THE STRUCTURE OF CERTAIN JURASSIC HOLOSTEAN FISHES WITH SPECIAL REFERENCE TO THEIR NEUROCRANIA

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INTRODUCTION

The term Holostei is in the process of being transformed from one expressing (or intending to express) some phylogenetic type of classification into one denoting a structural grade—a transformation commonly suffered by a term of long standing as the essential characters of its component genera are better understood. Unfortunately, understanding of this particular stage in Actinopterygian evolution is far from complete, and at present it is not possible to replace the old classification by one that will not have to be thoroughly revised in a few years' time. Since, therefore, the present work (which was essentially complete in 1940) deals primarily with the structure of a few Jurassic neurocrania the term Holostei may still serve conveniently to cover the families in which they are found, although the origin of these is largely unknown and their degree of relationship a matter of debate. It will be found that a study of neurocrania occasionally produces some new evidence on these problems, but for a more complete discussion on classification reference may be made to those works expressly dealing with the subject, especially Brough (1939), Rayner (1941) and Westoll (1944).

The dermal bones and body skeleton of the Jurassic fishes are often well preserved in the shales and limestones that make up a large part of the rocks of this period, but a very exceptional degree of preservation is necessary to enable the neurocranium to be described. Moreover, the earlier writers of the nineteenth century, primarily occupied in sorting the material into genera and species, were naturally concerned first with scales, fins, teeth and the general shape of the body, and secondly with the dermal bones where they were well preserved, so that it is not surprising to find, for instance, among the many descriptions of these fishes given by Agassiz (1833–1844), that references to the neurocranium are incidental and very rare.

The basis for all modern work is the *Catalogue of Fossil Fishes in the British Museum*, compiled by Smith Woodward between the years 1889 and 1901; from 1884 onwards this writer also published many papers on the Jurassic fish faunas. Among the material dealt with, a few uncrushed or partially crushed skulls are described, and it is from these that we get the first systematic accounts of the neurocranium. The genera concerned are:

Lepidotus *Dapedius*	(1893, 1895)	*Caturus* *Osteorachis*	(1895, 1897*a*)	*Eurycormus* *Aspidorhynchus*	(1890) (1918)

The neurocranium of *Dapedius* was also shortly treated by Frost (1913). These descriptions cover three families but are necessarily often incomplete, and it was not possible to make much correlation between the various bones and structures described. Since then Holmgren & Stensiö (1936) have published reconstructions and short descriptions of *Lepidotus* and *Hypsocormus*; an isolated Eugnathid cranium from the Portlandian has been described by Aldinger (1932), and *Leptolepis* by the author.

DESCRIPTION

This section gives an account of all the Jurassic neurocrania which the author has been able to examine except that of *Leptolepis*, already described (Rayner 1937). The bulk of the material so presented is new, but some of the specimens have been treated before, more or less shortly, by other writers. The dermal bones are not given in much detail except where previous accounts could be substantially supplemented or where they have some special structural or phylogenetic significance. In many cases the neurocrania were found isolated, or with insufficient of the remainder of the skeleton for specific identification. Those species which have been identified, however, are all described in the *British Museum Catalogue of Fossil Fishes*, Part III (Smith Woodward 1895), to which the reader is referred for matters of systematic position. The only exception to this is *Caturus porteri* which is newly founded.

The fishes examined were preserved in shale, clay or one of a variety of limestones; they were prepared by removing the matrix with a hand-needle, dental drill or pneumatic hammer, according to the size and delicacy of the specimen. In addition, one half of the specimen of *Caturus* from the Upper Lias was studied by means of serial sections and the construction of an enlarged model.

The following letters indicate some of the Museums from which the specimens were borrowed; others mentioned less frequently are given their full title in the text:

B.M.N.H.	British Museum (Natural History).
S.M.	Sedgwick Museum.

EUGNATHIDAE

The neurocranium in this family is described from *Caturus porteri* n.sp., from the Oxfordian, and an isolated cranium of the same genus, not specifically identifiable, from the Upper Lias. These two are dealt with separately, as the structures visible in one supplement those of the other. The Upper Liassic specimen is entirely uncrushed and provides some account of the internal structure; *C. porteri* exhibits most of the dermal bones and some of the neurocranial are distinguishable, but as the specimens are preserved in a soft clay and always distorted the proportions can only be deduced and the interior is unknown.

The neurocranium of *Caturus* is described in rather more detail than those that follow. It is better preserved and better known than that of any other Jurassic genus except *Leptolepis*, and the central position of the Eugnathidae among the Holostei, and in particular the relations of the family to *Amia*, make it a good starting point for description.

Caturus porteri n.sp.

1895, *Caturus* sp., Smith Woodward, p. 335.
1897*a*, *Caturus* sp., Smith Woodward, p. 292, plates viii, ix.

Diagnosis. *Caturus* in which the depth of the dentary at the last tooth is one-quarter the length of the dentigerous border, and in which the width of the maxilla is approximately one-fifteenth of its length.

Holotype. Head of fish, British Museum 29049; Oxford Clay, Christian Malford, probably *jason* zone (figure 36, plate 19).

Remarks. This species is very similar to *C. furcatus* Agassiz, in which the proportions given in the diagnosis are approximately one-fifth and one-twentieth; in addition, it can usually be distinguished by the more ornamented dermal bones and the greater number of teeth (about fifty on both dentary and maxilla); commonly also it is rather larger than *C. furcatus*, an average head measuring 12 cm. between snout and posterior margin of parietals. The body skeleton is unknown except for fragments of pectoral and caudal fins.

The species is not known at present outside the Oxfordian; the British, Peterborough and Sedgwick Museums contain a large number of specimens from the Oxford Clay of Peterborough and a few from Christian Malford. Smith Woodward (1895, 1897*a*), in describing the dermal and some of the neurocranial bones, distinguished these specimens as probably belonging to a new species but did not give it a name; that now given is after Dr Henry Porter, the author of *The Geology of Peterborough and its Vicinity* (1861), who made the pioneer vertebrate collection from the district, now in the Sedgwick Museum.

Roof and cheek of skull. The major bones of the skull roof are of the normal Holostean pattern—that is, large frontals, small quadrangular parietals and rather large dermopterotics. The very small dermosphenotic (often missing through accident) is characteristic of the genus, as is the division of the supraorbital series into a large number of ossicles which vary from specimen to specimen. Though these bones lack any regular ornamentation, with the exception of the parietals they usually have an irregular surface often with long radiating ridges covering the tubules of the sensory system.

The nasal and rostral lie loosely above the neurocranium and the former is only rarely preserved (figured by Smith Woodward 1897*a*, plate viii, figure 2, and in figure 40, plate 20). The position of the anterior nostril is shown by a rounded notch in the side of the nasal and a corresponding slight embayment in the antorbital. The posterior nostril presumably lay in the space above the hind part of the antorbital. All three bones overlap the premaxilla, the internal prolongation of which is uncertain in extent. The two premaxillae meet in the midline; these bones bear about fourteen close-set sharp teeth each, and the maxillae about fifty.

The pattern of the cheek plates is that characteristic of the Eugnathidae, as is the square-cut shape of the opercular with a horizontal ventral margin. The lower border of the subopercular is badly preserved and the extent of the interopercular unknown.

Latero-sensory system. The sensory canals of *C. porteri* are not directly visible except very occasionally as a slight ridge on the nasal. The bones bearing them are usually covered with a large number of pores, often difficult to distinguish from the surface ornamentation. Where these pores are aligned the course of the canals can sometimes be deduced from them. The canals are drawn with some certainty on the cheek bones, extra- and suprascapular in figure 1, but those on the skull roof and snout are more doubtful. On the hind part of the frontal there are often some lines of pores that probably follow the course of the sensory canals; if this is the case there is evidence of one canal passing from the frontal on to the anterior prolongation of the parietal, and a possibility of another from the frontal to the dermopterotic, but this group of pores is less compact. Thus there may be an anastomosis between the supra- and infraorbital canals near the hind margin of frontal, more or less as in *Amia*, but having no connexion with the dermosphenotic, which in *Caturus* is a very small bone, not touching the frontal. It has been impossible, however, actually to prove this anastomosis on any specimen of *C. porteri* that I have seen. The course of the canals of the snout is also very difficult to ascertain. The supraorbital canal can be traced as far as the centre of the nasal, and since no exit has been observed on the front and side margins of the bone it may terminate there as in *Amia*. The ethmoid commissure in the rostral is entirely deduced, for the one specimen that was found with the bone well preserved (S.M.J 4854, figure 40, plate 20) was too thick to show the course of any contained canal and too ornamented to identify any

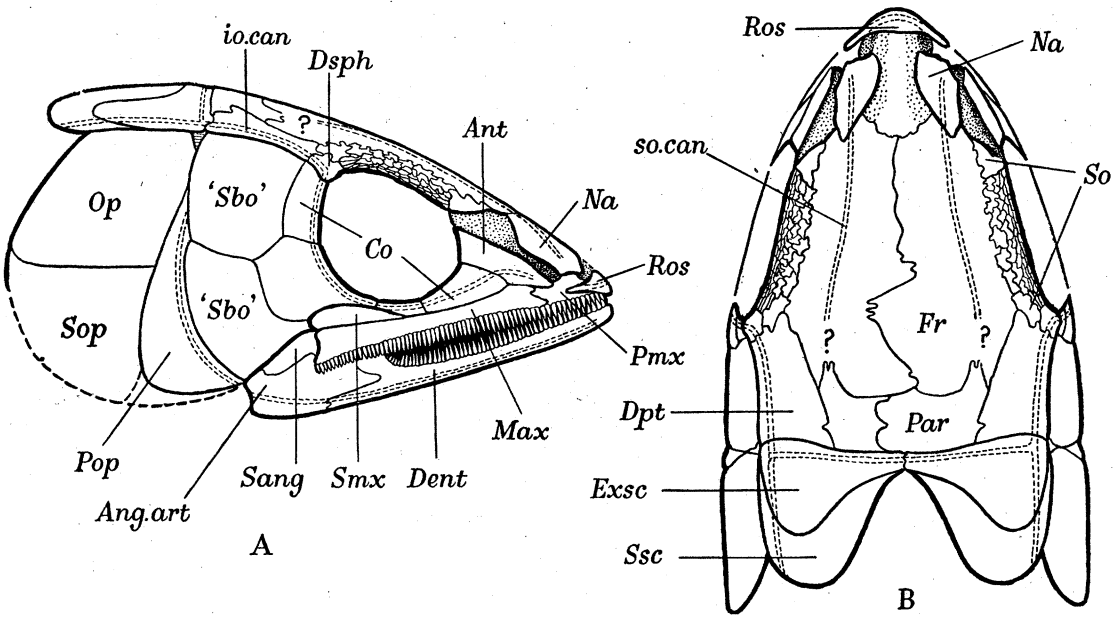

FIGURE 1. *Caturus porteri*, reconstructions of the dermal bones of the skull, after Rayner (1941). $\times \frac{1}{2}$. A, side view. B, dorsal view. *Ang.art.* angulo-articular; *Ant.* antorbital; *Co.* circumorbital; *Dent.* dentary; *Dpt.* dermopterotic; *Dsph.* dermosphenotic; *Exsc.* extrascapular; *Fr.* frontal; *io.can.* infraorbital sensory canal; *Max.* maxilla; *Na.* nasal; *Op.* opercular; *Par.* parietal; *Pmx.* premaxilla; *Pop.* preopercular; *Ros.* rostral; *Sang.* surangular; '*Sbo.*' 'suborbital'; *Smx.* supramaxilla; *So.* supraorbital; *so.can.* supraorbital sensory canal; *Sop.* subopercular; *Ssc.* suprascapular.

pores for certain; it is placed here on analogy with other Holostei. The infraorbital canal in the antorbital is only marked by a few pores along a line near the ventral margin. The great similarity of these bones with the corresponding elements of *Amia* suggests that there may have been an anastomosis of supra- and infraorbital canals between the two nostrils; that is, through the central parts of the antorbital and the space between it and the frontal; but if such existed it has not been traced in *Caturus*.

Lower jaw. This description is largely taken from an isolated mandible, B.M.N.H. P967. In general, the jaw consists of dentary, angulo-articular, prearticular and surangular; a mento-meckelian ossification probably existed, but it has not been possible to recognize it as the sutures of the anterior end are usually obliterated. In one or two of the smaller specimens there is a faint line close to the hind corner of the jaw, suggesting that the division between angular and articular elements persisted until fairly late in development. The dentary bears about fifty sharp teeth, all of about the same size. The prearticular has a large expanse on the inner side of the jaw and bears a great number of teeth, very small ones in patches near the hind end, and rather larger ones along the dorsal margin (largely obscured in B.M.N.H. P967). Some roughened areas below this bone and along the hind margin of the jaw result from the crushed fragments of a partially ossified meckelian bone.

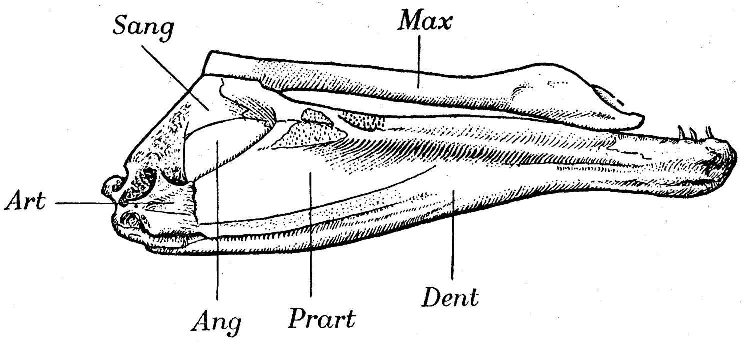

FIGURE 2. *Caturus porteri*, B.M.N.H. P967, maxilla and lower jaw viewed from the inside. × 1·0. *Ang.* angular; *Art.* articular; *Dent.* dentary; *Max.* maxilla; *Prart.* prearticular; *Sang.* surangular.

A large gular plate is seen between the mandibles and behind it about twenty-seven branchiostegal rays. The remainder of the visceral skeleton is unknown.

Postcranial skeleton, etc. The pectoral fins and some of the anterior scales are seen in the type specimen and in a number of those in the Peterborough Museum; some of the latter also include fragments of caudal fin, which must have been large, as in *C. furcatus*, and with much-jointed rays. All the specimens showing the body in *C. porteri* are squashed quite flat, dorsoventrally; the pectoral fins consist of about thirty or more rays inserted into a very short scaly lobe; they remain almost undisturbed on the ventral surface of the specimens, which suggest that the mean position of the fin web was roughly horizontal in life, and since the most anterior rays of each side lie farther apart than the posterior the base of the lobe must have been slightly higher on the flank in front than behind. Specimen no. 9, Peterborough Museum, shows the scaled lobe to be underlain by a number of elongated radials. The scales are small, quadrangular, and of about the same size all over the body.

Neurocranium. Some parts of this structure have been shortly described by Smith Woodward (1897*a*, p. 293); the present account agrees with that one, which also includes some of the neurocranial bones of *Osteorachis*, a genus very similar to *Caturus*, and which bears out the observations made on the latter. The following account is drawn chiefly from one specimen (unnumbered) in the Peterborough Museum (figures 37 and 38, plate 20); it consists of a crushed cranium with the dermal bones of the roof and some of those of the neurocranium recognizable; fragments of jaws, palate and the head of the right hyomandibular are plastered on to the ventral side. The hind surface now appears in the dorsal view because the roof of the skull has been thrust forwards and slightly to the right. The crushing is not complete and the bones of this region still indicate their original positions. They have a wrinkled surface whose irregularities sometimes follow the radial structure of the bones; in the original state the sutures were probably visible and some of them can still be traced along parts of their course.

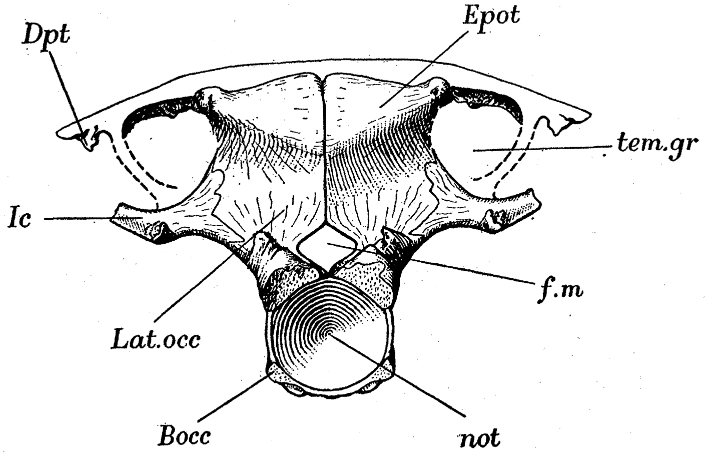

FIGURE 3. *Caturus porteri*, reconstruction of the neurocranium in hind view. × 1·0. *Bocc.* basioccipital; *Dpt.* dermopterotic; *Epot.* epiotic; *f.m.* foramen magnum; *Ic.* intercalar; *Lat.occ.* lateral occipital; *not.* notochord pit; *tem.gr.* temporal groove.

There is no sign of a supraoccipital on either posterior or dorsal surface. The epiotics protrude from under the parietals and meet each other closely in the mid-line; they have a rounded outstanding process near their lateral margins, and the posterior skull wall below this is slightly excavated. On either side of the epiotics lie the dermopterotics, which in life roofed the temporal groove. This hollow lodged the anterior ends of the trunk muscles as in Teleosts; it was rather large and has completely collapsed in this specimen, obscuring the bones around it. The extent of the lateral occipitals is deduced from the radiating ridges on the external surface rather than shown by their bounding sutures; they form a large part of the hind wall, meeting for some distance above the foramen magnum. Although the notochord pit has withstood the crushing well, no sutures can be seen in this region to mark the relative parts played by the lateral and basioccipital; very possibly they were fused, as frequently happens in other Holostei.

The intercalar (opisthotic of Smith Woodward's description) is the best preserved of the neurocranial bones; in the hind view it is seen to form a large, slightly irregular, process, presumably for ligamental attachment to the suprascapular, though the latter is not well enough known to confirm this. It has a clear junction with the lateral occipitals, but above this the boundaries are obliterated. The lateral wall of the skull is almost indecipherable in this specimen but can be supplemented by S.M. J 4853 (figure 39, plate 20), which has been completely flattened dorsoventrally, but in such a way as to leave the lateral walls (which must have faced outwards and downwards at about 45°) sufficiently undisturbed for a number of features to be recognizable. The intercalar has a large extent on the lateral wall, and forms the upper and anterior margin of the vagal foramen; the opposite border probably consisted of lateral and basioccipital, overlain perhaps in some specimens by an extension of the intercalar (cf. Smith Woodward 1897*a*, p. 293). The anterior expansion of the bone consists of a broad raised band overlapping the front end of the basioccipital and probably the parasphenoid as well; above and in front of this is an elongated hollow, containing a foramen for the 9th nerve, bordered on the upper side by a sharp ridge; the supratemporal branch of the nerve pierced this ridge. All the margins are incomplete, but there is some evidence of a indented border overlapping the parasphenoid; in the Peterborough specimen there are numerous strips of bone which have been thrust ventrally over the parasphenoid and basioccipital, some of which terminate in such indentations. This sliding of the intercalar, together with the compact nature of the bone seen where it is broken, suggests strongly that it is a superficial membrane ossification.

There is a mass of crushed bone in S.M. J 4853 lying dorsal and lateral to the intercalar in which it is impossible to discover any sutures, so that it is unknown whether there was an independent ossification in the posterior otic region (i.e. a Holostean 'opisthotic') or not; the largest fragment surrounds the foramen for the supratemporal branch of the glossopharyngeal, slightly above its passage through the ridge of the intercalar. There is an outstanding postorbital process formed from a rather large autosphenotic; behind this is the facet for the hyomandibular, which was originally cartilaginous, as shown by the irregular surface with minute rounded projections of bone.

The orbital surface has been thrust forward and has suffered more from crushing than the lateral walls; there is some evidence of a small myodome with openings separated by a stout basisphenoid, and also of a fragmentary pterosphenoid.* The ethmoid region was well ossified, and the Peterborough specimen bears a stout curved preorbital process, to which part of a tooth-bearing palatine remains attached. The parasphenoid bears an immense number of similar, minute teeth; the ascending and basipterygoid processes are broken but otherwise the bone is fairly complete. The forked hind end embraces the basioccipital, and there is a deep groove for the dorsal aorta. The foramina for the internal carotids are no longer distinguishable.

Caturus sp.

There is in the possession of the Bath Museum an isolated neurocranium (M 1288) in the Upper Liassic collection made by Charles Moore. With a large number of other vertebrates it comes from the 'Fish and Saurian bed' of Somerset (*exaratum* subzone), a soft limestone with nodules that often surround the fossils. Through the generosity of the Trustees of the Museum it has been possible to slice the specimen in two longitudinally, and examine the left half by means of serial sections; from these transfers were taken and an enlarged model of the neurocranium made. The details of this method are given in the Appendix. The exact mid-line was avoided in the slicing and remains on the surviving half, which has been prepared by excavation in the usual way.

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* This term is used in preference to 'alisphenoid' in these fishes in order to avoid confusion with the mammalian alisphenoid (for discussion see de Beer 1937, p. 439).

The specimen consists of an uncrushed neurocranium, ossified in two sections, postorbital and ethmoid, together with the right vomer and left autopalatine. On the skull roof the frontals, parietals and dermopterotics remain, though rather shattered at their margins, and portions of two scattered vertebrae have also been preserved. In shape the braincase is low and broad, the height being about half the width. The sutures are nowhere visible, neither on the surface nor in section, but the position of some of the bones may be recognized by their radiating fibres of perichondral bone on the exterior. An attempt is made to show these and other external features in figure 4; such delicate mouldings could not be shown on the model which is used for illustrating the main structural features of the cranium. The hindmost part of the basioccipital is broken off, and the foramen magnum, a triangular aperture, is also cut through by the fracture; a pair of occipital nerves can be seen leaving the cranial cavity on the broken surface. The notochord pit is badly preserved; it protruded well beyond the rest of the skull and seems to have been incomplete dorsally; a pair of neural arches articulated with its upper borders on either side of the foramen magnum.

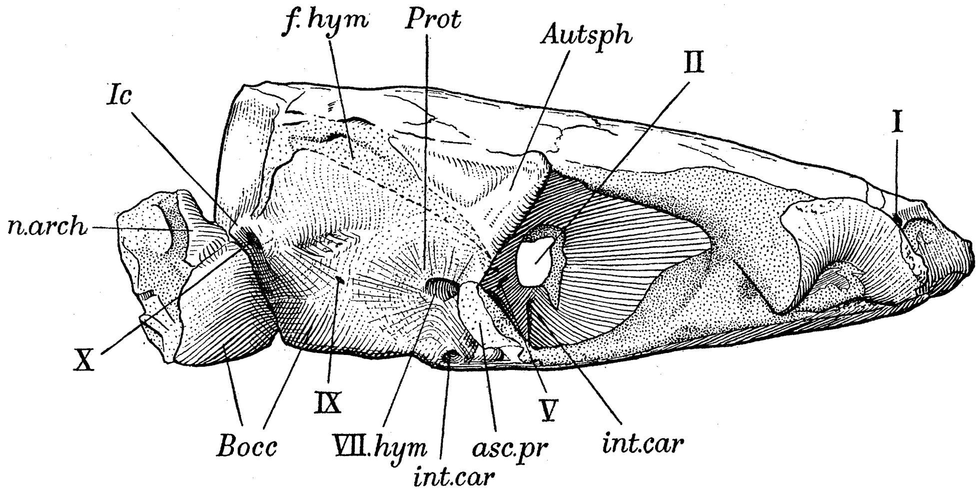

Figure 4. *Caturus* sp., a cranium in the Bath Museum, M 1288, cut through longitudinally and viewed from the right side; the autopalatine has been removed. × 1·1. *asc.pr.* ascending process of parasphenoid; *Autsph.* autosphenotic; *Bocc.* basioccipital; *f.hym.* hyomandibular facet; *Ic.* intercalar; *int.car.* foramen for internal carotid artery; *n.arch*, neural arch; *Prot.* pro-otic; I, olfactory canal; II, optic foramen; V, foramen for trigeminal nerve; VII, facial foramen; IX, foramen for glossopharyngeal nerve; X, foramen for vagal nerve.

The dorsal surface of the neurocranium was very irregular and only partly ossified, for in the central part of the postorbital section the bone is seen to disappear gradually until only isolated small spheres remain, now imbedded in the matrix, but originally marking the transition to cartilage; the same structure is found in the central parts of the ethmoid ossification. Elsewhere there is always a bony covering to the cranial cavity though its dorsal surface may be much excavated, especially internal to the postorbital process, the walls of which are only a few millimetres in thickness.

The posterior face of the skull is a broad low triangle, since the side walls face downwards and outwards at about 45°. There was originally some type of intercalar process at the junction of side and hind wall, at a point about midway between the skull base and roof, but only a slight projection remains. Below and slightly mesial to this projection is the foramen for the 10th nerve, an upward branch of which pierced the base of the process. There is a definite median ridge on the posterior wall above the foramen magnum, and the epiotics are marked by a pair of ledges protruding from under the parietals, clearly centres of ossification. The temporal groove is a deep pit lying, as usual, external to the epiotics and containing the anterior end of the trunk muscles. The outer wall is formed in part of the short ventral lamina of the dermopterotic and below that of the primary ossification of the lateral skull wall. The cavity is about 1 cm. deep, closed anteriorly partly by a thin wall of neurocranial bone (possibly epiotic) and laterally to this by a forward extension of the dermopterotic lamina.

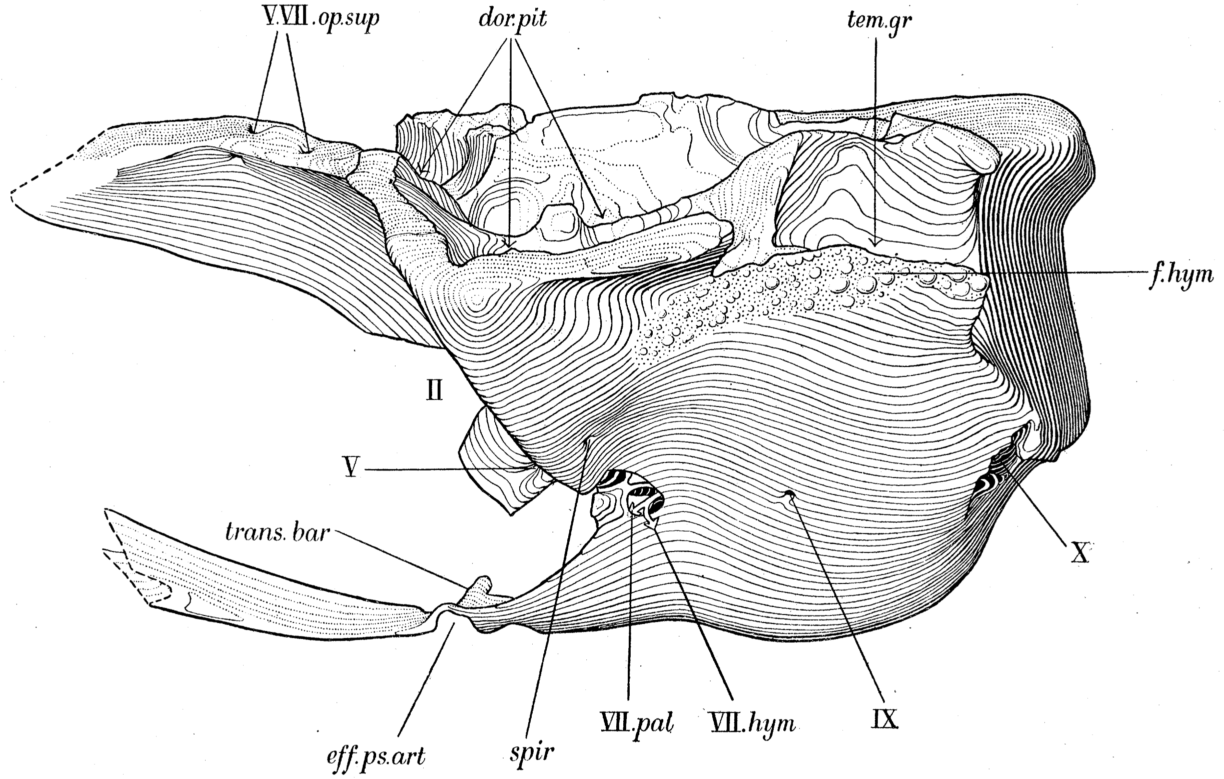

FIGURE 5. *Caturus* sp., a model of the postorbital section of the neurocranium in lateral view, slightly diagrammatic. × 2·5. The half specimen from which the model was made included rather less than an exact half of the cranium; its limits are shown in figures 6 and 7; the posterior part of the basioccipital was also broken off. *dor.pit*, pits in dorsal surface of neurocranium; *eff.ps.art.* entrance of efferent pseudobranchial artery; *f.hym.* facet for hyomandibular; *spir.* spiracular canal; *tem.gr.* temporal groove; *trans.bar*, transverse bar; II, optic foramen; V, foramen for trigeminal nerve; VII.*hym.* and VII.*pal.* course of hyomandibular and palatine branches of the facial nerve; V.VII.*op.sup.* foramen for superficial ophthalmic branches of trigeminal and facial nerves. IX, foramen for glossopharyngeal nerve; X, foramen for vagal nerve.

The lateral wall presumably consisted of the same bones as in *C. porteri*, but only the intercalar has any clear individuality, distinguished by radiating fibres stretching downwards and forwards; where the anterior parts of these were cut through in section they were seen to be well separated from the underlying cartilaginous bone, though nearer the centre of the intercalar this distinction was lost and fusion was complete. The extent of basioccipital and pro-otic is also indicated by a slight development of radial structure, but in this specimen, as in those of *C. porteri*, it is impossible to say whether there was a separate ossification in the posterior otic region or not. The hyomandibular facet was cartilaginous. The external opening of the spiracular canal lies in the upper part of the pro-otic; the passage runs upwards and slightly inwards and opens into the large dorsal pit internal to the postorbital process. The parasphenoid in this part of the skull is so badly damaged that little of the main body of the bone remains and is very difficult to distinguish from the primary neurocranial bones. There was a strong ascending process, now largely missing and marked only by its impression; it reached slightly above the facial foramen. A small protrusion from the anterior edge near the base probably represents the basipterygoid process.

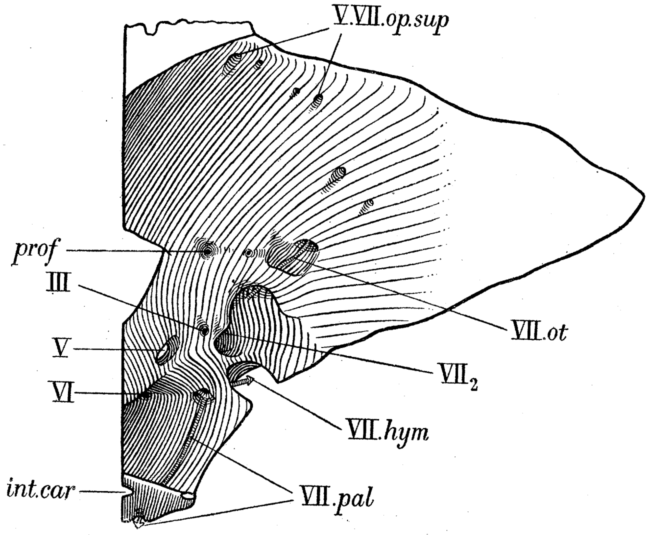

FIGURE 6. *Caturus* sp., model of neurocranium in front view, as if cut vertically just in front of the optic foramen and through the transverse groove in the basis cranii. × 2·5. *int.car.* foramen for internal carotid artery; *prof.* foramen for profundus nerve; III, foramen for oculomotor nerve; V, foramen for trigeminal nerve; VI, foramen for abducens nerve; VII.*hym.* and VII.*pal.* course of hyomandibular and palatine branches of facial nerve; VII.*ot.* course of otic branch of facial nerve; VII$_2$, second or buccal and superficial ophthalmic entrance to facial recess; V.VII.*op.sup.* foramen for superficial ophthalmic branches of trigeminal and facial nerves.

The bony interorbital septum is complete except for the rather large, confluent, optic foramina and a short unossified space between the orbitotemporal region and ethmoid ossification. The bone surface is slightly wrinkled in the ptero- and orbitosphenoid regions with some suggestion of radial structure. The myodome is rather small, its two openings widely spaced, and there is a facial chamber of rather complex structure completely separate from the trigeminal exit. The basisphenoid is massive and passes directly forward into the interorbital septum; the parasphenoid in the orbital region is largely covered by a thin sheet of cartilage bone continuous with that septum, but separated from a similar sheet that floors the myodome by a transverse gap which thus forms a pair of grooves in the base of the skull communicating with each other by a short tunnel in the interorbital septum.

The facial chamber is in direct communication with the facial foramen on the side wall of the cranium; the anterior margin of this foramen appears to have been formed from the ascending wing of the parasphenoid only, unsupported by the cartilaginous neurocranium. From it issued the hyomandibular branch of the 7th nerve; it also served for the passage of the jugular vein into the orbit and probably the external carotid as well. The chamber has two fairly large openings from the cranial cavity; the first is situated rather ventrally, and passing downwards and forwards from the cranial cavity opens immediately internal to the facial foramen; through it passed the hyomandibular nerve and the palatine branch, which turned forward into the myodome. The second entrance arises close to the first, both issuing from a latero-ventral extension of the interior of the brain-case which presumably

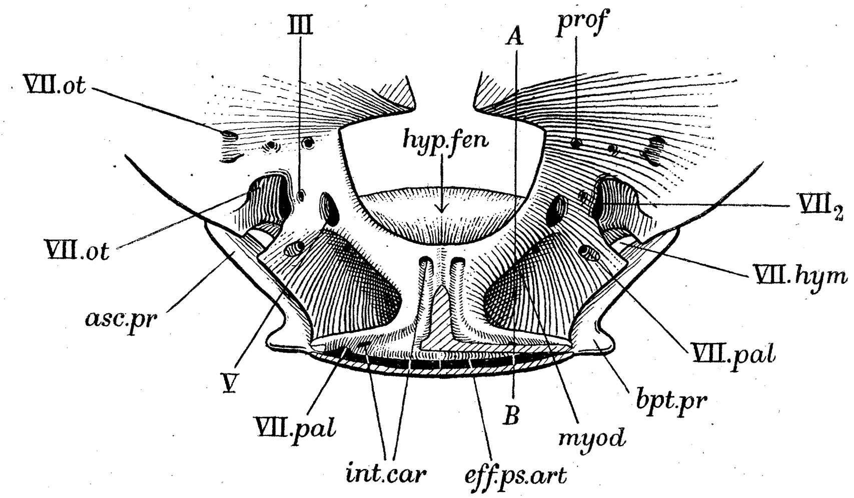

FIGURE 7. *Caturus* sp., reconstruction of the basal part of neurocranium cut vertically through the optic foramen and viewed from in front; on the left side part of the basis cranii is removed to expose the foramina in the raised bar that bounds the floor of the myodome. The line *AB* represents the limits of the model shown in figures 5, 6 and 8. × 2. *asc.pr.* ascending process of parasphenoid; *bpt.pr.* basipterygoid process of parasphenoid; *eff.ps.art.* groove for efferent pseudobranchial artery; *hyp.fen.* hypophysial fenestra; *int.car.* foramen for internal carotid artery; *myod.* myodome; *prof.* foramen for profundus nerve; III, foramen for oculomotor nerve; V, foramen for trigeminal nerve; VII.*hym.* foramen for hyomandibular branch of facial nerve; VII.*ot.* foramen for otic branch of facial nerve; VII.*pal.* foramen for palatine branch of facial nerve; VII_2, second or buccal and superficial ophthalmic entrance to facial recess.

therefore housed the trigemino-facial ganglionic complex; it may have been separated by membrane from the true cranial cavity. This second entrance lies above the first and is high and narrow and faces more laterally; it transmitted the buccal branches of the facialis and the superficial ophthalmic nerves. The roof of the chamber is overhanging; behind this overhang is a passage which leads directly into another small open recess. From this recess a small passage plunges upwards into the bone again; it represents the course of the otic branch of the facialis, and opens again into the dorsal pit not far from the upper aperture of the spiracular canal. The course of the superficial ophthalmic nerves is not quite clear; they may have accompanied the otic nerve through the roof of the facial chamber and emerged from the small upper recess, or they may have passed upwards and forwards directly from the chamber. The small slit-like apertures in this part of the orbital wall (pterosphenoid region) are almost certainly nutritive; some are seen to lose their individuality soon after entering the bone.

The trigeminus lay in rather a long passage in the pedicle that joins the ptero- and basisphenoid regions and separates the myodome from the optic foramen. Between this passage and the facial chamber is a smaller opening, directed somewhat downwards, which transmitted the oculomotor. The remaining neural aperture in this region is rather small and short, not far from the hind corner of the optic foramen; it faces forwards and very slightly upwards. I think that it probably represents an independent ophthalmicus profundus, a nerve which occurs in *Amia* and the foramen of which has been deduced roughly in this position in the Kansas Palaeoniscid B by Watson (1925, p. 843). In that case the trochlearis in *Caturus* must have entered through the optic foramen, which is fairly large. The only other neural structures to be described on the orbital surface are some upwardly directed canals near the dorsal margins of the cranium; these canals are common in Holosteans and may differ in number on the two sides of the head. They usually lie below the supraorbital sensory canal and served for the passage of one or more branches of the superficial ophthalmic nerves to the organs of the canal.

The base of the skull in *Caturus* is rather complex in structure. The internal carotids pierced the parasphenoid, and after passing inwards and forwards through the bone for a short distance emerged on to the floor of the myodome. The anterior part of this floor terminates in a raised bar, which is pierced by two apertures, the posterior serving the palatine nerve and the anterior and more mesial the internal carotid. Immediately in front of this ridge is the transverse gap in the cartilage bone already mentioned; it is bridged only by a strip of bone at each extreme lateral end, which rises slightly to form a thin arch between anterior and posterior basal plates. The efferent pseudobranchial arteries entered under these arches and occupied the transverse groove (floored by the parasphenoid); they probably anastomosed in the mid-line and turned outwards and upwards again as the ophthalmic arteries. The internal carotids turned upwards above them and entered the cranial cavity by two short vertical passages slightly below the optic foramen; their course is clearly marked by a pair of grooves in the basisphenoid region.

The myodome is rather short, measuring about 1·5 cm. in length and 1 cm. in height in longitudinal section, and probably little of it was surrounded by the basioccipital. There is a pair of small foramina for the 6th nerves in the hind part of the roof and a large median entrance for the hypophysis in the fore part, directly behind the internal carotid foramina.

The cranial cavity is rather large and high; a considerable lateral expansion in the orbitotemporal region suggests that the optic lobes were large, but otherwise, except for the more lateral parts of the labyrinth, the shape of the cavity seems to have borne little relation to the soft structures which it contained. This applies particularly to the posterior part, where the roof is high, and the hind wall descends almost perpendicularly to the foramen magnum. The floor of the cavity is very irregular, but, behind the hypophysial fenestra, in general is highest in the mid-line. On either side of this in the orbitotemporal region are the passages transmitting the trigeminus, and behind these a considerable pair of cavities which lodged the roots of the facialis and part at least of the trigemino-facial ganglia. Farther back there are a pair of deep saccular pits, whose smooth contours give no indication of a differentiated lagena. The glossopharyngeal nerve on either side traversed these pits, and still more posteriorly the roots of the vagus are represented by a pair of deep funnel-shaped passages.

The utriculus has not left much impression on the cranial wall, but the semicircular canals were almost entirely enclosed in it. The ampulla of the posterior canal is marked by a slight enlargement at its ventral end; those of the other two canals lay in a deep rounded hollow, the ampullary chamber, partly confluent with that containing the roots of the 7th nerve and directly behind and below the optic lobe expansion. This hollow is divided by a slight constriction into a larger hind part which enclosed the ampulla of the external canal and a smaller fore part containing that of the anterior.

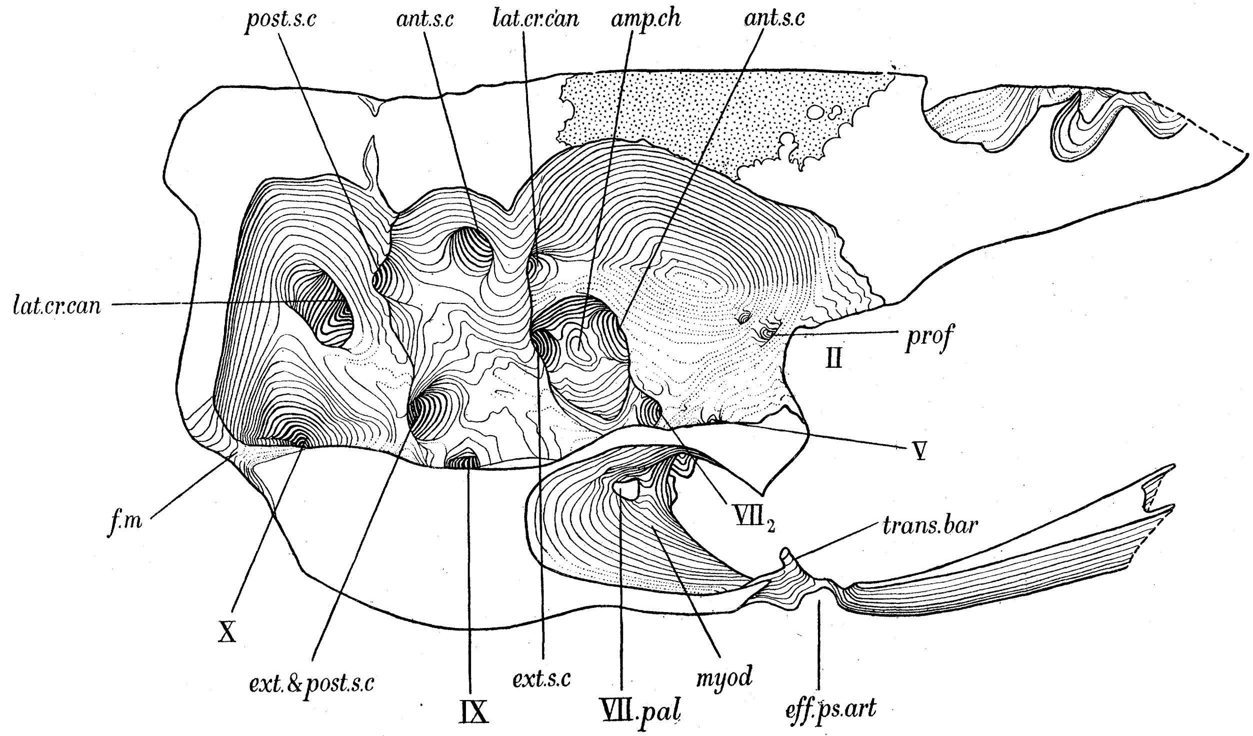

FIGURE 8. *Caturus* sp., model of neurocranium in mesial view. × 2·5. *amp.ch.* ampullary chamber; *ant.s.c.* anterior semicircular canal; *eff.ps.art.* entrance of efferent pseudobranchial artery; *ext.s.c.* external semicircular canal; *f.m.* foramen magnum; *lat.cr.can.* lateral cranial canal; *myod.* myodome; *post.s.c.* posterior semicircular canal; *prof.* foramen for profundus nerve; *trans.bar,* transverse bar; II, optic foramen; V, foramen for trigeminal nerve; VI, foramen for abducens nerve; VII.*pal.* foramen for palatine branch of facial nerve; VII_2, second or buccal and superficial ophthalmic entrance to facial recess; IX, canal for glossopharyngeal nerve; X, canal for vagal nerve.

There remains in this region of the skull a very puzzling feature for which at present it is difficult to suggest any satisfactory explanation. It is a large canal, called 'lateral cranial canal' for want of a better name, which arises from the cranial cavity above the root of the 10th nerve and behind the posterior semicircular canal; it passes forward under the arch of both posterior and anterior canals and above the external, and enters the cranial cavity again behind the optic lobes. In shape it is rounded but irregular, with a distinct ventral expansion in the middle of its length. It is not peculiar to this specimen, for not only does Aldinger (1932) figure a similar canal in *C. groenlandicus*, but there is also fairly good evidence for its existence in a cranium of *Dapedius*, described below. The function of this canal, if it had one, is quite unknown. In some Teleosts there are irregular enclosures in this part of the skull housing diverticulae of the air bladder (described by Ridewood (1891), Bridge

(1900), Assheton (1907) and Ballantyne (1927) among others), but they all differ on some important point from that in *Caturus*.

The posterior portion has a homologue in certain specimens of *Glaucolepis* and *Boreosomus* described by Nielsen (1942, pp. 43–45, 294–296) where there is an opening between that part of the cranial cavity lodging the medulla oblongata and the hindmost portion of the fossa bridgei, the latter being apparently unusually large and complex. The relations with the labyrinth are essentially the same, for this opening perforates the cranial wall through the loop of the posterior semicircular canal. Nielsen compares this aperture with Aldinger's canal and also considers them partly homologous. He finds Aldinger's idea that the canal was '? for an electric organ' unlikely, but does suggest that it may have served for some nerve or nerves connected with the unusually swollen medulla oblongata (Nielsen 1942, p. 102). My specimen of *Caturus*, being more complete than *C. groenlandicus*, shows the lateral cranial canal to have no external outlet at all, so that any nervous function seems ruled out—a conclusion which is supported by the fact that in *Boreosomus* the homologous opening is sometimes lacking. Moreover, Nielsen notes that there has hitherto been no function satisfactorily ascribed to the fossa bridgei, and that in *Acipenser* and *Polyodon* (the second of which has the communicating opening) it is filled with fatty tissue.

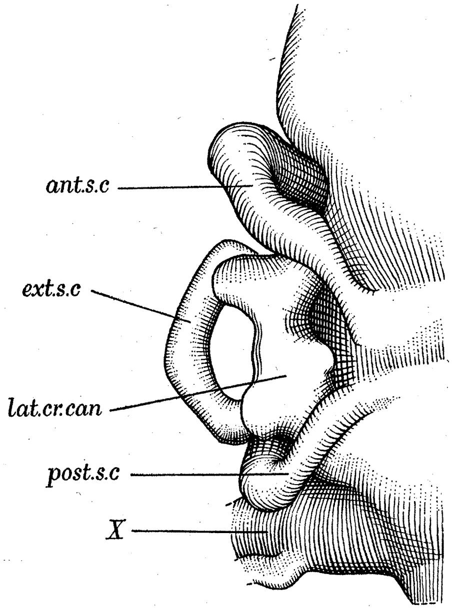

FIGURE 9. *Caturus* sp., reconstruction of the cranial cavity and labyrinth of the left side in dorsal view, drawn as if in cast. ×2·5. *ant.s.c.* anterior semicircular canal; *ext.s.c.* external semicircular canal; *lat.cr.can.* lateral cranial canal; *post.s.c.* posterior semicircular canal; X, vagus.

It would be interesting to know whether a lateral cranial canal was common among the Holostei; but, apart from *Dapedius*, no fossil genera are known with the interior of the skull so well preserved as *Caturus* and few are as well ossified. In *Lepidotus latifrons*, for instance, only parts of the posterior semicircular canal were found to be surrounded by bone, and if such a canal existed it would not be preserved in the fossil state. The same probably applies to the Pachycormidae. Serial sections through the larval forms of *Lepidosteus* showed no such structure in the cartilage of the otic region, nor does it exist in *Amia*, so far as can be ascertained from the literature. Thus the general impression is that in some form this curious structure was possibly of long standing in the earlier Actinopterygii (Nielsen thinks that it may be present in the Kansas Palaeoniscids, though I can find little positive evidence for this), but that it was much altered or lost in the later members.

The olfactory nerves were completely surrounded by bone except for a short space between the postorbital and ethmoid ossifications; the bone margins here are very irregular and the two ossifications may have been connected by cartilage. The ethmoid region was well ossified except for a narrow gap in the dorsal mid-line, and there is a pair of strong preorbital processes. On the right side the autopalatine is preserved; it is a stout triangular bone carrying a groove for articulation with the maxilla on the outer edge. The left vomer also remains, bearing several sharp teeth. The olfactory nerves enter the ethmoid ossification by a single passage and diverge inside the bone to emerge into a pair of rather large olfactory pits. The hind wall of these contains a short blind hollow, immediately lateral to the olfactory passage, which possibly contained glandular epithelium as in a few Teleosts.

Hitherto the only detailed account of neurocranial structure in this genus has been that of *Caturus groenlandicus* given by Aldinger (1932). This species consists of one specimen, an incomplete neurocranium, chiefly in cast; the labyrinth is fairly well preserved and part of the cranial cavity and myodome, but everything in front of the facial foramen is missing. Comparison between this species and that described above is therefore rather limited.

The remainder of the external wall of *C. groenlandicus* is distinctly like that of the earlier species, especially the intercalar process, its band of forward-reaching fibres, and the foramina of the vagus, facialis and internal carotids. Aldinger speaks of a trigemino-facial chamber, but as his specimen is broken off immediately in front of this cavity there may have been a separate trigeminal passage unsuspected by him. There is also a slight difference concerning the course deduced for the palatine nerve in the Portlandian and Upper Liassic specimens. In the latter it appears to have issued from the cranial cavity together with hyomandibular trunk through a large foramen; in *C. groenlandicus* Aldinger considers that it had a small separate opening leading directly into the myodome; in both cases the geniculate ganglion must be supposed to have lain inside the cranial cavity. The presence of a lateral cranial canal in the two fishes has already been noted and in general the otic region is decidedly similar.

A rather unexpected possibility emerges from a comparison of the cranial cavities. That of *C. groenlandicus* is mentioned as probably representing the actual outline of the brain (Aldinger 1932, p. 23), whereas in the Upper Liassic specimen it seems much more likely that there was a distinct space between the brain and skull wall; also I can find no trace of the structures in the roof of the cranial cavity that are indicated in *C. groenlandicus* (Aldinger 1932, figure 2). In small fishes the skull is sometimes found to have a closer adherence to the brain than in larger ones (see Edinger 1929), but in this case the Portlandian species is nearly twice the size of the other, so that the difference cannot be correlated simply with size. Thus arises the possibility that the later form actually had a thicker and more closely investing skull than the earlier; this progression is opposed to the general reduction in cranial ossification found among the Actinopterygii which is certainly borne out by other Holostei and the Teleosts. Before coming to such a conclusion, however, it is perhaps well to bear in mind that the systematic determination of isolated neurocrania is always a difficult matter, and that these two specimens may possibly not be so closely related as their nomenclature indicates.

The neurocranium of *Caturus* bears points of resemblance to both *Amia* and the Kansas Palaeoniscids (Watson 1925, 1928). The greater degree of ossification in *Caturus* makes the neurocranium superficially very unlike that of *Amia*, but the skull shape is not dissimilar and the bones, as far as they are known, have much the same distribution, especially as regards the rather large intercalar and lack of supraoccipital. The orbital surface and nerve apertures are abnormal in the recent genus owing to reduction in the size of the eye and myodome; nevertheless, there are some interesting points of agreement in the structure of the basis cranii and the course of the carotid and efferent pseudobranchial arteries. Allis describes the myodome of *Amia* as also being bounded in front by a raised bar (1897, p. 492 et seq.), in front of which is a transverse groove or canal, equivalent to the unossified tract of *Caturus*. The whole region in *Amia* is much reduced in height, and the basisphenoid bone, represented by a pair of ossicles at each end of the bar, is pierced by the internal carotid as it passes upwards into the cranial cavity; in one specimen the left basisphenoid was found to bridge the transverse groove as the corresponding ossification does in *Caturus*; in *Amia*, however, there is no anastomosis between the efferent pseudobranchial arteries, which is found in some Teleosts (Allis 1912) and is deduced in *Caturus* and in the Kansas Palaeoniscid B (Watson 1925).

The distribution of other orbital vessels and nerves in *Caturus* also has some points in common with those of the Kansas neurocrania—points which are not entirely confined to this genus, but are more obvious because it is better known. The isolated position of the trigeminal foramen, well removed from the facial, and consequent lack of a true trigemino-facial chamber, is an important resemblance; also the structure of the basis cranii, especially as seen in front view, is not unlike. These points probably also apply in some degree to the Semionotidae as well, but what is known and described below of the other Jurassic families suggests that they are more divergent in the structure of the orbitotemporal region.

SEMIONOTIDAE

Lepidotus

This genus has received more detailed treatment by previous writers than most other Jurassic fishes; the osteology as a whole is given fairly fully by Smith Woodward (1895, p. 77). *L. semiserratus* is described by the same author at some length (1897*b*), though only the external bones and body skeleton are considered. The neurocranium of more than one species is known from the following sources: Smith Woodward (1893, *L. latifrons*; 1916, *L. mantelli* and *Lepidotus* sp.), and Holmgren & Stensiö (1936, p. 479, *L. semiserratus*). Of these the two earlier works deal with broken crania and isolated bones, especially those of the occipital region, and the more recent is a reconstruction and description of a single very well preserved specimen. This specimen, kindly lent to me by Professor Stensiö, is the basis of this description also, but has been supplemented by another in the Sedgwick Museum (S.M. J4849).

Dermal and visceral skeleton. While investigating the neurocranial bones some features of the dermal skeleton were also recorded where they supplemented the existing descriptions. The distribution of the infra- and supraorbital sensory canals in this genus is rather clearer than in *Caturus*, and the great abundance of well preserved material makes it possible to give a partial description of their course on the hind part of the skull roof. The most complete evidence was afforded by some specimens of *Lepidotus minor*; B.M.N.H. P 6371 and Professor Watson coll. P 228 have a row of pores near the lateral edge of the parietal which mark the course of the supraorbital canal; they can be seen leading directly to the groove of the anterior pit-line. This is confirmed by the B.M.N.H. 36001 which shows the under side of the roofing bones; the supraorbital canal appears as a slight ridge, bearing a number of small nerve apertures on the frontal and one at least on the parietal. There is no evidence on this specimen for an anastomosis between supra- and infraorbital canals; if such existed it was probably between the secondary branches in the more superficial layers of the bones.

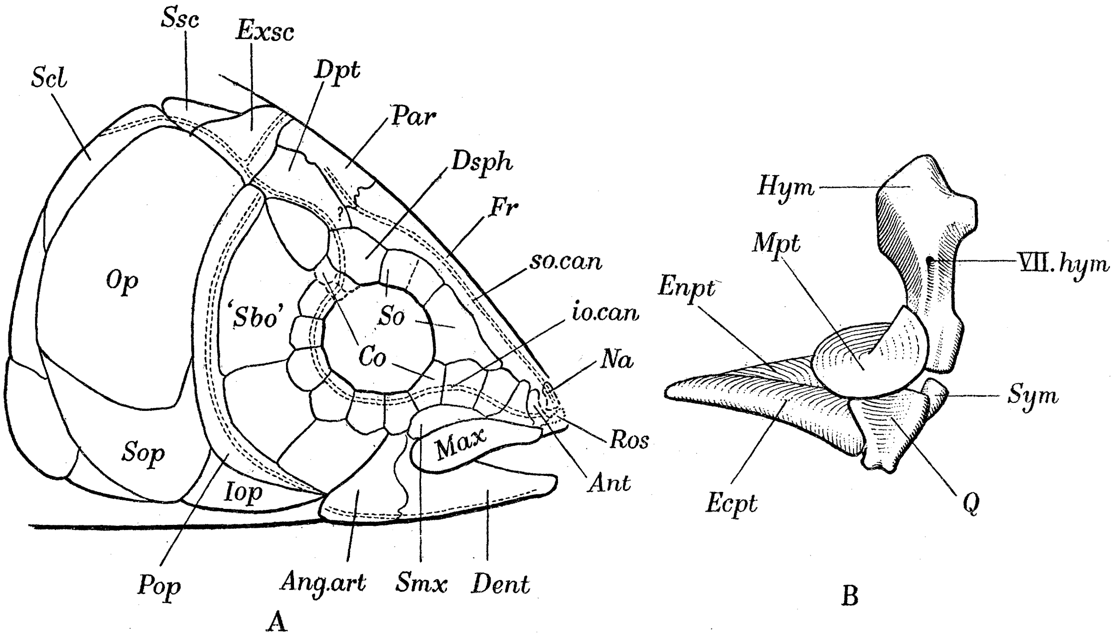

FIGURE 10. *Lepidotus semiserratus*. $\times\frac{1}{2}$. A, reconstruction of the dermal bones in lateral view, after Smith Woodward (1916, p. 27) with slight alterations. B, reconstruction of the left palate and hyomandibular. *Ang.art.* angulo-articular; *Ant.* antorbital; *Co.* circumorbital; *Dent.* dentary; *Dpt.* dermopterotic; *Dsph.* dermosphenotic; *Ecpt.* ectopterygoid; *Enpt.* entopterygoid; *Exsc.* extrascapular; *Fr.* frontal; *Hym.* hyomandibular; *io.can.* infraorbital sensory canal; *Iop.* interopercular; *Max.* maxilla; *Mpt.* metapterygoid; *Na.* nasal; *Op.* opercular; *Par.* parietal; *Pop.* preopercular; *Q.* quadrate; *Ros.* rostral; '*Sbo*'. 'suborbital'; *Scl.* supracleithrum; *Smx.* supramaxilla; *So.* supraorbital; *so.can.* supraorbital sensory canal; *Sop.* subopercular; *Ssc.* suprascapular; *Sym.* symplectic; VII.*hym.* foramen for hyomandibular branch of facial nerve.

Some of the sensory system is visible on the Stockholm specimen of *L. semiserratus*, where parts of the dermal pores have been removed to expose the main canals and many of their ramifying branches; the supraorbital canal is again seen to terminate on the parietal. The dermal bones of this species are well represented in Smith Woodward's restoration (1916, p. 27), and there are only a few additions to be made. The circumorbital series was found to vary in number occasionally, especially below the eye; there may be some small bones intercalated below the dermosphenotic, and the centre circumorbital above the eye is sometimes divided into two. The elements of the snout are always fragmentary and often missing; there are usually three anterior circumorbitals, and in front of these have been found remnants of two smaller bones containing portions of sensory canals; they are called nasal and antorbital from comparison with better known Holosteans. This region is poorly preserved in all species of *Lepidotus*, but Piveteau (1934, p. 74) also notes a pair of nasals meeting in the mid-line, and Holmgren & Stensiö (1936, p. 481) figure both bones, but not with exactly my positions. What is possibly a rostral has been found in one specimen of *L. minor* (B.M.N.H. P12211).

The lower jaw includes dentary, angulo-articular and a large, toothed, pre-articular; the upper part is usually covered by the circumorbitals, but a small surangular has been found by Smith Woodward (1916, p. 42, 'coronoid') in *L. mantelli* and Holmgren & Stensiö (1936) mention a similar bone in *L. semiserratus*.

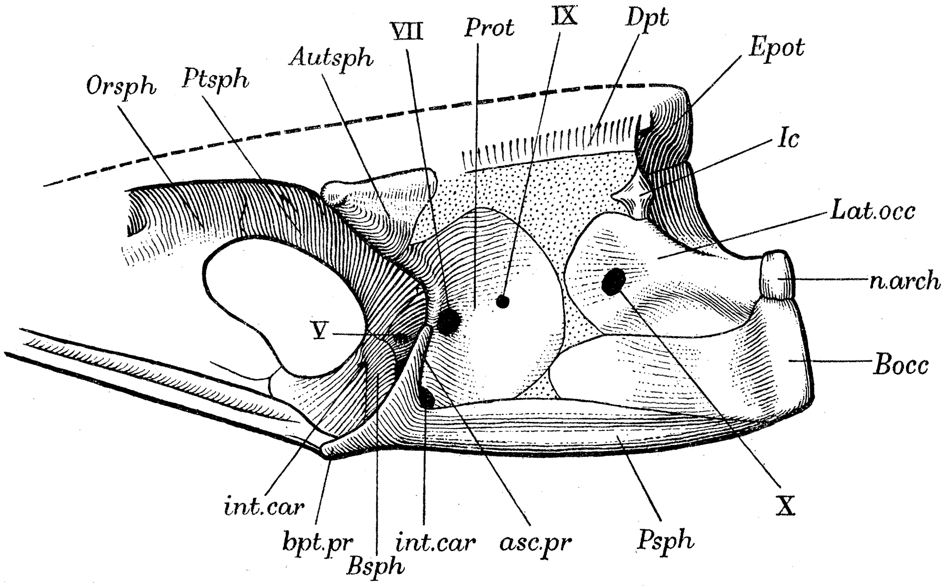

FIGURE 11. *Lepidotus semiserratus*, reconstruction of the neurocranium in side view, cartilage stippled. × 1·0. *asc.pr.* ascending process of parasphenoid; *Autsph.* autosphenotic; *bpt.pr.* basipterygoid process of parasphenoid; *Bocc.* basioccipital; *Bsph.* basisphenoid; *Dpt.* dermopterotic; *Epot.* epiotic; *Ic.* intercalar; *int.car.* foramen for internal carotid artery; *Lat.occ.* lateral occipital; *n.arch*, neural arch; *Orsph.* orbitosphenoid; *Prot.* pro-otic; *Psph.* parasphenoid; *Ptsph.* pterosphenoid; V, foramen for trigeminal nerve; VII, foramen for facial nerve; IX, foramen for glossopharyngeal nerve; X, foramen for vagal nerve.

The palate is described largely from one specimen of *L. semiserratus* (Professor Watson coll. P230); it consists of the normal Actinopterygian components. The metapterygoid is roughly circular, though not quite plane, the posterior margin interrupted by a V-shaped notch, the inner edge of which provides the ridge articulating with the basipterygoid process. The quadrate is small; the ectopterygoid rather large and broad transversely, and the entopterygoid similar but less well exposed. These two bones form the major part of the broad palatal arch. They have much the same relations in cross section as those of *L. mantelli* (Smith Woodward 1916, p. 41). The palatine is large and tooth bearing.

The elements of the hyoid arch are rarely seen except for the hyomandibular and anterior ceratohyal element, the latter being sometimes exposed between the lower jaws. Hypohyals and the posterior ceratohyals are also figured by Smith Woodward (1916, plate x, figure 2, where the posterior ceratohyal is labelled epihyal). The dermal shoulder girdle consists of cleithrum, supracleithrum and three post-cleithral scales; the first is long and curved and often hidden under the opercular bones. The suprascapular has a short, curved, ventral process near its external margin to which was attached the ligament connected to the neurocranium. The primary girdle is very rarely seen, but a bone (probably the scapula, but labelled coracoid) is figured by Smith Woodward (1916, plate viii, figure 1); it bears an obvious articulating surface facing backwards. This specimen (of *L. mantelli*) also exhibits fragments of elongated cartilage bones, the radials. The position of the pectoral fin is very similar to that deduced for *Caturus*, but the common preservation of *Lepidotus* as a three-dimensional object makes it much clearer; S.M.J 4855 is almost uncrushed and has all the fins in their natural positions and the pectoral extremely well preserved.

Neurocranium. In well preserved specimens of *Lepidotus* this structure has always been found to consist of distinct bones and to have considerable interspaces, once cartilaginous. There is no supraoccipital, the epiotics meeting each other closely; below them lie a pair of unusually large lateral occipitals, which entirely surround the foramen for the 10th nerve. A massive basioccipital is capped at the hind end by a pair of neural arches. The pro-otic is pierced on the lateral wall by both the glossopharyngeal and facial foramina, and this wall also contains a large unossified space between the pro-otic, lateral occipital and dermopterotic. The latter bears a slight ventral flange but there is no primary component. A small superficial intercalar is included in Holmgren & Stensiö's reconstruction (1936, p. 479) above the external upper angle of the lateral occipital; it was removed before the specimen was borrowed, but a crushed head of *L. minor* (Professor Watson coll. P228) has the remains of a small star-shaped bone in about this position. An 'opisthotic' (i.e. intercalar in modern terminology) is shown in Smith Woodward's figure of *L. mantelli* (1916, plate x, figure 1), but it was not possible to confirm any sutures on this part of the skull in that specimen; the 'facet for opisthotic' on *Lepidotus* sp. (1916, p. 38) is very probably correct, through it is not quite in the same place as that given by Stensiö.

The bones of the orbital surface are known only from the Stockholm specimen; there their limits are clear, but it is not always easy to be certain which are nerve foramina and which imperfections in the specimen. Figure 12 shows a drawing of the orbital surface of the right side as seen from in front; on the other side is an attempted reconstruction giving such foramina as are tolerably certain.

The myodome is small, its two openings separated by a massive basisphenoid; the optic foramen is rather large and confluent with the interorbital fenestra. The opening marked VII seems from its small size to have served for the facial nerve only, so that, as in *Caturus*, there was no true trigemino-facial chamber; there is an upwardly directed foramen and groove that marks the exit of one or both of the superficial ophthalmic nerves, and several passages piercing the upper part of the pterosphenoid are almost certainly for secondary branches serving the sensory organs of the supraorbital canal. I think that probably the trigeminus issued through the most anterior foramen in the pro-otic, close to the junction with the basisphenoid; it is very much in the same position as the trigeminal foramen of *Caturus*. The remaining smaller openings are not distinct enough to be interpreted on the evidence of a single specimen except that of the internal carotid, which entered the myodome from behind the ascending process of the parasphenoid and turned up in front of the basisphenoid, piercing it near the upper margin.

The parasphenoid in the Stockholm specimen is incomplete and the posterior part broken off short; it is supplemented by that seen in S.M. J4849, which has a long pair of ventral flanges extending the length of the basioccipital. The parasphenoid of *Lepidotus latifrons* (B.M.N.H. P6840) has complete ascending and basipterygoid processes; they are shorter and less distinct from one another than in fishes with a deeper skull, and were figured together by Smith Woodward (1893, p. 561) as a basipterygoid process. It is on the position and inclination of the ascending process that I differ from Smith Woodward in the interpretation of dorsal and ventral in this specimen. The basipterygoid process has distinct grooves on the dorsal surface for articulation with the ridge of the metapterygoid; both it and the ascending process are broken on the right (figured) side of the Stockholm specimen but may be seen in ventral view on the left. *L. latifrons* shows a rounded notch in front of the basipterygoid process, probably for the efferent pseudobranchial artery.

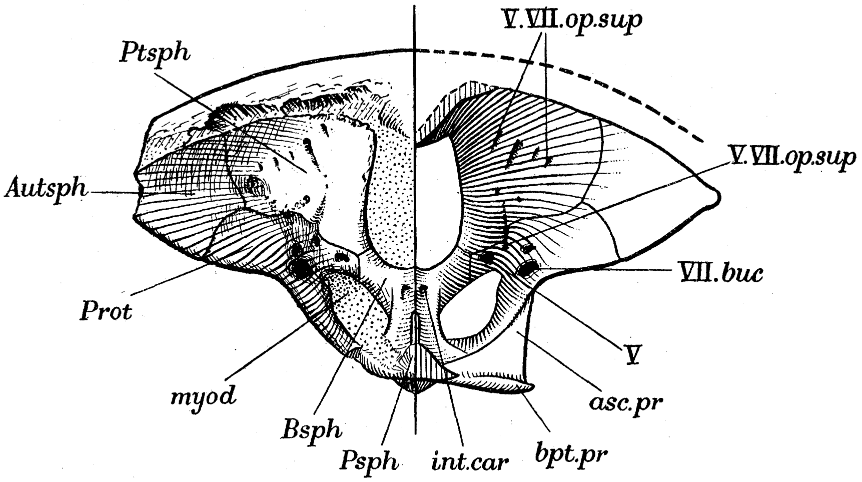

FIGURE 12. *Lepidotus semiserratus*, the neurocranium cut vertically through the interorbital fenestra and viewed from in front; on the left a drawing of a specimen in the Riksmuseum, Stockholm, on the right an attempted reconstruction. × 1·3. *asc.pr.* ascending process of parasphenoid; *Autsph.* autosphenotic; *bpt.pr.* basipterygoid process of parasphenoid; *Bsph.* basisphenoid; *int.car.* foramen for internal carotid artery; *myod.* myodome; *Prot.* pro-otic; *Psph.* parasphenoid; *Ptsph.* pterosphenoid; V, foramen for trigeminal nerve; VII.*buc.* foramen for buccal branch of facial nerve; V.VII.*op.sup.* foramen for superficial ophthalmic branches of trigeminal and facial nerves.

The ethmoid region is little known, but there was some cartilage bone investing the olfactory nerves and cartilage; I am rather doubtful of Holmgren & Stensiö's pre- and ectethmoid, for the bony mass exposed in the snout of their specimen seems rather too ventral in position to be neurocranial and is nearer that of an autopalatine.

The interior of the braincase of *Lepidotus* was largely walled with cartilage or membrane, but some important details can be deduced from B.M.N.H. P9998 (also figured by Smith Woodward 1916, p. 38), which contains part of the semicircular canals. Figure 13A shows the dorsal surface of the lateral occipital, pierced by the posterior canal on either side; the canal had a much greater part of its length in contact with this bone than with the epiotic, which it only just notches on the ventral surface. A distinct enlargement at the ventral end represents the ampulla. The only sign of the horizontal canal is a very short groove on the left lateral occipital; presumably the majority of it was enclosed in the cartilage wall in front, though possibly the pro-otic was concerned also. The basioccipital of this specimen contains a small section of the myodome.

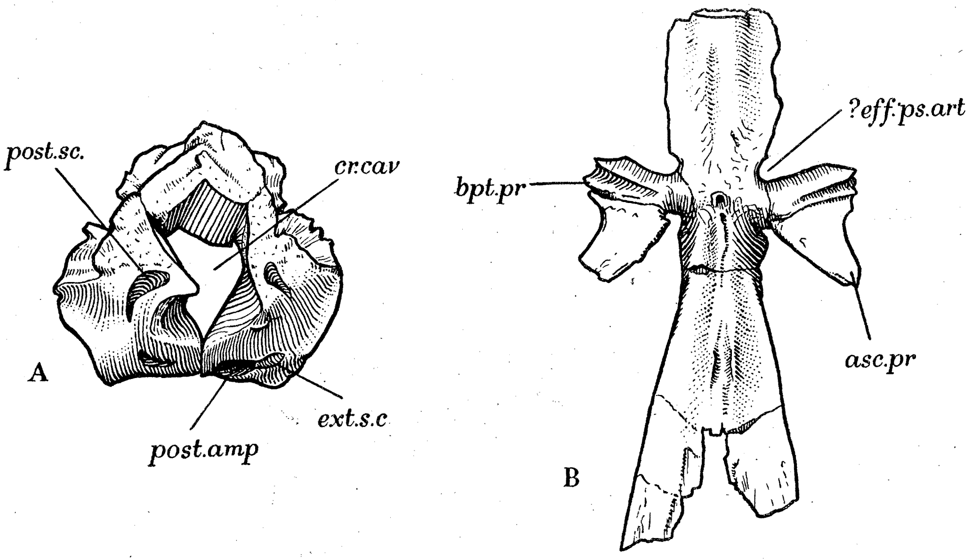

FIGURE 13. *Lepidotus latifrons*, B.M.N.H. P9998. A, dorsal surface of the lateral occipitals, showing portions of the labyrinth. × 1·0. B, parasphenoid in dorsal view. × $\frac{2}{3}$. *asc.pr.* ascending process; *bpt.pr.* basipterygoid process; *cr.cav.* cranial cavity; *? eff.ps.art.* ? notch for efferent pseudobranchial artery; *ext.s.c.* external semicircular canal; *post.amp.* ampulla of posterior semicircular canal; *post.s.c.* posterior semicircular canal.

Dapedius

The neurocranium of this genus is known from four specimens, each consisting of cranium only. Two of them, B.M.N.H. P3541 and P11177, from the Lower Lias of Lyme Regis, have been shortly described by Smith Woodward (1893) and Frost (1913) respectively. The third specimen, B.M.N.H. P11189, is also from the Lower Lias of Lyme Regis (Green Ammonite Beds—*davoei* zone), but has not been described, nor has the fourth, from the Upper Lias of Somerset (*exaratum* subzone), borrowed from the Bath Museum (M1280).

The braincase of *Dapedius*, unlike that of *Lepidotus*, is very well ossified; with the possible exception of the hyomandibular facet the whole structure in all four specimens appears to be without cartilaginous interspaces and has no visible sutures. The 'supraoccipital' in Smith Woodward's figures (1893, plate 1, figures 3 to 3*b*) probably is really a process composed of the two outstanding mesial edges of the epiotics. Such a median process has been found in a lesser degree in other Holosteans, but no large supraoccipital is known except in *Pholidophorus* and *Leptolepis*; moreover, in B.M.N.H. P11177 there is a slight median groove on the process suggesting a pair of bones. The hind region of the skull shows a pair of large temporal grooves and a long ventral canal for the dorsal aorta; in general, the occipital region of this genus is very dissimilar to that of *Lepidotus*.

On the side wall the external semicircular canal is marked by a faint ridge below the hyomandibular facet. There appears to have been a small, rounded basipterygoid process. The walls of the orbit are not unlike those of *Lepidotus*, allowing for the deeper shape of the skull, and the interorbital fenestra is still small, though rather different in outline. A basisphenoid is present in B.M.N.H. P3541 and P11177, so that its lack in P11189 and the Upper Liassic specimen is presumably due to accident; P11189 is a small skull not so well preserved in this region as the others. Three of the specimens show the nerve apertures of the orbital surface in a fairly good state of preservation, and it has been possible to excavate part of the cranial cavity of the Bath specimen since much of the hind wall and right side is broken away. The poor preservation of the fourth, B.M.N.H. P11177, makes the validity of some of the foramina described by Frost very doubtful; certainly his correlation of optic foramen and nerves is wrong.

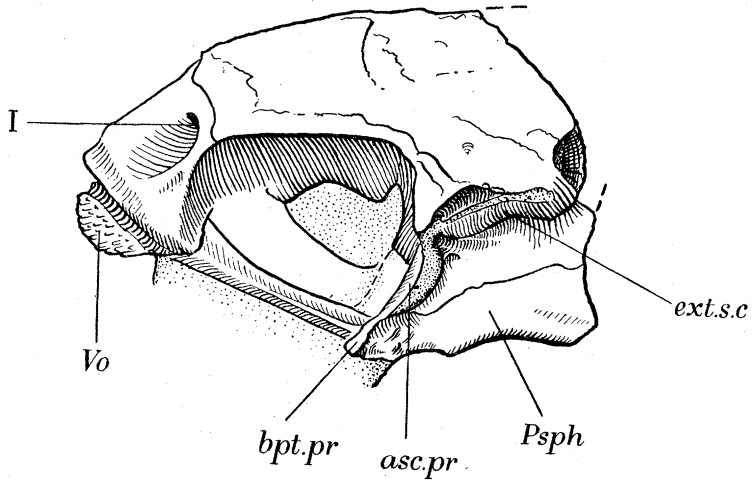

FIGURE 14. *Dapedius* sp., a cranium from the Upper Lias in the Bath Museum, M1280, viewed from the left side. × 1·5. *asc.pr.* ascending process of parasphenoid; *bpt.pr.* basipterygoid process of parasphenoid; *ext.s.c.* external semicircular canal; *Psph.* parasphenoid; *Vo.* vomer; I, olfactory canal.

Figure 15A is a slightly diagrammatic representation of what is visible of the cranial cavity in the Upper Liassic cranium. The floor is almost flat in the mid-line, but slopes slightly downwards at the foramen magnum and more steeply in front, presumably to the hypophysial fenestra, but with the basisphenoid missing it is difficult to be certain of this. On either side of the central line in the otic region is a deep pocket for the sacculus (unexcavated), which reduces the cranial floor to a narrow median ridge. The 10th nerve had its exit behind the saccular cavity; the 9th probably ran across it. The posterior semicircular canal appears for a short distance on the broken hind surface of the specimen; the position of the external canal has already been noticed on the lateral skull wall, so that the connexions of these two with the cranial cavity are fixed.

The shape and course of the lateral cranial canal is inevitably not so certain in this genus as in *Caturus*, since it was not possible to excavate it far. The position of the posterior opening, however, and its relations to the 10th nerve and posterior semicircular canal are so similar in the two genera that there can be little doubt that the structure exists in *Dapedius*. The anterior opening presumably lies in the large unexcavated hollow above the external semicircular canal; it appears to be much larger than the corresponding opening in *Caturus*, while the vertical pillar separating the lateral cranial canal from the utriculus is decidedly narrower. The result is that the canal is much more part of the cranial cavity in this genus—a fact which rather increases the difficulty of assigning to it any of those functions, suggested from comparison with living fishes or Palaeoniscoids, which were discussed when dealing with *Caturus*.

The position of the anterior semicircular canal can only be deduced from its entrances to the cranial cavity; it seems to have been rather longer than the posterior canal. The ampullary chamber is very large, and less clearly separated from the cranial cavity than that of *Caturus*, nor is there any impression to show whether the ampulla of the external canal was particularly enlarged. There are a number of nerve apertures in the floor of the chamber which lead out into the orbit or facial recess. Four of them have been traced to their respective external openings by holding the skull in front of a strong light and blocking all but one of the openings in turn; the calcite which fills the passages is sufficiently transparent to let light through for a short distance. The only foramen whose exit could not be traced by this means lay in the bottom of the ampullary chamber. It appeared to run more directly downwards than the others and probably did not transmit sufficient light to be visible; by removing the bone surrounding this region on the other (right) side this passage was seen to lead to the facial foramen on the side wall of the skull. It is large and probably transmitted the hyomandibular trunk; the palatine branch turned down immediately into the myodome. The chamber must have contained the trigemino-facial ganglionic complex; a second passage leads from it to the facial recess, and transmitted the remaining, buccal and otic, branches of the facialis.

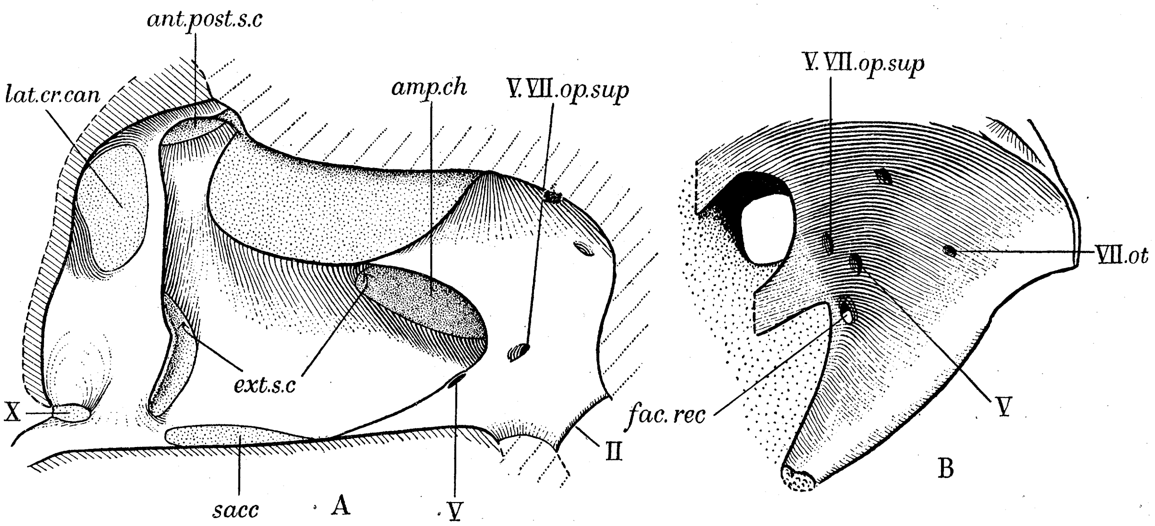

FIGURE 15. *Dapedius* sp., a cranium from the Upper Lias in the Bath Museum, M1280. × 6·6. A, a slightly diagrammatic drawing of the cranial cavity as if cut along the mid-line and viewed from the right, partially excavated; the skull is broken off behind the vagal foramen; matrix stippled. B, the orbital surface on the left side viewed from in front. *amp.ch.* ampullary chamber; *ant.post.s.c.* joint entrance of anterior and posterior semicircular canals; *ext.s.c.* external semicircular canal; *fac.rec.* facial recess; *lat.cr.can.* lateral cranial canal; *sacc.* saccular cavity; II, optic foramen; V, foramen for trigeminal nerve; VII.*ot.* foramen for otic branch of facial nerve; V.VII.*op.sup.* foramen for superficial ophthalmic branches of trigeminal and facial nerves; X, foramen for vagal nerve.

The trigeminus pierced the skull wall on the sharp angle between the ampullary hollow and the upward sweep of bone bordering the optic foramen; it emerged just above the facial recess, and slightly dorsal and anterior to this again is the superficial ophthalmic opening, which in B.M.N.H. P11189 leads into a dorsally directed groove. The trigemino-facial nerves therefore emerged more closely together in this genus than in *Lepidotus*. The remaining passage found between the cranial cavity and orbit is fairly large; it is too far dorsal for a neural canal and also faces slightly downwards. I have therefore taken it to be vascular. The autosphenotic region is pierced by the otic foramen in the usual manner, and there are an irregular number of upwardly directed foramina high up in the interorbital wall serving for branches of the ophthalmicus superficialis.

The ethmoid region floors the two large shallow nasal pits, the hind walls of which bear a pair of olfactory foramina. A pair of stout preorbital processes continue this wall ventrally and carry a shallow facet for the connexion with the palate. Fragments of vomer with tightly packed teeth are found in the Upper Liassic specimen.

Pachycormidae

Hypsocormus

The neurocranium of this genus is known from one specimen only, from the Lithographic Stone (Kimmeridgian) of Solenhofen; it has been borrowed from the Riksmuseum, Stockholm, and has already been shortly described and used as a basis for reconstruction by Holmgren & Stensiö (1936, p. 482). It consists of a well preserved cranium without visceral skeleton; dermal bones are present but are rather difficult to distinguish; the laterosensory system is also obscure, but the supraorbital canals are visible for a short distance on the frontals and single parietal. This bone is broken above the occipital region where it would have risen to the dorsal eminence characteristic of the hind part of the skull in this family.

On the ventral surface there is a pair of large teeth in sockets in the rostral region; behind are the vomers, distinct on this surface but apparently fused to the parasphenoid dorsally. At the side the lateral and pre-ethmoid are partially exposed; between them the neurocranium was cartilaginous, and probably farther forward in the rostrum also. The ethmoid bones form the floor of a shallow olfactory pit, roofed by a large nasal.

The bones of the postorbital part of the specimen are quite distinct from one another; they have been slightly crushed dorsoventrally, and those of the occiput especially are a little displaced. None of the nerve apertures of the orbit is visible except the optic foramen; a groove in the pterosphenoid, which in the uncrushed skull would have led forwards and upwards, may be assigned to the ophthalmicus superficialis. The exits of the 7th, 9th and 10th nerves and the jugular vein are unmistakable on the side wall, but lack of parasphenoid in this region makes it difficult to place the internal carotid. Stensiö's reconstruction, however, gives a very probable position for both bone and foramen.

The posterior otic region contains not only a small intercalar but another bone dorsal and anterior to it, called by Stensiö the opisthotic. Both it and the intercalar appear on the posterior face of the skull. The occipital bones have been slightly telescoped and their limits are a little doubtful. There seems to have been a large basioccipital and probably the usual two pairs of bones above it, lateral occipital and epiotic, but there is no primary element to the pterotic. There is a small knob of bone appearing from under the parietal on the left side (or possibly fused to it); this might be a supraoccipital, as considered by Stensiö, or more likely, I think, from the evidence of *Pachycormus*, the dorsal margin of the epiotic. Behind the skull a number of neural spines are exposed.

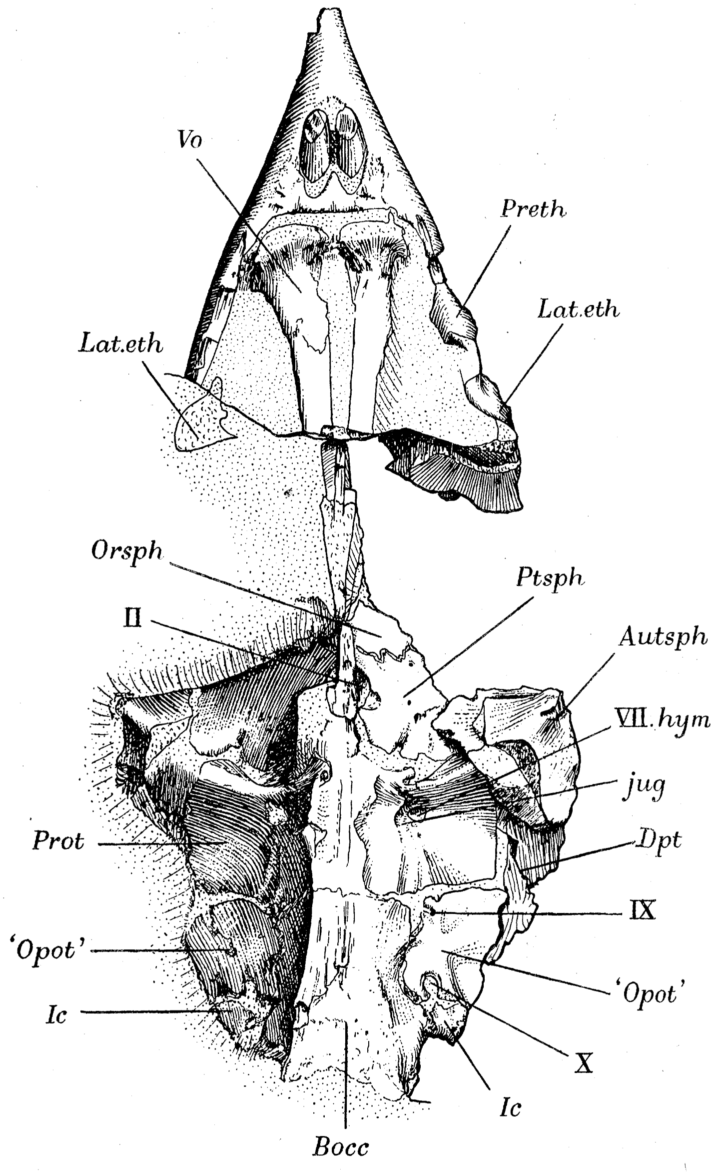

FIGURE 16. *Hypsocormus* sp., a cranium from the Riksmuseum, Stockholm, in ventral view. × 1·0. *Autsph.* autosphenotic; *Bocc.* basioccipital; *Dpt.* dermopterotic; *Ic.* intercalar; *jug.* jugular canal; *Lat.eth.* lateral ethmoid; '*Opot.*' 'opisthotic'; *Orsph.* orbitosphenoid; *Preth.* pre-ethmoid; *Prot.* pro-otic; *Ptsph.* pterosphenoid; *Vo.* vomer; II, optic foramen; VII.*hym.* foramen for hyomandibular branch of facial nerve; IX, foramen for glossopharyngeal nerve; X, foramen for vagal nerve.

Pachycormus

The skull of this genus is usually distorted and not very well preserved and the neurocranium therefore unexposed or unrecognizable; two specimens of *P. curtus*, however, from the Upper Lias (S.M. J4850 and B.M.N.H. 32443) were found with these bones, or some of them, preserved.

S.M. J4850 was prepared to show as much of the skull as possible; the inward collapse of the hyomandibular has completely destroyed the structure of the otic and occipital regions, but the orbitosphenoid, autosphenotic and part of the lateral ethmoid are roughly in place. The specimen also shows some of the palate, ento- and metapterygoid and quadrate, and the jaws, the lower especially massive, with small sharp teeth. The occipital elevation is in the form of a rounded crest, including both frontal and parietal; it has no immediate support from the neurocranium beneath for the partly broken bones expose an area of matrix below.

Although B.M.N.H. 32443 is considerably smaller and more crushed than the Sedgwick Museum specimen, the bones on the left side of the neurocranium are very well exposed because the dermal roof is the only other part of the skull preserved, and it has been thrust to one side. There is a stout rounded rostrum covered with a fine granulation, and bearing a number of sharp teeth along the ventral margin. The nasal, frontal, parietal and dermopterotic are all incomplete but recognizable; a number of pores of the supraorbital sensory canal are found on the frontal and three sections of pit-line on the parietal. The collapse of the roofing bones has obscured the fronto-parietal crest, but its fragments are preserved in the arched surfaces of these bones. As in S.M. J4850 there appears to have been no other osseous support to this structure.

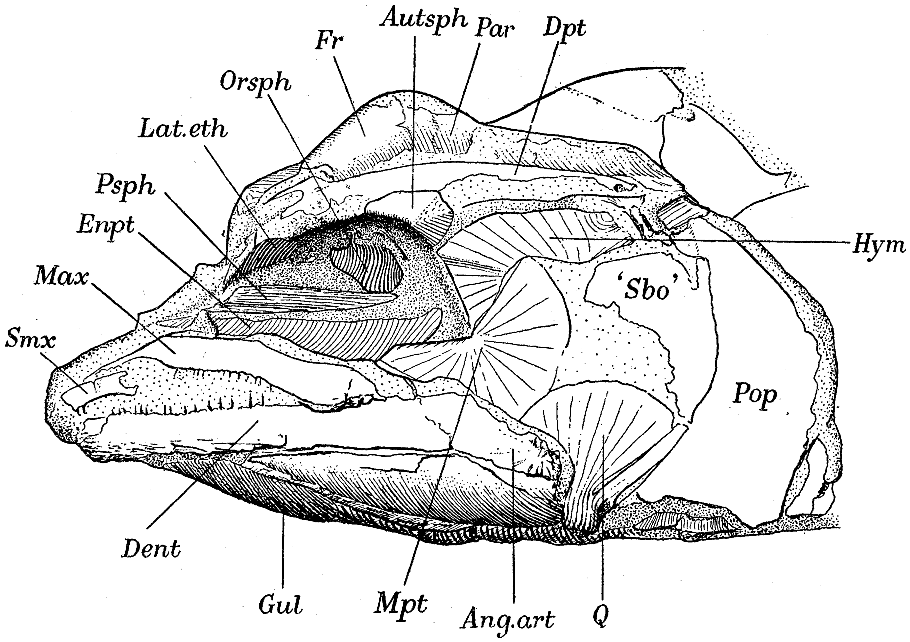

FIGURE 17. *Pachycormus curtus*, S.M. J4850. × 1·0. *Ang.art.* angulo-articular; *Autsph.* autosphenotic; *Dent.* dentary; *Dpt.* dermopterotic; *Enpt.* entopterygoid; *Fr.* frontal; *Gul.* gular; *Hym.* hyomandibular; *Lat.eth.* lateral ethmoid; *Max.* maxilla; *Mpt.* metapterygoid; *Orsph.* orbitosphenoid; *Par.* parietal; *Pop.* preopercular; *Psph.* parasphenoid; *Q.* quadrate; '*Sbo.*' 'suborbital'; *Smx.* supramaxilla.

The solid walls of the notochord pit have prevented the basioccipital from being much disturbed, but the lateral occipital has suffered more, and the epiotic is entirely displaced. There is no sign of any supraoccipital, though its absence cannot be absolutely proved owing to the general distortion of this part of the skull. The remaining bones are well preserved and their approximate relations to each other can be easily deduced; they are clearly very like those of *Hypsocormus*.

The 'opisthotic' and intercalar are separate and distinct, each with a small expanse on the hind wall; that of the former is damaged and it may have been larger originally. The vagal foramen lies between these two bones, surrounded by a complex of grooves; some of these are connected with an occipital nerve foramen in the basioccipital and others may be merely irregularities of the surface. There does not appear to be any certain opening for the glossopharyngeal preserved, but the anterior part of the 'opisthotic', which contains it in *Hypsocormus*, is obscured and broken in *Pachycormus*. This injury has removed the total thickness of bone in the upper anterior part of the 'opisthotic', exposing the matrix of the inner side. This appears as a smooth-surfaced cone, the apex towards the centre of the bone and the base at the pro-otic margin; it is, I think, the cast of the external semicircular canal. Excavation of the internal surface of the pro-otic revealed a similar structure, though here preserved as a shallow groove in the actual bone, which would in that case represent the anterior half of the canal.

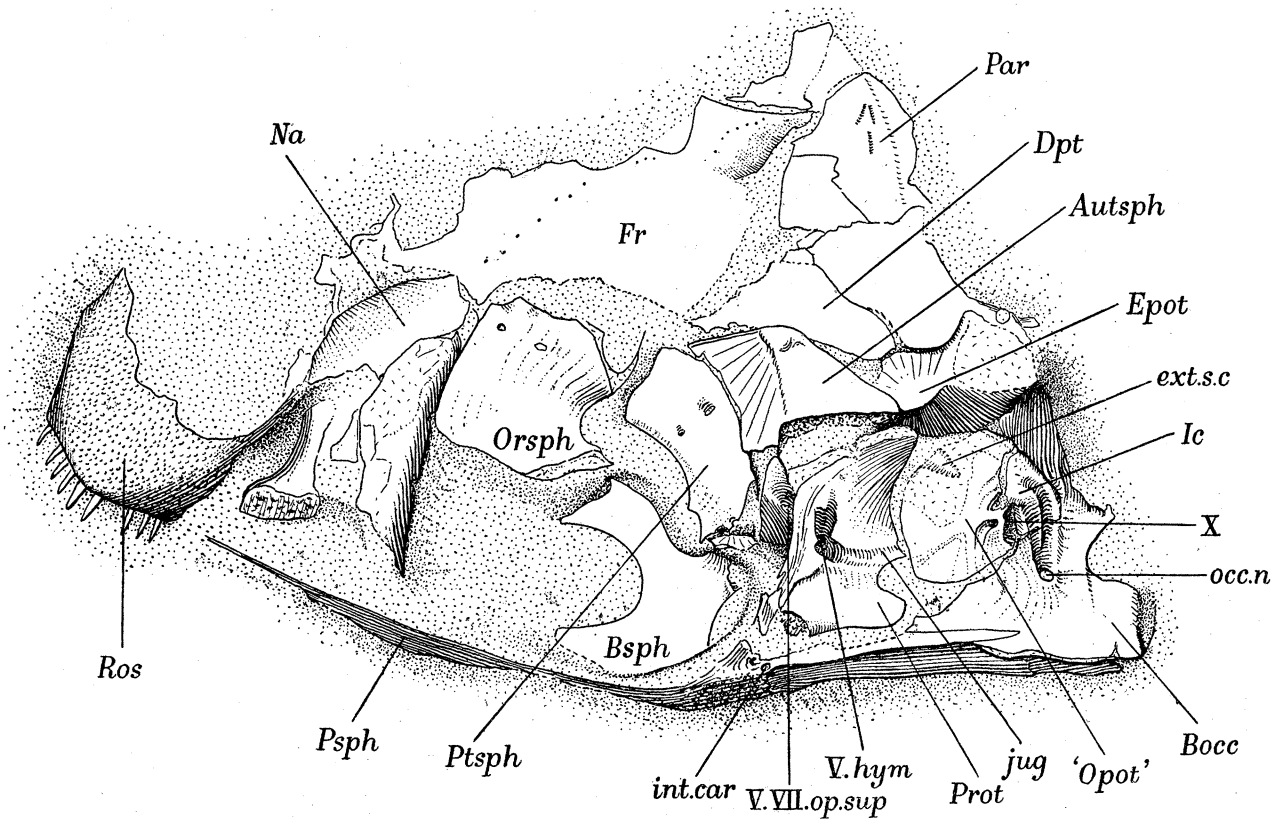

FIGURE 18. *Pachycormus curtus*, B.M.N.H. 32443. ×3. *Autsph.* autosphenotic; *Bocc.* basioccipital; *Bsph.* basisphenoid; *Dpt.* dermopterotic; *Epot.* epiotic; *ext.s.c.* external semicircular canal; *Fr.* frontal; *Ic.* intercalar; *int.car.* foramen for internal carotid artery; *jug.* jugular canal; *Na.* nasal; *occ.n.* foramen for occipital nerve; '*Opot.*' 'opisthotic'; *Orsph.* orbitosphenoid; *Par.* parietal; *Prot.* pro-otic; *Psph.* parasphenoid; *Ptsph.* pterosphenoid; *Ros.* rostral; VII.*hym.* foramen for hyomandibular branch of facial nerve; V.VII.*op.sup.* foramen for superficial ophthalmic branches of trigeminal and facial nerves; X, foramen for vagal nerve.

The side face of the pro-otic has distinct passages for the jugular vein and the hyomandibular branch of the 7th nerve; together these passages lead into the facial chamber which opens at once into the orbit. Only one entrance from the cranial cavity is seen, but it was not possible to excavate the chamber entirely without injuring the specimen. Slightly above and mesial to the orbital opening is another, rather large, which faces upwards and slightly forwards; it served for the passage of the ophthalmicus superficialis, and two small apertures in the pterosphenoid probably represent branches of these nerves. The adjoining margins of this bone, pro-otic, and basisphenoid, have been thrust apart and slightly injured by a horizontal sheet of some element of the other side; thus the exit of the trigeminus cannot be fixed with certainty, nor those of the eye-muscle nerves or internal carotid, though there are signs of a small aperture between the pro-otic and pterosphenoid and a rather larger one between the latter and the basisphenoid. The optic foramen is large and elongated, bounded by ptero-, basi- and orbitosphenoid; the cross-section of the olfactory canal is exposed on the hind sutural margin of the last.

The large preorbital process is somewhat shattered and has much of the bone surface removed except on the posterior face; in shape and position it seems to correspond to the lateral ethmoid of *Hypsocormus*. The parasphenoid is badly damaged around the ascending process and internal carotid foramen, which nevertheless are recognizable. In front of these the ventral surface bears a large number of fine teeth. The existence of a basipterygoid process is doubtful; it cannot be traced on either side.

ASPIDORHYNCHIDAE

Aspidorhynchus

Two isolated crania of this genus have been found from the Great Oolite of Kingsthorpe, Northampton; they have been briefly described and one figured by Smith Woodward (1918, p. 96). A more thorough preparation has made it possible to study the outside of these neurocrania in greater detail.

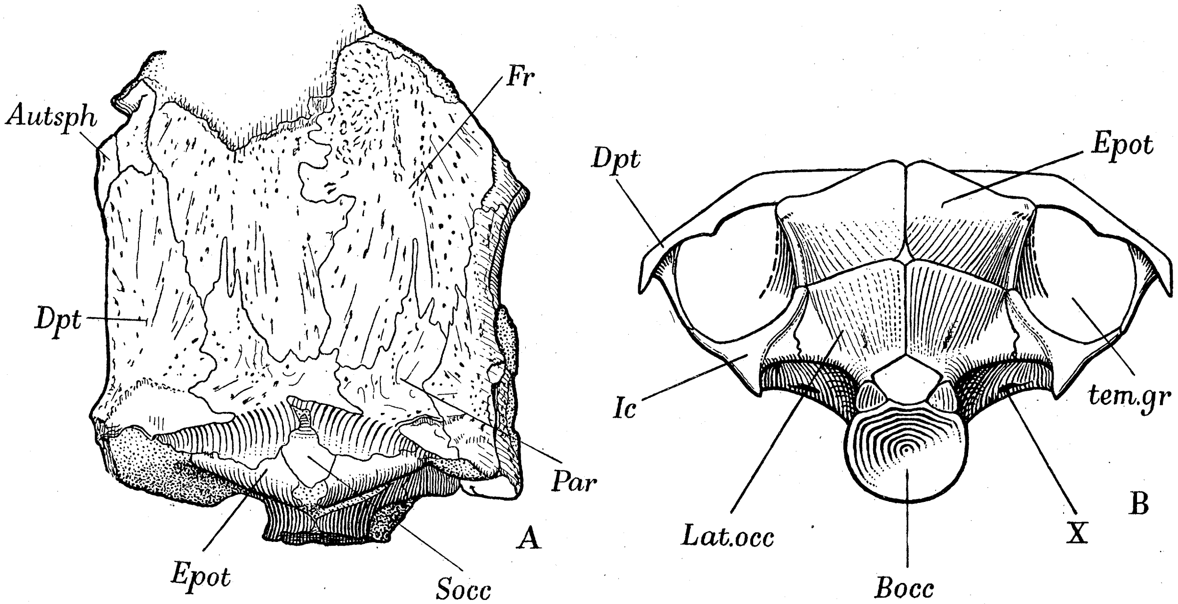

FIGURE 19. *Aspidorhynchus* sp. × 1·5. A, B.M.N.H. 9843 in dorsal view. B, reconstruction of the neurocranium in hind view. *Autsph.* autosphenotic; *Bocc.* basioccipital; *Dpt.* dermopterotic; *Epot.* epiotic; *f.m.* foramen magnum; *Fr.* frontal; *Ic.* intercalar; *Lat.occ.* lateral occipital; *Par.* parietal; *Socc.* supraoccipital; *tem.gr.* temporal groove; X, foramen for vagal nerve.

Dermal bones. A few of these remain on B.M.N.H. 9843, the whole of the parietals and dermopterotics and the hind part of the frontals being preserved. The sutures are much indented and the surface has a close-set ornamentation of pits and furrows; in consequence it has been impossible to distinguish the sensory canals on this specimen, but their position is shown on B.M.N.H. 9844, in which the dermal bones have been damaged or entirely removed except for the dermopterotics. Here the canals occasionally remain as calcite infillings, and elsewhere they are marked by grooves in the impression of the under surface. The supraorbital canal is thus seen to pass directly on to the parietals. B.M.N.H. 9843 is entirely without ethmoid region; 9844 is broken in two along the hind wall of the orbits and consequently across the frontals; on the anterior part the impression of these bones can be traced for a short way beyond the preorbital process, but here the specimen is broken and nothing of the rostrum remains.

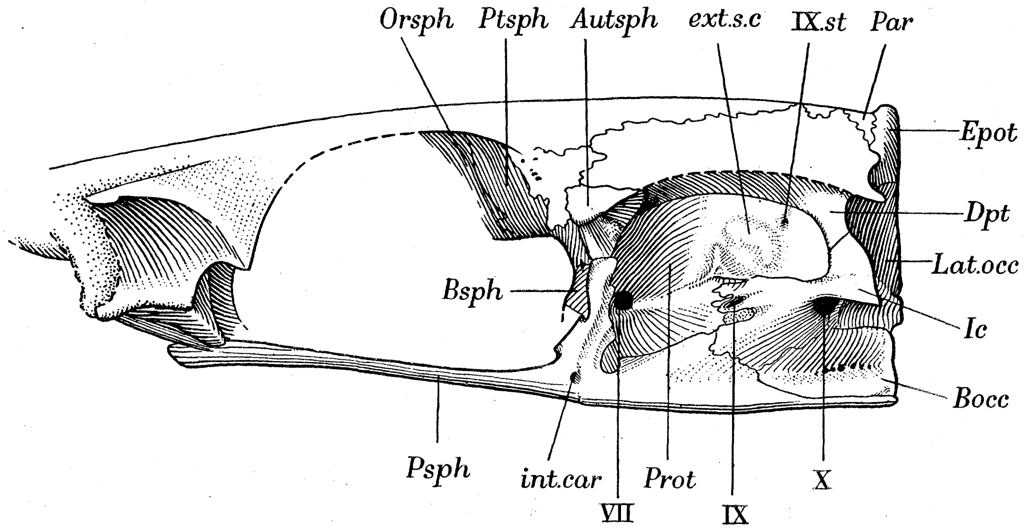

FIGURE 20. *Aspidorhynchus* sp., reconstruction of the neurocranium in lateral view. × 1·5. *Autsph.* autosphenotic; *Bocc.* basioccipital; *Bsph.* basisphenoid; *Dpt.* dermopterotic; *Epot.* epiotic; *ext.s.c.* external semicircular canal; *Ic.* intercalar; *int.car.* foramen for internal carotid artery; *Lat.occ.* lateral occipital; *Orsph.* orbitosphenoid; *Par.* parietal; *Prot.* pro-otic; *Psph.* parasphenoid; *Ptsph.* pterosphenoid; VII, foramen for facial nerve; IX, foramen for glossopharyngeal nerve; IX.*st.* foramen for supratemporal branch of glossopharyngeal nerve; X, foramen for vagal nerve.

Neurocranium. Most of this description is based on B.M.N.H. 9844 (figures 42 and 43, plate 21), which is entirely uncrushed and shows all the bones of the orbital and side walls perfectly, but those of the posterior surface are indistinguishable from one another and slightly damaged, and the restoration of the hind view is taken from 9843 (figure 41, plate 21), which is slightly distorted. An important feature of the skull is the small supraoccipital shown in this specimen; it appears on the dorsal surface only, between the parietals and epiotics; its forward extent is unknown, but it clearly had no posterior spine and did not appear on the skull roof in the living fish, for it would be entirely covered by the extrascapulars. The intercalar has a large expanse on the side wall and might therefore appear to take a substantial part in the skull wall, but this is not the case, for on the right side of 9843 most of the anterior part is broken away, showing the bone to consist of superficial splints only with a compact appearance unlike the cancellar structure of cartilage bone. Even in the two known specimens the intercalar is not constant in its relation to the 10th nerve. In 9844 it surrounds the opening entirely; in 9843 the lower margin is formed by the lateral occipital. The latter has several rather irregular foramina in its side wall, including at least one for an occipital nerve.

The large pro-otic may be divided for description into the anterior portion representing its usual extent in Holostean fishes, and the posterior part containing a small dorsally directed foramen for the supratemporal branch of the 9th nerve and a crescentic ridge marking the position of the external semicircular canal. There is no sign of suture between the two parts, but the grain of the bone suggests a radial structure in the anterior part centred on the facial foramen, while there is no directional structure in the posterior part.

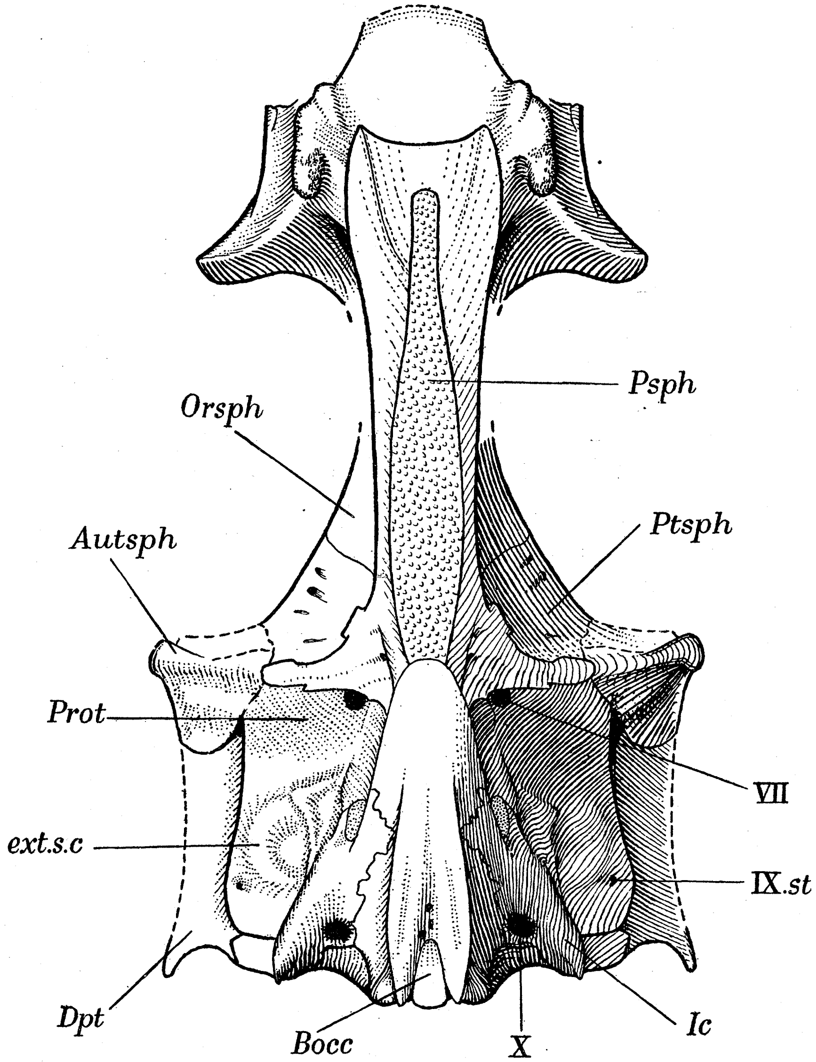

FIGURE 21. *Aspidorhynchus* sp., reconstruction of the neurocranium in ventral view. × 1·5. *Autsph.* autosphenotic; *Bocc.* basioccipital; *Dpt.* dermopterotic; *ext.s.c.* external semicircular canal; *Ic.* intercalar; *Orsph.* orbitosphenoid; *Prot.* pro-otic; *Psph.* parasphenoid; *Ptsph.* pterosphenoid; VII, foramen for facial nerve; IX.*st.* foramen for supratemporal branch of glossopharyngeal nerve; X, foramen for vagal nerve.

Below the ridge of the external semicircular canal is another, triangular and sharp, which together with the longitudinal ridges on the pro-otic and intercalar may mark muscle insertions, possibly of the adductors of the hyomandibular and palate, and farther back on the intercalar, the levators of the branchial arches. The only other suggestion of muscular attachment is a roughening on the autosphenotic, possibly for the dilator operculi.

There is no distinct facet for the hyomandibular and it probably articulated with the large ventral flange of the dermopterotic, below which the dorsal margin of the pro-otic shows on its inner side the granulated surface that marks an original junction with cartilage.

The anterior face of the autosphenotic is partially overhung by a thin irregular bony fringe, the significance of which is obscure. The bones of the rest of the orbital surface are complete and well preserved in 9844 except for the basisphenoid and anterior part of the orbitosphenoid. Part of the former is found in 9843 as a small ossification on the left side roughly in place below the pedicle of the pterosphenoid; it is one of the two arms of the normal Y-shaped bone, the other being lost; the stem was apparently unossified.

The myodome has been excavated for nearly a centimetre; the backwardly converging side walls and roof are formed by the pro-otic and a narrow floor by the parasphenoid.

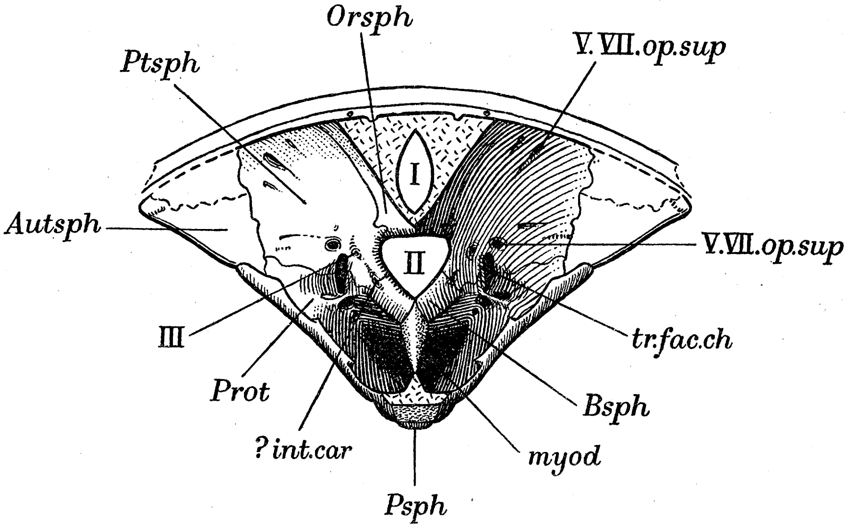

FIGURE 22. *Aspidorhynchus* sp., reconstruction of the neurocranium cut through vertically just in front of the optic foramen and viewed from in front. × 1·5. *Autsph.* autosphenotic; *Bsph.* basisphenoid; *? int.car.* ? foramen for internal carotid artery; *myod.* myodome; *Orsph.* orbitosphenoid; *Prot.* pro-otic; *Psph.* parasphenoid; *Ptsph.* pterosphenoid; *tr.fac.ch.* trigemino-facial chamber; I, olfactory canal; II, optic foramen; III, foramen for oculomotor nerve; V.VII.*op.sup.* foramen for superficial ophthalmic branches of trigeminal and facial nerves.

Probably it extended only a short distance into the basioccipital. The two arms of the basisphenoid apparently formed a complete floor to the cranial cavity between the hind border of the optic foramen and the myodome roof, with no space for a hypophysial fenestra. The hypophysis must therefore have lain entirely within the cranial cavity, lodged in a depression bounded behind by a strong transverse ridge on the floor of this cavity and in front by the rising border of the pro-otic bridge where it curves up to meet the basisphenoid.

The trigemino-facial chamber is unusually large and high. It has one entrance into the cranial cavity at the hind end placed ventrally and mesially; from this must have entered both roots of the trigemino-facial ganglion. The superficial ophthalmic nerves issued from a foramen above and in front of the main orbital opening of the chamber, and branches of these nerves account for the upwardly directed passages in the pterosphenoid. The trigeminus, together with the buccal branch of the facialis, passed directly into the orbit by the main elongated opening; the hyomandibular branch by a ventral aperture farther back, to turn outwards at once through the side wall of the skull, the palatine branch at the same time diverging inwards into the uppermost part of the myodome. Shortly behind this palatine foramen is another for the abducens. The pedicle of the pterosphenoid contains a small aperture which leads directly into the cranial cavity without any connexion with the trigemino-facial complex and was probably for the oculomotor. A slit-like opening crossing the suture between the pterosphenoid and basisphenoid may have transmitted the internal carotid.

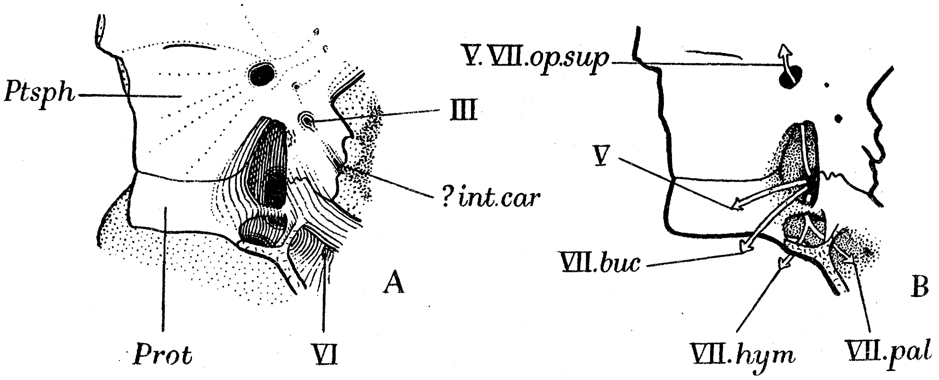

FIGURE 23. *Aspidorhynchus* sp. × 3. A, B.M.N.H. 9844, the trigemino-facial chamber and surrounding structures. B, a reconstruction of the course of the trigeminal and facial nerves. *? int.car.* ? foramen for internal carotid artery; *Prot.* pro-otic; *Ptsph.* pterosphenoid; III, foramen for oculomotor nerve; V, course of trigeminal nerve; VI, foramen for abducens nerve; VII.*buc.* course of buccal branch of facial nerve; VII. *hym.* course of hyomandibular branch of facial nerve; VII.*pal.* course of palatine branch of facial nerve; V.VII.*op.sup.* course of superficial ophthalmic branches of trigeminal and facial nerves.

The under side of the ethmoid ossification and anterior part of the parasphenoid is exposed in 9844; the former is a solid structure without divisions, but in this specimen at least does not continue far into the rostrum. There is a slight anterior myodome and a roughened ridge at the base of the preorbital process for articulation with the palate. Nothing is known of the olfactory capsules. Between the ethmoid bone and the orbitosphenoid there is a small patch of bone in the interorbital septum.

PHOLIDOPHORIDAE

Pholidophorus

The neurocranium of this genus is only known in the type species, *P. bechei*, from the Lower Lias, and even here specimens are rare and only moderately preserved. In consequence the interpretation of this structure has depended considerably on that of *Leptolepis*, which is very similar, and a fairly full description of which has been already published (Rayner 1937).

Dermal skeleton. The bones of the snout in this genus are better preserved than in many Jurassic fishes and allow a restoration to be made of the sensory canals and nasal apertures. The posterior of these openings is completely enclosed in the nasal; the anterior lies between the rostral and antorbital. The latter is commonly imperfect or missing in fossil Holosteans (exceptions are *Caturus* and *Dapedius*), but in *Pholidophorus* it is found fairly frequently, and, more important, it can be seen to carry the junction of three branches of the sensory canal, showing the supra- and infraorbital canals in this genus to form a closed circuit around the eye.

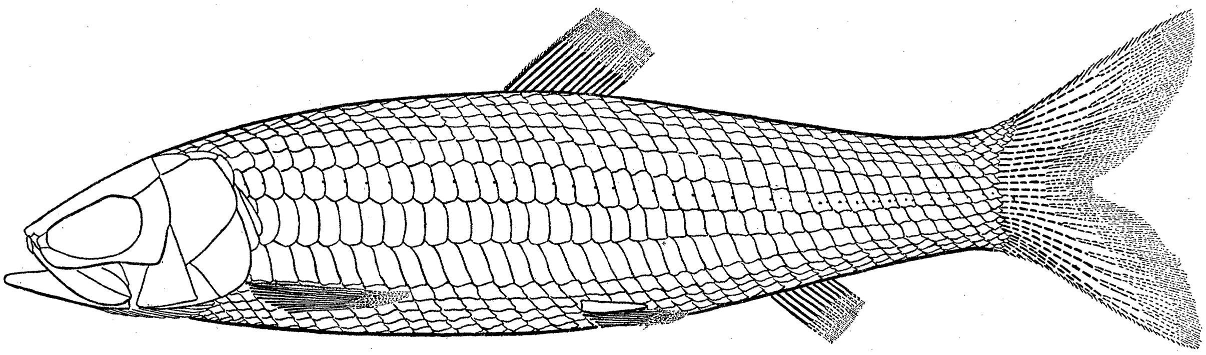

FIGURE 24. *Pholidophorus bechei*, reconstruction. × 1.

Figures 25 and 26 illustrate the variation found in this species in the development of the supraorbital sensory canal; the sensory tract may continue on to the parietal as a closed canal and the anterior pit-line be short, or it may be represented on this bone by a long pit-line extending to the anterior suture, or the canal may stop short well within the frontal and be supplemented by a pit-line on that bone as well; finally, traces of the anterior pit-line may be missing altogether. Professor Watson coll. P372 shows both the last two possibilities, one on each side of the head. The middle pit-line is always well developed, especially on the dermopterotic. The supraorbital canal gives off a few short branches while passing through the frontal; on most of the roofing bones the course of the sensory canals can only be deduced from the pores of such branches, but on the thinner elements (e.g. nasal) it may show up as a slight ridge. The frontals, parietals and dermopterotics are often so closely welded together that their bounding sutures are not distinguishable. The extra- and suprascapular are but loosely attached to the remainder of the skull; the latter has not been found complete at the anterior margin, nor is it known whether it bore the usual downward process for attachment to the intercalar or not, but this was probably the case. The premaxilla is small and stout; it lies in an embayment in the anterior surface of the maxilla and bears some large, low, rounded teeth; there is no underlying process connected with the neurocranium. The maxilla for most of its length is long, slim and slightly curved; it bears very minute denticulations on its outer border. In the neighbourhood of the premaxilla it narrows and thickens to a curved beak disappearing under the ethmoid region.

The lower jaw is composed of three elements, dentary, prearticular and angulo-articular. In one specimen only have teeth been found preserved (B.M.N.H. 38109); they were about six small delicate pegs, placed at a little distance from the anterior point of the jaw, larger than the denticulations of the maxilla but not comparable with the stout rounded teeth of the premaxilla. These last probably closed on the bare surface of the mandible in front. One specimen, S.M. J3828, where the jaws are seen from below shows a narrow gular with median vertical ridge lying between them.

The palatal bones are only known in fragments in any one fish, but from such fragments and the general shape of the skull it is apparent that they must have closely resembled those of *Leptolepis*. The quadrate has the usual triangular shape with a rounded process for articulation with the lower jaw; the palatine appears as a stout single ossification lying unattached below the parasphenoid in B.M.N.H. 3586*c*. The metapterygoid is rather

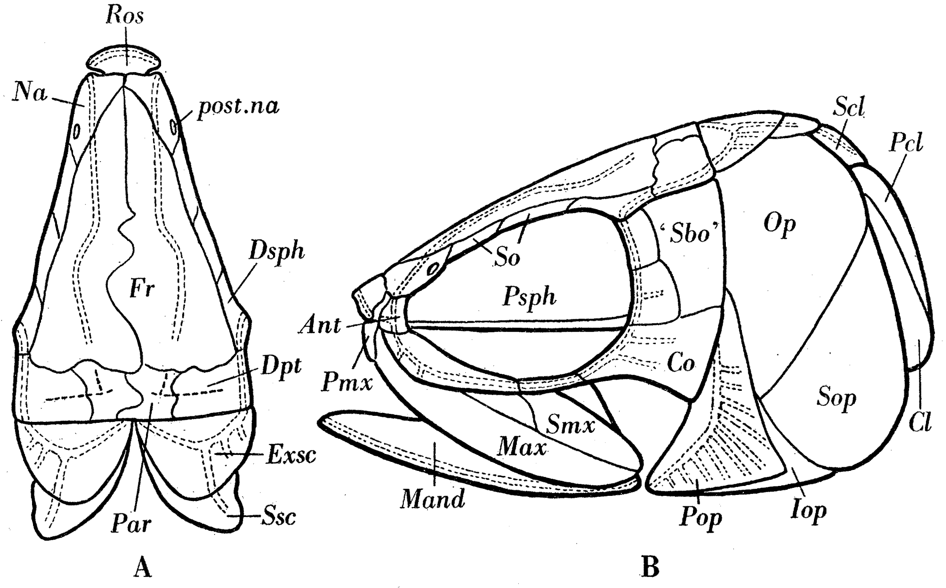

FIGURE 25. *Pholidophorus bechei*, reconstruction of the dermal bones of the skull, from Rayner (1941). × 2. A, dorsal view. B, side view. *Ant.* antorbital; *Cl.* cleithrum; *Co.* circumorbital; *Dpt.* dermopterotic; *Dsph.* dermosphenotic; *Exsc.* extrascapular; *Fr.* frontal; *Iop.* interopercular; *Mand,* mandible; *Max.* maxilla; *Na.* nasal; *Op.* opercular; *Par.* parietal; *Pcl.* postcleithrum; *Pmx.* premaxilla; *Pop.* preopercular; *post.na.* posterior nasal aperture; *Psph.* parasphenoid; *Ros.* rostral; '*Sbo*'. 'suborbital'; *Scl.* supracleithrum; *Smx.* supramaxilla; *So.* supraorbital; *Sop.* subopercular; *Ssc.* suprascapular.

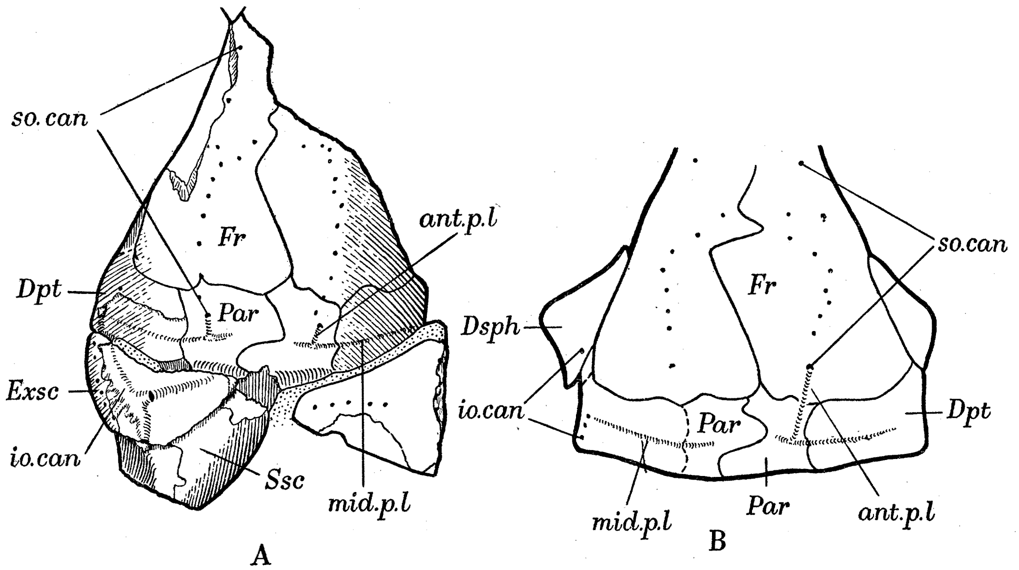

FIGURE 26. *Pholidophorus bechei*, showing the posterior roofing bones and latero-sensory system. × 3. A, B.M.N.H. 19010. B, Professor Watson coll. P372. *ant.p.l.* anterior pit-line; *Dpt.* dermopterotic; *Dsph.* dermosphenotic; *Exsc.* extrascapular; *Fr.* frontal; *io.can.* infraorbital sensory canal; *mid.p.l.* middle pit-line; *Par.* parietal; *so.can.* supraorbital sensory canal; *Ssc.* suprascapular.

better preserved; the body is a large semicircular wing lying above the quadrate and bearing a well developed dorsal process with a groove on its posterior face for articulation with the basipterygoid process of the parasphenoid. Scarcely anything can be seen of the ento- and ectopterygoid.

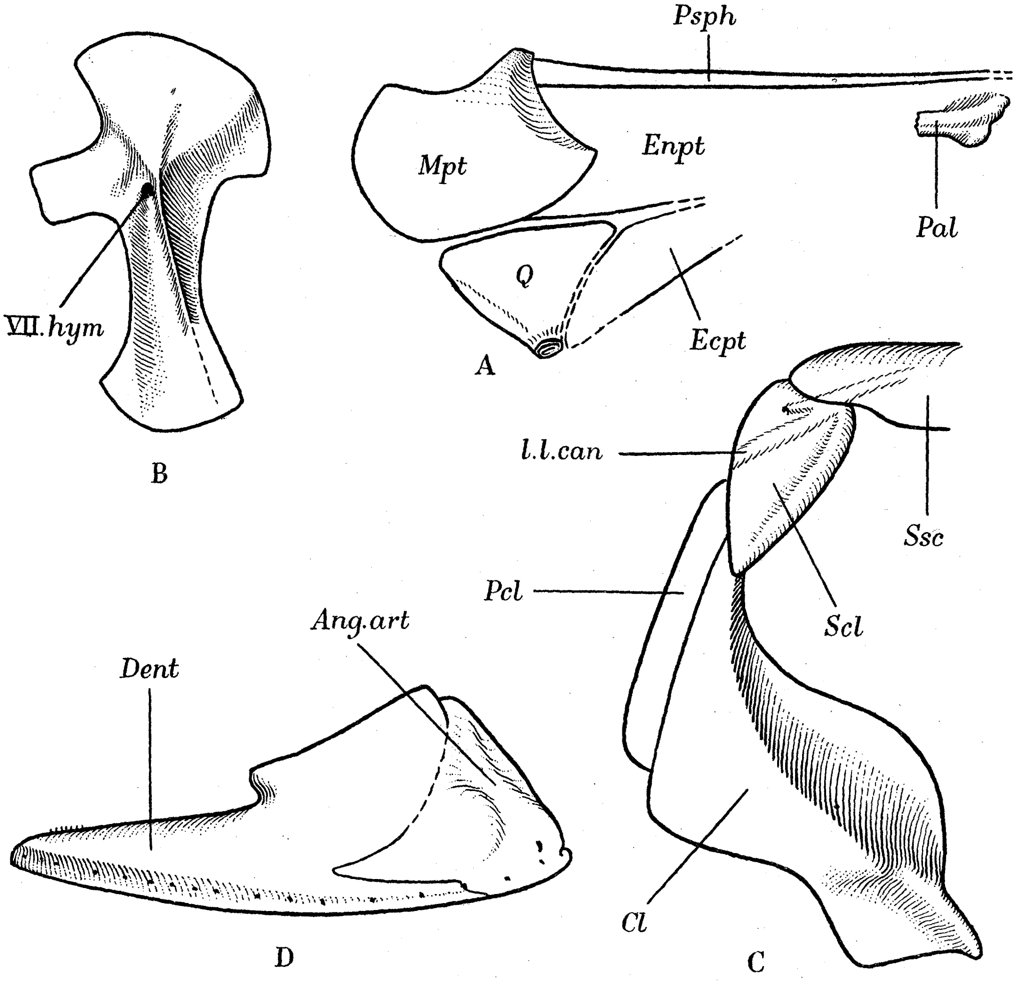

FIGURE 27. *Pholidophorus bechei*, reconstructions of various parts of the skeleton. × 4. A, right palate. B, right hyomandibular. C, dermal bones of the right pectoral girdle. D, left lower jaw. *Ang.art.* angulo-articular; *Cl.* cleithrum; *Dent.* dentary; *Ecpt.* ectopterygoid; *Enpt.* entopterygoid; *l.l.can.* main lateral line canal; *Mpt.* metapterygoid; *Pal.* palatine; *Pcl.* postcleithrum; *Psph.* parasphenoid; *Q.* quadrate; *Scl.* supracleithrum; *Ssc.* suprascapula; VII.*hym.* foramen for hyomandibular branch of facial nerve.

The hyoid and branchial arches are also poorly preserved, the hyomandibular alone being known sufficiently for description. It articulated with the neurocranium by a broad thick head and has a strong vertical ridge and stout opercular process. The hyomandibular branch of the facial nerve entered near the upper anterior corner and emerged on the outer surface somewhat below the level of the opercular process. As far as can be seen it continued in a groove behind the vertical ridge until near the lower end of the bone, but the preservation is never very good in this region. Fragments of bone show the remaining visceral arches to have been well ossified, and there were certainly two separate elements to the ceratohyal, bearing a large number of branchiostegal rays.

Neurocranium. Only three specimens showing this structure have been found—B.M.N.H. P1052 and 19010, and S.M. J4851; the first of these (figure 45, plate 21) is almost uncrushed, but the others have all the bones somewhat displaced. The neurocranium was very well ossified, and B.M.N.H. P1052 shows only those sutures bounding the intercalar and supraoccipital and that between the ptero- and basisphenoid. These are in the same positions as the corresponding divisions in *Leptolepis*; the crania of the two genera are also very alike in general shape, and it is very probable that the bone pattern was essentially the same. The bone names are therefore used here for convenience in describing regions of the neurocranium, although the extent of some of the ossifications is a matter of inference.

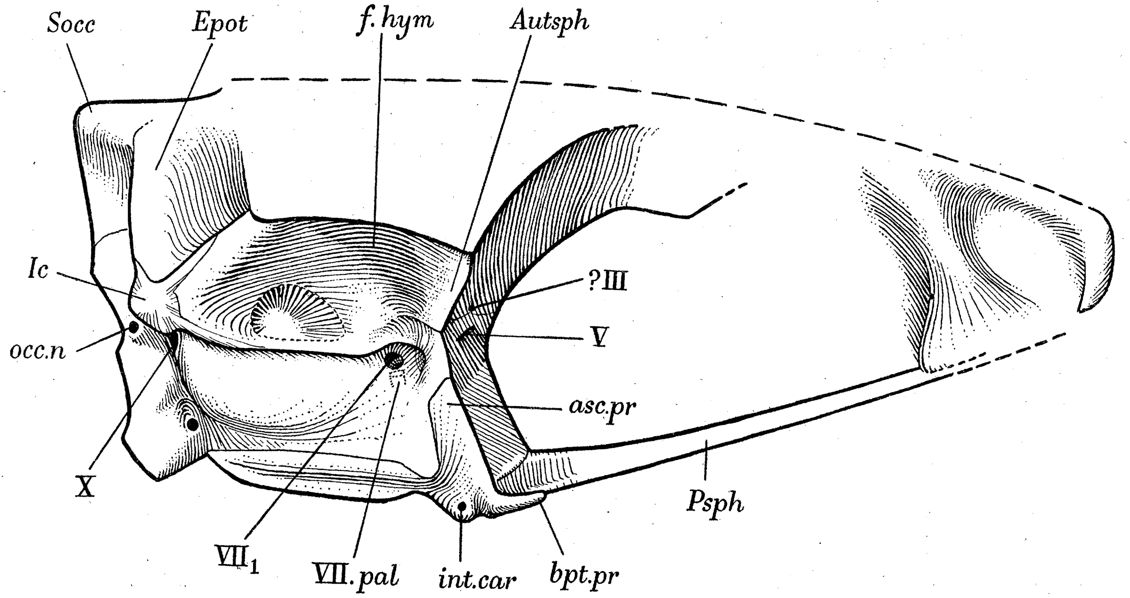

FIGURE 28. *Pholidophorus bechei*, reconstruction of the neurocranium in side view. × 5. *asc.pr.* ascending process of parasphenoid; *Autpt.* autopterotic; *bpt.pr.* basipterygoid process of parasphenoid; *Epot.* epiotic; *f.hym.* facet for hyomandibular; *Ic.* intercalar; *int.car.* foramen for internal carotid artery; *occ.n.* foramen for occipital nerve; *Psph.* parasphenoid; *Socc.* supraoccipital; ? III, ? foramen for oculomotor nerve; V, foramen for trigeminal nerve; VII.*pal.* passage for palatine branch of facial nerve; VII_1, entrance of hyomandibular root of facial nerve; X, foramen for vagal nerve.

The large supraoccipital does not appear on the roof of the skull as it does in *Leptolepis*, but is covered by the parietals and extrascapulars; nor has it any median crest on the hind surface, only a rounded elevation which passes smoothly into the epiotic of either side. The latter contains part of the posterior semicircular canal; it occupies only a little of the posterior surface and then turns inwards and forwards under the skull roof to form the inner wall of the temporal groove. The forward extent of this hollow is unknown; its outer wall is the autopterotic, which is sufficiently damaged in B.M.N.H. P1052 and S.M. J4851 to show that it was largely occupied by the external semicircular canal. The junction of autopterotic and epiotic is capped by a small intercalar, irregular in outline and bearing long splints of bone overlying its neighbours. The two lateral occipitals meet above the foramen magnum and an occipital nerve emerged close to it; the exact shape of this opening and of the notochord pit are unknown. There is a short canal for the dorsal aorta, from which at least one fair-sized artery arose dorsally; the canal is delicate and always rather crushed, so that there may have been other arteries whose foramina are not preserved.

The upper half of the side wall of the neurocranium is at a broad angle with the lower and faces downwards and outwards. In front of the autopterotic region there is a hyomandibular facet, curving downwards anteriorly, and a strong postorbital process. Below the hyomandibular facet and external semicircular canal lies a deep pit, apparently ossified throughout, and bounded below by a sharp horizontal ledge; the position of both pit and ledge suggest that they were connected with the levator muscles of the branchial arches.

There is a pronounced saccular bulge in that part of the auditory capsule surrounded by the basioccipital which fades away anteriorly in the pro-otic region. The trigemino-facial complex is represented on the side wall by the following foramina, somewhat sunk below the overhanging autosphenotic: a large opening leads immediately into the orbit and carried the jugular vein and buccal branches of the facial nerve; the smaller one farther back is almost at once divided into two by a transverse bar, the upper, hindermost of these passing directly into the cranial cavity and the other into a canal leading downwards and forwards inside the bone. The first of these two foramina transmitted the main trunk of the facial nerve, from which arose the buccal branch, and also the hyomandibular trunk which immediately turned outwards to pierce the hyomandibular bone. The palatine branch occupied the second foramen and descending passage; its course is seen again as a groove on the dorsal surface of the parasphenoid, but whether between these points it ran through the myodome or emerged on to the outer surface cannot be determined.

The orbital surface of the neurocranium is described almost entirely from B.M.N.H. P1052 with slight additional evidence from 19010. The two orbits are entirely confluent above the parasphenoid except for the latero-ventral walls of the olfactory canal. This orbitosphenoid portion of the orbital surface, and also the pterosphenoid, are only slightly curved, outwards and downwards, and posteriorly the wall turns out rather abruptly to pass into the anterior face of the autosphenotic. The facial chamber is no more than a short tunnel for the jugular vein and buccal branches of the facial nerve, the entry of which has been described on the lateral wall. In B.M.N.H. 19010, where the myodome has been partially excavated, the facial chamber is seen to be floored by a sharp, narrow ledge between the pro-otic outer wall and the basisphenoid wing; this ledge at the same time is roof to part of the myodome.

Slightly below the ventral margin of the pterosphenoid is a large elongated foramen facing downwards and forwards; from its size and position it is taken to be that of the 5th nerve, and thus lies just outside the facial chamber, not so far removed from it as in *Caturus* or *Lepidotus*, but not sufficiently within it to transform the cavity into a true trigemino-facial chamber as is found in the later members of this stock, *Leptolepis* and the Teleosts. A well-marked, rounded groove rises dorsally from the facial chamber and is connected with an upward facing opening in its dorso-median wall; the aperture and groove almost certainly mark the course of the superficial ophthalmic nerves, which thus arise almost from within the facial chamber. There are two small passages in the pterosphenoid, similar to those which in *Leptolepis* are tentatively assigned to minor branches of the ophthalmicus superficialis (p. 325 below). In *Pholidophorus* there is also another, with a slight groove above it, close to the ventral margin, which may represent the oculomotor; the region immediately anterior to the facial chamber is poorly preserved, however, and it is not possible to be certain that the oculomotor did not issue elsewhere. The otic foramen is found in the anterior face of the autosphenotic as in *Leptolepis*; the roof of the myodome similarly shows a small aperture for the abducens nerve.

The cranial cavity and auditory capsule are unknown except for the short and fragmentary portions of the semicircular canals already described. The wall of the cavity does not appear to have been thickly ossified, and the roof consisted mainly of membrane or cartilage beneath the dermal bones. The myodome was large, but its exact backward extent is not known, nor whether it communicated with the aortic canal. It was almost certainly floored by the parasphenoid; this bone bears a rather short ascending process, the base of which is continuous with that of the basipterygoid process; the latter is long and slender with a shallow groove on the anterior surface. Just in front of this region the lateral flange of the parasphenoid is pierced for the efferent pseudobranchial artery. The internal carotid entered the parasphenoid shortly behind the base of the ascending process of that bone, passed inwards and forwards through a short canal and emerged in the region of the basisphenoid; there is no further evidence as to its course, but presumably it turned upward and entered the cranium through the optic foramen.

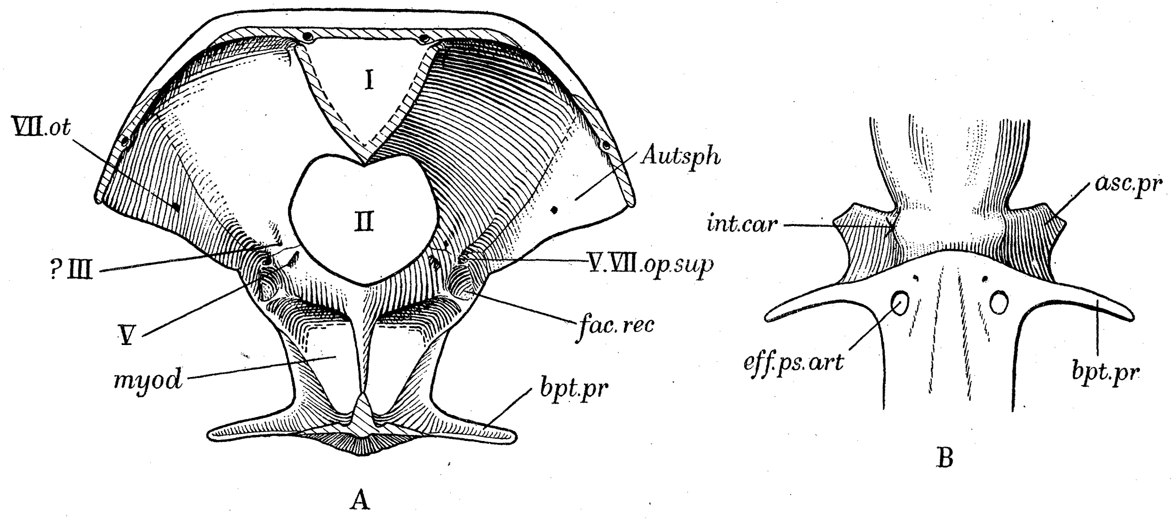

FIGURE 29. *Pholidophorus bechei.* × 5. A, reconstruction of the neurocranium cut through vertically in front of the optic foramen and viewed from in front. B, central section of the parasphenoid in ventral view. *asc.pr.* ascending process; *Autsph.* autosphenotic; *bpt.pr.* basipterygoid process; *eff.ps.art.* foramen for efferent pseudobranchial artery; *fac.rec.* facial recess; *int.car.* foramen for internal carotid artery; *myod.* myodome; I, olfactory canal; II, optic foramen; ? III, ? foramen for oculomotor nerve; V, foramen for trigeminal nerve; VII.*ot.* foramen for otic branch of facial nerve; V.VII.*op.sup.* foramen for superficial ophthalmic branches of trigeminal and facial nerves.

The preorbital part of the neurocranium can only be deduced from several crushed and fragmentary specimens. There is a fairly stout preorbital process, which is also the hind wall of the large olfactory chamber. The anterior border of this hollow is the ethmoid or pre-ethmoid ossification which closely underlies the rostral, and which has a pair of recurved lateral horns similar to those of that bone.

Postcranial skeleton, etc. The dermal shoulder girdle consists, as usual, of cleithrum, supra- and postcleithrum; the anterior portion of the cleithrum is strongly curved and concave outwards, the posterior slightly convex. The primary girdle is normally situated beneath the latter and is either hidden or so broken as to make the bone unrecognizable. In one specimen, S.M. J3830, however, fragments of the scapula have been seen showing it to be similar to that of *Leptolepis*. The pectoral fin comprises about twenty-two lepidotrichia. The base is overlapped by a number of small scales continuous with those of the belly; probably they covered a slightly movable base to the fin-web. The pelvic fins contain about fourteen lepidotrichia, the dorsal twelve and the anal nine. Each ray branches twice, and the first of each fin is bordered by numerous small fulcra.

The vertebrae consist of stout separate pleuro- and hypocentra opposed to one another. Their number is uncertain since they can be seen only in slightly distorted specimens where the scales are disturbed. The caudal fin consists of twenty-eight lepidotrichia; the lower lobe bears small fulcra similar to those on the other fins, but the upper has very much larger ones. The greatest length of the upper lobe is formed by the first ray and that of the lower by the sixth; the lepidotrichia divide three times and possibly more, the finest branches being not easily distinguishable.

The scales are stout, and smooth or with very faint concentric markings. There are four deepened rows on the flank but they are not always very clearly distinguished from their neighbouring rows, and the difference fades away towards the tail. The scales articulate by means of a stout peg and socket. Their hind border is smooth and slightly convex; the scales of the second deepened row bear the sensory canal which opens by a small pore at the hind margin of each; in addition, near the tail some of the scales have another pore in the centre.

LEPTOLEPIDAE

Leptolepis

Only a few points concerning the autopterotic and the nerves of the orbit are given here, since a description of the genus has already been published (Rayner 1937). The most dorsal and posterior bone of the otic region was in that work called supratemporo-intertemporal (e.g. p. 59) and thought to be indivisible from the dermal bone of that name, here called dermopterotic; further examination of the material has shown that in one specimen at least (Professor Watson coll. P507, figure 44, plate 21) the two ossifications are separate, and that the ventral is a true cartilage bone, an autopterotic, containing part of the external semicircular canal. The epiotic similarly contains part of the posterior so that the two bones are very like those of *Pholidophorus*.

With regard to nerves of the orbit, *Leptolepis* and *Philodophorus* are so much alike in other respects that it seems very improbable that they should differ seriously in the distribution of the major nerve trunks. One specimen of the latter, which is the rather better preserved in this respect, shows the position of the trigeminal and superficial ophthalmic nerves clearly (p. 323 above); the most important point is that the latter apparently issue from the back of the facial chamber, and therefore it is likely that they had a similar position in *Leptolepis*. They were originally thought to issue through a pair of smaller foramina in the pterosphenoid in this genus; these also exist in *Pholidophorus*, and as they have been seen in more than one specimen of each genus they are apparently stable structures; they are always close together and about equal in size, and possibly represent branches of the ophthalmic nerves.

If this revised position of the ophthalmicus superficialis is correct some alterations in the positions of other nerves is necessitated. Both the facialis and the superficial ophthalmic nerves emerged through the larger, posterior, entrance of the trigemino-facial chamber; the hyomandibular branch turned outwards and backwards on to the lateral skull wall, the buccal and otic branches forward into the orbit, and the ophthalmicus superficialis upwards and forwards close to the skull wall. The trigeminus occupied the anterior entrance, and the oculomotor issued through the small foramen just in front of it. The profundus and ciliaris trunk lay in the smallest, most ventral passage, and the trochlearis entered through the optic foramen.

DISCUSSION

Comparison with Palaeoniscoids

A survey of the Actinopterygian neurocranium and its development may conveniently begin with some general comparisons between the Jurassic forms just described and those known from earlier rocks; the latter have received more attention than the former and the following genera are known fairly completely:

'Kansas Palaeoniscids A and B'	(Watson 1925, 1928), Upper Carboniferous
Birgeria	(Stensiö 1921), Eotrias
Saurichthys	(Stensiö 1925), Eotrias
Perleidus	(Stensiö 1932), Eotrias
Ospia	(Stensiö 1932), Eotrias
Broughia	(Stensiö 1932), Eotrias
Australosomus	(Piveteau 1934), Eotrias
Glaucolepis	(Nielsen 1942), Eotrias
Boreosomus	(Nielsen 1942), Eotrias

In addition, Watson (1928) has described a specimen of *Cosmoptychius* from the Lower Carboniferous, and another, more imperfect, of *Elonichthys*; Case (1937) has briefly described a Palaeoniscid very similar to those from Kansas.

It is well known that the evolution of the cranium in bony fishes has involved a general lightening of the skull, even resulting in the partial replacement of bone by cartilage or membrane. In particular, the dorsal surface in all known Jurassic neurocrania has large pits or even lacunae in the ossification, whereas the Palaeoniscoid neurocranium is commonly rather more complete. Another primitive character that appears to be partly connected with this difference in ossification is the rather widely spaced positions of the neural apertures of the orbit; this is seen in the Kansas crania, especially in the forward position of the trigeminus, which traverses a considerable thickness of bone before reaching the exterior; the same applies to *Caturus* in rather a lesser degree, and slightly to *Lepidotus*, but *Leptolepis* and *Aspidorhynchus* have different and more specialized arrangements of nerve passages, collected more closely together.

The Palaeoniscoids had large eyes and a fairly large myodome, and the interorbital septum was largely membranous. The eyes remain fairly large in all the Jurassic forms, though in the Eugnathidae, Semionotidae and Pachycormidae there is a considerable development of bone in the interorbital septum. The reduction of eyes and myodome in *Amia* and *Lepidosteus* is an obvious case of parallel development; the line leading to the Teleosts kept the rather large eyes, and the myodome extends even farther backwards into the basioccipital region.

The difference in the appearance of the ethmoid region results from the different shape of the snout; the Palaeoniscoid rostrum is broad and blunt and the neurocranium underlying it was probably similar in outline. In the Kansas specimens there is a broad olfactory plate continuous with the very massive supraorbital ridges which overhang the eyeball. The same type of structure is found in *Australosomus* (Piveteau 1934, p. 15) which is rather better preserved in this region. The narrow, rather pointed snout of the Holostei leaves little room for any great skeletal expansion around the olfactory pits, and usually there is not much development of neurocranial bone above the eyes, so that the preorbital processes are more pronounced.

The semicircular canals of the Palaeoniscoids show up on the external surface as they do not in the more generalized Jurassic Holostei; the anterior and posterior form slight curved ridges on the dorsal surface, and the external is marked by a prominent ridge on the lateral wall. The majority of the Jurassic fishes have in contrast a fairly smooth outline and the canals are well sunk in the cranial walls; the same applies to *Amia* and *Lepidosteus*, allowing for the replacement of bone by cartilage. *Pholidophorus* and *Leptolepis* stand well apart in this, for the posterior, and particularly the external, canals jut out prominently beyond the surrounding parts of the cranium, and the labyrinth in general lies more dorsally.

Another important difference in this region between Palaeoniscoid and later neurocrania is the loss in the latter of the vestibular fontanelle—the long slit in the lateral wall between the occipital and otic regions which contains the vagal foramen. It is found in all the better known pre-Jurassic crania except *Birgeria* and *Saurichthys*; Piveteau (1934, p. 14) notes the correspondence between this fontanelle and the space in the developing chondrocranium of *Amia* between the otic capsule and occipital arcade (as figured by Pehrson 1922, p. 20), and recognizes them both as the division between palaeocranium and neocranium, the evidence of which remains in adult pre-Jurassic fishes but is lost in the adults of later forms.

An aortic canal is characteristic of the Palaeoniscoids and also of the Perleididae and Parasemionotidae, which in most respects are nearer the Kansas type of cranium than those of Jurassic fishes. Among the latter it is found in *Leptolepis*, *Pholidophorus* and *Dapedius*. Its occurrence in the last is particularly interesting since it is not found in the related *Lepidotus*; the structure is therefore not of primary systematic importance as was once thought (Rayner 1937, p. 70), when its discovery in *Leptolepis* was apparently evidence of a greater affinity between this genus and the Kansas Palaeoniscids than possessed by genera without one.

The existence of a basipterygoid process in fossil Holostei has hitherto been only supported by isolated references (e.g. Smith Woodward 1893, *Lepidotus*, and Frost 1913, *Dapedius*); the structure was discussed by the author (1937, pp. 70–72), and it was stated that the presence of such a process in *Leptolepis* was supplemented by the discovery of a similar one in one specimen of *Lepidotus*. Since then it has been found in *Dapedius*, *Pholidophorus* and probably in *Caturus* as well. This strengthens the suggestion that its presence in the Holostei is not due to parallel evolution, dependent on feeding habits, since it is found among the predacious Eugnathids, Semionotids with a grinding mechanism, and *Leptolepis* and

Pholidophorus with delicate jaws and very few fine teeth and which probably lived on plankton.

There remains a general point concerning not neurocrania, but the course of the sensory canals in the bony fishes. In the account of *Pholidophorus* it was mentioned that the posterior section of the supraorbital canal appeared to be a particularly variable region, and in other genera some attention was paid to the course of the canals on this part of the head because they were once supposed to constitute a distinction between the Palaeoniscoids (supraorbital canal continued on to the parietals) and the Holosteans—e.g. *Amia* (fusion of supra- and infraorbital canals behind the eye). This difference lost much of its importance when Watson (1925, p. 867) found a Liassic Palaeoniscoid, *Oxygnathus*, with the 'Holostean' pattern, and later the 'Palaeoniscid' nature of that in *Leptolepis* was discovered (Piveteau 1934, p. 73; Rayner 1937).

Further research on the fossil Holostei suggests the continuation of the canal on to the parietal to be the more common; at least it is found in *Lepidotus*, *Aspidorhynchus*, *Pholidophorus* and *Leptolepis*; *Caturus* produces no decisive evidence, though the arrangement of the pores on the parietal is on the whole suggestive on an underlying canal. As far back as 1889 Allis produced evidence which suggests that the arrangement in *Amia* may be a secondary one, a point noticed by Watson (1925, p. 820). The supra- and infraorbital canals develop separately, in the normal Holostean pattern, with separate innervation of their organs. The connexion between the dermosphenotic and frontal is due to an anastomosis after both canals have been fully formed (Allis 1889, p. 472); there is another primary pore belonging to the supraorbital canal behind the anastomosis, in the adult the trunk of a dendritic system, the surface pores of which penetrate the parietal and frontal. In young specimens the organs of the anterior pit-line lie directly behind this pore in the line of the canal, and the first of them is occasionally enclosed in it (Allis 1889, p. 506). It may be supposed that the development of a canal on the parietal is due to a greater number of pores being enclosed than in *Amia*, and that the variation found in *Pholidophorus* is variation in this degree of enclosure. Although the development of *Amia* shows its supraorbital-infraorbital anastomosis to be secondary, in the adult it has the appearance of a fundamental distinctive feature; no such deep-seated anastomosis has been found in any of the fossil genera investigated, though in some specimens of *Caturus porteri* it is perhaps suggested by the arrangement of the pores; this, however, does not rule out the possibility of fusion between secondary branches, which in many cases are very extensive.

Variation in the neurocranial bones

In this section the distribution of the neurocranial bones will be considered before going on to the more controversial problems of homologies and evolution. In addition to the evidence supplied by the fossil genera already described considerable use has been made of Allis's description of *Amia* (1897) and some original observations made on the neurocranium of *Lepidosteus*.

The degree of cranial ossification varies among the Jurassic fishes without direct systematic significance, for the fusion of the separate bones into a solid cranium in the adult may occur independently in different genera, species and even specimens. *Lepidotus* and *Dapedius* belong to the same family, but the former has a skull of separate bones with wide spaces of cartilage between some of them, while the neurocranium of the latter has always been found fused. The skull of the *Caturus* from the Upper Lias is a single piece; that from the Oxford Clay shows a number of sutures. Lastly, only one specimen of *Leptolepis* had all the bones of the side and hind walls distinct, the others exhibiting various degrees of fusion. This indiscriminate fusion suggests that the degree of ossification is partly dependent on the age of the fish, and that a young specimen of *Pholidophorus* probably had distinct bones very similar to those known in *Leptolepis*, which it so closely resembles in shape. Only in a poorly ossified skull, such as that of *Lepidotus*, were the separate ossifications retained throughout life. Although the skull pattern in the adult may thus be obscured, the morphological units can still be deduced where slightly immature specimens are known.

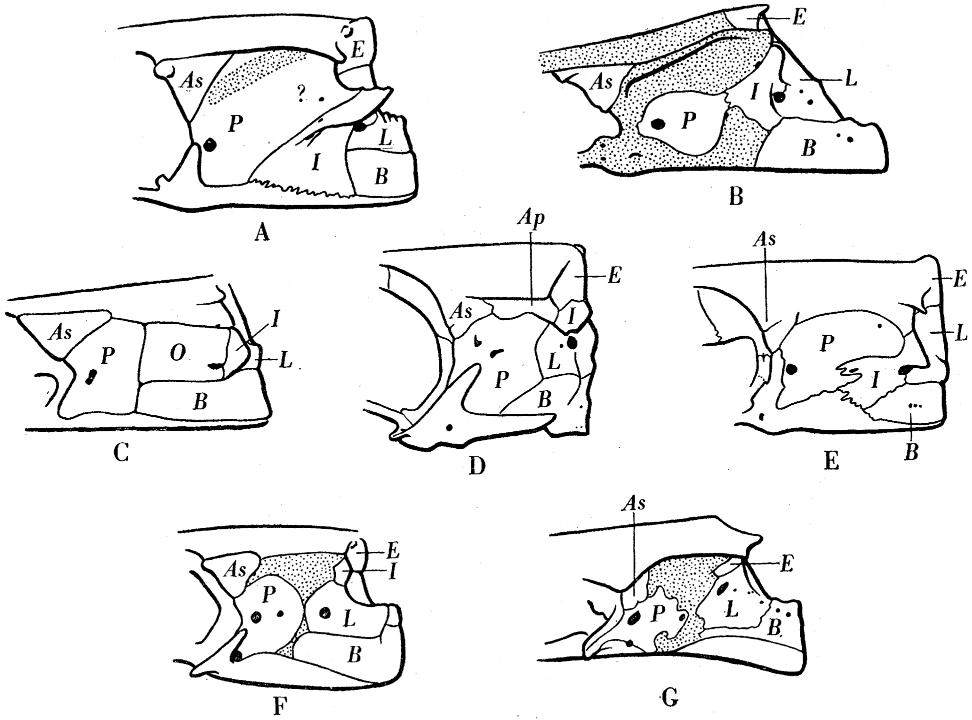

FIGURE 30. Holostean neurocrania in side view, slightly diagrammatic, from Rayner (1941). A, *Caturus*; B, *Amia*; C, *Hypsocormus*; D, *Leptolepis*; E, *Aspidorhynchus*; F, *Lepidotus*; G, *Lepidosteus*. *Ap.* autopterotic; *As.* autosphenotic; *B.* basioccipital; *E.* epiotic; *I.* intercalar; *L.* lateral occipital; *O.* 'opisthotic'; *P.* pro-otic; cartilage stippled.

Figures 30 and 31 illustrate the distribution of bones in the postorbital section of the Holostean neurocranium. It will be seen that they can be arbitrarily divided into those which remain constant in position, and those that vary in lesser or greater degree, fuse with neighbouring bones, or even totally disappear. The first category contains the pro-otic, autosphenotic and basioccipital. The pterosphenoid, orbitosphenoid and basisphenoid are not figured, being rather less well known, but where the boundaries have been seen they are very much alike.

The second category includes the epiotic, lateral occipital, supraoccipital, intercalar, autopterotic and 'opisthotic'. The variation found in the first two is probably of not very great importance. The epiotic has universally a very similar position on the outside of the skull except where there is a large supraoccipital (*Pholidophorus* and *Leptolepis*); internally it has always been found to have some connexion with the posterior semicircular canal except, apparently, in *Amia*, where the reduced ossification has resulted in only occasional contacts between the neurocranial bones and the labyrinth (Stensiö 1921, p. 155). In one specimen of *Lepidotus* the posterior canal made only a slight groove in the epiotic. The lateral occipital also has certain fundamental relations to the foramen magnum, vagus, and occipital nerves, and articulates with the neural arches; the anterior and dorsal limits vary, however, so that in *Lepidotus* the bone encloses much of the posterior semicircular canal and abuts on the external, and is said by Stensiö (1921, p. 156) to have similar relations in a well-ossified specimen of *Lepidosteus*, although in those seen by me this was not the case. Such variation in the peripheral parts of a bone is clearly only part of individual differences between specimen and specimen.

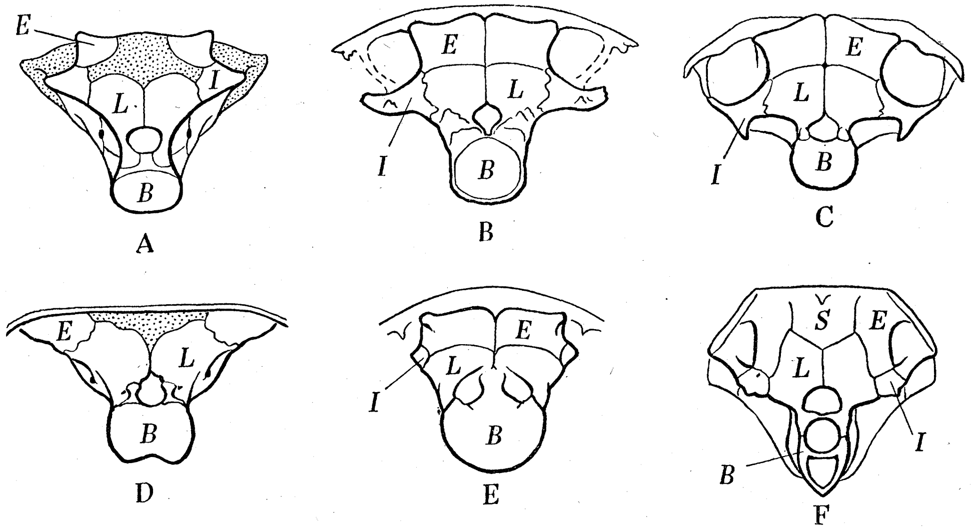

FIGURE 31. Holostean neurocrania in hind view, slightly diagrammatic. A, *Amia*; B, *Caturus*; C, *Aspidorhynchus*; D, *Lepidosteus*; E, *Lepidotus*; F, *Leptolepis*. *B.* basioccipital; *E.* epiotic; *I.* intercalar; *L.* lateral occipital; *S.* supraoccipital; cartilage stippled.

The supraoccipital is found as a large bone in *Leptolepis* and *Pholidophorus*, and as a very small one, on the dorsal surface only, in *Aspidorhynchus*. The variation in the size of the intercalar appears more important than it is, for its large extent in some genera (*Aspidorhynchus* and *Caturus*) is due to superficial fibres of bone overlying the solid skull wall. Its inconstant relations to the foramen for the 10th nerve may be put down to similar superficial differences; this is supported by *Aspidorhynchus*, in which those relations are not exactly the same in the two known specimens. Other variations in the size of this bone in Teleosts are given by Vrolik (1873). The absence of an intercalar in *Lepidosteus* is almost certainly connected with the modified mechanics of the shoulder girdle in that fish, for the downward process of the suprascapular lies directly against the hind wall of the skull in a slight hollow in the epiotic, and the ligamental connexion with an intercalar is no longer necessary. The presence of the bone in *Lepidotus* is accompanied by a normal suprascapular and descending process, well removed from the cranium. All the evidence supplied by the Holostei goes to show that the intercalar is rightly named in these fishes, and also in the Teleosts, and is a membrane bone; this was clearly set forth by Allis in 1909 (p. 58), who writes of it as being of 'unquestionably pure ectosteal origin' and mentions the ligamentous connexion with the suprascapula.

The Holostean 'opisthotic' has only been found in *Pachycormus* and *Hypsocormus*. The autopterotic is known from direct evidence in *Leptolepis* and may be supposed to occur separately in young specimens of *Pholidophorus*, for the neurocrania of these genera are almost indistinguishable in shape and such sutures as are visible very similar.

Among the Palaeoniscoids the following are known with separate neurocranial ossifications: *Birgeria*, *Cosmoptychius* and *Elonichthys* and certain specimens of *Glaucolepis*. Those of *Birgeria* consist of three large pieces called by Stensiö sphenoid and pro-otico-opisthotic (paired), a smaller pair of autosphenotics, and there is also the remains of a basioccipital; the rest of the occipital region and all the ethmoid region is missing. The sphenoid forms part of the hind wall of the orbits and closes the cranial cavity in front; its short thick ventral stem separates the two openings of the myodome. The 2nd, 3rd and 4th nerves and the ophthalmicus superficialis pierce the bone, and the 5th notches the hind border. The 'pro-otico-opisthotic' extends as far forward as the hind margin of the 7th nerve; it contains portions of both external and posterior semicircular canals, and reaches the whole height of the skull in the posterior otic region (see Stensiö 1921, pp. 152–182).

The specimen of *Cosmoptychius* described by Watson is almost certainly an immature one; it contains a large basioccipital, an opisthotic and a very small autosphenotic; there is also a large parasphenoid and a small incomplete basisphenoid. The opisthotic appears to contain both external and posterior semicircular canals, and the exit of the 10th nerve is marked by a notch between it and the basioccipital. *Elonichthys* is less easy to interpret: there is certainly a large parasphenoid and basioccipital similar to those of *Cosmoptychius*, and another ossification in the anterior part of the neurocranium, labelled pro-otic by Watson; there may be another farther back, an opisthotic, but the specimen is not well enough preserved for this to be certain.

The descriptions given of *Glaucolepis* and *Boreosomus* given by Nielsen (1942) show that they are fairly similar to the Kansas specimens, and *Boreosomus* also resembles these in having a neurocranium ossified in a single piece. *Glaucolepis* has normally two elements, one occupying the ethmoid, orbitotemporal and dorsal otic regions, the other the occipital and ventral otic regions, the dividing line being the vestibular fontanelle and extensions thereof; there are also two minute median bones, in the nasal septum and floor of the cranial cavity. There were found, however, a few poorly ossified specimens of *G. magna* (Nielsen 1942, pp. 91–93), and these showed other separate elements, some which are not unlike those of *Cosmoptychius*. The large occipital element was distinct as before, and I agree with Nielsen that it is probably the homologue of the basioccipital in that genus. The remainder were much less clearly defined, but Nielsen notes a pair of separate autosphenotics, a pair of thin plates in the 'crista supraorbitalis' (dorsal surface of the orbitotemporal region), a possible pair of sphenoids with resemblances to the unpaired bone of *Birgeria*, and implies other primary elements under the ascending wing of the parasphenoid and in the dorsal otic region.

There are a few living fish probably more closely related to the Palaeoniscoids than to the higher Actinopterygii—*Polypterus* and *Calamoichthys*, *Polyodon*, *Acipenser* and *Scaphi-*

rhynchus, etc., but all have the proportion of bone in the skull reduced in varying degrees compared with their ancestors. *Polypterus* has been described by Lehn (1918) and more fully by Allis (1922). It is fairly well ossified externally, but a considerable proportion of the neurocranium is built of cartilage. This structure contains, according to Allis, one large bone in the otic region, the opisthotic, which is traversed by both external and posterior semicircular canals and also contains a membrane element equivalent to the Holostean intercalar; the basioccipital extends sufficiently far upwards to close the foramen magnum and that for the vagus, and also surrounds a long aortic canal. The auto- and dermosphenotic are fused (postfrontosphenotic of Allis). The remaining bone entering into the neurocranium is the parasphenoid whose ascending process reaches far enough upwards and backwards to surround the foramen for the hyomandibular branch of the 7th nerve—and, indeed, partially lines the jugular canal. Van Wijhe (1882, p. 257) and Stensiö (1921, p. 157) record a small independent pro-otic. The interorbital region is occupied by a large sphenoid bone reaching from the trigeminal aperture to the ethmoid region, and also forming the floor of the cranial cavity and roof of the short myodome in the place usually occupied by the pro-otic bridge.*

The neurocranial ossifications in *Acipenser* are very small and not always present; they are figured and briefly described by Parker (1882) and by Holmgren & Stensiö (1936). Parker mentions an ecto-ethmoid, orbitosphenoid, alisphenoid and a pro-otic which surrounds the trigeminal foramen. Holmgren & Stensiö (p. 438) repeat these names with some reservations; they also describe an 'opisthotic', a bony plate in front of the vagus, and a 'lateral occipital', a larger element on the mesial side of the temporal groove. *Polyodon* (Bridge 1878) is totally without bone in the neurocranium except for two pairs of rudimentary ossicles in the posterior otic region.

The progressive reduction of bone in the evolution of the Actinopterygian skull is known to have occurred in more than one branch of the group, and the reduction has involved the division of an original solid cranium into separate bones. This progression has been commented on by Watson (1925), Stensiö (1932), Piveteau (1934) and Holmgren & Stensiö (1936). A mechanical corollary may be added to it in the higher Actinopterygii; the massive skull of the lower forms was composed of compact bone with a cancellar, not radial, structure; the Teleostei, on the other hand, are known to have typically a neurocranium of separate bones of radiating fibres in which the mechanical structure is one of girders and struts supplemented by very thin sheets of bone. The Jurassic Holostei show only an occasional slight development of radial structure, thus falling into place between the other two groups.

Some problems of homology and evolution

Within the ground covered by the present work neurocranial homologies can probably be best treated in two separate, though allied, parts. First those within the group of Jurassic Holosteans, and secondly the comparison of these with the known Palaeoniscoid ossifications. For the most part earlier opinions have been concerned chiefly with homologies in rather

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* Since this was written, Pehrson (1947) has published a detailed study of the development of the dermal bones of *Polypterus*; he treats the neurocranial more briefly but does mention a small pro-otic seen in two specimens at the 30 and 37 mm. stages.

a broad sense; they include important comments by Stensiö and Aldinger. Stensiö refers to the general problem of ossification thus (1932, p. 297):

> 'As the endocranium of all the Chondrostei which tend to develop in a direction to the *Holostei* is ossified in a single piece or is occupied by two large unpaired elements, this shows also that the endocranium of the *Holostei* originally consisted of one or a few ossifications. It seems therefore highly probable that the numerous bones in the endocranium of the Post-Triassic *Holostei* have arisen independently in each large group from one or a few original ones. Only by adopting such a view can we understand and explain the considerable differences which, for instance, are to be found in the development of the bones in *Lepidotus*, *Lepidosteus*, *Hypsocormus* and *Amia*.
>
> 'As thus, in both Crossopterygians and Actinopterygians, the original single or the original few unpaired bones of the endocranium seem to have become subdivided independently of each other in the different larger groups, it follows that the various bones originated by these subdivisions are not homologous in the different groups. Thus the numerous bones in the endocranium of the Mesozoic Coelacanthids are not homologous with either the possibly similarly shaped and situated bones in the endocranium of the *Chondrostei*, *Holostei* and *Teleostei*, nor of course are the rather numerous bones in the endocranium of *Birgeria*, homologous with the bones in the endocranium of *Amia* or Teleosts etc.'

Holmgren & Stensiö (1936, p. 236) repeat this assertion of separate fragmentation and non-homology, but their remarks are confined to the major divisions of Crossopterygii and Actinopterygii ('grosseren Teleostomengruppen') and would probably receive general agreement; it is only on the narrower problem of homologies within the Holostei that I find myself in opposition to Stensiö, for reasons which are set forth later.

Aldinger (1932), who shortly discusses the problem of ossification, also comments on the differences in neurocranial ossifications in the Holosteans and Teleosts, especially the variation in the development of the opisthotic. He arrives at much the same conclusions as Stensiö regarding the independent origin of the ossifications in the major vertebrate groups, though he would admit the probability of homology inside the Teleosts, for instance. In leading up to these conclusions (p. 46) he makes an interesting comment on the possible origin of this variation:

> 'Aus diesen Überlegungen folgt, dass die Unterschiede in der Ausbildung der Ersatz-Verknöcherungen in den einzelnen Fischstämmen durch die abweichende Lage der Ossifikations-zentren verursacht werden.'

It is convenient here to consider this question of embryonic growth centres in more detail. The total number of these necessary, in theory, for the formation of the postorbital section of the Holostean and Teleostean cranium are shown in figure 32. The basi-, ptero- and orbitosphenoid are excluded as before, and also the parasphenoid, being a membrane bone not fundamentally concerned in the structure of the braincase. These figures are based on *Leptolepis*; the various other Holostean patterns can be derived by the following alterations:

Lepidotus: no supraoccipital or 'opisthotic'.
Lepidosteus: no supraoccipital or 'opisthotic'.
Caturus: no supraoccipital, ? 'opisthotic' (skull imperfect).
Amia: no supraoccipital or 'opisthotic'.
Pachycormus and *Hypsocormus*: probably no supraoccipital.
Aspidorhynchus: no opisthotic in adult, ? present in early ontogeny.

If the pro-otic, epiotic, intercalar, lateral and basioccipital are considered to be homologous it follows that any bones bordered by these in different genera should also be homologous, unless one of them can be shown to be a fresh development. An example of such a development can probably be supplied by the supraoccipital; among the Jurassic skulls it only appears in the Aspidorhynchidae and in the Pholidophorid-Leptolepid-Teleost line; and is it very different in extent in these two appearances. On the other hand, the status of the 'opisthotic' and autopterotic is much more difficult to resolve; the former is confined to the Pachycormidae, the latter to the Pholidophorid-Teleost branch. They have similar, but by no means identical, positions in the braincase. The whole shape of this structure is very different, and clearly the two branches are as divergent as any among the Holostei. The two names are kept at present, since it is more satisfactory to leave the matter open than to suggest a homology which may be false.

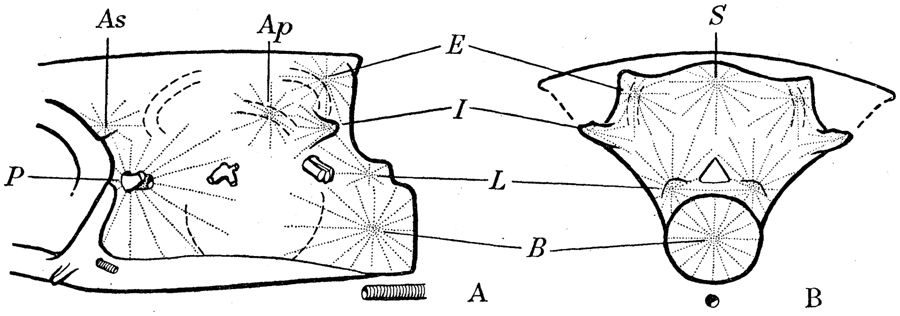

FIGURE 32. Diagram of the ossification centres in the Holostean neurocranium with approximate relations to nerves, blood vessels and labyrinth; A, in lateral view. B, in hind view. *Ap.* autopterotic (or approximate position of 'opisthotic' in Pachycormidae); *As.* autosphenotic; *B.* basioccipital; *E.* epiotic; *I.* intercalar; *L.* lateral occipital; *P.* pro-otic; *S.* supraoccipital.

Apart from this anomaly, however, it is contended that the remainder of the bones of the postorbital section of the neurocranium are essentially homologous; their remarkably constant distribution is well seen in figures 30 and 31. In general not very great importance is attached to the detailed relations of bones to nervous and related structures, though they are given as a guide to the positions of bones in figure 32; it is rather the whole organization of the neurocranium that is considered. Otherwise it might, for instance, be supposed that the epiotics of *Lepidotus* and *Leptolepis* were not homologous, because in the latter they enclose a large part of the posterior semicircular canal and in the former there is only a short groove for its reception on the ventral surface of the bones, a larger part being contained in the lateral occipital.

It will also be noticed that the assumption of homology in these forms is accompanied by the idea that such variations as have occurred are brought about by the disappearance of some bones, rather than by their fusion, whole or in part, with others, for they do not vary much in extent between family and family except as necessitated by the different forms of the skulls. The large pro-otic of *Aspidorhynchus* is an obvious exception to this, and differs quite remarkably from the same bone in other fish; this suggests that it may include an 'opisthotic' element incorporated during ontogeny (though there is no direct evidence of this in the specimens) rather than an unusual backward extension of the pro-otic proper.

It was the proposition of a single fundamental plan for the Holostean neurocranium that was the mainstay of the argument for a monophyletic origin of the group considered in an earlier review (Rayner 1941); since then it has been countered by Westoll (1944, p. 95) who says 'the similarly constituted endocrania merely indicate retention of similar generalized ancestral conditions'. This leads up to the second part of this problem and a consideration of the neurocranial ossifications in Palaeoniscoid and allied fishes. Of the genera mentioned on p. 331 only *Cosmoptychius*, *Birgeria* and *Polypterus* concern us here, and chiefly the first. *Birgeria* and *Polypterus* have been treated in great detail by Stensiö (1921) and Allis (1922) respectively, including the problem of what Holostean elements may be represented in their bones. But they are both aberrant types and one would not look for much likeness between them and the much more generalized *Cosmoptychius*. Nevertheless, there are some similarities between the three. A striking feature is a large bone, here called opisthotic after Allis (1922), which contains both external and posterior semicircular canals. The most constant bone in the otic region of Holosteans and Teleosts, the pro-otic, is only occasionally present; the parasphenoid plays rather a larger part in the architecture of the braincase, and in *Polypterus* and *Birgeria* there is a large 'sphenoid' bone in the orbitotemporal region.

Turning to *Cosmoptychius* itself, it is apparent at first sight that the neurocranial bones have no *direct* connexion with those of the Holostei since they are too few and too large. This is not to say, however, that there is no homology between them. Considering the matter again as a question of growth centres, it is theoretically possible to derive the Palaeoniscoid pattern of autosphenotic, opisthotic and basioccipital, from the diagram constructed for the Holosteans and Teleosts by suppression of some of the centres and the greater extension of the few remaining elements. Thus the pro-otic is not developed, at least not at this stage, nor the epiotic, lateral or supraoccipital. The opisthotic has grown very large and enclosed the posterior as well as the external semicircular canal, and the basioccipital has an unusual dorsal extension. Alternatively, the greater extent to the remaining bones might be due to fusion of a larger number of rudiments; the Holostean epiotic and 'opisthotic' forming the Palaeoniscoid opisthotic, the lateral occipital perhaps incorporated with the basioccipital.

It may be noted in passing that there are commonly these two methods of viewing related bone patterns, a theory of fusion of several rudiments being opposed to a theory of the growth of one bone at the expense of its neighbours; the problem is reviewed by de Beer (1937, pp. 502–512). In the present case, with no positive evidence such as radial bone structure, it seems impossible to choose between them, but both allow an essential homology between the bone rudiments of Holostean and Palaeoniscoid.

By way of summary of this aspect, therefore, we can say that the evidence does uphold the idea of a single fundamental plan of neurocranial ossifications in the bony fishes; this would, indeed, be likely on theoretical grounds alone, since the bones of the skull roof, for instance, also have a common basic plan, recognizable even in the most specialized types; and skull roof and neurocranium are among the most stable elements in the fish head. On the other hand, it must be emphasized that nearly all the information on neurocrania comes from either the later Actinopterygii or from the most divergent of the Palaeoniscoids. Concerning many of the more central stocks, and the important Triassic 'Sub-Holostei' we know only very few specimens, showing either a single adult ossification, or one, essentially similar, in which the vestibular fontanelle is extended to divide the structure into two large ossifications. It is partly because of this great gap in our knowledge that I feel dubious about accepting the view that the strongly similar braincase of the Jurassic Holostei is merely the retention in many parallel stocks of a pattern present in the embryonic ossifications of a *large* number of Palaeoniscoids and Sub-Holostei. This may be so, but we have no evidence for it. With regard to the general problem of Holostean ancestry I have little to add to my earlier summary (Rayner 1941, p. 234), since the conclusions derived from a detailed study of neurocrania were available for that review. The homogeneous nature of the braincase was the strongest argument for a monophyletic origin, the opposite view being supported by the divergence of the families at their first appearance, and particularly the occurrence of *Acentrophorus* (the first Semionotid) as early as the Upper Permian. This second view is favoured by Westoll (1944, p. 94) in the course of a general survey of Palaeoniscoid descendants. The reader is accordingly referred to these two works for a discussion of this problem and for comments on classification.

There remain, however, a few studies to be added to certain evolutionary sequences in the group. The origin of the Eugnathidae from the Parasemionotidae is the one well established link between the Holostei and 'Sub-Holostei'—and is one of the best reasons for considering the Holostei a 'grade' and not a natural order. This link has been strengthened by the discovery of a new genus, *Promecosomina*, from the Middle and Upper Trias of New South Wales by Wade (1941). This form has a skull which in many ways resembles those of the Parasemionotidae, but it also has a semiheterocercal tail. Wade makes other comparisons with the Semionotidae and Eugnathidae, and while not agreeing with him in all details I do find certain similarities with the less specialized Eugnathids.

There is another link which has not received its due attention, perhaps, and that is the structure of the lower jaw. Among the Parasemionotidae it is well known in *Ospia*, and in describing that genus Stensiö (1932, p. 258) notes the likeness to that of *Eugnathus* and *Amia*. It is, indeed, a likeness closer than that supplied by any other part of the skull, the mandibular structure retaining an almost identical plan through the morphological series *Ospia*, *Eugnathus*, *Sinamia*, *Amia*.

The derivation of *Lepidosteus* from *Lepidotus* is borne out by both the dermal and neurocranial skelton, but especially the latter. The long rostrum of *Lepidosteus* naturally has distorted the dermal bones, and there is little resemblance here except the chain of small square circumorbitals common to both. The neurocranium of *Lepidosteus* was for a long time left almost undescribed except by Agassiz (1843), whose description is for modern readers somewhat hampered by the obsolete nomenclature, though the figures remain excellent. For present purposes the short account given by Holmgren & Stensiö (1936, p. 469) describes the neurocranium, nerves and blood vessels adequately; the bones are also illustrated in the present work from dried skulls in the British Museum and the University Museum of Zoology, Cambridge (figures 33 and 34).

The orbital region does not partially enclose the eye as in fossil Holosteans, and the curved wall of bone characteristic of the front view of the neurocranium in them is not found in *Lepidosteus*—a corollary of the reduction in ossification and size of eye. In side and hind view the neurocranium of *Lepidotus* and *Lepidosteus* have a greater likeness; the distribution of bone and cartilage in a well ossified specimen of the latter is essentially the

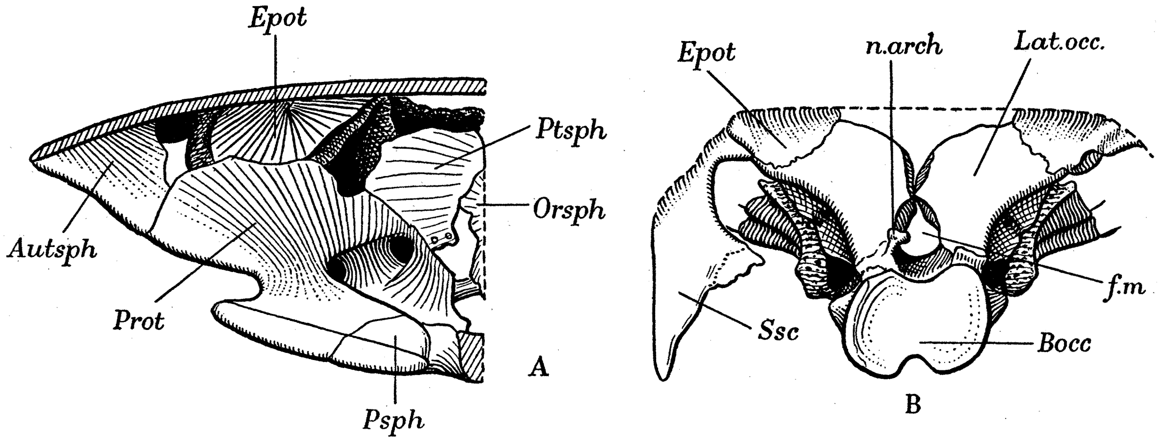

FIGURE 33. *Lepidosteus*. A, front view of half a dried cranium in the Zoological Department, British Museum (Natural History), as if cut through immediately in front of the orbitosphenoid. × 1. B, hind view of a specimen in the University Museum of Zoology, Cambridge, dermal roofing bones omitted. $\times \frac{2}{3}$. *Autsph.* autosphenotic; *Bocc.* basioccipital; *bpt.pr.* basipterygoid process of parasphenoid and pro-otic; *Epot.* epiotic; *f.m.* foramen magnum; *Lat.occ.* lateral occipital; *n.arch*, neural arch; *Orsph.* orbitosphenoid; *Prot,* pro-otic; *Psph.* parasphenoid; *Ptsph.* pterosphenoid; *Ssc.* suprascapular.

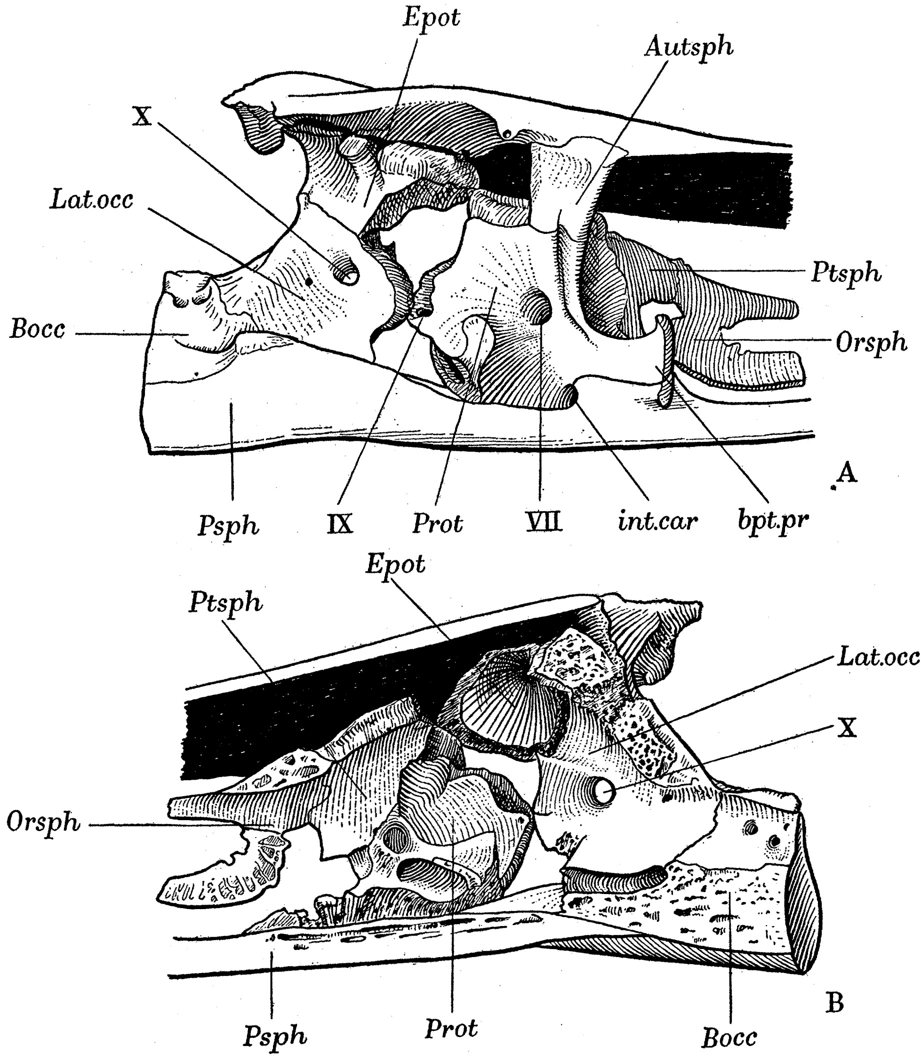

FIGURE 34. *Lepidosteus*, half a dried cranium in the Zoological Department, British Museum (Natural History). × 1. A, viewed from the side and slightly from below. B, mesial view. *Autsph.* autosphenotic; *Bocc.* basioccipital; *bpt.pr.* basipterygoid process of parasphenoid and pro-otic; *Epot.* epiotic; *int.car.* foramen for internal carotid; *Lat.occ.* lateral occipital; *Orsph.* orbitosphenoid; *Prot.* pro-otic; *Psph.* parasphenoid; *Ptsph.* pterosphenoid; VII, foramen for facial nerve; IX, foramen for glossopharyngeal nerve; X, foramen for vagal nerve.

same as in the former, except that there is a large area of cartilage between the epiotics of *Lepidosteus*, due to the dorsoventral flattening of the skull and the consequent outward migration of these bones. The position of the 9th and 10th nerves is similar, and both fishes have one or two neural arches attached to the skull (actually fused to the basioccipital in *Lepidosteus*). The distribution of the semicircular canals is very alike when the greater proportion of cartilage in the living fish is taken into account; the epiotic is in contact with a small section of the posterior canal in both, and though my specimens showed no contacts between the lateral occipital and labyrinth, Stensiö (1921, p. 156) records the enclosure of part of the external canal. The lack of intercalar in the living fish has already been noticed as a structural adaptation.

The Semionotid neurocranium, being known in both *Lepidotus* and *Dapedius*, gives an opportunity for examining some differences in cranial structure possibly related to the very different external form of these two genera. The discrepancy in ossification has already been mentioned, which with variation in other families suggests strongly that this feature is not of systematic importance. The presence of deep temporal grooves and the general excavation of the hind region of the skull in *Dapedius* and the lack of these in *Lepidotus* is presumably a reflexion of the importance of the trunk muscles, and may perhaps be correlated also with the long dorsal fins of *Dapedius*; in any case the swimming mechanism of a deep bodied form may be expected to differ from that of a longer, more cylindrical one such as *Lepidotus*. Another important difference already mentioned is the presence of an aortic canal in *Dapedius* and its absence in *Lepidotus*.

A third important line leads from the Pholidophoridae through the Leptolepidae to the most primitive teleost family, the Elopidae. Hitherto it appears to have been commonly supposed that all the Teleosteans are offshoots of this single stock, which is characterized in particular by an autopterotic and a large supraoccipital in the braincase, and, except in the basal Pholidophoridae, a lower jaw consisting of dentary and angulo-articular elements only. Thus it is a radical innovation when Smith Woodward (1942) suggests that some of the Teleostei may have been derived from other Holostean families. His examples concern certain specialized fishes already present in the Cretaceous—the Apodes (eels), the Enchodontidae (allied to the Myctophidae) and certain of the Acanthopterygians. He draws comparisons with these and the Macrosemiids, Eugnathids and Semionotids respectively. The structures concerned are mainly jaws and fin fulcra and in one case (Apodes) scales, but having studied the skulls of several of the living fishes, and the literature on them, I can find little support in the cranial bones for any such derivation. Aberrant though some of them are they still seem to possess the fundamental Leptolepid characters, but probably further research, especially among the Cretaceous faunas, is needed to establish this definitely.

There are a few points concerning the *Pholidophorus-Leptolepis* line which remain for consideration. It is often very difficult to separate species of these two, and the small differences between *Leptolepis* and the Elopidae mostly represent a further stage in the same line of evolution. The two Jurassic genera have been described from their type species, and certain crucial differences between these are summarized below; the points concerning prearticular, vertebrae, scales and fulcra are evolutionary stages in the main stock; the remainder are specializations of *Leptolepis*.

Pholidophorus bechei	*Leptolepis bronni*
Frontals tapering irregularly but gradually	Frontals narrowing to parallel-sided strips between the nasals
Nasals stout, half as broad as long	Nasals delicate (exact dimensions unknown)
Prearticular present	Prearticular absent
Highest point of coronoid elevation reached at three-quarters of the length of the jaw from the anterior end	Highest point of coronoid elevation reached at one-third of the length of the jaw from the anterior end
Height of coronoid elevation two-fifths the length of jaw	Height of coronoid elevation half the length of jaw
Point of articulation of lower jaw beneath hind margin of orbit	Point of articulation of lower jaw beneath centre of orbit
Vertebrae divided into pleuro- and hypocentra	Vertebrae complete rings
Fulcra on all fins	Few fulcra on dorsal lobe of caudal fin only
Scales stout and rhombic	Scales thin and cycloid

The group also contains a morphological sequence concerning certain cartilage and membrane bones. The snout of *Pholidophorus* has already been commented on as being unusually well preserved; the rostral is distinct from the underlying neurocranium and can clearly be seen to carry a sensory canal, the ethmoid commissure. In *Leptolepis* all the foremost bones of the head are much less massive, so that the nasal is rarely preserved and the antorbital has never been seen. The rostral here is indistinguishable from the ossification of the ethmoid region, the commissure is no longer a canal, and usually the only trace is a short groove representing a pit-line, though sometimes this may have been situated in the skin above. The development of this bone (usually called ethmoid) in a number of cases among the Teleostei shows it sometimes to consist of dermal and cartilaginous elements fused; sometimes it is single from the start but has the anatomical relations of both elements; sometimes a membrane ossification acquires direct contact with the cartilage later. These variations are noted by de Beer (1937, p. 500), who also discusses the history of these elements (p. 498) and others which in Teleosts consist of fused dermal and cartilaginous rudiments. He says that it certainly looks 'as if the supraethmoid [i.e. rostral of this work] had gradually invaded the cartilage and given rise to the ethmoid'. But if the sequence *Pholidophorus*-*Leptolepis*-primitive Teleost is truly evolutional in this, the single bone of the last represents phylogenetically both dermal rostral and cartilaginous ethmoid, now fused and sunk beneath the surface.

This sequence is paralleled by the fusion and sinking of the auto- and dermopterotic. In the adult Teleosts these components are commonly fused, the latter being much reduced, sometimes to a series of ossicles bearing the sensory canal. In this case de Beer doubts the theory, sometimes advanced, that the pterotic (or sphenotic) resulted from the sinking of the membrane bone, for the cartilaginous element arises from internal as well as external perichrondral lamellae. The palaeontological history of the bone shows this origin to be impossible as the autopterotic is a distinct bone in the Jurassic genera, or at least has been found as such in one specimen of *Pholidophorus* and a small (perhaps slightly immature) one of *Leptolepis*. It is again a case of fusion, with reduction of the dermal element.

CONCLUSIONS

1. The neurocrania of the Jurassic Holostean fishes have a remarkably similar bone pattern; the most important differences concern the supraoccipital and posterior otic regions.

2. This pattern differs materially from that found in the few earlier fishes in which separate ossifications are known, but nevertheless, a broad system of homology between the two is theoretically possible.

3. The earlier (Palaeoniscoid) crania commonly, but not always, contain a large basioccipital element, another in the posterior otic region, an autosphenotic and sometimes a 'sphenoid' in the base of the skull; the pro-otic is not an important member.

4. The undivided neurocranium of the remaining Palaeoniscoids and 'Sub-Holosteans' may be partly divided into anterior and posterior parts by the vestibular fontanelle. This is lacking in the Jurassic skulls.

5. Because of these and other differences the Jurassic Holosteans are considered as perhaps a natural group, but neither the evidence for nor against this view is entirely conclusive.

6. The degree of ossification in the Holostean neurocranium varies among the Jurassic families with only minor systematic significance. The progressive lightening of the Actinopterygian skull as a whole, however, is confirmed by a comparison between the living derivatives and their Mesozoic ancestors.

7. The variations of the infra- and supraorbital canal systems on the hind part of the skull roof seen in certain Palaeoniscoids and Holosteans is not of great importance. It may be caused by different degrees of anastomosis of secondary branches during growth, and also by the varying amounts of enclosure of the anterior pit-line organs in the supraorbital canal.

8. The established links between the Parasemionotids, Eugnathids and Amiids are strengthened by the similarity between the lower jaws in these families and also by a comparison of the neurocrania in *Caturus* and *Amia.*

9. No satisfactory function can be assigned to the lateral cranial canal found by Aldinger and myself in *Caturus* and deduced by me in *Dapedius*. It has no opening to the exterior.

10. The neurocranial bones of *Lepidotus* and *Lepidosteus* are sufficiently alike to confirm the derivation of the latter from the former.

11. Within the Pholidophorid-Leptolepid-Teleost stock the ethmoid and pterotic bones develop phylogenetically from the fusion of cartilaginous and dermal components.

APPENDIX

The method used for making the sections is an adaptation of that described by Caldwell (1935). The half specimen of *Caturus* was imbedded in plaster of Paris, the sliced median surface to be ground facing upwards. This first surrounding of plaster was set in a rectangular casing, two sides of which were at a measured right angle and also perpendicular to the surface to be ground. An outer layer of plaster was added, so that throughout the grinding these two guiding lines showed on the surface and were also reproduced in the transfers. An additional means of orientation was produced by scoring two vertical lines on the sides of the inner block, thus forming fixed points on the transfers, which were very useful when making a rapid survey of the sections in tracing the successive outlines of any particular structure.

The plaster was left to set hard for some weeks, and then the back of it was cemented with Canada balsam on to a thin glass plate, and that on to an aluminium plate. The latter carried two screws, the free ends of which projected on the same side as the plaster block. The grinding was done by hand with carborundum powder on a square sheet of plate glass, levelled beforehand. The aluminium plate was frequently tested with a spirit-level also, and kept horizontal by adjusting the two screws; these did not move on the plate glass, but on another small sheet, slightly below, and well greased with vaseline to prevent wear. It is the exact horizontality of both plate glass and aluminium plate that ensures that the sections are parallel, so that the levelling must be frequent and accurate. The plate glass was found to become appreciably worn in the centre of the grinding field after about 2 mm. of the specimen had been removed, and usually it was turned through 90° after about 1 mm., except at the end of the series when the area of the specimen had decreased considerably.

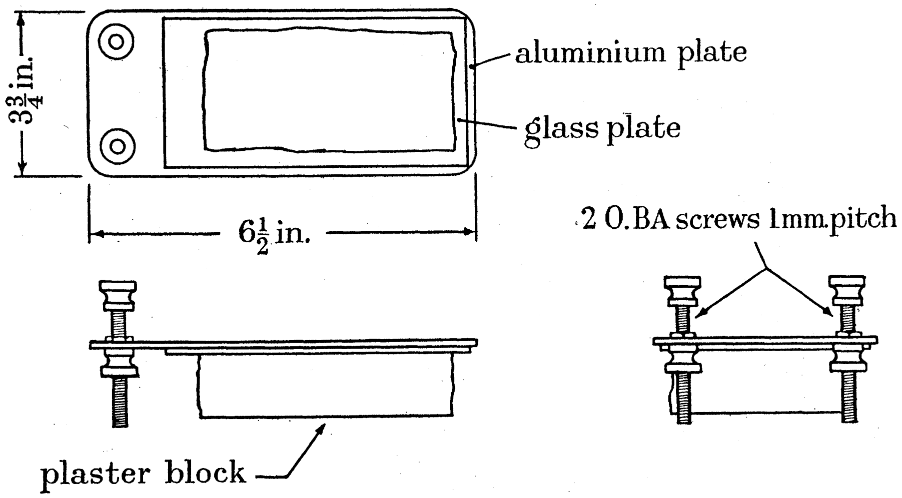

FIGURE 35. Plaster block and aluminium plate, etc., used in grinding *Caturus*.

At the beginning a medium grade of carborundum powder was used except for the last 0·02 mm. or so of each section when it was replaced by a finer grade, to leave the surface as smooth as possible; at the end of the series the finer grade was used throughout.

The transfers were taken every 0·1 mm.; 'taking' a transfer involves the following processes. The ground surface was washed and then etched with dilute (about normal) hydrochloric acid, and then washed again. If a photograph was wanted it was stained with a solution of alizarin in 90 % alcohol, which colours bone a vivid crimson; this stain is bleached by acid, however, and if the bone was thin and delicate it was found convenient to wash with very dilute alkali after the etching, any residual alkali only turning the stain to a dark purple. After staining, the specimen was washed again, with absolute alcohol; it was then dried and covered with a layer of 'Durofix' to which slightly more than its own volume of amyl acetate had been added. This preparation dries in about 3 hr. and peels off as a more or less transparent transfer; these transfers were finally mounted between glass plates. Other solvents may be used instead of amyl acetate, e.g. acetone, which has the advantage of drying in about an hour but gives a less satisfactory reproduction of the etched surface.

Except where the bone was exceedingly thin it was reproduced clearly in the transfers as transparent patches and lines, in contrast to the opacity caused by the much more grainy surface of the limestone matrix. Where there was much crystalline calcite this was also reproduced transparently, and may be a little difficult to distinguish from the bone, but when seen under a binocular microscope the outline of the cranium in each section was quite distinct.

The transfers were left on while the ground surface was photographed, as they had the clarifying effect of a varnish. Photographs were not taken at fixed intervals, but when any important structure appeared, i.e. about every six to eight sections near the mid-line and less frequently towards the lateral margin; three of them are reproduced in figures 46 to 48, plate 22. The transfers are in the Sedgwick Museum.

The second part of the process consisted of drawing enlargements of each transfer and making a wax cast from them, and finally a plaster model from the cast. The drawing apparatus was a small projection lantern fitted with an extra mirror; the transfers were enlarged by $7\frac{1}{2}$ diameters and drawn on tracing paper. The wax sheets were made in the usual manner by rolling out the melted wax on a lithographic stone, but the paper was stuck to the stone by wetting it in turpentine, not water, which causes much less stretching, an important point with large drawings.

The wax sheets can be used to build up a model themselves, but in the case of *Caturus* their large size and the thinness of some parts of the bone made it difficult to prevent a slight warping, and it was found more satisfactory to make a negative or cast of the wax and fill it with plaster of Paris at intervals of about 2 cm. If the surface of each successive layer is roughened and pitted there is little danger of their coming apart when the wax is removed. The removal of the wax is the most difficult part of this method, especially where it is deeply imbedded in plaster. In order to make the removal as easy as possible the model was built in two halves; these were placed on a tray over a coal range, and it was found that if they were slowly heated there for some hours the wax melted even in the internal cavities and the sheets of paper could be removed fairly easily when the plaster was cool.

This is a convenient way of making a model that is rather large and intricate, and also there is no danger of warping, as wax may do under its own weight. It was found necessary, however, to exaggerate the thickness of the bone in one or two places so that the plaster was not less than 0·5 cm. thick, or there was a possibility of its cracking when heated, or of the different layers coming apart.

The work was done at the Zoology Department, University College, London, and at the Sedgwick Museum, Cambridge; thanks are due to Professor D. M. S. Watson for facilities for working in London, and Professor O. T. Jones and Mr A. G. Brighton for those at Cambridge.

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The *Aspidorhynchus*, *Pholidophorus* and *Leptolepis* crania shown in plate 21 were photographed by the staff of the Riksmuseum, Stockholm, through the courtesy of Professor Stensiö; figure 35 was drawn by Mr G. H. Rayner, and figures 25 and 30 are reproduced by permission of the Council of the Cambridge Philosophical Society.

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FIGURE 36

(*Facing p.* 344)

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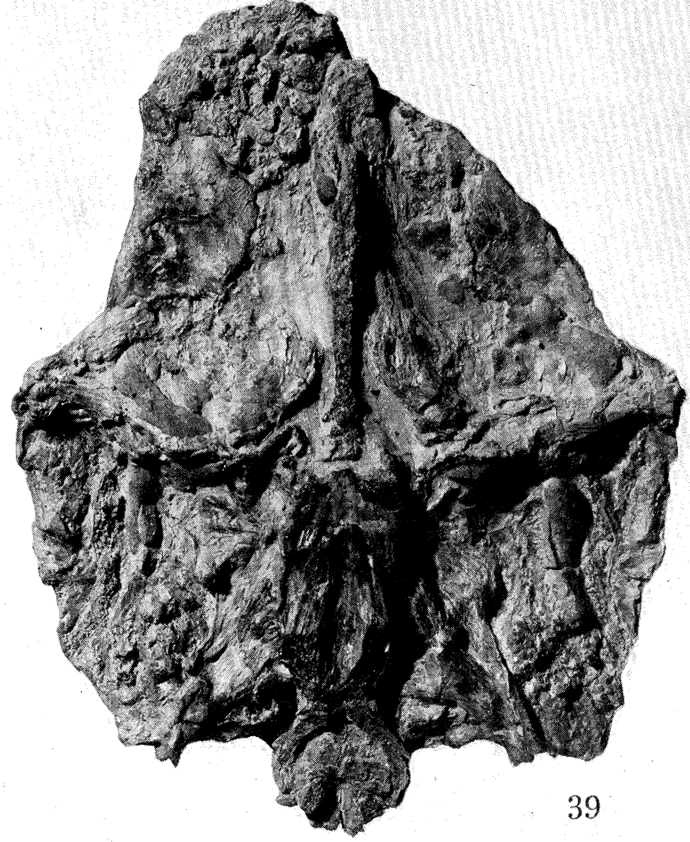

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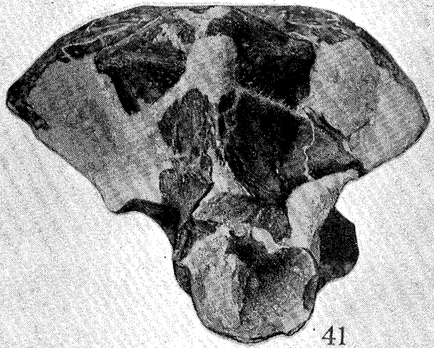
Figures 37 to 40



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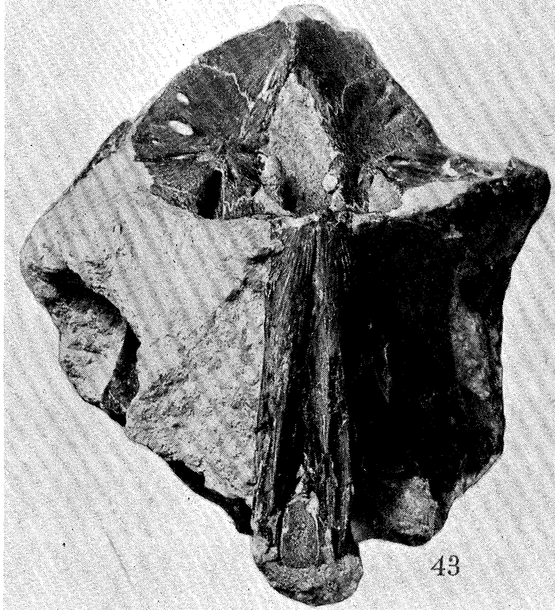

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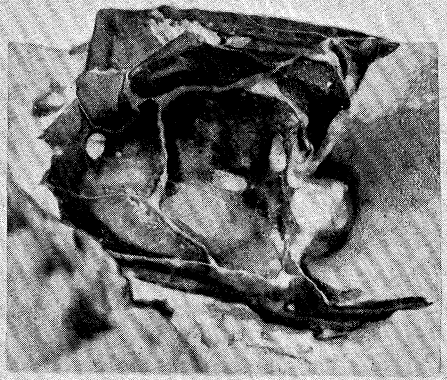

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Figures 41 to 45

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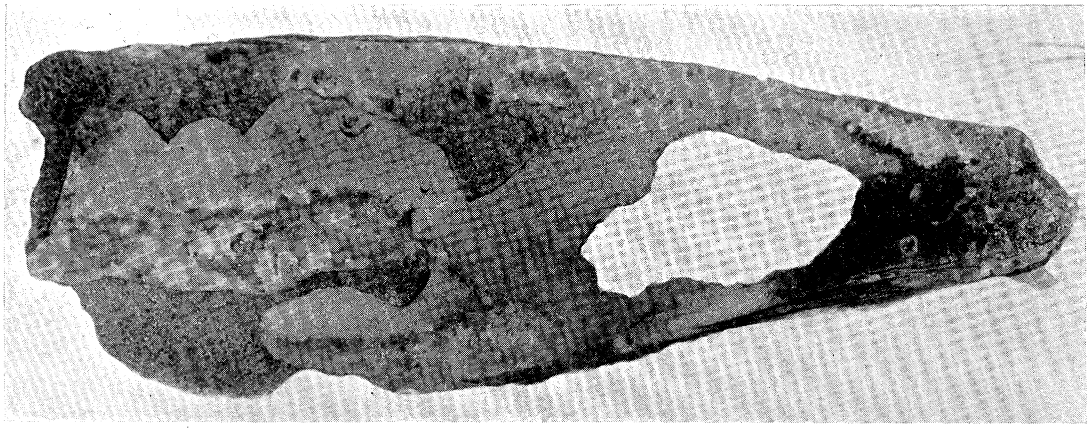

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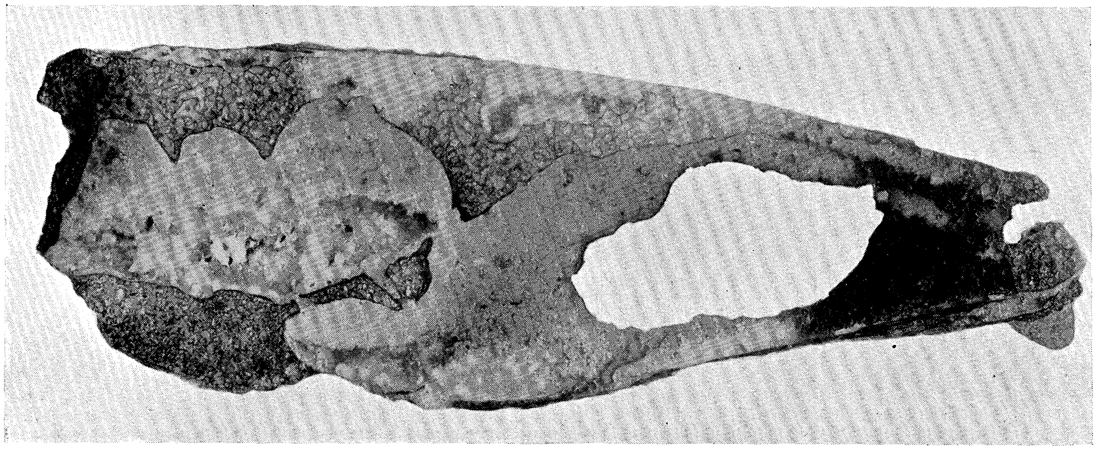

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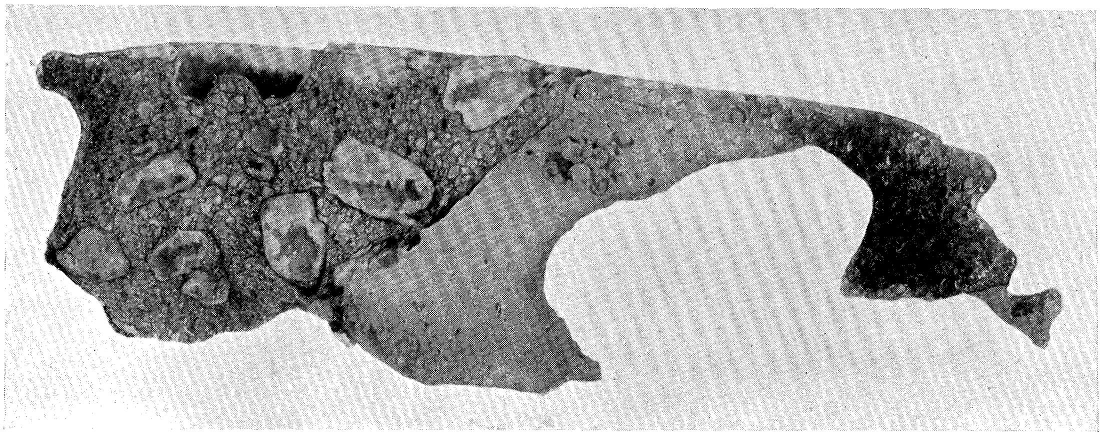

FIGURES 46 TO 48

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DESCRIPTION OF PLATES 19 TO 22

PLATE 19

FIGURE 36. *Caturus porteri*, B.M.N.H. 29049, holotype, in ventral view. × $\frac{3}{4}$.

PLATE 20

FIGURE 37. *Caturus porteri*, a cranium in the Peterborough Museum in dorsal view. × 1.

FIGURE 38. *Caturus porteri*, the same specimen as in figure 37, in ventral view. × 1.

FIGURE 39. *Caturus porteri*, S.M. J 4853, in ventral view. × 1.

FIGURE 40. *Caturus porteri*, S.M. J 4854, the snout showing rostral and nasals. × $\frac{2}{3}$.

PLATE 21

(All these figures have been slightly retouched.)

FIGURE 41. *Aspidorhynchus* sp., B.M.N.H. 9843, neurocranium in hind view. × 1·5.

FIGURE 42. *Aspidorhynchus* sp., B.M.N.H. 9844, neurocranium in side view. × 1·5.

FIGURE 43. *Aspidorhynchus* sp., the same specimen as in figure 42 in ventral view. × 1·5.

FIGURE 44. *Leptolepis bronni*, Professor Watson coll. P 507, neurocranium in side view. × 7·5.

FIGURE 45. *Pholidophorus bechei*, B.M.N.H. P 1052, neurocranium in side view. × 4·5.

PLATE 22

FIGURE 46. *Caturus* sp., longitudinal section no. 32·50 through the foramen magnum, optic foramen, cranial cavity and myodome. × $1\frac{1}{2}$.

FIGURE 47. *Caturus* sp., longitudinal section no. 31·30 through the optic, trigeminal and abducens foramina, and foramen magnum. × $1\frac{1}{2}$.

FIGURE 48. *Caturus* sp., longitudinal section no. 27·40 through the facial recess, the passage for the vagus, several portions of the labyrinth, and two of the dorsal pits. × $1\frac{1}{2}$.

FIGURE 36

PLATE 19

FIGURE 36. *Caturus porteri*, B.M.N.H. 29049, holotype, in ventral view. × $\frac{3}{4}$.

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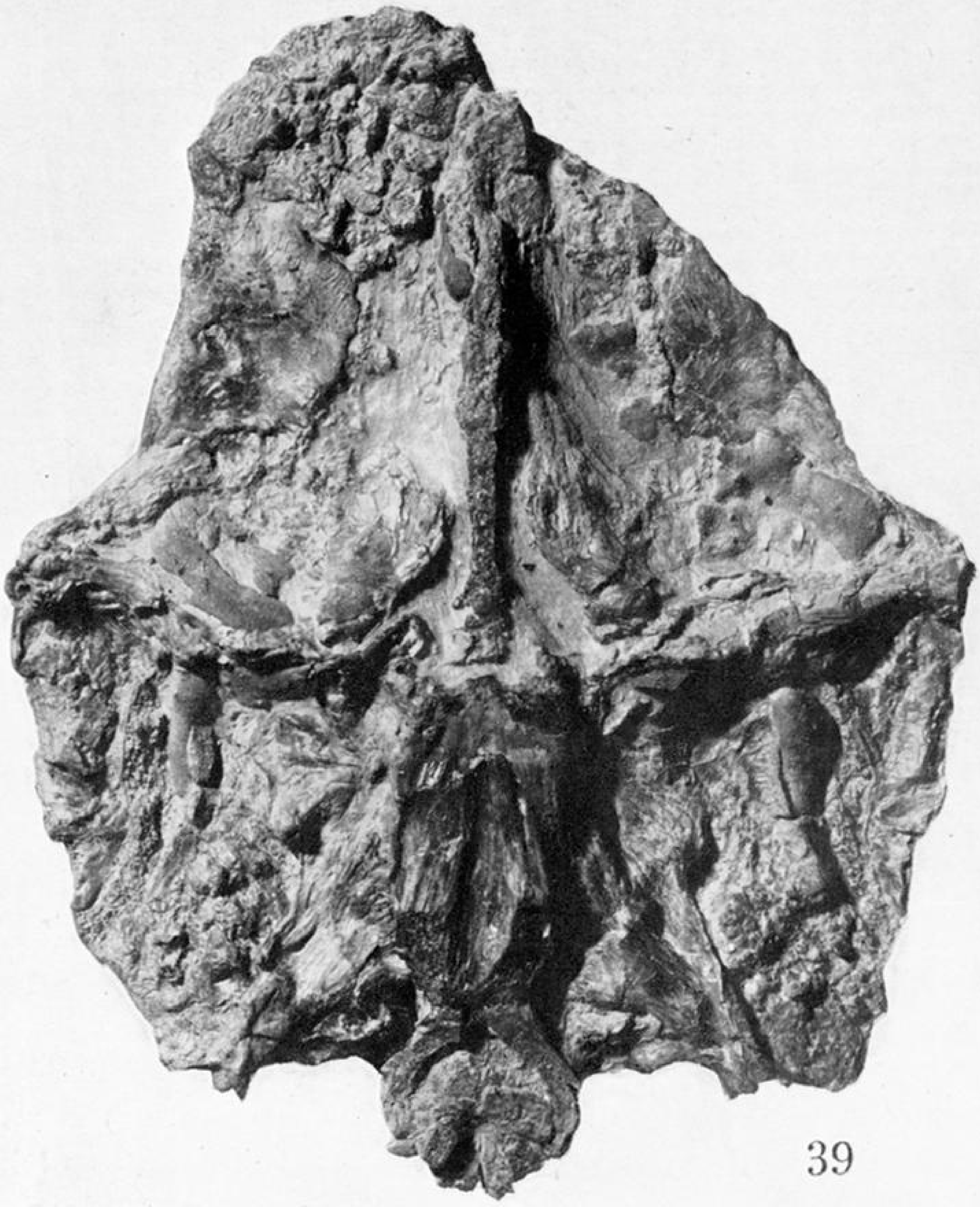

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FIGURES 37 TO 40

PLATE 20

FIGURE 37. *Caturus porteri*, a cranium in the Peterborough Museum in dorsal view. × 1.

FIGURE 38. *Caturus porteri*, the same specimen as in figure 37, in ventral view. × 1.

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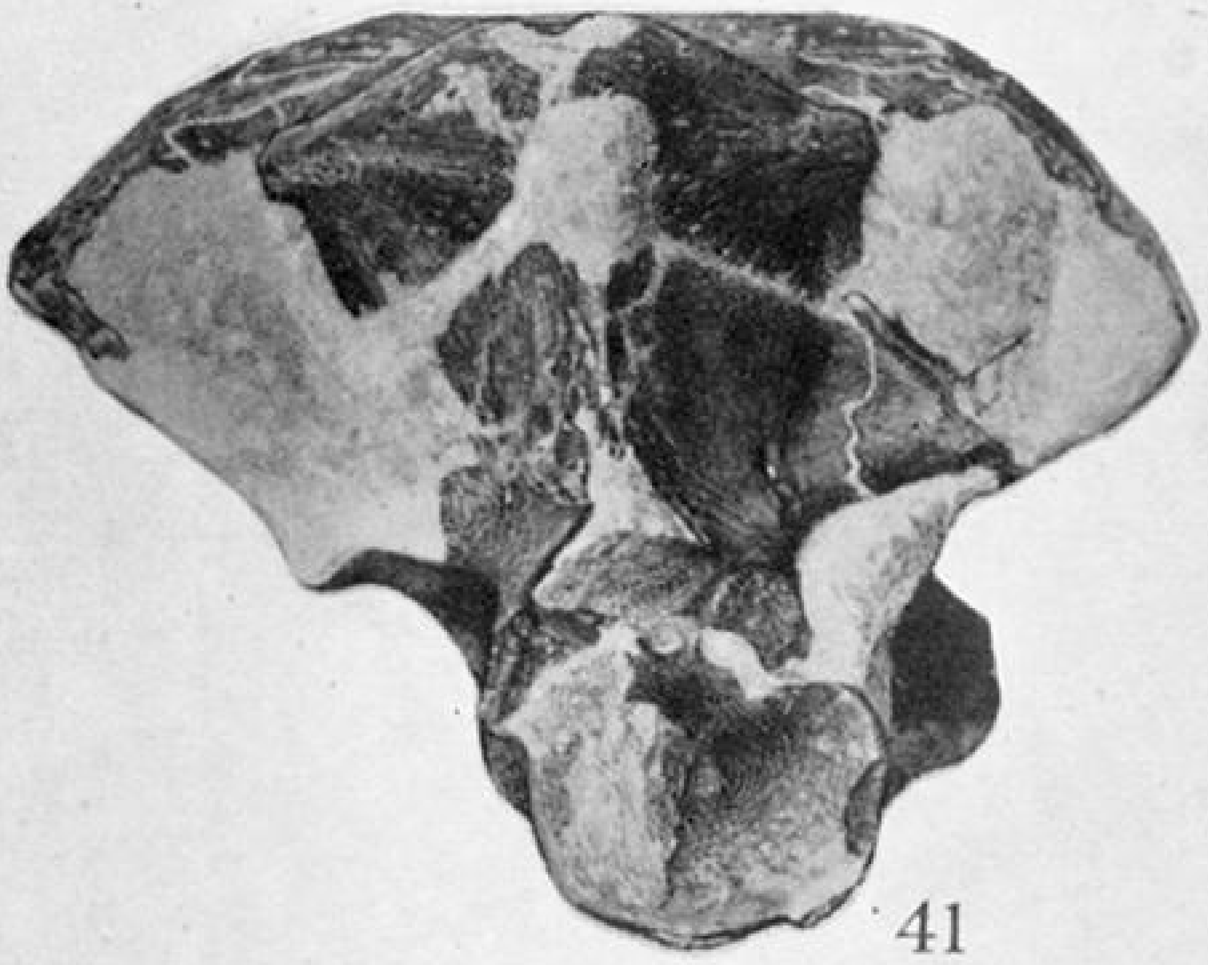
FIGURE 40. *Caturus porteri*, S.M. J 4854, the snout showing rostral and nasals. × $\frac{2}{3}$.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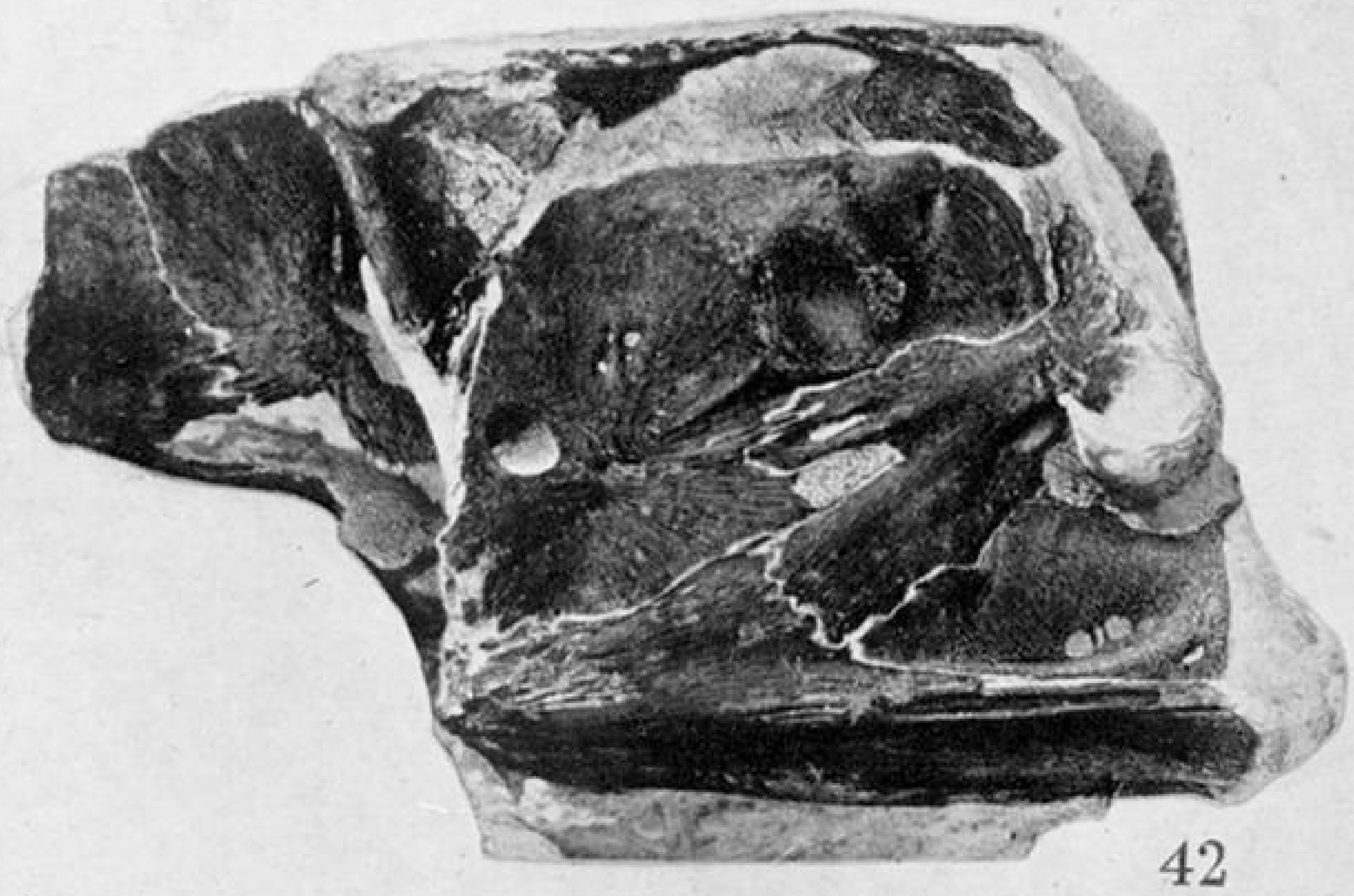
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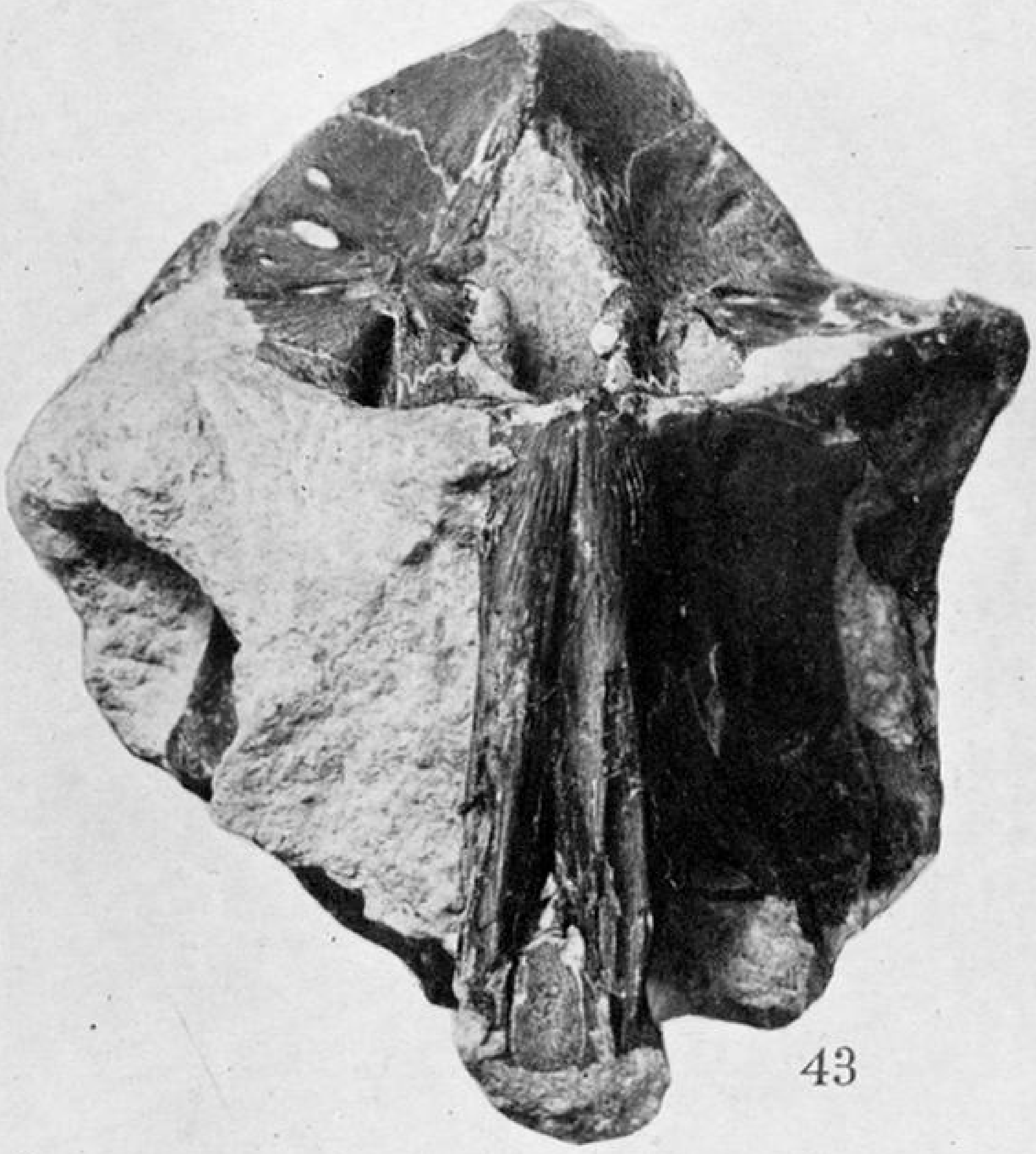
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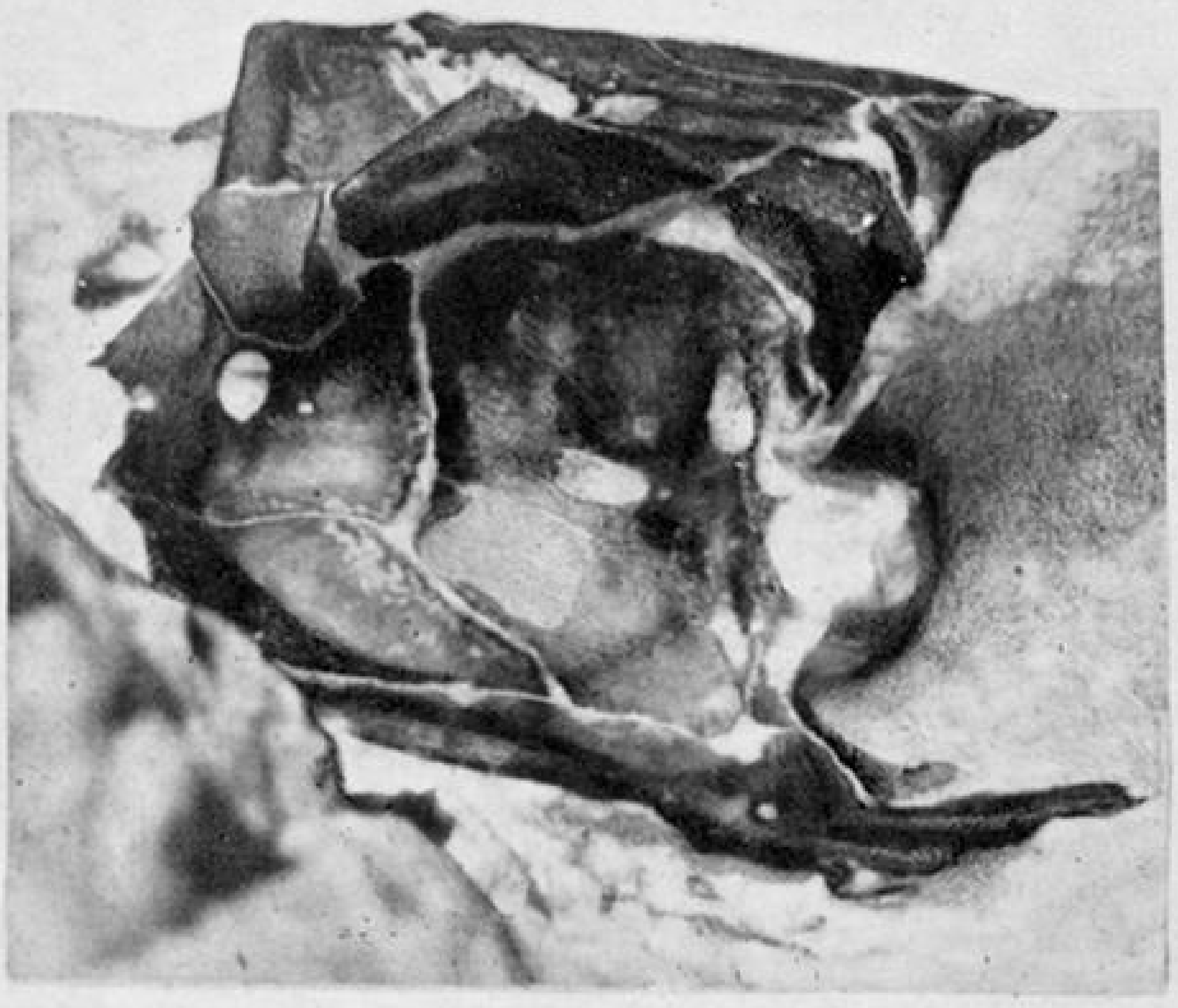
44


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Figures 41 to 45

Plate 21

(All these figures have been slightly retouched.)

Figure 41. *Aspidorhynchus* sp., B.M.N.H. 9843, neurocranium in hind view. × 1·5.

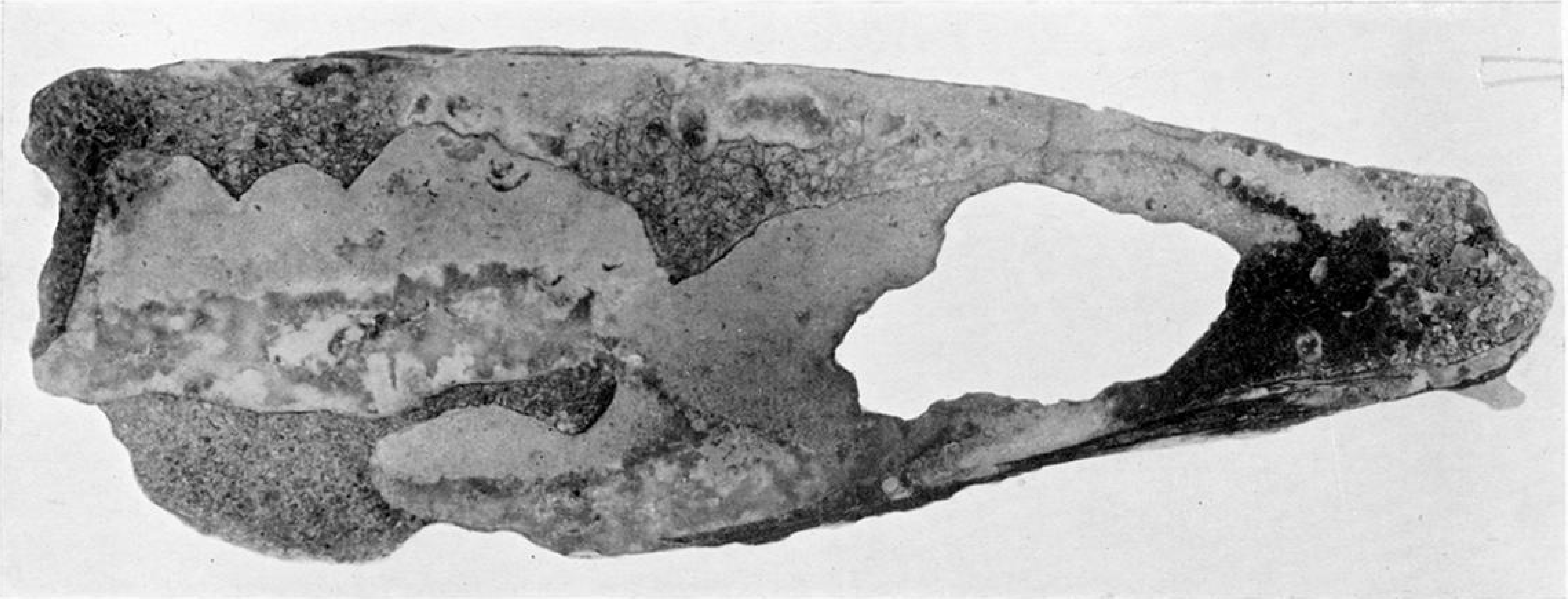
Figure 42. *Aspidorhynchus* sp., B.M.N.H. 9844, neurocranium in side view. × 1·5.

Figure 43. *Aspidorhynchus* sp., the same specimen as in figure 42 in ventral view. × 1·5.

Figure 44. *Leptolepis bronni*, Professor Watson coll. P507, neurocranium in side view. × 7·5.

Figure 45. *Pholidophorus bechei*, B.M.N.H. P1052, neurocranium in side view. × 4·5.

46



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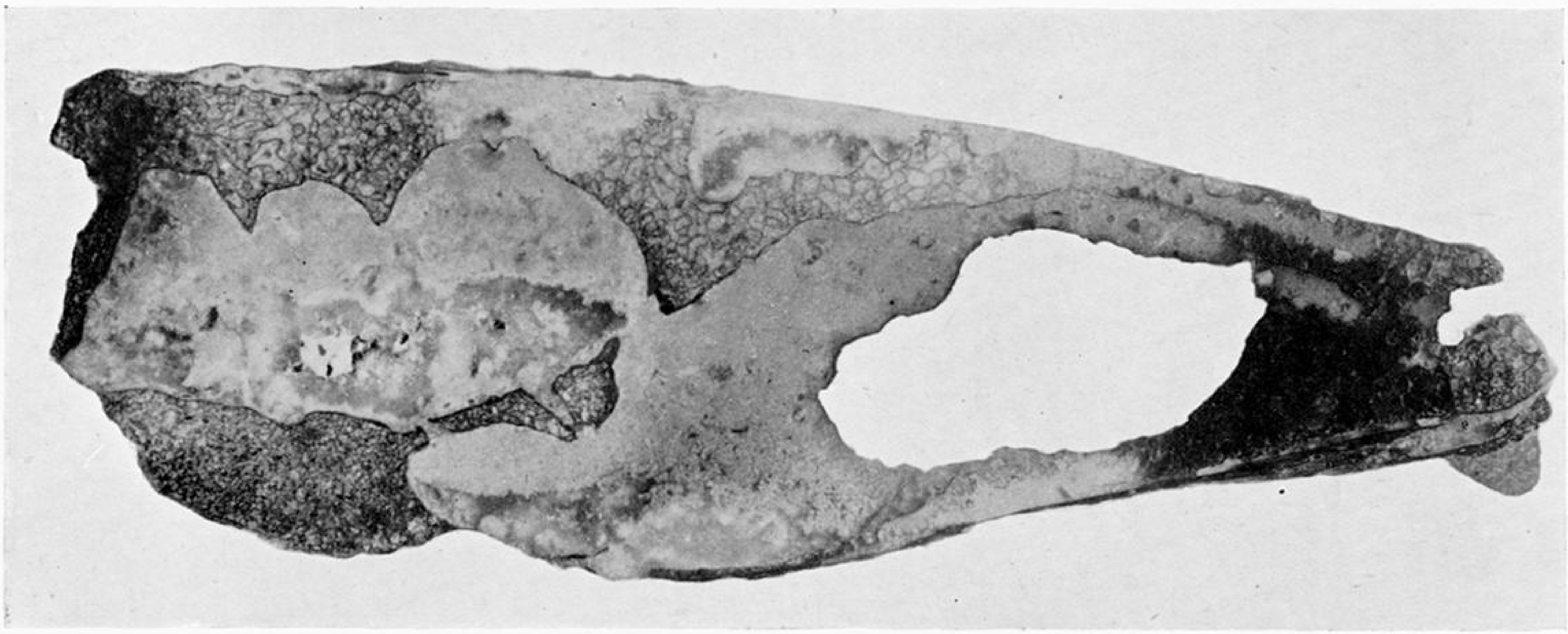

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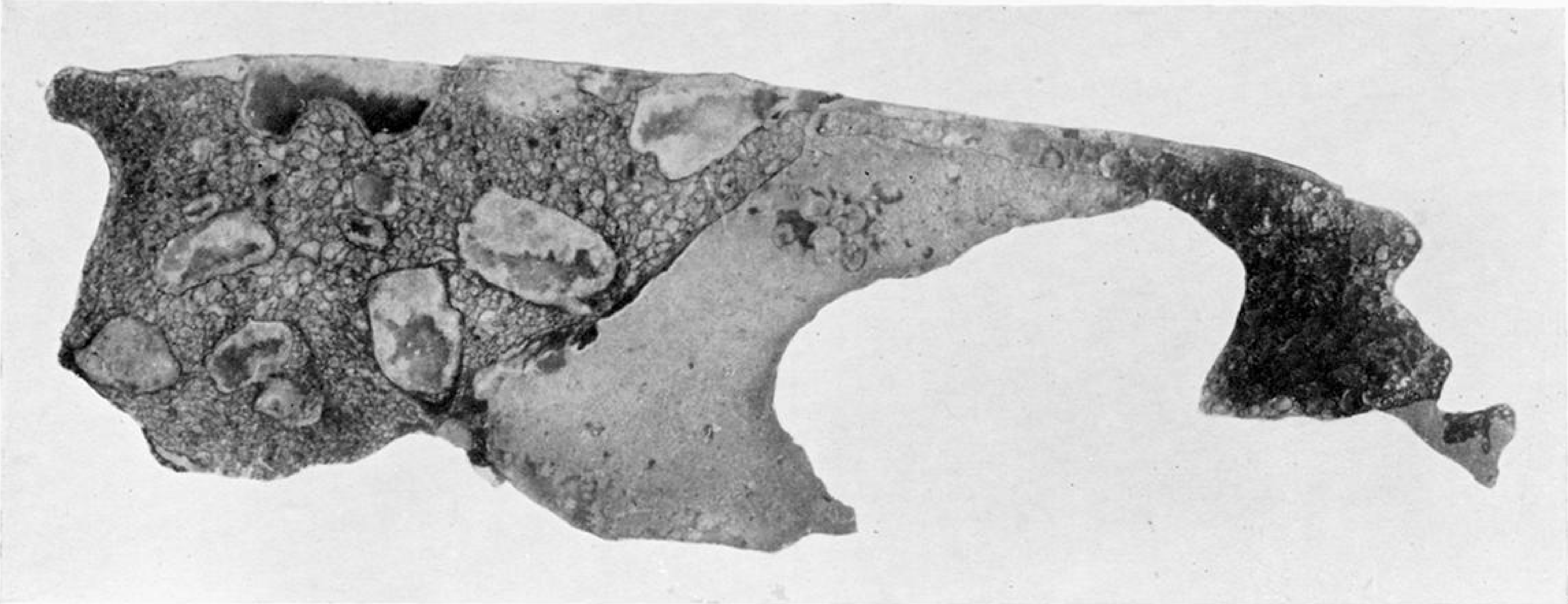

Figures 46 to 48

Plate 22

Figure 46. *Caturus* sp., longitudinal section no. 32·50 through the foramen magnum, optic foramen, cranial cavity and myodome. × 1½.

Figure 47. *Caturus* sp., longitudinal section no. 31·30 through the optic, trigeminal and abducens foramina, and foramen magnum. × 1½.

Figure 48. *Caturus* sp., longitudinal section no. 27·40 through the facial recess, the passage for the vagus, several portions of the labyrinth, and two of the dorsal pits. × 1½.