articulates with the opisthotic. The surface for articulation is divided into two parts by a groove which is directed obliquely forwards towards the endocranial cavity. The groove corresponds in position to a similar groove on the ventral surface of the opisthotic, so that when the two bones are articulated, they enclose a channel, the possible function of which will be discussed below.

The dorsal surface of the stapes, lateral to the opisthotic facet, is of smooth bone and is continuous anteriorly with the smooth lateral surface of the basisphenoid. The stapes thus lies in the posterior part of the floor of the cranioquadrate passage; over its dorsal surface would have passed the vena capitis lateralis; the hyomandibular branch of the facial (VII) nerve also emerged onto the dorsal surface. The shaft of the stapes lies against the posterior edge of the quadrate ramus of the pterygoid, which is here overlapped by a ventral flange from the squamosal. In well-ossified individuals a distinct facet is developed on the anterior face of the stapes shaft. BMNH R2133 shows the stapes, quadrate, squamosal and pterygoid in articulation, and it is clear from this specimen that the facet on the stapes articulates largely with the squamosal, and has only a small contact with the pterygoid. The facet on the stapes is seen as a rugose area reaching from the distal end of the bone almost the full length of the shaft. Dorsally the rugosity ends in a ridge which twists ventrally on the shaft as it nears the stapes head. The facet for the pterygoid and squamosal has not been noted on the stapes of Ophthalmosaurus by previous authors.

The stapes has a second contact with the pterygoid along the ventral edge of the stapes head which rests on the dorsal surface of the medial flange of the pterygoid. There is no distinct facet, however, on the stapes for this contact. Between this proximal contact and their more distal union, the stapes and pterygoid enclose a space which may have allowed passage for the stapedial artery. In primitive reptiles, such as pelycosaurs and captorhinomorphs, the stapedial artery pierces the stapes; in the majority of modern forms, however, there is no stapedial foramen, and the artery passes forwards either above or below the stapes. Appleby (1961) reconstructed the stapes-pterygoid contact as leaving no space for the passage of the stapedial artery, and he concluded it must have passed forwards above the stapes. As reconstructed here, however, there is a space below the stapes and above the pterygoid, which could have accommodated the artery: no other structure is likely to have taken this course. On the anterior edge of the stapes head, there is a slight notch which may mark the course of the artery as it ascended, after having passed below the stapes, to pass over the basipterygoid process.

The postero-ventral edge of the stapes shaft normally bears a tubercle, which Appleby (1961) suggested might be for the attachment of a hyoid ligament. The tubercle shows a variable degree of development, even between the right and left sides of the same individual (HM V1893). The stapes of Ichthyosaurus is angulate and roughened in the same position, and it was suggested by McGowan (1973a) that this was a site of muscle origin. I would similarly interpret the tubercle in Ophthalmosaurus to be for muscle origin. One specimen, BMNH R4522, shows a second projection from the head of the stapes which I suggest might have connected with the ceratohyal of the hyoid apparatus, and can, therefore, be regarded as the homologue of the hyoid process which is present in the development of all extant reptile groups (Lombard and Bolt 1979). The summit of this process is pitted for the attachment of cartilage, and is directed ventro-laterally. Just lateral to it on the shaft is a roughened area of bone which is pierced by small nutrient foramina, and this appears to be the equivalent of the muscle tubercle in other specimens. The hyoid process of R4522 appears to be joined by a ridge to the postero-ventral corner of the stapes head; this feature suggests that when, in other individuals, the process is not a distinct structure, it is in fact coalesced with the postero-ventral corner of the stapes head (see figure 6).

The distal extremity of the stapes ends in a flat, triangular facet, directed laterally and slightly anteriorly, which articulated with the stapedial pit on the quadrate. The bone surface is pitted for the application of intercalary cartilage which intervened in this union.

It was pointed out above that when the stapes and opisthotic are articulated, they enclose a channel which is directed antero-medially towards the endocranial cavity. Possibly as a result of poor ossification, McGowan (1973a) found that in Ichthyosaurus the channel was marked only as a groove on the stapes, and left no mark on the opisthotic. Because of its close association with the stapes head, he concluded the groove transmitted the stapedial artery which, he suggested, gained access to the endocranial cavity after passing over the stapes head. Such a course is unknown among living reptiles: the stapedial artery passes forwards extracranially along the lateral wall of the braincase. The channel is therefore more likely to have transmitted a nerve outwards from the brain cavity.

When the otic capsule is reconstructed (see below), the channel appears to emerge from the ventralmost region of the otic capsule in the vicinity of the cochlear recess of the osseous labyrinth of the inner ear. This suggests the channel may have transmitted the glossopharyngeal (IX) nerve, as suggested by Andrews (1910) and Appleby (1956). In the majority of living reptiles the nerve passes out behind the otic capsule and exits from the skull via the vagus foramen. In some forms, however, such as the Scincidae and some turtles, the nerve takes an intra capsular course through the cochlear portion of the otic capsule before emerging from the skull via a separate foramen (Bellairs and Kamal 1981). If this interpretation is correct, the stapes of Ophthalmosaurus is unusual both in its position immediately ventral to the exit of the ninth cranial nerve and in its close association with this nerve as it runs across the stapes head.

One further possible interpretation is that the foramen transmitted the hyomandibular branch of the facialis (VII) nerve, which in living reptiles exits from the anterior edge of the otic capsule (Stark, 1979; Hopson 1979). The relationship between the nerve and the stapes head would seem to agree with this interpretation. The hyomandibular branch of the facialis nerve, after leaving the cranium, normally passes backwards over the head of the stapes, medial to the dorsal process. If this is the correct interpretation, then the anterior half of the facet on the stapes for the opisthotic could be the equivalent of the dorsal process. The choice between these two possible interpretations - that the foramen was the exit either of nerve IX or VII - depends on whether the nerve exited anterior to or posterior to the otic capsule. Unfortunately, because of incomplete ossification of the capsule, this cannot be distinguished.

PALATAL COMPLEX

Quadrate (Figure 8)

The quadrate consists of a medial pterygoid lamella and a lateral occipital lamella which is visible in occipital view and bears the articular condyle ventrally. Laterally this occipital lamella is embayed to form the quadrate foramen. The quadrate is orientated vertically in the skull and the occipital lamella lies in a transverse plane which faces posterolaterally, whilst the pterygoid lamella faces postermedially.

The whole of the dorsal and medial edge of the quadrate is of irregularly pitted, unfinished bone, indicating they were continued in cartilage. Anteriorly this cartilage would probably have reached the epipterygoid, though this bone has never been identified in Ophthalmosaurus. Dorsally the cartilage articulated with the squamosal by slotting into its deeply grooved ventral surface. The medial face of the pterygoid lamella is roughened, and the ventral two thirds of this face was closely applied to the quadrate flange of the pterygoid, with the exception of a small area which received the stapes. The dorsal one third of the pterygoid lamella was overlapped by a flange from the squamosal.

The stapes facet is an oval recess situated roughly midway up the medial face of the pterygoid lamella, near the angle between this lamella and the occipital lamella. The posterior edge of the recess is raised into a roughened ridge to which may have attached ligaments from the stapes. The floor of the recess shows an irregular growth of unfinished bone which probably indicates the attachment of the short intercalary cartilage which lay between the stapes and quadrate. Ventral to the stapedial recess, in well-ossified individuals, there is present a raised tubercle, which in some cases takes the form of an elongate ridge. The surface of which is perforated by minute foramina. It is positioned at the edge of the overlapping pterygoid and it is interpreted as the point of origin of ligaments binding the quadrate to the pterygoid.

The internal, or anterior, face of the quadrate forms a smoothly concave surface which makes a large contribution to the hindwall of the adductor chamber. It is likely that from this surface arose the M. adductor mandibulae posterior, and usually a central depression is visible which may mark its origin. In some individuals, e.g. HM V1899, a second more dorsal depression is distinguishable which may mark the origin of part of the M. adductor mandibulae externus complex, which may take origin here in living reptiles (Haas 1973) and in the primitive reptile Eocaptorhinus (Heaton 1980).

The condylar surface of the quadrate is irregularly pitted for the application of articular cartilage. The condyle consists of two elongate bosses separated by a groove. The more mesial region of the condylar surface faces ventrally and the bosses and groove are approximately transversely orientated. Laterally, however, the condylar surface curves both dorsally and anteriorly so that the lateral portion faces more laterally, and the bosses and groove become anteriorly orientated. The more posterior boss is the larger of the two and articulates mainly with the concave anterior face of the articular bone, whilst the smaller anterior boss articulated with the antero-lateral part of the glenoid fossa of the lower jaw, formed on the surangular bone.

Immediately above the condylar surface the lateral edge of the quadrate bears a rugose facet for the quadratojugal, and above this facet the lateral edge is emarginated for the large quadrate foramen. The dorsal tip of the quadratojugal meets the cartilage-covered lateral edge of the quadrate again above the foramen. Through this foramen would have passed a vein from the upper jaw (Romer 1956).

Dorsally on the occipital face of the quadrate a change in the surface texture of the bone may mark an area of overlap by the lateral lamina from the squamosal.

Epipterygoid

No example of this bone has been recognised amongst the known Ophthalmosaurus material. It is ossified in the genus Ichthyosaurus (McGowan 1973a), but it is not certain whether its absence in Ophthalmosaurus is due to its failure to ossify, or to its loss during collection.

Pterygoid (Figures 9 and 6)

The pterygoids are the largest elements in the dermal palate. Each is composed of an anterior sheet-like palatal ramus, and a more complex posterior quadrate ramus. In its posterior section, bordering the interpterygoid vacuity, the mesial margin of the bone is thickened and rounded. More anteriorly, however, this margin develops a thin ventral shelf which is roughened for its contact with the parasphenoid rostrum. The original rounded thickening of the medial margin increases in height anteriorly and becomes sharper; this coincides with a narrowing of the palatal exposure of the bone so that in this anterior region the pterygoid lies in a vertical rather than a horizontal plane. In this anterior region the two pterygoids unite ventrally, and hold between them the parasphenoid rostrum which is excluded from palatal view and probably persists until the level of the anterior edge of the internal naris (Sollas 1916). The lateral edge of the palatal ramus of the pterygoid is sharply angled posteriorly as it forms the anterior border of the subtemporal fenestra. At this point on the pterygoid, there is usually developed, in other reptile groups, a descending transverse flange. This flange is not present in any known ichthyosaur. The presence of a transverse flange of the pterygoid is usually taken to be a primitive reptilian character and it may have developed as an aid to inertial feeding (Heaton 1980).

The ventral surface of the pterygoid, inside its postero-lateral angle, bears a rounded depression which may mark the point of origin of muscle slips from the M. adductor mandibulae internus pterygoideus, which in living reptiles may originate from both the dorsal and ventral surfaces of the pterygoid (Haas 1973). In front of this region the pterygoid contacts the palatine via an interdigitating transverse suture. Anterior to this the lateral edge of the pterygoid contacts the vomer by a simple narrow overlap onto the medial edge of the latter bone. This edge of the pterygoid bears fine serrations for this union. More anteriorly, the relationship of the two bones reverses and the mesial edge of the vomer comes to lie on a narrow shelf developed on the ventral edge of the thin anterior extension of the pterygoid. The curved lateral surface of the pterygoid above this shelf is closely held by the medial surface of the vomer. Thin anterior extensions of the pterygoids persist for a short distance applied to the mesial surfaces of the vomers, excluded from the palatal surface by the union of the latter bones along the midline of the palate. Evidence from serial sectioning of Ichthyosaurus (Sollas 1916) suggests that the pterygoids may have persisted for a short distance anterior to the internal naris, though their anterior extremities are unknown in Ophthalmosaurus.

The quadrate ramus of the pterygoid is separated from the palatal ramus by a neck formed by emarginations for the sub-temporal fenestra laterally, and the interpterygoid vacuity mesially. The quadrate ramus is drawn out into three winged processes extending laterally, mesially and dorsally. The lateral and dorsal wings together form a flat surface, facing laterally, dorsally and slightly anteriorly, against which lay the pterygoid lamella of the quadrate. A flange from the squamosal overlaps the mesial surface of the dorsal wing, and this flange also wraps around the anterior edge of the wing which is serrated for this contact. Near its base, the posterior edge of the dorsal wing of the pterygoid has a brief contact with the shaft of the stapes.

The mesial wing of the quadrate ramus extends mesially as a shelf beneath the stapes to contact the ventral surface of the basisphenoid. The shelf thus formed would serve as a bony floor to the cranioquadrate passage and, presumably, the middle ear cavity.

The anterior edges of the mesial and dorsal wings of the pterygoid come together to form a socket into which fits the basipterygoid process of the basisphenoid.

During the course of this study I have not found any trace of a facet on the pterygoid for the epipterygoid, further suggesting that this element may have remained unossified in Ophthalmosaurus.

The posterior edge of the mesial and lateral wings of the quadrate ramus bears strong irregular serrations and pittings which extend onto the ventral surface of the bone. These are interpreted as the marks of muscle slips of the subvertebral group of the hypaxial series, which in other reptile groups normally insert on the basal tubera. Pronounced basal tubera are not present in Ophthalmosaurus, and it may be that these muscles have migrated onto the pterygoid.

Palatine (Figures 9 and 10)

The palatines have previously been poorly known in Ophthalmosaurus. Andrews (1910) only tentatively identified a pair of bones (BMNH R4693-5) as palatines. My own study has supported this identification, however, I consider the bone figured by Andrews (figure 18) as a right palatine to be in fact from the left side. Appleby (1956, figure 11) figured a bone which he identified as a right palatine of specimen P8 (R220). Having studied this specimen, I consider the bone to be a left vomer, seen in dorsal view in his figure. Other specimens of the Leeds collection which were unavailable to Andrews, and which include palatine bones are BMNH R4753 and HM V1129. Although, because of the delicacy of this palatal element, these palatines are poorly preserved, it is possible, by comparisons with Lower Jurassic forms (McGowan 1973a), to reconstruct the form of the palatine with reasonable certainty (figure 10).

The palatine is an elongate, plate-like bone on the lateral edge of the dermal palate. Anteriorly, the bone divides into two tongue-like projections which form between them the posterior, lateral and much of the mesial border of the internal naris. In its posterior section, the palatine meets the pterygoid in a transverse interdigitating suture. Along its mesial border it contacts the vomer by a simple overlap onto that bone. Anteriorly, at the point of division into two anterior projections, the mesial edge of the palatine develops a small shelf which runs beneath the vomer. The edge of the palatine here twists upwards and expands as the mesial anterior projection which lies flat against the lateral surface of the vertical expansion of the vomer. The surface which contacts the vomer is rugose and finely ridged and faces ventro-mesially.

In its most posterior region, the lateral border of the palatine is free from contact with surrounding bones, but more anteriorly it develops a complex, tongue-and-groove suture with the maxilla. The thin lateral anterior projection of the palatine extends forwards along the mesial edge of the maxilla.

The mesial and lateral anterior projections of the palatine form the sharply angled posterior border of the internal naris. In the angle of the naris the lateral projection develops, from its dorsal surface, a blunt tubercle of bone which may have aided in the support of the tissues forming the walls of the nasopharyngeal duct.

Both the dorsal and ventral surfaces of the palatine are pierced by a number of foramina which are particularly numerous on the dorsal surface around the narial border. It is likely that they transmitted the nerves and blood vessels supplying the nasal tissues - possibly these were branches of the nasal artery and palatine nerve. A series of grooves running across the dorsal surfaces of the palatines of BMNH R4753 probably served the same function.

Vomer (Figures 9 and 11)

Like the palatine, this bone has previously been poorly known in Ophthalmosaurus. Andrews (1910) again only tentatively identified one incomplete example of this bone amongst the Leeds collection material.

Other specimens, not then available to Andrews, show his identification to be correct (HM V1129, BMNH R4753). Andrews had, however, misorientated the bone, so that his figure 19 is in fact a right vomer, rather than a left; and the palatal surface shown by Andrews is actually the dorsal edge of the vomer.

The vomer is a very long, narrow element in the anterior region of the palate. In its midsection, it develops a vertical expansion, from its dorsal surface, which forms much of the mesial border of the internal naris. No vomer is complete posteriorly, but evidence from a Liassic skull, BMNH 33157, which is preserved in the round, has enabled me to produce the reconstruction in figure 9.

The thin posterior extremity of the vomer would probably have been wedged between the palatine laterally and the pterygoid mesially. More anteriorly the vomer widens, maintaining its contact with the latter two bones. This union was by a very narrow overlap of the edges of the vomer onto the bones beneath. Such a contact could not have been strongly bound. More anteriorly, however, in the vicinity of the vertical expansion of the vomer, the surface area of contact increases and the facets become rugose, reflecting a stronger union. In HM V1129, the facet for the pterygoid is seen as a broad, elongate channel running along the ventral edge of the mesial side of the vertical expansion. The channel continues, becoming narrower, along the medial surface of the tapering anterior extension of the vomer. The floor of the channel is evenly rounded, but is marked by numerous striations. The lateral surface of the pterygoid is held closely in this channel, and the union is further strengthened by the presence of a groove along the ventral edge of the vertical expansion into which the pterygoid slots.

The facet for the mesial projection of the palatine is seen as a roughening in the posterior region of the lateral surface of the vertical expansion. The vertical expansion of the vomer takes the form of a thin vertical sheet lying in a sagittal plane. In lateral view it is seen to have an irregular outline. In the well-ossified BMNH R4753 the vertical expansion is seen as a relatively complex structure. In lateral view its surface is divided into two shallowly concave areas, one posterior and one anterior, by an oblique ridge which originates at the highest point of the dorsal edge of the bone and descends anteriorly to the ventral surface. The ridge is highest in its dorsal region, and here its summit is pulled out into a series of three spinous projections which point in a dorso-lateral direction. Immediately below the projections the ridge flattens out to a low gentle fold and lies in the floor of what appears to be a channel connecting the anterior and posterior concavities.

The ventral border of the vomer in the region of the posterior concavity forms the mesial edge of the internal naris. Rising vertically from this edge the posterior concavity is interpreted as the mesial wall of the functional equivalent of the choanal tube of Sphenodon and modern squamates (Parsons 1970). It is thus the morphological homologue of the vomerine cushion. The choanal tube of living reptiles is that portion of the cavum nasi proprium which lies ventral to the concha, and which forms a direct air passage between the vestibulum and the choana; it does not have a sensory function and is therefore lined by non-sensory respiratory epithelium. I interpret the anterior concavity of the vomer as forming part of the floor and medial wall of the vestibulum nasi. The vestibulum is the non-sensory entrance chamber leading from the external naris to the cavum nasi proprium. The low ridge between the anterior and posterior concavities is interpreted as the morphological homologue of the post-vestibular ridge. A reasonable interpretation of the function of the spinous projections on the vomer might be that they gave support to the soft tissues of the nasal capsule.

The anterior half of the vomer has contact with its own counterpart medially and with the premaxilla laterally. The surface for contacting the premaxilla is developed at about the level of the anterior concavity as an elongate, roughened facet on the rounded ventral edge of the vomer. Anteriorly this facet extends along the whole length of the lateral surface of the bone, but loses its rugosity. The vomers meet one another along their medial surfaces a little in front of the premaxillary facet, and in so doing they exclude the pterygoids from palatal view. These latter bones persist for a short distance above the vomers before ending.

The thin, tapering anterior extensions of the vomers become flattened bars inclined dorso-laterally to lie flat against the mesial surfaces of the premaxillae. They continue anteriorly running between the premaxillae for about half the length of the latter bones. From BMNH R3893 it appears that they do not become excluded from the palatal surface by union between the premaxillae as do the vomers of Ichthyosaurus (Sollas 1916); but instead they are held between the ventral edges of the premaxillae.

THE SKULL ROOF

Squamosal (Figures 6, 12, and 13)

The squamosal is a bone of complex shape which lies at the posterior corner of the skull roof and forms the posterior boundary of the temporal vacuity. It can be described as being composed of three main rami, lateral, medial and ventral in their orientation. The lateral ramus forms the posterior half of the lateral border of the temporal opening and unites with the postfrontal anteriorly by a strong interlocking tongue-and-groove joint which strengthens an otherwise weak point in the border of the temporal opening. The ventral edge of the lateral wing of the squamosal is thickened and roughened posteriorly forming a facet against which abuts element B (for an explanation of the nomenclature of this bone, see Chapter 3, section 2). Above this facet the lateral surface of the squamosal bears a shallow groove which received an overlap from element B. More anteriorly the internal surface of the ventral edge of the squamosal is roughened to receive the dorsal edge of the postorbital which underlaps here. The sharp dorsal edge of the lateral ramus is finely striated on its inner surface. These markings may indicate the origin of part of the M. adductor mandibulae externus, which in Sphenodon and living lizards may take origin here (Haas 1973).

The mesial ramus of the squamosal is a thickened bar of bone which abuts against and overlaps onto the postero-lateral end of the parietal. Again this contact is strengthened by a series of ridges and grooves. Two deep grooves on the ventral surface of the squamosal receive a pair of prominent ridges on the parietal. The mesial ramus tapers anteriorly along the posterior edge of the parietal.

Projecting from the occipital surface of the mesial ramus of the squamosal is a small horizontal shelf of bone which receives the paroccipital process in a facet developed on its ventral surface in the angle formed between the shelf and the main body of the bone. This facet is relatively smooth and difficult to distinguish in the majority of individuals, but in well-ossified specimens the facet becomes complex. In these cases (BMNH R2133, R4753) it appears as two separate facets: one on the ventral surface of the bony shelf, and one smaller facet on the main body of the squamosal. The distal end of the paroccipital process bears a corresponding double facet for the articulation.

In the middle of the occipital face of the squamosal there is present a prominent tubercle which may be flanked by a smaller tubercle. The bone surface surrounding these tubercles is marked by fine striations radiating outwards from them. The tubercles are taken to represent a major site of origin for the M. depressor mandibulae which in living reptiles originates from the dorsal occipital surface (Haas 1973).

The ventral ramus of the squamosal is developed as a series of laminae which in effect wrap around and hold much of the dorsal and anterior edge of the quadrate. The most extensive lamina, the mesial lamina, extends down the mesial surface of the pterygoid lamella of the quadrate. In BMNH R2133 (figure 6) this lamina is split for the entrance of a small blood vessel to the quadrate beneath. Ventrally the lamina overlaps the dorsal edge of the pterygoid and, at its most ventral limit, the lamina intervenes between the pterygoid and the shaft of the stapes, developing a facet for the latter bone. More anteriorly the mesial lamina wraps around the anterior edge of the quadrate, and in so doing it also envelops the dorsal edge of the pterygoid. A number of tubercles, which may mark the origin of fibres from the M. adductor mandibulae externus complex, are developed on the folded anterior edge of the mesial lamina.

The dorsal edge of the occipital face of the quadrate is covered laterally by the short, lateral lamina of the squamosal. The lateral edge of this lamina is notched to expose the lateralmost tip of the dorsal edge of the quadrate. The latter bone slots between and is held by the laminae of the ventral ramus of the squamosal which form a deep groove for this purpose (figure 13). Much of the depth of this groove was filled by the cartilage capping the dorsal edge of the quadrate.

Parietal (Figures 12 and 13)

The parietal forms the mesial boundary of the upper temporal fenestra. From its postero-lateral edge extends a thickened bar of bone which is overlapped by the squamosal - the union between the two bones being achieved by strong ridges and grooves. The ventral surface of the thickened bar forms the roof of a slit-like opening which is the equivalent of the post-temporal fenestra of primitive tetrapods.

Just mesial to the postero-lateral bar, projecting from the main body of the bone, is a narrow shelf which overlaps onto the dorsal surface of the supraoccipital. At the junction between the main body and the shelf, the dorsal surface of the parietal bears a roughened depression which may have served for the attachment of occipital muscles of the dorsal axial series.

The main body of the parietal unites with the corresponding bone of the opposite side in the midline by a complexly grooved and thickened facet. Anterior to the facet the two bones diverge allowing posterior extensions of the frontals to intervene. At this point the parietal takes part in the parietal, or parapineal, foramen.

The whole of the anterior region of the parietal is overlapped to a considerable degree by the frontal, whose overlapping posterior edge interlocks with the dorsal surface of the parietal along an irregular line. The antero-lateral edge of the parietal has contact with both the prefrontal and postfrontal bones by a complex system of interlocking laminae; however, the contact with the prefrontal is obscured from dorsal view by the overlapping postfrontal and frontal. The prefrontal sends a narrow tongue posteriorly to reach towards the superior temporal opening. This tongue slots between two laminae developed on the antero-lateral corner of the parietal, and as it does so its posteriormost tip enters the border of the temporal opening. The dorsalmost lamina of the parietal overlaps the prefrontal to only a small degree, and it is itself overlapped by the frontal; but the ventralmost lamina is drawn out anteriorly into a long point which runs along the orbital ridge on the ventral surface of the prefrontal (figure 13). The facet on the parietal for contact with the postfrontal is small in area: it is developed on the dorsal surface of the parietal just above the point where the prefrontal enters the temporal opening. The postfrontal abuts onto this facet in a simple overlap. This postfrontal-parietal contact is almost completely obscured on the dorsal surface of the skull roof by the overlap of the postero-lateral corner of the frontal onto the postfrontal.

It can be seen from the foregoing account that at this small point in the border of the temporal opening a total of four bones come together in a system of interlocking layers. A vertical section through the skull roof at this point would reveal a maximum of five layers of bone - from dorsal to ventral these would be the frontal, postfrontal, parietal, prefrontal and parietal. It would seem that a series of laminae such as this would lend great strength to an otherwise weak point at the junction between bones surrounding the temporal opening.

The lateral edge of the parietal curves downwards at the border of the temporal opening, thus sheathing dorsally the lateral wall of the braincase, and providing an extra bony surface for the attachment of the jaw adductor muscles. The lateral edge is drawn down as a pointed descending process developed midway along the bone. The ventral tip of the process probably united with the epipterygoid, which may have remained unossified; such a contact occurs in Ichthyosaurus (McGowan 1973a). Andrews (1910) interpreted a deeply grooved region on the ventral surface of the parietal, just anterior to the descending process, as the facet for the epipterygoid. The condition in Ichthyosaurus makes this seem unlikely, and I would interpret this feature as the point of origin of muscle slips, perhaps of the M. levator pterygoidei, which in some living lizards takes origin from the ventral surface of the lateral edge of the descending process of the parietal. McGowan (1973a) refers to a comparable feature on the parietal of Ichthyosaurus as the extraencephalic depression, but he does not suggest a function for it.

No obvious scarring is present on the dorsal and lateral surfaces of the parietal, but it is assumed that to some extent these surfaces were covered by the fleshy origins of the adductor muscles. In living lizards and *Sphenodon*, the M. pseudotemporalis and the M. adductor mandibulae externus medialis are the most important muscle divisions to take origin here.

The ventral surface of the parietal has to some extent been moulded to accommodate the underlying structures of the brain. The posterior half of the main body of the bone bears a rounded excavation on its ventral surface. The floor of the depression is irregular and marked by striae which radiate outwards from its centre. Laterally, the depression is bounded by the descending process, and anteriorly by a transverse ridge. This ridge is also present in *Ichthyosaurus* where it is drawn out into a spatulate flange of bone directed antero-ventrally. Anterior to the transverse ridge the mesial region of the ventral surface of the parietal is again slightly concave and marked by striae, but this impression is less clearly demarkated. A second, faint, anterior impression is also distinguishable just lateral to the first. Therefore in *Ophthalmosaurus* there are three impressions on the ventral surface of the parietal - one rounded posterior impression, and two less distinct anterior impressions (figure 13). A fuller discussion of the brain will be presented in a later section, but it is sufficient to say here that, in agreement with McGowan (1973a), I interpret the posterior and more mesial anterior impressions as, respectively, the impressions left by the optic lobe of the mesencephalon, and the cerebral hemisphere of the telencephalon. The more lateral anterior impression seems to be associated with the impressions left by the olfactory lobes of the telencephalon.

Frontal (Figures 12 and 13)

The frontals are small, paired median elements in the skull roof which, in their dorsal exposure, enclose almost the entire parietal foramen at their posterior edge. In dorsal exposure, the frontal bone of each side forms an interdigitating suture with the parietal, nasal and postfrontal. These sutures, in fact, involve a system of extensive overlapping, the significance of which will be discussed in a later section.

The posterior half of the ventral surface of the frontal bone bears a series of ridges and grooves into which locked the underlapping anterior extension of the parietal. Anteriorly the frontal bone surface in this area is ridged and grooved. Contact with the postfrontal is less extensive and is achieved by interlocking tongues with a limited overlap. Obscured from dorsal view by the postfrontal-nasal contact is a broad contact between the frontal and prefrontal in which the lateral edge of the frontal is underlapped by a mesial flange from the prefrontal.

The frontals meet one another along the midline in a straight suture, however the medial edges are here deflected downwards thus offering a large surface area for bonding by connective tissue. The deflected medial edges also form a ventral median ridge which may have aided in the support of each side of the telencephalon of the brain.

The entire exposed ventral surface of the frontal bone bears endocranial impressions which are continuous with those on the parietal, nasal and prefrontal. It is thought that the frontals formed a roof over the anterior part of the cerebral hemisphere, and the posterior region of the olfactory lobes (see later).

The exposed dorsal surface of each frontal bone is pitted by a number of small nutrient foramina. This may be interpreted as an area of the skull roof to which the dermis was particularly closely applied.

Postfrontal (Figures 12 and 13)

The postfrontals take the form of thickened struts of bone which take part both in the border of the temporal opening and in the orbital rim. Posteriorly the mesial edge of each bone is strongly grooved to receive a tongue of bone from the squamosal. The posterior edge of the bone is developed into two blunt tongues. The more dorsal of these overlaps the lateral surface of the squamosal, whilst the ventral tongue fits into a slot on the postorbital. The latter bone sends a tongue beneath the postero-lateral edge of the postfrontal which is here grooved for its reception.

Along its midline, the ventral surface of the postfrontal is raised into a robust, rounded ridge which forms part of the orbital rim. The mesial slope of the ridge forms a gently concave surface facing ventromedially into the temporal opening. This surface is peppered by small nutrient foramina which may indicate the fleshy origin of part of the M. adductor mandibulae externus. The lateral slope of the postfrontal ridge is drawn out into a flange which forms a bony shelf projecting over the orbit, and which is continuous with similar supraorbital flanges on the postorbital and prefrontal.

Anteriorly the ventral surface of the postfrontal is extensively underlapped by the prefrontal bone and the bone surface here is strongly grooved for this contact. The antero-mesial edge of the ventral surface of the bone bears a small facet which abuts against and overlaps the parietal. In dorsal view the postfrontal is seen to form an interdigitating sutural contact with the nasal and frontal, but with neither of these bones is there an extensive overlap.

Prefrontal (Figures 12 and 13)

The prefrontal is a large bone of complex shape which nevertheless has only a small exposure on the skull roof. It takes part prominently in the orbital rim, and also to a lesser extent in the border of the external naris. Its central axis is in the form of a thickened, rounded strut of bone which forms the curved anterior section of the orbital rim. From this central strut extend wide flanges mesially and laterally. Posteriorly, however, these flanges and central strut merge together to form an expanded sheet. Only the lateral flange of the prefrontal is exposed on the dorsal surface of the skull roof. It is effectively a bony shelf, projecting over the orbit, which, together with similar flanges from the postorbital and postfrontal, probably formed a protective cover for the eyeball. These supraorbital shelves will be discussed in a later section.

The remaining dorsal surface of the prefrontal is overlapped by neighbouring bones, and is for this reason ridged and roughened. The mesial flange of the prefrontal is overlapped by the nasal and frontal, and itself overlaps an anterior extension from the parietal.

From the dorsal surface of the prefrontal, along the axis of the central strut, there is developed a projecting ridge which has a parabolic outline in lateral view. This ridge slots into a deep groove on the ventral surface of the lateral edge of the nasal bone, which here broadly overlaps onto the prefrontal. Ventral to this ridge the mesial surface of the central strut of the prefrontal forms the lateral wall of a rounded depression, on the ventral skull roof, which may have housed the olfactory lobes of the brain.

Distally, the central strut of the prefrontal reaches ventrally, as a pillar between the external naris and the orbit, to articulate with the lachrymal by means of a complex arrangement of interlocking tongues. The pillar of the lachrymal and prefrontal thus formed would play a role in resisting vertical compression forces which, because of the large orbit and posteriorly placed external nares, would be particularly large here. The most distal tip of the central strut also abuts against the maxilla; this contact is obscured from view on the lateral surface of the skull and has not been noted previously.

The sheet-like posterior portion of the prefrontal is overlapped largely by the postfrontal. The bone tapers posteriorly to a point which extends beneath the overlying frontal and postfrontal to reach the border of the temporal opening; here its tip also contacts the parietal.

Nasal (Figures 12, 13 and 14)

The nasals are large, elongate bones in the posterior region of the snout, which meet each other along a straight butt joint in the midline. In their midregion they form the dorsal edge of the external naris.

Anteriorly the nasals are overlapped by the premaxillae, and their tapering anterior extremities run concealed beneath the latter bones for some distance.

Posteriorly the nasals form an interdigitating suture with the postfrontal and frontal, whilst broadly overlapping the latter bone. More laterally they overlap the prefrontals which slot into a deep groove on their lateral edges. In this vicinity the nasals do not contact the lachrymals as suggested by Andrews (1910).

In their midregion the nasals are sharply angled along a longitudinal line so that their lateral surface lies in a plane at right angles to their dorsal surface. In the same region the dorsal surfaces slope downwards towards the midline to form an internasal depression. There is no evidence, in Ophthalmosaurus, for an internasal foramen here, a feature reported by McGowan (1973a) to be present in Ichthyosaurus.

The external narial opening on the nasal is complex in form. It can be described as being in two parts. The anterior portion is a simple smooth sharpened edge. This edge widens posteriorly into a flat horizontal surface which is drawn out laterally into a flared edge which projects outwards from the narial border. As Andrews (1910) pointed out, this flared surface forms a funnel-shaped channel into the posterior portion of the narial opening. The flared edge curls downwards towards the hind edge of the narial opening. Its actual bony edge is usually damaged, presumably because in life the bone was very thin. Just inside the nostril, between the anterior and posterior portions, the bone surface is raised and sometimes develops a blunt spur of bone which is visible in lateral view as a projection in the midline of the nostril - further adding to its bipartite character. Presumably this projection, together with similar spurs on the lachrymal and maxilla in the border of the naris, supported soft tissues of the nasal capsule. It is possible that these could be muscular tissues associated with a valvular mechanism. Insufficient evidence is available from the preserved hard parts to allow a reconstruction to be made of the nasal vestibulum and any valvular structures that may have been present in life. However, it is reasonable to assume that ichthyosaurs did possess valvular nostrils since these are widespread amongst living reptiles, both aquatic and terrestrial (Parsons 1970). The same lack of evidence prevents me from proposing a functional explanation for the apparent bipartite structure of the external naris.

One further feature of the narial border is a smooth notch or channel, at the posterior edge of the opening, which is present in some specimens, for example, HM V1129 (figure 13). In other specimens the notch is not developed, but instead the external bone surface in this region is pierced by one or more vascular foramina, for example in P5. The notch or foramina may have transmitted nerves and blood vessels to fleshy structures surrounding the posterior region of the nostril, and this might be regarded as further evidence for a valvular mechanism.

Immediately anterior to the narial border the ventral edge of the nasal is thickened and roughened to form a facet which articulates with the maxilla. This contact is obscured from the skull surface by the premaxilla.

Lachrymal (Figure 14)

This is a small, triangular bone which is rather superficially placed, lying against the lateral surface of the maxilla. The bone surface for this contact is fairly smooth and there is no interdigitation, suggesting the union was relatively weakly bonded. The lachrymal sends out a long extension posteriorly along the dorsal edge of the maxilla. This extension is grooved ventrally to receive the dorsal edge of the jugal. The apex of the triangle of the lachrymal unites strongly with the prefrontal by means of interdigitating tongues. Anteriorly, the ventral edge of the lachrymal has a brief contact with the premaxilla. The smooth antero-dorsal edge of the lachrymal forms part of the ventral border of the external naris; midway along this edge is developed a spur of bone which may have supported soft tissues of the nasal capsule.

On its external surface the lachrymal develops a crescent-shaped ridge, which follows the curvature of the orbit, and which is peppered by nutrient foramina on its rostral surface. It is possible that the lachrymal ridge aided in the support of thickened dermis which continued onto the supraorbital flanges on the prefrontal, postfrontal and postorbital bones, thus forming a protective rim around the eye.

Postorbital (Figure 14)

This is a narrow, bow-shaped element in the posterior margin of the orbit. Ventrally the bone is deeply grooved to receive the dorsal edge of the jugal. Above this contact the posterior edge of the bone forms a heel, the internal surface of which is roughened and ridged for contact with the quadratojugal. Above this heel the posterior edge of the postorbital is faintly roughened for contact with the ventral portion of element B, which here twists round this posterior edge to overlap onto the dorsal surface of the expanded upper portion of the postorbital. The upper portion of the bone develops a lateral flange which contributes to the orbital rim. This portion also contacts the squamosal along its dorso-medial edge, and the postfrontal by a tongue-and-groove union of its anterior extremity with that bone.

Quadratojugal (Figure 4a,b)

The quadratojugal is a small, crescentic element which has only a very narrow exposure on the lateral surface of the skull. The jugal is received in a groove on the external surface of its ventral section. Above this facet the midpoint of the posterior edge of the bone projects to form a cup-like facet, directed ventrally and slightly mesially, for articulation with the quadrate. Just above this facet, on the internal surface of the quadratojugal there is present a triangular depression which may have been the site of attachment of ligaments binding together the quadrate and quadratojugal.

The dorsal section of the quadratojugal bears a roughened prominence on its external surface, just above the quadrate facet. This prominence articulates with the overlapping postorbital. Extending dorsally from this point is a deep groove which received the ventral tongue of element B. The quadratojugal figured by Andrews (1910) was more triangular and less elongate than the bone figured here (figure 4). This difference is due to the fact that in larger individuals, in this case BMNH R4753, the quadratojugal grows proportionally more elongate as the orbit enlarges.

Jugal

The jugal is a slender, bow-shaped bar forming the ventral border to the orbit. Anteriorly it overlaps the maxilla and its internal surface bears a number of ridges and grooves for this purpose. It also receives the lachrymal in a groove on its antero-dorsal edge. On its external surface the posterior extremity of the bone is coarsely ridged and grooved for articulation with the postorbital which envelops its dorsal edge. Beneath this overlap the ventral edge of the jugal lies against the quadratojugal, resting in a groove on that bone.

As the jugal curves upwards behind the orbit, its ventral edge is more or less sharply angled, and the bone here is frequently roughened, indicating, perhaps, the attachment of a ligament.

Maxilla

The maxilla is a bone of complex shape which is largely obscured from external view. It is very much reduced relative to the premaxilla, which has taken over the role of major tooth bearer. Evidence from BMNH R3893 suggests, however, that the maxilla bears approximately thirteen teeth. Isolated maxillae usually show little evidence of tooth implantation, as there are no bony sockets formed; however, R3893 possesses tooth fragments partially embedded in matrix along the alveolar groove, and it is clear that teeth were present as far back as the level of the external naris.

A projecting flange of bone, developed from the internal surface of the maxilla, forms the smooth floor of the alveolar groove. Just internal to the tooth row, this flange is deflected upwards and becomes part of the palatal surface, interlocking with the palatine by means of tongue-like processes developed from its edge. The most posterior of these processes forms part of the antero-mesial border of the sub-temporal fenestra. Anteriorly, the dorsal surface of the mesial flange of the maxilla lies in the floor of the nasal capsule, and is well supplied in this region with nutrient foramina. Foramina also penetrate the ventral surface of the mesial flange, in the floor of the alveolar groove. These maxillary foramina probably transmitted branches of the inferior orbital artery, the infraorbital nerve, and the palatine nerve, all of which supplied the tissues of the nasal capsule and the alveolar groove.

In its anterior region the maxilla slots into the alveolar groove of the premaxilla,so that most of its dorsal and lateral surface is covered by that bone. In this region the maxilla is seen as a mere slender splint on the lateral surface of the snout, beneath the premaxilla, but most of the bone is here concealed. Posteriorly the lateral surface of the maxilla is again largely concealed by the overlapping jugal. In its mid-region the lateral surface develops,from its dorsal edge,a series of jagged, posteriorly directed peaks which are largely concealed from view by the overlapping lachrymal. The posteriormost peak receives,on its lateral surface,the distal tip of the prefrontal. A smaller, anterior peak is just visible in the border of the external naris, behind the overlapping lachrymal. It lies near a similar spur of bone on the lachrymal, and the two prominences may have supported soft tissues of the nasal capsule. Like the spurs of bone in the narial border of the nasal, they may have afforded anchorage to muscle strands involved in a valvular mechanism. Immediately anterior to this anterior peak, the dorsal edge of the maxilla follows the smooth curve of the narial border; more anteriorly still, the edge contacts the nasal.

As reconstructed here, the maxilla is excluded from entering the narial border, at least in external view, by the lachrymal-premaxilla contact. However, internally it lies along almost the entire ventral border of the naris. This reconstruction differs from that of Andrews (1910) who shows the lachrymal and premaxilla failing to make contact.

Premaxilla (Figures 9 and 14)

The premaxillae are very long bones which form the major part of the elongate rostrum; in length they occupy just over half the entire length of the skull. In cross-section each premaxilla is λ-shaped, with the alveolar groove enclosed between the main stem of the λ, which is the lateral wall of the bone, and its ventral branch, which is a mesial flange of bone running the entire length of the premaxilla. Posteriorly the lingual and labial walls of the alveolar groove both project backwards from the main body of the bone and receive the maxilla in the fork between them. Here the lateral surface of the mesial wall just enters the anterior border of the internal narial opening. The maxilla lines the alveolar groove for a short distance anterior to these posterior premaxillary projections, but in front of this bone the floor of the alveolar groove starts to show faint tooth impressions which become stronger anteriorly. These impressions show as round, shallow depressions, at the base of the lingual wall, separated from one another by very low transverse septa. The labial wall may in addition bear grooved markings opposite the depressions on the lingual wall.

The teeth were not fused to the bone of the upper and lower jaws, but would probably have been attached by connective tissue to the floor and labial wall of the alveolar groove. It is largely for this reason that the teeth are frequently lost prior to deposition, and an exact tooth count is therefore impossible. However, BMNH R3893 retains fragments of tooth roots,embedded in matrix,along the whole length of the tooth row as far back as the posterior border of the external naris. From this specimen it is estimated a total of about forty teeth were present in each half of the upper tooth row, and the premaxilla probably held about twenty-seven of these. The nature of the tooth implantation has been partly responsible for the long-held belief that Ophthalmosaurus was edentulous (McGowan 1976, for example), or possessed teeth only in the anterior half of the jaws (Andrews 1910, Müller 1968). Other ichthyosaur genera from the Lower Jurassic of England and Germany also possessed teeth held in an open groove (McGowan 1973a, 1979), but the conditions of deposition in these Lower Jurassic limestones and shales were such that the animals became embedded quickly, before much tooth loss could occur. It seems that the deposition of the Oxford Clay forms occurred less rapidly, and rarely were more than a few teeth recovered during collection.

Towards the front of the tooth row, the tooth impressions become more socket-like and smaller, indicating that the teeth became smaller towards the front of the jaws. The tooth fragments of R3893 correspondingly reduce in size anteriorly.

When the premaxillae are articulated together, the lingual wall of the alveolar groove descends below the level of the labial wall, so that the former is visible in lateral view. In addition, the labial walls slope obliquely outwards rather than lie vertically as do the lingual walls. These differences can be understood by examining the orientation of the tooth roots in R3893. The base of each tooth abuts against the lingual wall, and the teeth lie with their sides against the labial wall. Consequently, the tooth bases lie in a plane inclined at about 45° to the vertical. In the most anterior teeth, this angle is lessened and they lie more vertically. Despite the strong oblique orientation of the tooth bases, however, the actual crowns would lie at about 20° to the vertical as a result of a marked lingual curvature.

On the skull roof, the right and left premaxillae come together a little posterior to their mid-point. At this level they enclose between themselves the nasals, which extend anteriorly along a channel formed between the dorsal edge of the premaxillae and the lingual wall of the alveolar groove. Running through the ventral part of this channel in the rostrum are the thin anterior extensions of the vomers which are applied closely to the mesial surface of the lingual wall for almost its entire length.

The lateral surface of the premaxilla bears a deep longitudinal groove which begins just in front of the external naris. Opening into the floor of the groove are a number of foramina which become smaller and more abundant towards the tip of the snout, corresponding with the diminishing depth of the groove. In broken premaxillae the foramina can be seen to connect with a hollow intraosseous channel running the length of the premaxilla. In addition, a few foramina on the internal surface of the premaxilla also connect up with this channel. The channel opens out posteriorly onto the internal surface of the bone,at a point just anterior to the start of the external longitudinal groove. This system of grooves and channels most probably transmitted nerves and blood vessels which supplied the soft tissues on the external surface of the snout. Romer (1968) suggested the groove might be evidence for the presence of a horny bill, or fleshy lips. However, I do not regard the presence of these nutrient channels to be sufficient evidence for the presence of such structures. At the tip of the rostrum the premaxillae diverge from one another,leaving a space which was presumably cartilage-filled.

Element B (Plates 1 and 2)

This is a problematic bone which will be discussed further in a later section. As preserved in Ophthalmosaurus it is seen from BMNH R2740 and R4753 to be a thin, triangular element which overlaps onto the dorsal edge of the postorbital and sutures with the ventral edge of the lateral wing of the squamosal. Anteriorly it meets the postfrontal by a narrow extension.. From the postero-ventral corner of the bone is developed a descending narrow tongue which extends ventrally along the internal surface of the posterior edge of the postorbital, intervening between this bone and the quadratojugal. The posterior edge of the bone is incomplete in both the known examples and so its occipital exposure cannot be accurately determined.

LOWER JAW (Figure 15)

Articular

This is a compact, rounded bone which ossifies in the posterior end of the mandibular cartilage and which, together with the surangular, forms the articular surface of the lower jaw. The lateral face of the bone is of finished bone which is roughened for its application to the mesial surface of the surangular. In matching the contours of this latter bone, the lateral face of the articular has developed a horizontal groove across its midregion. The mesial surface of the bone is again of finished bone but it is saddle-shaped, being convex dorso-ventrally, whilst in an antero-posterior direction it is concave. The ventral edge of the mesial surface is roughed for an overlap by the pre-articular. The rounded posterior border of the articular is of unfinished bone, and would have been continued in cartilage which may have projected backwards as a retro-articular process. The thin, unfinished dorsal edge of the bone connects the posterior border of the bone with the anterior articular surface. This takes the form of a gently concave oval surface which is pitted,for the application of articular cartilage,and which faces antero-dorsally and slightly mesially. The long axis of the oval concavity of this surface aligns with the long axis of the posterior boss of the quadrate condyle, and it is with this boss that it was in articulation. The ventral edge of the articular is again irregularly pitted and was continued anteriorly in the mandibular cartilage.

Surangular

This is a large, important bone in the posterior region of the mandible. Posteriorly it forms the lateral wall of the adductor (Meckelian) fossa, and behind this it contacts the articular on its mesial surface. The rounded posterior margin of the surangular is crennate and would have been applied to the cartilage which capped the articular bone.

The ventral edge of the surangular was in contact along its entire length with the angular bone, but in the region of the adductor fossa the latter bone in addition sheathes part of its lateral surface. The area for this contact is seen as a depression which is overhung by a horizontal ridge which is roughened and prominent, and may mark the insertion of the M. adductor mandibulae externus superficialis. In its dorsal region, the lateral surface of the surangular bears an oval depression, marked by striae, which corresponds to the area identified by McGowan (1973a) as for the insertion of the M. depressor mandibulae in Ichthyosaurus.

Just anterior to the articular bone the dorsal edge of the surangular is inflected outwards, and here its dorsally inclined mesial surface is roughened. This area was probably covered by the articular cartilage of the glenoid fossa, and this antero-lateral portion of the fossa rotated against the anterior boss of the quadrate condyle. In front of the glenoid the dorsal edge of the surangular ascends smoothly to a slightly mesially directed peak. The entire mesial surface of this peak is covered by fine striations which also extend along a rounded ridge extending postero-ventrally from the peak. The striations are taken to mark the area of insertion of the M. adductor mandibulae externus group, which in living lizards and Sphenodon normally inserts onto an aponeurotic sheet or tendon, the basal aponeurosis, which attaches to the dorsal edge of the mandible (Haas 1973). The form of the surangular peak in Ophthalmosaurus suggests that there was a similar tendinous insertion here.

Anterior to the surangular peak, the dorsal edge of the bone is raised into a low crest whose mesial side is rugose. This is interpreted as the coronoid process onto which probably inserted the M. adductor mandibulae internus pseudotemporalis division, as in extant lizards.

Lower down the mesial surface of the surangular, at the level of the coronoid process, there is developed an elongate foramen which probably transmitted blood vessels and nerves between the adductor fossa and the external surface of the jaw. On the lateral surface of the surangular, the nerves and blood vessels exited via a variable number of foramina situated just anterior to the insertion of the M. adductor mandibulae externus superficialis. The more anterior of these foramina open into a deep groove running along the lateral surface of the surangular for a short distance, just ventral to the dentary.

In front of the coronoid process the dorsal edge of the surangular is overlapped by the thin posterior extremity of the dentary. Its area of overlap increases anteriorly until, about halfway along the mandible, the surangular is enveloped completely by the dentary and it continues as a narrowing splint running along a groove on the mesial surface of that bone. The angular has contact with perhaps the entire ventral edge of the surangular, however the anteriormost extremities of these elements are not known, and so neither are their exact relationships in this region.

The mesial surface of the dorsal edge of the surangular has a narrow contact with the dorsal edge of the pre-articular, at a level just anterior to the coronoid process; and in front of this region the splenial has a similar contact. Below these narrow lines of bony contact the mesial surface of the surangular is slightly concave, and the bone here has a frosted appearance. This surface faced the Meckelian canal and to it would have attached membranes lining its walls and, more ventrally, the Meckelian cartilage.

Pre-articular

The pre-articular was referred to as the coronoid by Andrews (1910). The latter bone has not been identified in Ophthalmosaurus. The pre-articular is a slender element exposed on the mesial surface of the posterior region of the mandible. Because of its delicate nature, few examples are well preserved, but information on its form has been obtained from BMNH R2180 and HM V1893. The bone consists of a narrow posterior region and a thin expanded anterior section which becomes wafer-thin at its extremity. The posterior portion lies against the internal surface of a mesial flange of the angular, and in this position it forms the dorsal part of the mesial wall of the adductor fossa. Its posterior extremity sheathes the ventral edge of the articular. Just anterior to this region, the mesial side of the pre-articular is marked by a distinct rugosity which spreads ventrally onto the angular bone. The rugosity possibly marks the insertion of a mesial portion of the pterygoideus division of the M. adductor mandibulae internus which probably also sent a lateral portion beneath the angular, to insert on the lateral surface of the retro-articular process. Similar relationships of this muscle are seen in living lizards and Sphenodon (Haas 1973).

More anteriorly the pre-articular increases steeply in height, at about the level of the surangular peak, to form a thin mesial wall to the adductor fossa. Its ventral edge appears to continue to run along the mesial dorsal edge of the angular, but its exact relationship to that bone is uncertain. However, it is apparent that ventrally the pre-articular lies on the mesial side of the Meckelian canal, whilst its dorsal edge arches laterally to touch the surangular on the lateral wall of the canal. The tapering anterior extension of the pre-articular is obscured from mesial view by the overlapping splenial.

Coronoid

Andrews (1910) described the pre-articular as the coronoid bone, but the true homology of the former bone was later realised (e.g. Romer.1956). No true coronoid element has been identified in Ophthalmosaurus, and there is no evidence of its presence from the remaining jaw elements. However, McGowan (1973a) reported a very slender splint of bone, in the mandible of Ichthyosaurus, which he homologised with the coronoid. If this is the case, it could be that the coronoid was reduced and lost in the Ophthalmosaurus lineage.

Splenial

This bone has an extensive exposure on the lingual surface of the mandible, and in its anterior limit it contributes to the jaw symphysis. Posteriorly the splenial forms a point which lies in a groove on the angular. More anteriorly, the bone increases in height and in so doing its dorsal edge encroaches upon and obscures the pre-articular. In this region the dorsal edge is interrupted by a notch which lies adjacent to a foramen (as shown in specimen P1) which is interpreted as having transmitted the chorda tympani branch of the VII cranial nerve into the Meckelian canal. It seems likely that this nerve also pierced the pre-articular bone which here underlies the splenial.

In its midsection, the dorsal edge of the splenial has a narrow contact with the surangular, but more anteriorly, as the latter bone is reduced, this contact is replaced by the dentary. Below its dorsal edge, the splenial bows outwards lingually, to enclose the Meckelian canal, before curling its ventral edge beneath the angular, in this way revealing itself on the lateral surface of the mandible. In its anterior section, the splenial forms a fork, each branch of which bears on its mesial surface a strongly rugose facet for the symphysial union. Forking of the bone at the symphysis allows the Meckelian canals of each of the separate jaw rami to become confluent.

Angular

The angular lies along the ventral edge of the mandible and forms the floor of the Meckelian canal. Posteriorly it sheathes the bones surrounding the adductor fossa - the surangular laterally and the pre-articular mesially. Along its dorsal surface, in the floor of the adductor fossa, lay the Meckelian cartilage and its posterior ossification, the articular.

The posterior edge of the angular is, like the surangular, finely crennate, and was applied to the cartilage capping the articular. The mesial surface of the angular, in this posterior region, bears a rugosity which may mark the insertion of the medial part of the M. pterygoideus, as noted in the description of the pre-articular.

Anterior to the adductor fossa, the angular is seen in cross-section to have a rounded ventral margin and a double-grooved dorsal margin. The more lateral of these dorsal grooves carries the ventral edge of the surangular, whilst the more mesial groove lies open in the floor of the Meckelian canal, and along this groove probably lay the Meckelian cartilage. A third groove, which is much shallower, lies low down on the mesial surface of the angular, and this received the ventral edge of the splenial.

In its anterior section, the angular becomes cut off from exposure on the surface of the mandible by the dentary and splenial which meet below it. The angular continues anteriorly as a thin splint running inside the jaw ramus between the surangular and dentary, laterally, and the splenial mesially.

Dentary

The dentary is exposed mainly on the dorsal and lateral surfaces of the jaw. In its posterior limit, just below the coronoid process, it is a thin splint which widens anteriorly as it spreads over the dorsal edge of the surangular and down the lateral surface of the jaw. The dorsal edge of the dentary forms the alveolar groove which starts to bear teeth at a level one-third of the way along the lower jaw, or at the level of the posterior border of the external naris. In this region the groove is not marked by impressions of the tooth roots, but BMNH R3893 shows embedded tooth fragments here. As in the upper jaw, the tooth impressions become smaller, more marked and socket-like towards the front of the lower jaw. A further similarity to the upper tooth row is seen in the high lingual wall of the alveolar groove, which is visible above the labial wall in lateral view. The tooth bases abut against the lingual wall, and the teeth lie with their sides against the labial wall.

For most of its length the dentary is applied to the lateral surface of the surangular, and for this purpose its mesial surface is deeply grooved. In the symphysial region, however, beyond the anterior end of the surangular, the dentary retains a mesial groove. The two opposed grooves on each dentary formed a canal which carried forwards the contents of the Meckelian canal to the tip of the mandible. Just posterior to the symphysis,the ventral edge of the dentary contacts the angular bone, and more anteriorly, in the region of the symphysis, the dorsal and ventral edges of the dentary contact the splenial.

In lateral view, the dentary exhibits a deep longitudinal groove which is associated with foramina which lead into an intraosseous canal running the length of the bone. This is closely similar to the system of canals and foramina seen in the premaxilla, and it is presumed to have had the same function - that is, it served to transmit nerves and blood vessels to supply the tissues on the external surface of the mandible. Like the premaxilla, the dentaries diverge at their tips to leave a space which was presumably cartilage-filled.

The Dentition

Ophthalmosaurus can be seen to have possessed approximately forty teeth in each ramus of the upper and lower jaws, as estimated from BMNH R3893, and from counts of the tooth impressions in HM V1129 and BMNH R4753. As mentioned previously, the teeth were not fused to the jaw bones, but were probably attached by connective tissue by their basal surfaces and labial sides. The teeth decrease in size towards the anterior region of the jaws. The largest teeth in "adult' specimens measured approximately 3.73 cm in total length (estimated from incomplete teeth of HM V1129) and 1.14 cm in maximum width across the base. The largest teeth were in the middle of the tooth row. Using McGowan's (1976) index for tooth length (10 x largest crown length/ jaw length), Ophthalmosaurus appears to have relatively small teeth when compared to all the other taxa in McGowan's (1976) study. The tooth length index obtained for three specimens, BMNH R2181, HM V1129 and BMNH R2180, is, respectively, 0.216, 0.183 and 0.140. Interestingly, smaller specimens appear to have relatively larger teeth - these specimens have jaw lengths respectively of 50 cm, 79 cm and 95 cm. However, because of the rarity of teeth in Oxford Clay ichthyosaur material, and the fragmentary nature of the few teeth preserved, these ratios are considered to be subject to relatively large errors, and should be treated with caution.

Each tooth is gently curved so that its lingual side is shorter than its labial side. The crown is a pointed cone, the enamel of which bears fine longitudinal ribbing. The base of each tooth is swollen and slightly compressed transversely. It accounts for approximately two thirds of the total length, though this proportion varies with the size of the tooth, larger teeth having proportionately longer bases. Just below the crown, each tooth exhibits a region in which the tooth surface is smooth, and only faintly marked by plications which are continuous with the ribbing on the enamelled crown. This smooth area appears to be free of cementum, and the dentine is exposed. Below this smooth band the tooth base is enveloped by a layer of cementum. In this region the surface of the tooth base is thrown into fine, longitudinal, slightly anastomosing folds. These folds are surface features resulting from the underlying labyrinthine infolding of the orthodentine in this region (Plicidentin of Schultze 1969). In this region the pulp cavity becomes fragmented by the infolded dentine, and the tooth base then assumes a characteristic solid appearance. Schultze (1969) has shown that the folds in the dentine of ichthyosaur teeth are widely spaced, allowing cementum from the surface of the tooth to penetrate between the opposed orthodentine layers of each fold. Since the outermost zone of orthodentine is the globularzone (of Schultze), then cementum is seen between globularzone layers. In cross-section, cementum can also be seen inside the plicidentin layer, having penetrated upwards from the lower edge of the tooth.

Schultze (1969) has shown that this type of labyrinthine infolding is not directly comparable to that seen in the teeth of rhipidistians or of lower tetrapods. It is a commonly held assumption that the striated crowns of ichthyosaur teeth indicate an infolding of the enamel which occurs in more typical labyrinthodont teeth (e.g. Romer 1956). This is not, however, the case: the enamel of ichthyosaur teeth is simply plicated.

From BMNH R3893, it appears that at any one time a large number of teeth are undergoing resorption at their bases. However, the tooth row is too imperfectly preserved to allow an exact description of the pattern of tooth replacement. It is evident, though, that the replacement teeth develop lingually and lie in a résorption pit at the base of the mature tooth; in the upper tooth row of R3893, several such replacement teeth are still in place.

Some examples of isolated teeth, for example, HM V1129 and BMNH R2181, show evidence of tooth wear (figure 16c). These wear facets are found on either the distal or mesial sides of the tooth crown. The tips of the teeth, when complete, show little evidence of wear. This pattern of wear would be consistent with the occurrence of abrasion between the distal and mesial sides of the crowns of the upper and lower teeth, as they interlock when the jaws come together.

This kind of dentition in which there are numerous sharp, recurved teeth which interlock like crossed swords, is also seen in several other aquatic reptile groups such as plesiosaurs, mesosaurs and mosasaurs. The possession of this kind of dentition is generally regarded as an adaption to a piscivorous diet, or to a diet of active invertebrates such as belemnoid cephalopods.

Sclerotic Plates

One specimen, BMNH R4753, possesses a complete sclerotic ring with fifteen individual plates; however, Andrews (1910) reconstructs the ring as possessing fourteen plates. Each plate comprises a flattened inner corneal portion, whose edge takes part in the aperture of the sclerotic ring, and an outer, curved orbital portion. The orbital portion of the sclerotic plate lies at an angle of about 130° to the corneal part, so that when the ring is complete, it is markedly domed. There is no apparent inflection at the rim of the central aperture of the ring. An inflection here is normally present in living reptiles possessing a prominent scleral sulcus which increases the curvature of the cornea. It can be inferred from this that Ophthalmosaurus lacked a prominent scleral sulcus. From specimen R4753 it was possible to estimate the ratio of the internal diameter of the sclerotic ring to its external diameter. The value obtained was 0.4, which is relatively large amongst reptiles (Underwood 1970). The significance of the apparent lack of a scleral sulcus, and the large size of the sclerotic aperture will be discussed in a later section.

At the junction between the corneal and orbital parts of the sclerotic plates, both the external and internal surfaces bear irregular tuberosities from which radiate striated markings. The internal sculpturing may have marked the attachment of muscle fibres passing from the scleral ossicles to the ciliary body. These muscles in living forms (Crampton's and Brücke's muscles) are important in accommodation (Underwood 1970).

The internal border of the sclerotic ring, at the edge of the aperture, is relatively smooth in contrast to the external border which is irregularly crennate. The union between individual sclerotic plates is achieved by neighbouring plates slotting together by means of thin interlocking laminae developed from their edges. The joint is seen in cross-section, therefore, not as a simple overlap, but as a complex interdigitation. The sutural line visible on the surface at each union is relatively straight, but becomes wavy at the corneal edge, particularly on the internal surface of the sclerotic ring.

Hyoid Apparatus

The hyoid apparatus is represented by a pair of blunt-ended, curved rod-like bones. In cross-section the bones are slightly flattened. At each extremity is an oval, flattened surface which bears the characteristic irregular pitting that indicates the application, in life, of cartilage. McGowan (1973a) followed Sollas (1916) in homologising these rods in

Ichthyosaurus with the cornu hyale of living reptiles, which is the anteriormost of the, typically, three cornua which attach to the corpus hyoideum. This first cornu, however, typically remains cartilaginous in living forms, whereas the second, middle cornu branchiale I is usually well-ossified (Romer 1956), and often takes the form of a pair of curved rods. It seems more likely that the ossified cornu in Ophthalmosaurus is the homologue of the cornu branchiale I.

The reason for Sollas' decision of interpretation was that his serial sectioning of this region revealed an array of other bones which he painstakingly reconstructed to form a complex hyoid apparatus which, he acknowledged, bore little resemblance to any living reptile, but which he thought resembled the branchial apparatus of some living amphibia. These other elements were posterior to the hyoid rods, and it seems more likely that they were displaced cervical ribs, indeed the occipital region of this skull does appear to have undergone a degree of displacement. The theoretical basis of Sollas' and McGowan's interpretation seems, therefore, rather doubtful.

POSTCRANIAL SKELETON

The Atlas-Axis Complex (Figures 17 and 18)

The atlas and axis pleurocentra are completely fused even in very young individuals. Usually an indication of their primitively separate nature is left in the form of a vertical thin ridge of unfinished bone running down the side of the pleurocentral complex. The anterior face of the atlas is concave with a central pit in the majority of specimens. The bone surface of this face is slightly irregular, contrasting with the posterior face of the axis. The ventral edge of the atlas face is continuous with what would have been a cartilage-covered ridge on the ventral surface of the pleurocentral complex (figure 19). The cartilage-covered surface of the atlas face is also continuous, dorso-laterally with broad surfaces for articulation with the neural arches and ribs. The antero-ventral edge of the atlas is seen in side view to be bevelled, and this may indicate the presence of a separate atlantal intercentrum.

The floor of the neural canal is a concave area of smooth bone which is slightly raised above the surrounding pitted bone surface. On either side of the neural canal are elongate depressions in which were located the pedicels of the atlas and axis neural arches. The rib facets are poorly defined and vary in position both between individuals and between right and left sides of the same individual (figure 17c,d). Frequently the rib facets merge with the neural arch facets. These are features which reflect the relatively low degree of ossification in the pleurocentral complex. In some cases (HM V1061, V1611, right side) the diapophysis and parapophysis of both the atlas and axis amalgamate as a prominent mass of irregularly pitted bone. In other cases the parapophyses can be distinguished lying postero-ventral to the diapophyses which themselves may or may not be distinct (HM V1916). This variability does not seem to be correlated with size as is evident from the variation that can occur between the right and left sides of an individual (e.g. HM V1611).

The posterior face of the axis is more deeply concave, smoother and more sharply edged than the atlas face. Its ventral edge is constricted to form a medial keel which gives the bone a heart shape in posterior view. There is no separately ossified axis intercentrum, in contrast to some Liassic forms.

Neither the atlas nor the axis neural arches fuse to the pleurocentra. The atlas neural arch is in two distinct halves (figure 18), but all the succeeding neural arches are fused to form a single arch. Andrews (1910) indicated that the arches of the first few vertebrae after the atlas remained unfused, but my study does not support this. The atlas neural arch comprises a thickened pedicel, which ends in a rounded facet for articulation with the pleurocentrum, and a short blade-like neural spine which unites medially with its fellow. On the posterior edge of the neural spine is a distinct zygapophysis for articulation with the axis neural arch. Anteriorly there is a roughened tubercle which may have articulated with a proatlas, however this has not been recognised in any ichthyosaur. As an indication of its original separation into two halves, the posterior edge of the axis neural spine remains deeply split, and in this way it overlaps extensively the anterior edge of the third cervical neural spine. In appearance the axis neural spine resembles the succeeding neural spines except that its spine is a little lower. Its anterior edge is overlapped by the atlas arch which articulates also with its prominent anterior zygapophysis. The distal extremity of the spine is grooved indicating it would have been capped in cartilage.

The Vertebral Column (Figures 19 - 23)

The presacral vertebrae show no clear-cut division into a cervical and trunk series, a feature which reflects the loss of functional importance of a distinct neck in Jurassic ichthyosaurs. Appleby (1956) defined the cervical series to include those vertebrae which retain a contact between the neural arch facet and the diapophysis. Under this definition there would be approximately 20 - 25 cervical vertebrae, although Appleby reports one specimen with only 11 in this series: this specimen, I think, is unlikely to be complete (LM 100'1949/75).

It appears that the process of loss of contact between the diapophysis and neural arch facet is a gradual one, taking place over a series of at least 5 vertebrae (figure 19), and that the final separation occurs at a variable point in the column. There is,therefore,no clear difference in form between so-called cervical and dorsal vertebrae. Furthermore, inspection of Liassic forms, which are embedded often as complete skeletons, reveals that the separation of the diapophysis occurs far behind the pectoral girdle in a region of the column where the ribs are elongate, and ventral gastralia are present. This is clearly well into the dorsal, or trunk region of the column. I would suggest Appleby's division into cervical and trunk vertebrae is not correct. It seems clear that the true neck region occupied only the first few anterior trunk vertebrae, and its distinctness from the rest of the trunk has been lost. The point at which the diapophysis leaves the neural arch facet will be used to mark a division between anterior and posterior trunk vertebrae.

Difficulties also arise in the determination of the position of the sacrum. The sacrum of Jurassic ichthyosaurs has lost bone-to-bone contact with the vertebral column, though some ligamentons attachment may have been present. For this reason, the sacral vertebrae are not easily distinguishable from the rest of the series. Andrews (1910) defined the first caudal vertebra, for convenience, as that in which the diapophysis and parapophysis merge to support a unicipital rib. This may not correspond exactly to the true position of the sacrum, but nevertheless it is a useful reference point. The vertebrae behind this vertebra and before the tail bend will be referred to as anterior caudal vertebrae, whilst those behind the tail bend will be referred to as posterior caudal vertebrae. One feature which lends support to the proposal that the sacrum is positioned around vertebrae 42 is illustrated by figure 36: in "adult" specimens (R4753 and R2133) there is a sudden increase in central height at this point in the column. Interestingly, this increase in height is not shown by juveniles (specimen V1611 in the figure). The sudden increase in central height may be taken to mark the start of the caudal series. A large cross-sectional area of the vertebral centra here may indicate the importance of this section of the column in generating thrust during swimming movements.

One further consequence of the disarticulated nature of the Oxford Clay material is that it is impossible to be sure whether a series of vertebrae in any specimen is complete. In fact no specimen appears to have been collected with a complete vertebral column, but some specimens have at least nearly complete portions of the column. It is assumed, therefore, that specimens in which there are no obvious gaps in a section of the column, and which display maximum vertebral numbers for that section, have probably complete vertebral counts for that section. Table 3 shows vertebral counts for specimens which are thought to have nearly complete sections of the vertebral column; the description below is based largely on these specimens. The most complete individual was SM J63920 - 64037. Large sections of the vertebral column of this specimen were preserved as blocks held together by matrix and it is reasonably certain that the column is nearly complete, with perhaps only a shortfall in the number of vertebrae in the anterior caudal region. From the available data, then, it is estimated that there were between 120 and 130 total vertebrae; of these, 20 - 25 were in the anterior trunk region, and about 19 were present in the posterior trunk region. Possibly 30 were anterior caudal vertebrae, although this is the least certain regional count. About 5 vertebrae were involved in the tail-bend region, though this is not an absolutely distinct region, and approximately 50 - 55 vertebrae were present in the posterior caudal region, behind the tail bend.

Anterior Trunk Vertebrae

The first few vertebral centra behind the atlas-axis complex are somewhat heart-shaped owing to the development of a low median ventral keel which is comparable to the keel on the atlas-axis (figures 19a,b; 20a,b). The keel in this region of the neck may have formed a surface for the attachment of the subvertebral muscles. By vertebra 6 or 7 the keel disappears and the centra take on a rounded ventral contour. The anterior and posterior faces of each centrum are deeply concave with a central pit. A segment of the centrum immediately below the neural canal is thickened, so that the anterior and posterior faces of the centrum develop a convex triangular area beneath the neural canal. The thickening, which is usually more marked on the posterior face, can be thought of as providing extra resistance to compression forces along the column. The neural arch facets are narrow concavities which extend the whole length of the dorsal surface of the centra. The neural arches are almost invariably preserved separately from the centra indicating that cartilage persisted at their union. However, in one well-ossified individual, BMNH R8737, neural arches have been preserved still attached to the centra in a series of vertebrae from the 7th to the 15th. The suture between the neural arch pedicels and the centra appears to be fused only in its posteriormost region and, anteriorly, some cartilage persisted. The union is still a weak one, and in less well-ossified individuals it seems the suture did not fuse. Even when some fusion has occurred, the fragile nature of the union would account for the frequency with which the arches and centra are preserved separately.

The diapophysis in the anterior trunk region is confluent with the neural arch facet, and is situated towards the anterior edge of the centrum. In the first few anterior trunk vertebrae the parapophysis is situated below the diapophysis about halfway down the side of the centrum. Moving posteriorly along the column the parapophysis "migrates" posteriorly on the centrum and leaves the anterior edge, though it still remains connected to this edge by a ridge. In the same section of the column, the diapophysis starts to move ventrally on the centrum and detach itself from the neural arch facet. This process becomes complete at around the level of vertebrae 20 to 25 (figure 19c). Throughout the anterior trunk region, there is a steady increase in size of the vertebral centra, in terms of both cross-sectional area and length.

The neural arches of the first few anterior trunk vertebrae resemble that of the axis vertebra except for a rapid increase in height of the spines which takes place between the 3rd and 6th vertebra (figure 18). The 3rd to 6th neural arches are, like the axis arch, split deeply along the posterior edge of the spine; presumably as a remnant of their original ossification from two centres. This groove also divides the posterior zygapophysis of each arch into two postero-ventrally facing facets which articulate with the anterior zygapophyses of the succeeding vertebra. The anterior edges of the 3rd to 6th neural spines are sharply ridged to slot into the groove on the posterior edge of the preceeding spine; similarly the anterior zygapophyses are separated by a median ridge which slots between the posterior zygapophyses. In this way the neural arches interlock with some degree of overlap. This arrangement would have restricted the lateral mobility of the neck as part of the adaptations in the Jurassic ichthyosaur body towards a fusiform shape.

By the 9th neural spine these ridges and grooves become very slight with the result that a single zygapophysial surface is present both anteriorly and posteriorly. The anterior zygapophysial surface is slightly concave, whilst the posterior one is convex. These surfaces appear to have been cartilage-covered, and their arrangement would seem to have allowed a high degree of mobility in all directions. This feature reflects the loss of the importance of the primitive supportive function of the vertebral column, as the column has become primarily used as a compression member during swimming movements.

The neural spines of the anterior trunk region appear to slope quite strongly backwards relative to an axis running through the centre of the vertebral centra. This may be explained by the fact that in articulated Liassic specimens the dorsal series is strongly arched, and the neck region descends steeply towards the skull. Towards the 25th vertebra the neural spines become broader in lateral view, reflecting the increase in length of the vertebrae. Here and throughout the column the distal end of each neural spine is deeply grooved for the application of a cartilage cap.

Posterior Trunk Series (Figures 19 and 20)

Throughout this region, from about vertebra 25 to 45, the centra continue to increase in size; at around vertebra 42 or 43 there is a sudden increase in central height, marking the start of the caudal series (figure 36).

From vertebra 25 the diapophysis and parapophysis move rapidly down the sides of the centrum, though, until about the 38th or 39th vertebra a constant distance is maintained between them. In this region the parapophysis is situated below and anterior to the diapophysis. After the 39th vertebra the diapophysis diminishes in size and moves towards the parapophysis until at around vertebra 42 or 43 (figure 19e) the two become confluent, reflecting the merging of the capitulum and tuberculum of the rib. At this point the single rib facet is elongate and situated ventrally and anteriorly on the centrum.

Throughout the posterior trunk region the neural spines become wider in lateral view, but at the same time they diminish in height (figure 21), having obtained a maximum height at around vertebra 25.

Caudal Series (Figures 20 - 23)

From about vertebra 43 to 60 the centra remain large in cross-sectional area, but throughout this region the centra diminish in length so that throughout the anterior caudal region they appear more flattened and disc-like. Shortening of the centra in this region suggests that there was an increase in flexibility of the column, whilst the maintenance of a maximum central diameter would ensure a large load bearing capacity of this region. These features can be interpreted as an indication of the importance of the anterior caudal region in the generation of the lateral swimming movements of the tail.

One further feature of the posterior trunk and anterior caudal vertebrae is the development at around vertebra 26 of a low median ventral keel on the centrum (figure 19d). At about vertebra 29 the summit of the keel develops a median groove, thus splitting the keel in two. The double keel becomes single once more at around vertebra 36. Throughout the succeeding vertebrae the keel becomes sharper, and by around vertebra 50 a pair of low lateral keels develop on either side. In this region also a pair of nutritive foramina become prominent one on either side of the median keel. Where the lateral keels meet the anterior and posterior edges of the centra, these edges thicken forming what are interpreted as facets for haemal arches. By about vertebra 61 the haemal arch facets become more prominent, whilst the median keel is diminished. This ventral keeling is not pronounced in every individual, but it is well shown in HM V1611, BMNH R2180, R3533, R2157 and R2141. It appears to be less prominent in larger specimens, and this might at first seem to be of taxonomic importance. However, larger specimens are commonly more susceptible to crushing which obscures the keeling. Large specimens which display keeling are BMNH R8737 and R2157.

Throughout the anterior caudal region, the centra remain fairly uniform in size and appearance. A single rounded rib facet is present low down near the anterior edge of the centrum. More posteriorly, however, at around the 66th vertebra the centra diminish rapidly in diameter, and at the same time they become proportionately wider transversely. Here also the rib facet extends along the whole length of the centrum, and becomes positioned higher up the sides. The edges of the centra in this region are less sharply defined indicating that the anterior and posterior faces would have been invested in a greater amount of cartilage.

The neural spines decrease in height rapidly throughout the anterior caudal region (figure 21), and become steeply posteriorly inclined. The zygapophysial surfaces are reduced to small, almost horizontal facets which appear to have allowed a great deal of flexibility.

At the tail bend, around vertebra 75, is found a series of about 5 specialised vertebrae (figures 22, 23). The anteriormost of this series have the rounded cross-section of the anterior caudal vertebrae and they possess rib facets midway down their sides. They differ, however, from the anterior caudal vertebrae in that their edges are irregular and tuberculous indicating a greater degree of investment in cartilage, and possibly also ligaments. In some well-ossified vertebrae, e.g. BMNH R2188 these vertebral centra may develop a convex anterior face which articulates with the concave posterior face of the preceding vertebra; they are therefore procoelous. This feature, in fact, misled Andrews (1910) who interpreted two of these centra as a basioccipital bone ossified in two parts.

These procoelous centra form a ball and socket joint, in effect, which would allow not only lateral and vertical movement at the tail bend, but also a degree of rotation. The procoelous nature of the centra at the tail bend was first noticed for the genus Ichthyosaurus by Seeley in 1908. A functional interpretation of the procoelous vertebrae at the tail bend will be presented in a later section.

The posterior tail bend vertebrae have centra which differ from the anterior centra in that they are vertically elongate and do not bear rib facets. They do not show marked procoely. However, they resemble the anterior centra in their roughened and tuberculous bone surface.

All the vertebral centra in the region of the tail bend show a slight wedge-shape in lateral view, the ventral surface being shorter than the dorsal surface. When the centra are articulated (figure 23) it is seen that the neural canal of each slopes downwards relative to the preceding centrum. These two features contribute to a significant downward curvature of the vertebral column at the tail bend (figure 22). The disarticulated nature of the Oxford Clay material means that it is impossible to estimate the angle of the tail bend with any certainty. However, McGowan (1973b), using measurements taken from well-preserved articulated Liassic specimens of Stenopterygius, estimated the angle between a line through the long axis of the skull and preflexural column, and a line from the tail tip to the tail bend. The resultant angle gave a measure of the tail bend angle; this was between 18° and 35° for the specimens measured, and the angle showed an increase during ontogeny. Ophthalmosaurus was an ichthyosaur with a similar body form to Stenopterygius, and it is reasonable to assume that the tail bend angle did not differ greatly between these genera.

The neural arches at the tail bend are also specialised (figure 23). The neural spines are transversely widened and low, with a thickened, nodular appearance. They are almost vertical in orientation and there is virtually no development of zygapophysial surfaces. The posteriormost neural arches are similar in appearance except that they are smaller, in correspondnece with their smaller centra, and the spines are narrower and show less thickening. The thickened, tuberculous nature of the neural arches at the tail bend suggests that in life they were heavily invested in ligamentous connective tissue which strengthened the tail bend.

The posterior region of the tail, behind the tail bend, consists of an estimated 55 small, uniform vertebrae which gradually diminish in size towards the tail tip, becoming tiny discs less than one centimetre in diameter at the distal tip. The centra in the posterior caudal region are slightly laterally compressed and are longer than those in the anterior caudal region. Their edges are more sharply defined, indicating more extensive ossification. In one specimen with an apparently complete posterior tail section, SM J63920 - 64037, some of the more distal centra can be seen to be slightly wedge-shaped, but this wedging is the reverse of that found at the tail bend: that is, their dorsal surfaces are shorter than the ventral surfaces, with the effect that there would have been a slight upturning of the tip of the tail. Such an upturning is also visible in some Liassic specimens, such as Stenopterygius quadriscissus BMNH R4086, which possesses the preserved outline of the tail fin. Specimens such as this show clearly that the tail fin itself was recurved at its ventral and dorsal extremities.

After the tail bend the neural arch facets persist towards the tip of the tail, however neural arches themselves, from this region, have not been recognised amongst the Oxford Clay material. It is likely that they were very much reduced, as is seen in Liassic forms. Rib facets are not present on any of the posterior caudal vertebrae. Facets for the haemal arches appear in the caudal region at around vertebra 50, and they can be described as thickenings of the anterior and posterior edges of the centra on either side of the midline. The facets persist posteriorly throughout the caudal region, however haemal arches themselves have not been identified. It is likely that they were either very small and easily overlooked on collection, or they remained unossified.

Ribs (Figure 24)

The ribs, like the vertebrae, are not sharply differentiated into regions. Ribs are present from the atlas to the anterior tail bend vertebrae. The first 42 or 43 ribs are double-headed, dichocephalous; the remainder being single-headed, or holocephalous, as a result of the fusion of the capitulum and tuberculum. The anteriormost trunk ribs are short and slender, tapering rapidly to a point. Evidence from articulated Liassic specimens suggests that, in correlation with the reduced neck region, there would have been only two or three pairs of these short, pointed ribs and that posterior to these the ribs rapidly elongate.

The capitulum and tuberculum of the anterior trunk ribs are widely separated. The surfaces articulating with the vertebrae are irregularly pitted, showing that cartilage intervened in this contact. It is clear that a relatively large amount of cartilage was present here, and this leads to uncertainty in orientating the ribs on the vertebral column. However, the ribs on the mounted skeleton of Ophthalmosaurus, in the British Museum (Natural History), do not appear to be incorrectly mounted. This skeleton was used as the basis of the reconstruction (figure 35).

The rib shafts in the anterior trunk region are flattened, strongly curved bars, which taper distally to a flattened tip. Proximally their anterior and posterior dorsal edges are thickened for the attachment of the axial musculature. Below these edges both the anterior and posterior faces of the rib shaft are grooved, indicating further sites of muscle attachment (figure 24a).

Towards the posterior trunk region, the ribs become shorter, more slender and tapering. Here also the tuberculum becomes dorso-ventrally compressed and less robust. The bone between the capitulum and tuberculum thins to form a web. Small muscle tubercles are present on the anterior face of the rib head, one near the dorsal edge, and another between the capitulum and tuberculum. In this region the ribs extend horizontally and slightly posteriorly (figure 24b). At a level on the column around vertebra 40 to 43 the tuberculum further diminishes in size, and at the same time the capitulum elongates and the two rib heads grow closer together. It seems that the single rib head of the caudal vertebrae is brought about by two combined processes: a reduction in size of the tuberculum and a fusion of the capitulum and tuberculum. Appleby (1956) has tried to distinguish between these two processes, and he has argued that the holocephalous nature of the caudal ribs results solely from a loss of the tuberculum, so that the single rib head is the homologue of the capitulum. I would argue that such a distinction cannot be made between these two processes, and that the single rib head represents both the capitulum and tuberculum.

Posterior to vertebra 42, the holocephalous caudal ribs are short, distally tapering elements. The rib head is vertically elongate, with its long axis inclined slightly posteriorly. The distal end of the rib is horizontally flattened and it bore a cartilage tip (figure 24d). More posteriorly still, the caudal rib shafts become reduced to horizontally flattened nubbins of bone, and the rib head becomes rounded (figure 24e,f). There is no clear evidence for sacral attachments, and specific sacral ribs are not distinguishable. Facets for the ribs on the vertebrae appear to persist until the anterior two or three vertebrae of the tail bend; the ribs here are reduced to mere nodules of bone (figure 23b).

PECTORAL GIRDLE AND FORELIMB

Scapula (Figures 25 and 26)

The scapula consists of an expanded proximal end, which takes part in the glenoid, and a narrow, elongate scapular blade. The proximal end of the bone is deeply and irregularly pitted, and there is no well-formed glenoid socket, indicating that a substantial amount of cartilage took part in the glenoid articulation. The proximal surface is shallowly S-shaped in end view; the posteriormost half of the S is expanded to form a broad articular surface, in two parts, for contact with the coracoid anteriorly and the humerus posteriorly. The anterior half of the S does not make contact with bone, but it is likely that it met, via cartilage, the region of the coracoid in front of the anterior notch (see below). The anterior section of the S terminates in an acromion process which extends along the anterior edge of the scapula as a raised ridge of unfinished bone to which a thin layer of articular cartilage was applied. The middle section of the S was opposed, in life, to the anterior coracoid notch, or anterior fenestra of the coracoid. In the majority of individuals this section of the S is unfinished like the remainder of the proximal edge of the bone; however, in a few well-ossified individuals such as BMNH R2160, R2140, R2152, the bone here is a finished edge. This variation in the extent to which the endochondral pectoral girdle is ossified does not appear to be strictly size-dependent, since some very large scapulae and coracoids, for example, BMNH R2149, R4753, do not show a finished edge here. Johnson (1979) found, similarly, a large amount of individual variation in the extent of ossification in the endochondral pectoral girdle of Stenopterygius.

The distal edge of the scapular blade is irregularly pitted and grooved indicating that a suprascapular cartilage was applied to it. In lateral view the external surface of the scapula displays a rounded concavity which leads mesially into the anterior bend of the S-shaped proximal edge of the bone. The concavity probably offered an attachment surface for muscles going to the humerus. Spreading along almost the entire anterior edge of the scapula is a flattened, roughened facet to which was applied the distal horn of the clavicle. This clavicular facet is broadly visible on the external surface of the bone. Much of the external surface of the scapular blade bears rugosities which probably indicate the sites of attachment of muscles involved in the movement of the forelimb. In Ophthalmosaurus, it does not appear possible to delimit, with any confidence, the attachment sites for specific locomotory muscles, as has been attempted by Johnson (1979) for the pectoral girdle of Stenopterygius.

The internal surface of the scapula is slightly concave in its proximal region. The remainder of this surface is relatively featureless despite the fact that it was probably an important site of muscle origin (Johnson 1979).

Coracoid (Figures 25 and 26)

Like the scapula, this endochondral element displays considerable individual variation in the extent to which ossification has progressed, and as a result of this there is a large variation in shape. In overall shape and proportions, the coracoid resembles that of Stenopterygius. Johnson (1979) also found a large amount of individual variation in the coracoid of this genus.

The bone is an ovoid plate-like element which bears a rounded excavation or notch in its anterior border. When the scapula and coracoid are in articulation, the anterior notch is completed laterally by the scapula to form a fenestra in the scapulo-coracoid plate. Johnson (1979) refers to this as the fenestra coracoscapularis (Furbringer 1876), which is a term applied to a morphologically similar fenestra in extant lizards. It would appear, however, that insufficient evidence is available to demonstrate strict homology, and I would suggest it is misleading to apply such a specific term to this fenestra. It is quite possible, however, that the fenestra had a similar function to the fenestra coracoscapularis of extant lizards, which is associated with the site of origin of a muscle inserting on the humerus (the M. scapulo-humeralis anterior in lizards (Romer 1956)). The shape of the anterior coracoid notch varies between individuals, being widely open in some, for example, BMNH R2137 (figure 25) and R4753, whilst in others the notch is smaller and more closed, indicating more extensive ossification, for example BMNH R2160 and HM V1872 (figure 34). This variation is not strictly size-dependent, for example, BMNH R4753 and R2149 are large, well-ossified individuals with large, open notches.

The intercoracoidal facet is seen as an ovoid thickening of the medial edge of the bone. Its surface is irregularly pitted, even in large individuals, and it is clear that a certain amount of cartilage intervened between the two coracoids. The articular surfaces are inclined to the plane of the coracoids so that when in articulation, the two coracoids form an angle of about 125° between themselves.

The lateral margin of the coracoid is similarly thickened to form an elongate irregularly pitted surface. The anterior region of this surface curves slightly mesially and articulates with the scapula. The larger, more posterior portion faces laterally and takes part in the glenoid. When the scapula and coracoid are articulated, it is seen that the region of the glenoid is very poorly ossified, and there is no well-defined socket. Because of the extensive cartilage here, the orientation of the humerus cannot be accurately determined. This differs from the condition in <u>Stenopterygius</u>, in which Johnson (1979) regards the bone surface of the glenoid as accurately reflecting the form of the socket in life.

The whole of the anterior and posterior edges of the coracoid are of unfinished bone which would have been continued in cartilage. When the pectoral girdle is articulated it is seen that the cartilage of the anterior edge would have had contact, laterally, with the anterior edge of the scapula. The cartilaginous anterior edge of the coracoid would probably also have reached towards and contacted the clavicles. In some large specimens the medial anterior corner of the coracoid is planed off on its ventral surface to form a triangular, irregularly pitted surface. This surface was in contact, via cartilage, with the posterior median stem of the interclavicle.

The thin posterior edge of the coracoid forms a rounded curve. In some well-ossified individuals the posterior edge is interrupted by a slight excavation just posterior to the glenoid. In one such specimen the excavation is of finished bone (SM J63920) and forms a slight concavity in the posterior margin, though this is not so deep as the anterior coracoid notch. In two known specimens from the Oxford Clay, this point on the posterior margin of the coracoid is deeply emarginated, to form a distinct posterior notch. These specimens are BMNH R2133, the type specimen of <u>Ophthalmosaurus icenicus</u>, and LM 100'1949/20. These two specimens are discussed more fully above.

The internal and external surfaces of the coracoid are relatively flat and featureless. On the internal surface, however, the medial intercoracoidal edge is raised markedly above the flat surface, whilst on the external surface the lateral glenoid edge is markedly raised. These differences can conveniently be used to distinguish between the dorsal and ventral surfaces of isolated coracoids which are otherwise difficult to orientate.

<u>Clavicles</u>

The clavicles are elongate, curved elements which, from their medial expanded region, taper distally to a point. The medial extremity of each bone is digitiform and meets the bone of the opposite side along a complexly interdigitating line. There is no overlap at this union between the clavicles of each side, and furthermore the bones do not maintain a contact along the whole length of the line; instead, the two bones diverge at a point along their line of contact to expose the underlying interclavicle. In the majority of specimens the suture between the clavicles does not fuse, nor do the clavicles fuse with the interclavicle. However, in very well-ossified individuals, which are presumably very old, for example, BMNH R3535, all three bones fuse together and the sutures become very difficult to distinguish.

The whole of the medial section of the clavicle is folded around the lateral bar of the interclavicle, so that the posterior surface of this section of the bone is seen to be deeply grooved. The bone surface here is rugose and bears numerous striations which indicate close bonding to the interclavicle. The anterior, or external, surface in this region is smooth and convex. It is likely that muscles involved in the movement of the forelimb covered this surface, as reconstructed for Stenopterygius (Johnson 1979).

Lateral to its straight medial section, the clavicle curves dorsally. In this region the internal (posterior) surface of the bone becomes more shallowly concave, but maintains its rugosity and striated markings beyond the region of overlap with the interclavicle. These markings are interpreted as indicating a contact with anterior cartilaginous extensions of the coracoid and scapula.

More laterally still, the clavicle narrows to a horn-like extension. At the point of narrowing, the ventral edge of the bone is in some specimens sharply angled; in others the transition is less abrupt, and there is no sharp angle. The internal surface of the ventral angle is marked by a shallow depression, the bone surface of which is rugose. When the shoulder girdle is articulated the depression is seen to receive the acromion process of the scapula. Lateral to this point, the tapering horn of the clavicle is applied to the antero-ventral edge of the scapula, and for this purpose its internal surface is coarsely striated.

Interclavicle

The interclavicle is a T-shaped bone consisting of a posteriorly-directed median stem and an anterior transverse bar. The transverse bar is held firmly by the clavicles which envelop most of its convex external face; the external face is here roughened for this contact. Ventrally the external surface of the bone bears a prominent irregular tuberosity which is left exposed between the medial extremities of the clavicles. The tuberosity may mark the point of origin of muscle slips which insert on the pectoral limb. The internal surface of the interclavicle is concave and deeply grooved, reflecting the shape of the internal surface of the clavicles.

The median stem of the interclavicle tapers and flattens towards its distal extremity becoming blade-like. The external, or ventral, surface of the stem is coarsely striated, and in some specimens exhibits a raised ridge about halfway along its length. These features may indicate the origin of muscles inserting onto the pectoral limb. The internal surface of the median stem is convex proximally, but becomes shallowly concave distally. The convex area is roughened and may be tuberculous; this roughening extends onto the internal surface of the transverse bar. The concave region of the stem bears numerous coarse longitudinal striations. When the pectoral girdle is articulated, it is seen that the median stem of the interclavicle is applied to the ventral surface of the intercoracoidal suture; the roughening of the internal surface of the stem is then interpreted as an indication of its contact with the cartilage which was present both at the suture and extending from the anterior edges of the coracoids. There is no indication of a ridge and groove system by which the interclavicle and coracoids of Stenopterygius are reported to have articulated (Johnson 1979).

Humerus (Figures 27 - 30)

The humerus is a short, robust element which expands considerably at the proximal and distal ends of its constricted shaft. The distal articular surface is expanded in the plane of the paddle; this plane is referred to as antero-posterior even though it may not correspond to the antero-posterior long axis of the body. The long axis of the proximal head of the humerus lies at an angle of about 45° to that of the distal head, and this at first gives the impression that the shaft of the humerus undergoes a torsion. This is not, however, the case: the proximal head is greatly expanded by two well-developed trochanters on the dorsal and ventral surfaces of the bone, and this results in the long axis running through these prominences rather than through the anterior and posterior edges of the bone (see figure 28).

The proximal articular surface is gently convex and, even in large individuals, it is deeply pitted, indicating that a cartilaginous epiphysis was present throughout growth.

The cartilage-covered surface extends onto both the dorsal and ventral trochanters. The ventral trochanter is the larger of the two, and it is comparable in position with the deltopectoral crest of primitive reptiles (Johnson 1979). It is positioned near the anterior edge of the humerus and the ridge of the trochanter reaches distally more than halfway along the shaft. Both the anterior and posterior slopes of the ridge are convex. It is likely that the ventral trochanter was an important insertion point for muscles involved in the movement of the forelimb. Johnson (1979) has produced a reconstruction of these muscles in Stenopterygius.

The dorsal trochanter is positioned towards the mid-region of the dorsal surface, and it differs in form from the ventral trochanter in that its ridge reaches distally only midway down the shaft, and the surfaces sloping away on either side of the ridge are concave, particularly on the anterior side; this gives the ridge a sharper relief than the ventral trochanter.

The shaft of the humerus is smoothly constricted in its midline, but in dorsal view the constriction is seen to be less marked along the posterior margin of the shaft. Here the posterior edge of the humerus is sharpened to form a ridge.

The distal articular surface of the humerus is elongate in the plane of the paddle, and, like the proximal surface, it is deeply pitted for the application of cartilage which intervened between the propodial and epipodials. The distal surface is composed of two large, rounded, concave surfaces which are separated by a high ridge, and a third, smaller, triangular surface situated at the anterior edge of the bone. The third, anterior, articular surface gives a pointed outline to the anterior edge of the distal surface of the humerus. This anterior articular surface has been considered by previous authors to be diagnostic of the genus Ophthalmosaurus, since it is not present in any other ichthyosaur genus (Seeley 1874, Andrews 1910, Appleby 1956). The three distal articular facets on the humerus are interpreted as, respectively, for the ulna posteriorly, radius and a pre-axial accessory element.

On both dorsal and ventral surfaces of the humerus shaft, just proximal to the ulnar facet there is frequently developed a muscle tubercle. The exact positions of these tubercles vary. They may be positioned relatively high on the shaft, well separated from the distal edge of the bone, for example BMNH R2157, or they may be on the distal edge, for example HM V1893 (figure 27). In some specimens, one or other tubercle is absent from the humerus shaft. A study of specimens BMNH R3702 (figure 30) and R2856, both of which are preserved with the radius and ulna cemented to the humerus by hardened matrix, reveals that when one or other tubercle is absent from the humerus, it is, instead, developed on the proximal edge of the ulna. In R3702 the tubercle is "shared" between humerus and ulna. The variability in the presence of tubercles on the distal edges of isolated humeri led Andrews (1910) and Appleby (1958) to suggest that this may be a sexual character. The preceding observation would seem to negate this proposition.

Disarticulated ichthyosaur humeri have in the past presented difficulty in their correct right/left and anterior/posterior orientation, and consequently in the orientation of the paddle as a whole. The problems are even greater for skeletons from the Oxford Clay, which are never embedded in matrix, and which were almost all collected around the turn of the century. There is, therefore, a lack of knowledge of the position of the paddle on deposition. The result of this is that there has been disagreement amongst previous authors on the correct orientation of the paddle of Ophthalmosaurus. For example, Andrews (1910) in figure 36 shows what he interprets as a left humerus in ventral view. Seeley (1874) figures a similar humerus in the same orientation, but he refers to it as a right humerus in dorsal view. I consider both interpretations to be incorrect, and I interpret the figured humeri as being from the left side and seen in dorsal view. The same errors were noted by Johnson (1979) who described a simple method by which the correct orientation of isolated humeri of Stenopterygius can be achieved: of the two proximal trochanters, one (the dorsal trochanter) is situated in the middle of the dorsal face of the bone, and the other (the deltopectoral crest) is on the opposite face towards the anterior edge. One additional feature is that the posterior margin of the bone is sharper than the anterior margin. This method can be tested on other Liassic skeletons which are so well preserved and articulated that there is no doubt about the correct orientation of the paddles. I have found it reliable for all the Jurassic ichthyosaur humeri I have studied.

As a result of these errors of interpretation, the entire forepaddle of Ophthalmosaurus has been antero-posteriorly reversed by all previous authors, and also dorso-ventrally reversed by some. It has, therefore, been widely accepted that the third distal articular facet on the humerus of Ophthalmosaurus was for the articulation with a postaxial element which was generally homologised with the pisiform. The revised interpretation presented here indicates that the third distal facet is, instead, for a preaxial accessory element.

Epipodials (Figure 30)

As a result of the errors of interpretation noted above, the ulna has previously been described as the radius and vice versa. The ulna is the larger of the two bones and is usually slightly longer than the radius in the direction of the long axis of the paddle. Its dorsal and ventral faces are of smooth finished bone and are usually more or less pentagonal in outline. These faces converge posteriorly towards the posterior free edge of the element which is relatively thin. This edge is unfinished, but relatively smooth and lacks the pitting that is characteristic of cartilage-covered bone surfaces; instead, fibrous connective tissue may have been applied to this edge. At the distal corner of the posterior edge of the ulna, there is normally present a small facet which articulated with a post-axial accessory element. Johnson (1979) homologised a similar ossicle in Stenopterygius with the pisiform. The remaining four borders of the ulna are wide, and their surfaces are deeply and irregularly pitted suggesting that cartilage intervened between the ulna and its surrounding bones. The widest of these borders is convex and was in articulation with the concave posterior distal facet of the humerus. In some cases the dorsal and ventral edges of the humeral facet of the ulna are raised to form a tubercle for muscle insertion which may be shared between the humerus and ulna. The remaining two borders of the ulna, which contact the radius and intermedium, are variable in their length, reflecting the variable degree to which the intermedium wedges between the radius and ulna. In some specimens, for example, BMNH R2853, HM V1893, the ulna and radius hardly make contact and so both bones are effectively four-sided rather than pentagonal.

The radius is surrounded on all sides by other bones, and so all its borders are irregularly pitted for the application of cartilage. The broadest edge articulates with the humerus whilst the narrowest edge articulates with the most proximal element of the preaxial accessory digit.

The preaxial element articulating with the humerus is ovoid in outline and slightly wedge-shaped, so that its outer free border is narrower than the inner border, which articulates with the ulna. The long axis of the bone lies parallel with the long axis of the paddle. All borders of the bone are deeply pitted, indicating that in life it was embedded in cartilage, and, furthermore, that the anterior edge of the paddle was completed in cartilage.

Carpus and Digits

The radius, ulna and proximal preaxial accessory ossicle are normally easily recognised amongst the disarticulated remains of the Leeds collection, and their arrangement in relation to the humerus is obvious. However, the remaining elements of the paddle resemble one another very closely and they all have the appearance of more or less rounded bony discs. In the majority of cases these are disarticulated, and so the arrangement of the bones of the carpus and digits is uncertain.

The reconstruction of the forepaddle of Ophthalmosaurus presented here is based on two specimens, BMNH R3534 and P3, both of which retain some of the more proximal elements of the paddle embedded in hardened matrix, and relatively little disturbed. Additional, very valuable information concerning the arrangement of the whole paddle, including more distal elements, has been obtained from a pencilled diagram which was found together with the paddles of R3702 in the British Museum (Natural History) collections. The handwriting on the diagram matches that in the manuscripts of Alfred Leeds, which are stored in the BM (NH) archives. The caption on the diagram reads "Plan of paddle marked with red ink dot". A dot is marked on both the forepaddles of R3702, and both paddles have been reconstructed and fixed onto a board. The pattern in which the paddle bones have been arranged differs from that in Leeds' diagram, and I would think it unlikely that the reconstructions were done by Leeds himself. The number of phalanges of the right paddle of R3702 matches better Leeds' diagram, and the reconstruction in figure 30 is based on this right paddle. A tracing of Leeds' diagram is presented in figure 29.

The importance of Leeds' diagram lies in the fact that, derived from twenty years' experience of collecting from the Oxford clay, Alfred Leeds possessed a unique knowledge of the arrangement of the paddles before their removal from the clay, and their consequent disarticulation. Andrews (1910) pointed out that he based his own knowledge of the humerus and paddle upon the knowledge of Alfred Leeds. Unfortunately, Andrews reversed the forelimb antero-posteriorly, and it appears this incorrect interpretation was influenced by Leeds (Andrews, 1910, p.51). This one error, however, does not, in my opinion, lessen the accuracy of the overall plan of the paddle recorded in Leeds' diagram.

Discussion on Terminology

The terminology used here to describe the digits of the paddle, and their component parts, is slightly modified from that of McGowan (1972a, 1976) and Johnson (1979). McGowan identified a primary digit as one arising from the distal edge of a distal carpal element. He distinguished these from accessory digits which he identified as those originating from outside the distal carpal series. An accessory digit may touch a distal carpal element by the free (lateral) edge of the carpal, but never by its distal edge. McGowan included in his definition of primary digits those extra digital rows which result from "digitial bifurcation". This is the apparent splitting of a row of ossicles in a digit to form two rows, and it is a phenomenon that occurs frequently in the Liassic genus Ichthyosaurus (McGowan 1974b). The concept of digital bifurcation is, on closer inspection, seen to be inappropriate: when a row of ossicles develops between two primary digits, it can only be arbitrarily decided which of the two neighbouring primary digits has "split" to produce two "daughter" digits. This can be seen from figure 42c, which is a tracing of the paddle used by McGowan to demonstrate bifurcation. The inappropriateness of the concept when applied to the genus Stenopterygius was recognised by Johnson (1979). In this genus the new digit is apparently formed anew, between two primary digits, and the ossicles of the new digit are smaller than the phalanges in each of the neighbouring primary digital rows. Johnson, however, retained the usage of the term "bifurcation", believing it still to be applicable to Ichthyosaurus.

It is clear that there are here two different hypotheses concerning the developmental processes that result in the appearance of new digits in the paddle. Either a primary digit has split in development, or an additional digit has been added to the paddle. It seems unlikely that two different developmental processes have developed in two different genera to produce the same result - hyperdactyly. For the reasons noted above, that it is only arbitrarily decided which digit has "split" in Ichthyosaurus, and that it is apparent that an entirely new digit has arisen in Stenopterygius, I would suggest that the second mentioned developmental process is the more likely one to have taken place. I would therefore suggest that the term "digital bifurcation" is inappropriate for Jurassic ichthyosaur paddles, and that new digits arising between primary digits in the paddle should be referred to as "intermediary digits".

This proposition has the additional advantage that it is no longer necessary to make the distinction, that McGowan made, between additional digits forming at the edges of the paddle, which he named accessory digits, and new digits arising as a result of apparent "bifurcation", which he referred to as primary digits. Under the proposition presented here, both types of digit would be seen as having arisen from fundamentally the same developmental process.

For the remaining components of the paddle, the terminology adopted here is illustrated in figure 30. A preaxial accessory digit is one positioned on the leading edge of the paddle, and its ossicles are not supported by a distal carpal. Similarly, a postaxial accessory digit lies on the trailing edge of the paddle. There are two of these, denoted $poax^1$ and $poax^2$. The components of accessory digits, and intermediary digits, are referred to as ossicles, to distinguish them from the phalanges of primary digits. Distal carpals are denoted by the Arabic numerals 1 to 4, and metacarpals by Roman numerals I to IV. p_1^{I} refers to the first phalange of primary digit I. Similarly, p_4^{III} refers to the fourth phalange of primary digit III.

Description

The proximal row of carpals comprises a radiale, intermedium and ulnare. In addition to these, there appears to have been present a posterior element comparable to the pisiform of Stenopterygius (Johnson 1979); this is the element numbered 4 by Leeds in his diagram (figure 29). The pisiform articulated with the ulnare, and also contacted the ulna. There was also present a preaxial accessory element lying distal to the preaxial element in contact with the humerus. This more distal preaxial element articulated with the anterior edge of the radiale, and it was the second ossicle in the preaxial accessory digit.

The radiale, intermedium and ulnare are pentagonal to hexagonal elements which articulate with one another along short borders lying parallel to the long axis of the paddle. The intermedium wedges to a variable degree between the radius and ulna. The proximal and distal borders of the proximal carpals are aligned obliquely to the long axis, so that the transverse line traced along the proximal and distal borders of these elements is zig-zagged. The same zig-zagged arrangement is seen between the distal carpals and the phalanges, but the effect is less marked owing to the more rounded contours of the phalanges. Such a zig-zagged arrangement was noted by Johnson (1979) in the carpus of Stenopterygius. She pointed out that it has the effect of preventing transverse lines of weakness in the carpus, whilst retaining flexibility.

The pisiform is a small element whose straight free edge is thinner than the remaining rounded edges. On the basis of Alfred Leeds' diagram, there appears to have been a second element on the posterior border of the carpus, just distal to the pisiform, and these two elements form the base of a postaxial row of accessory ossicles comprising approximately 10 elements. The paddle drawn by Leeds is unlikely, however, to be complete distally, so the final count for any digit is uncertain. Leeds also figures a single element of a second postaxial accessory digit, and there may, in life, have been such a digit. The preaxial accessory digit appears to have comprised a total of 6 elements. Apart from the pisiform, all the ossicles of the accessory digits are round and disc-like with pitted roughened borders, to which was applied cartilage or perhaps dense fibrous connective tissue. They do not differ in form from the more distal elements of the primary digits, but they tend to be smaller than the latter bones at any one transverse level.

There are four distal carpals. These are smaller than the proximal carpals, but they resemble them in form except that their distal margins are slightly less angular, reflecting the increase in cartilaginous investment of the bones towards the distal end of the paddle.

The metacarpus and manus comprise a row of four metacarpals, each supporting a primary digit. The metacarpals retain a slight angularity, but otherwise they resemble the succeeding phalanges. The disc-like phalanges are arranged in four rows which, from Leeds' diagram, appear to curve anteriorly from the distal carpals; the curve diminishes more distally. A certain amount of hyperphalangy is present: each digit appears, from Leeds' diagram, to have consisted of 7 phalanges, except for digit III which has 8. As already mentioned, it is unlikely that this represents the full complement of phalanges, since it is evident, from Liassic skeletons, that there are usually numerous small terminal phalanges which are frequently disturbed or lost prior to deposition, and in <u>Ophthalmosaurus</u> these might be easily overlooked on collection, or lost before deposition. However, R3702 does possess the largest phalangeal complement of any paddle in the Leeds' collection. Furthermore, it seems that the ossification of these terminal phalanges varies widely between individuals, as Johnson (1979) discovered for Stenopterygius.

The phalanges decrease in size distally and change from ovoid to round in shape. In the well-preserved, embedded paddles of Stenopterygius the phalanges are spaced further apart distally, and this feature has been reconstructed for Ophthalmosaurus in figure 30. Johnson suggested that the more distal phalanges were embedded in dense connective tissue, though it is equally likely that they were surrounded by cartilage.

It is not known whether intermediary digits occurred in Ophthalmosaurus; however, there is some evidence for it in the type specimen of the American form Baptanodon discus (discussed above). The embedded forepaddle of this specimen possesses an intermediary digit arising between p_1^{I} and p_1^{II}. I have studied this specimen and find agreement with Gilmore's (1905) figure of this paddle, except that this author refers to the paddle, incorrectly, as a pelvic paddle.

Pelvic Girdle (Figure 31)

The pelvic girdle is very much reduced in comparison with the pectoral girdle, and it has lost all bony contact with the vertebral column. It comprises only two elements, a slender ilium and a fused, plate-like puboischium.

The ilium takes the form of a rod which curves and also twists at its distal end. This allows the sidedness of each isolated bone to be determined, since, when in its life position, the ilium would curve posteriorly, but also twist mesially so that its distal section lies closer to and alongside the vertebral column. Both the proximal and distal ends of the bone are pitted and unfinished, indicating the presence here of cartilage. The proximal end seems to have contributed only very little to the acetabulum. The dorso-mesial surface of the distal section of the ilium is rugose. This is interpreted as the point of attachment of ligaments anchoring the pelvis to the sacral region of the vertebral column. In some specimens, for example, HM V1899, the proximal lateral surface of the bone bears longitudinal striations which may indicate the origin of muscles involved in moving the hindlimb.

The pubis and ischium are fused to form a single elongate plate. However, a remnant of their original separation is indicated by a slit-like opening near to and parallel with the anterior edge of the plate. This is sometimes accompanied by a second opening positioned lower down, and there may be an additional notch in the ventral edge of the bone. Andrews (1910) referred to the more dorsal slit as the obturator foramen. It is doubtful, however, that this opening is the homologue of the latter foramen, which is a distinct nerve foramen in the pubis of primitive reptiles. However, it is possible that the slit has taken over the function of that foramen in Ophthalmosaurus.

The proximal articular surface of the pubo-ischium is triangular in end view and is irregularly pitted for the application of cartilage. The facet for the ilium is seen as a slight down-turning of the antero -mesial corner of the proximal surface. It is apparent that a large pad of cartilage intervened between the two bones. The rest of the proximal surface is involved in the acetabulum which would have been largely formed in cartilage.

Below its thickened proximal end the pubo-ischium flattens out to form a plate. Its anterior edge, however, is thickened and deflected laterally so that its anterior face lies at an angle of 90° to the rest of the plate. This edge is considered to be formed by the pubis. The posterior edge of the plate is thin and sharp. The pubo-ischiadic plate widens towards its ventral edge which is convexly curved. This edge is deeply grooved and irregularly pitted indicating that it was originally continued in cartilage. There is no evidence of a contact between the pubo-ischia of each side.

Hindlimb (Figures 28, 32 and 33)

The femur is very reduced relative to the humerus, suggesting that its function in steering during swimming was less important. In length the femur is a little over half that of the humerus. It differs in overall proportions, however, in that the proximal end of the femur is more massive than its distal end.

As with the humerus, problems are encountered in the orientation of isolated femora. Unfortunately, in this case comparisons with embedded British Liassic skeletons are less useful because the dorsal and ventral trochanters are both in almost the same position towards the anterior margin of the paddle (the anterior margin itself can be distinguished from these skeletons). This means that it is difficult to distinguish between dorsal and ventral aspects of femora. The problem is compounded by the fact that the hindlimb and girdle are smaller than, and less firmly attached in life to, the rest of the skeleton, so that the hindlimbs are more frequently lost or disturbed at deposition. The problem of the orientation of the humerus of Ophthalmosaurus was resolved by Johnson's study of the forelimb of Stenopterygius; a similar study is needed for the hindlimb. Nevertheless, a provisional interpretation will be presented here. Andrews (1910) noted that the major features of the femur closely resembled those of the humerus of Ophthalmosaurus, and he orientated the femur in a similar way. The interpretation presented here suggests that, as with the humerus, Andrews had reversed the bone antero-posteriorly and dorso-ventrally, but, given these errors, I would orientate the femur in a similar way to the humerus, so that the more anterior trochanter is ventral.

The proximal articular surface of the femur is convex and irregularly pitted, indicating the presence of a cartilaginous epiphysis (figure 28). The anterior edge of the head is greatly widened by the development of two very similar trochanters - the more anterior being interpreted as the ventral trochanter. In primitive reptiles, generally, the prominent internal trochanter on which inserts the M. puboischio femoralis externus, is positioned antero-ventrally on the bone; in contrast, on the dorsal surface of the femur of primitive reptiles, there is usually developed a more posteriorly placed prominence for the puboischio femoralis internus.

That the trochanters are comparable in position to the dorsal and ventral trochanters of the humerus may be an indication that similar locomotory movements were carried out by both limbs. The dorsal trochanter is distinguished from the ventral trochanter in that its summit is narrower and the anterior face of its prominence is more concave than that of the ventral trochanter. Extending distally from the prominence of the dorsal trochanter is a low ridge whose summit is roughened for muscle attachment. The ventral trochanter does not display a distal ridge, but a generalised roughening of the shaft occurs just distal to the prominence of the trochanter. The posterior faces of the two trochanters form broad planes which converge towards the sharpened posterior margin of the shaft of the femur. A certain amount of roughening of the posterior margin is detectable which may indicate muscle attachment.

The distal articular surface of the femur, unlike that of the humerus, consists of only two separate articular surfaces, for the tibia and fibula (figure 28). These are seen as ovoid concavities - the anteriormost, for the tibia, being the larger of the two. The distal articular surface is irregularly pitted, showing that cartilage intervened between the propodial and epipodials. The anterior extremity of the distal surface is extended to form a blunt projection whose tip is of unfinished bone. It is reasonable to suppose that the blunt projection was continued in cartilage which appears to have been present along the preaxial margin of the hind paddle.

Epipodials, tarsus and digits

There is less certainty of the arrangement, in life, of the bones of the hind paddle, than of the forepaddle. There is no partially embedded hindpaddle known to me amongst the Leeds Collection, and neither is there a diagram by Alfred Leeds of the hindpaddle. Perhaps the most reliable evidence of the structure of the hindpaddle derives from Andrews' (1910, figure 40) reconstruction, since he at least based his reconstruction on the knowledge of Alfred Leeds.

The following description, therefore, is based largely on Andrews' reconstruction, with the modification that he had antero-posteriorly reversed the femur and hindpaddle from its correct orientation. Andrews did not state which specimen his figure was based on, but it seems to correspond to BMNH R4693-5.

The tibia is the larger of the epipodial elements, and it is deeper along the long axis of the paddle. The tibia is slightly angulate, with all its borders irregularly pitted indicating that it was surrounded by cartilage. The fibula is roughly ovoid in shape, with a straight medial border for articulation with the tibia. The postaxial border of the fibula is sharpened and does not display the irregular pitting of the other borders, indicating that only a thin layer of connective tissue or cartilage was applied to it; in this feature it resembles the postaxial border of the ulna and pisiform.

The remaining bones of the hindpaddle are ovoid and disc-like and closely resemble one another. Their borders are pitted indicating that they were embedded in cartilage, and there does not seem to have been any close contact between the elements. It is not possible, from their arrangement, to homologise with any certainty the remaining bones of the hindpaddle with those in the tarsus and pes of primitive reptiles. Andrews reconstructs these bones as being arranged in three rows arising from the tibia and fibula. This reconstruction seems reasonable, since in other genera, from the Upper Lias, the hindpaddles often possess one fewer primary digit than the forepaddle. For example, this is seen in Stenopterygius quadriscissus, BMNH R4086 and R3300 (personal observation), and in five other Stenopterygius species (McGowan 1979, plates 1 - 4). Lower Liassic genera appear to vary with regard to this feature, but the hindpaddle is often neglected in published descriptions so that the feature is not well known.

In Andrews' reconstruction, two of the three digital rows comprise only three elements distal to the epipodials, whilst the middle row comprises four elements. It is likely that some of the phalanges are missing from this specimen, as Andrews himself pointed out. When dealing with Leeds' collection specimens, it is frequently found that the paddle bones from the fore and hind limbs have been put together in the same box, and it is impossible to separate them. It is reasonable to suppose, however, that the number of phalanges in each digital row of the hindpaddle is substantially smaller than in the digits of the forepaddle. This is a feature which is found consistently in Liassic specimens.

Gastralia

The gastralia are delicate rods of bones which are rarely preserved amongst the Leeds collection material. HM V1916 possesses a number of fragments of gastralia, but unfortunately they are not complete enough to allow a reconstruction of the plastron to be made. In Liassic ichthyosaur taxa, the plastron is formed from two pairs of slender, lateral rods which articulate with each other by their overlapping ends (Owen 1881). The more medial member of the pair on each side articulates with a slightly angled median rod which is thickened at its point of curvature in the midline.

Genus Grendelius McGowan, 1976

Synonymy: None

Type species: G. mordax, McGowan, 1976

Additional British species: None

Diagnosis: As for monotypic species below.

Grendelius mordax McGowan, 1976

Synonymy: None

Holotype: A nearly complete skull with associated postcranial material in the Sedgwick Museum, Cambridge, catalogue no. J68516. The specimen was described and figured by McGowan (1976, text figures 1, 2, 3).

Preservation of Holotype: The skull of J68516 is better preserved on its left side, and because of its fragility it is now supported in a glass fibre mould with the left side exposed. The skull has been laterally crushed: displacement of the skull elements is greater in the region of the orbit than in the snout. The postorbital region, and the region of the temporal vacuity are incomplete. The basioccipital, basisphenoid, exoccipitals, fragments of posterior pterygoids and right surangular are preserved separately. Postcranial remains are fragmentary and include vertebral centra from the anterior and posterior trunk region and rib fragments. Limb and girdle fragments are extremely friable and in need of preservation; these include fragments of two scapulae, a clavicle and two coracoids.

Locality and Horizon of Holotype: The specimen was discovered in 1958, during excavation work near Stowbridge, Norfolk (National grid reference: TF604069). It lay approximately one metre below the top of the Kimmeridge Clay in the Wheatleyensis Zone; the horizon is then Middle Kimmeridgian (Upper Jurassic).

Diagnosis: A lack of paddle material has led to uncertainty in the taxonomic position of this species. However, its large size, and the robust nature of the skull, jaws and teeth, and the relatively small eye are all features apparently characteristic of the Temnodontosauridae, and they are not found in the other Jurassic ichthyosaur family, the Ichthyosauridae. The lack of paddle and other postcranial material also restricts the search for specifically diagnostic characters to the skull. McGowan's (1976) diagnosis for this species consists of a series of ratios calculated from skull measurements. None of these values is particularly distinctive when compared with those values from the twelve other taxa used by McGowan for comparison with Grendelius. McGowan's classification relies on a phenetic technique which simultaneously compares all the characters (in this case, skull ratios) of all the taxa studied. These characters are only diagnostic, therefore, when considered together. Grendelius does not, then, show any unique derived characters in its skull proportions. The only autapomorphy I have been able to distinguish is used in the following diagnosis:

> Member of the family? Temnodontosauridae (order Ichthyopterygia, suborder Ichthyosauria, infra-order Ichthyosauri) possessing: a basioccipital with a relatively small extracondylar area which

is only narrowly visible in posterior view.

Description: (Plate 4, figs. 37, 38)

The holotype possesses a fairly large skull, with a lower jaw length of 123.0 cm; the tip of the dentary and the posterior edge of the surangular are incomplete, however, so that in life the jaw measurement would have been a few centimetres greater. If skull length is taken as an approximate indication of actual body size (see McGowan, 1972b), then G. mordax can be described as a moderately large ichthyosaur. Using data from McGowan (1972b) and Camp (1980), out of twenty other ichthyosaur taxa only five exceed G. mordax in skull length (120.2 cm). A further indication of large body size is the relatively large diameter of the vertebral centra. The largest well-preserved mid-trunk centrum of the holotype is 9.30 cm in height. For comparison, a large specimen of Ophthalmosaurus, BMNH R4753 has a corresponding central height of 8.5, jaw length 94.0 cm.

The orbit is both relatively and absolutely smaller than that of Ophthalmosaurus, despite the larger skull of Grendelius. Its greatest horizontal diameter is 21.5 cm; this may be compared to 28.0 cm in the largest Ophthalmosaurus skull, BMNH R3013 (adjusted for distortion). The remains of at least four sclerotic plates are present in the left orbit and they appear to occupy a segment which would be about one third of the complete sclerotic ring. It is estimated, therefore, that a complete ring would contain approximately twelve plates. This contrasts with Ophthalmosaurus which possesses fifteen plates. The radial width of the sclerotic ring is 6.05 cm. Other bones visible in the orbit of the holotype skull are palatal elements, almost certainly the pterygoids which have been crushed upwards to the side of the skull.

The postorbital segment of the skull is badly damaged. Nevertheless, McGowan (1976) interpreted the postorbital segment as being narrow, compared to the Liassic *Temnodontosaurus*, and the Triassic *Cymbospondylus*, both with similar skull proportions to *Grendelius*. He took this as indicative of a more posteriorly positioned orbit in *Grendelius*. Since the postorbital bone is badly fragmented, and the greatest part of the quadratojugal is missing, I find this interpretation, that *Grendelius* has a narrow postorbital segment and a posteriorly placed orbit, questionable. The postorbital portion of the jugal of *Grendelius* is widely expanded, compared to taxa with narrow postorbital segments such as *Ophthalmosaurus* and *Stenopterygius*; these taxa display narrow, bow-shaped jugals. Although the postorbital region of the holotype is damaged, it appears that the posterior edge of the jugal forms a long suture with a fragment of bone which must be part of the quadratojugal (figure 37). This latter bone is obviously very incomplete, and in life it would have contributed to a much broader cheek than is now present.

The jugal extends far anteriorly beneath the orbit towards the vicinity of the narial opening where it forms a complex, interdigitating suture with the premaxilla. This union would have excluded the maxilla from entering the narial opening in lateral view, but it would enter the narial border beneath the overlying premaxilla and jugal. The maxilla is just visible in the narial border of the holotype because part of the overlying premaxilla has flaked away. The configuration of bones surrounding the narial opening contrasts with that seen in *Ophthalmosaurus* where the jugal does not reach far enough anteriorly to meet the premaxilla, but instead, the lachrymal and premaxilla meet to exclude the maxilla from the narial border in external view. The lachrymal is crushed, but is apparently of similar form to that of *Ophthalmosaurus*.

The prefrontal is difficult to distinguish in the holotype with certainty, because of crushing in this region. However, it appears to be relatively small compared with the prefrontal of *Ophthalmosaurus*. The relatively small orbit of *Grendelius* has resulted in a relative reduction of all the circum-orbital bones, when compared with *Ophthalmosaurus*, with the exception of the lachrymal.

The postfrontal bone appears as a thickened, smoothly rounded bar above the orbit. There is no sign of the supraorbital flange seen in *Ophthalmosaurus*. This could be a result of crushing, but alternatively it could be that the smaller eye of *Grendelius* was not in need of protection from supraorbital flanges. The mesial edge of the postfrontal is finished bone, and forms part of the lateral border of the temporal opening. This opening is incomplete posteriorly, however, and it is not possible to distinguish the bones forming the posterior border of the opening.

The postorbital is distinguishable by its union with the jugal below and its contribution to the posterior border of the orbit, but neither the squamosal nor an element B is identifiable.

A fragmentary area of bone lying dorsal on the specimen to the postfrontal is interpreted as both frontal and parietal bones, but the suture between them is reconstructed only tentatively.

More anteriorly on the skull roof there is present a large nasal bone. It reaches towards and meets the postfrontal, thus excluding the prefrontal from entering the temporal opening in external view; this is a feature also seen in *Ophthalmosaurus*, where the prefrontal reaches the temporal opening beneath the overlying nasal and postfrontal. Laterally the nasal forms the dorsal border of the narial opening. Although it is crushed, the nasal appears to resemble that of *Ophthalmosaurus* in that it possesses a lateral flange in the posterior half of the narial opening. The flange is now crushed down onto the skull surface, but, without the crushing, it would probably have given a bi-partite appearance to the nostril, as in *Ophthalmosaurus*. The nostril is 8.68 cm in its longest diameter. Above the nostril the nasal is sharply angled (as in *Ophthalmosaurus*) along a longitudinal line which marks the transition from the dorsal surface of the skull to the lateral surface. As a result of crushing, however, the angle now appears as a rounded ridge, and the dorsal skull surface is visible in lateral view. The nasals are relatively longer than those of Ophthalmosaurus. In external exposure they reach more than halfway along the snout (measured from the anterior edge of the orbit to the tip of the premaxilla). In Ophthalmosaurus the nasals are concealed from external view by the premaxillae at a point just posterior to the midpoint of the snout.

The maxilla makes a relatively large contribution to the ventral edge of the snout, as noticed by McGowan (1976). It disappears from view at a point 20.3 cm anterior to the anterior edge of the naris. This compares with 4.0 cm for Ophthalmosaurus. McGowan expressed relative length of the maxilla in terms of the premaxillary ratio - the ratio of the distance from the tip of the premaxilla to the anterior tip of the maxilla (the premaxillary segment) to the jaw length. This ratio is less appropriate for this purpose than one which expresses length of premaxillary segment to snout length, since it fails to take into account variations in the length of the orbital segment of the skull, which is greatly influenced by orbital size variations. Thus McGowan's (1976) premaxillary ratios for Grendelius and Ophthalmosaurus are respectively 0.44 and 0.46. These do not accurately represent the great difference in maxillary length actually seen. When the ratios are expressed as length of premaxillary segment to snout length, the values obtained are respectively 0.59 and 0.73 - a more accurate representation.

The maxilla of Grendelius has a smaller exposure posteriorly than that of Ophthalmosaurus, owing to the more extensive overlap in Grendelius of the jugal.

The premaxilla of Grendelius enters the posterior border of the external naris, as in Ophthalmosaurus, and sends a tongue of bone both dorsal and ventral to the narial opening. The dorsal tongue reaches further posteriorly than is the case in Ophthalmosaurus.

A longitudinal vascular groove, into which open a number of foramina, is present along the premaxilla and dentary. The groove appears to be characteristic of ichthyosaurs later than the Lower Lias. In Lower Liassic and Triassic specimens that I have studied, the vascular foramina are more scattered and there is not the same degree of development of a distinct groove.

The premaxilla is relatively deep and robust compared to that of Ophthalmosaurus, but it is most noticeably more robust in its anterior section, which does not taper as it does in the latter genus. This seems to be correlated with the fact that the teeth in Grendelius do not decrease in size noticeably towards the anterior tip of the jaws, whereas in Ophthalmosaurus there is a marked reduction in tooth size anteriorly in the tooth row.

McGowan (1976) expressed snout robustness by the ratio of snout depth at the midpoint of the snout to jaw length. His values for Grendelius and Ophthalmosaurus respectively were 0.89 and 0.54 (these values must have been multiplied by 10, although McGowan does not state this). My own measurements give values respectively of 0.80 and 0.65.

The lower jaw, like the snout, is more robust than that of Ophthalmosaurus. McGowan's jaw depth ratios (ratio of depth of jaw, measured at midpoint, to jaw length) are 0.72 and 0.47 for Grendelius and Ophthalmosaurus respectively. Posteriorly the lower jaw is incomplete since the posterior edge of the surangular is damaged and part of the angular is missing.

The form of the teeth is similar to that in Ophthalmosaurus. The teeth are conical and slightly recurved, with pointed crowns which bear numerous longitudinal ridges. The roots are swollen and are presumably invested in cement. The teeth of Grendelius are, however, both absolutely and relatively larger than the teeth of Ophthalmosaurus.

McGowan expresses relative tooth length by the ratio 10 x crown length of longest tooth / jaw length. McGowan (1976) estimates this ratio for Grendelius to be 0.37. My own measurements do not agree with McGowan's values, and give a ratio of 0.20. I cannot explain this large difference. The crown length of the largest complete tooth of Grendelius was found to be 2.42 cm, whilst the whole tooth length was 5.34 cm. For the largest available specimen of Ophthalmosaurus with relatively complete teeth, specimen BMNH R2180, the tooth length index was calculated as 0.14. As all these measurements are likely to be subject to relatively large errors, the apparent difference in tooth length index between the two genera must be treated with caution. McGowan (1976) gave a tooth length index for Ophthalmosaurus as 0.00, since he believed the genus to be edentulous.

As in the tooth row of Ophthalmosaurus, the maxillary teeth are relatively small, and the teeth increase in size anteriorly. The number of teeth visible in the maxillary tooth row is 23 in Grendelius (10 in Ophthalmosaurus). There are likely to be more than 23 actually arising from the maxilla, since this bone continues to form the alveolar groove for a short distance anteriorly, hidden by the premaxilla from lateral view. The total number of teeth in each half of the upper tooth row is 53 in Grendelius (40 in Ophthalmosaurus). There was probably a similar total count in the lower tooth row.

The most striking difference in dentition between Grendelius and Ophthalmosaurus is seen in the teeth in the anteriormost tooth row. In Ophthalmosaurus the teeth gradually decrease in size anteriorly so that they are very small at the slender tips of jaws. In contrast to this pattern the teeth remain large throughout the anterior half of the tooth row of Grendelius, and at the tips of the jaws they are near the maximum size. This is a pattern also seen in other members of the Temnodontosauridae, such as Temnodontosaurus platyodon, T.risor and T. eurycephalus (McGowan, 1974a).

It is suggested that these taxa probably fed on larger prey than Ophthalmosaurus and other members of the Ichthyosauridae, and that during feeding the large anterior teeth were used to hold prey, much as in extant crocodiles. In contrast to this, Ophthalmosaurus and other Ichthyosauridae probably fed on smaller, swift prey and the anterior teeth were not used for holding the prey.

The basioccipital, basisphenoid and exoccipitals were preserved separately from the rest of the skull, and were figured by McGowan (1976) (see also figure 38). The posterior face of the basioccipital bears the occipital condyle which is convex with a notochordal pit situated some way above the centre of the condyle. The condylar surface is of slightly roughened, "unfinished" bone and takes up almost the entire posterior face of the basioccipital. The extracondylar area is restricted to two very narrow regions of relatively smooth bone, which are situated on either side of the condyle, and are barely visible in posterior view. McGowan (1976) interpreted these smooth areas of bone as facets for the stapes, and he compared them to the much more extensive "stapedial facets" on the basioccipital of Ophthalmosaurus. These latter "facets" in Ophthalmosaurus are actually the smooth extracondylar surfaces (figure 1), and the true stapedial facets are areas of pitted bone surface immediately anterior to these surfaces, as are the true stapedial facets in Grendelius. However, McGowan was correct in showing that the smooth, extracondylar areas on the basioccipital of Ophthalmosaurus are more extensive and more prominent in posterior view than those of Grendelius. One further difference between the two basioccipitals is in the notochordal pit which is more central in Ophthalmosaurus, (compare figures 1 and 38).

The opisthotic facets, situated just above the stapedial facets, are not as distinct as they are on the basioccipital of Ophthalmosaurus. The anterior face of the basioccipital of Grendelius is a flattened surface of pitted bone to which cartilage would have been applied in life. A slight vertical groove divides the face in two. McGowan (1976) noted that there is no development of a basioccipital peg in *Grendelius*, in contrast to *Ophthalmosaurus*. This does not appear to be a significant difference between the genera since the development of a basioccipital peg in *Ophthalmosaurus* is variable.

The basisphenoid is shaped, in ventral view, quite differently to that of *Ophthalmosaurus*. The basipterygoid processes are anteriorly pointed and more prominent than in the latter genus. Just posterior to these processes the ventral surface of the bone is deeply grooved for the transmission of the palatine nerve . The ventral surface of the basisphenoid is distinctly roughened in an area that reaches medially around the posterior edge of the carotid foramen. This roughening is for contact with the pterygoids of either side which underlap the basisphenoid here. In *Ophthalmosaurus* no such roughening is detectable, (compare figures 1 and 38).

The opening for the entrance of the carotid artery is situated at the end of a raised, rounded ridge in the midline of the ventral surface of the bone. The opening is therefore raised above the level of the ventral surface, in contrast to the condition in *Ophthalmosaurus*.

The exoccipitals show no unusual features, except for the presence of an additional third small nerve foramen which is situated anteriorly on the lateral face of each bone. In *Ophthalmosaurus* only two lateral foramina are present. The third exit is presumably for a root of the hypoglossal nerve, as are the two more posterior foramina. Fragments of the pterygoids and right surangular are present, but are not well enough preserved for description.

There are approximately fifty vertebral centra preserved amongst the material of the holotype. These are from the anterior and posterior trunk regions, but are not in series. They are relatively larger than the vertebrae of *Ophthalmosaurus*. The height of one of the earliest posterior trunk centra, in which the diapophysis is separate from the neural arch facet is 9.05 cm whereas a similar centrum of *Ophthalmosaurus* (BMNH R4753) is 7.53 cm in height.

The centra differ slightly in form from those of *Ophthalmosaurus*. The ventral border of the anterior and midtrunk centra, when seen in anterior view, have a slightly parabolic contour, in contrast to the more rounded ventral contour of these centra in *Ophthalmosaurus*. The diapophysis, at the point on the column where it is just separate from the neural arch facet, is completely free of the anterior edge of the centrum. In *Ophthalmosaurus* the diapophysis remains attached to the anterior edge of the centrum by a thin cartilage-finished ridge. The nutrient foramina piercing the sides of the centra tend to be fewer in number, larger and more constant in their position than are the numerous, scattered foramina in the centra of *Ophthalmosaurus*.

The remaining postcranial skeleton is very fragmentary and consists mainly of the remains of ribs. There are, however, some girdle remains. Two poorly preserved scapulae are present. The more complete scapula is large, measuring 27.0 cm in greatest length, but it is incomplete proximally. A large, distally incomplete clavicle is also present. This measures 30.0 cm in a straight line from distal to proximal extremities.

Two poorly preserved coracoids are present. Each displays an anterior notch together with facets for the scapula, humerus and coracoid of the opposite side. The posterior and postero-medial borders of both coracoids are incomplete, but the evidence suggests that there was no posterior notch. The more complete coracoid, as preserved, measures 19.0 cm in length whilst the greatest distance between the intercoracoidal facet and the glenoid is 20.0 cm. In general shape and proportions, the coracoids appear to resemble those of *Ophthalmosaurus*, but, though incomplete, they appear to be relatively larger than the coracoids of the latter genus.

It is unfortunate that no limb material was preserved except for a single phalange.

Referred specimens:

The following two specimens are only tentatively referred to Grendelius mordax. Only the first specimen displays diagnostic features of the basioccipital, but in the size and form of other bones both specimens appear to resemble the holotype.

(a) BMNH 45984-7: This specimen was referred to Ichthyosaurus dilatatus (nomen dubium) by Lydekker (1889a). It consists of twenty-one presacral vertebral centra with associated fragmentary skull bones and incomplete teeth. The basisphenoid resembles that of the holotype, and the basioccipital shows the characteristic reduced extracondylar area. The teeth resemble those of the holotype and the centra indicate that the specimen would have been of a similar size.

(b) A specimen in the Swindon Museum (uncatalogued), which was described by Delair (1972) and referred to Macropterygius trigonus (nomen dubium). The specimen is very incomplete and consists of thirteen anterior trunk vertebral centra with an associated quadrate, basisphenoid, coracoid, rib, neural arch and jaw fragments. Fragments of large teeth are also preserved. Only one half of the basisphenoid is present, but its shape resembles that of the holotype. Delair compared the basisphenoid of BMNH 45984-7 with that of this specimen and concluded that the two bones differed significantly in form. From my own study of both specimans, I would suggest that the differences are size-related. 45984-7 is a larger specimen (the heights of centra around vertebra 25, where the diapophysis is just separate from the neural arch facet are 8.10 cm and 7.28 cm respectively. The basisphenoid of 45984-7 is larger and has slightly more pointed basipterygoid processes, probably as a result of more extensive ossification in the tips of the processes.

Genus *Nannopterygius* Von Huene, 1922

Synonymy: None

Type species: *Nannopterygius enthekiodon* (Hulke, 1871)

Additional British species: None

Diagnosis: As for monotypic species below.

Nannopterygius enthekiodon (Hulke, 1871)

Ichthyosaurus enthekiodon	Hulke, 1871
Ichthyosaurus entheciodon	Lydekker, 1888 (unjustified emendation)
Nannopterygius entheciodon	(Lydekker, 1888) Von Huene, 1922
Nannopterygius euthecodon	Von Huene, 1923 (lapsus calami)
Nannopterygius enthekiodon	(Hulke, 1871) McGowan, 1979.

Discussion of synonymy:

In 1871 Hulke described a near complete ichthyosaur skeleton from the Kimmeridge Clay of Kimmeridge Bay, Dorset, under the new name *Ichthyosaurus enthekiodon*. The specific name was a reference to the nature of the teeth which were said by Hulke to be distinctive in possessing a cement investment of the tooth base. The specific name was emended to *entheciodon* by Lydekker in 1888. An explanatory note for this emendation (appearing in Lydekker 1889a) gave the reason that the name *Enthekiodon* was used previously by Hulke (1870), in a generic sense, applied to isolated teeth from the same locality. Lydekker considered it necessary to emend the specific name; I consider the emendation unjustified.

In 1922 Von Huene erected the new genus Nannopterygius for the reception of this species. He considered the extremely reduced paddles to be sufficiently unique to warrant the erection of a new genus. Von Huene and Kuhn (1934) retained Lydekker's emended specific name; however McGowan (1979) recognised Hulke's (1871) original spelling. In 1923 Von Huene misspelt the specific name as euthecodon.

Holotype:

A near complete, but poorly preserved embedded skeleton, BMNH 46497. The specimen possesses an almost complete, but disrupted skull. The vertebral column is present in series as far as the mid-caudal region. Both incomplete forepaddles, pectoral girdle and one incomplete hindpaddle are present together with a fragment of pelvic girdle. Numerous ribs are present. The specimen is now mounted behind glass on a gallery wall in the British Museum (Natural History). Hulke (1871) first described and figured the specimen (Plate XVII).

Locality and Horizon of Holotype:

The specimen was collected from Kimmeridge Bay, Dorset. Although Hulke (1871) did not state that the specimen was collected from the Kimmeridge Clay, subsequent authors have inferred that this was so, and the information on the specimen itself indicates that this is its horizon. There is no further detail known of the locality or horizon.

Range:

Kimmeridgian, Upper Jurassic.

Diagnosis:

Although the paddles are incomplete, so that there is some uncertainty as to the correct family to which the species belongs, the relatively large eye, slender skull, and unequal size of the fore- and hindpaddles are features which indicate the species belongs to the Ichthyosauridae.

Member of the family Ichthyosauridae (order Ichthyopterygia, suborder Ichthyosauria, infra-order Ichthyosauri) possessing:

(1) Extremely reduced fore- and hindpaddles.

(2) Relatively large posterior trunk and anterior caudal vertebral centra.

Referred specimens:

Lydekker's (1889a) catalogue referred four other specimens to the species. These were BMNH 46497a, R1197, 46473e, 47424. None of these specimens includes diagnostic material. I have been unable to find any other diagnostic material during this study.

Description (Plate 5, figure 39)

The specimen is of a moderately sized individual, embedded so that only its right side is exposed. The near complete right lower jaw ramus measures approximately 60.0 cm in length. The skull is disrupted and incomplete, but the premaxillae and bones in the region of the orbit are still present. The right premaxilla measures 25.2 cm long, but is incomplete anteriorly. The snout appears to have been relatively slender, judging from the slender premaxillae and lower jaw bones.

The orbital region of the skull is very disrupted. The postorbital has moved anteriorly and the jugal has its anterior end rotated dorsally. Because of this distortion, the exact orbital diameter is unknown, but an estimate can be made from the apparent position the postorbital would have occupied before its disturbance, as judged from the position of the posterior end of the jugal. This estimate gives an orbital diameter of 13.0 cm. The ratio of orbital diameter / jaw length thus obtained is 13.0/60.0 = 0.22. This compares with 0.27 and 0.17 for Ophthalmosaurus and Grendelius respectively.

Of the bones in the orbital region, the lachrymal, postorbital, jugal, postfrontal and possibly the quadrate are identifiable, but are too poorly preserved for description. The posterior end of the jugal does, however, appear to be narrow suggesting that Nannopterygius possessed a narrow postorbital region, as did Ophthalmosaurus.

The remains of approximately fifteen teeth are present in the jaw region. None has a complete root, but the largest complete crown measures 0.88, giving a tooth length index (McGowan, 1976) of 0.147. This compares to 0.140 for a large Ophthalmosaurus specimen (BMNH R2180) and 0.20 for Grendelius. Hulke (1871) placed great emphasis on the characteristics of the teeth, in particular the bulbous, cement-invested tooth bases. This character is, however, found in all the known ichthyosaur taxa from the Upper Jurassic and it is common also amongst forms from the Liassic and Cretaceous. The teeth show no distinctive features, and resemble those of Ophthalmosaurus.

A total of 65 ± 1 vertebral centra are present, all but seven of which are in series. Neural spines are visible on all but the most posterior eleven centra. The most posterior centra present are from the mid-caudal region. The anterior trunk centra are poorly preserved and it is impossible to determine at which centrum the diapophysis has separated from the neural arch pedicel; however, the two rib facets are merged to form a single elongate rib facet at centrum number 42. The presacral count is therefore identical to that of Ophthalmosaurus. Only a few centra are well enough preserved to allow measurements to be taken. The fourth anterior trunk centrum measures 4.70 cm in height and 2.41 cm in length. From this point on the column, the centra increase in height to reach a maximum at around the forty-second vertebra - taken to be the position of the sacrum. The heights of the fourth, twenty-seventh, forty-second and fifty-second centra are recorded on figure 36. These measurements indicate that the centra in the sacral region were as large as those of the largest specimens of *Ophthalmosaurus*, whereas the anterior trunk centra were relatively small, reflecting the relatively small head size. Such relatively large sacral and anterior caudal centra may indicate that the vertebral column of *Nannopterygius* was capable of generating greater thrust than an *Opthalmosaurus* specimen of equivalent body-weight (assuming, as McGowan 1972b) does that head length is directly proportional to body weight). The greatly reduced limbs of *Nannopterygius* may in some way be correlated with the relatively powerful tail.

McGowan (1972c) distinguishes two separate mechanisms by which ichthyosaurs may produce propulsive thrust. These are lateral swimming movements of the tail, and sculling movements of the paddles. He proposed that in taxa such as *Platypterygius* which have large, narrow-based paddles with high aspect ratio (length/width), and a relatively small tail, the fins were important in generating forward thrust. If this interpretation is valid, in *Nannopterygius* the powerful tail would be the major thrust generator, and the reduced paddles would probably simply serve as hydrofoils.

Numerous ribs are preserved in the holotype material, but they show no unusual features.

The pectoral girdle is represented by both coracoids, scapulae and fragments of the clavicles. All the elements of the pectoral girdle appear to be relatively small compared with the pectoral girdle of *Ophthalmosaurus*. The coracoids are articulated together and are exposed in ventral view. They are unusually long compared with their width. The ratio of length to width of the left coracoid is (13.00 cm / 7.78 cm) 1.67 compared to (19.00 cm / 18.00 cm) 1.06 for *Ophthalmosaurus* (BMNH R4753). Figure 39 shows the outline of the pectoral girdle of *Nannopterygius*. Most of the increased length of the coracoid appears to be in the region of the bone anterior to the lateral facets for the scapula and humerus. These facets appear to project far laterally, but this effect is exaggerated by a slight embayment in the lateral edge of the coracoid immediately posterior to the humerus facet. The posterior embayment is not edged by finished bone, unlike the anterior coracoid notch which is widely open.

The left scapula is exposed in ventral view on the right of the coracoids. Its greatest length is 11.5 cm, and its proximal width is 8.58 cm. The right scapula is incomplete, and the clavicles are too fragmentary to allow description.

Both incomplete forepaddles are present. The left forepaddle is preserved separately from the rest of the skeleton, but has been mounted on the specimen in a position just ventral to the coracoids. The paddle consists of a humerus (in ventral view), radius, ulna, intermedium, radiale and one distal carpal. The humerus is very much reduced (measured relative to jaw length) in comparison to the humerus of *Ophthalmosaurus*. The ratios of greatest humerus length to jaw length for *Nannopterygius* and *Ophthalmosaurus* (R4753) are 0.116 (6.96 cm / 60·0 cm) and 0.159 (15.0 cm / 94·0 cm) respectively. The humerus bears only two distal facets, for the radius and ulna, showing no sign of the third distal facet which is characteristic of *Ophthalmosaurus*. A prominent ventral trochanter (equivalent of the deltopectoral crest) is present towards the anterior edge of the proximal end of the bone. Although poorly preserved, the radius appears to be smaller, and less wide transversely, than the ulna.

The right paddle consists of a humerus, ulna, and eight other scattered limb bones.

The pelvic girdle is represented only by a fragment of bone which may be part of the ischium. The girdle is not complete enough to determine whether the pubis and ischium were separate or fused as in *Ophthalmosaurus*.

The hindpaddle is represented by the femur and fibula. The femur, like the humerus, is reduced in size. The ratio of femur length to jaw length is 0.08 (4.79 cm / 60.00 cm) compared to 0.09 (8.42 cm / 94.00 cm) for R4753. However, the difference in relative size of the femur is slight between the two genera, reflecting the more equal length of the humerus and femur in *Nannopterygius*. The ratio of humerus to femur length is 1.45 (6.96 cm / 4.79 cm) in *Nannopterygius* and 1.78 (15.00 cm / 8.42 cm) in *Ophthalmosaurus* (R4753).

The femur bears two distal facets for articulation with the epipodials, as does the femur of *Ophthalmosaurus*.

Genus Brachypterygius Von Huene, 1922

Synonymy: None

Type species: B. extremus (Boulenger, 1904a)

Diagnosis: As for monotypic species below

Brachypterygius extremus (Boulenger, 1904a)

Ichthyosaurus extremus Boulenger, 1904a.

Discussion of synonymy:

In 1904 Boulenger published a preliminary diagnosis of a new species of ichthyosaur which he named Ichthyosaurus extremus. Later that year (1904b) he published a more complete description of the specimen which comprised a right humerus and forepaddle preserved in an articulated condition.

In 1922 Von Huene considered the configuration of the paddle sufficiently distinct to warrant the erection of the new genus Brachypterygius for its reception.

Holotype:

An embedded right forepaddle; some of the paddle elements have been replaced in an unnatural position and are now held in plaster. The specimen is BMNH R3177 and comprises humerus, radius, ulna, radiale, ulnare, intermedium and fifty two other elements. The paddle is exposed in dorsal view. Boulenger (1904b) described and figured the specimen in Textfigure 83c.

Locality and Horizon of Holotype:

When Boulenger (1904 a,b) published his description of the holotype, he stated that the specimen had been in the possession of a Miss Mary Ashley, and later a Mr. H.E. Lansdown of Bath, who donated the specimen to the British Museum (Natural History) in 1904. Boulenger stated that the locality and horizon of the specimen were unknown. Six years later, Andrews (1910), in a footnote (page 54) stated that the humerus of the holotype was found to be closely similar to an isolated humerus, in the Passmore collection (specimen no. J1608, now in the O.U.M.) which was known to be from the Kimmeridge Clay of Swindon, Wiltshire. Andrews concluded the holotype must also have been derived from the Kimmeridge Clay. The data now attached to the specimen indicate that the holotype locality was Smallsmouth Sands, Weymouth.

Diagnosis:

Member of the family Ichthyosauridae (order Ichthyopterygia, suborder Ichthyosauria, infra-order Ichthyosauri) possessing:

(1) Humerus with three distal facets, the middle facet being smaller than the other two and articulating with the intermedium which wedges between radius and ulna.

Distribution:

Diagnostic material is known from the counties of Dorset, Cambridgeshire and Wiltshire.

Range:

Upper Jurassic; Kimmeridgian to Portlandian stage.

Referred specimens:

(1) O.U.M. J1608 - an isolated humerus which shows the distinctive three distal facets. The proximal end of the humerus is crushed in an antero-posterior direction. The specimen is from the Portland Rock of Swindon (Portlandian stage). A cast of this specimen is housed in the British Museum (Natural History) (R3420).

(2) O.U.M. J29864 - an isolated right forepaddle consisting of humerus, radius, ulna, radiale, intermedium, ulnare, four distal carpals, four metacarpals, and twenty-eight phalanges arranged in four rows. The specimen is from the Kimmeridge Clay of Ely, Cambridgeshire. All elements are cemented together by hardened matrix. There are, in addition, thirteen isolated phalanges. The humerus has been partially restored in plaster.

(3) O.U.M. J1586, 1585 - two isolated humeri in the Passmore collection - labelled as femora. Derived from the Portland Rock of Swindon.

Description (figures 40, 41)

The humerus of the holotype (figure 40) is incomplete and dorsoventrally crushed at its proximal end, so that the dorsal trochanter is obliterated. Evidence from specimen J29864 (figure 41) shows that the uncrushed humerus bears no unusual features and displays the usual dorsal and ventral trochanters as seen in Ophthalmosaurus. The proximal end of the bone is expanded, but below this the shaft of the humerus narrows before expanding again distally. The posterior edge of the humerus is sharply ridged compared to the anterior edge, a feature which is seen in the humeri of all Jurassic ichthyosaurs. Distally the humerus forms three distal facets for articulation with the radius, intermedium and ulna. The facets for the radius (anteriorly) and ulna (posteriorly) are more or less equal in size and each lies at an angle to the much smaller facet between them. This latter articulating surface receives the intermedium which wedges between the radius and ulna, preventing these two bones from making their usual contact.

The area of contact between the humerus and intermedium is greater in the holotype than in J29864, and this is interpreted as being due to a more advanced state of ossification in the holotype.

The radius and ulna are both four-sided, disc-like bones, with all four sides in contact, via cartilage, with other elements in the epipodial region. The ulna is slightly bigger than the radius in both the holotype and J29864. The large intermedium contacts the mesial borders of the radius and ulna. Compared to the intermedium of Ophthalmosaurus, this element is enlarged in the direction of the long axis of the paddle; it is roughly hexagonal in shape, and makes contact with seven other paddle elements, one of which is the humerus. The smallest of these contacts are with the radiale and ulnare. Distally, the intermedium contacts two distal carpals by their proximal edges. The radiale and ulnare are smaller than the intermedium and are roughly four-sided. They each contact two elements laterally and two distal carpals distally. The remaining two contacts are with the radius, or ulna and intermedium. The four distal carpals are all similar in shape. Their proximal edges wedge between the more proximal row of carpals so that the line between the two rows of bones is zig-zagged, much as in the paddle of Ophthalmosaurus. It was mentioned in the description of that genus that this arrangement avoids transverse lines of weakness in the paddles. However, in contrast to this condition of their proximal edges, the distal edges of the distal carpals align themselves along a straight transverse line. This feature is found in both the holotype and J29864.

Each distal carpal supports one metacarpal and digit. The metacarpals are roughly rectangular with their long axes arranged transversely across the paddle. In the holotype, metacarpals 2 and 3 appear to be fused, though the suture between them is still visible. Fusion at this point suggests there was little movement between the bones of the paddle here.

The elements of the carpus and metacarpus in *Brachypterygius* are arranged in longitudinal rows which lie parallel to the long axis of the humerus and paddle as a whole. This condition is in contrast with that seen in *Ophthalmosaurus*, where the metacarpals and the first row of phalanges are shifted slightly anteriorly so that the rows are inclined to the long axis of the paddle. More distally in the *Ophthalmosaurus* paddle, the phalangeal rows straighten out, giving a curved appearance to the longitudinal rows of bones. In the *Brachypterygius* paddle, however, the four longitudinal rows of bones, comprising the primary digits, are straight and orientated longitudinally throughout the whole paddle.

The phalanges are arranged in four rows extending distally from the metacarpals. At the level of the third phalange (p_3; for nomenclature see description of paddle of *Ophthalmosaurus*), in the holotype paddle, there appears to be a sudden decrease in size of the phalangeal elements. This suggests that beyond this level the paddle has been reconstructed. J29864, however, is in its natural articulation and there is no sudden decrease in size, and the digits comprise a greater number of phalanges than is suggested by the reconstructed holotype. Reconstruction of the holotype paddle has abruptly shortened the paddle, giving it an unnatural spade-like shape. The longest digit in J29864 comprises nine phalanges, and it is likely that more would have been present distally. The longest digit in the holotype (digit II) comprises only seven phalanges, and the terminal elements are extremely small.

From specimen J29864 it is clear that the metacarpals and phalanges of *Brachypterygius* were more closely packed and angular than those of *Ophthalmosaurus*. This suggests ossification had proceeded further in the metacarpals and more proximal phalanges of *Brachypterygius*. The apparent transverse lines of weakness and lack of zig-zagging seen between the distal carpals and metacarpals continues to a less marked degree between the transverse rows of phalanges.

There are two accessory digits in the paddle of the holotype, one preaxial and one postaxial. Although these digits appear to have been reconstructed, I do not doubt that preaxial and postaxial accessory digits were present in life. The most proximal elements of each digit are of unusual shape, with pointed extensions from their proximal edges. (The postaxial element has been replaced upside-down so that the extension is directed distally.) It is likely that contact would have been made with the humerus via thin bands of cartilage.

The remaining elements of the accessory digits are simple discoidal ossicles which decrease in size distally. J29864 does not possess any accessory ossicles cemented to the paddle edges, but the lateral edges of the digits I and IV are angled and cartilage-finished, suggesting that accessory digits were present. In the holotype there are nine postaxial and ten preaxial accessory ossicles.

As reconstructed, the accessory ossicles are more rounded than the phalanges of the primary digits at any one level. This feature is also seen in the paddle of Ophthalmosaurus.

The Brachypterygius paddle possesses five bones at the level of the distal end of the humerus, in contrast to the three bones present at this level in Ophthalmosaurus. In this respect, Brachypterygius apparently possessed the broadest paddle, at the level of the distal end of the humerus, of all known ichthyosaur taxa.

Note on the genera Brachypterygius and Grendelius:

It is unfortunate that the known material of Brachypterygius comprises only forepaddle material. It is equally unfortunate that known Grendelius material lacks any associated paddle material. It is quite possible that, should more material be discovered at a future data, it may be found that Grendelius and Brachypterygius are congeneric. At present, however, the two taxa must remain as separate genera.

SECTION 2: BRITISH UPPER JURASSIC ICHTHYOSAURS: REJECTED NAMES

The following are rejected names for British Upper Jurassic taxa which are listed in alphabetical order of the species name. The single rejected genus name is listed at the end.

Ichthyosaurus aequalis Philips, 1871.

status: nomen dubium.

comment: Philips referred to a single caudal vertebra from the Kimmeridge Clay, but he did not designate a specific type, nor give its whereabouts, nor figure it. The feature said to distinguish the centrum was the position of the rib facet midway down the sides of the centrum. This feature is characteristic in general of middle caudal Jurassic ichthyosaur centra. For this reason I do not consider the material to be distinctive, and it is therefore designated nomen dubium - a name of uncertain application, because it is impossible to ascertain to which taxon the type should be referred (Jeffrey 1977). McGowan (1976) regarded this species as a taxon dubium.

Ichthyosaurus chalarodeirus Seeley, 1869.

status: nomen nudum.

comment: Seeley named as I. chalarodeirus a single axis centrum, from the Kimmeridge Clay, which he catalogued as part of the collection in the Sedgwick Museum. No description or figure was given. Mention of a specimen in a museum collection does not constitute an indication under Article 16 b(i) of the International Code of Zoological Nomenclature. Furthermore, I do not consider the material distinctive. McGowan (1976) regarded this species name as a nomen nudum.

Ichthyosaurus dilatatus Philips, 1871.

status: nomen dubium.

comment: Philips did not designate a holotype nor give a figure, but simply referred to a "considerable number" of vertebrae from the Oxford Clay and Kimmeridge Clay. He briefly described the centra, giving some measurements. He stated that the vertebrae were broader than those of I. trigonus and thicker than those of I. thyreospondylus. These features I consider likely to be due to individual variation in vertebral proportions, or to the mistake of comparing vertebrae from slightly different regions in the column. Delair (1959) cited cervical and dorsal vertebrae in the Oxford University Museum (J12494/1-8) as type specimens. I do not consider these vertebrae to be distinctive. McGowan (1976) regarded I. dilatatus as a taxon dubium.

Ichthyosaurus hygrodeirus Seeley, 1869.

status: nomen nudum.

comment: Seeley named as I. hygrodeirus a single axis centrum, from the Kimmeridge Clay, which he catalogued as part of the collections in the Sedgwick Museum. This name is rejected for the same reasons given for I. chalarodeirus. McGowan (1976) regarded this name as a nomen nudum.

Ichthyosaurus megalodeirus Seeley, 1869.

status: synonym of Ophthalmosaurus icenicus.

comment: Seeley described and catalogued a specimen, in the Sedgwick Museum, which he named I. megalodeirus. I consider the specimen to be indistinguishable from O. icenicus. Although I. megalodeirus predates O. icenicus, I do not consider that I. megalodeirus should take priority, following Article 23 (a-b) of the International Code of Zoological Nomenclature, which states that for the sake of stability, a long-established name in its accustomed meaning should not be replaced by its senior synonym.

Ophthalmosaurus monocharactus Appleby, 1956.

status: synonym of *O. icenicus*.

comment: For the reasons for the rejection of this name - see the discussion of synonymy of *O. icenicus*.

Ichthyosaurus ovalis Philips, 1871.

status: nomen dubium.

comment: Philips did not designate a type nor give a figure, but simply referred to vertebral centra from the Kimmeridge Clay. He stated that the centra have an oval outline of face and are higher than broad; some measurements were given. I consider these features to be likely to be either the result of individual variation, or of crushing. Delair (1959) cited two vertebrae in the Oxford University Museum (J12488/1-2) as types of this species. I do not consider these specimens to be distinctive. McGowan (1976) regarded *I. ovalis* as a taxon dubium.

Ophthalmosaurus pleydelli Lydekker, 1890.

status: synonym of *O. icenicus*.

comment: for reasons for rejection, see discussion of synonymy of *O. icenicus*.

Ichthyosaurus thyreospondylus Owen, 1839.

status: nomen dubium.

comment: Owen briefly described five vertebrae (since destroyed) in the Bristol Museum, and gave a few measurements. The feature taken by Owen to be distinctive was the presence of a triangular convexity lying dorsally on the articulating faces. I have observed this feature frequently on well-preserved centra of all Upper Jurassic taxa, and so I do not consider it distinctive. McGowan (1976) regarded *I. thyreospondylus* as a taxon dubium.

Ichthyosaurus trigonus Owen, 1839.

status: nomen dubium.

comment: Owen briefly described a single vertebral centrum, giving some measurements. He stated that the centrum was distinctive in possessing a triangular contour in end-view. From his description it appears that the centrum is from the cervical region, and in this region of the column the centra of all Upper Jurassic taxa commonly appear triangular as a result of the presence of a ventral keel. I do not therefore consider this feature to be specifically distinctive. McGowan (1976) regarded I. trigonus as a taxon dubium.

Macropterygius Von Huene, 1922.

status: nomen dubium.

comment: Von Huene erected this genus for the reception of I. trigonus, I. dilatatus and I. ovalis together with three other Upper Jurassic taxa from abroad which are all regarded as taxa dubia by McGowan (1976). Since all the member species of this genus are designated nomina dubia, it is concluded that Macropterygius should also be regarded as a nomen dubium.

CHAPTER 3 : DISCUSSION

SECTION (1) : CLASSIFICATION OF THE ICHTHYOPTERYGIA

Historical Introduction

In 1814 Sir Everard Home recognised a new group of fossil reptiles for which, in 1819, he proposed the generic name Proteosaurus. In the previous year, König (1818) had applied the name Ichthyosaurus to the group, in recognition of its many fish-like characteristics, and this name became generally accepted. Conybeare, in 1821, grouped the ichthyosaurs and plesiosaurs together in the new order Enaliosauria, on the basis of their shared marine nature. The term Enaliosauria continued in general usage until 1860 when Owen separated the ichthyosaurs and plesiosaurs into the orders Ichthyopterygia and Sauropterygia.

Owen noted that members of the order Ichthyopterygia were distinguished from the Sauropterygia by the extreme shortness of the neck, giving them a fish, or whale-like appearance. Twenty-five years previously, however, de Blainville (1835) had already separated the orders Ichthyosauria and Plesiosauria; but his proposal remained largely ignored, despite the chronological priority of his ordinal name.

Owen (1860) included all members of the Ichthyopterygia in the single genus Ichthyosaurus, of which there were stated to be more than thirty species, all of which were derived from the Jurassic, mainly Liassic, deposits of Europe.

The first sub-division of the order was attempted by Kiprianoff (1881), who distinguished two groups of ichthyosaurs: the latipennipedes and the longipennipedes, though he did not subdivide the single genus Ichthyosaurus on this basis. The latipennipedine species were said to differ from the longipennipedines in the following seven characters: they possessed (1) shorter and broader fore- and hind-paddles, (2) a shorter snout, (3) a greater number of digits in both paddles, (4) no notching along the anterior border of the fore-paddles, (5) a pelvic girdle which was more weakly developed than the pectoral girdle, (6) a proportionately larger eye, and (7) a shorter and broader tailfin.

Kiprianoff further subdivided the latipennipedines into two groups typified by the two species Ichthyosaurus communis and I. campylodon. The two groups were said to differ in the size of the snout and in the nature of the teeth.

The longipennipedines were divided by Kiprianoff into platyodont-type species and tenuirostrine-type species, typified by I. platyodon and I. tenuirostris respectively. Again the distinction was based largely on the nature of the teeth.

By 1887 three further genera of ichthyosaurs had been named; these were Ophthalmosaurus Seeley, which was thought by some authors to be synonymous with Baptanodon Marsh; the third genus was Mixosaurus Baur. Baur (1887a) thus split the order into three families, the Mixosauridae, Ichthyosauridae and Baptanodontidae (to include Ophthalmosaurus). Baur further noted that the genus Ichthyosaurus could probably be split into two or more further genera.

In the following year, Lydekker (1888) presented a classification of the order which largely followed Kiprianoff's scheme in that it split the genus Ichthyosaurus into two groups which Lydekker called the latipinnates and longipinnates. Lydekker followed Kiprianoff in subdividing the latipinnates into the same two subgroups, but he introduced a third subgroup to the longipinnates. This additional subgroup was typified by the species Ichthyosaurus acutirostris, and was thus referred to as the acutirostrine subgroup.

Neither Kiprianoff's nor Lydekker's subdivisions were made at a taxonomic level higher than the species, and therefore they retained the genus Ichthyosaurus for both groups. Unlike Baur (1887a), Lydekker classified the whole of the Ichthyopterygia under the single family, the Ichthyosauridae.

During the early years of this century, new finds of ichthyosaurs from the Triassic of California and Nevada demonstrated that in the Triassic, as in the Jurassic, there were present broad- and narrow-paddled forms. Merriam (1902) identified a new family of narrow-paddled ichthyosaurs from the Upper Trias which he named the Shastasauridae. Boulenger (1904b) subsequently attempted to establish the latipinnates and longipinnates as distinct phylogenetic lineages connecting the Triassic forms with their presumed descendants in the Jurassic; a third lineage was reserved for the Triassic genus *Shastasaurus* and the Jurassic *Ophthalmosaurus*, neither of which he considered fitted comfortably into the latipinnate/longipinnate scheme. Boulenger reserved the genus name *Ichthyosaurus* for the Jurassic latipinnate species, whilst he included the Jurassic longipinnates in the genus *Proteosaurus* Home.

In the same year as Boulenger's publication, Jaekel (1904) independently published a similar proposal to split the genus *Ichthyosaurus*. Jaekel proposed to abandon the genus name *Ichthyosaurus*, and erected the generic names *Stenopterygius* and *Eurypterygius* for the longipinnate and latipinnate species respectively.

The theory that the latipinnate/longipinnate distinction could be applied to Cretaceous ichthyosaurs was first put forward by Broili (1907). He described *I. platydactylus*, a form with an extremely broad paddle, but which he nevertheless classified in a subgroup of the longipinnates. In so doing, Broili highlighted an important feature of Lydekker's (1888) classification which recognised the configuration of the carpus to be of fundamental importance in distinguishing between latipinnate and longipinnate paddles. Lydekker considered the single variant of breadth of the paddle to be insufficient and imprecise in making the distinction, but he considered that the two groups could easily be separated by reference to the number of distal carpal elements lying in contact with the distal edge of the intermedium. In latipinnate paddles there were said to be two distal carpals making this contact, whereas in longipinnate paddles there was only one.

On this basis, I platydactylus could be classified as longipinnate.

The following year, Merriam (1908) published his own phylogenetic scheme for the order. He based his scheme largely on the consideration of two characters - the nature of the rib articulation, whether uni- or bi-cipital, and the morphology of the forepaddle. Merriam recognised the difficulty in producing a satisfactory phylogeny based on these characters, since they do not strictly correlate. Because of this he placed most emphasis on the nature of the rib articulation, since he considered this to be "fundamental", whereas the forepaddle would be more subject to convergence, being "in closer touch with the environment".

Merriam's resulting scheme shows a primary dichotomy into (a) taxa with a unicipital rib-head, to which he applied the family name Mixosauridae, and (b) taxa under the family name Ichthyosauridae, which possessed bicipital rib-heads, which he considered to be the more primitive condition. In each of these lineages both lati- and longipinnate forms were present and, though Merrian did not state it, this implies that convergence had occurred for one or other of these character states. The broad-paddled Mixosaurids were designated as the sub-family Mixosaurinae, whilst the narrow-paddled Mixosaurids were put in the sub-family Shastasaurinae.

Merriam split the Ichthyosauridae into a broad-paddled lineage containing the sub-family Baptanodontinae and also latipinnate members of the genus Ichthyosaurus. The second, narrow-paddled, lineage contained the longipinnate members of Ichthyosaurus.

Merriam had in this way created a paraphyletic group (the descendent group, the Baptanodontinae had been removed) which he named the Ichthyosaurinae, and which included both lati- and longipinnate members of the genus Ichthyosaurus. Merriam followed Lydekker (1888), Fraas (1891) and Kiprianoff (1881) in not removing the longipinnate species from the genus Ichthyosaurus.

The first attempt to apply the latipinnate/longipinnate distinction to the whole order, from the Triassic to the Cretaceous, was made by Von Huene (1922, 1923).

Unlike Merriam's phylogenetic scheme, that of Von Huene based the primary dichotomy on the configuration of the forepaddle, the nature of the rib articulation being considered less important. Thus Von Huene traced two lineages, which he termed the Latipinnatidae and Longipinnatidae (though he did not assign them a rank) from the Triassic through to the Cretaceous. Von Huene proposed that the mixosaurs were ancestral to the latipinnate members of the genus *Ichthyosaurus*, which he renamed *Eurypterygius* after Jaekel. The Longipinnatidae were further divided into two lineages - one leading to the Liassic genus *Stenopterygius*, and the other to the longipinnate members of the genus *Ichthyosaurus*, which he renamed *Leptopterygius*.

Each lineage was subdivided into the constituent genera which Von Huene arranged in diagrammatic form as a branching tree, linked to show ancestor-descendant relationships. In determining relationships between genera, Von Huene looked for morphological similarities expressed in the common possession of a number of diverse characters; there was no attempt made to distinguish primitive from advanced characters.

In 1951 Von Huene raised the latipinnates and longipinnates to the rank of separate sub-orders - the Latipinnati and Longipinnati.

Despite Von Huene's attempt to establish a fundamental division of the whole order in this way, later authors continued to restrict the terms latipinnate and longipinnate to the Jurassic genera, and to the less numerous Cretaceous genera. Thus Kuhn (1934) divided the order Ichthyosauria into five families: the Omphalosauridae, Mixosauridae, Shastasauridae, Eurypterygiidae (latipinnate) and Stenopterygiidae (longipinnate).

The same basic scheme was used by Romer (1956, 1966). However, Romer elevated the Ichthyopterygia (Owen 1860) to the rank of subclass, with the single constituent order Ichthyosauria, De Blainville (1835). Romer maintained the same five families of Kuhn, with the minor difference that he replaced the name Eurypterygiidae (Jaekel 1904) by the family name Ichthyosauridae (Bonaparte 1841).

Although his classification did not reflect any phylogenetic relationship between the Triassic families and the longipinnate and latipinnate families, Romer (1956) did suggest that the Ichthyosauridae could be readily derived from the Mixosauridae, whilst the Shastasauridae made good ancestors for the Stenopterygiidae.

In 1972 a final attempt was made by McGowan to establish the latipinnates and longipinnates as two phylogenetically distinct groups. By applying a concise terminology to describe the configuration of the ichthyosaur forepaddle, he provided a more precise method with which to distinguish lati- or longipinnate forefins (see descriptive section on forepaddle of Ophthalmosaurus).

In addition to differences in the configuration of the forepaddle, McGowan found that the two groups could be distinguished by differences in the skull, and that both sets of characters could distinguish latipinnates and longipinnates from the Triassic through to the Cretaceous. McGowan then inferred that the Triassic taxa were ancestral to the Liassic taxa. Thus he proposed the mixosaurs gave rise to the Liassic latipinnates whereas the narrow-paddled Merriamia was presumed to be closely related to the ancestral longipinnate. By comparing forefin and cranial characters between the Triassic taxa and their presumed Liassic descendants, he identified three specific evolutionary trends which, it appeared, occurred throughout the Ichthyosauria, but at different rates in the two lineages. However, McGowan's list of salient distinguishing characters, in particular those of the skull, was heavily dependent on data from Liassic taxa, owing to the relative poverty of material from the Triassic and post-Liassic horizons. Because of this, his trends are less convincing, and his distinguishing characters are less useful when applied to the whole order.

In subsequent publications, McGowan (1974a,b) erected the suborders Latipinnati and Longipinnati, but did not publish a complete classification of their constituent families.

In a later publication (1976), McGowan revealed evidence that caused him to question the validity of the latipinnate/longipinnate division. Using the technique of multivariate analysis, McGowan found that members of the Upper Liassic genera *Stenopterygius* and *Leptopterygius* - traditionally thought of as "typical" longipinnates - had close phenetic affinity with the latipinnate species of the genera *Mixosaurus* and *Ichthyosaurus*. McGowan resolved the problem temporarily by suggesting that perhaps *Stenopterygius* and *Leptopterygius* should be classified as latipinnate rather than longipinnate.

In a later paper (1979), which reviewed the Upper Liassic genera *Stenopterygius*, *Leptopterygius* and *Eurhinosaurus*, McGowan returned to the problem. He found that many of the characters which, in 1972, he had thought were exclusively latipinnate characters were, in fact, also found in the "typical" longipinnate species from the Upper Lias. He concluded there were no unequivocal distinctions between the two groups, and that a "systematic dichotomy of the group is probably unjustified".

In the same year, Appleby (1979) published a new classification of the subclass Ichthyopterygia in which he elevated the latipinnates and longipinnates to the rank of separate orders, the Latipinnatoidea and Longipinnatoidea. Appleby added two new orders: the Mixosauroidea, to accommodate *Mixosaurus*, and the Heteropinnatoidea, to include taxa which were described as "composite forms" displaying a melange of latipinnate and longipinnate features.

Appleby's main thesis was that the Heteropinnatoidea represented a stage of evolution which was transitional between the Triassic longipinnates and the Liassic latipinnates, and from this Appleby sought to refute the proposals of previous authors that the mixosaurs were ancestral to the latipinnates.

A number of criticisms can be made of Appleby's classification. Firstly, Appleby's Heteropinnatoidea is, in fact, a paraphyletic group (a monophyletic group from which one or more descendant groups have been removed - in this case the Latipinnatoidea). Paraphyletic groups are considered, even by traditional evolutionary taxonomists, to be undesirable at low taxonomic rank.

Secondly, one of the three heteropinnatoid species, Leptopterygius tenuirostris is said by Appleby to show "every gradation from longipinnates to latipinnates in McGowan's (1972a) sense" within the species. This species was classified by McGowan (1974b) as the latipinnate Ichthyosaurus tenuirostris. Appleby does not give a set of derived (apomorphic) characters diagnostic of the Heteropinnatoidea but, rather, he sees the variability in the expression of latipinnate characters as characterising the taxon, as though this variability is an expression of the intermediate position of the heteropinnatoids in the evolutionary transition from longipinnates to latipinnates. He erects two further species of heteropinnatoids. One of these, Protoichthyosaurus prostaxalis accommodates four specimens which were previously recognized as abnormal individuals of I. communis (McGowan, 1974b, p.11). In these specimens the variability of expression of latipinnate characters goes to the extreme: in each individual one of the paddles can be classified (using McGowan's 1972a criteria) as latipinnate whilst the opposite paddle is longipinnate. To Appleby, this demonstrates their heteropinnatoid, and thus intermediate, nature. A more sensible interpretation is that ichthyosaur paddles can show a large amount of variability in their configuration. This would seem to be correlated with the hyperphalangy and hyperdactyly present which may result in a certain loosening of the control over the "pattern" produced during development. For this reason, McGowan's criteria do not succeed in every individual case.

In the case of L. tenuirostris above, the fact that a whole species does not fall neatly into either a latipinnate or a longipinnate category calls into question either the validity of the taxonomic distinction, or the effectiveness of McGowan's criteria, or both.

A more detailed criticism of the latipinnate/longipinnate question will be presented below. For the reasons given above, that the Heteropinnatoidea are not characterised by unique apomorphic characters, and that the characters, given by Appleby as diagnostic, are variable between individuals of a species and between right and left sides of the same individual, I suggest that the Heteropinnatoidea is an invalid taxon.

In 1980, Mazin proposed a new classification of the Ichthyopterygia (his usage as a superorder) based on the techniques of phylogenetic, or cladistic classification. He designated the early Triassic taxa Grippia, Phalarodon, and Omphalosaurus as plesions (plesiomorphic sister group of all groups that succeed it in a hierarchy of relationships, see Patterson and Rosen 1977) of the order Euichthyopterygia which includes all other ichthyosaur taxa. The Euichthyopterygia were split into the suborders Mixosauria, containing the family Mixosauridae, and the Ichthyosauria with three families, the Shastasauridae, Ichthyosauridae and Leptopterygidae.

The whole scheme does not differ greatly from either Kuhn's (1934) or Romer's (1956, 1966) classification, despite the different technique used.

Mazin's study of the early Triassic ichthyosaurs led him to question the validity of the characters employed by previous taxonomists. These were the nature of the rib articulation and the configuration of the fore-paddle.

(a) Nature of the rib articulation

Mazin agreed with McGowan (1972a) that the presence of dichocephalic and holocephalic ribs varied with the position in the vertebral column in the majority of ichthyosaur taxa. For example, the forms characterised as possessing holocephalous ribs by Merriam (1908), for example, Shastasaurus and Cymbospondylus, actually possessed dichocephalous ribs in the anterior trunk region. Both Mazin and McGowan concluded that the nature of the rib articulation had little value for use in the classification of the ichthyosaurs.

(b) Configuration of the forepaddle : the latipinnate/longipinnate question

McGowan's criteria for the distinction between latipinnates and longipinnates, as set out in McGowan (1972a), are as follows:

	Longipinnates	Latipinnates
	Forefin	
1.	Three primary digits.	Four primary digits.
2.	Three distal carpals.	Four distal carpals.
3.	Intermedium supporting one digit.	Intermedium supporting two digits.
4.	Total digital count probably not exceeding five in pre-Cretaceous taxa.	Total digital count often exceeding five in pre-Cretaceous taxa.
5.	Digital bifurcation probably not occurring.	Digital bifurcation usually occurring.
6.	Radius probably notched.	Radius rarely notched.
7.	Notching probably occurring in other elements.	Notching occurring in other elements but generally restricted to taxa from lower horizons.
8.	Distal phalanges often widely spaced.	Distal phalanges not widely spaced.
9.	Phalanges relatively large and few in number.	Phalanges relatively small and numerous.

	Longipinnates	Latipinnates
	Skull	
10.	Ratio of the diameter of the orbit to the length of the jaw probably not exceeding 0.20 in Lower Liassic taxa.	Ratio of diameter of orbit to the length of jaw exceeds 0.20 in Lower Liassic taxa.
11.	Ratio of the internal diameter of the sclerotic ring to the diameter orbit probably less than 0.33 in Lower Liassic taxa.	Ratio of internal diameter of sclerotic ring to the diameter of orbit probably always exceeds 0.37 in Lower Liassic taxa.
12.	Ratio of the distance tip of snout to anterior tip of maxilla to the length of jaw probably less than 0.40 in Lower Liassic taxa.	Ratio of the distance tip of snout to anterior tip of maxilla to the length of jaw probably at least 0.40 in Lower Liassic taxa.

N.B. The vague terminology used (McGowan's) is significant.

Mazin (1980) showed that Grippia longirostris, Utatsusaurus hataii (Shikama et al 1978) and the genus Mixosaurus possessed forepaddles which could not be classified as either latipinnate or longipinnate by these criteria. In Mixosaurus the intermedium contacts three distal carpals and in all three genera there are five distal carpals and five primary digits.

Mazin also concluded that Appleby's heteropinnates were further evidence that the criteria could not differentiate two distinct groups even amongst the Jurassic forms, to which the concept was first applied. By reference to the forepaddles of various Jurassic ichthyosaurs, Mazin illustrated that character (3), above, was far from being a rigorous criterion for distinguishing between latipinnates and longipinnates. This point is further illustrated in figure 42, which shows forepaddles of two specimens of Stenopterygius; 42b could easily be classified as latipinnate since the intermedium has large contacts with distal carpals 2 and 3 (for nomenclature, see figure 30), whereas 42a is longipinnate in that the intermedium has contact with only one distal carpal. This slight anterior shift in the row of distal carpals relative to proximal carpals which is illustrated in figure 42b, occurs frequently in Stenopterygius and is also observable in the traditional longipinnate Temnodontosaurus platyodon (McGowan 1974a, fig. 4c,d). The problem of the anterior displacement of the distal carpal row confused McGowan 1974b, p.27) so that he had difficulty classifying Ichthyosaurus tenuirostris as either latipinnate or longipinnate, but on balance decided this taxon was latipinnate. Appleby (1979) "resolved" the same problem by classifying the taxon as heteropinnate.

Characters (4) and (5) are, in fact, two correlates of the same phenomenon - that digital bifurcation (see description of forepaddle of Ophthalmosaurus) results in hyperdactyly. Digital bifurcation (or more appropriately, the presence intermediary digits) occurs variably in latipinnates, see figure 42c,d. Intermediary digits also occur in the traditional longipinnate Stenopterygius (Johnson, 1979, p.69).

Characters (6) and (7) show a large amount of individual variation. In the "longipinnate" Stenopterygius, for example, Johnson (1979, p.70) regards this variability as reducing the diagnostic value of the characters in the latipinnate/longipinnate distinction.

Notching of the radius and anterior paddle elements is actually seen in all the latipinnate Liassic taxa reviewed by McGowan (1974b). The only difference is in the frequency with which notching occurs between the two groups.

Characters (8) and (9) really only express a characteristic feature of the genus Ichthyosaurus, that is,the paddle elements of this taxon are closely spaced, like paving stones, unlike the more widely spaced phalanges of "longipinnates". However, McGowan does not take into account either the pavement-like paddle of the "longipinnate" Platypterygius (McGowan, 1972c) or the widely-spaced paddle of Ophthalmosaurus (figure 30), a traditional latipinnate.

In summary, characters (3) to (9) are either variable, lacking in rigour, or present in both "latipinnates" and "longipinnates".

Characters (1) and (2) at first appear to be fundamental differences between latipinnates and longipinnates. However, Johnson (1979) showed that the "longipinnate" Stenopterygius possessed four primary digits and four distal carpals - the latipinnate number. McGowan (1972a) had regarded the fourth carpal and digit as a postaxial accessory digit. Johnson showed that there was no detectable difference between this digit and the other three primary digits. The paddles of Lower Liassic longipinnates (McGowan 1974a), where known, also reveal a fourth postaxial digit which is reasonably interpreted as a fourth primary digit, though this may be reduced in size. I would argue that all post-Triassic ichthyosaurs possess a forepaddle with four distal carpals and four primary digits. The only difference between the "longipinnate" and "latipinnate" arrangement is a slight posterior displacement of the distal carpal row in "longipinnates", and in some taxa the fourth digit is reduced. This latter character has been used as a taxonomic character in the classification of the order which is proposed below.

McGowan's remaining three skull characters maintain that the "latipinnates" possessed relatively larger eyes and shorter maxillae than longipinnates. However, he restricts the values given for relative orbital diameter and relative maxillary length to Lower Liassic taxa, so that, in effect, the differences expressed are merely differences between the genera Ichthyosaurus and Temnodontosaurus (see McGowan, 1974a,b). When, for example, the Upper Liassic "longipinnate" Stenopterygius is compared with these genera, the values for relative orbital diameter and relative maxillary length (McGowan, 1979) fall within the range of those for Ichthyosaurus rather than Temnodontosaurus. McGowan (1972a) explains this anomaly by postulating that there was a parallel trend in time in latipinnates and longipinnates towards increase in orbital diameter and decrease in maxillary length. However, characters (10) to (12) appear of little use in distinguishing between "latipinnates" and "longipinnates" from horizons other than the Lower Liassic.

I conclude, therefore, that the evidence above supports McGowan's (1979) and Mazin's (1980) proposals that the latipinnates and longipinnates should no longer be considered as distinct phylogenetic lineages.

Systematic Background

For the last fifteen years or so, Systematic Biology has been dominated by a continuing debate between three opponent schools of taxonomic methodology. The traditional school, applying an evolutionary, or eclectic, method of classification came to be challenged firstly by advocates of phenetic classification, or numerical taxonomy, and secondly by the Hennigian school of phylogenetic systematics, or cladistics.

Evolutionary taxonomists attempt to produce classifications which simultaneously take into consideration the degree of similarity, or difference (in practice, usually morphological) between organisms, and also the phylogenetic relationships between them; furthermore both clades and grades are used in this method (see later). A major criticism of the eclectic school has been the lack of a distinct methodology by which this compromise position in classification can be reached. Traditional methodology has been criticised for being largely an ad hoc procedure; the classifications and phylogenetic hypotheses produced depend heavily on the intuitive skills of the taxonomist, and therefore, according to some of its cladistic opponents, lack the objectivity of legitimate scientific methodology (by which is generally meant the methodology enunciated by Popper (1959)).

The phenetic, or numerical (a less accurate name since many pheneticists do not use numerical methods (McNeill 1979)) approach to taxonomy at first purported to produce classifications which were more objective than other classifications. Later, the concept of "naturalness" in classification became emphasised by pheneticists (a concept which traditional taxonomists

(Mayr, 1974) and some cladists (Farris, 1977) have claimed applies to their classifications.

The concept of a natural classification was most effectively formulated by J.S. Mill in 1872:

> "The ends of scientific classification are best answered when the objects are formed into groups respecting which a greater number of general propositions can be made, and those propositions more important, than could be made respecting any other groups into which the same things could be distributed ... a classification thus formed is properly scientific or philosophical, and is commonly called a Natural, in contradistinction to a Technical or Artificial, classification or arrangement."

When analysed further, Mill's criterion yields the following two qualifying criteria. The first is that character states "should be homogeneous within taxa and heterogeneous between them" (Sokal, in Farris 1977). The second criterion concerns the predictivity of classifications, which is characterised by Fitch (1979):

> "The essence of predictivity in the sense used here is the degree to which a specific classification agrees with characters not used in the formulation of that classification."

Mill's criterion of naturalness was reformulated by Gilmour (1961) and later adopted by pheneticists as a philosophical basis for their classifications.

In a subsequent review, Farris (1977) coined the term "Gilmour-natural" to describe classifications which are natural in the Mill-Gilmour sense.

The phenetic approach to classification has been characterised by McNeill (1979) as an approach which "with the most thorough knowledge possible uses all available characters of the object being classified, without any a priori selection of certain characters or types of characters as inherently more important than the rest". This approach is sometimes referred to as clustering by overall similarity.

The pheneticists claim superiority of their methodology over the traditional school in a number of respects. First, they apply a distinct methodology: by searching for the maximum possible number of characters, with no a priori weighting, the pheneticists claim to avoid subjective bias and get as close as possible to a Gilmour-natural classification; no attempt is made to distinguish between primitive and derived characters.

The phenetic approach to classification stresses the importance of the role classification plays in communication between biologists. To achieve this, a pheneticist seeks to produce a simplification of genetically controlled similarities and differences between organisms (McNeill, 1979). The clustering techniques employed to achieve this simplification depend largely on the principle of parsimony. This has inherent difficulties in that opponents would argue that "false" similarities between organisms can occur as a result of convergence and character correlation. Present-day pheneticists do, however, employ some weighting of characters, in particular a posteriori weighting, which is used to improve the resolution of previously discerned groups (McNeill 1979).

A further feature of phenetic classification is that it distinguishes very definitely between classification and phylogeny reconstruction. Phenetic classifications do not attempt to reflect phylogeny, and in this way they aim to avoid the influence on their classifications of preconceived ideas of evolutionary relationship. Nevertheless, hypotheses concerning phylogeny can be constructed using phenetic techniques developed initially by Camin and Sokal (1965), who use a "minimum evolutionary step" method. Phylogeny reconstruction, however, is considered to be a separate, although complementary, procedure to classification by most pheneticists (McNeill, 1979).

The evolutionary or eclectic approach proposes that classification should reflect not only morphological similarity but also the phylogenetic relationships between the groups under consideration.

The cladistic approach to classification, in contrast, originally aimed only to represent phylogeny, and, more specifically, one aspect of phylogeny - that of cladogenesis, or the sequence of branching of sister groups. More recently, however, a change of emphasis has occurred so that cladistics now aims to represent only the emergence of unique derived characters, and not necessarily the branching of sister groups (Hull, 1979). This so-called "transformation" of cladistics has resulted in a shift in emphasis away from phylogeny reconstruction, and, in some cladists, a loss of interest in the mode of evolution itself. Platnick (1979) clarifies the arguments behind "transformed" cladistics.

The cladists have claimed that their methodology is more objective than that of the traditional school, since it makes use of the hypothetico-deductive method of scientific enquiry enunciated by Popper (1934, 1959).

Gaffney (1979) provides an illustration of cladistic methodology by reference to the simplest case of a "three-taxon-statement". Here three monophyletic taxa are compared for degree of relatedness.

Three alternative hypotheses can be set up which state that, either A and B are more closely related to each other than either is to C, or that A and C are more closely related than either is to B, or that B and C are more closely related than either is to A. A search for synapomorphies, derived characters shared between any two of A, B and C, is then carried out.

Falsification of, for example, hypothesis I - AB-C, occurs when B and C share a synapomorphy, but A does not. One hypothesis should remain unfalsified.

When, however, many characters are looked at, it can happen that all three hypotheses are falsified by one or more character distributions. This occurs when one or other apparent synapomorphy is "false" in the sense that the shared derived characters are a result of parallel or convergent evolution. This, obviously, does not apply to "transformed" cladists who, when faced with the problem of this apparently "false" synapomorphy, regard the "mistake" as being due to "overestimating the generality of a character, by confusing it with what is in actuality a different character" (Platnick, 1979).

When faced with this contradiction, cladists apply the principle of parsimony so that the hypothesis which is falsified the fewest number of times is accepted.

A second form of cladistic use of parsimony (see Panchen, 1982) involves the confrontation between several incompatible cladograms which may be based on different sets of characters. The accepted cladogram is then the one to which the majority approximate.

Both cladist uses of parsimony have been criticised by Panchen (1982). The first use, as in the three-taxon-statement introduces potential inaccuracies which may result from character correlation, and also from the fact that only a relatively small number of synapomorphies are used which may contain a ratio of "true" to "false" synapomorphies which is unrepresentative of the full suite of possible synapomorphies. The second use of parsimony is illegitimate because the number and type of synapomorphies being compared between different cladograms are not the same.

Even without the inherent difficulties in the cladist use of parsimony, Panchen argues that the cladistic methodology, despite its claims (for example, in Gaffrey 1979), fails to apply the Popperian hypothetico-deductive method. Many cladists, in practice, confuse Popperian falsification with the logicians' modus tollens. Furthermore, the cladists' use of falsification contrasts with Popper's concept of falsification owing to their incorrect use of parsimony (see Panchen 1982).

Because of their incorrect application of the hypothetico-deductive method, Panchen argues, the cladists cannot justify their claim to methodological superiority over traditional taxonomy.

There are a number of other methodological principles which have been criticised by non-cladists. The most important of these in present-day cladistics concerns the problems of ranking and the cladist attitude to paraphyletic groups.

Cladistic classifications, derived from cladograms, require an enormous number of ranks. The cladogram must be broken up so that every clade is a taxon and every level of bifurcation in a lineage represents an additional rank. Furthermore, the convention of equal rank for sister groups necessitates the assignment of very high ranks to fossil species which may be the sole representatives of the sister groups of taxa of high rank. Patterson and Rosen (1977) propose means of reducing the problem of classifying fossil species, but the problem of rank explosion remains and has led opponent taxonomists to state that cladistic classifications are impractical for use as tools of communication amongst biologists (Gingerich 1979).

The cladistic attitude to paraphyletic groups is the cause of further conflict. Cladists only recognise monophyletic groups: in their usage this is a group which includes a hypothetical ancestor with all its descendants. Traditional taxonomy allows the removal from a monophyletic group of one or more monophyletic descendant groups which are judged to have reached a higher "grade" of evolutionary development, so that the remaining members of the original group now comprise a paraphyletic group. An example is that the Reptilia is a paraphyletic group following the removal of the Aves.

This cladist convention is attacked for producing classifications which include groups lacking in homogeneity, and therefore such groups are less useful in communication than are traditional classifications.

Gingerich (1979) argues that cladistic classifications are less stable than traditional classifications since minor alterations at one level in the hierarchy will have widespread effects; thus, being less stable, such classifications are less effective as tools for communication.

In conclusion, the cladistic approach has contributed much of value to the field of systematics. Most importantly, the insistence on more rigorous methodological principles and the emphasis on the use only of derived characters to show relationship have forced traditional taxonomists to tighten up what was a rather loose attitude to methodology.

However, what cladistic analysis has achieved in terms of rigour has, some would argue, been at the price of a loss of usefulness in their classifications. Opponents argue that classifications should have a broader information content than just sister group relationships; that is, they should express divergence in terms of differences in the degree of similarity between groups. Cladistic classifications, furthermore, are too unstable and complex to be useful in everyday biology.

Phenetic classifications also have disadvantages. They depend for their effectiveness on the availability of a large number of characters. Thus phenetic techniques are most useful in classifying extant organisms, and are less useful in the classification of fossil groups, the members of which may be very incomplete. Furthermore, the refusal of pheneticists to incorporate information regarding phylogeny into classification is seen by their opponents as being too narrow an approach to classification.

In the following classification of the order Ichthyopterygia, I have chosen to apply an eclectic approach to taxonomy. However, I have incorporated a cladogram in order to illustrate phylogenetic relationships within the group, and throughout I have emphasised the importance of shared derived characters in exposing these relationships.

The Classification of the Ichthyopterygia

Order ICHTHYOPTERYGIA Owen, 1860

The generally accepted diagnosis of the order is that given by Romer (1956). In essence, this takes the form of a description based on the features evident in the better-known Jurassic forms. There is no attempt to distinguish primitive from derived characters.

Mazin (1980) has studied the earliest (and in his opinion, the most primitive) ichthyosaurs known, which are derived from the Lower Triassic of Spitzberg. This study revealed the following characters which are believed to be synapomorphies, defining the order Ichthyopterygia (Class Reptilia).

Diagnosis

(1) Neural arches remain unfused to the amphicoelous centra in adults. (In Lower Triassic ichthyosaurs, the centra are as broad as they are long, but in later taxa the "characteristic ichthyosaurian" disc-like centra develop.)

(2) Toothbases with a simple infolding of the primary dentine. (The infolding becomes more complex in later forms. It has been argued in the past that this infolding is a primitive character retained from the rhipidistian (if not the labyrinthodont) condition. However, Schultze (1969) has shown that the type of infolding seen in the ichthyosaur tooth base is not comparable to any other type of reptilian, amphibian or rhipidistian labyrinthine infolding. For this reason, it seems likely that the ichthyosaurian infolding is derived; it perhaps developed as a strengthening adaptation. This seems even more likely in view of the hypothesis proposed in the next section concerning the ancestry of the Ichthyopterygia.)

(3) Caudal vertebrae showing specialisations for the support of a tail fin.

(The Triassic forms possess caudal centra, in the region of the presumed tail fin, which are laterally compressed and whose neural arches are posteriorly inclined in the anterior section of the tail, but are anteriorly inclined further posteriorly. In later forms the centra remain laterally compressed, but the neural arches are lost from the posterior region of the tail which supports the hypocaudal lobe of the tail fin.)

(4) Eye relatively large.

(This feature is seen in the earliest ichthyosaur genera including Grippia (Mazin, 1980), Utatsusaurus (Shikama, 1978) and Mixosaurus (McGowan, 1972a). It may indicate an early specialisation of the group in which sight becomes a dominant sense.)

In previous classifications, the order has been characterised by the presence of a single superior temporal opening of unique construction (e.g. Williston, 1925). It now seems likely that the superior opening of ichthyosaurs is the homologue of that of diapsids, and that the ichthyosaurs have lost the original inferior temporal opening. This possibility will be discussed further in the following section. The ichthyosaur temporal opening cannot, therefore, be used as an autapomorphy of the order Ichthyopterygia.

Mazin (1980) concluded that Grippia longirostris represented the most primitive ichthyosaur taxon known. It possesses the following characters which are believed to represent the plesiomorphic condition for the Ichthyopterygia. Mazin regarded Grippia as the plesiomorphic sister group of all other ichthyosaurs. Some of the following primitive characters are also primitive reptilian characters.

(1) Relatively short snout.

(Later forms possess the characteristic "ichthyosaurian" long snout.)

(2) Large parietals and frontals.

(These are reduced in size in later forms.)

(3) The parietal, or parapineal, foramen is situated between the parietals.

(In all other taxa the foramen is positioned at the suture between the parietals and frontals.)

(4) The large postorbital and large quadratojugal both take part in the border of the superior temporal opening.

(In later forms both bones are excluded.)

(5) Large maxilla.

(In later forms this is reduced in size.)

(6) A dorsal process of the maxilla excludes the lachrymal from the narial border.

(This character is present in *Mixosaurus* and *Cymbospondylus* (Mazin 1980). In post-Triassic ichthyosaurs the maxillary-nasal contact remains, but the lachrymal extends to the naris by overlapping the latter contact.)

(7) Heterodonty.

(The posterior teeth in the tooth row are rounded and blunt, presumably as an adaptation for crushing. The anterior teeth are specialised for piercing, and are sharp and pointed. Heterodonty is present in the genera *Grippia*, *Phalarodon*, *Omphalosaurus*, and *Mixosaurus* but all later ichthyosaurs display isodonty - all the teeth being sharp and pointed.)

(8) Maxillary teeth in two rows.

(9) Subthecodont tooth implantation.

(This type of implantation is seen in at least part of the tooth row of all Triassic taxa (Mazin 1980, Merriam 1908). In post-Triassic taxa, the tooth sockets more or less disappear and the teeth are held in an open longitudinal alveolar groove.)

(10) Pelvic girdle large and plate-like, and scapula spatulate and distally expanded.

(11) Pelvic girdle probably has some form of bony contact with vertebral column (Mazin 1980).

(12) Pentadactyl limbs, little specialised for aquatic locomotion (see figure 48). Primitive features of limbs include:

(a) Radius, ulna, tibia and fibula elongate;

(b) Metapodials elongate;

(c) Phalanges constricted in the midline.

(In later forms pentadactyly is modified in various ways; the radius, ulna, tibia, fibula and metapodials and phalanges all become disc-like.)

(13) Hindlimb equal in size to the forelimb.

(14) Lack of a tail bend.

(The true hypocercal tail is present only in Jurassic taxa.)

Mazin (1980) designated Grippia, Phalarodon and Omphalosaurus as plesions. This term was introduced by Patterson and Rosen (1977) to apply to fossil groups or species which are the plesiomorphic sister groups of all those groups that succeed them in the synapomorphy scheme. These three taxa, on present knowledge, share no derived characters other than those that define the order Ichthyopterygia, and so it would be inappropriate to classify them together in a "grade group". Phalarodon and Omphalosaurus are more incomplete and less well-known than Grippia. For this reason, I propose to classify them as incertae sedis since future discoveries may clarify their taxonomic position.

Suborder GRIPPIDIA Wiman, 1933 (as order)

Diagnosis:

Members of the order Ichthyopterygia characterised by the possession of a large number of primitive ichthyopterygian characters. Among the characters listed by Mazin (1980) for Grippia, unique derived characters are:

(1) Presence of a pair of fossae (for the insertion of ? M. adductor mandibulae internus pseudotemporalis) at suture between postfrontal, parietal and frontal.

(2) Teeth possessing a distinct neck between crown and root. (As far as I am aware, these characters are not present in either primitive reptiles or the proposed ancestral diapsids (see later section), and so they can be taken as diagnostic characters for the suborder.)

Family: GRIPPIIDAE (fam. nov.)

Genus: Grippia Wiman, 1928 (1 species)

Range: known only from the Lower Trias, Spathian, of Spitzberg.

Incertae sedis: Omphalosaurus, Phalarodon.

Suborder MIXOSAURIA Mazin, 1980

Diagnosis:

Ichthyopterygians which retain many primitive ichthyopterygian features such as a pentadactyl limb, lack of a tail bend, heterodonty, maxillary process excluding lachrymal from the naris, plate-like pelvic girdle, expanded scapula. Characters which show an advance over those of Grippia include

(1) elongate, "typically ichthyopterygian" pointed snout,
(2) parapineal foramen situated at fronto-parietal suture,
(3) reduction of metapodials to disc-like bones,
(4) reduction of hindlimb.

The first two advanced characters are shared with all other ichthyopterygians (except Grippia); but the third and fourth advanced characters are considered to be diagnostic of the Mixosauria.

(Reduction of the metapodials and of the hindlimb has also occurred in the suborder Ichthyosauria (below), but these two characters would appear to be likely candidates for convergence, since they are clearly correlated with adaptation to aquatic locomotion. This is also the conclusion reached by Mazin (1980). The alternative hypothesis that these two characters could be synapomorphies uniting the Mixosauria with the Ichthyosauria is considered less likely since this would mean that the heterodonty of the Mixosauria must be a character reversal: this is considered unlikely.)

Family: MIXOSAURIDAE Baur, 1887a

Genus: Mixosaurus Baur, 1887a (6 species)

Range: Middle Trias, Anisian to Ladinian, of North America, Europe, Spitzberg, Indonesia and China.

Suborder: ICHTHYOSAURIA de Blainville, 1835 (as order)

Diagnosis:

Ichthyopterygians possessing the shared derived character of isodonty.

Infraorder: UTATSUSAURI (inf.ord. nov.)

Diagnosis: as family below.

Family: UTATSUSAURIDAE (fam. nov.)

Diagnosis:

Ichthyosaurians retaining many primitive features including elongate metapodials, pentadactyl limb, lack of a tail bend, spatulate scapula, plate-like pubis and ischium, subthecodont tooth implantation.

Unique derived characters include

(1) a loss of the radial infolding of the primary dentine in the tooth base, giving a smooth-walled pulp cavity, (assuming ichthyosaurian infolding is derived);

(2) reduction in size of the pelvic girdle and hindlimb.

(This latter character also occurs in the Ichthyosauridae and the Mixosauria. As already mentioned, this character is likely to be developed convergently since it is correlated with aquatic locomotion.)

Genus: *Utatsusaurus* Shikama et al, 1978.

Range: Lower Trias, late Scythian, of Japan.

Incertae sedis: *Svalbardosaurus* Mazin, 1980.

(Mazin (1980) proposed a relationship between *Svalbardosaurus* and *Utatsusaurus* on the basis of similarities in tooth morphology. However, *Svalbardosaurus* appears to retain infolding of the tooth base, and so this relationship seems to me uncertain.)

Infraorder: ICHTHYOSAURI (inf.ord. nov.)

Diagnosis:

Ichthyosaurians characterized by

(1) reduction or loss of the fifth primary digit in fore- and hind-paddles;

(2) humerus with a median constriction;

(3) reduction of the metapodials.

Family: SHASTASAURIDAE Merriam, 1902

Diagnosis:

Members of the infraorder Ichthyosauri which retain many primitive characters, such as a foramen between radius and ulna, a plate-like pelvic girdle, scapula which is distally expanded, and lack of a hypocercal tail. Shared derived characters defining the family are:

(1) reduction and almost complete loss of the fourth distal carpal and primary digit (see figure 42g) in fore- and hindlimbs.

(In some cases, there are a few postaxial accessory ossicles which may be remnants of the fourth digit (for example, in _Merriamia_ (Merriam 1908) and _Shonisaurus_ (Camp 1980), see figure 42i). Reduction of the fourth digit also occurs in the Temnodontosauridae (see below), however, in this case the reduction of the digit is not as complete as in the Shastasauridae, even though the Temnodontosauridae are later in time. Furthermore, the alternative hypothesis, that reduction of the fourth digit is a true synapomorphy uniting these two families, is considered unlikely, since this would necessitate the condition that development of a hypocercal tail, reduction of the pelvic girdle and shortening of the epipodials (characters 18-20 in the cladogram, figure 43) had arisen convergently in the Ichthyosauridae and in the _Shastasaurus-Temnodontosaurus_ group. For these reasons it is thought more likely that reduction of the fourth digit has occurred convergently in the Temnodontosauridae. This conclusion was also reached by Mazin (1980).)

Genera: Shastasaurus Merriam, 1895 (5 species)
Delphinosaurus Merriam, 1905
Merriamia Boulenger, 1904b
Shonisaurus Camp, 1976 (3 species)
Toretocnemus Merriam, 1902

Range: Upper Trias (Carnian-Norian) of North America.

Incertae sedis: Pessosaurus Hulke, 1873
Cymbospondylus Leidy, 1868

(This latter genus has traditionally been included in this group, but the structure of the limbs is imperfectly known, and it is from a lower horizon (Anisian) than the rest; I conclude it is best to designate the genus incertae sedis at present. Pessosaurus is known from only fragmentary remains and so is here designated incertae sedis.)

Family: ICHTHYOSAURIDAE Baur, 1887a

Diagnosis:

Members of the infraorder Ichthyosauri which possess the following shared derived characters:

(1) Forelimb with four distal carpals and four primary digits equally developed (figure 42);

(2) Pelvic girdle no longer plate-like.

(3) Hindlimb reduced relative to the forelimb.

Genera: Ichthyosaurus De La Beche and Conybeare, 1821 (4 species)
Stenopterygius Jaekel, 1904 (8 species)
Ophthalmosaurus Seeley, 1874.
Nannopterygius Hulke, 1871
Brachypterygius Boulenger, 1904a

Range: Jurassic (Hettangian to Kimmeridgian) of Europe and America.

Family: TEMNODONTOSAURIDAE McGowan, 1974a

Diagnosis:

Members of the infraorder Ichthyosauri, generally of large size, which retain the primitive character of equal-sized fore- and hindlimbs. The shared derived character defining the family is reduction of the fourth distal carpal and digit in the forefin, but never its complete loss (see figure 42e).

Genera: Temnodontosaurus Lydekker, 1889b (4 species)

Leptopterygius Von Huene, 1922 (4 species)

Eurhinosaurus Abel, 1909.

Platypterygius Von Huene, 1922 (7 species)

(Platypterygius is assigned with less certainty to the Temnodontosauridae since its forepaddle is secondarily widened so that it possesses eight digits. Previous authors have considered only three of these to be primary digits, the remaining five are then accessory digits. Thus the genus has been aligned with Temnodontosaurus and Leptopterygius. Until further evidence is put forward, I propose to follow the classification of previous authors.)

Range: Lower Liassic (Hettangian) to Upper Cretaceous (Santonian) of Europe, America, Australia, India, U.S.S.R.

Incertae sedis: Grendelius McGowan, 1976

(Grendelius is assigned with uncertainty to this family since no paddle material is known. However, the robust nature of the skull, jaws and teeth of the genus, and its large size contrast with the members of the Ichthyosauridae, and so it is thought appropriate to include the genus here until further evidence becomes available.)

Order: ICHTHYOPTERYGIA

Suborder: GRIPPIDIA

Family: GRIPPIIDAE

Grippia longirostris

Phalarodon fraasi } incertae sedis

Omphalosaurus (2 sp.) } incertae sedis

Suborder: MIXOSAURIA

Family: MIXOSAURIDAE

Mixosaurus (6 sp.)

Suborder: ICHTHYOSAURIA

Infraorder: UTATSUSAURI

Family: UTATSUSAURIDAE

Utatsusaurus hataii

Svalbardosaurus crassidens, incertae sedis

Infraorder: ICHTHYOSAURI

Family: SHASTASAURIDAE

Shastasaurus (5 sp.)

Shonisaurus (3 sp.)

Delphinosaurus perrini

Toretocnemus californicus

Cymbospondylus (3 sp.) } incertae sedis

Pessosaurus polaris } incertae sedis

Family: ICHTHYOSAURIDAE

Ichthyosaurus (4 sp.)

Stenopterygius (8 sp.)

Ophthalmosaurus icenicus

Brachypterygius extremus

Nannopterygius enthekiodon

Family: TEMNODONTOSAURIDAE

Temnodontosaurus (4 sp.)

Leptopterygius (4 sp.)

Eurhinosaurus huenei

Platyptergius (7 sp.)

Grendelius mordax, incertae sedis

Phylogenetic Relationships

The cladogram in figure 43 illustrates the phylogenetic relationships between the members of the Ichthyopterygia, as revealed by this study.

SECTION 2 : ORIGINS AND RELATIONSHIPS OF THE ICHTHYOPTERYGIA

Since 1860, when Owen placed the ichthyosaurs and plesiosaurs in separate orders, the ichthyosaurs have been regarded as a taxonomically isolated group of reptiles. One of the main reasons for their isolation was the presence in the ichthyosaur skull of a single superior temporal opening, bordered by an apparently unique combination of bones.

The earliest workers on ichthyosaur skull morphology (Owen 1839, 1858, 1881; Seeley 1880) encountered difficulties when trying to homologise the bones in the temporal region of the skull, and a certain amount of controversy has surrounded this problem until the present day.

The difficulties have centred around the homology of two of the bones in the temporal region,which are labelled A and B in figure 44. This is the nomenclature used by Romer (1968) in a paper which discussed this problem.

It should be noted that most of the descriptive studies which deal with the temporal region were based on well-preserved material from the Lias of England and Germany. The Triassic taxa have been, until very recently, known only from poorly preserved material.

In Liassic ichthyosaur skulls, element A is a large triradiate bone which forms the whole of the posterior half of the border of the superior temporal opening. It is an important structural element in that it forms the posterior corner of the skull roof; the quadrate slots into a groove on its ventral edge, and the bone articulates with the paroccipital process in occipital aspect.

To the earlier workers, this bone appeared to have the relationships of the squamosal bone of more typical reptiles with fenestrated skulls; from about 1890 to 1922 a concensus was reached and the bone was named the squamosal. This left the problem of deciding the true homology of element B.

The first description of this bone was given by Owen in 1881, from a study of the Lower Liassic genus Ichthyosaurus. Owen described the bone as a "broad, thin, flat, irregularly-shaped bony plate, smooth and subconvex outwardly, wedged into an interspace between the postfrontal, postorbital, zygomatic (quadratojugal), tympanic (quadrate) and mastoid (element A) bones". He named the bone a "supersquamosal", and, finding it impossible to discover its homology, concluded it must be a supplemental sclerodermal plate covering what would have been an inferior temporal opening.

Table 2 shows that much disagreement has surrounded the nomenclature of elements A and B.

Table 2 : Nomenclature of A and B

	Element A	Element B
Owen (1858)	mastoid	supersquamosal
Seeley (1876)	squamosal	supraquadrate
Baur (1887b)	supratemporal	squamosal
Fraas (1891)	squamosal	supratemporal
Gilmore (1905)	"	"
Andrews (1910)	"	"
Sollas (1916)	"	"
Watson (1914)	squamosal	no commitment
Von Huene (1922)	supratemporal	squamosal
Broom (1936)	tabular	squamosal
Romer (1948)	supratemporal	squamosal
Appleby (1956)	?tabular	squamosal
" (1961)	supratemporal	squamosal
Romer (1968)	squamosal	-
McGowan (1973a)	squamosal	-

By the turn of the century, the majority of workers agreed that one of the two bones must be a retained member of the temporal series, the elements of which are reduced or lost in the majority of reptile lineages.

Baur (1887b) was the first to homologise the "extra" temporal bone of ichthyosaurs with the reduced member of the temporal series in the skull of the Lacertilia, and so he named element A the supratemporal; element B then became the squamosal. Other workers (Gilmore 1905, Andrews 1910, Sollas 1916) found it hard to accept that the retained supratemporal could be such a large and structurally important bone in the skull roof, and so these workers switched the nomenclature around - element B was then the supratemporal whilst element A became the squamosal.

Von Huene recognised that no conventional tetrapod has a temporal series element situated ventral to the squamosal on the cheek, and so he once more reversed the two names. For the next forty-five years or so, this nomenclature was the accepted one, apart from minor disagreements as to whether element A was the supratemporal or tabular.

It became generally accepted that the ichthyosaur skull was unusual in the configuration of the temporal region (figure 46). In no other reptile group possessing a superior temporal opening was there a large supratemporal or tabular meeting the postfrontal below the opening. The most widely used system of reptile classification this century has been the system, developed by Osborn (1903) and Williston (1925), which is based on the nature of the temporal openings in the skull.

Under this system, the ichthyosaurs were placed in a separate order (or superorder of Osborn). However, Williston grouped the ichthyosaurs with three other orders in the subclass Parapsida. These orders possessed a single upper temporal opening, and they included the lizards, mesosaurs, araeoscelids and the ichthyosaurs.

The Parapsida became regarded by subsequent authors as an unnatural group, and the most widely accepted classification of the last thirty years, that of Romer (1956, 1966), removed the ichthyosaurs to a distinct subclass, the Ichthyopterygia. It became widely held that the unique temporal opening, in which a large supratemporal or tabular took part, must have arisen very early in reptilian evolution, and perhaps arose independently from an anapsid condition (Von Huene 1922, Romer 1956, Appleby 1961).

In 1968 Romer challenged the accepted interpretation of the ichthyosaur temporal region. He described the well-preserved skull of a Cretaceous ichthyosaur. The temporal region was intact, and here Romer could find no trace of element B. Instead, a large quadratojugal occupied its place. Romer then looked at a number of other acid-prepared skulls in the BMNH, and again found no evidence of an element B. A literature survey revealed that authors often reported element B to be missing or crushed beyond recognition. These findings led Romer to suggest that element B had never existed as a discrete element in the skull of ichthyosaurs. He suggested that when it had been reported present in the skull, authors had been misled by broken flakes from the postorbital or quadratojugal.

Five years later, McGowan (1973a) published the results of a study of acid-prepared Liassic ichthyosaur skulls during which he independently reached the same conclusion as Romer (1968), that element B did not exist.

Under the interpretation of Romer and McGowan (figure 45), the ichthyosaur temporal opening looks less unusual and resembles the euryapsid type of opening seen in the sauropterygians, here illustrated by the nothosaur Simosaurus. Colbert (1969) and McGowan (1973a) both suggested that the ichthyosaurs should be included in the subclass Euryapsida, though Romer (1968) was more hesitant about this.

The present study of Ophthalmosaurus has led me to disagree with the findings of Romer and McGowan. An element B is present as a separate bone in the cheek of this genus (figure 14, plates 1, 2)

Andrews (1910) described and figured element B, in Ophthalmosaurus, as a small, triangular element situated just below element A on the cheek. Romer (1968) postulated that Andrews had mistaken for element B the dorsal half of the quadratojugal, which appeared to be separated from its ventral half by the overlapping postorbital. However, my own study of the skull of Ophthalmosaurus has revealed that element B is present as a distinct element (see descriptive section).

In the course of the present study, I have seen at least three other Liassic ichthyosaur skulls which possess a distinct element B. These are BMNH 32681, 33157 - both labelled Ichthyosaurus longifrons (the latter specimen being the type) - and SM J35176, labelled Ichthyosaurus zetlandicus (all three specimens are classified by McGowan (1974a) as Leptopterygius acutirostris). These specimens are preserved in-the-round, with very little crushing. The majority of the English Liassic ichthyosaur skulls I have studied are preserved in a compressed condition, and crushing usually makes it uncertain whether element B is present or not in the cheek.

Element B is present, however, in at least some ichthyosaur taxa. It is apparently absent from the skull of Platypterygius americanus, described by Romer (1968). The specimens of Ichthyosaurus, described by McGowan (1973a), I find to be imperfectly preserved in the temporal region and, unlike McGowan, I do not consider there to be sufficient evidence to conclude that element B was not present.

Mazin (1980) has shown conclusively that the skull of Grippia, one of the earliest, and in his opinion the most primitive ichthyosaur known, does not possess an element B (figure 47). Instead, a large quadratojugal spans the whole cheek behind the postorbital, and, in this genus, both these bones contribute to the border of the temporal opening. Mazin (1981) has also described the cheek region of another taxon, MNHN SVT 331, which remains unnamed. This specimen derives from a horizon just below that of *Grippia*, and it therefore represents the earliest known ichthyosaur remains. The cheek region of this taxon again shows no evidence of an element B.

There are then two possible hypotheses concerning the homology of the bones in the temporal region. The first states that the primitive ichthyopterygian condition is the possession of an element B, which can then be homologised with the squamosal; element A is then the supratemporal or tabular (figure 46). Under this hypothesis, the temporal region of *Grippia* and MNHN SVT 331 must represent the derived condition, element B having been lost extremely early in their respective lineages.

The second hypothesis states that *Grippia*, MNHN SVT 331, and *P. americanus* display the primitive ichthyopterygian condition, and that element B, when present in the skull, is a neomorph. Element A can then be homologised with the squamosal (figure 45).

Mazin (personal communication) believes that the absence of element B from the temporal region of the two earliest, and in his opinion, the most primitive, ichthyosaur taxa is evidence in support of the second hypothesis. Until more detailed knowledge is available of the incidence of element B in the skull of ichthyosaur taxa, I am prepared to accept the second hypothesis as the more likely.

Each of these above hypotheses has important implications for the problem of the origins and relationships of the Ichthyopterygia.

Under the first hypothesis the ichthyosaur skull displays a number of apparently primitive tetrapod characters. The most striking of these is the retention of a large supratemporal or tabular. In its size and relationships to surrounding elements, the bone closely resembles the retained temporal series member in the skull of procolophonids and pareiasaurs (and, incidentally, of the amphibian microsaurs) (figure 46). The temporal series bone in these forms is most often homologised with the tabular on the basis that it receives the paroccipital process, as does the tabular of Rhipidistia and primitive tetrapods, and it also takes part, with the paroccipital process, in the formation of the walls of the post-temporal fossa (Panchen 1972).

In ichthyosaurs (according to hypothesis I) and procolophonids and pareiasaurs, the paroccipital process shows no tendency to reach towards or contact the cheek region. In all other primitive reptiles such as captorhinomorphs, millerosaurs and pelycosaurs, the paroccipital process reaches horizontally towards the suspensorial region, although actual bony contact may be prevented owing to incomplete ossification of the paroccipital process. Pelycosaurs, procolophonids and pareiasaurs, however, unlike captorhinomorphs, retain a tabular-paroccipital contact and this has been interpreted as evidence that the pelycosaurs, procolophonids and pareiasaurs are closer to the primitive reptilian condition than are captorhinomorphs (Panchen 1972, Kemp 1980, Heaton 1980). In millerosaurs (Gow 1972), the paroccipital process passes beneath the supratemporal and tabular to contact the squamosal - there being no actual bony contact with the tabular.

The failure of the paroccipital process of ichthyosaurs to reach towards the squamosal has influenced many authors in the past to suggest that ichthyosaurs originated very early in reptilian evolution (e.g. Romer 1948, Appleby 1956), and it has even been suggested that they arose independently from amphibians (Von Huene 1937, 1944, 1956, Nielsen 1954). Another apparently primitive feature, interpreted as supporting an early origin of the group, was the labyrinthine infolding of the teeth. The doubtfulness of the primitiveness of this character was discussed above.

If hypothesis I were correct, then it would follow that the Ichthyopterygia arose very early in reptile phylogeny, and possibly from a group more primitive than the known captorhinomorphs.

Under hypothesis II, which I consider the more acceptable, the Ichthyopterygia would appear to have originated much later in reptilian phylogeny, and their nearest relatives can be sought amongst fenestrated reptile groups. Under this hypothesis the skull of Grippia (figure 47 a) exemplifies the primitive ichthyopterygian condition. The bones contributing to the border of the superior temporal fenestra are the parietal, squamosal, quadratojugal, postorbital and postfrontal. The temporal opening of Grippia differs from that of all other ichthyosaurs in that the postorbital figures prominently in the border of the opening, and prevents the postfrontal-squamosal contact that is characteristic of all later ichthyosaurs. Because of this, the temporal opening of Grippia resembles the euryapsid-type seen in the sauropterygians even more closely than Romer's (1968) and McGowan's (1973a) interpretation had allowed (figure 45); this apparently strengthens the case for a relationship between the sauropterygians and ichthyopterygians.

The question of the origins and relationships of the Euryapsida (usually taken to include the Sauropterygia and Placodontia) has remained problematic until the present day. Recent theories have, however, suggested that the euryapsid skull may be derived from an ancestral diapsid condition. The upper temporal opening, of sauropterygians at least, is identical with that of diapsids. Kuhn-Schnyder (1961, 1963, 1967) proposed that the emarginated ventral border of the cheek of nothosaurs and plesiosaurs was the remnant of a lower temporal opening and that the euryapsid line had lost the lower temporal bar, the reduced quadratojugal having, in the process, lost all contact with the jugal (figure 45 a,c). This theory was proposed originally by Jaekel (1910), but was largely ignored.

More recently, Carroll (1981) has described reptilian remains from the Permian of Madagascar which he believes are possible sauropterygian ancestors, and which he considers to be morphologically intermediate between eosuchians, primitive diapsids, and nothosaurs. These forms have an open cheek similar to that of nothosaurs, suggesting that the lower temporal bar has been broken.

The idea that ichthyosaurs may have originally possessed a lower temporal fenestra was first put forward by Owen (1881) and later by McGregor (1905), who suggested phytosaurs as their nearest relatives. Triassic ichthyosaurs display a distinct emargination of the lower border of the cheek (see Grippia, figure 47). In Jurassic forms the emargination is much less noticeable because of an overall shortening of the postorbital section of the skull, this is at an extreme in Ophthalmosaurus (figure 14) in which the postorbital region is extremely narrow.

Unlike the condition seen in the cheek of nothosaurs, however, the quadratojugal and jugal of ichthyosaurs show a broad contact above the emargination. This means that, if the emargination had resulted from the modification of a lower temporal fenestra, the quadratojugal and jugal would have had to re-establish a contact above the opening in the cheek. An alternative explanation for the jugal-quadratojugal contact was given by Ginsburg (1968).

Ginsburg compared the ichthyosaur cheek embayment with that seen in Pleurosaurus and related forms. In this group of reptiles, the jugal and quadratojugal also contact one another above the cheek embayment. Ginsburg stated that, because the pleurosaurs are believed by him to be incontestable diapsids, this is evidence that a similar process of loss of the lower temporal arch could have occurred in ichthyosaurs. The mechanism proposed by Ginsburg for this loss was that the jugal-quadratojugal arch had moved dorsally and had become applied to the upper temporal arcade, thus closing the lower temporal opening, but leaving a ventral cheek emargination. Dr. P. Janvier informs me (personal communication) that supporting evidence for this mechanism can be found in the cheek of some Pleurosaurus specimens, where the junction between the jugal-quadratojugal bar and the postorbital-squamosal bar is seen to be imperfectly consolidated.

Without fossil evidence of any intermediate stages in the breakdown or modification of the lower temporal arch, it is still a possibility that the ichthyosaur cheek emargination may be no more than a simple emargination which is present in a number of reptile groups such as turtles (Romer 1956) and the procolophonids Procolophon and Owenetta (Gow 1977). However, on present knowledge it seems reasonable to uphold the hypothesis that the ichthyosaur skull, and the sauropterygian skull may both have been derived from an ancestral diapsid condition.

There is very little evidence, though, from the rest of the skeleton, in support of any particular close relationship between sauropterygians and ichthyosaurs. Shared derived characters such as posteriorly positioned nasal openings, elongate premaxillae and loss of the transverse flange of the pterygoid are probably aquatic specialisations and could possibly have developed convergently.

Mazin (1980) has suggested a close relationship between placodonts and ichthyosaurs. The placodonts have been regarded as a problematic, apparently aberrant group whose relationship to other reptile groups has been much debated.

They have most often been classified, along with the nothosaurs and plesiosaurs in the subclass Euryapsida. Romer (1956) regarded them as a suborder of the Sauropterygia, but later removed them from such a close relationship with the plesiosaurs and nothosaurs by placing them in a separate order of the subclass Euryapsida (Romer 1966, 1971).

Kuhn-Schnyder (1963, 1967, 1980) disagreed with Romer. He regarded the placodonts as an isolated group which bear no close relationship to the sauropterygians. He noted that the quadratojugal of placodonts is a large bone which forms a large part of the cheek and contributes to the lower border of the temporal opening (figure 47 b). This contrasts with the quadratojugal of sauropterygians which is greatly reduced. Kuhn-Schnyder argued that the temporal opening of placodonts is not comparable to that of sauropterygians. Although the quadratojugal-jugal bar of placodonts is ventrally arched, as in the latter group, he argued that the large size of the quadratojugal and its persistent contact with the jugal, is evidence that the group never possessed a lower temporal opening. Other differences which, to Kuhn-Schnyder, weighed against a close relationship between the two groups were seen in the vertebral column. Nothosaurs possess a zygosphene-zygantrum articulation (accessory neural arch articulations situated above the zygapophyses), whilst placodonts possess a hyposphene-hypantrum articulation (accessory neural arch articulations below the zygapophyses). Furthermore, sauropterygians tended towards an increase in vertebral numbers, whilst placodonts tended towards a reduction.

It is apparent that the configuration of the temporal opening and cheek of the placodont Placochelys is very similar to that of the primitive ichthyosaur Grippia (figure 47). The main difference is that in Grippia the postfrontal contributes to the temporal opening, whereas it does not in Placochelys; however, in the placodont Placodus the postfrontal does enter the opening (Romer 1966).

Mazin (1980) postulated that the cheek of placodonts is derived with respect to that of sauropterygians. He described a possible evolutionary transition from an ancestral diapsid condition (figure 47 c) . The first stage in this transition was a breakdown of the lower temporal arcade and a reduction of the quadratojugal, which gave the sauropterygian skull configuration. This would be followed by a secondary dorsal expansion of the quadratojugal and jugal, so that they meet one another above the ventral cheek emargination, and the quadratojugal invades the border of the superior temporal opening. This is the primitive condition for both placodonts and ichthyosaurs. The ichthyosaur lineage was then characterised by an expansion of the postfrontal and squamosal so that they meet below the temporal opening, excluding the quadratojugal from its border. Mazin suggests that the Ichthyopterygia and Placodontia share two synapomorphies. These are the development of the secondary contact between the jugal and quadratojugal, and the possession of heterodonty. Heterodonty is present in all known placodonts except *Helveticosaurus* and is manifested by the presence of specialised blunt crushing teeth in the posterior region of the tooth row, together with conical or peg-like teeth in the anterior tooth row. Heterodonty is considered to be the primitive condition for ichthyosaurs by Mazin (1980); in primitive ichthyosaur genera such as *Grippia* and *Mixosaurus* the posterior teeth are blunt and specialised for crushing, whereas the anterior teeth are conical and specialised for piercing.

Helveticosaurus is usually considered to be a primitive placodont (Romer 1966). However, it lacks many of the derived characters of later placodonts, and for this reason Romer considered it to be very close to the nothosaur lineage. It displays a marginal dentition of sharp, recurved teeth, and shows no evidence of heterodonty. Mazin (1980) classified *Helveticosaurus* as the plesiomorphic sister-group of all other placodonts, but its true relationships remain uncertain.

Ginsburg's (1968) proposed mechanism for the loss of the lower temporal opening in ichthyosaurs (see above) has different implications for the interrelationships of ichthyosaurs, placodonts, and sauropterygians. In this case the placodont and ichthyosaur condition would have developed directly from the primitive diapsid condition by the dorsal migration of the lower temporal arcade, and its application to the upper temporal arcade. The sauropterygian condition may be derived from this by a secondary reduction of the quadratojugal; or alternatively, it may be derived independently from the diapsid condition by the breakdown of the temporal arcade as before.

Further research may provide evidence in support of one or other of these possible phylogenetic pathways, and it may also test the proposed relationship between placodonts and ichthyosaurs.

Loss of the lower temporal arcade occurs separately in the diapsid groups Prolacertilia (Prolacerta, Macrocnemus, Tanystropheus), sphenodontids (Clevosaurus) and squamates. A number of functional explanations have been proposed for the repeated loss of the arcade. These include proposals that the loss is correlated with the development of a streptostylic quadrate (e.g. Romer 1956) or with middle ear function (Robinson 1973). Neither of these explanations would appear to apply to the sauropterygians, placodonts and ichthyosaurs, which have immovable quadrates and whose hearing was presumably less acute than in terrestrial diapsids.

Rieppel & Gronowski (1981) have put forward the hypothesis that the loss of the lower temporal arcade in prolacertids, sphenodontids and squamates may be correlated with an expansion of a postero-ventral portion of the M. adductor mandibulae externus superficialis over the lateral surface of the jaw. The advantage of such an expansion is the attainment of maximum muscle fibre length which allows a large range over which contraction can occur (large excursion range), and also allows maximum force to be generated on contraction (Rieppel & Gronowski 1981).

Room for the expansion of the M.a.m. externus superficialis can only be obtained either by a bulging outwards of the lower temporal arcade, as occurs in Sphenodon, or by its loss.

This hypothesis gives a possible functional explanation for the loss of the lower temporal arcade in ichthyosaurs, placodonts, and sauropterygians. The description of the lower jaw of Ophthalmosaurus reveals a possible site of insertion of the M.a.m. externus superficialis (figure 15) fairly low down on the lateral surface of the surangular. The insertion area is situated lower on the external surface of the jaw than it is in the primitive reptile Eocaptorhinus (Heaton 1979) which Rieppel takes as illustrating the primitive condition from which expansion of the M.a.m. externus superficialis is derived. It is possible, therefore, that this expansion has also occurred in the ichthyosaurs in correlation with the loss of the lower temporal arcade.

Under hypothesis II as explained above, the temporal regions of some Jurassic ichthyosaurs, including Ophthalmosaurus, possess a neomorph - element B (figure 44). It is reasonable to look for a possible functional explanation for the development of the neomorph. Under this hypothesis the primitive ichthyopterygian condition is the possession of a large quadratojugal spanning the whole depth of the postorbital region of the skull. In some Jurassic ichthyosaurs, the postorbital region has become very narrow in correlation with an increase in orbital diameter (McGowan 1972 b). This process is at an extreme in Ophthalmosaurus (figure 14). It seems reasonable to propose that the development of a neomorph by the splitting of the narrowed quadratojugal into separate dorsal and ventral halves may be correlated with the narrowing of the postorbital region.

Addendum

In 1972 Young and Dong described a problematic reptile, from the (?)Lower Triassic of the Hunang Province region of China, under the name of Hupehsuchus nanchangensis. The authors noted that the body and head of Hupehsuchus superficially resembled that of the primitive ichthyosaur Grippia, in that it possessed an ichthyosaurian-like elongate snout, shortened neck, long body and relatively reduced hind limbs. The skull, however, was clearly diapsid, and this latter feature persuaded the authors to classify the reptile as a somewhat aberrant member of the Thecodontia.

A cast of the specimen is now in the British Museum (Nat. Hist.). The description of Young and Dong does not reveal the presence of any of the synapomorphies of the Ichthyopterygia, and at present it is not possible to state with any certainty whether or not Hupehsuchus bears any close relationship to the Ichthyopterygia. Further research on better-preserved material may answer this question.

Two recent papers by Tarsitano (1982, 1983) once more put forward a case for the diapsid origin of ichthyosaurs. Tarsitano suggests that a number of features of the ichthyosaur skull, postcranial skeleton and presumed reproductive strategy can be interpreted as evidence for their origin from within the Eosuchia. Some of these proposed lines of evidence, I would suggest, can be criticised.

Tarsitano notes that the jugal of lizards is characteristically boomerang-shaped as a direct result of the reduction of a posterior branch of the jugal during the breakdown of the lower temporal arcade. He points out that the jugal of ichthyosaurs is also boomerang-shaped, and he states "Thus, a similar reduction pattern producing identical results calls for the original condition to have been the same, namely a diapsid skull". He further comments, "had the skull of ichthyosaurs not been of diapsid ancestry, the reduction of the temporal region with the enlargement of the eye would not have produced the temporal architecture of the ichthyosaur skull".

This seems to me to be stating the case too emphatically. It is, of course, a possibility that the similar end result, namely jugal shape, in ichthyosaurs and lizards is the result of a similar reduction pattern from an originally diapsid skull, but there is no evidence that such a reduction pattern has necessarily occurred, since there are no fossil intermediates. The possibility is not ruled out that the boomerang-shaped jugal and temporal architecture is the result of an entirely different process, and from a different ancestral condition.

Tarsitano disagrees with the interpretation of Romer (1968) and McGowan (1973a) concerning the pattern of bones in the temporal region of the ichthyosaur skull. In agreement with both these authors, however, he does not believe an element B exists in the ichthyosaur skull. His disagreement concerns the bone occupying the space of element B - this was thought by Romer and McGowan to be the large quadratojugal. From a study of one specimen of the Upper Liassic genus Leptopterygius acutirostris (G.I.T. 1576), Tarsitano concluded that the quadratojugal is a small ventral element,and the space for element B is taken up by a ventral flange from the squamosal. My own study of skulls of Ophthalmosaurus and of Leptopterygius acutirostris (BMNH 32681, 33157) has shown that this space is occupied by a separate skull bone, element B, and there is a distinct suture between it and the squamosal.

Tarsitano argues that his interpretation, that is,a small ventral quadratojugal overlapped by a large ventral flange from the squamosal, resembles the pattern characteristic of diapsids. This piece of evidence can be criticised on two counts: firstly, Tarsitano has misidentified element B as the squamosal (interestingly, his figures illustrate the squamosal as differentiated into a dorsal region and a ventral flange; he depicts the ventral flange (my element B) as separated from the dorsal region by a broken line). Secondly, the primitive ichthyopterygian condition (according to Mazin 1980) is the possession of a large quadratojugal occupying the whole depth of the cheek, as in Grippia. Therefore the small ventral quadratojugal of later ichthyosaurs is not a true synapomorphic character showing a relationship with diapsids.

Tarsitano states that the small ventral quadratojugal of ichthyosaurs has lost all contact with the jugal, and he sees this as evidence in favour of a breakdown having occurred in an original lower temporal bar. However, in Ophthalmosaurus, Grippia (Mazin, 1980) and Ichthyosaurus (McGowan, 1973a), and in all the ichthyosaur skulls I have studied,the jugal and quadratojugal maintain contact. It was, however, explained above that the jugal-quadratojugal contact does not preclude a diapsid origin for the group. It was also pointed out that this contact may indicate a relationship between placodonts and ichthyosaurs.

Tarsitano briefly explains a hypothesis (to be more fully discussed in a later paper) that states that the lower temporal fenestra inevitably develops first in any fenestrated reptilian skull, and only later, as a result of expansion of the Mm. adductor mandibulae internus pseudotemporalis and externus medialis, does the upper temporal fenestra develop. The hypothesis relates to the low angle of insertion necessary for periosteal invasion by these muscles, which can only be achieved in the ancestral "cotylosaur" skull by their attachment to the lower part of the temporal and cheek regions. Thus, according to Tarsitano, no reptile should ever develop only an upper temporal fenestra, and therefore the ichthyosaurs, placodonts and sauropterygians must have a diapsid origin.

Tarsitano cites as further evidence for a diapsid origin of ichthyosaurs, placodonts and sauropterygians the presence of an internal trochanter on the femur (the trochanter is reduced in ichthyosaurs and plesiosaurs). Tarsitano states that an internal trochanter is an eosuchian-lacertilian character. The traditional interpretation of the primitive reptilian femur (see Romer 1956) describes the presence of an internal trochanter. The trochanter in this position on the femur of eosuchians and lacertilians is better developed, but since the presence of an internal trochanter is a primitive reptilian character, I do not consider its presence in ichthyosaurs, placodonts and sauropterygians to be good evidence for a diapsid origin.

The final piece of evidence upheld by Tarsitano as being in favour of a diapsid origin for ichthyosaurs derives from the presumed viviparous nature of the group. Unlike the embryos of crocodiles and turtles, those of saurians do not obtain calcium for their growing skeletons from the egg shell. Therefore, only saurians amongst living reptiles have the option to develop viviparity. Tarsitano sees this as indicating that ichthyosaurs share a common eosuchian origin with the Lacertilia, although he admits this evidence is somewhat circumstantial.

Despite these criticisms, Tarsitano reaches the same conclusion as the present study, that it is likely that ichthyosaurs, sauropterygians and placodonts originated from a diapsid ancestral group. However, his proposed evidence appears to depend too strongly on data from the specialised Upper Liassic ichthyosaur taxa, without any consideration of evidence from the earliest and most primitive members of the order such as <u>Grippia</u> (Mazin 1980). The accuracy of Tarsitano's interpretation of the skull must also be questioned.

SECTION 3: FUNCTIONAL CONSIDERATIONS OF THE MORPHOLOGY OF OPHTHALMOSAURUS

I. Reconstruction of the Mandibular Adductor and Abductor Muscles

The mandibular muscles of extant reptiles are generally identified according to the classification of Luther (1914), who classified the jaw muscles according to their position relative to the branches of the trigeminal (V) nerve. The mandibular muscles are divided into three groups: the adductor mandibulae, constrictor dorsalis and constrictor ventralis groups. The present study will deal only with those muscles responsible for opening and closing the jaws, that is the adductor mandibulae muscle group, and the depressor mandibulae muscle, which is a member of the branchial musculature and is innervated by the facial (VII) nerve.

The adductor mandibulae group is subdivided into three sheets, each identified according to their position relative to the trigeminal nerve.

1. The M. adductor mandibulae externus:

   This is itself usually further differentiated into three slips: (a) M. a. m. externus superficialis, (b) M. a. m. externus medialis, and (c) M. a. m. externus profundus. In practice, however, these three slips are rarely easily separated in living reptiles (Haas 1973, Schumacher 1973).

2. The M. adductor mandibulae internus:

   This is in two subdivisions: (a) M. a. m. internus pseudotemporalis and (b) M. a. m. internus pterygoideus.

3. M. adductor mandibulae posterior:

   This muscle is not usually further differentiated.

This basic plan applies to all living reptile groups; however, there are numerous variations in the topography of the jaw muscles between these groups which result from particular specialisations in skull morphology and feeding function.

The turtles possess an unfenestrated skull which shows marked specialisations in jaw function. The M. a. m. externus is enlarged relative to the M. a. m. internus and posterior. Jaw adduction is effected by horizontal traction in the M. a. m. externus and M. a. m. internus pterygoideus which is transformed into a vertical component by means of a fulcrum at the trochlear process of the quadrate, or the pterygoid (Schumacher 1973). Because of these specialisations, the turtle skull does not provide a good model for the reconstruction of the jaw muscles of ichthyosaurs.

At first sight the crocodilian skull approaches the ichthyosaur skull in form. However, a typical crocodilian skull differs from the skull of Ophthalmosaurus in that it is dorso-ventrally flattened, the quadrates are strongly inclined, and the superior temporal fenestrae are relatively small in size. In typical crocodilians, the vertical jaw adductors, that is, the M. a. m. externus and posterior and the M. a. m. internus pseudotemporalis, are less important in adduction than is the M. a. m. internus pterygoideus which has a more horizontal action. This is correlated with the relatively small size of the superior temporal fenestrae and the very large lateral descending flanges of the pterygoids from which originate the horizontal adductors.

The skull of Ophthalmosaurus shows more similarity with ichthyophagous crocodile taxa, such as Gavialis and Tomistoma, which have elongate, slender snouts, relatively large superior temporal fenestrae and relatively short lateral descending pterygoid flanges. Langston (1973) suggests that the large superior temporal fenestrae, and hence the more important vertical jaw adductors seen in longirostrine crocodiles, are correlated with the development of a quick-snapping bite with strong holding power for use when feeding on active prey in water. It appears that the skull of Ophthalmosaurus displays similar adaptations, and for this reason the longirostrine crocodile skull provides a reasonable model for the reconstruction of the adductor muscles of Ophthalmosaurus.

The skulls of generalised members of the Lacertilia have relatively large superior temporal fenestrae and the M. a. m. externus and posterior and the M. a. m. internus pseudotemporalis are more important adductors than is the M. a. m. internus pterygoideus. In addition, lizard skills are generally less flattened and have larger orbits than those of crocodiles, and for these reasons it is thought that the lizard skull makes a good model for the reconstruction of the adductor muscles of Ophthalmosaurus.

Evidence for the possible sites of attachment of the jaw adductors was noted in the descriptive section on Ophthalmosaurus. This evidence has been used in a comparison with the skulls of lizards and crocodiles (Haas 1973, Schumacher 1973) in order to produce the following reconstruction of the jaw adductor and abductor muscles of Ophthalmosaurus. Figure 49 shows this reconstruction.

1. M. a. m. externus

In living lizards (Haas 1973) this muscle originates from bones surrounding the superior temporal fenestra. The three component parts of this muscle, when separable, have slightly different origins: the M. a. m. externus superficialis takes origin from the posterior part of the temporal arch, and from the dorsal end of the quadrate. The M. a. m. externus medialis may fill most, or only the posterior part of the superior temporal fenestra, originating from the parietal and the posterior half of the squamosal and supratemporal. The M. a. m. externus profundus is the deepest layer, lying next to the braincase; it may take origin from the prootic and quadrate and the parietal.

In crocodiles, the M. a. m. externus is not clearly subdivided (Schumacher 1973), and many of its fibres do not attach directly to the skull roofing bones, but instead originate from the cranial adductor tendon which is connected to the ventral skull roof and the descending process of the quadrate. In Ophthalmosaurus there is no evidence of a strong ridge on the ventral skull roof to which such a tendon would attach (as in crocodiles), and so it seems more likely that the M. a. m. externus had a more direct origin from the bones surrounding the temporal opening, as in lizards.

In Ophthalmosaurus, the dorsal edge of the lateral ramus of the squamosal bears markings which may indicate the origin of the Mm. a. m. externus medialis and superficialis - though separate attachment areas for these slips cannot be distinguished. It is likely that these slips also attached to the posterior and mesial aspects of the squamosal, in the border of the temporal opening, and to the parietal, though markings are not present. The ventral ridge on the postfrontal may have offered an additional surface for the origin of these muscle slips.

The mesial lamina of the squamosal, which folds round the anterior edge of the quadrate, bears markings which may mark the origin of the M. a. m. externus profundus. As noted in the descriptive section, markings on the dorsal, internal surface of the quadrate, on the prootic and on the anterior surface of the opisthotic may mark the attachment of the M. a. m. externus profundus division.

In living lizards and crocodiles, the M. a. m. externus inserts onto the dorsal edge of the surangular, posterior to the coronoid process. In lizards this attachment is largely via a tendon or aponeurotic sheet referred to as the basal aponeurosis. The surangular of Ophthalmosaurus possesses a well-developed lateral projection referred to above as the surangular peak, and this may have been the site of a similar tendinous insertion.

2. M. a. m. internus

In the majority of lizards the M. a. m. internus pseudotemporalis is subdivided into a superior and a deep portion. The superior portion of the muscle originates from the antero-lateral surface and the descending lateral surface of the parietal, and it fills the anterior half of the superior temporal fenestra.

The deep portion arises from the epipterygoid. The M. a. m. internus pseudotemporalis may partly insert on the basal aponeurosis, and partly on the coronoid process.

In crocodiles this muscle has a similar origin and insertion to that of lizards (Schumacher 1973).

The dorsal and lateral surface of the parietal of *Ophthalmosaurus* is not scarred, but it is assumed the M. a. m. internus pseudotemporalis took origin from the extensive bony surface here. It presumably inserted onto the coronoid process as in lizards.

The M. a. m. internus pterygoideus of lizards is generally subdivided into dorsal and ventral parts. The dorsal portion may take origin from both dorsal and ventral surfaces of the pterygoid, and it inserts on the ventro-medial surface of the surangular, behind the jaw articulation. The more superficial ventral portion originates mainly from the dorsal aspects of the pterygoid; it wraps around the ventral edge of the retroarticular process to insert on the lateral surface of the surangular, thus forming the "masticatory cushion" which is exposed in lateral view.

The M. a. m. internus pterygoideus of crocodiles has a similar origin and insertion to that of lizards, but the muscle is much more strongly developed, and the areas for its attachment on the pterygoid are extensive. The pterygoid of *Ophthalmosaurus* does not possess large descending lateral flanges for the origin of this muscle and it is concluded that the M. a. m. internus pterygoideus of *Ophthalmosaurus* resembled more the condition of this muscle in lizards.

The dorsal surface of the pterygoid of *Ophthalmosaurus* bears no obvious scarring, but the M. a. m. internus pterygoideus may have had a fleshy attachment over this surface and to a ridge on the mesial edge of the bone. The ventral surface of the bone possesses a rounded depression which may mark points of origin of the muscle.

The M. a. m. internus pterygoideus of Ophthalmosaurus presumably inserted on the lateral surface of the retroarticular process, though no distinct markings were observed. The mesial surfaces of the prearticular and angular bones are distinctly roughened, and it may be that slips from the dorsal portion of the muscle inserted here.

3. M. a. m. posterior

This muscle in living lizards originates from the anterior surface of the quadrate and inserts well posteriorly onto the walls of the adductor fossa.

In crocodiles the M. a. m. posterior is fused to the M. a. m. externus (Schumacher 1973) and, indeed, in lizards the M. a. m. posterior is not always clearly definable (Haas 1973).

The quadrate of Ophthalmosaurus bears a central depression on its anterior face which may mark the origin of the M. a. m. posterior. It is likely that this muscle inserted onto the cartilage lining the walls of the adductor fossa, and no clear markings are detectable on the bones themselves.

4. The Jaw Abductor Muscle: The M. depressor mandibulae

In living lizards and crocodiles, this muscle takes origin from the dorsal occipital surface and inserts on the retroarticular process.

The posterior corner of the squamosal of Ophthalmosaurus bears a prominent tubercle, or in some cases a pair of tubercles. The bone surface surrounding these tubercles is roughened. These markings are taken as evidence for the origin here of the M. depressor mandibulae. The muscle presumably inserted onto the retroarticular process, which is composed of the surangular and angular bones, though presumably a cartilaginous cap extended the process and increased the surface area for attachment of this muscle.

The reconstruction presented here and figured in figure 49 does not differ greatly from that given by McGowan (1973a) for the genus Ichthyosaurus.

II Reconstruction of the Brain of Ophthalmosaurus (figure 13)

Hopson (1979) reviews the various pitfalls involved in the interpretation of fossil reptile endocasts. It is known that amongst living reptiles the degree to which the endocast reveals the size and shape of the brain varies considerably. A number of factors influence the shape of the endocast, for example, the thickness of the dural envelope, the degree of development of intradural venous sinuses and the extent to which cartilage contributed to the braincase. Therefore caution must be used in the interpretation of the cranial impressions noted in the descriptive section on Ophthalmosaurus, particularly since there is no known closely related living model for comparison. The following interpretation of the brain of Ophthalmosaurus is then to be viewed with a certain amount of caution.

Much of the braincase remained unossified in Ophthalmosaurus, and in Jurassic ichthyosaurs generally, a feature which is probably correlated with their aquatic nature. However, the ventral surface of the skull roof bears a number of encephalic impressions, and these, together with the ossification in the basisphenoid, basioccipital and supraoccipital, give some indication of the flexure and relative proportions of the brain. The following reconstruction of the brain of Ophthalmosaurus agrees largely with that given by McGowan (1973a) for Ichthyosaurus.

1. Flexure

Two features of the skull of Ophthalmosaurus suggest that the brain underwent a certain degree of compaction and flexure. First, the nerve cord entered the skull at a steep angle directed antero-ventrally. This is the result of a strong arching of the cervical and mid-dorsal region of the vertebral column. The occiput then faces postero-dorsally and the floor of the foramen magnum (on the basioccipital) slopes antero-ventrally. The skull can be oriented horizontally by reference to the horizontal semicircular canal. The nerve cord can then be seen to enter the foramen magnum from above at an angle of about 40° to the horizontal.

The second feature to suggest the brain underwent flexure is the large size of the orbits and the extreme shortening of the temporal region. In recent reptiles, enlarged orbits have the effect of "crowding" the brain backwards (Stark 1979).

Both these features would introduce compaction and flexure to the brain. The first feature would emphasize pontine flexure (between the metencephalon and myelencephalon of the hindbrain) and the second would emphasise cephalic flexure (between the forebrain and midbrain) (Hopson 1979).

2. Hindbrain (Myelencephalon and Metencephalon)

The anteriormost part of the floor of the foramen magnum (figure 1) probably accommodated the medulla oblongata. At about this level the vagus foramen opens as a notch in the front border of the exoccipital. This probably allowed exit for nerves IX, X and possibly XI. Immediately posterior to this nerve XII exits by two separate foramina in the exoccipital.

Anterior to the basioccipital the floor of the hindbrain would have been continued onto the basisphenoid (figure 2), though deep pitting of the dorsal surface of this bone suggests that the brain was not closely applied to the bone surface. The exits for nerves V, VI and VIII are not represented on the ossified remains of the braincase, but nerve VII may have exited from the anterior edge of the otic capsule between the opisthotic and stapes (see description of the stapes).

Dorsally the cerebellum of the metencephalon would have been roofed by the supraoccipital bone which is inclined anterodorsally and extends beneath the posterior shelf of the parietal. In the majority of living reptiles the cerebellum does not leave a clear impression on the braincase because it is normally overlain by the longitudinal venous sinus (Hopson 1979). There is evidence for the presence of a substantial venous sinus beneath the supraoccipital of Ophthalmosaurus: the major portion of the arch of the supraoccipital may have allowed exit for veins from this sinus, and the foramina in the supraoccipital may have served a similar function (see descriptive section). McGowan (1973a) suggested that the cerebellum of Ichthyosaurus was a large structure, and that this would be expected in reptiles adapted for movement in an aquatic medium. He based this conclusion on the size of the encephalic impression on the supraoccipital and the posterior shelf of the parietal (this latter shelf is actually extracranial - the shelf being underlapped by the supraoccipital bone). I would suggest that it is impossible to make a reliable estimate of the size of the cerebellum in these two ichthyosaur genera, because the extent of the venous sinus is unknown and because of a general lack of ossification of the sides of the braincase in this region.

The ascending dorsum sellae is at the level of the transition between the hindbrain and midbrain. At this level the pontine flexure of the brain would cause the midbrain to lie obliquely in the skull.

3. Midbrain (Mesencephalon)

The reptilian mesencephalon is not normally represented on the endocast because the optic tecta are partially overlapped by the cerebral hemispheres (Stark 1979), and are often covered by a very thick dural envelope. The longitudinal venous sinus and its branches may also further obscure it (Hopson 1979).

However, the optic lobes do become exposed on the dorsal surface of the brain in macrophthalmic species (Stark 1979), and under these circumstances they may be represented on the endocast. Endocasts of pterosaurs, for example, show prominent optic lobes (Hopson 1979).

It is not, therefore, surprising to find impressions on the ventral skull roof of Ophthalmosaurus which may be interpreted as having been formed by the optic lobes. These are a pair of rounded posterior impressions on the parietal, at the same transverse level as the dorsum sellae. That they are not impressions of the cerebral hemisphere of the telencephalon of the forebrain is evident from the fact that a second anterior impression on the parietal is more likely to have accommodated the cerebrum. Furthermore, the paired impressions are placed far behind the parietal foramen, which accommodated an outgrowth from the forebrain in the region behind the cerebrum. It appears, then, that the optic lobes of Ophthalmosaurus, and of Ichthyosaurus (McGowan 1973a) were unusually large. This is additional evidence that sight played an important role in the life of these forms.

4. Forebrain (Diencephalon and Telencephalon)

Projecting ventrally from the diencephalon is the pituitary body which lay in the pituitary fossa of the basisphenoid. However, it is unlikely that the fossa in the basisphenoid accurately reflects the size of the pituitary since, in living reptiles, arteries, venous sinuses and frequently extrinsic eye muscles also occupy the fossa (Hopson 1979).

From the same region of the reptilian diencephalon is developed a dorsal outgrowth, the parietal eye/pineal complex (Quay 1979). The evidence remaining for the presence of this structure in Ophthalmosaurus is the parietal foramen which is developed at the junction between the frontal and parietal bones.

The cerebral hemispheres have left elongate,median impressions on the ventral surface of the parietals,which appear to be continuous with similar impressions on the frontals (figure 13). The parietal foramen is positioned quite far forwards in the skull, and the cerebral hemispheres appear to extend behind it. This may at first seem anomalous, but Quay (1979) has shown that in living reptiles an anterior shift of the parietal foramen occurs when the forebrain becomes inclined, usually as a result of a particularly large orbit. This seems the most likely explanation for this condition in Ophthalmosaurus and other ichthyosaurs.

The olfactory lobes of the telencephalon appear to have left clear rounded impressions on the ventral surface of the nasal bones, which are continuous with impressions on the medial side of the orbital ridge of the prefrontal (figure 13). The impressions also appear to continue onto the frontal bones, and parietal bone, lying lateral to the cerebral impressions. The lateral anterior impression on the parietal may therefore mark the posterior limit of the olfactory lobes,which appear to flank the cerebrum in this region.

If the olfactory lobes have been correctly identified, it appears that they are large relative to the cerebral impressions, and that the brain endocast was wider across this region than across the cerebrum. This would agree with the findings of Hopson (1979) who points out that the cerebrum of many fossil reptiles is relatively narrow, possibly because of the small size of the dorsal ventricular ridge.

McGowan (1973a) found that the olfactory lobes of Ichthyosaurus did not extend further anteriorly than the frontal bones. If this is the case, then it appears that the olfactory lobes of Ophthalmosaurus were more extensive than those of this latter genus.

5. Otic Capsule

The otic capsule is ossified from centres in the supraoccipital, opisthotic and prootic. Ossification is incomplete so that none of these bones has direct bony contact with the others, and the walls would have been completed in cartilage. Despite this problem the capsule can be reconstructed with reasonable confidence (see figure 7). The orientation of the supraoccipital is easily determined since it has close contact with the exoccipitals, which articulate closely with the basioccipital. The opisthotic, similarly, can be oriented with reference to the stapes below it. The prootic can then be oriented by finding the "best fit" position from the clearly marked impressions on it of the horizontal and anterior vertical semicircular canals. As shown in the descriptive section, impressions of the anterior and posterior vertical semicircular canals, the common crus, the horizontal semicircular canal and the ampullae of the anterior vertical and posterior vertical canals are distinguishable in the ossified capsule walls, allowing a reasonably accurate reconstruction of the osseous labyrinth. Less information is available, however, on the form of the ventral region of the osseous labyrinth - the cochlear recess. A small impression on the basioccipital may represent a part of the cochlear recess. If so, it appears that the cochlear recess was positioned ventral and slightly posterior to the semicircular canals. The head of the stapes is positioned largely ventral to the region of the cochlear duct, and only a small part of the stapes head could have had any contact with this region. The greatest part of the stapes head abutted against the basioccipital and basisphenoid bones.

III Sight, Olfaction and Hearing in Ophthalmosaurus

The orbit of Ophthalmosaurus is extremely large amongst known reptiles, and it is the second largest amongst the Ichthyopterygia (Shonisaurus (Camp 1980) possesses the largest eye amongst ichthyosaurs.) It can be inferred from the large orbit, with boundaries well-defined by the prefrontal and postorbital bones, that the eye of Ophthalmosaurus was also relatively large amongst reptiles (Underwood 1970), and hence it is likely that sight was of fundamental importance to the life and habits of this genus. The optic lobes of the brain are also interpreted as being unusually large, adding further evidence for the importance of sight.

In the descriptive section it was noted that the sclerotic ring of Ophthalmosaurus was markedly domed and showed no apparent inflection at the rim of the central aperture. These features suggest that the ring lacked a prominent scleral sulcus (Underwood 1970).

Amongst living reptiles the marine turtles characteristically lack a scleral sulcus. This owes to the loss of importance of the cornea as a refracting surface in these forms, as a result of adaptation to almost exclusively underwater vision (Underwood 1970). If the interpretation of the sclerotic ring of Ophthalmosaurus is correct, then this would indicate that the eye was adapted primarily for underwater vision. McGowan (1973a) reached a similar conclusion for the eye of Ichthyosaurus.

The sclerotic aperture of Ophthalmosaurus was shown in the descriptive section to be relatively large amongst reptiles. The ratio of the internal diameter to the external diameter of the sclerotic ring was calculated to be approximately 0.4. Underwood (1970) finds that a ratio larger than 0.33 indicates a relatively large cornea which, in itself, would tend to reduce the scleral sulcus. A large cornea and pupil aperture are seen in living reptiles showing adaptations to vision in dim light. It would appear that the eye of Ophthalmosaurus was adapted for underwater vision in relatively low light intensities. A similar conclusion was reached by McGowan (1973a) for Ichthyosaurus.

The olfactory lobes of the brain, as reconstructed above, appear to be well-differentiated and relatively large, suggesting the sense of olfaction was fairly well-developed.

There is no development of a secondary palate in ichthyosaurs, unlike the condition in crocodiles and cetaceans, and in turtles (which possess an extended primary palate). The external naris of ichthyosaurs must have communicated directly with the buccal cavity. Presumably a laryngeal valve would prevent water entering the lungs from the buccal cavity, and under these conditions the external naris could remain open for olfactory sampling of the water.

The stapes of Ophthalmosaurus is a massive bone which is directed ventrolaterally, reaching between the braincase proximally and the quadrate distally. Further extensive contacts are made with the pterygoid and squamosal along the stapedial shaft. Some cartilage may have intervened at these latter points of contact, and pads of cartilage almost certainly intervened at the contacts with the quadrate and braincase.

There was apparently no conventional fenestra ovalis in Ophthalmosaurus, and only a small part of the stapes head can have come into close association with the perilymphatic cistern. The greater part of the head abutted against the basioccipital and basisphenoid. There is no evidence from the skull of Ophthalmosaurus for the presence of a tympanum.

Four of the five stapedial processes thought to be present on the primitive pretetrapod stapes can be identified in Ophthalmosaurus. These are the otic, dorsal, hyoid and quadrate processes. The stapes, then, in its proportions, orientation and form appears to resemble the primitive reptilian condition (Lombard and Bolt 1979). However, it is not known whether this resemblance is primitive or convergently derived, since the stapes of the most primitive ichthyosaurs is unknown, and the ancestry of the Ichthyopterygia is not known with any certainty.

The majority of living lizards have ears which are adapted for the perception of relatively high-frequency, air-borne sound impinging on a tympanic membrane . The stapes of these forms is a delicate rod which inserts in the fenestra ovalis and has a distal connection to the tympanic membrane . The stapes is relatively mobile with no firm attachments to surrounding structures.

In lizard genera with decreased sensitivity to air-borne sound, for example, the burrowing forms Holbrookia and Callisaurus and some amphisbaenians such as Anniella (Baird 1970), the stapes develops firm attachments to the quadrate or other bones, and there is enlargement of the footplate together with varying degrees of thickening of the tympanic membrane and reduction of the middle ear cavity.

The slender, mobile stapes and light tympanic membrane of forms perceiving air-borne sound function to match the acoustic impedance at the tympanic membrance with that of air in order that sound energy is effectively transmitted to the inner ear for its perception.

The impedance-matching function of the ear is less important for burrowing forms whose hearing depends increasingly on the reception of low-frequency substrate-borne vibrations, and the changes seen in the tympanum and middle ear of these forms are correlated with this.

As described, the stapes and middle ear of Ophthalmosaurus bears no resemblance to those of living reptiles which possess "aerial" ears, and it is clear that the ear would not function well for the reception of high-frequency air-borne sound.

The acoustic impedance of the periotic fluid is approximately the same as that of water, and so for an animal whose ears are adapted to function in an aquatic medium there are virtually no problems of impedance-matching. For this reason, the middle ear ossicles of whales are massive and the acoustic impedance of the tympanum and middle ear is high (Alexander 1968). It is possible, therefore, that the massive stapes of Ophthalmosaurus with its extensive bony connections was capable of transmitting water-borne sound waves to the inner ear.

An animal perceiving water-borne sound is faced with an additional problem of the localisation of the sound source. Directional hearing has been studied mainly in mammals, where it has been found that differences in intensity and in the time of arrival of sound at each ear are the cues for the detection of the direction of the sound source.

Sound travelling in air is largely reflected from the head surface so that a sound-shadow is cast by the head. The ear further from the sound source receives sound at a lower intensity than the nearer ear, and this gives information about the direction of the source. Longer wavelengths, however, can reach around the head to the further ear with little reduction in intensity, and under these conditions the later time of arrival of the sound at the further ear gives the cue for direction.

Sound travelling in water, which has virtually the same density as body tissue, is not reflected from the body surface and, instead, the sound is conducted, mainly through bone, to reach the further ear with virtually no loss of intensity. Presumably a difference in arrival time at each ear can still be detected, but nevertheless there is a marked reduction in the capacity for directional hearing unless the ears can be acoustically isolated from sound reaching them by conduction through the bones of the skull.

The otic capsule of whales is only loosely connected by ligaments to the rest of the braincase, and the capsule and middle ear are surrounded by cavities (evaginations of the tympanic cavity) which are filled with albuminous foam. The cavities themselves are surrounded by fatty or other connective tissue. In addition, the bone of the otic capsule is extremely dense, making it unlikely to resonate with the lighter bones of the skull. These features of the cetacean ear allow the operation of the extremely efficient directional hearing that is characteristic of the group (Slijper 1962).

The living crocodiles also show a certain degree of acoustic isolation of the inner ear. Many of the bones in the posterior region of the skull show extensive pneumatisation, being penetrated by branching canals which extend from the middle ear cavity (Iordansky 1973).

The otic capsule of Ophthalmosaurus appears to be an integral part of the braincase, despite the fact that cartilage intervened between its component bones and the rest of the braincase. There does not appear to be any evidence for its effective acoustic isolation.

The stapes has extensive attachments to the quadrate, squamosal and pterygoid, and was apparently not isolated from vibrations reaching it through these connections. It appears likely that sound could have reached the inner ear by conduction through various pathways in the skull bones, such as the squamosal-opisthotic pathway, the pterygoid-stapes and quadrate-stapes pathways and possibly the supraoccipital-skull roof pathway. The apparent lack of a tympanum suggests that sound was received by various bones in the surface of the skull and conducted to the inner ear by a variety of pathways. It therefore seems unlikely that Ophthalmosaurus possessed a well-developed capacity for perceiving the directionality of sound.

IV Structural Considerations of the Skull of Ophthalmosaurus

A notable feature of the skull of post-Triassic ichthyosaurs, and one which is well-demonstrated in the skull of Ophthalmosaurus, is the degree to which many of the bones of the skull roof overlap one another.

In the descriptive section, considerable overlapping was noted between the parietal, frontal, prefrontal and postfrontal, and also between the frontal, nasal and prefrontal. In the snout, both the maxilla and nasal are extensively overlapped by the premaxillae, so that the snout in cross-section has a tubular construction, with three layers of bone - the premaxillae externally, nasals and anterior extensions of the vomers forming the innermost layer.

A similar large number of overlapping joints between bones (known as scarf joints) is found repeatedly in various crocodilian taxa. Langston (1973) interprets these structural features as adaptions to strengthen the elongate crocodilian skull against longitudinal torsional and shearing stresses during feeding. In the slender-snouted fish-eating crocodiles such as Gavialis, the snout has taken on a tubular structure with no transverse sutures owing to a retreat posteriorly of the nasal bones. The snout of Ophthalmosaurus has a similar tubular structure, but the elimination of transverse sutures has been achieved by modifying the nasal-premaxillary suture to an extensively overlapping longitudinal joint.

The prefrontal, postorbital and postfrontal bones of Ophthalmosaurus display lateral flanges which together form a bony supraorbital shelf. Similar supraorbital shelves were developed in the extinct marine thalattosuchian crocodilians as outgrowths from the prefrontal bones. It is thought that these shelves protected the eye from sudden or fast movements in water (Langston 1973). In other crocodilians osteodermal eyelids carry out this function; osteoderms are lost repeatedly in the most highly aquatic crocodilians, and in the thalattosuchians the prefrontal bones took over their function of protection for the eye.

It is likely that the supraorbital shelves in Ophthalmosaurus served to protect the very large eye, as in thalattosuchians, and,as in this group, there is no evidence for the presence of osteoderms in ichthyosaurs.

V Skull Kinetism

The skulls of many reptiles display a certain amount of kinetism between skull components. Kinetism is extensively present throughout the Lacertilia, where an amphikinetic skull may be regarded as the typical saurian condition (Frazzetta 1962).

In the amphikinetic skull as many as five different kinds of movement can be detected. Kinesis may occur between the braincase and the rest of the skull (the maxillary segment), and this is termed metakinesis (Frazzetta 1962). Movement may also occur at various points within the maxillary segment : the quadrate may be freely movable, articulating dorsally with the squamosal and paroccipital process; this is termed streptostyly. The palate (or basal unit) may be movable relative to the skull roof and braincase, with kinesis occurring at the basipterygoid process and to a lesser extent at the union between the anterior palate and the maxilla. Mesokinesis refers to movement between the anterior part of the skull (or muzzle unit) and the parietals (or parietal unit). The movement here causes complementary movement between the muzzle unit and the basal unit. The epipterygoid bone often forms a movable link between the parietal unit and basal unit, with kinetic joints at its union with each unit.

In some burrowing forms, such as Anniella, the stapes is firmly attached to the quadrate, and so forms a structural part of the kinetic mechanism (Frazzetta 1962). The stapes of Ophthalmosaurus may also be considered as playing a structural part in skull kinesis.

In the descriptive section it was shown that the bones of the skull roof of Ophthalmosaurus were firmly united, often by extensive overlapping scarf joints. There was no evidence for the presence of mesokinesis. The quadrate is firmly held in a deep groove on the ventral surface of the squamosal. Extensive flanges from this latter bone spread down its posterior and anterior faces. In addition, the quadrate forms an extensive contact with the quadrate flange of the pterygoid. The nature of these extensive bony contacts makes it unlikely that the quadrate was movable relative to the parietal unit or palate.

The braincase of Ophthalmosaurus articulates with the rest of the skull at the distal end of the paroccipital processes, at the distal end of the stapes, at the basipterygoid processes, at the dorsal edge of the supraoccipital and at the parasphenoid rostrum. There is no fusion at any of these points even in large specimens. The surfaces for contact between the paroccipital process and squamosal, and between the stapes and quadrate, all show evidence for the presence of cartilage. The contact between the stapes shaft and the pterygoid and squamosal may also have been mediated by cartilage. The dorsal edge of the supraoccipital underlaps the posterior shelf of the parietal and was continued in cartilage which presumably met the cartilage of the braincase. It is possible that movement could occur at all these points of contact between the braincase and the rest of the skull. Anteriorly, the dermal parasphenoid is fused to the basisphenoid, and the parasphenoid rostrum extends in the midline between the pterygoids. It is quite possible that a sliding contact was present here.

It can be envisaged that the braincase of Ophthalmosaurus was capable of a rocking movement, with the paroccipital process and stapes both acting as axes for the rotation. The supraoccipital would then slide back and forth beneath the parietals. The paroccipital process is directed more laterally and slightly more posteriorly than is the stapes which lies more in a transverse plane, directed ventro-laterally (see figure 7). These differences may indicate that the paroccipital process could have acted as the major axis for rotation, with movement of a twisting nature at its distal end, whilst the stapes may have shown more of a sliding action along its own longitudinal axis. Movement of the braincase anteriorly would cause rotation at the basipterygoid processes, and also a sliding movement between the parasphenoid rostrum and pterygoids.

The possible advantage of such metakinesis in Ophthalmosaurus may have been its function as a shock-absorbing mechanism which protected the brain from damage during rapid and sudden jaw adduction in feeding.

The presence of a movable articulation between the basipterygoid processes and the palate raises the question of the possibility of movement of the palate relative to the braincase and the rest of the skull. In living Lacertilia this particular movement is brought about by the action of the muscles of the constrictor dorsalis group - the Mm. levator pterygoidei and protractor pterygoidei. For the palate to be free to move, its contacts with the muzzle unit anteriorly and with the quadrate posteriorly must show evidence of mobility. The pterygoid of Ophthalmosaurus is firmly held by both the squamosal and quadrate posteriorly, and it is unlikely that movement could occur here. Similarly the palatines form a complex interdigitating union with the maxilla, and the vomer unites with the premaxilla by extensively overlapping surfaces. It appears unlikely that movement could occur to any degree between the palate and the rest of the skull, and it is concluded that the movable basipterygoid articulation simply allowed kinesis of the braincase relative to the rest of the skull.

McGowan (1973a) reached the conclusion that the skull of Ichthyosaurus was probably akinetic; he did, however, note that the contacts between the braincase and the rest of the skull remained unfused, but nevertheless he dismissed the possibility of metakinesis.

VI Swimming

It is evident that in even the earliest ichthyosaurs the tail showed adaptations which reveal its primary function in generating forward thrust during swimming; in these forms there is evidence for the presence of a tailfin (Mazin 1980), though this probably did not possess a large epicaudal lobe. Skin impressions preserved on specimens of the Jurassic genus Stenopterygius show the tail of this genus to be shark-like in form, with well-developed epicaudal and hypocaudal lobes. McGowan (1973b), in a study of the functional morphology of the tail of Stenopterygius, suggested that the hypocaudal lobe, being supported by the down-turned vertebral column, was deflected less with each lateral tail movement than was the epicaudal lobe. This results in the forward propulsive thrust of the tail being accompanied by a net downward thrust which, together with downthrust at the centre of gravity, would counteract the upthrust at the centre of buoyancy and downthrust provided by the hydrofoils of the pectoral fins.

During lateral movements of the tail, the greater stiffness of the hypocaudal lobe would cause it to lag behind the epicaudal lobe with the result that rotation would occur at the tailbend. In the descriptive section it was noted that the tailbend centra of Ophthalmosaurus were procoelous so that they formed a ball and socket union. This arrangement would accommodate the rotation occurring at the tailbend.

McGowan (1972b,c) proposed that there were functionally two distinct types of ichthyosaur forefin. The first is a low aspect ratio (length/width ratio), broad-based fin (evidence from skin impressions) which McGowan suggests is used primarily as a hydroplane for stability and fine control during swimming. The second type is a slender, high aspect ratio, narrow-based forefin which McGowan suggests was used mainly for sculling (or subaqueous flying as was described by Robinson (1975) in a study of plesiosaur locomotion). The thrust produced by these fins augmented that produced by the tail.

It seems unlikely that there would be a clearcut distinction in function between the two types of fin or paddle. Probably all ichthyosaurs used their paddles to some extent as hydroplanes, and most ichthyosaurs, with the possible exception of Nannopterygius which had tiny limbs and girdles, probably were capable of making sculling movements with their forepaddles during slower swimming.

McGowan (1972b) considered the forepaddle of Ophthalmosaurus to be of the narrow-based sculling type. The present study has found that the forepaddle of Ophthalmosaurus resembles that of Stenopterygius, which is also considered to possess the sculling-type of paddle by McGowan. It is possible, however, that both genera used the forepaddle for sculling and also as a hydroplane.

APPENDIX

Catalogue of specimens referred to Ophthalmosaurus icenicus

The following specimens were catalogued by Andrews (1910) and are part of the Leeds Collection housed in the B.M.N.H. The Leeds no. refers to the catalogue numbers given to the specimens by Alfred Leeds. Unfortunately this catalogue is now missing (A.C. Milner, personal communication).

Diagnostic material

R2180 (Leeds no. 76) figd. Andrews (1910 Text figs. 7, 8c, 10, 11, 12, 13, 17, 20, 22, 29, 31AB).

R2181 (Leeds no. 66) figd. Andrews (1910 Plate 1, figs. 7, 8).

R2740 figd. Andrews (1910 Plate 1, figs. 9, 10).

R2160 (Leeds no. 65) figd. Andrews (1910 Text fig. 36D)

R2853 (Leeds no. 85) figd. Andrews (1910 Text fig. 37, 38, 39ABC)

R2149 (Leeds no. 70)

R2138 (Leeds no. 64)

R3013 (Leeds no. 91) figd. Andrews (1910 Plate 1, figs. 1 - 6)

R2185

R2155

R2132 (Leeds no. 61)

R2150, 2150a (Leeds no. 77) figd. Andrews (1910 Text fig. 24AB)

R2152 figd. Andrews (1910 Text fig. 24EF)

R2173 (Leeds no. 56)

R2135 (Leeds no. 71) figd. Andrews (1910 Text fig. 25)

R2137 (Leeds no. 63) figd. Seeley (1893, fig. 1)
figd. Andrews (1910 Text figs. 30, 31CD, 32, 33AB, 34, 35)

R2147 (Leeds no. 68)

R2134 figd. Seeley (1874 Plate XLVI, fig. 3)
figd. Andrews (1910 Text fig. 36ABC)

R3533 figd. Andrews (1910 Text fig. 19)

R3535 figd. Andrews (1910 Text fig. 15)

R3534 figd. Andrews (1910 Text fig. 27)

Material which is not diagnostic, but which is referred to the species on basis of agreement in form of the bones:

R2162 (Leeds no. 31) figd. Andrews (1910 Text figs. 1, 2, 3C-F, 5, 14)

R2161 (Leeds no. 90) figd. Andrews (1910 Text figs. 3AB, 6B)

R2191

R2153

R2143 (Leeds no. 82)

R2174

R2163

R2188

R2148 (Leeds no. 69)

R2141

R2157 (Leeds no. 29)

R2139 (Leeds no. 73)

R2164 figd. Andrews (1910 Text fig. 6A)

R2175 figd. Andrews (1910 Text fig. 24CD)

R2169 (Leeds no. 80) figd. Andrews (1910 Text fig. 28)

The following specimens, now in the BMNH, were catalogued by Neaverson (1922) and are part of the Leeds collection, but were originally housed in the Geological Collections of the University of Liverpool. The catalogue numbers are those of that institution.

Diagnostic material

4530

4531

Material which is non-diagnostic, but which agrees in form with the species, and is thus tentatively referred to it:

4521

4522

4523

4524

4525

4526

4527

4528

4529

The following specimens are part of the Leeds Collection in the BMNH, but were not catalogued by Andrews (1910).

Diagnostic material:

R2856 a humerus, with radius and ulna cemented to it by hardened matrix.

R2186 a humerus, radius, ulna and pre-axial accessory ossicle.

R3702 two almost complete forepaddles (right and left). The radius, ulna and intermedium are cemented in the right paddle which comprises 53 other paddle bones. Accompanying the specimen was a pencilled diagram by Alfred Leeds showing a plan of the paddle. Figd. Andrews (1910 Plate 11, figs. 1, 4).

R3893 an almost complete skeleton including a dorso-ventrally compressed, articulated skull, pectoral girdle and forepaddles, pelvic girdle and femora, vertebral column comprising 66 centra and some neural arches - the posterior caudal region is missing, numerous ribs. The bones of the occiput, sclerotic rings, vertebral column, ribs, pectoral girdle and limbs and femora are now part of the mounted skeleton of *O. icenicus* on exhibit in the BMNH. The right puboischium of this specimen is deformed.

R3894 premaxilla, vomer, vertebral centra, neural arches, coracoids, scapulae, humeri of a young individual.

R4752 left forepaddle, some of the proximal elements are cemented to the humerus.

R4753 Incomplete skeleton of a large individual comprising disarticulated, near-complete skull and mandible, sclerotic rings, hyoid apparatus, 48 vertebral centra, neural arches, numerous rib fragments, complete pectoral girdle, humeri, paddle bones, femora, puboischia.

Non-diagnostic, but tentatively referred material:

R2140 scapula

R2154 sclerotic ring

R2172 single paddle bone

R2146 figd. Andrews (1910 Text figs. 8AB, 16) vertebral centra, squamosal and other skull bones.

R4124 58 caudal vertebrae, now part of the mounted skeleton of O. icenicus in main gallery, BMNH.

R4399 basioccipital, cut in half, cut sides polished.

R4693-5 hindpaddle, sclerotic plates, puboischium, palatine. figd. Andrews (1910 Text figs. 18, 41)

R4754 puboischium, unusual in that pubis and ischium fail to fuse ventrally.

R4755 small clavicle, poor preservation.

The following material in the BMNH is diagnostic, and is derived from the Oxford Clay, but is not part of the Leeds collection:

R6217 humerus and paddle bones.

The following material in the BMNH is diagnostic and is derived from the Kimmeridge Clay:

42283 left humerus showing 3 distal facets, catalogued by Lydekker (1889a) as *Ichthyosaurus trigonus*. Kimmeridge Clay of Isle of Portland.

47885 left humerus, catalogued by Lydekker (1889a), Kimmeridge (?) Clay, Oxford district.

46474 crushed right humerus, catalogued by Lydekker (1889a), Kimmeridge (?) Clay, Wiltshire (?).

Material in the Hunterian Museum, Glasgow, not recorded in any previously published catalogue. Leeds Collection, Oxford Clay, Peterborough district.

Diagnostic material:

V1049-1059 (Leeds no. 40?) Three skull bones, teeth, vertebral centra, 2 coracoids, scapula, interclavicle, clavicle and forelimb of a small individual.

V1063 ilia, ischiopubis, femur.

N.B.: preservation of the bones suggests they may belong to V1049-59. (The Hunterian Museum Leeds Collection remained in packing cases from 1917-1966, after this length of time information was lacking as to which bones belonged to specific individuals. Drs. K. Ingram and I. Rolfe had to infer that bones packed together belonged to the same individual.)

V1070 large, incomplete and poorly preserved skeleton which has previously been mounted on display.

V1080 right forepaddle.

V1129 Very well preserved disarticulated bones of the skull and mandible of a moderately large individual. Almost every skull bone is represented;left prefrontal, figd. Andrews (1910 Plate 11, figs. 2, 2a).

V1611 (Leeds no. 73) 72 vertebral centra, 7 neural spines, disarticulated skull and mandible, scapula, rib fragments of a small individual.

V1711 (Leeds no. 132) 6 trunk centra, scapula, femora, left humerus, 12 paddle bones of a small individual.

V1857 humerus of a large individual.

V1859 quadrates, basioccipital, 54 centra, humeri, phalange and 2 articulars of a medium-sized individual.

V1863 humerus.

V1868 (Leeds no. 82) occipital bones, 102 poorly preserved centra, humerus, radius, ulna, radiale, intermedium, ulnare, phalanges, femur, fibula of a moderately large individual.

V1871 (Leeds no. 80) skull bone fragments, 73 centra, coracoids, scapula, puboischium, ilium, humeri, paddle bones, femur, of a small individual.

V1869 (Leeds no. 72) 58 centra, occipital bones, humeri of a moderately large individual.

V1873 (Leeds no. 81) atlas/axis, 66 centra, coracoids, scapula, humerus, phalanges.

V1875 skull fragments, atlas/axis, 76 centra, coracoids, scapulae, humeri, epipodials, carpus and phalanges, femur.

V1876 humerus and 13 paddle bones of a large individual.

V1887 humerus, epipodials, carpus and phalanges of a large individual.

V1888 (Leeds no. 78) occipital bones, ischiopubis, clavicle, interclavicle, coracoids, scapulae, humeri and paddle bones, femur, tibia.

V1889 (Leeds no. 178) prootic, atlas/axis, 27 centra, scapula, coracoid, clavicle, humerus, femur and paddle bones.

V1891 2 incomplete forepaddles.

V1893	basioccipital, exoccipital, articular, 2 stapes, 2 surangulars, 2 angulars, parietal, 36 teeth, neural arches, 2 forepaddles of a large individual.
V1894	16 centra, 19 neural arches, coracoid, 2 humeri, ulnae, intermedia, radii, 28 phalanges of a large individual.
V1897	2 incomplete forepaddles.
V1898	(Leeds no. 135) basioccipital, articular, atlas/axis, ischiopubis, humerus, paddle bones, 2 femora and paddle bones of a large individual.
V1899	quadrates, articulars, 5 caudal ribs, 2 ilia, clavicle, 2 humeri, 35 paddle bones of a large individual.
V1900	stapes, quadrate, articular, hyoid, 11 centra, 2 incomplete forepaddles, and 1 femur.
V1902	1 humerus, epipodials, carpus and 8 other paddle bones of a large individual.
V1904	humerus, radius, 11 paddle bones.
V1905	(Leeds no. 139) humerus, epipodials, paddle bones of a large individual.
V1907	1 mounted forelimb.
V1908	1 humerus.
V1915	1 small humerus.
V1923	2 humeri, radius, ulna, 2 pre-axial accessory ossicles, 4 paddle bones, 1 tibia.
V1924	mounted forepaddle, large individual, incomplete.
V1926	basioccipital, 9 cervical centra, 2 small humeri.

Material in the Leicester Museum, collected from the Oxford Clay, Peterborough district. Catalogued by Appleby (1958):

Diagnostic material:

100'1949/17

100'1949/21

100'1949/28

100'1949/36

100'1949/204

100'1949/223 figd. Appleby (1958, plate V)

The following specimens are non-diagnostic, but are tentatively referred to *O. icenicus* and were figured by Appleby:

100'1949/39	figd. Appleby (1956 fig. 14) (1961 figs, 5,7)
100'1949/45	figd. Appleby (1956 fig. 3) (1961 fig. 26)
100'1949/50	figd. Appleby (1956 fig. 21) (1958 Plates II, III)
100'1949/64	figd. Appleby (1956 figs. 2, 4, 5, 6, 12, Plate 3, fig. 2, also basis of figs. 14, 21) (1958 basis of Plates II, III) (1961 fig. 1b, basis of figs. 5, 6, 7)
100'1949/79	figd. Appleby (1956 basis of fig. 21) (1958 basis of Plates II and III) (1961 basis of figs. 6, 7)
100'1949/198	figd. Appleby (1956 basis of figs. 14a, 21) (1958 basis of Plate III) (1961 basis of figs. 6, 7)

Material in the Peterborough Museum, Oxford Clay, Peterborough district. Catalogued by Appleby (1958) and Cross (1975). Appleby's (1958) catalogue numbers are cited in brackets following Peterborough Museum's new catalogue numbers.

Diagnostic material:

R35

R190

R220 (P8) figd. Appleby (1956 fig. 1, 4A, 11, 13, 17, 18, Plates 1, 2 fig. 2) (1958 Plate I and basis of plate III) (1961 fig. 11b) cited by Appleby as type of O. monocharactus.

R15, 43, 93, 221 (P9) one individual

R67, 96, 223 (P11) more than one individual, figd. Appleby (1956 fig. 8)

R217 (P3) figd. Appleby (1958 Plate VII)

(P6) figd. Appleby (1958 Plate IV)

(P7) figd. Appleby (1956 Plate 3, fig. 1)

R214, R224 (P12) more than one individual

R95, 225 (P14)

R227 (P17)

R228 (P18)

R94, R229 (P20)

R232 (P23)

(P26) Leicester Museum's transferred specimen no. 418'1956/78.

(P27) Leicester Museum's transferred specimen no. 418'1956/68.

Material in the Oxford University Museum not previously cited in a published catalogue:

Diagnostic material:

J899 2 humeri from the Kimmeridge Clay of the Oxford district.

Material in the Sedgwick Museum, Cambridge: from the Oxford Clay, Peterborough district.

Diagnostic material:

J66699 - 746 coracoids, scapulae, vertebral centra, incomplete fore-

	paddles.
6.7 - 6.13	catalogued by Seeley (1869) as *Ichthyosaurus megalodeirus*. A moderately large specimen consisting of disarticulated bones of the skull and mandible, ribs, scapulae, femora, left humerus, coracoids, hyoid, paddle bones, atlas/axis, 95 centra.
J63920- J64036	incomplete skull, coracoid, humeri, paddle bones, 122 centra.
J64037- J64117	skull bones, 74 centra, 2 humeri, paddle bones, femur, scapula.
J65451 & J65452	2 isolated humeri.

From the Kimmeridge Clay:

J29796	isolated humerus; no locality given.

Material in the Manchester Museum. Leeds Collection material from the Oxford Clay of the Peterborough district, sold to Manchester Museum by the BMNH in 1912.

Diagnostic material:

L10311c	2 right humeri, 2 ulnae.
L10311a	right humerus.
L10306	under this number are numerous disarticulated skull bones and 3 small humeri.

Material in the National Museum of Wales, Cardiff. Leeds Collection, Oxford Clay, Peterborough district.

Diagnostic material:

19.96.G26.1	left humerus
19.96.G3	partial skeleton.

Material in the Dorset County Museum, Dorchester.

Diagnostic material:

G82	right humerus; figd. Mansell-pleydell (1890, fig. 3) as type of O. pleydelli.

LIST OF ABBREVIATIONS OF MUSEUM NAMES

B.M.N.H.	British Museum (Natural History), London
G.I.T.	Geologisches Institut Tübingen, Tübingen
H.M.	Hunterian Museum, Glasgow
L.M.	Leicester Museum and Art Gallery, Leicester
M.N.H.N.	Muséum national d'Histoire naturelle, Paris
O.U.M.	Oxford University Museum, Oxford
P.	City Museum and Art Gallery, Peterborough
S.M.	Sedgwick Museum, Cambridge

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Figure 1

Basioccipital of Ophthalmosaurus icenicus, B.M.N.H. R4522.

a) occipital, b) dorsal, c) anterior, d) lateral view.

Scale = 5 cm.

con = condylar surface; for = foramen magnum; f.ex = facet for exoccipitals; f.op = facet for opisthotic; f.st = facet for stapes; coch = cochlear recess; f.bsph = facet for basisphenoid; no = notch; not = notochordal pit.

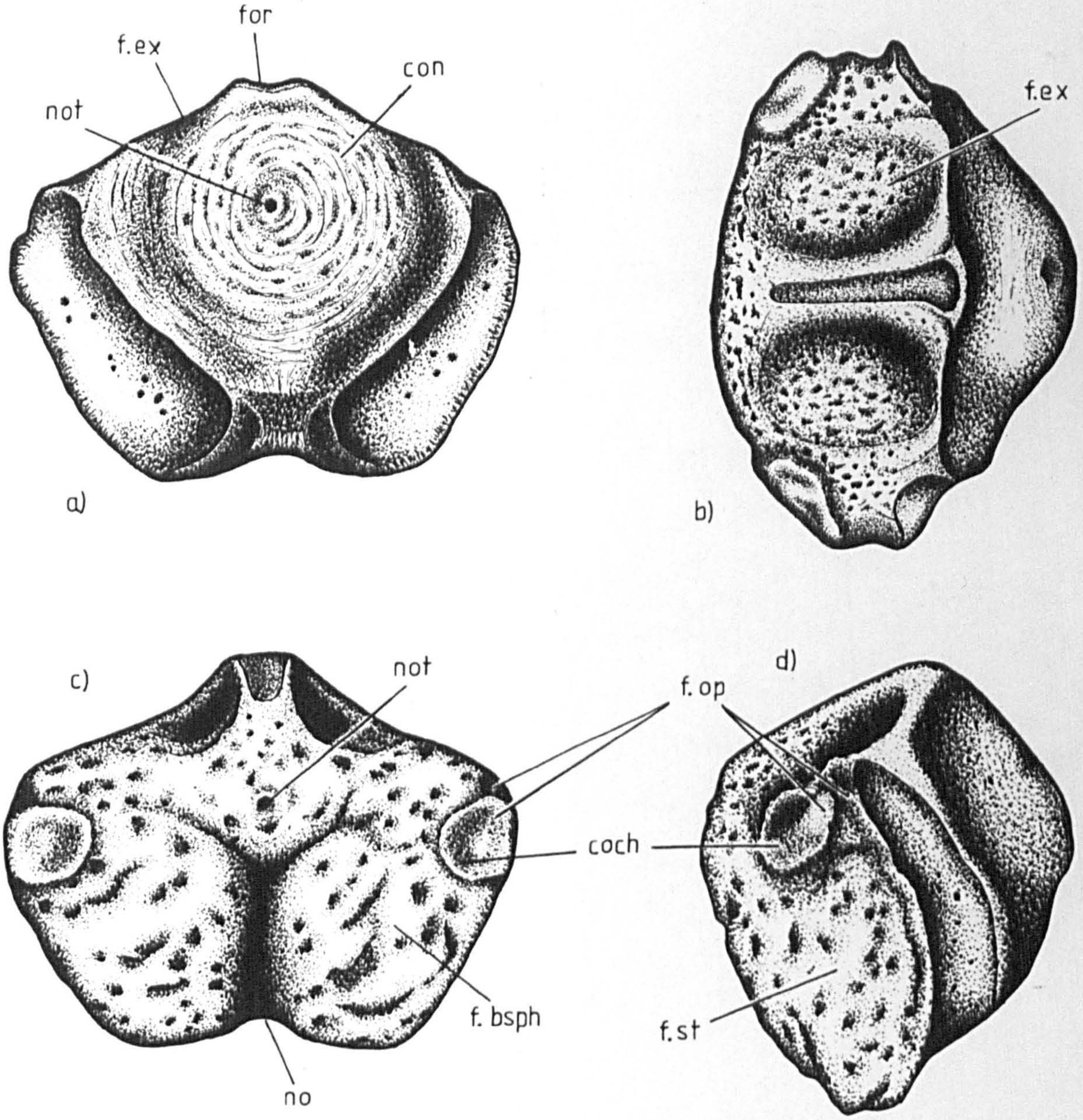

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Figure 2

Basisphenoid of Ophthalmosaurus icenicus, B.M.N.H. R4522.

a) lateral, b) anterior, c) ventral, d) dorsal view.

Scale = 5 cm.

b.pt.pr = basipterygoid process; c.for = carotid foramen; d.sell = dorsum sellae; e.m. = pit for origin of eye muscle; f.bocc = facet for basioccipital; f.pt = facet for pterygoid; f.st = facet for stapes; gr = median groove; no = notch marking anterior extremity of upturned notochord; pal = groove for palatine ramus of facial (VII) nerve; para = parasphenoid base; pit.foss = pituitary fossa; trab = impressions of trabecular cartilages.

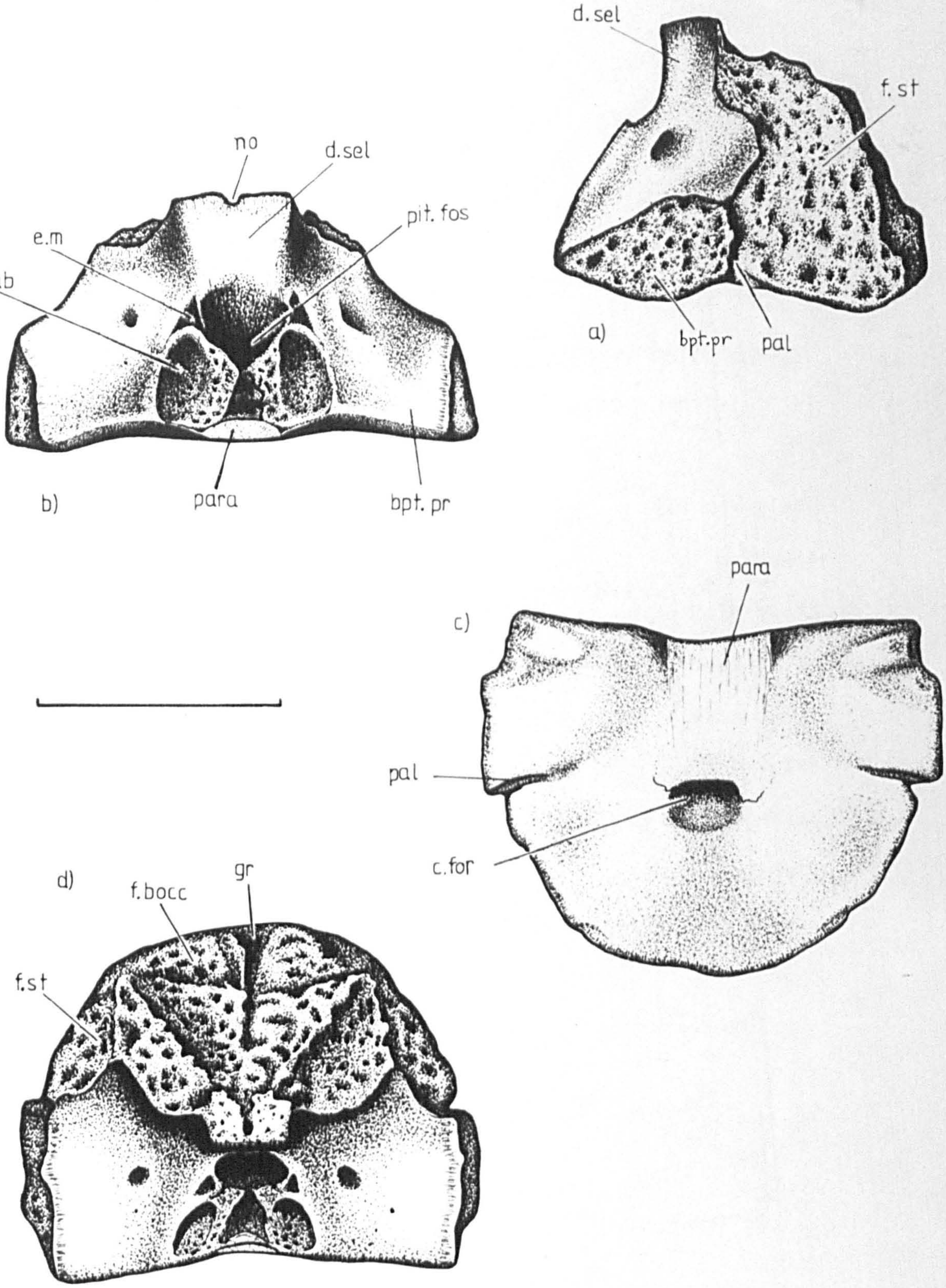
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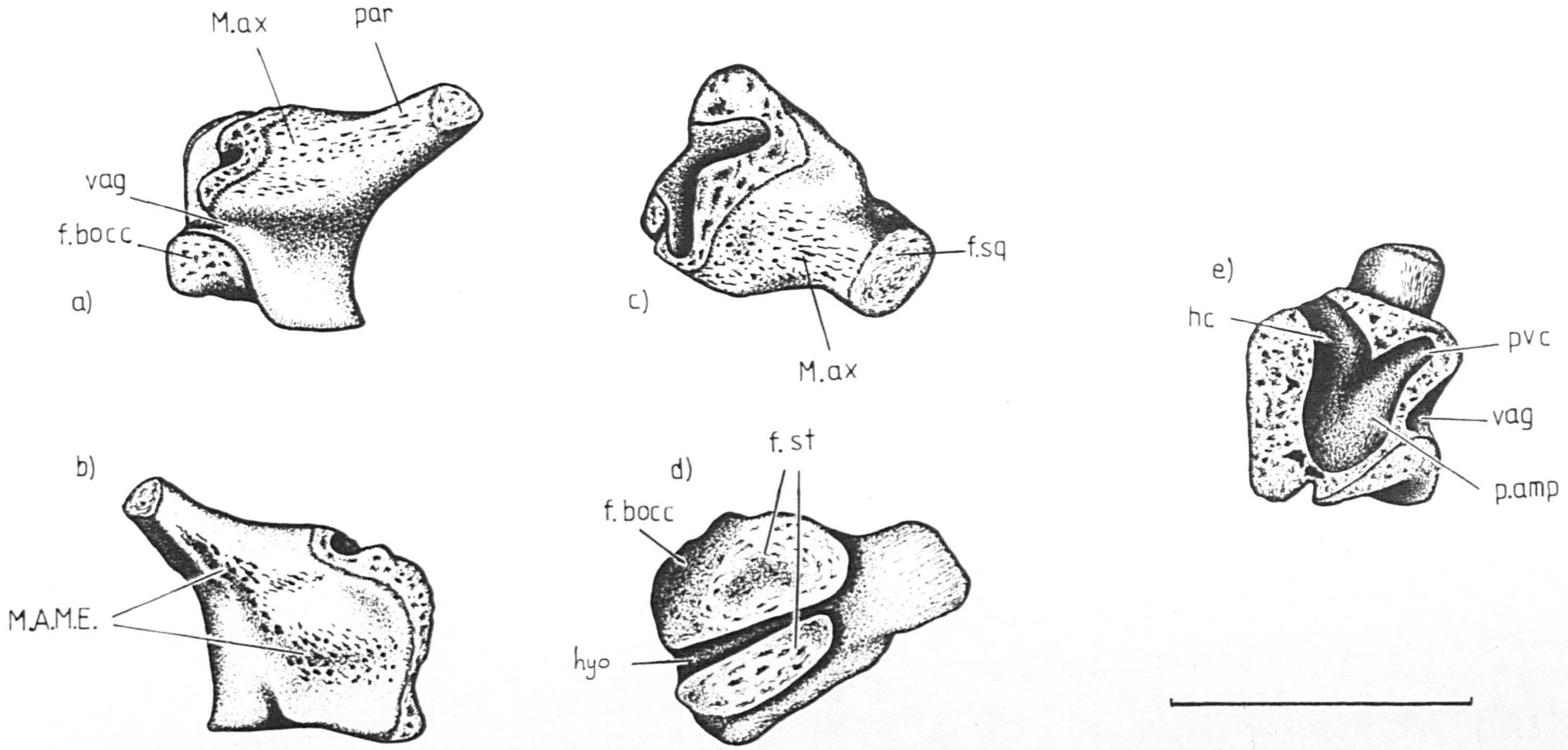
Figure 3

Opisthotic of Ophthalmosaurus icenicus, B.M.N.H. R4522.

a) posterior, b) anterior, c) dorsal, d) ventral, e) medial view.

Scale = 5 cm.

f.bocc = facet for basioccipital; f.sq = surface for articulation with squamosal; f.st = facet for stapes; h.c. = impression of the horizontal semicircular canal; hyo = groove for exit of hyomandibular branch of facial (VII) nerve or glossopharyngeal (IX) nerve; M.a.m.e. = site of origin of M.adductor mandibulae externus; M.ax = axial muscle insertion; p.amp = impression of posterior ampulla; par = paroccipital process; p.v.c. = impression of posterior vertical semicircular canal; vag = vagus foramen.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hyo
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pvc
vag
p.amp

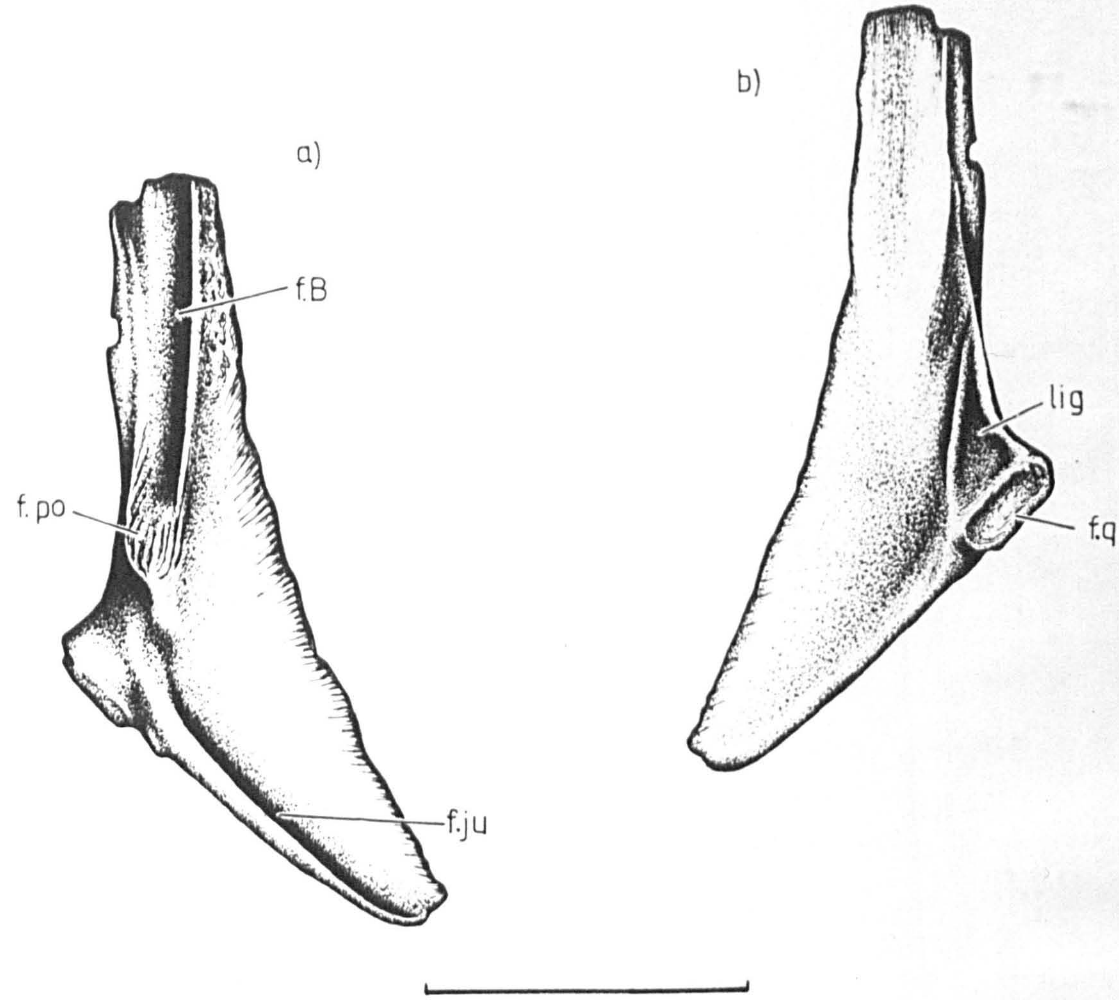
Figure 4

a),b) Right quadratojugal, and c),d) Right prootic of *Ophthalmosaurus icenicus*, B.M.N.H. R4753 and R4522 respectively.

a) lateral, b) medial, c) external, d) internal view.

Scale = 5 cm.

amp = ampulla of anterior vertical canal; a.v.c. = anterior vertical semicircular canal; f.B = groove for reception of ventral tongue of element B; f.ju = groove for reception of jugal; f.po = facet for postorbital; f.q = facet for quadrate; h.c = horizontal canal impression; lig = site of attachment of ligaments binding quadratojugal to quadrate; ri = ridge for jaw adductor muscles; sac = impression of sacculus; ut = impression of utriculus.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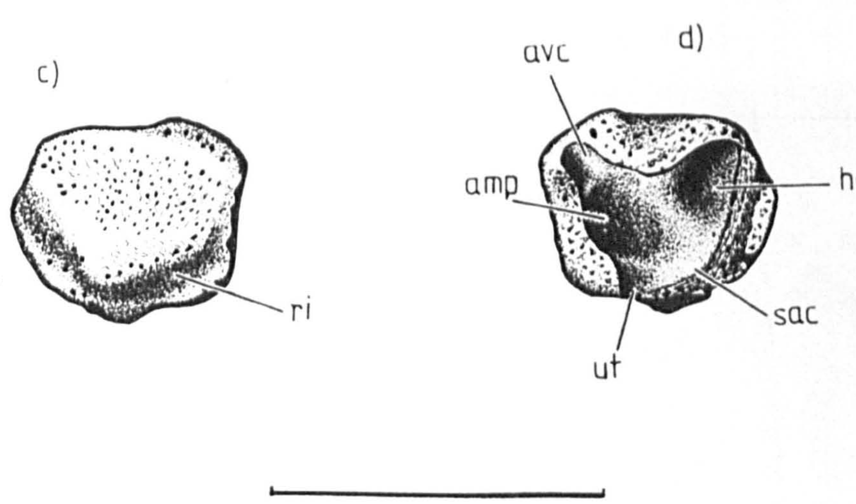
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Figure 5

a),b),c),d) Right stapes, and e),f) Left exoccipital of *Ophthalmosaurus icenicus*, B.M.N.H. R4522.

a) posterior, b) anterior, c) dorsal, d) ventral, e) medial, f) lateral view.

Scale = 5 cm.

f.bocc = facet for basioccipital; f.bsph = facet for basisphenoid; f.opis = facet for opisthotic; f.pt.sq.= facet for articulation with pterygoid and squamosal; f.pt = facet for pterygoid; f.quad = facet for quadrate; f.socc = facet for articulation with supraoccipital; gr = groove for hyomandibular branch of facial (VII) nerve or glossopharyngeal (IX) nerve; hy = hyoid process; hyp = foramina for hypoglossal (XII) nerve; M.occ = site of insertion of occipital muscles; msc = muscle scar; st.ar = path of stapedial artery; vag = vagus foramen.

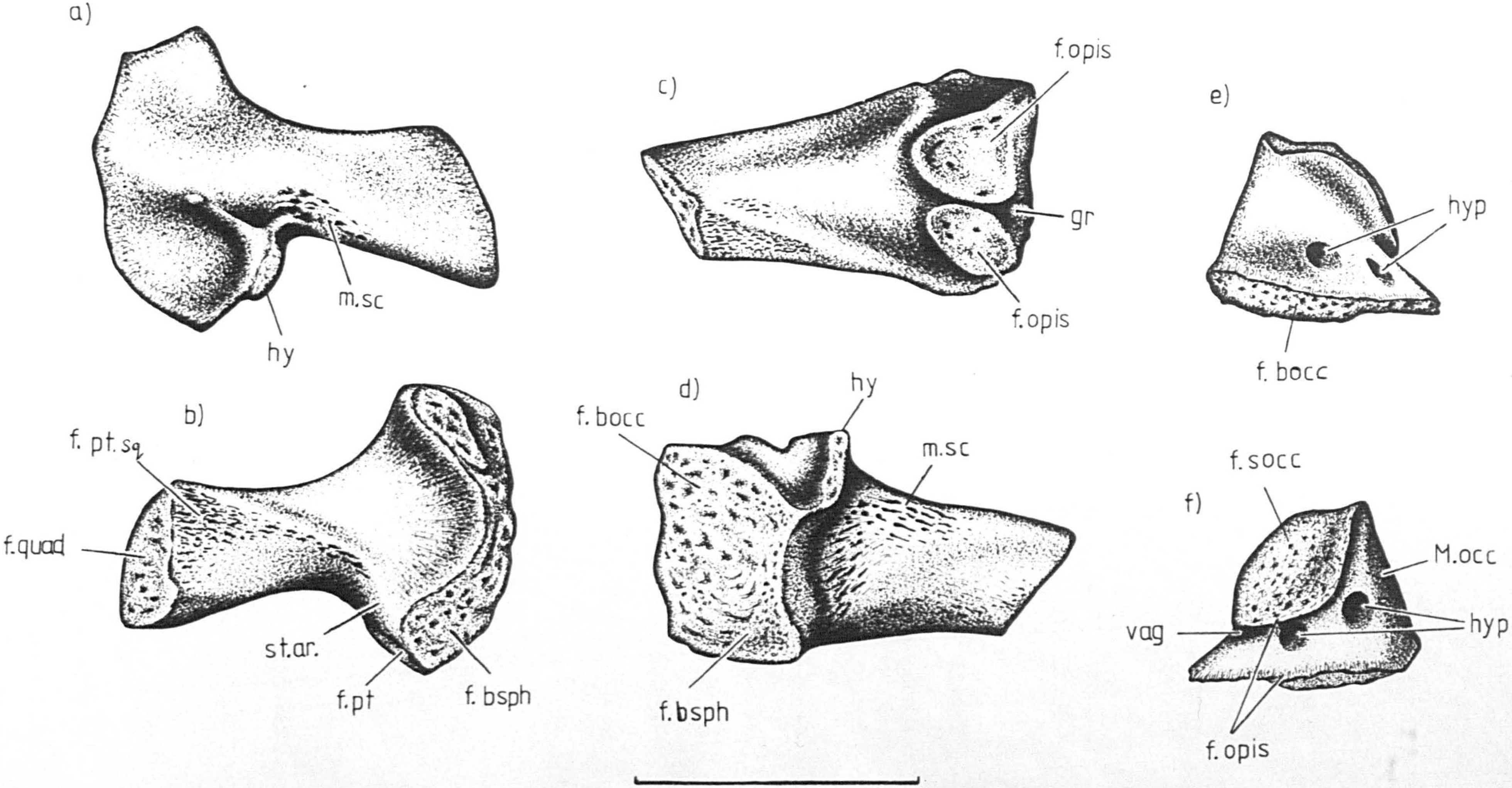
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Figure 6

Reconstruction of occiput of Ophthalmosaurus icenicus, based on B.M.N.H. R2133, R2161, R3893, R4753; H.M. V1901.

Scale = 10 cm. Cartilage stippled.

B = element B; bocc = basioccipital; b sph = basisphenoid; exoc = exoccipital; opis = opisthotic; p = parietal; pt = pterygoid; qj = quadratojugal; quad = quadrate; quad.f = quadrate foramen; sq = squamosal; st = stapes; subv = subvertebral muscle attachment scar; soc = supraoccipital.

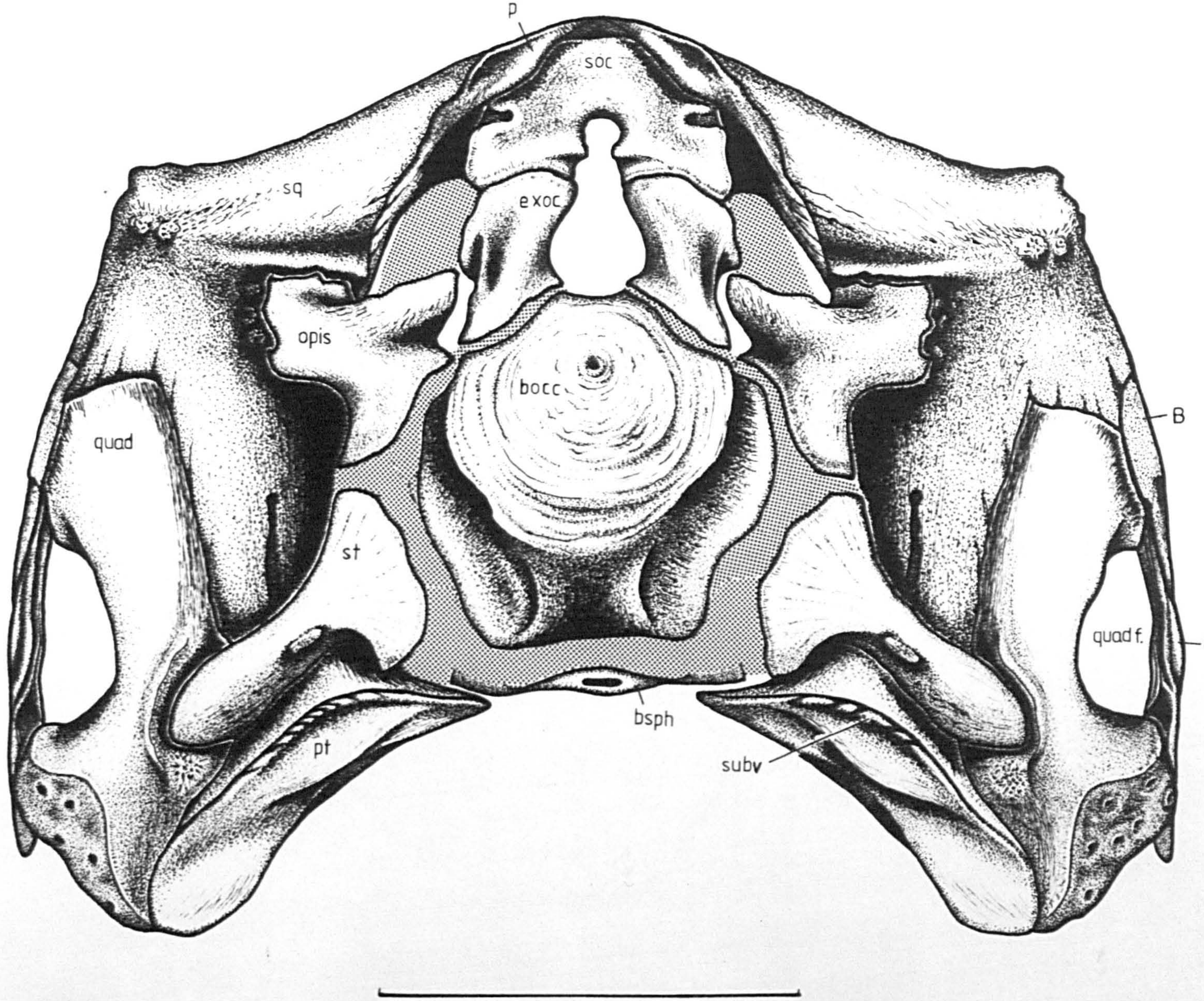
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Figure 7

Reconstruction of braincase and otic capsule of Ophthalmosaurus icenicus, based on B.M.N.H. R2161. Side view.

Scale = 5 cm. Cartilage stippled. Semicircular canals reconstructed.

bocc = basioccipital; b sph = basisphenoid; exoc = exoccipital; for = foramen for glassopharyngeal or facial nerve; for' = foramen in supraoccipital for passage of vein; opis = opisthotic; pal = groove for palatal ramus of facial nerve; pro = prootic; socc = supraoccipital; st = stapes.

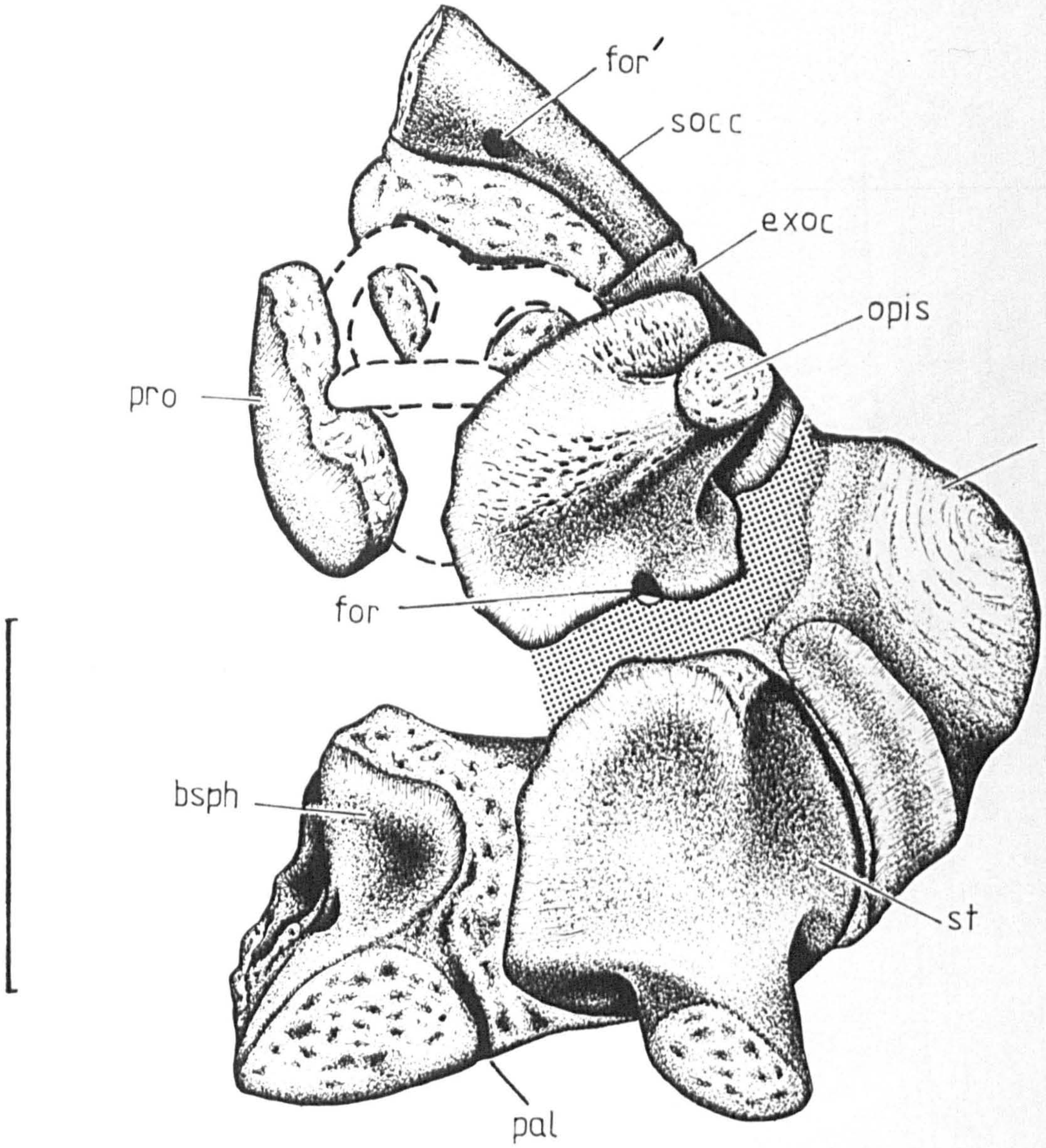

for′
socc
exoc
opis
pro
bocc
for
bsph
st
pal

Figure 8

Quadrate of Ophthalmosaurus icenicus, H.M. V1878.

a) posterior, b) lateral, c) anterior view.

Scale = 5 cm.

cond = articular condyle; f.artic = condyle boss articulating with articular; f.pt = surface for articulation with pterygoid; f.qj = facet for quadratojugal; f.sq = surface for articulation with squamosal; f.st = stapes facet; f.sur = condyle boss articulating with surangular; M.a.m.e. = origin of M.adductor mandibulae externus; M.a.m.p. = origin of M.adductor mandibulae posterior; occ.l = occipital lamella; pt.l = ptergyoid lamella; q.for = quadrate foramen; tub = tubercle for ligaments to pterygoid.

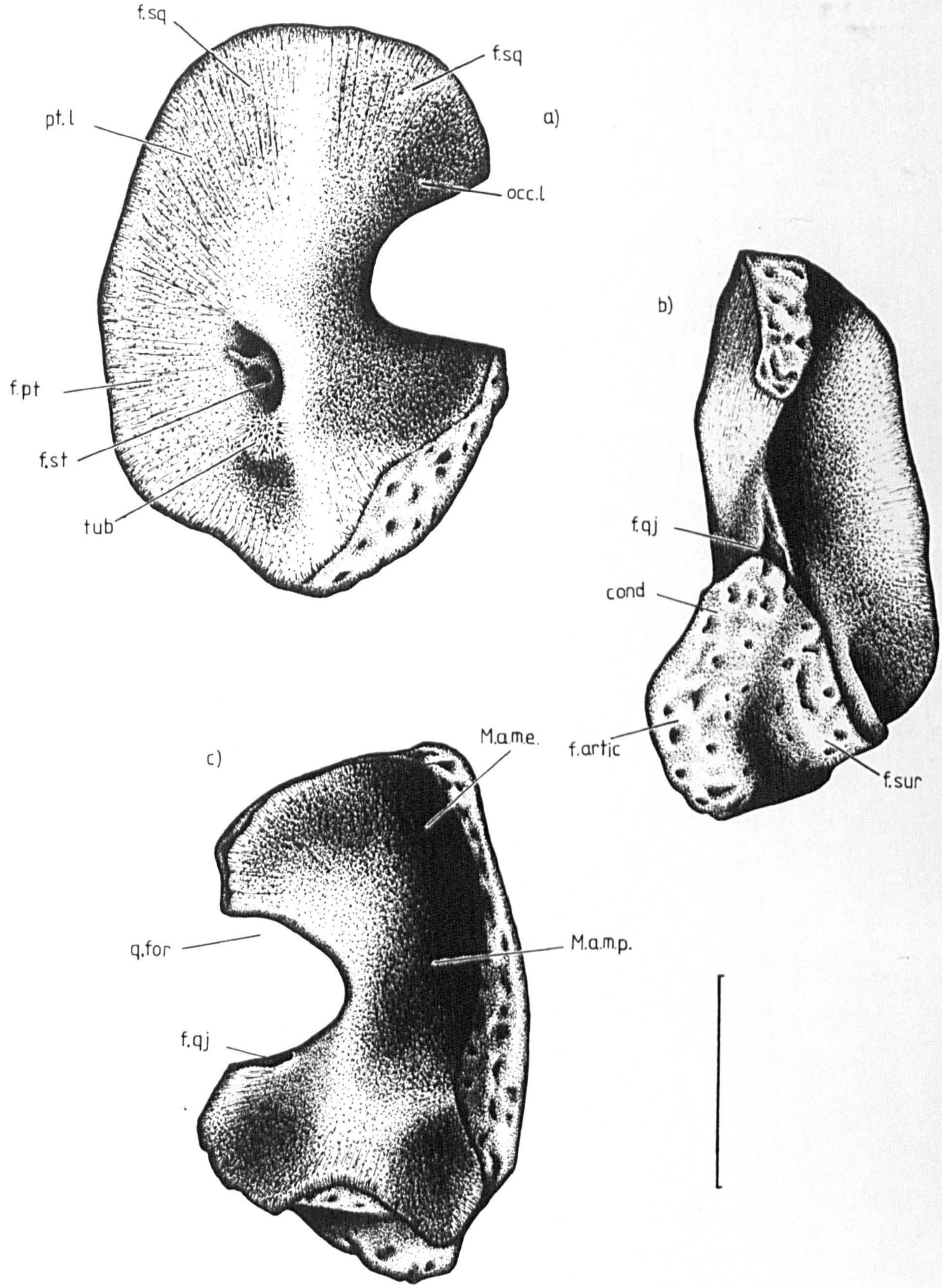

f.sq
f.sq
a)
pt.l
occ.l
b)
f.pt
f.st
tub
f.qj
cond
f.artic
f.sur
c)
M.a.m.e.
q.for
M.a.m.p.
f.qj

Figure 9

Reconstruction of palate of Ophthalmosaurus icenicus, based on B.M.N.H. R3893, R2180, H.M. V1129.

Scale = 10 cm.

alv = alveolar groove; bocc = basioccipital; b sph = basisphenoid; i.nar = internal naris; ju = jugal; M.a.m.i.p = origin of M.adductor mandibulae internus pterygoideus; max = maxilla; pal = palatine; pas = parasphenoid; pt = pterygoid; qj = quadratojugal; quad = quadrate; st = stapes; vo = vomer.

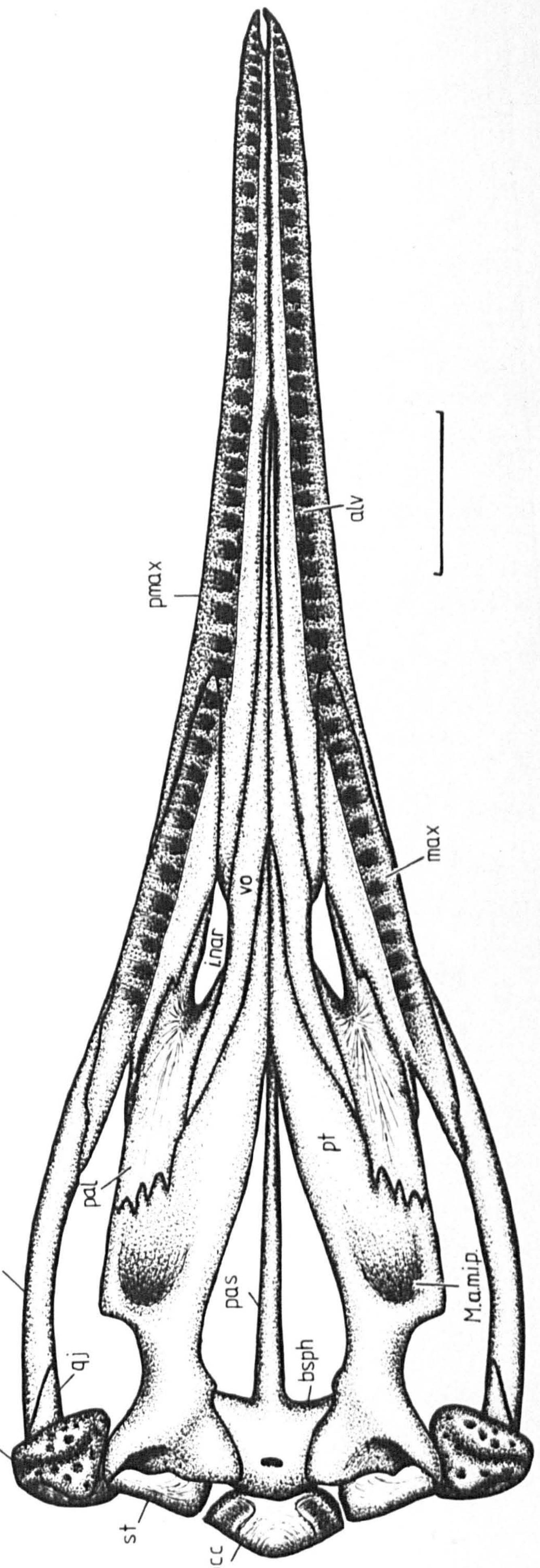

pmax
alv
max
vo
i.nar
pt
pal
ju
M.a.m.i.p.
pas
qj
bsph
quad
st
bocc

Figure 10

Left palatine of Ophthalmosaurus icenicus, B.M.N.H. R4753.

Reconstructed outline based on a number of other specimens.

a) ventral, b) dorsal view.

Scale = 10 cm.

f.max = surface for contact with maxilla; f.pt = suture with pterygoid; f.vo = surface for contact with vomer; int.nar = internal naris; nutr = nutrient foramina and grooves; proj = projection possibly for supporting soft tissues of nasal capsule.

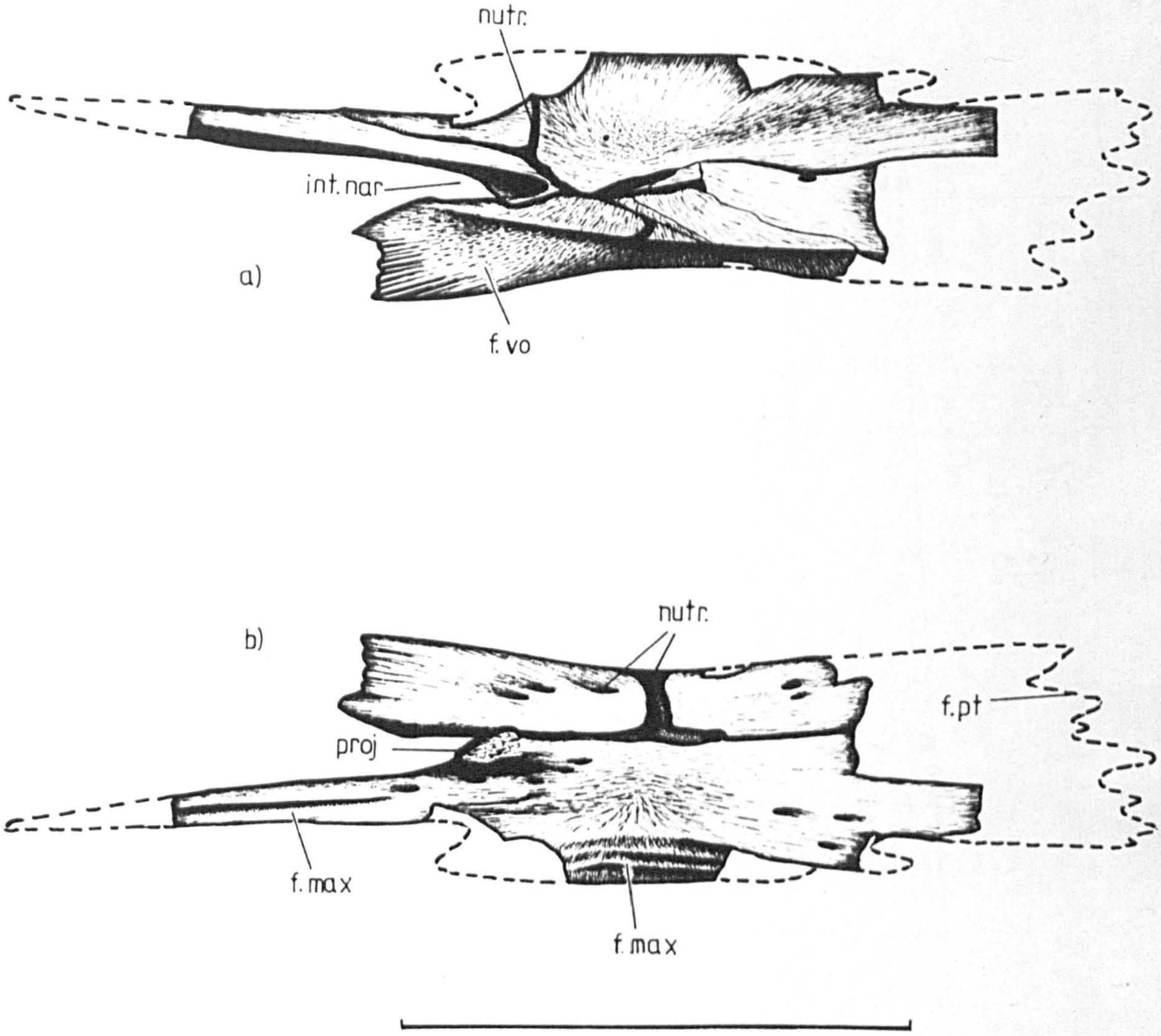

nutr.
int. nar
a)
f. vo
b)
nutr.
proj
f. pt
f. max
f. max

Figure 11

Vomer of Ophthalmosaurus icenicus.

a) lateral and b) dorsal left vomer of B.M.N.H. R4753. c) medial and d) dorsal left vomer of H.M. V1129. In both cases, reconstructed outlines based on the respective right vomers.

Scale = 10 cm.

choan = medial wall of choanal tube; f.pal = edge contacting palatine; f.pmax = surface for contact with premaxilla; f.pt = facet for pterygoid; gr.pt = groove for pterygoid; nar = medial border of internal naris; ri = ridge separating vestibulum and choanal tube; sp = spinous projections; vert.pr = vertical projection; vest = wall of vestibulum nasi.

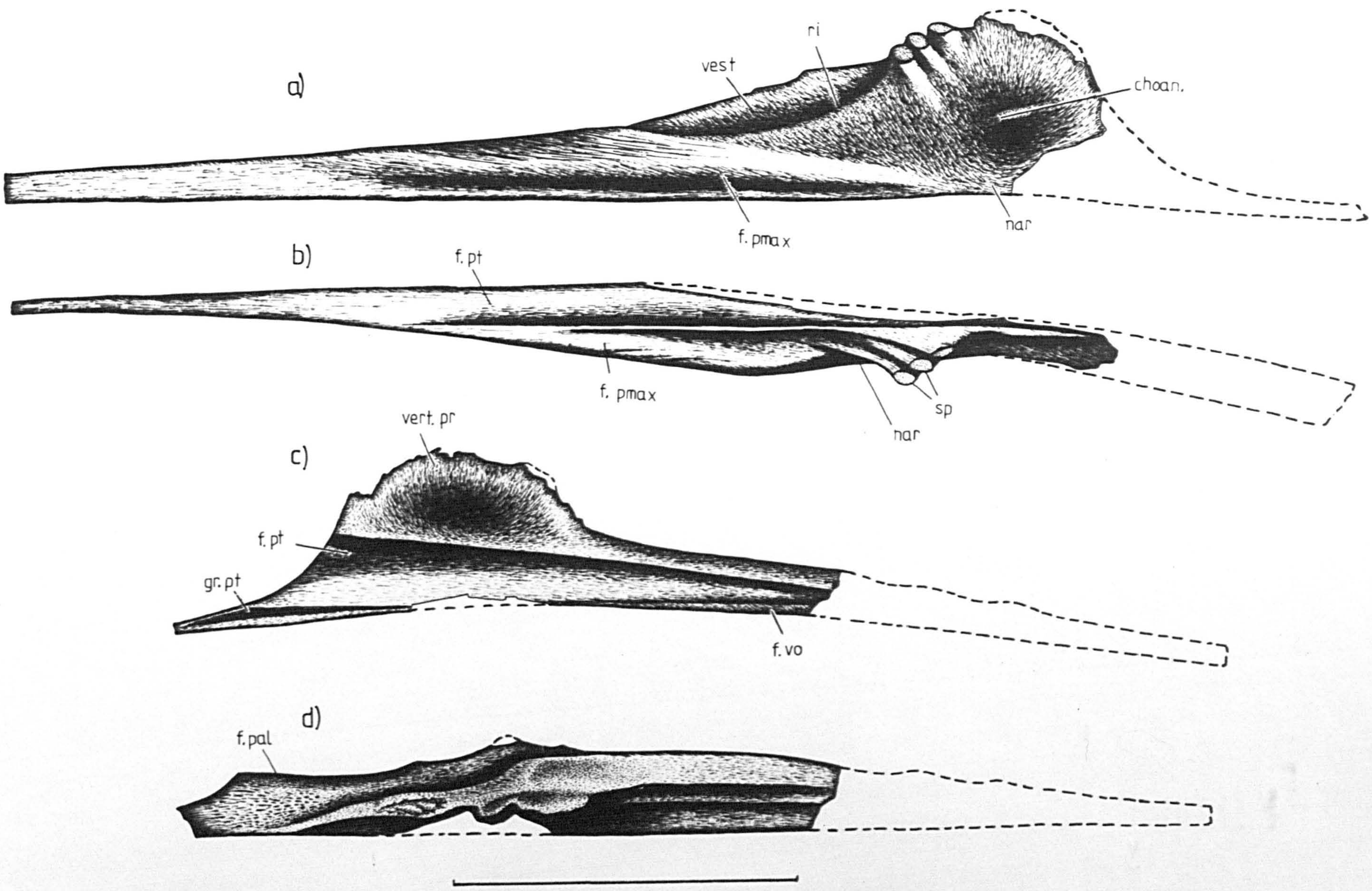

a)
vest
ri
choan.
f. pmax
nar
b)
f. pt
f. pmax
sp
nar
c)
vert. pr
f. pt
gr. pt
f. vo
d)
f. pal

Figure 12

Reconstruction of skull roof of Ophthalmosaurus icenicus, based on B.M.N.H. R3893 and H.M. V1129. Dorsal view.

Scale = 10 cm.

B = element B; fr = frontal; ju = jugal; lach = lachrymal; max = maxilla; nar = naris; nas = nasal; par = parietal; pf = postfrontal; pmax = premaxilla; prf = prefrontal; po = postorbital; sq = squamosal.

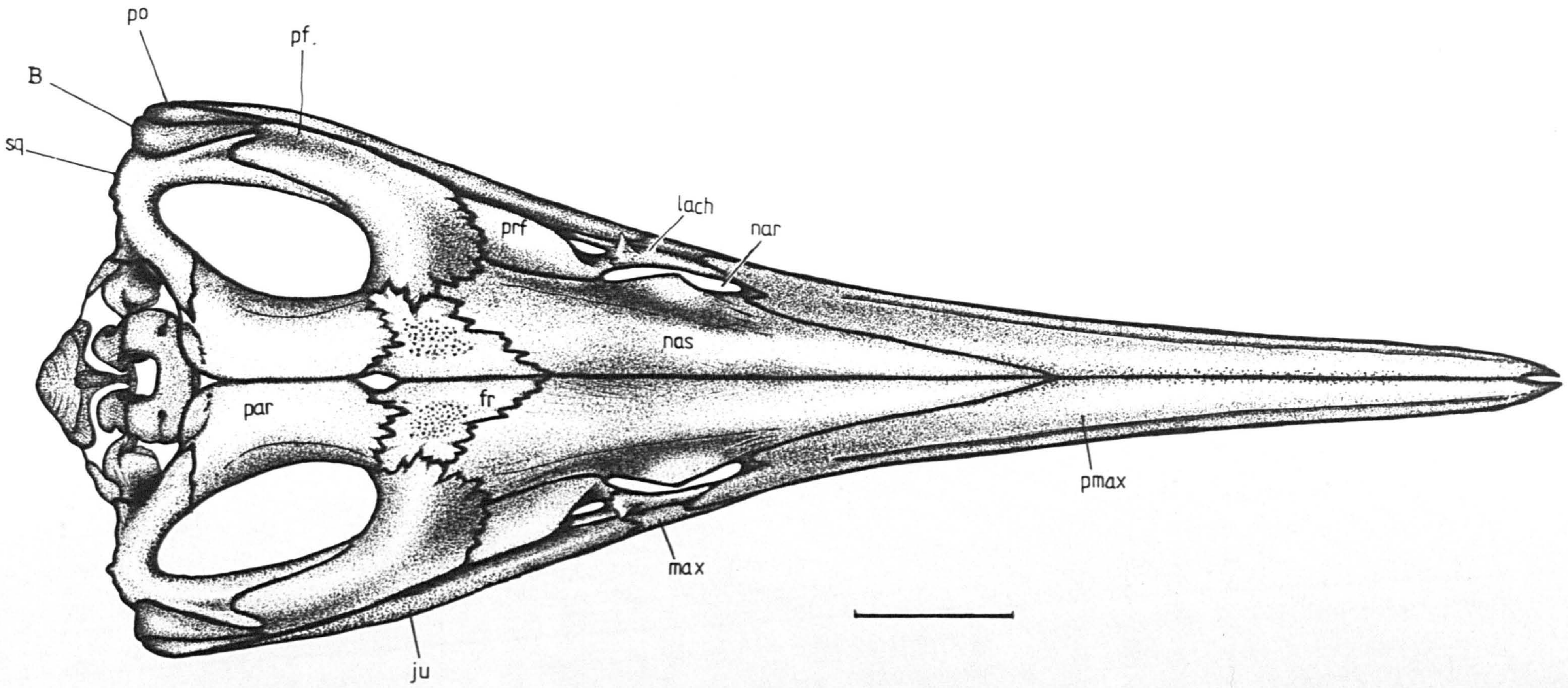

po
B
sq
pf.
prf
lach
nar
nas
par
fr
pmax
max
ju

Figure 13

Reconstruction of skull roof of Ophthalmosaurus icenicus, based on H.M. V1129. Ventral view.

Scale = 10 cm.

cer = impression of cerebral hemisphere on parietal; f.B = facet for element B; f.epi = facet for epipterygoid; f.lach = facet for lachrymal; f.max = facet for maxilla (broken here); f.op = facet for opisthotic; f.par = facet for parietal of opposite side; f.po = facet for postorbital; f.quad = groove for articulation with quadrate; fr = frontal; f.socc = shelf overlapping supra-occipital; lat.fl = lateral lamina of squamosal; med.fl = medial lamina of squamosal; M.l.pt = origin of M.levator pterygoidei; na = nasal; nar = flared edge of external naris; olf = impression of olfactory lobe; opt = impression of optic lobe; par = parietal; para = parapineal foramen; pref = prefrontal; pof = postfrontal; proj = projection at midpoint of naris; sq = squamosal; vasc = vascular channel.

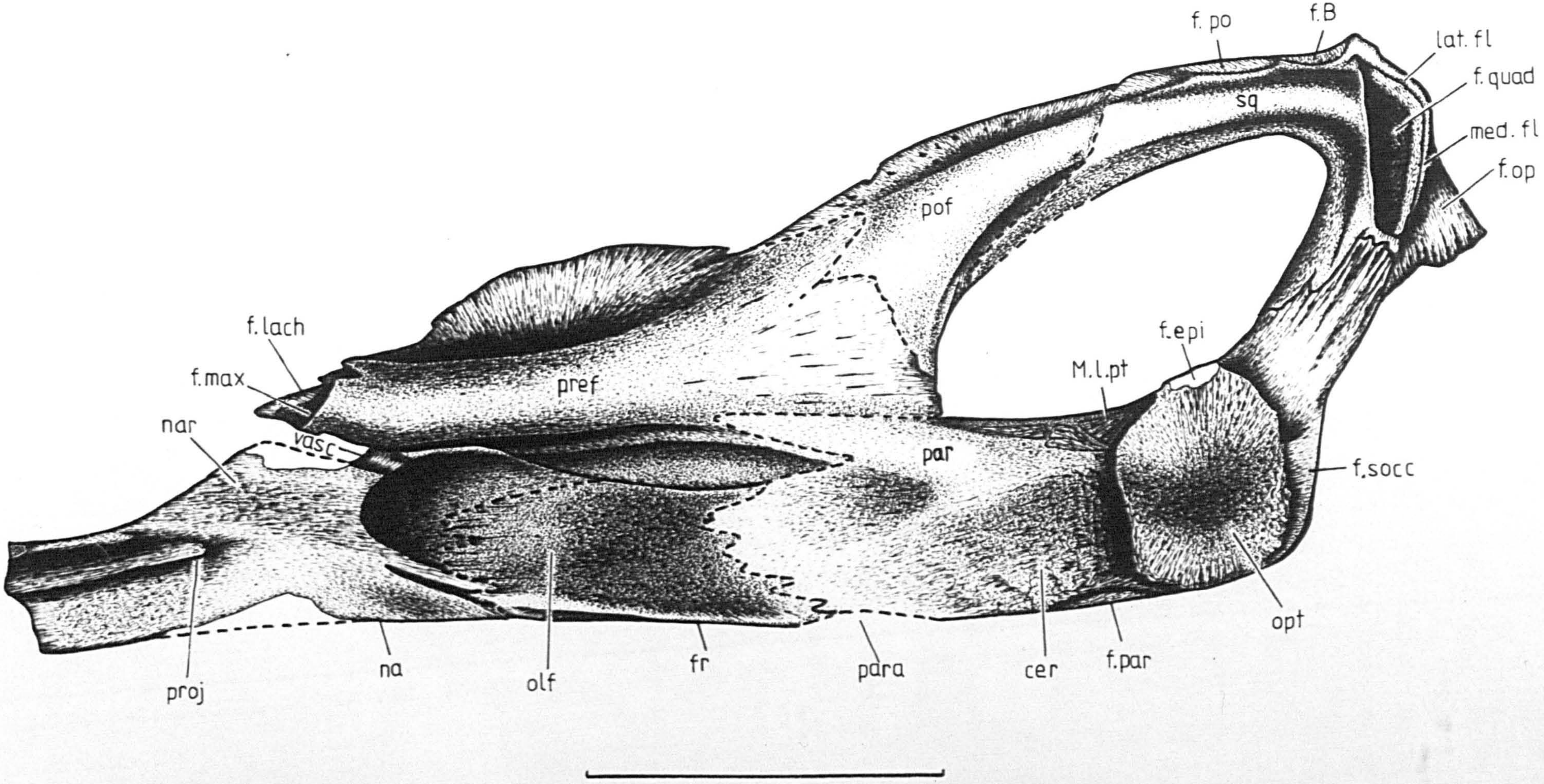

f. po
f.B
lat. fl
f. quad
sq
med. fl
f. op
pof
f. lach
f. epi
M. l. pt
f. max
pref
nar
vasc
par
f. socc
proj
na
olf
fr
para
cer
f. par
opt

Figure 14

Reconstruction of skull of <u>Ophthalmosaurus icenicus</u>, based on B.M.N.H. R3893, R4753. Side view.

Scale = 10 cm.

an = angular; B = element B; d = dentary; ju = jugal; lach = lachrymal; max = maxilla; na = nasal; pmax = premaxilla; po = postorbital; pof = postfrontal; pref = prefrontal; q = quadrate; qj = quadratojugal; sa = surangular.

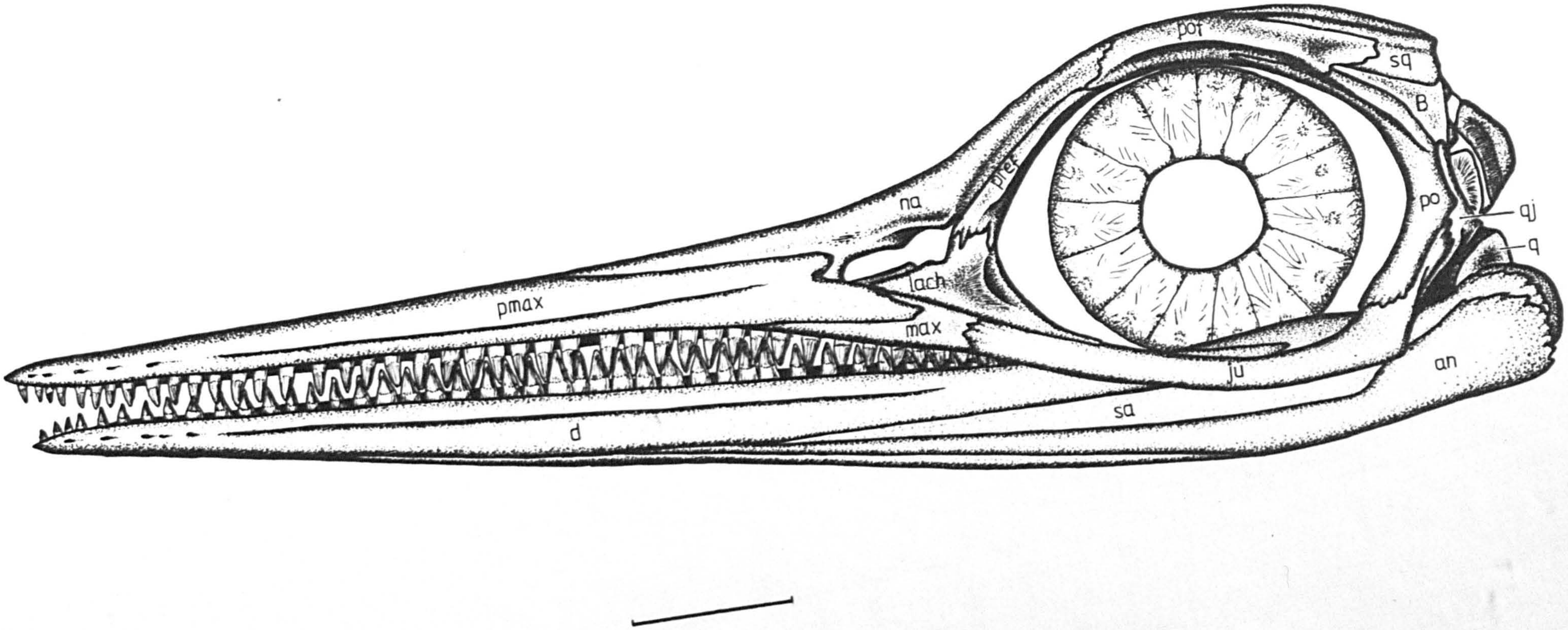

pof
sq
B
pref
na
po
qj
q
lach
pmax
max
ju
an
sa
d

Figure 15

Reconstruction of lower jaw of Ophthalmosaurus icenicus, based on B.M.N.H. R3893, H.M. V1893.

a) external; b) internal view.

Scale = 10 cm.

ang = angular; art = articular; ch.t = foramen for chorda tympani; cor = coronoid process; d = dentary; gl = glenoid fossa; M.a.m.e. = insertion of M.adductor mandibulae externus on surangular peak; M.a.m.i. = insertion of M.adductor mandibulae internus pterygoideus; M.a.m.e.sup. = insertion of M.adductor mandibulae externus superficialis; Meck = continuation of Meckelian canal on medial surface of dentary; p.art = prearticular; sa = surangular; spl = splenial; sym = symphysial facet.

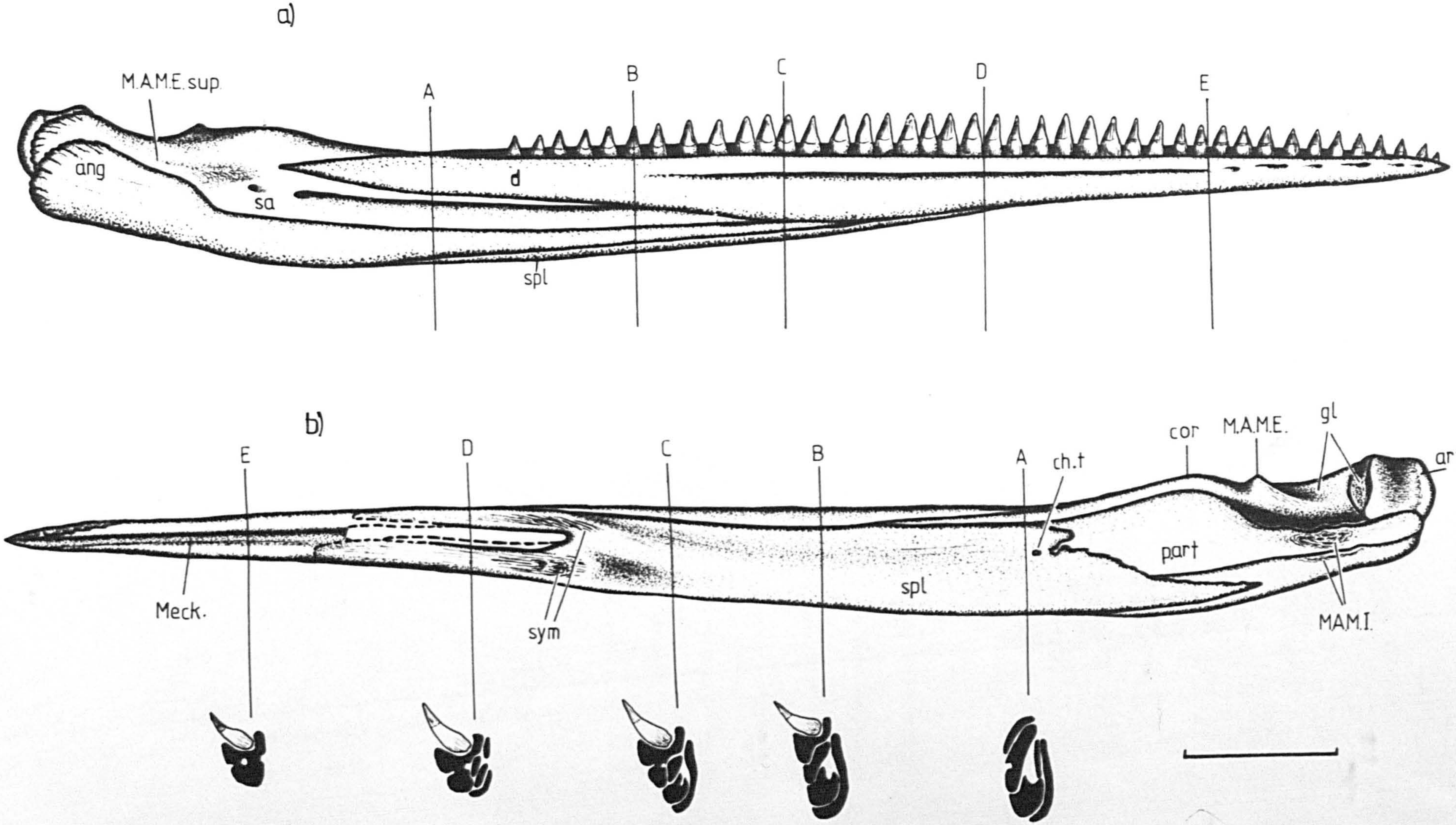

a)
M.A.M.E.sup.
ang
sa
d
spl
A
B
C
D
E
b)
E
D
C
B
A
ch.t
cor
M.A.M.E.
gl
art
Meck.
sym
spl
part
M.A.M.I.

Figure 16

Teeth of Ophthalmosaurus icenicus. H.M. V1129.

a),b) anterior tooth, c)d)e) teeth from middle of tooth row.

(c) has an abnormal root.)

Scale = 1 cm.

cem = cementum-covered tooth base; cr = crown, enamel-covered;

den = exposed dentine; fac = wear facet; lab = labial side;

lin = lingual side; res = resorption pit.

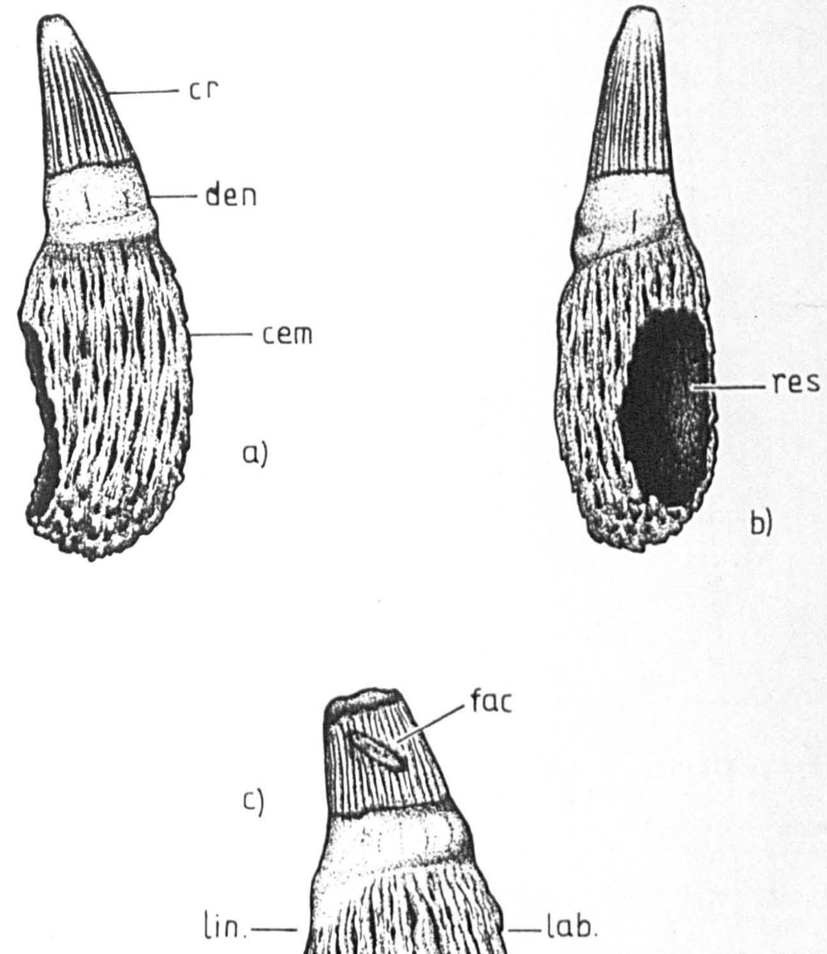

cr
den
cem
a)
res
b)
fac
c)
lin.
lab.
d)
e)

Figure 17

Atlas-axis complex of Ophthalmosaurus icenicus. H.M. V1916.

a) anterior, b) posterior, c) lateral from right, d) lateral from left view.

Scale = 5 cm.

diap = diapophyses; para = parapophyses.

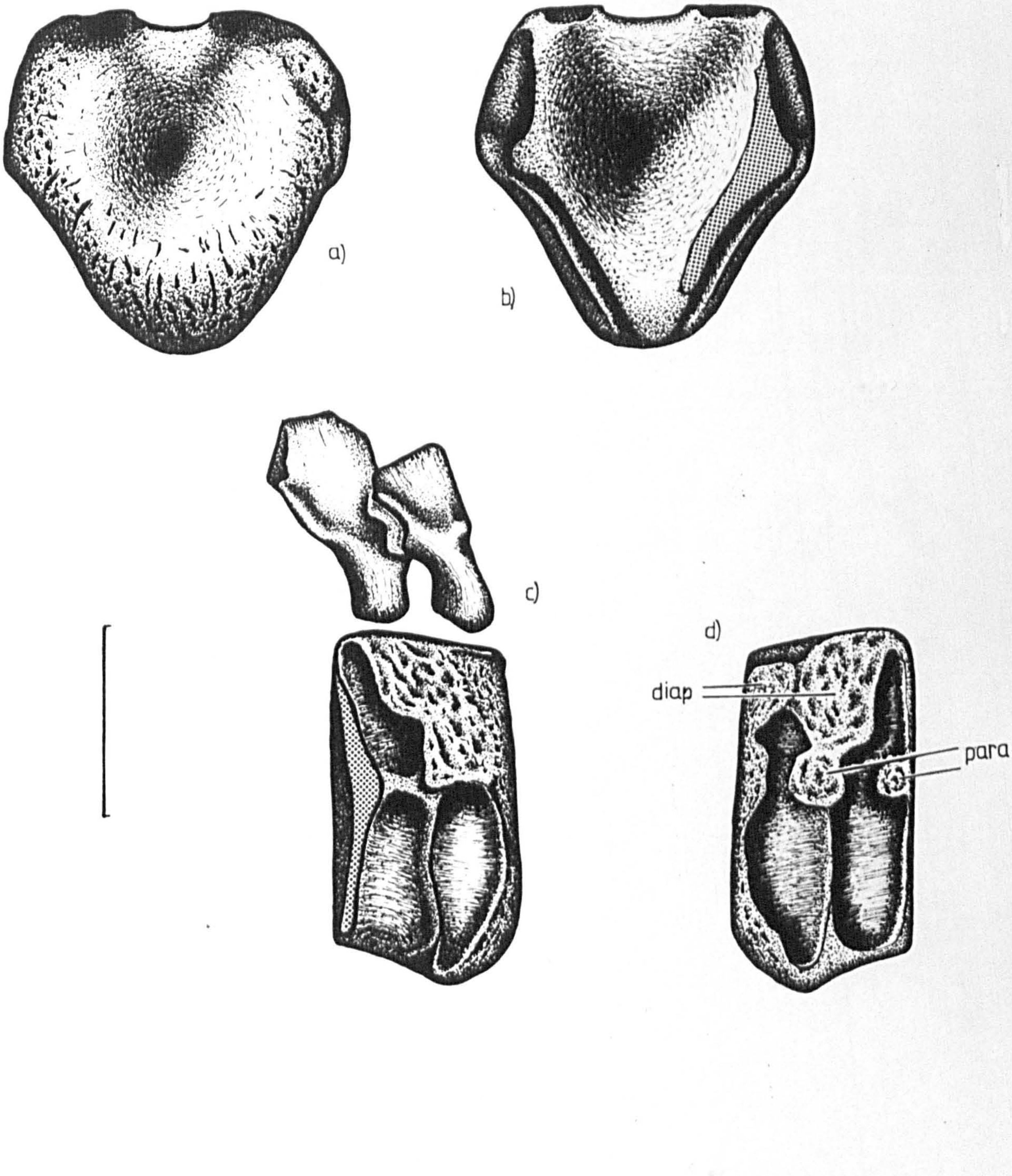

a)
b)
c)
d)
diap
para

Figure 18

Neural arches of atlas-axis and 3rd to 6th cervical vertebrae. of *Ophthalmosaurus icenicus*. H.M. V1894.

a) lateral, b) anterior, c) posterior view.

Scale = 5 cm.

az = anterior zygapophysis; pz = posterior zygapophysis.

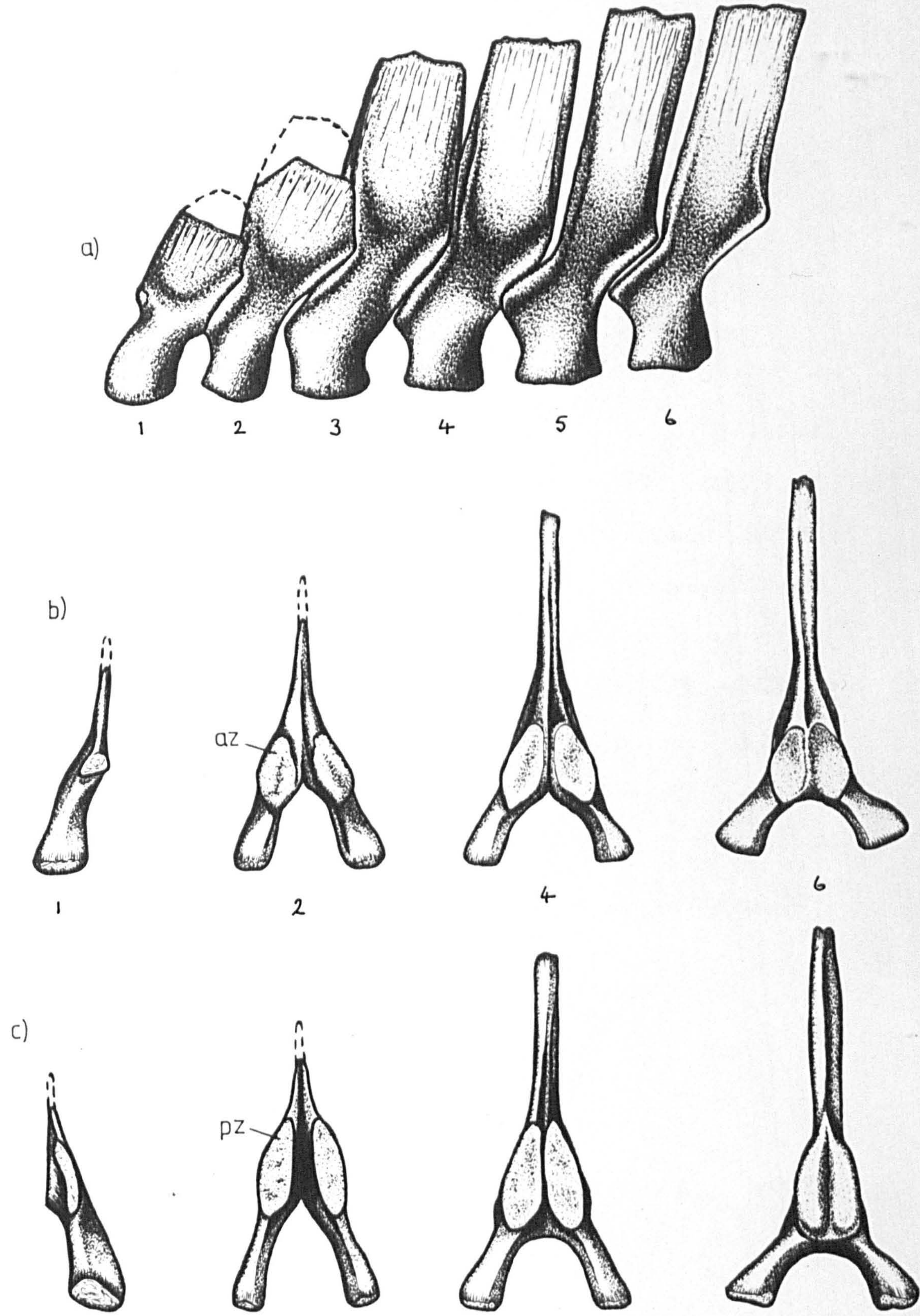

a)
1
2
3
4
5
6
b)
az
1
2
4
6
c)
pz
1
2
4
6

Figure 19

Series of vertebral centra of Ophthalmosaurus icenicus.

H.M. V1611.

a) left lateral view of 1st - 7th anterior trunk centra, b) ventral view of same, c) left lateral view of 22nd - 27th middle trunk centra to show separation of diapophysis from neural arch pedicel, d) ventral view of 27th centrum to show ventral keel, e) left lateral view of posterior trunk vertebrae 39 - 44 to show coalescence of diapophysis and parapophysis.

Scale = 5 cm.

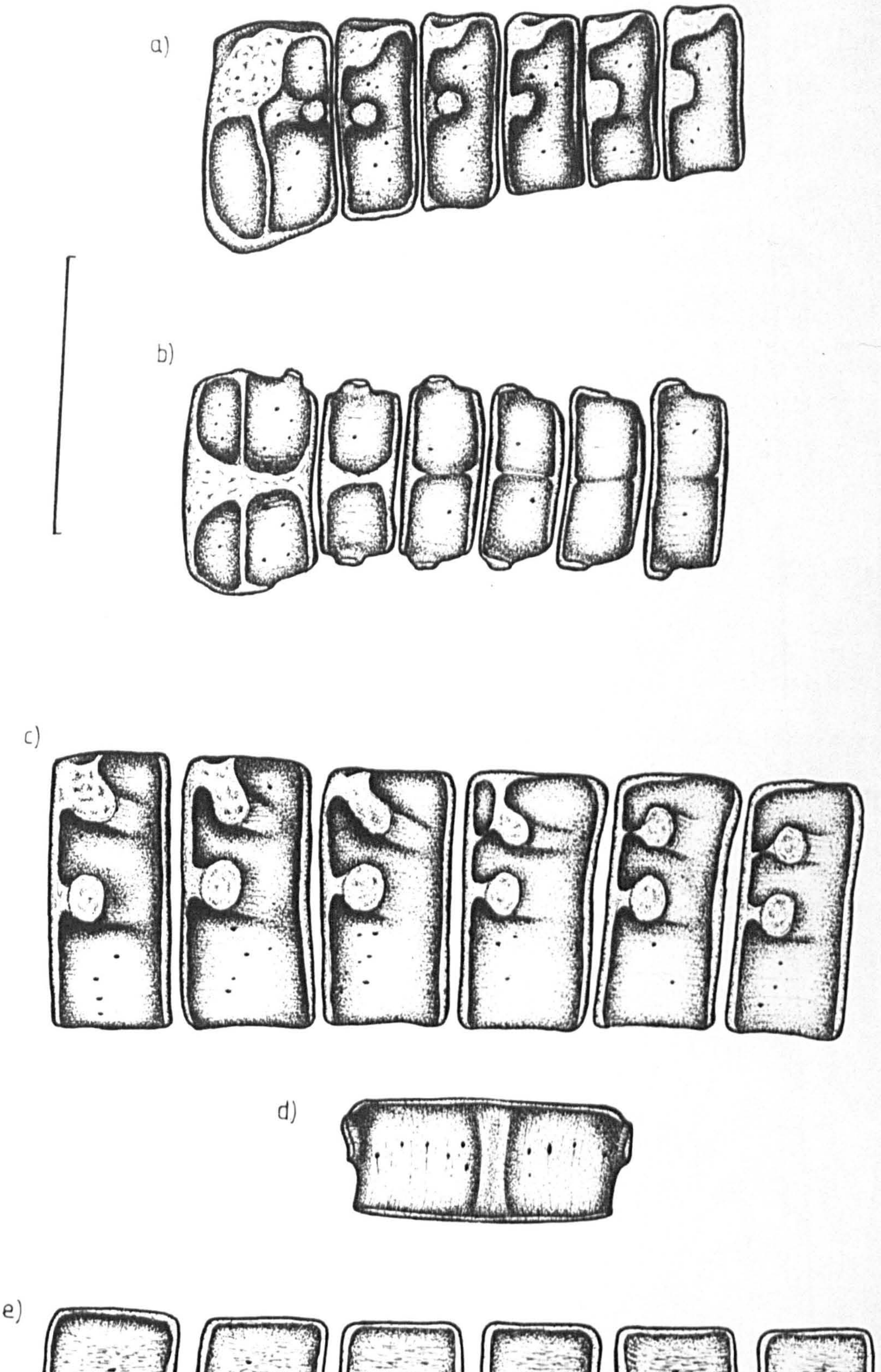

a)
b)
c)
d)
e)

Figure 20

Vertebral centra of Ophthalmosaurus icenicus, H.M. V1916.

a) anterior, b) left lateral view of anterior trunk vertebra from cervical region; c) anterior, d) left lateral view of posterior trunk vertebra; e) anterior, f) left lateral, g) ventral view of anterior caudal vertebral centrum; h) anterior, i) left lateral, j) ventral view of posterior caudal vertebral centrum.

Scale = 5 cm.

f.hae = facet for haemal arch.

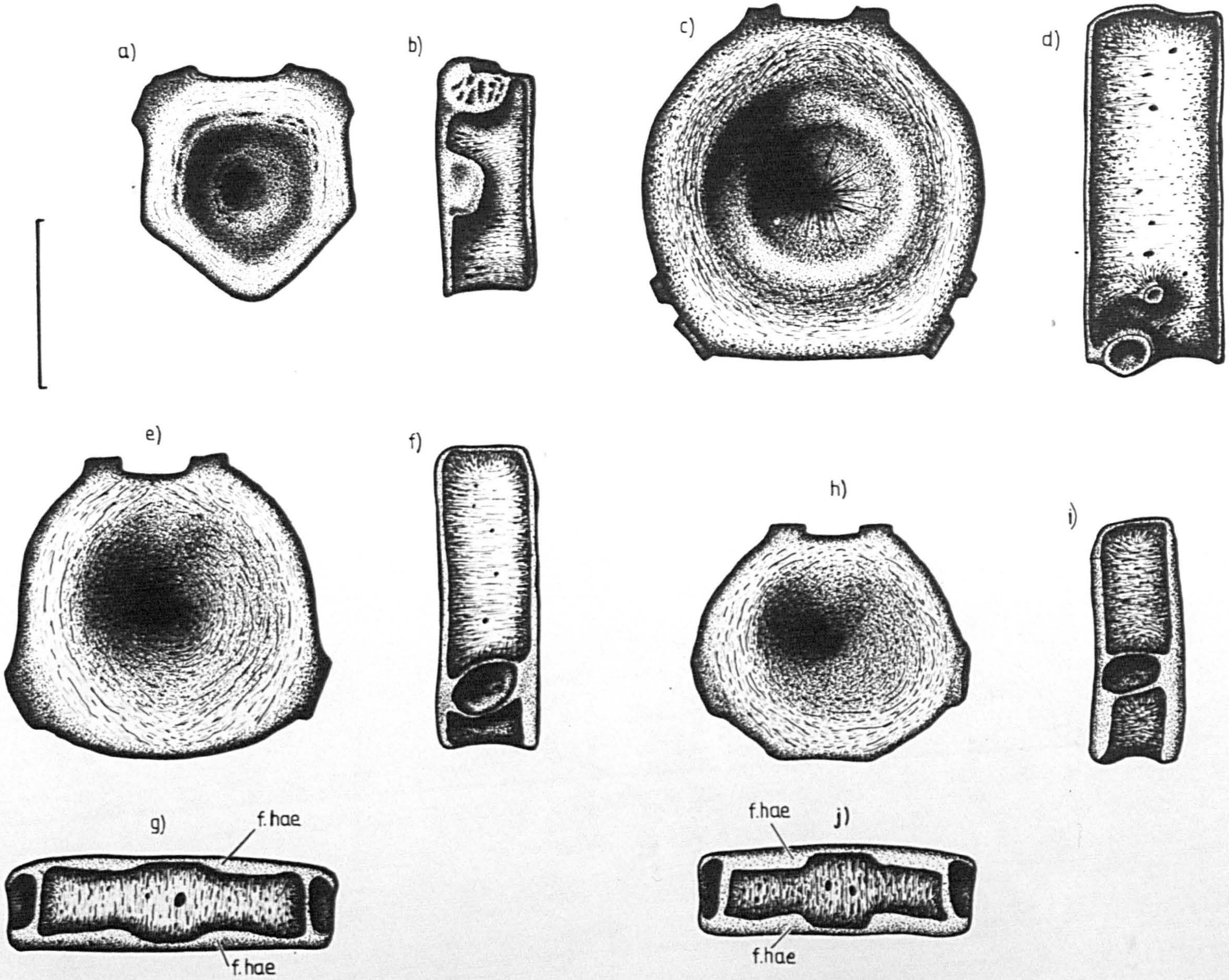

a)
b)
c)
d)
e)
f)
h)
i)
g)
f. hae
f. hae
f. hae
j)
f. hae

Figure 21

Neural spines of Ophthalmosaurus icenicus, H.M. V1916.

a) left lateral view of middle trunk to middle caudal neural spines (not in series), b) anterior, c) posterior view of same.

Scale = 5 cm.

az = anterior zygapophysis, pz = posterior zygapophysis.

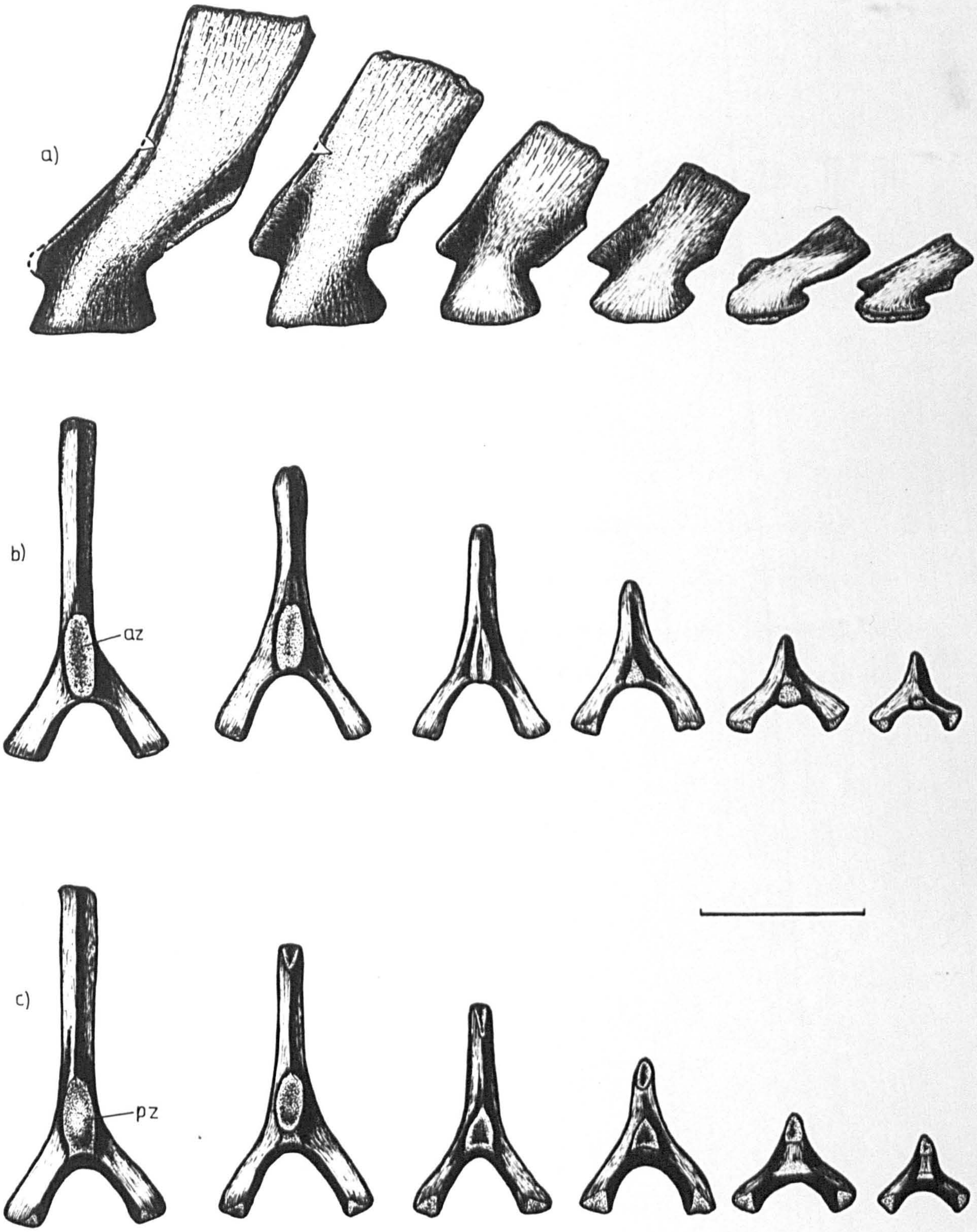

a)
b)
az
c)
pz

Figure 22

Outline of posterior caudal vertebral centra of *Ophthalmosaurus icenicus* reconstructed to show the tailbend. B.M.N.H. R8653, (probably incomplete posteriorly).

Scale = 10 cm.

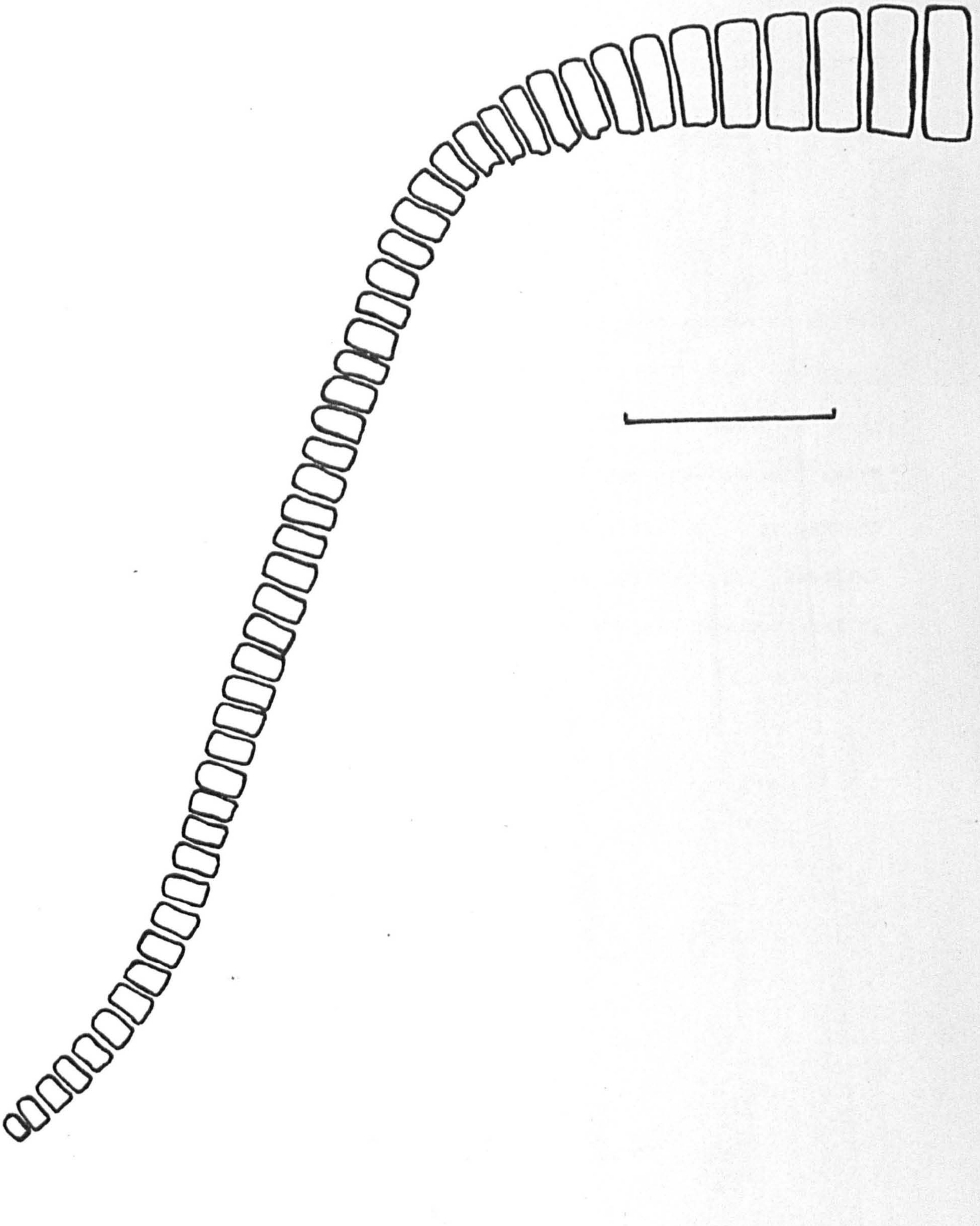


Figure 23

Vertebral centra and neural spines of tailbend of *Ophthalmosaurus icenicus*. H.M. V1916.

a),b) anterior view of anterior tailbend vertebral centra - b) has a small associated rib. c)d) anterior view of posterior tailbend centra. a') - d') left lateral view of same. e) reconstruction of tailbend. f) anterior view of neural spines of tailbend vertebrae. g) left lateral view of same.

Scale = 5 cm.

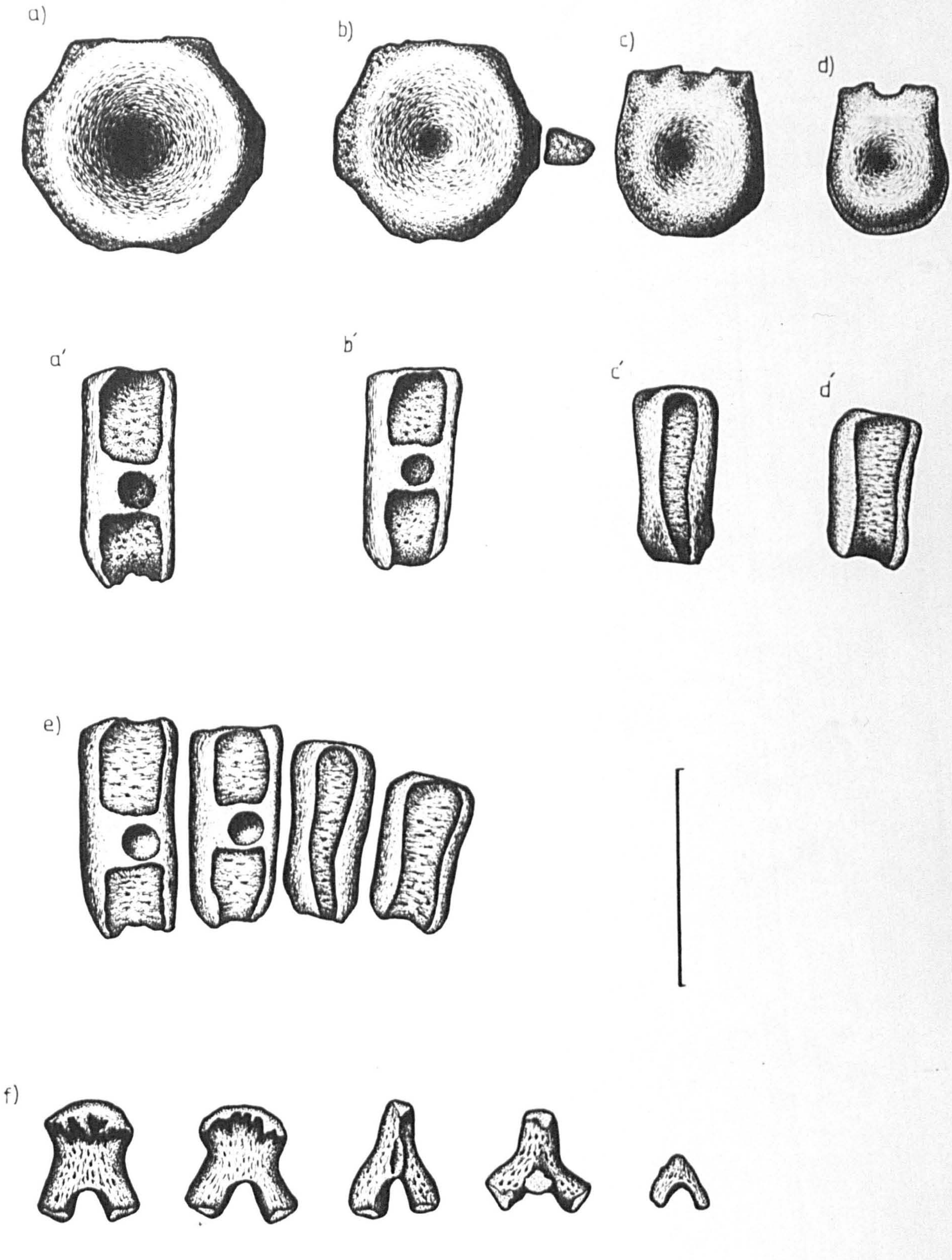

a)
b)
c)
d)
a´
b´
c´
d´
e)
f)
g)

Figure 24

Ribs of Ophthalmosaurus icenicus. H.M. V1916.

a) - f) posterior view of middle trunk to late caudal ribs (not in series). d') - f') dorsal view of d,e,f. a") - f") anterior view of same.

Scale = 5 cm.

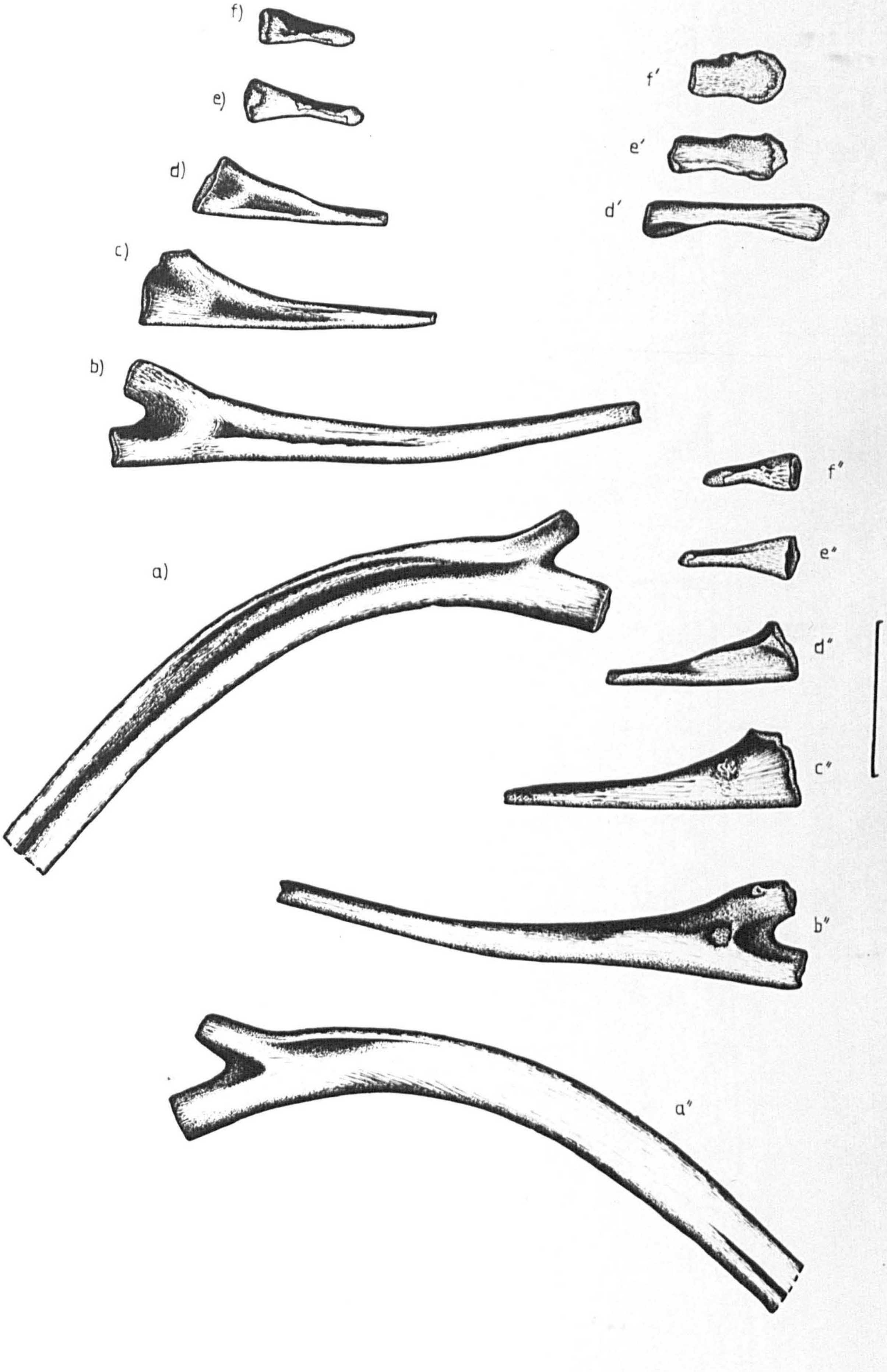

f)
e)
d)
c)
b)
a)
f'
e'
d'
f"
e"
d"
c"
b"
a"

Figure 25

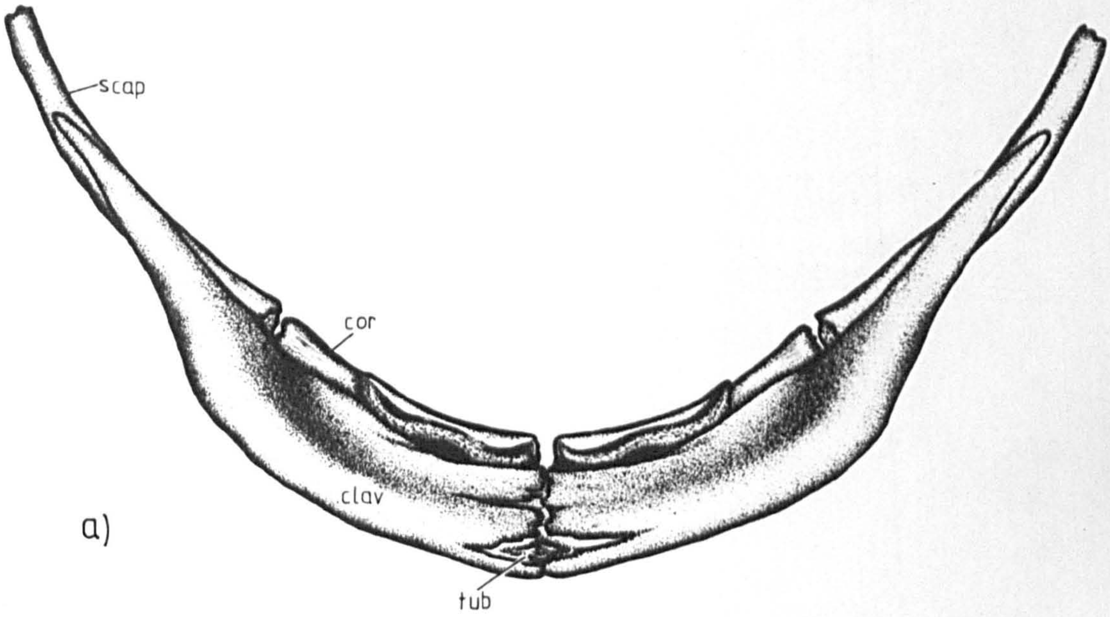
Reconstruction of pectoral girdle of Ophthalmosaurus icenicus, B.M.N.H. R2137.

a) anterior view. b) dorsal view.

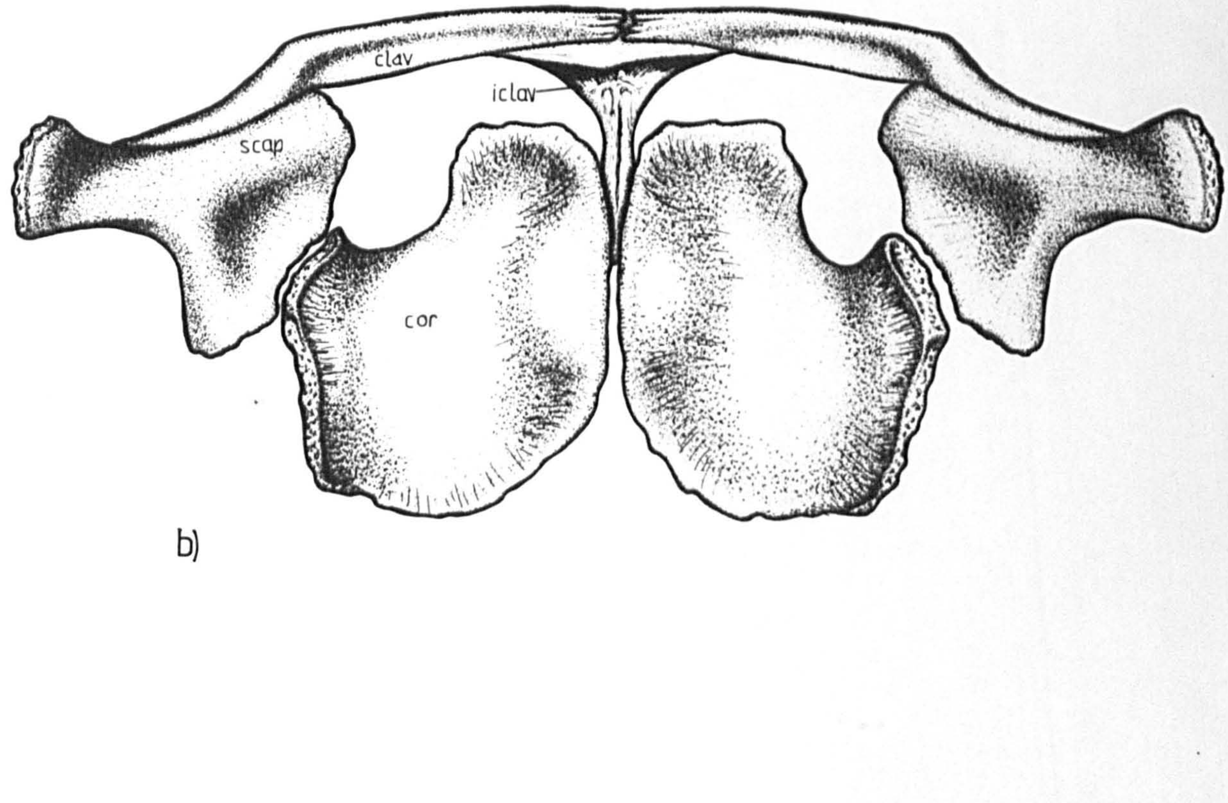
Scale = 10 cm.

clav = clavicle; cor = coracoid; iclav = interclavicle;

scap = scapula ; tub = tubercle on interclavicle.



a)



b)

Figure 26

Reconstruction of pectoral girdle of *Ophthalmosaurus icenicus*, B.M.N.H. R2137.

Left lateral view.

Scale = 10 cm.

clav = clavicle; cor = coracoid; iclav = interclavicle;

scap = scapula.

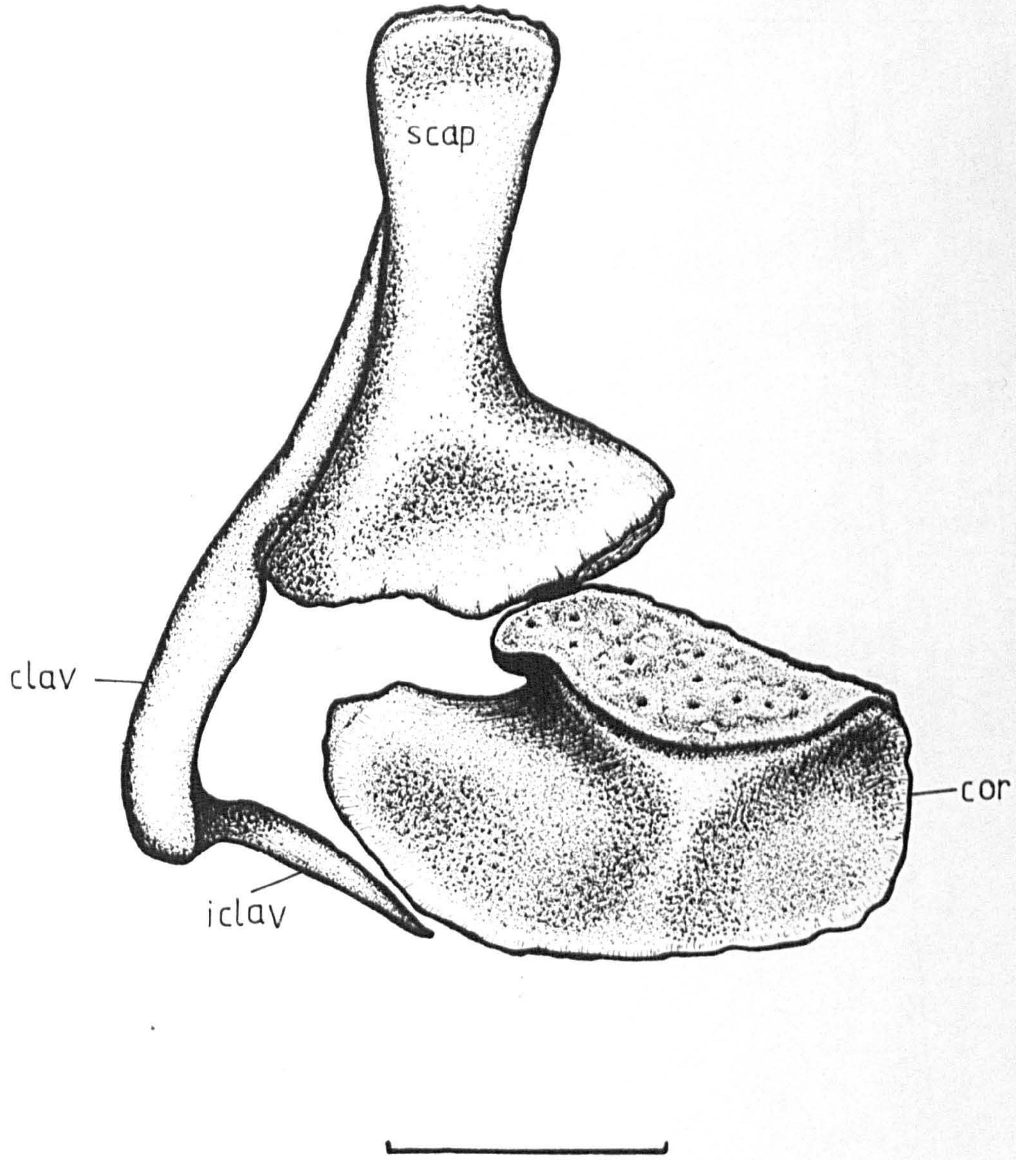

scap
clav
cor
iclav

Figure 27

Left humerus of Ophthalmosaurus icenicus, H.M. V1893.

a) ventral, b) posterior, c) dorsal, d) anterior view.

Scale = 10 cm.

dt = dorsal trochanter; tub = tubercles on dorsal + ventral surfaces of distal edge; vt = ventral trochanter.

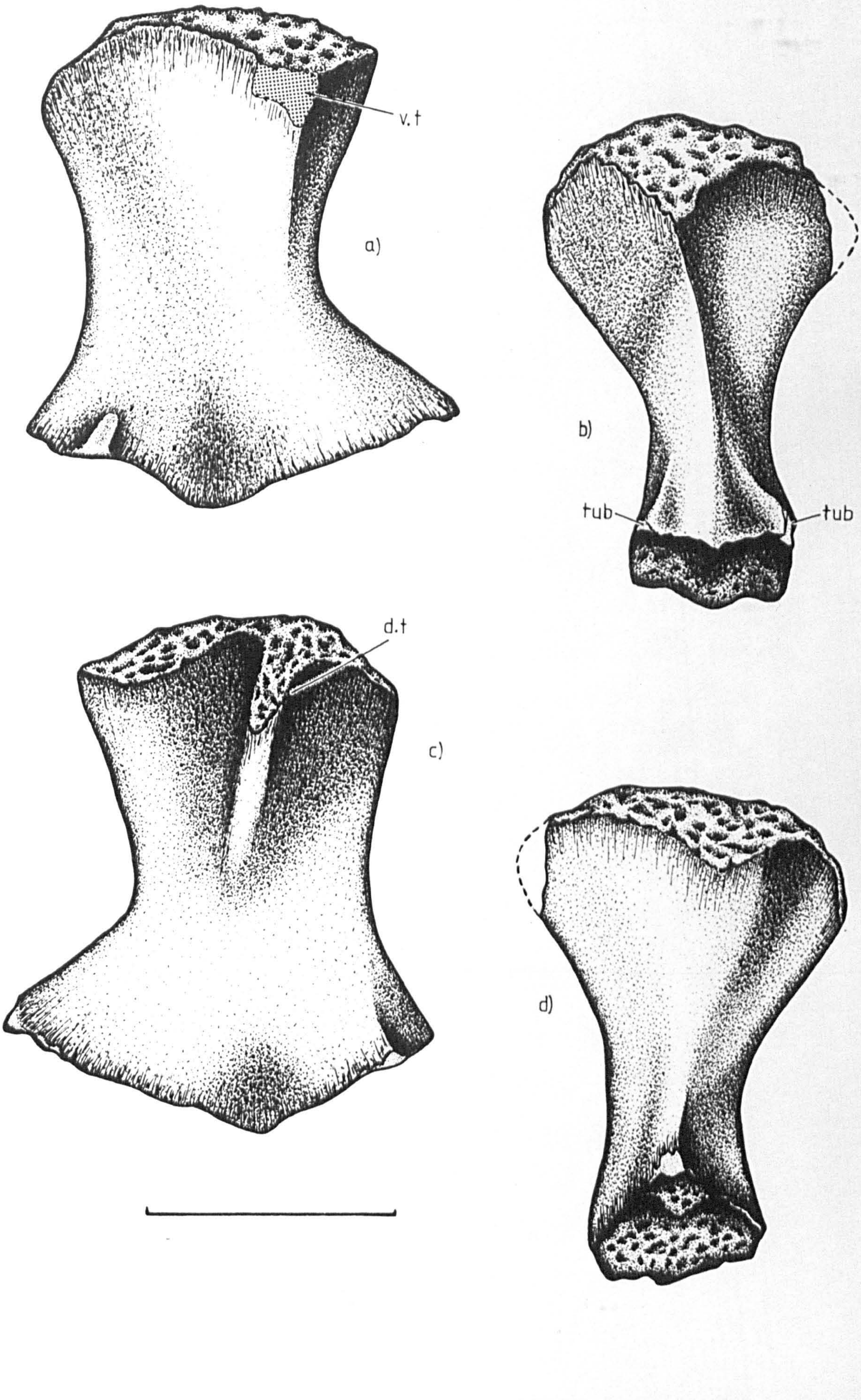

v.t
a)
b)
tub
tub
d.t
c)
d)

Figure 28

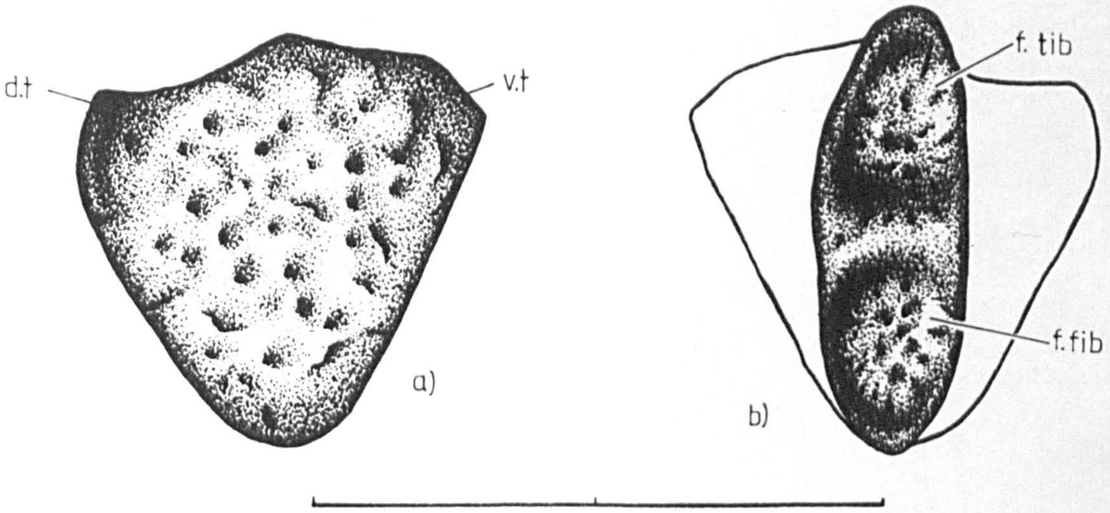
Proximal and distal articular surfaces of femur and humerus of Ophthalmosaurus icenicus.

a) proximal left femur, and b) distal left femur of H.M. V1916.

c) proximal left humerus, and d) distal left humerus of H.M. V1893.

Scale = 10 cm.

d.t. = dorsal trochanter; f.fib = facet for fibula; f.preax = facet for preaxial accessory epipodial element; f.rad = facet for radius; f.tib = facet for tibia; f.uln = facet for ulna; v.t. = ventral trochanter.


d.t
v.t
a)
f. tib
f. fib
b)

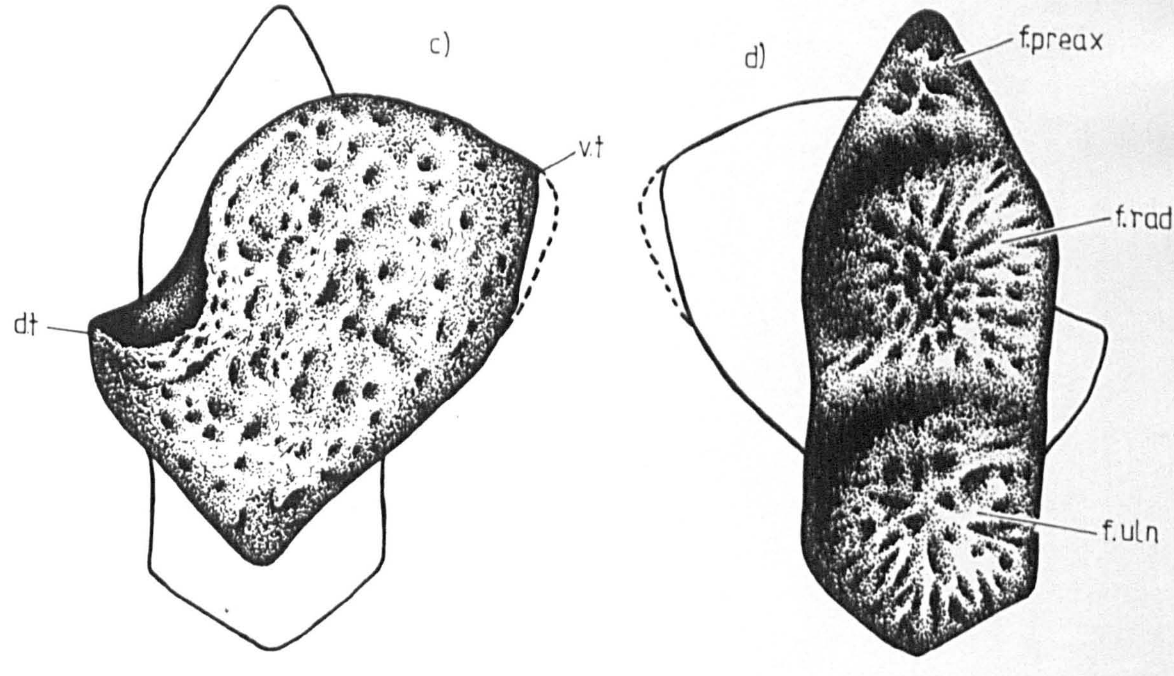
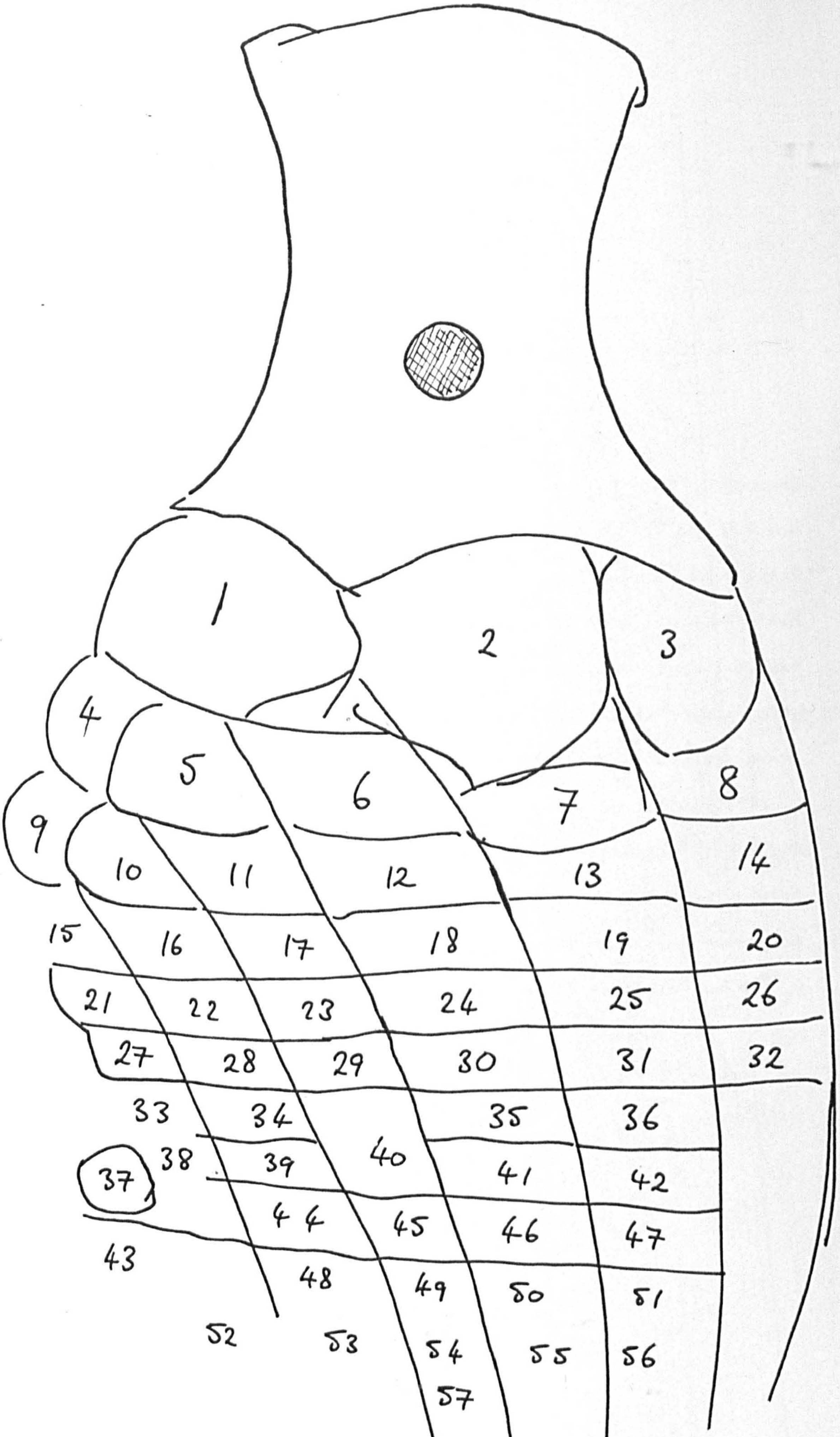

c)
v.t
dt
d)
f.preax
f.rad
f.uln

Figure 29

Tracing of outline drawing of plan of paddle of Ophthalmosaurus icenicus. Right paddle of B.M.N.H. R3702. Original drawing has caption in Alfred Leeds' handwriting which reads: "Plan of paddle marked with red ink dot." Numbers are those of Alfred Leeds.


1
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7
8
9
10
11
12
13
14
15
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17
18
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20
21
22
23
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56
57

Figure 30

Reconstruction of right forepaddle of *Ophthalmosaurus icenicus*.

B.M.N.H. R3702. Dorsal view.

Scale = 10 cm.

hum = humerus; int = intermedium; pisi = pisiform; pre = preaxial accessory element; r = radius; rad = radiale.

Nomenclature slightly modified from McGowan (1972a):

1 - 4 = distal carpals.

I - IV = metacarpals.

dig I - IV = primary digits I - IV.

preax = preaxial accessory digit.

poax = postaxial accessory digits 1 and 2.

p_1^{IV} = 1st phalange of primary digits I and IV.

p_4^{III} = 4th phalange of primary digit III.

p_1^{I} = 1st phalange of primary digit I.

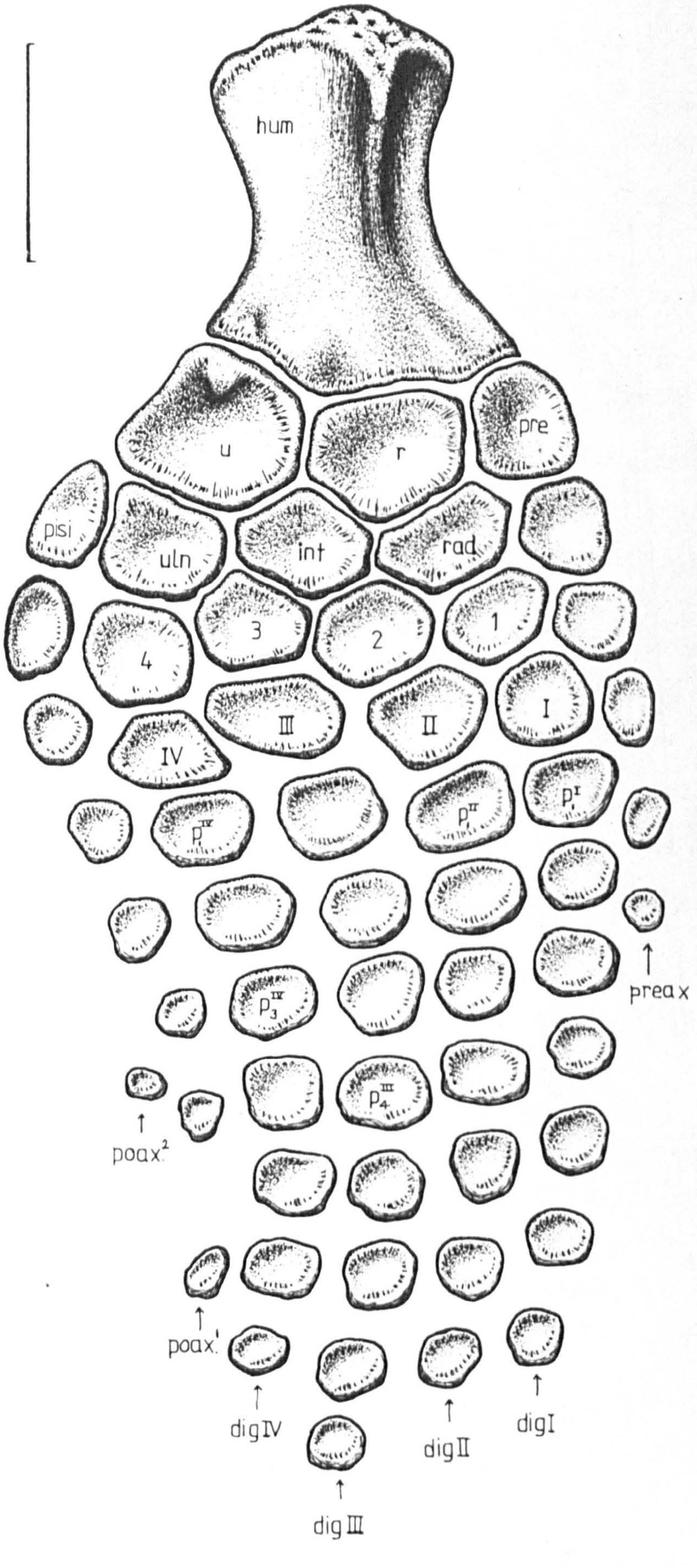

hum
u
r
pre
pisi
uln
int
rad
4
3
2
1
IV
III
II
I
p_1^{IV}
p_1^{II}
p_1^{I}
preax
p_3^{IV}
p_4^{III}
poax.²
poax.¹
dig IV
dig III
dig II
dig I

Figure 31

Left pelvic girdle of Ophthalmosaurus icenicus. H.M. V1916.

a) lateral, b) mesial view.

Scale = 10 cm.

acet = acetabulum; f.il = facets for ilium; for = foramen marking suture between pubis and ischium; il = ilium; lig = area for ligamentous attachment to vertebral column; no = notch marking original suture between pubis and ischium; pubisch = puboischium.

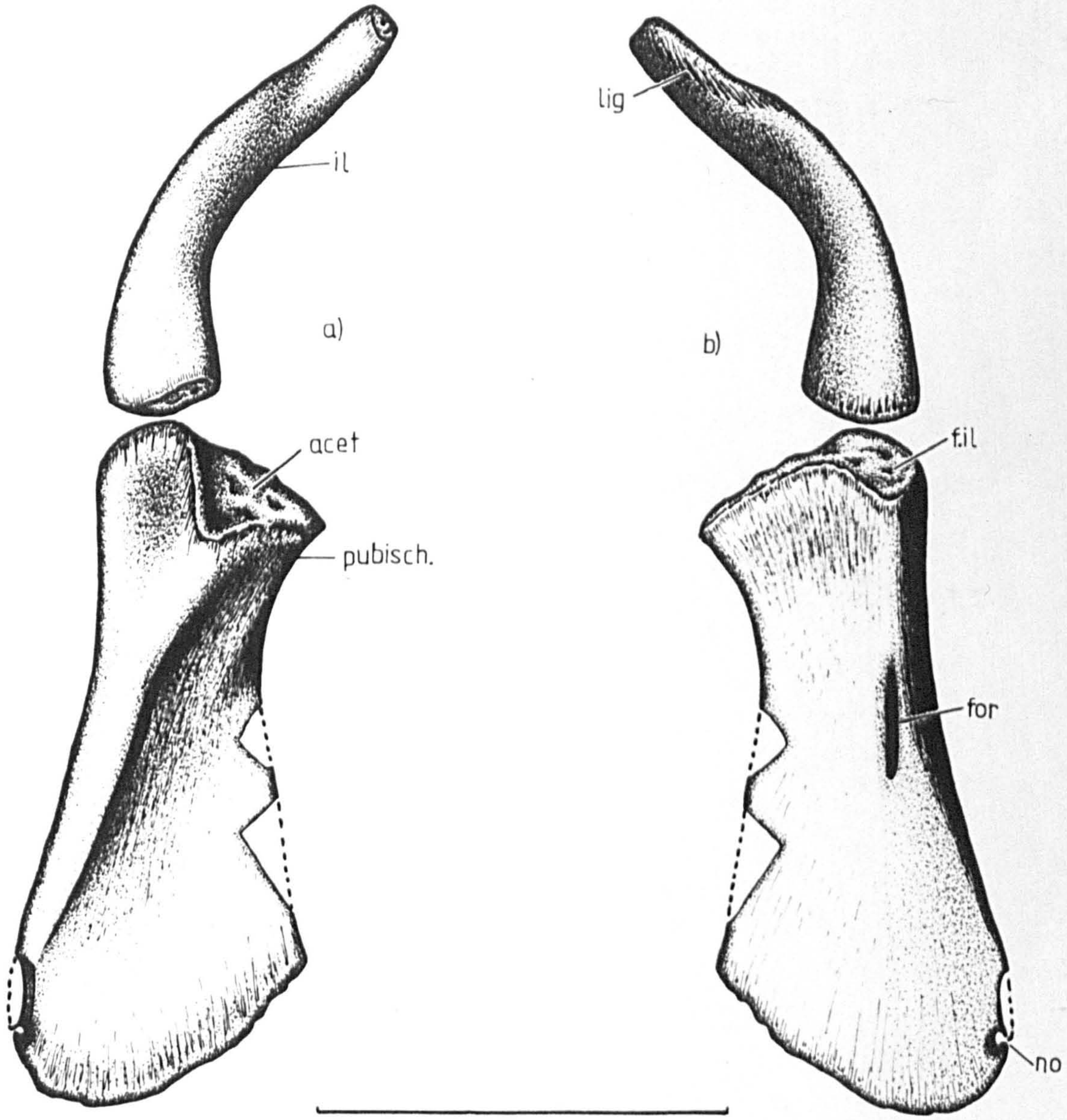

il
lig
a)
b)
acet
f.il
pubisch.
for
no

Figure 32

Left femur of Ophthalmosaurus icenicus. H.M. V1916.

a) ventral, b) dorsal, c) anterior, d) posterior view.

Scale = 10 cm.

d t. = dorsal trochanter; m.sc = muscle scar; proj = anterior blunt projection; v t. = ventral trochanter.

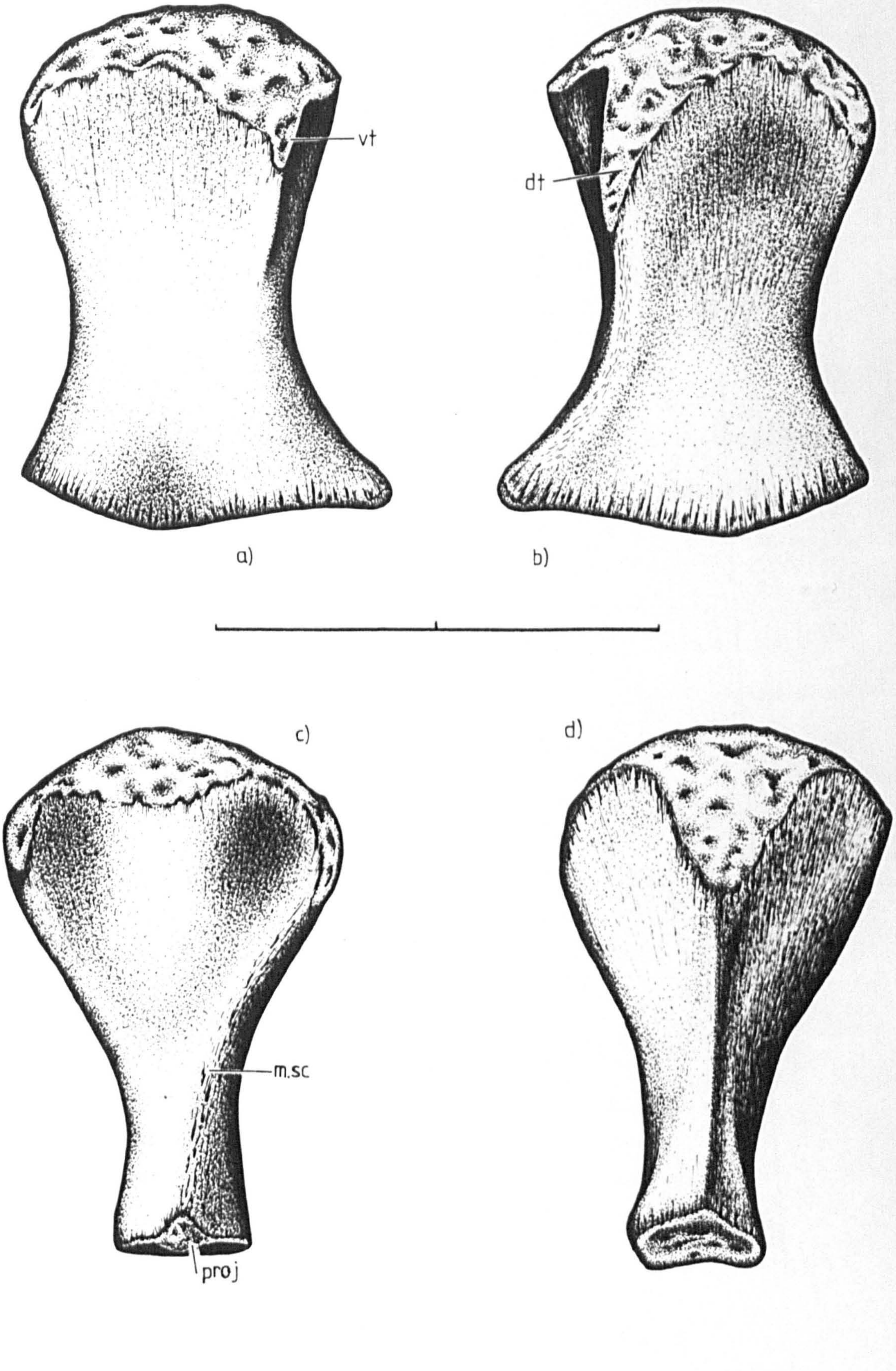

vt
dt
a)
b)
c)
d)
m.sc
proj

Figure 33

Reconstruction of right hind paddle of Ophthalmosaurus icenicus, based on Andrew's (1910) figure 41. B.M.N.H. R4693 - 5. Dorsal view.

× $^2/_3$.

d.t. = dorsal trochanter; fem = femur; fib = fibula; tib = tibia; I - III = digital rows I - III.

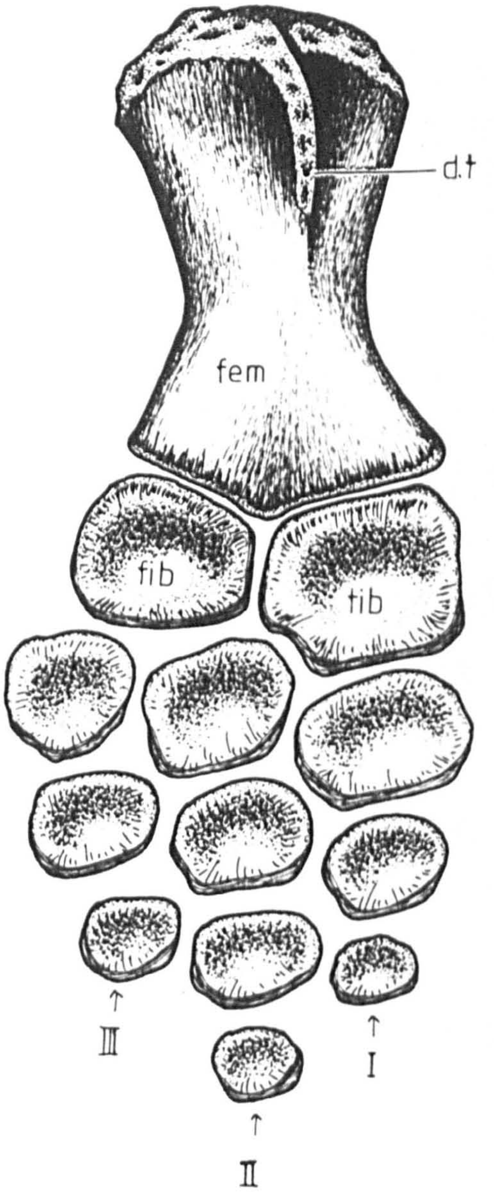

d.t
fem
fib
tib
III
I
II

Figure 34

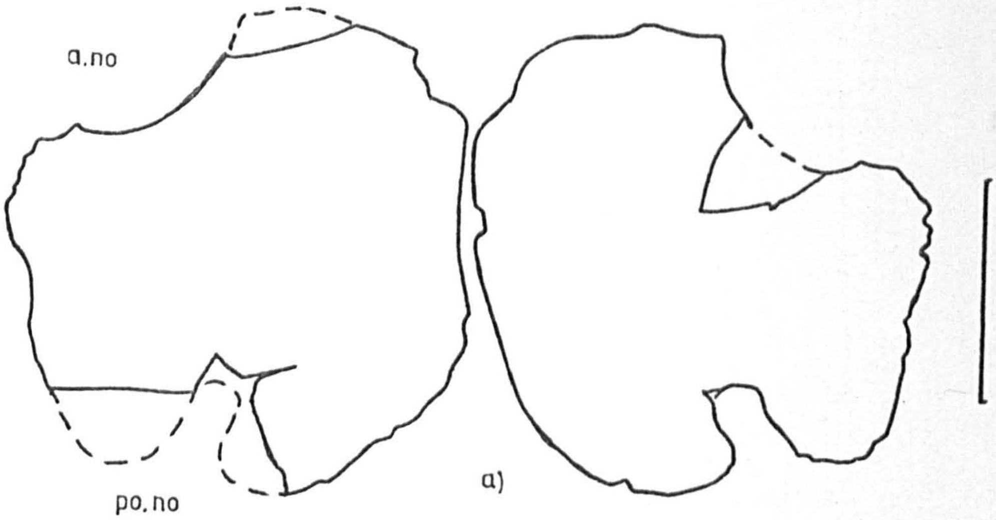
Line drawings of coracoids, dorsal view, of *Ophthalmosaurus icenicus*.

a) B.M.N.H. R2133 (type specimen). b) L.M.100′1949/20.

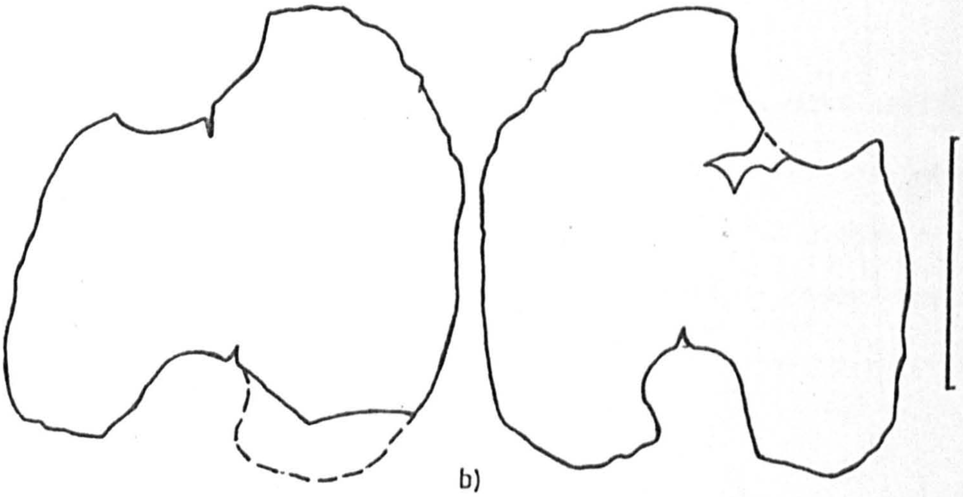
c) H.M. V1872. a) and b) both possess abnormal posterior notches.

Scale = 10 cm.

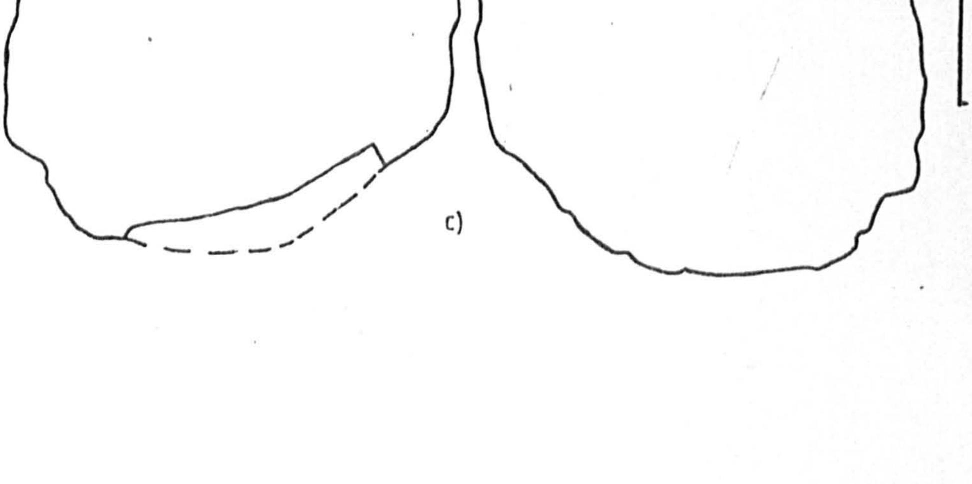
a.no = anterior notch; po.no = posterior notch.



a)



b)



c)

Figure 35

Outline reconstruction of *Ophthalmosaurus icenicus*, whole skeleton. Based on mounted skeleton in B.M.N.H., and information from other specimens. Mounted skeleton contains the following specimens:- R4124, R3893, R3702, and unspecified others.

Scale = 50 cm.

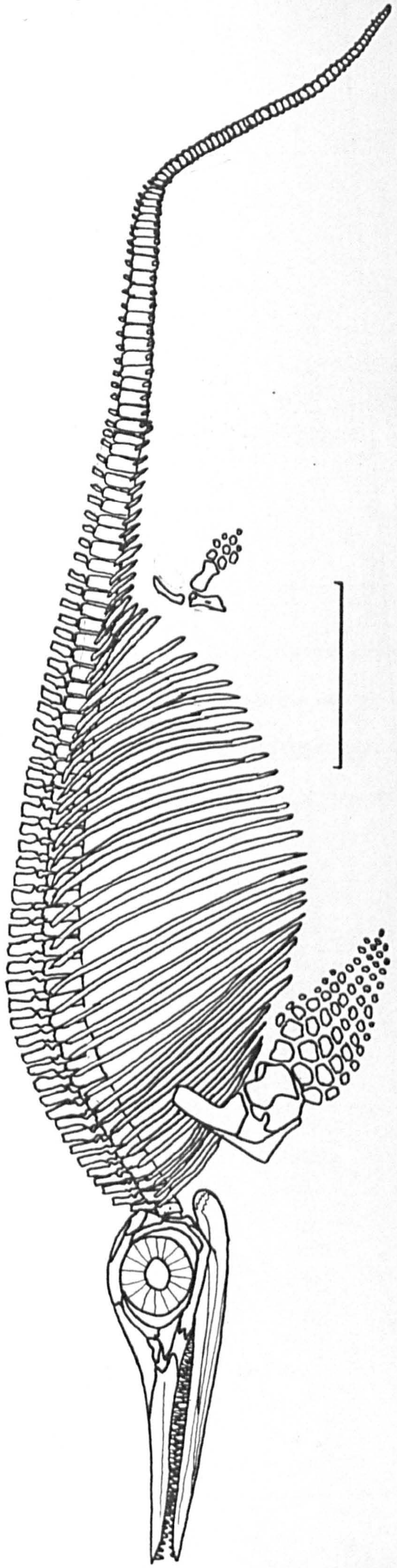


Figure 36

Graph of central height against position of centrum in the vertebral column (centra numbered from the head) for specimens of *Ophthalmosaurus icenicus* (B.M.N.H. R4753, R2133, H.M. V1611) and *Nannopterygius enthekiodon*.

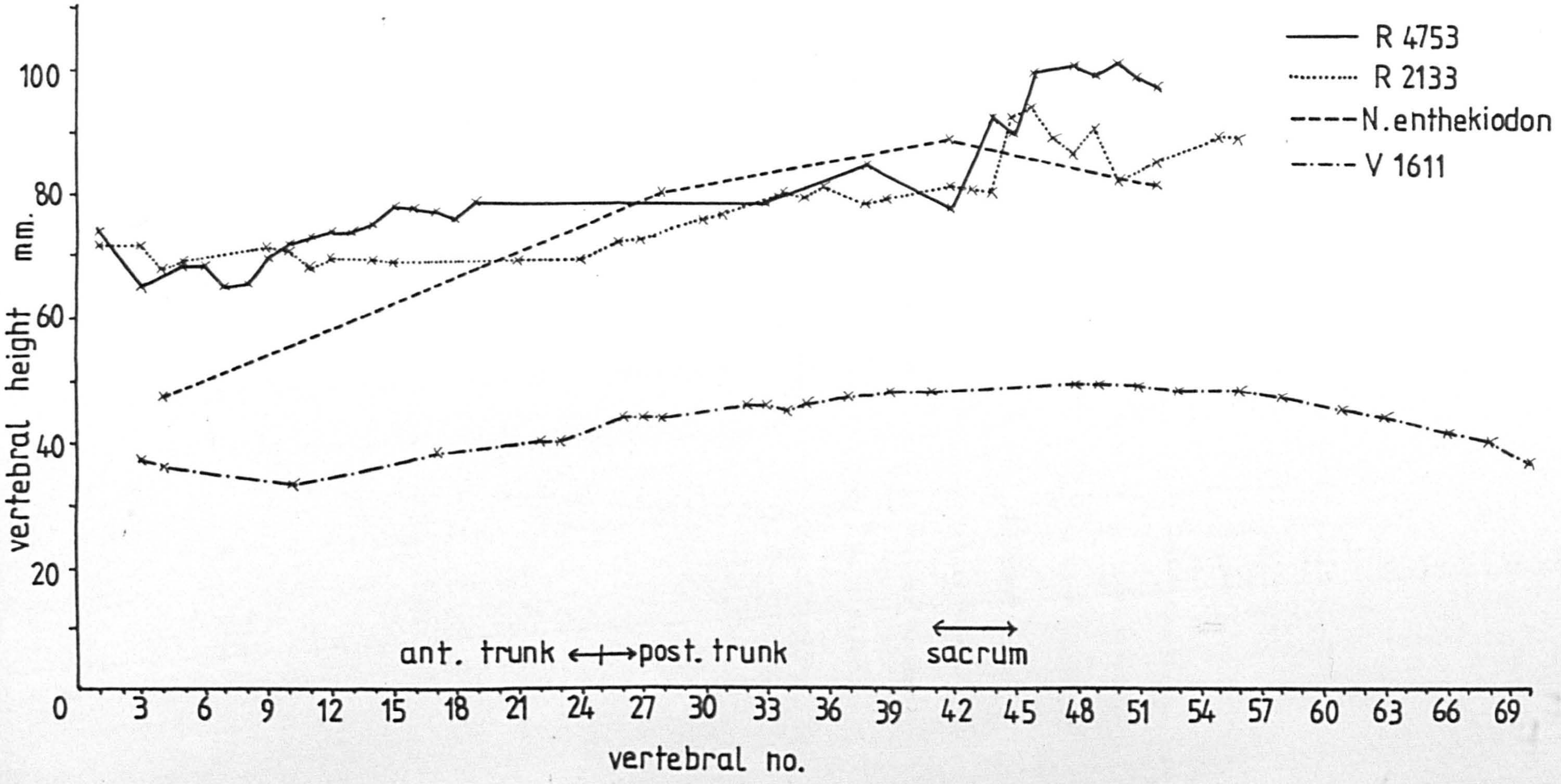

R 4753
R 2133
N. enthekiodon
V 1611
vertebral height mm.
100
80
60
40
20
0
3
6
9
12
15
18
21
24
27
30
33
36
39
42
45
48
51
54
57
60
63
66
69
vertebral no.
ant. trunk ←+→ post. trunk
sacrum

Figure 37

Line drawing of skull of Grendelius mordax, S.M. J68516. Reconstructed sutures are in broken line.

Scale = 10 cm.

ang = angular; d = dentary; fr = frontal; ju = jugal; lach = lachrymal; max = maxilla; na = nasal; nar = naris; par = parietal; pmax = premaxilla; po = postorbital; pof = postfrontal; pref = prefrontal; sa = surangular; scl = sclerotic ring; spl = splenial.

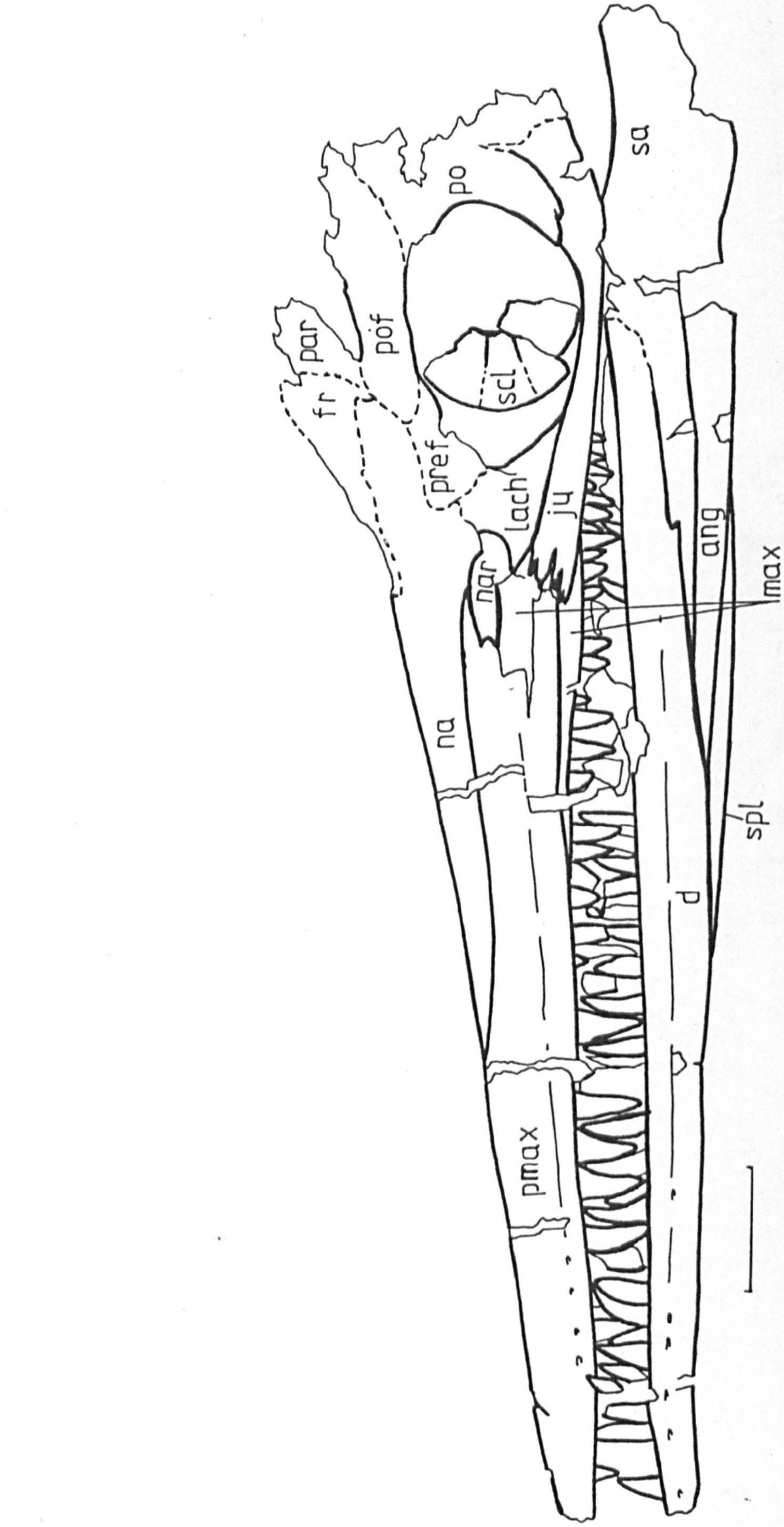

par
fr
pof
po
sa
scl
pref
lach
ju
nar
na
max
ang
spl
d
pmax

Figure 38

Basioccipital and basisphenoid of Grendelius mordax. S.M. J68516. a) basioccipital in lateral, and b) posterior view. c) basisphenoid in ventral view.

Scale = 10 cm.

b.pt.pr. = basipterygoid process; con = condyle; c.for = carotid foramen; ex.con = extracondylar area; f.ex = facet for exoccipital; f.op = facet for opisthotic; f.pt = facet for pterygoid; f.st = facet for stapes; not = notochordal pit; pal = groove for palatine ramus of facial (VII) nerve; para = base of parasphenoid.

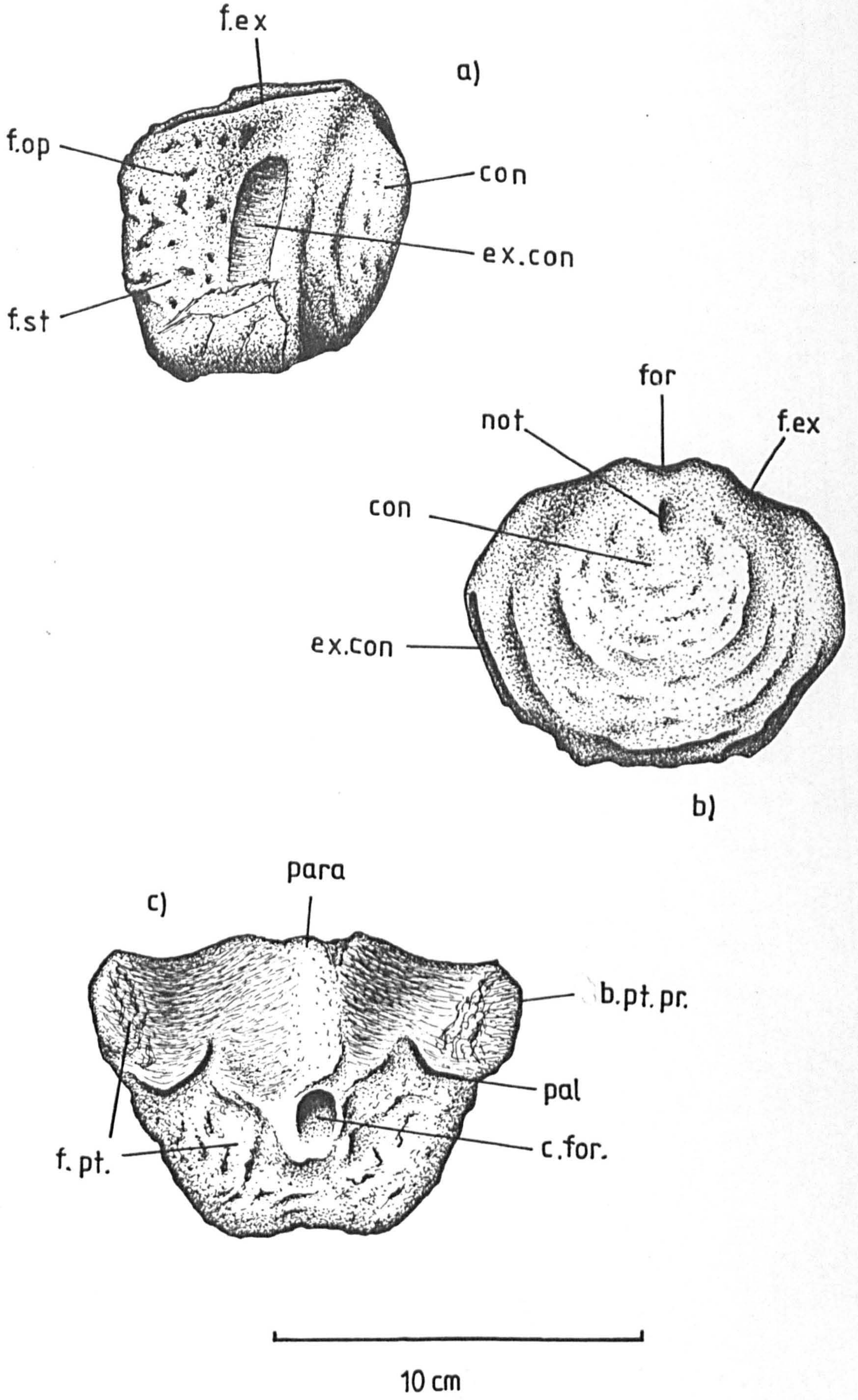

f.ex
a)
f.op
con
ex.con
f.st
for
not
f.ex
con
ex.con
b)
para
c)
b.pt.pr.
pal
c.for.
f. pt.
10 cm

Figure 39

Outline drawing of pectoral girdle and forepaddles of <u>Nannopterygius enthekiodon</u>. B.M.N.H. R46497. Coracoids and left scapula seen in ventral view. Left paddle detached and mounted below the rest of the specimen.

Scale = 10 cm.

cor = coracoid; clav = clavicle; l.hum = left humerus; l.scap = left scapula; r.hum = right humerus; r.scap = right scapula.

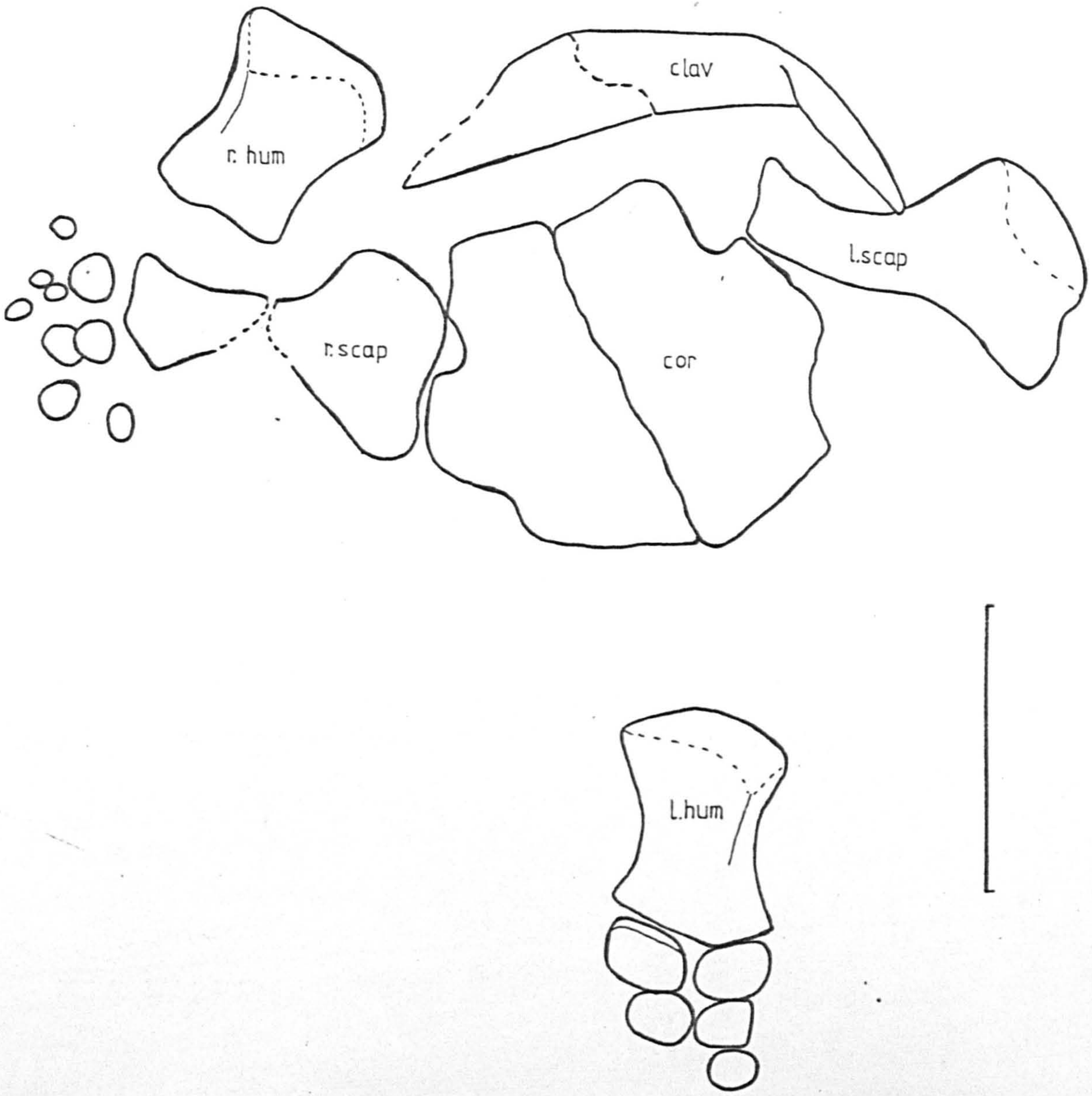

r. hum
clav
l.scap
r.scap
cor
l.hum

Figure 40

Dorsal right forepaddle of type specimen of *Brachypterygius extremus*. B.M.N.H. R3177. Humerus crushed proximally. Scale = 10 cm.

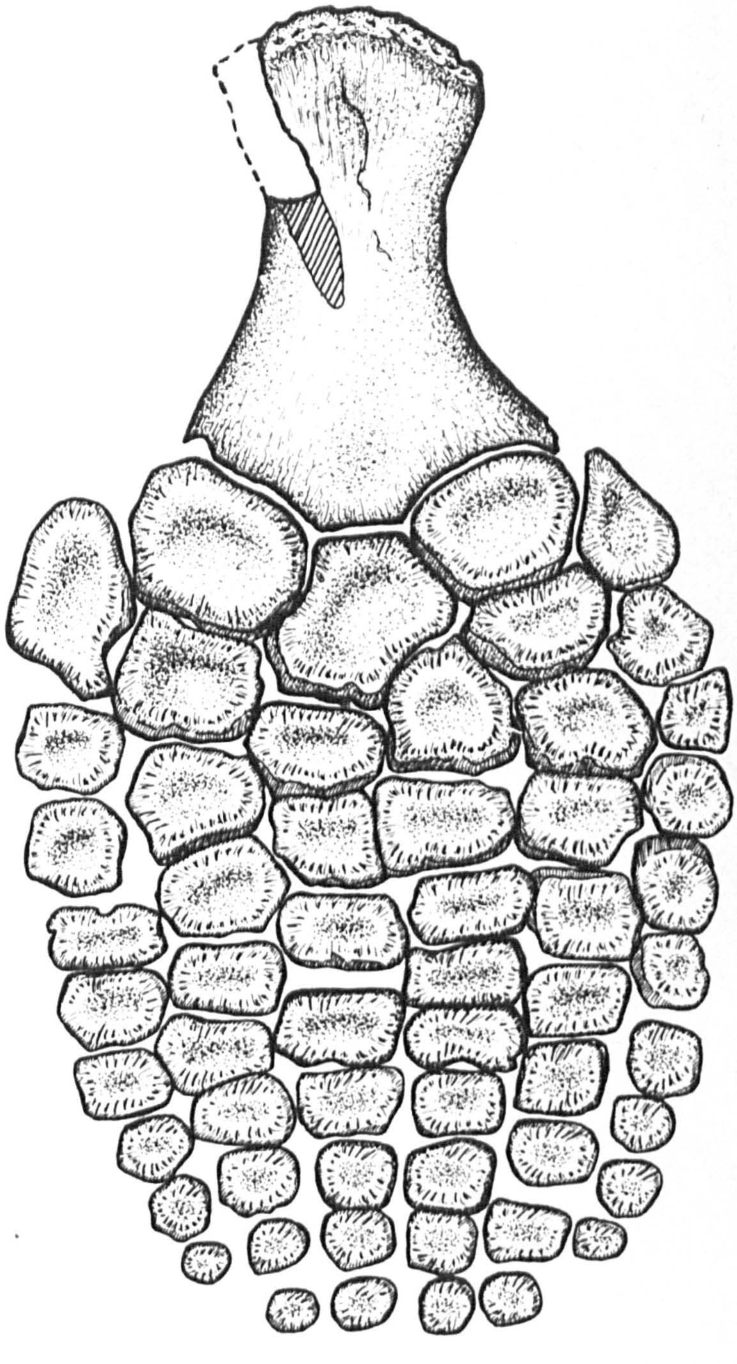


Figure 41

Dorsal right forepaddle of Brachypterygius extremus. S.M. J29864.

Humerus partially reconstructed in plaster, distally.

Scale = 10 cm.

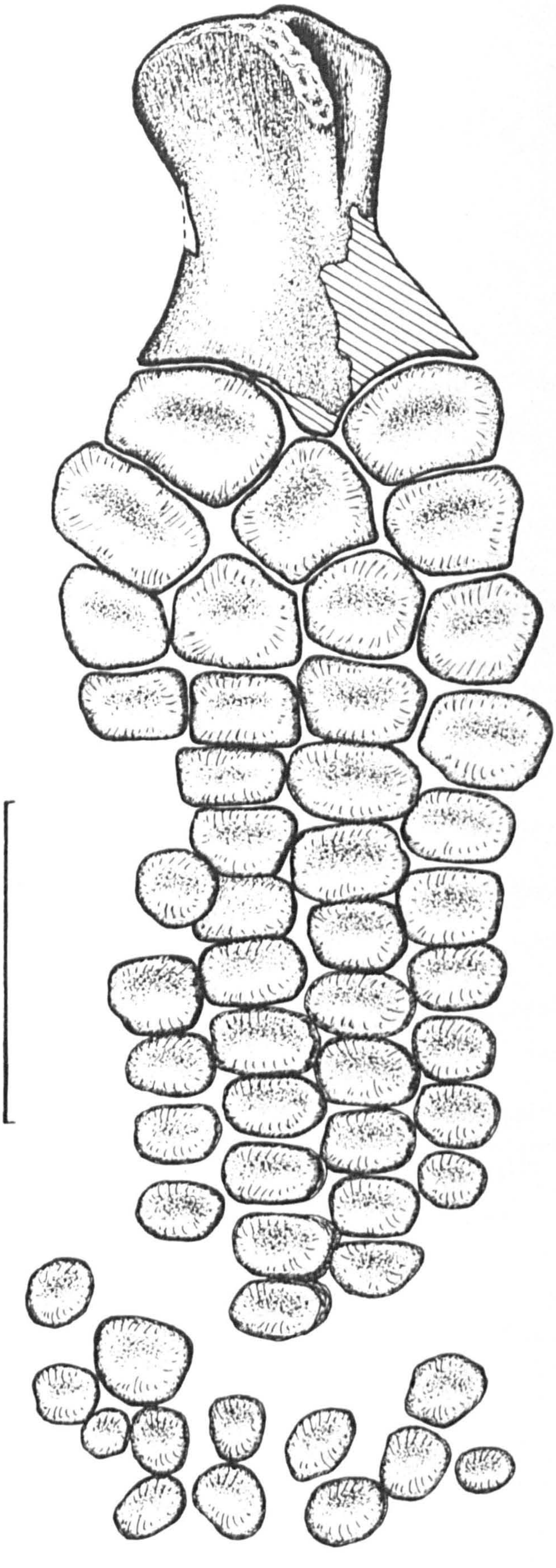


Figure 42

Ichthyosaur forepaddles.

a) from McGowan (1972a) *Stenopterygius quadriscissus*, a traditional longipinnate, showing longipinnate configuration.

b) *S. quadriscissus*, O.U.M. J2163, showing latipinnate configuration, including intermediary digit.

c) *Ichthyosaurus communis*, showing intermediary digits (from McGowan 1972a). d) *I. communis*, without intermediary digits (from McGowan 1972a). e) *Temnodontosaurus platyodon*, traditional longipinnate (from McGowan 1974a). f) *Mixosaurus cornalianus*, traditional latipinnate. (from McGowan 1972a). g) *Merriamia zittelli*, traditional longipinnate (from McGowan 1972a).

h) *Ichthyosaurus tenuirostris*, traditional longipinnate, B.M.N.H. R498. i) *Shonisaurus popularis* (from Camp 1980).

i = intermedium; r = radius; u = ulna; 1 - 5 = distal carpals.

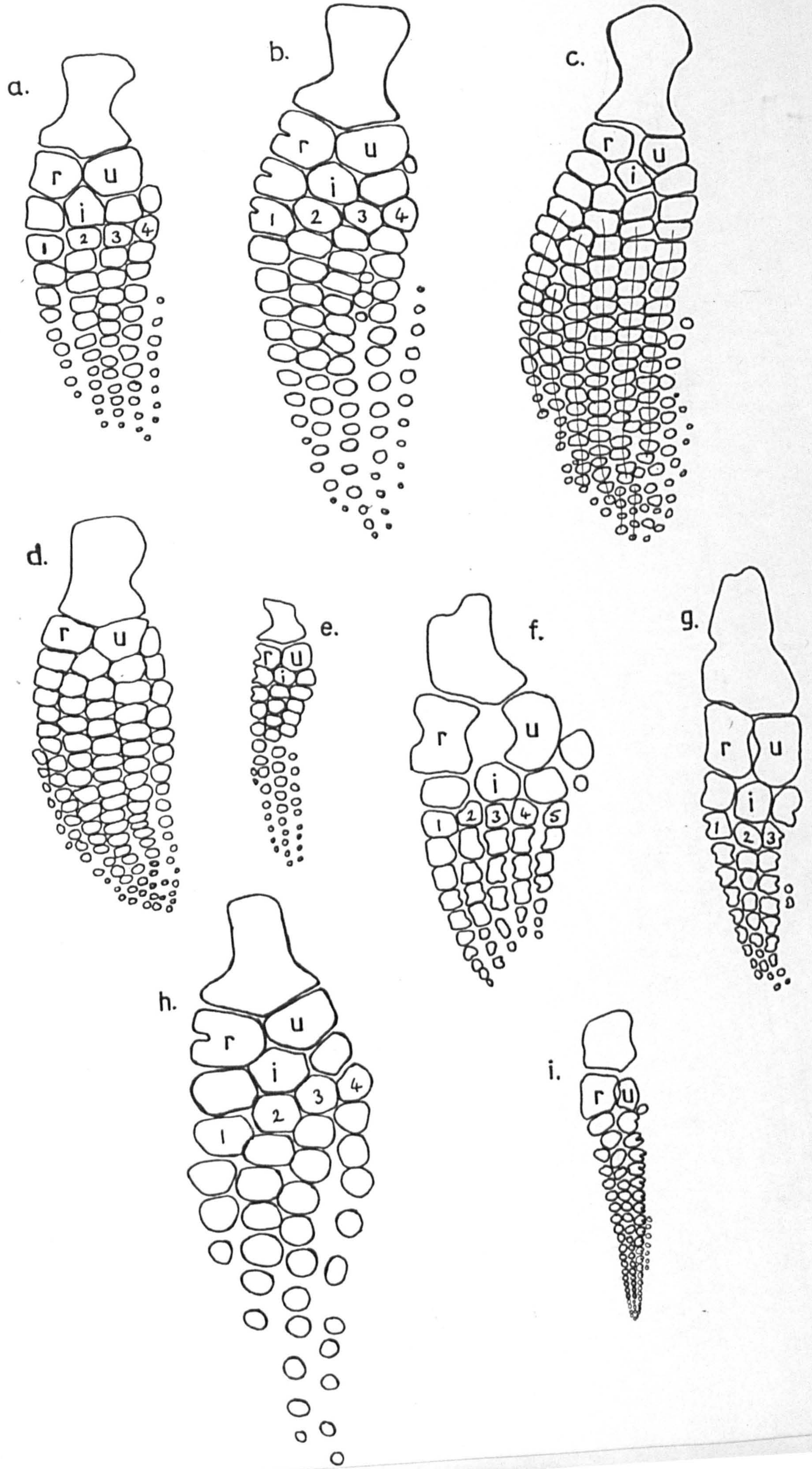

a.
r
u
i
1
2
3
4
b.
r
u
i
1
2
3
4
c.
r
u
i
d.
r
u
e.
r
u
i
f.
r
u
i
1
2
3
4
5
g.
r
u
i
1
2
3
h.
r
u
i
1
2
3
4
i.
r
u

Figure 43

Phylogenetic relationships within the Ichthyopterygia.

Derived (apomorphic) characters used in the cladogram .

(1) Neural arches remaining separate from centra. (2) Specialised tail vertebrae. (3) Infolding of primary dentine in tooth base. (4) Relatively large eye. (5) Special fossae for origin of M.adductor mandibulae. (6) Teeth necked between root and crown. (7) Parapineal foramen situated at fronto-parietal suture. (8) Elongate snout. (9) Reduction of metapodials. (10) Reduction in size of hind limb. (11) Isodonty. (12) Loss of infolding of tooth base. (13) Reduction or loss of 5th primary digit. (14) Median constriction of humerus. (15) Reduction of metapodials. (16) Extreme reduction of 4th distal carpal and primary digit IV. (17) Pelvic girdle no longer plate-like. (18) Hypocercal tail. (19) Shortening of epipodials. (20) Hindlimb and pelvic girdle reduced. (21) Fused pubo-ischium. (22) Reduction of 4th distal carpal and primary digit IV.

The unique derived character (21) separates the family Ichthyosauridae into the following sub-families: Ichthyosaurinae, Merriam 1908 (to include _Ichthyosaurus_, _Brachypterygius_ and _Nannopterygius_) and Ophthalmosaurinae (nom.nov.) to include _Ophthalmosaurus_ and _Stenopterygius_.

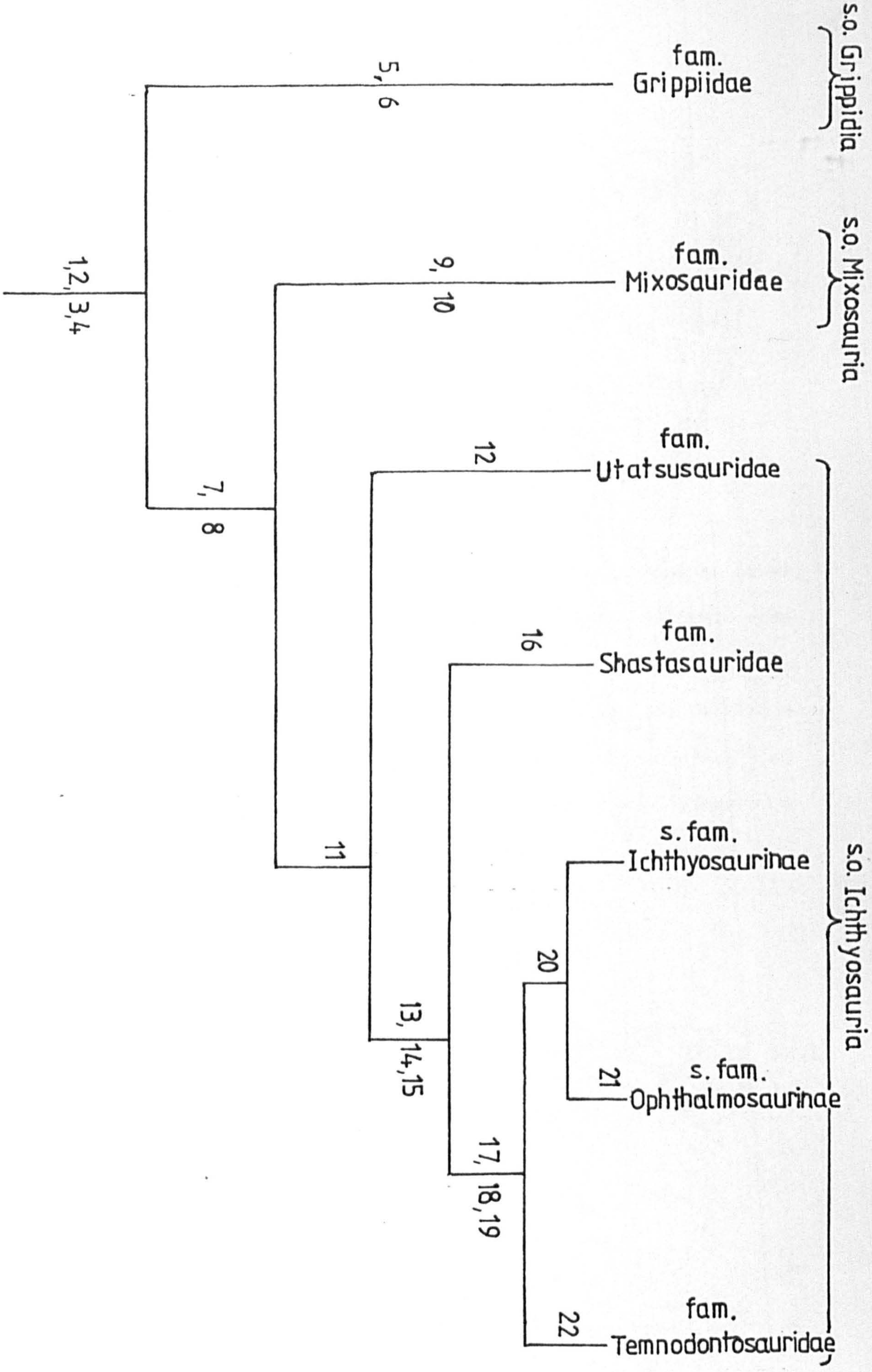
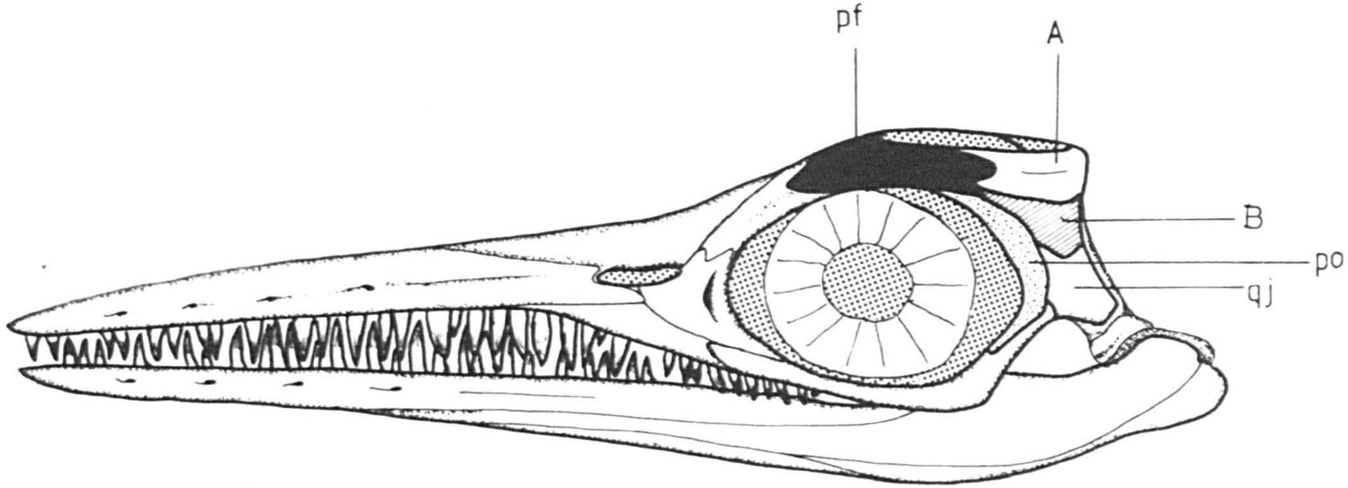
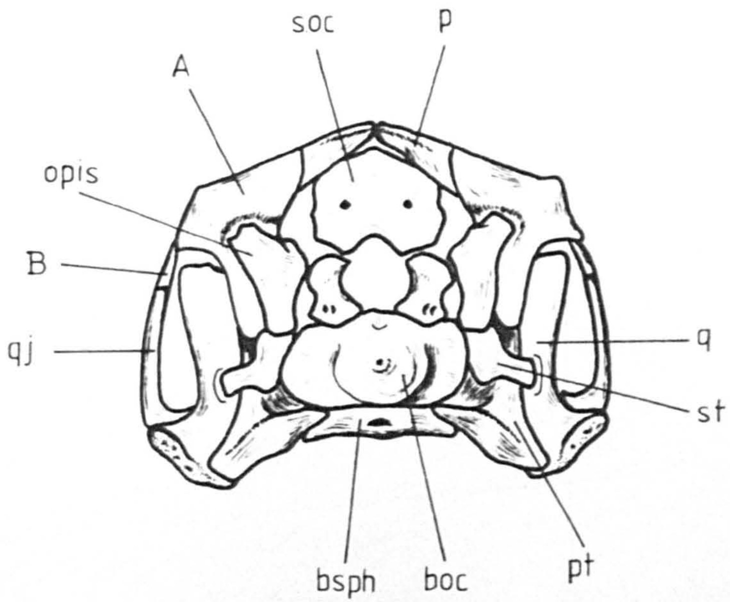

1,2, 3,4
5, 6
fam. Grippiidae
s.o. Grippidia
7, 8
9, 10
fam. Mixosauridae
s.o. Mixosauria
11
12
fam. Utatsusauridae
13, 14,15
16
fam. Shastasauridae
17, 18,19
20
s. fam. Ichthyosaurinae
21
s. fam. Ophthalmosaurinae
22
fam. Temnodontosauridae
s.o. Ichthyosauria

Figure 44

Skull of Ichthyosaurus in side, dorsal and occipital view to show elements A and B.

A = element A; B = element B; boc = basioccipital; bsph = basisphenoid; opis = opisthotic; p = parietal; pt = pterygoid; po = postorbital; pf = postfrontal; q = quadrate; qj = quadratojugal; soc = supraoccipital; st = stapes.


pf
A
B
po
qj


soc
p
A
opis
B
qj
q
st
bsph
boc
pt

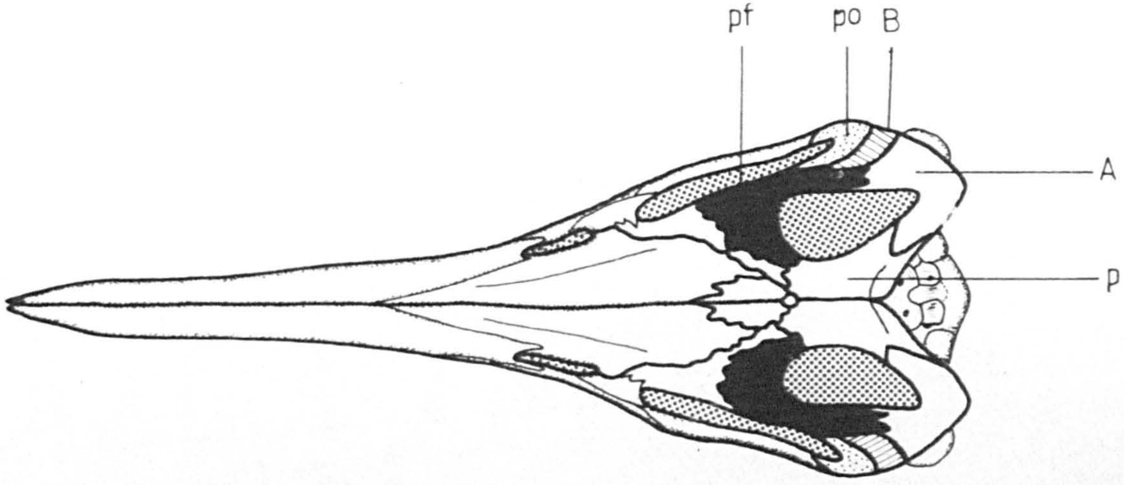
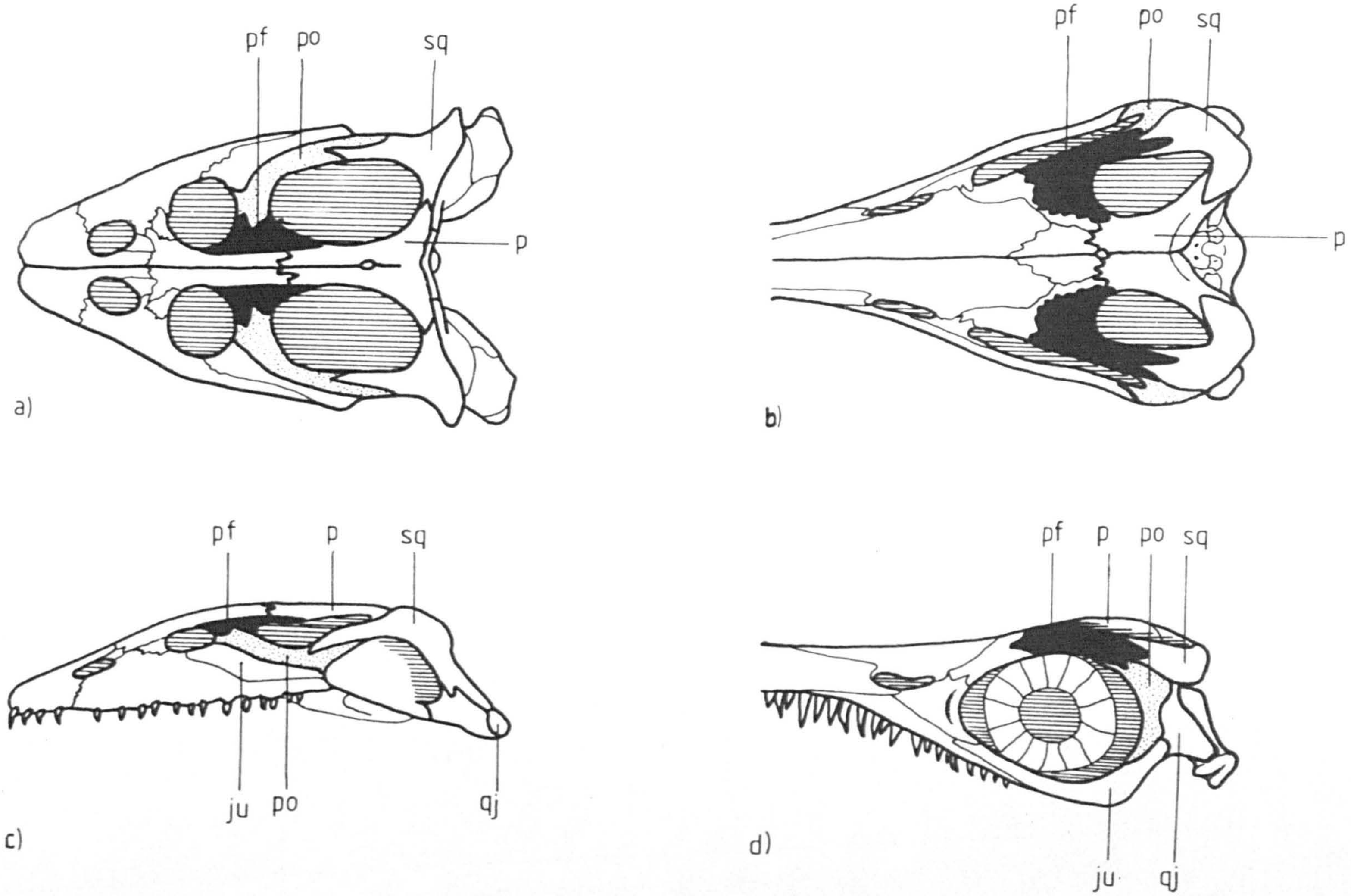

pf
po
B
A
p

Figure 45

Skulls of Simosaurus a),c) and Ichthyosaurus b),d).

a),c) euryapsid pattern. b),d) ichthyosaur skull under interpretation of Romer (1968) and McGowan (1973); also primitive ichthyopterygian condition for hypothesis II.

ju = jugal; p = parietal; pf = postfrontal; po = postorbital; qj = quadratojugal; sq = squamosal.



a), c), Simosaurus
[after Kuhn-Schnyder, 1980]

b), d), Ichthyosaurus
[after Romer, 1968]

Figure 46

Traditional interpretation of ichthyosaur skull a),b), compared to skulls of the procolophonids, Procolophon c),d) and Owenetta, e). a) and b) are also primitive ichthyopterygian condition for hypothesis I.

pf = postfrontal; po = postorbital; qj = quadratojugal; sq = squamosal; tab = tabular.

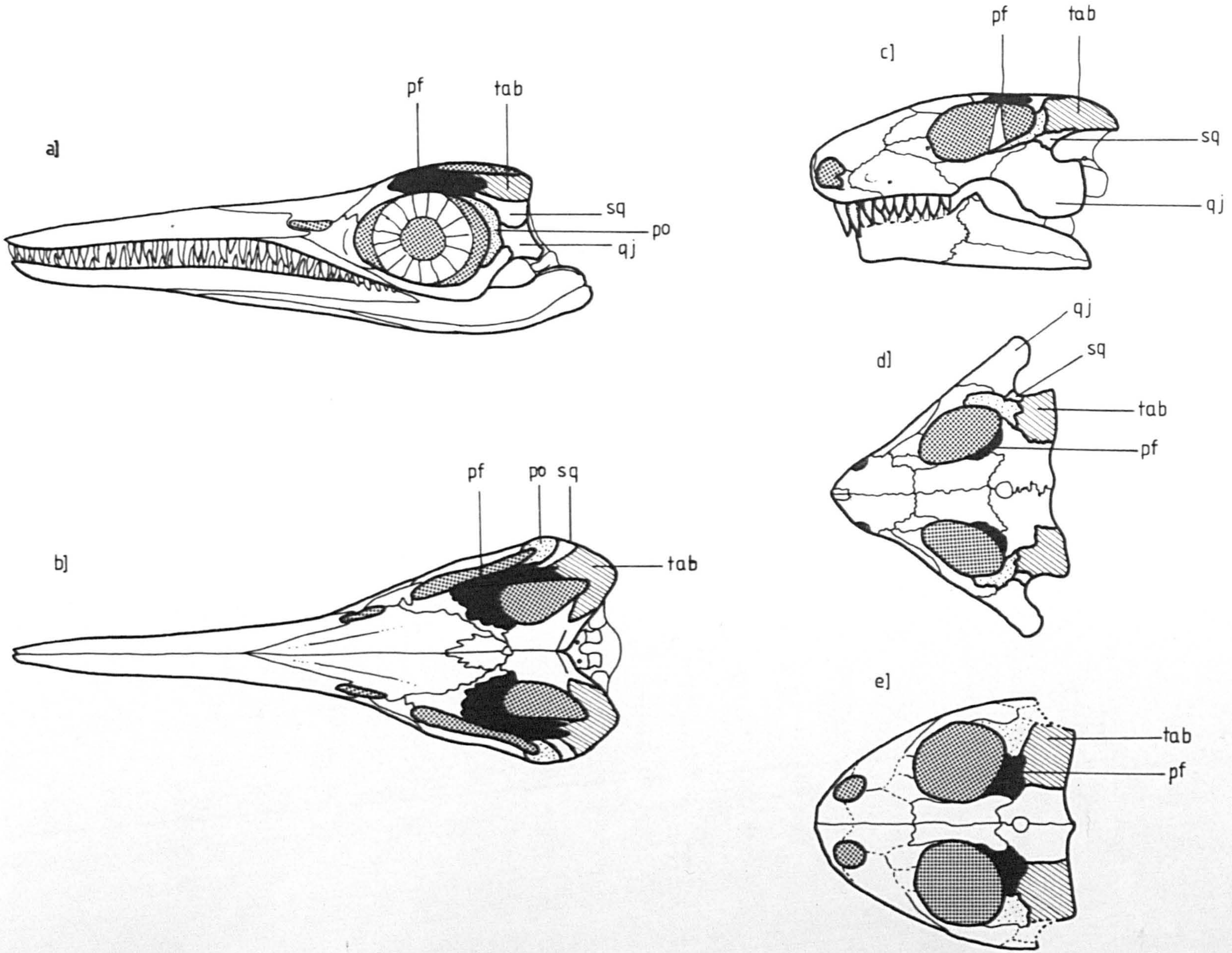

a]
pf
tab
sq
po
qj
b]
pf
po
sq
tab
c]
pf
tab
sq
qj
d]
qj
sq
tab
pf
e]
tab
pf

Figure 47

Skulls of a) Grippia longirostris (after Mazin, 1980), b) Placochelys (after Kuhn-Schnyder, 1980), and c) Petrolacosaurus (after Kuhn-Schnyder, 1980). (Not all to same scale.)

a) = primitive ichthyopterygian condition.

b) = placodont skull pattern.

c) = primitive diapsid pattern.

ju = jugal; p = parietal; pf = postfrontal; po = postorbital;

qj = quadratojugal; sq = squamosal; st = supratemporal.

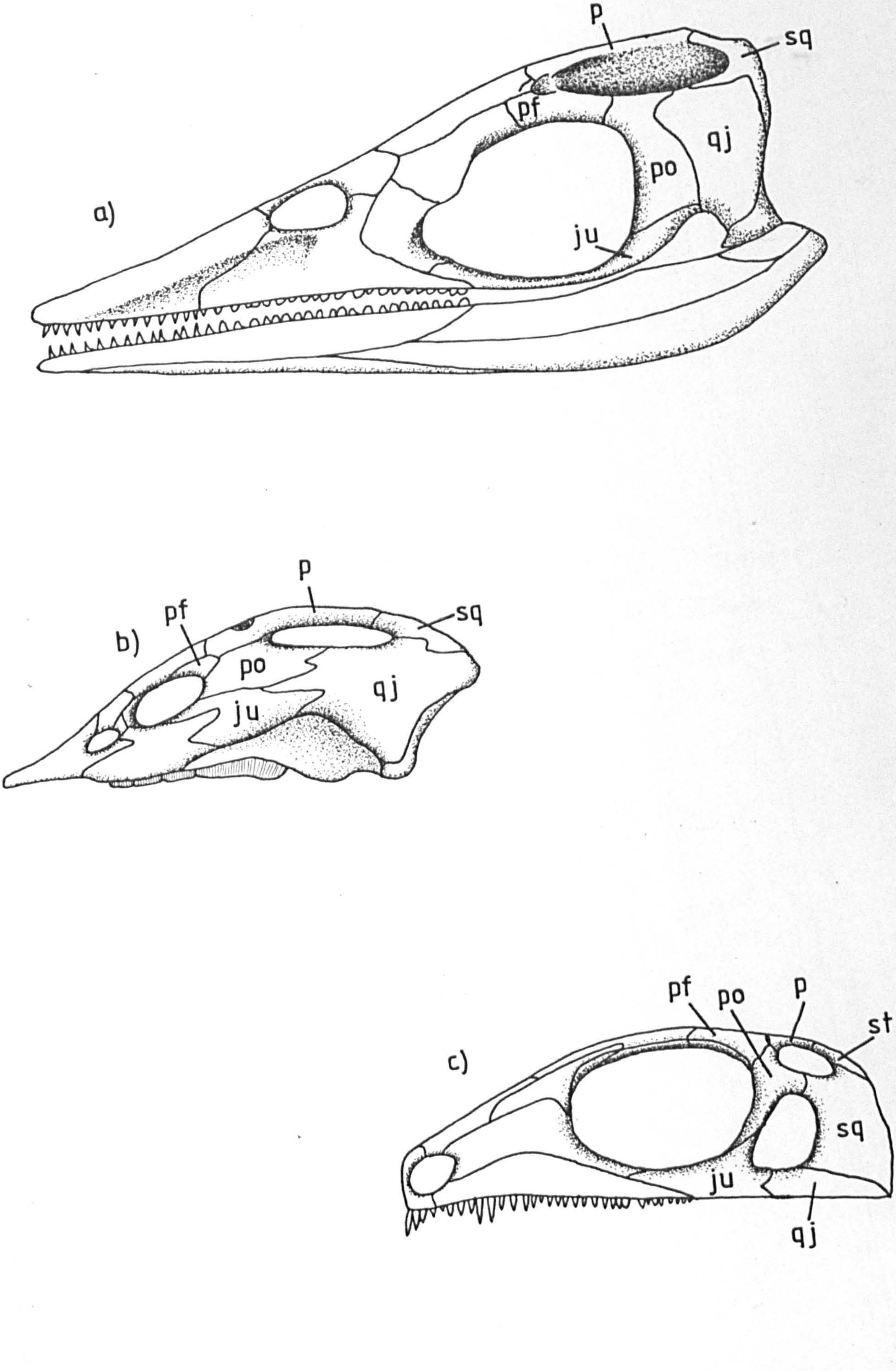

a)
p
sq
pf
qj
po
ju
b)
pf
p
sq
po
qj
ju
c)
pf
po
p
st
sq
ju
qj

Figure 48

Forepaddle of *Grippia longirostris* (from Mazin, 1980).

i = intermedium; p = pisiform; r = radius; u = ulna;

1 - 5 = distal carpals; I - V = metacarpals (primitively elongate).

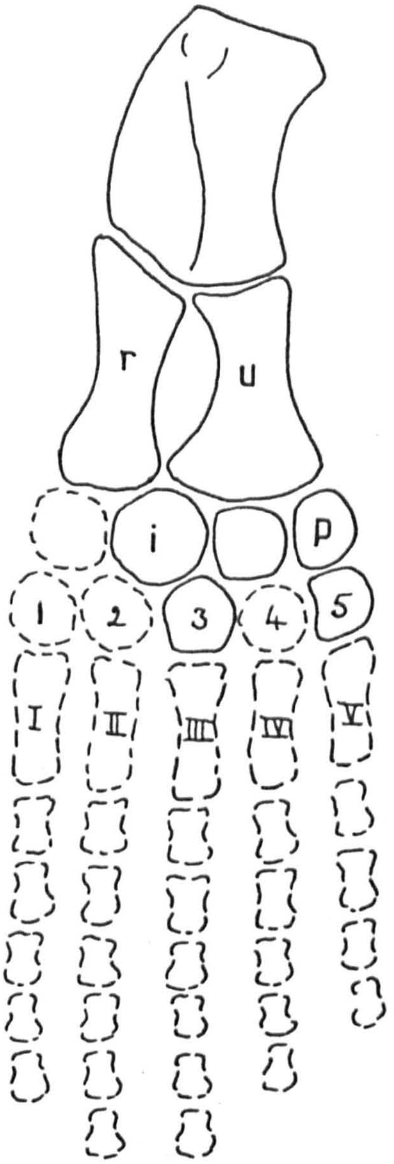

r
u
i
p
1
2
3
4
5
I
II
III
IV
V

Figure 49

Reconstruction of jaw adductor and abductor muscles of Ophthalmosaurus icenicus.

M.a.m. = M.adductor mandibulae.

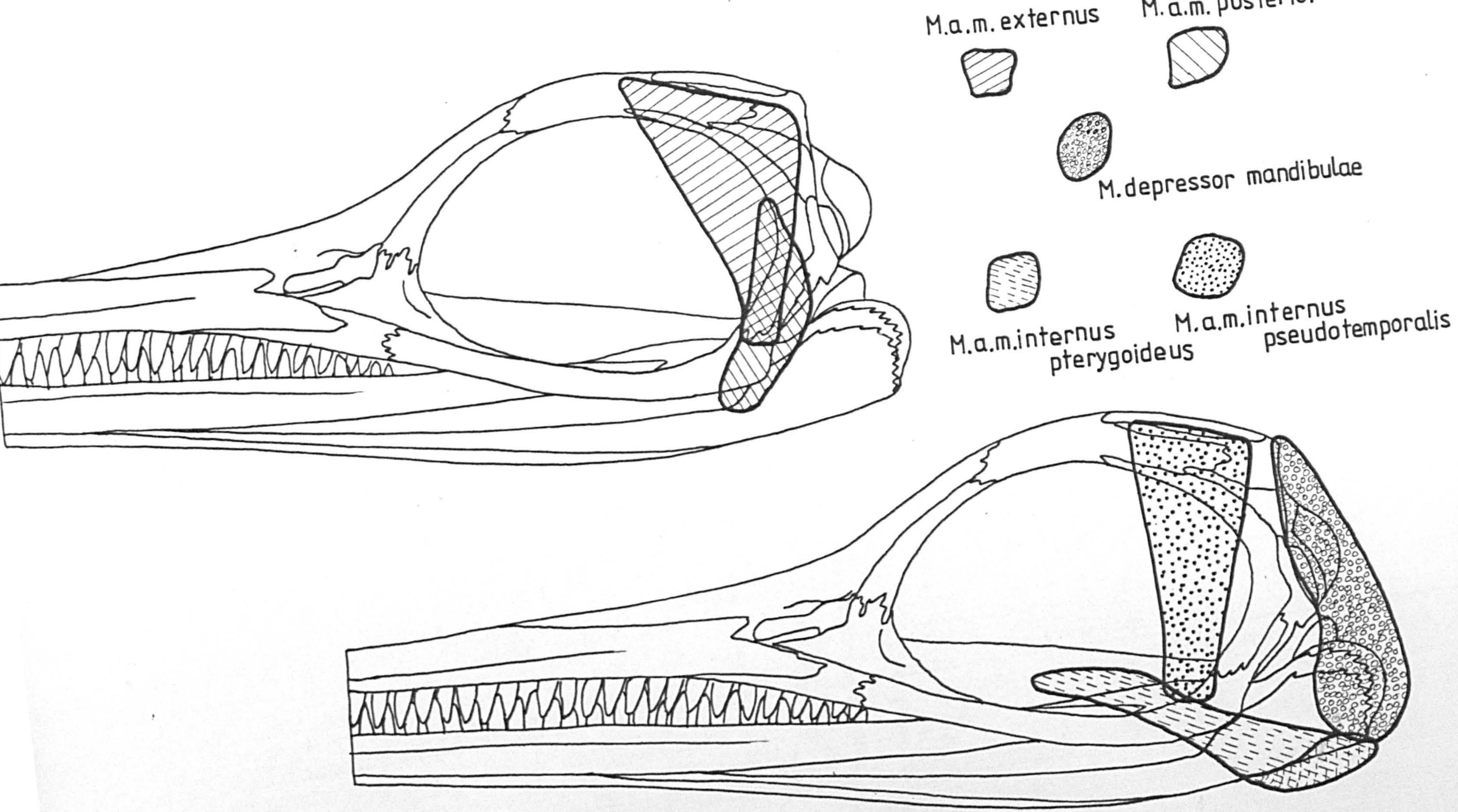

M.a.m. externus
M.a.m. posterior
M.depressor mandibulae
M.a.m.internus pterygoideus
M.a.m.internus pseudotemporalis

Table 3

Vertebral column counts for specimens of Ophthalmosaurus icenicus. Andrews' reconstruction was given in Andrews (1910). R4124 and R3893 are two specimens making up the vertebral column of the mounted skeleton in the B.M.N.H.

specimen	ant. trunk	post. trunk	ant. caudal	tail bend	post. caudal	total
SMJ 63920-64037	25	19	21	4	51	120
H.M. V 1611	25	18	29			72
" V 1871	27	19	25		1	72
" V 1868	25	16	← 61 →			102
" V 1873	28	13	← 27 →			68
" V 1875	27	16	← 35 →			78
B.M.N.H. R 2160	20	18	← 32 →			70
" R 2133	19	19	← 20 →			58
" R 2150	21	18	← 36 →			75
" R 4753	23	13	← 12 →			48
" R 3533	22	16	← 15 →			53
Andrew's reconstructn.	19	19	34	5	45	122
R 4124 + R 3893	19	19	38	5	43	124

Plate 1

Specimen No. B.M.N.H. R4753 showing element B.

Scale = 10 cm.

B.= element B; po = postorbital; pof = postfrontal; sq = squamosal.


10 cm
sq
B
po
pof

Plate 2

Specimen No. B.M.N.H. R2740, showing element B.

Scale = 10 cm.

The bones in the postorbital region are slightly disarticulated.

The specimen has been acid-prepared to show element B more clearly.

B = element B; po = postorbital; pof = postfrontal; sq = squamosal.


pof
10 cm
sq
B
po

Plate 3

Coracoids of *Ophthalmosaurus icenicus*. L.M.100'1949/20. Ventral view.

Scale = 10 cm.

a.no = anterior notch; p.no = posterior notch.


a.no
p.no

Plate 4

Skull of Grendelius mordax, type specimen, S.M. J68516.

Scale = 10 cm.

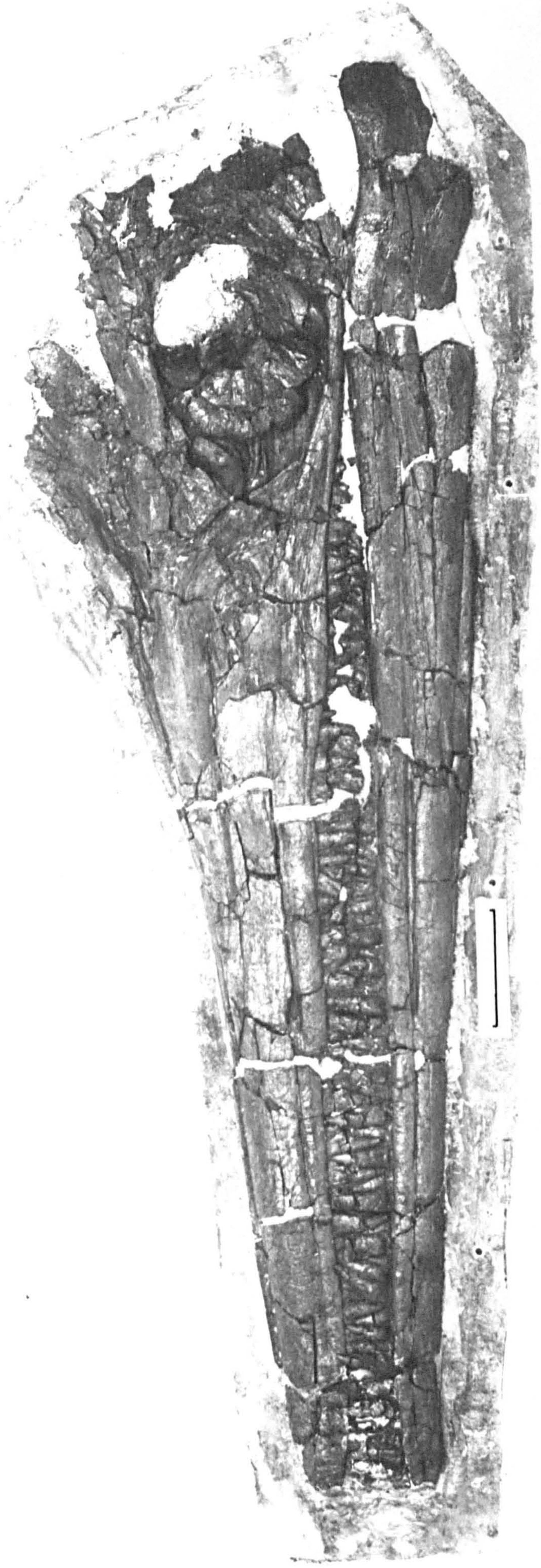
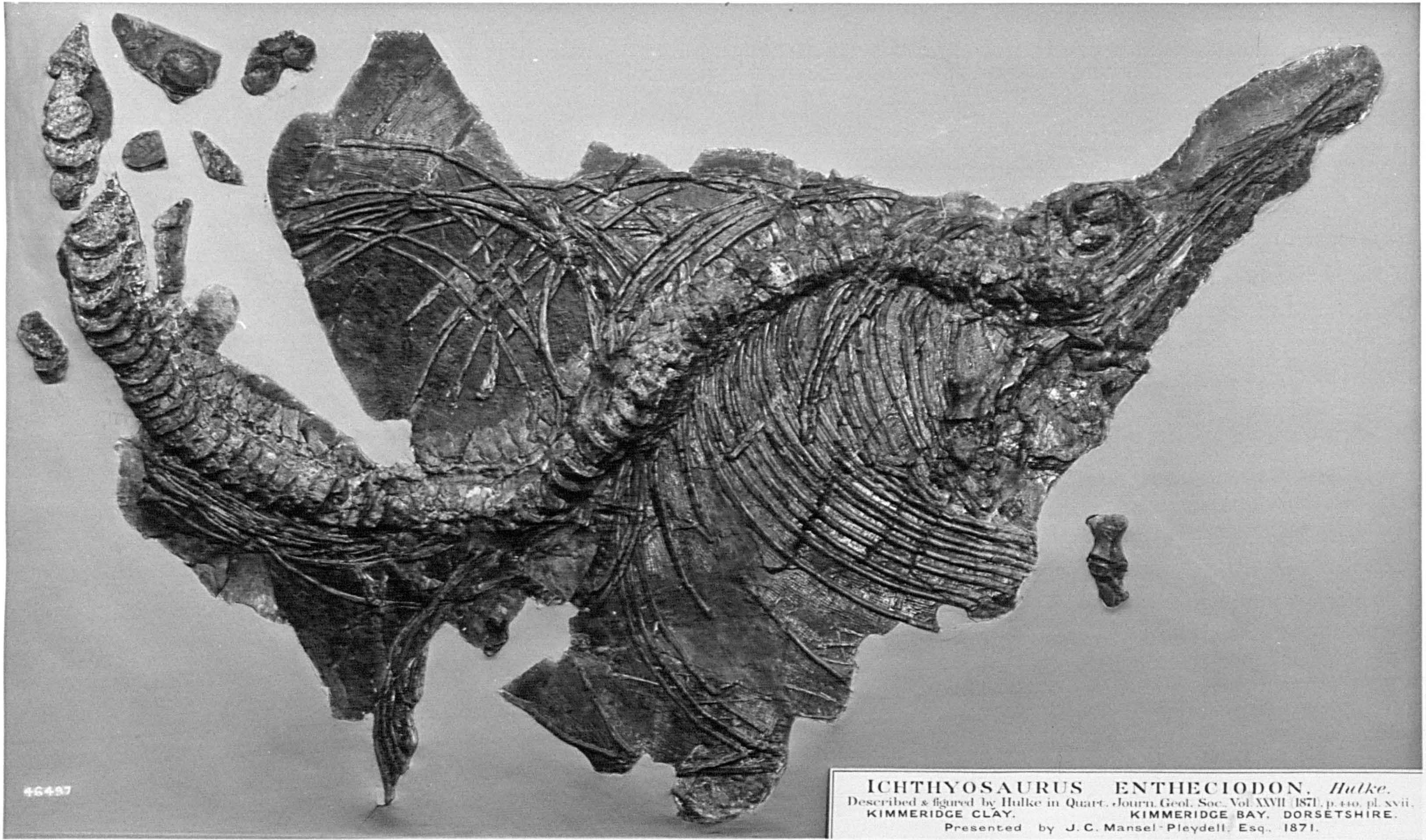


Plate 5

Type specimen of *Nannopterygius enthekiodon*. B.M.N.H. R46497.


46497
ICHTHYOSAURUS ENTHECIODON, *Hulke.*
Described & figured by Hulke in Quart. Journ. Geol. Soc., Vol. XXVII (1871), p. 440, pl. xvii.
KIMMERIDGE CLAY.
KIMMERIDGE BAY, DORSETSHIRE.
Presented by J. C. Mansel-Pleydell, Esq., 1871.