THE BRAINCASE OF PHOLIDOPHORID AND LEPTOLEPID FISHES, WITH A REVIEW OF THE ACTINOPTERYGIAN BRAINCASE

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The Mesozoic pholidophorid and leptolepid fishes stand at the base of the Teleostei. In this paper the neurocranium and the dermal bones intimately associated with it, the roofing bones and the vomer and parasphenoid, are described more or less completely in six Jurassic pholidophorids (*Pholidophoroides limbata*, *Pholidophorus bechei*, *P. germanicus*, *P. minor*, *P. macrocephalus* and an unnamed Callovian *Pholidophorus* sp.) and four Jurassic leptolepids (*Leptolepis coryphaenoides*, *L. dubia*, and two unnamed *Leptolepis* spp., one from the Sinemurian and one from the Callovian). These species provide a morphological series which illuminates many problems of actinopterygian evolution and anatomy, and a detailed comparison is made with teleosts and living and fossil holosteans and chondrosteans. In the course of these comparisons, new material of *Perleidus*, parasemionotids, *Heterolepidotus*, *Caturus*, *Lepidotes* and *Pachycormus* is described, and previously described fossil holostean braincases are reinterpreted.

The braincase of relatively advanced leptolepids proves to be teleost-like in every way, but the pholidophorids include forms with far more primitive braincases. There are few absolute differences in the braincase between pholidophorids and leptolepids, for the two groups intergrade in the Lower Jurassic and the Sinemurian *Leptolepis* is in many ways intermediate between *Pholidophorus bechei* and more advanced leptolepids. Among the braincases described here, 36 trends are recognized, from a relatively primitive pholidophorid condition to a more advanced leptolepid condition. Almost without exception, the leptolepid condition is the one found in generalized members of all teleostean cohorts. Evidence from the braincase strongly favours a monophyletic origin of extant teleost groups within the leptolepid grade, and there is no indication that any teleost is more closely related to pholidophorids than to leptolepids.

Although far more primitive than leptolepids, pholidophorids are related to leptolepids and teleosts by several specializations in the braincase, of which the most important are extension of the myodome into the basioccipital, presence of a strut across the subtemporal fossa formed by the prootic and intercalar, presence of a median mesethmoid and anterior myodome bone and a median vomer, and the form of the basipterygoid process. The most striking primitive features of the pholidophorid braincase are the obliteration of sutures between the cartilage-bones, terminating growth in full-grown individuals; the presence of a complete cranial fissure, perichondrally lined from the vestibular fontanelle upwards; the presence of two ossification centres absent in most leptolepids and in teleosts, an endochondral intercalar and an opisthotic; the primitive position of the ossification centre of the pterotic, in the postero-dorsal shoulder of the otic capsule; the extensive basisphenoid; the presence of an aortic canal; the presence of an endoskeletal partition separating the post-temporal fossa and fossa bridgei; the presence of a spiracular canal and a lateral cranial canal; the narrow, endochondral lateral commissure; the short posterior portion of the parasphenoid; and the presence in the snout of a pair of dermal bones, primitively toothed, which line the anterior part of the nasal pit, beneath the rostral, and separate the premaxillae. The new term lateral dermethmoids is introduced for these bones: they also occur in *Ichthyokentema* and *Pachycormus*, while in most leptolepids and in teleosts they are fused with the rostral and more or less completely incorporated in the mesethmoid. These bones are held to be the homologues of the nasal process (previously called ascending process) and medial part of the premaxilla of living and fossil holosteans: separation of the premaxilla into a lateral dermethmoid and a mobile premaxilla of pholidophorid or teleost type is a specialization.

Among the primitive features of the pholidophorid braincase, some are typical of holostean level actinopterygians, but others, especially the complete perichondrally lined fissura otico-occipitalis, are only found in palaeoniscoids and *Australosomus*, and pholidophorids closely resemble these forms in the shape and proportions of the braincase.

The principal anatomical conclusions concern the history of the cranial fissure, the ossification pattern of the actinopterygian braincase, and the history of the actinopterygian snout. Closure of the fissura otico-occipitalis in pholidophorids and leptolepids involves loss of the opisthotic and the endochondral portion of the intercalar (primitively the intercalar is entirely endochondral), a shift in the ossification centre of the pterotic, and extension of the occipital bones into the otic region (the new term epioccipital is introduced for the 'epiotic' of teleosts and some holosteans, which primitively had no connexion with the otic capsule, and is probably not homologous with the 'epiotic' of *Lepisosteus*). In some other actinopterygian groups closure of the fissure has had similar consequences, while in some groups the fissure persists after closure as a suture, without extension of neighbouring bones across it. The pholidophorids have more endochondral ossification centres in the braincase than leptolepids and teleosts, but *Perleidus*, parasemionotids and caturids are found to have an ossification pattern similar to that in pholidophorids. It is proposed that the number of ossification centres in the neurocranium has generally decreased, not increased, during actinopterygian evolution, and the ossification pattern of all groups is interpreted along these lines. The 'postrostral' of palaeoniscoids appears to be the homologue of the rostral of holosteans and pholidophorids, and the history of the snout bones of actinopterygians is reviewed, culminating in the compound ossifications in the complex rostrum of teleosts. Other anatomical conclusions include the precise homology between the spiracular groove on the parasphenoid of primitive actinopterygians and the 'prespiracular' groove of rhipidistians, and the inferred presence in many primitive actinopterygians of subcephalic muscles of the type found in *Polypterus*.

1. INTRODUCTION

The Mesozoic pholidophorid and leptolepid fishes are of outstanding interest because they stand in the same relation to living teleosts as do their contemporaries, the late Triassic and Jurassic mammals and 'quasi-mammals', to living mammals. Like those early mammals, the pholidophorids and leptolepids have centred in many discussions on whether the teleosts as a whole or various teleostean subgroups could have evolved from either leptolepids or pholidophorids, and on whether one or both of these groups should be included in the Teleostei. Such discussions have been given freer rein by the fact that only a handful of leptolepids and pholidophorids are at all well known, and no comprehensive account of the structure of either group exists.

For several years I have been accumulating acid-prepared material of a variety of Jurassic pholidophorids and leptolepids, with the intention of compiling a comparative anatomy of the two groups, to serve as an atlas of primitive teleostean osteology for the use of ichthyologists; to evaluate the relevance of these fishes to the main teleostean lineages; and to discover their relations to holosteans and more primitive actinopterygians. But the resulting closely spaced morphological series of pholidophorids and leptolepids proves to be central to so many problems of actinopterygian evolution and anatomy that I have found it necessary to make detailed comparisons with various extinct actinopterygian groups, and a further series of preparations was made to give adequate comparative material of such groups. An account of the whole skeleton along these lines will be too large for a single publication, and I have decided to publish the results piecemeal. This paper deals only with the neurocranium and the dermal bones intimately associated with it, the roofing bones and the vomer and parasphenoid. A second paper will cover the remainder of the skull, and a third the postcranial skeleton. Points raised by the structure of the braincase are fully discussed here, but an assessment of the phylogenetic relations of the pholidophorids and leptolepids will conclude the third paper in the series.

Pholidophorids and leptolepids are conventionally regarded as two families, Pholidophoridae Woodward (1890) and Leptolepididae Nicholson & Lydekker (1889), each the type of a separate order (Pholidophoriformes, Leptolepiformes). Both families are first recorded in marine deposits in the Middle Trias (Gardiner 1967). They intergrade to some extent in the Lower Jurassic (Nybelin 1966) and are common throughout the Jurassic. The last pholidophorids occur in the Purbeck and Wealden of Europe, near the Jurassic/Cretaceous boundary, and include freshwater occurrences. Many species of *Leptolepis* have been described from the Lower Cretaceous and the lower part of the Upper Cretaceous, and Arambourg (1950, 1955, 1968) has advocated the transfer of the majority of these to the genus *Clupavus* Arambourg, placed in a separate family Clupavidae. So little is known about most of these Cretaceous forms that nothing useful can be said of them: some are definitely more advanced teleosts, others could be leptolepids (see Patterson (1970*b*) for a review of the Clupavidae and Cretaceous *Leptolepis* species; Waldman (1971) has since described a freshwater *Leptolepis* from the Lower Cretaceous of Australia and Taverne (1973*b*, *c*) has commented on *Clupavus*).

Pholidophorids and leptolepids were mostly small, fusiform fishes, ranging in length from 5 cm or less in leptolepids (*Leptolepis africana* Gardiner, *L. brodiei* Agassiz), 6.5 cm in pholidophorids (*Pholidophorus pusillus* Agassiz, *P. caffii* Airaghi, *P. higginsi* Egerton), to a maximum of about 30 cm in leptolepids (*L. dubia* (Blainville)), 40 cm in pholidophorids (*P. macrocephalus* Agassiz). The majority of pholidophorids and leptolepids are found in marine beds, but there are several freshwater occurrences of both groups.

All leptolepids have minute teeth, restricted in number and distribution, and they appear to have been microphagous. Pholidophorids have a more robust and extensive dentition, and in keeping with their slightly greater size, most of them were probably predators. This has been confirmed for three of the larger species dealt with here, *P. germanicus* Quenstedt, *P. macrocephalus* and a Callovian *Pholidophorus* sp., by the discovery of leptolepid bones among their stomach contents. Many *Leptolepis* species were shoaling fishes, if such a deduction is permissible from the occurrence of many individuals on a slab. The only such multiple occurrences I have seen among pholidophorids are in the diminutive Upper Triassic species, and most pholidophorids were probably solitary. There is thus some evidence for a biological difference between the pholidophorids and leptolepids, the latter being eaten by the former.

Traditionally, pholidophorids are distinguished from leptolepids chiefly by the squamation, pholidophorids having thick, rhomboid, enamelled scales, leptolepids thin, cycloid scales, which, despite many statements to the contrary, are without ganoin (Schultze 1966). But this line of demarcation was certainly crossed several times (Nybelin 1966, p. 428), and at present it is not possible to regard either group as strictly monophyletic. A better assessment of the status of the two groups should emerge from this series of papers, and from work in progress by Professor O. Nybelin. In the following, the names 'pholidophorid' and 'leptolepid' are used only as vernacular terms, corresponding to the Pholidophoridae and Leptolepididae of Danil'chenko (1964), Lehman (1966) and others. The name pholidophorid as used here is therefore not equivalent to the Pholidophoridae *s. s.* of Nybelin (1966).

In these terms, the pholidophorids comprise the following well established genera:

Pholidophorus Agassiz: a 'dustbin' genus ranging from the Middle Trias to the Wealden and containing many nominal species. The type-species is *P. bechei* Agassiz from the Lower Lias.

Pholidophoroides Woodward: Lower Lias only, two species.

Pholidophoropsis Nybelin: Lower Lias only, two species.

Pholidolepis Nybelin: Lower Lias only, one species.

The following genera are normally included in the Pholidophoridae, but they have either been insufficiently investigated or not compared closely enough with *Pholidophorus* to be regarded as established:

Pholidophoristion Woodward: Kimmeridgian and Purbeck of Europe, two species.

Baleiichthys Rohon: Jurassic of Siberia and China, three species.

Hungkiichthys Liu & Wang: Middle Jurassic of China, one species.

Prohalecites Deecke: Middle and Upper Trias of Europe, two species; may be a 'subholostean' according to Brough (1939).

Eurycormus speciosus Wagner, the type-species of the genus, from the Kimmeridgian of Bavaria, is also a pholidophorid, since it has uroneurals and a *Pholidophorus*-like skull and vertebral column (Patterson 1973). Other species or specimens described as *Eurycormus* (Woodward 1895; Wenz 1968) are probably caturids.

The family Archaeomenidae Goodrich (1909), including *Archaeomene* Woodward, *Aetheolepis* Woodward, *Aphnelepis* Woodward and *Madariscus* Wade from the Jurassic of Australia, *Wadeichthys* Waldman (1971) from the Lower Cretaceous of Australia, and *Oreochima* Schaeffer (1972) from the Jurassic of Antarctica, are not yet clearly distinguished from the pholidophorids in my opinion (Waldman (1971) and Schaeffer (1972) give diagnoses of the Archaeomenidae, and Waldman discusses supposed differences from the pholidophorids).

The leptolepids comprise only one well established genus, *Leptolepis* Agassiz, another 'dustbin' genus, ranging from the Middle Triassic to the Cretaceous, with many species. The type-species is *L. coryphaenoides* (Bronn) from the Upper Lias.

Luisichthys White, from the Oxfordian of Cuba, is always placed in the leptolepids, but it is a large, tarpon-like fish, deep-bodied and with a single row of teeth in each jaw. *Haplospondylus* Cabrera, from the Lower Cretaceous of Argentina, is based on a single imperfect specimen which is not determinable from the original description.

The Upper Jurassic and/or Lower Cretaceous genera *Anaethalion* White, *Pachythrissops* Woodward, *Thrissops* Agassiz, *Allothrissops* Nybelin, *Tharrhias* Jordan & Branner and *Vidalamia* White & Moy-Thomas have been included in the Leptolepididae in one or another recent account, but all belong elsewhere, *Anaethalion* and *Pachythrissops* with the elopiform teleosts

(Nybelin 1971; Forey 1973*a*), *Allothrissops* and *Thrissops* with the ichthyodectids (Rosen & Patterson, ms.), *Tharrhias* with the gonorynchiforms (Santos & Valença 1968; Patterson, in press) and *Vidalamia* with the Amiidae (Wenz 1971).

Many nominal species of *Pholidophorus* and *Leptolepis* are based on such poorly preserved fossils that their relationships will probably never be known. Detailed work on other species will certainly result in their transfer to other taxa, and it is obvious from the braincases described below that some of the species here included in *Pholidophorus* and *Leptolepis* must belong in other genera. But since a reliable assessment of the taxonomic position of these species can only be based on a study of the whole skeleton, I have not introduced any new names or resurrected any old ones.

Apart from descriptions and illustrations of the dermal roofing bones, which have been provided by many authors, previous work on the pholidophorid and leptolepid braincase is almost entirely due to Rayner (1937, 1948), who described the braincase in the type-species of *Pholidophorus* and *Leptolepis*, *P. bechei* and *L. coryphaenoides*. Patterson (1967) published a restoration of the braincase of *L. dubia* in ventral view, and Wenz (1968) commented on and illustrated the occipital region and parasphenoid of *L. coryphaenoides*.

The braincases described here are mostly from new, acid-prepared material, in some cases of more or less complete skeletons, in others of fragments or isolated bones from bone-beds or stomach contents. Species of *Pholidophorus* and *Leptolepis* are differentiated on proportions and meristic characters, unavailable in the majority of the specimens described here, so that the specific identity of some of the material is doubtful or not discoverable. It is hoped that the new anatomical information will outweigh a lack of taxonomic precision.

For the loan of specimens, I am indebted to the authorities of the Institute of Geological Sciences, London; the Sedgwick Museum, Cambridge; the Hancock Museum, Newcastle-upon-Tyne; and the Mineralogisk Museum, Copenhagen, especially to Dr S. E. Bendix-Almgreen of that institution. Mrs Jean Parry Evans generously donated several specimens which she had collected at Lyme Regis. For unpublished information, I am grateful to Dr B. G. Gardiner, Dr P. H. Greenwood and Mr Keith Mitchell; for discussion and comment to Dr Greenwood and Dr R. S. Miles, and for assistance to Miss Alison Longbottom. The photographs were mostly taken by Mr T. W. Parmenter.

2. MATERIAL AND METHODS

(*a*) *Pholidophorid and leptolepid material and preparation methods*

The pholidophorid and leptolepid material described in this paper is listed below, in ascending stratigraphical sequence. Specimens referred to by a registered number without prefix or with the prefix P. are in the Department of Palaeontology, British Museum (Natural History). Other institutions are abbreviated as follows: GSM, Institute of Geological Sciences, London; MMK, Mineralogisk Museum, Copenhagen; SM, Sedgwick Museum, Cambridge.

(i) *Sinemurian* (*Lower Lias*)

Pholidophorus bechei Agassiz; Lyme Regis and Charmouth, Dorset. The mechanically prepared braincases described by Rayner (1948), 19010, P.1052 and SM J4851 (figure 8), were available, as were the complete fishes described by Nybelin (1966). 19010 has been further prepared mechanically to expose the fossa bridgei (figure 7). In addition:

P.51682, an incomplete, isolated braincase (figures 1–5, plate 8) recovered by Mrs Jean

Parry Evans during acid preparation of a series of pliosaur vertebrae, evidently part of the stomach contents of the reptile. The determination of this specimen is open to question as it can only be directly compared with *P. bechei*, since the braincase of the other Lower Lias pholidophorids is still unknown, but the preserved roofing bones (frontals, parietals and dermopterotics) agree exactly with *P. bechei* and differ from other Lower Lias pholidophorids such as *Pholidophoroides* (cf. figures 61, 82). The braincase agrees with those of *P. bechei*, and at present there is no reason for not giving it this name.

P.51160, P.51683, two crushed, incomplete fishes, acid-prepared, showing fragments of the braincase.

Pholidophoroides limbata (Agassiz); Charmouth, Dorset.

P.40588/9, a complete fish, in counterpart, in a nodule from the 'Flatstones' (*obtusum* subzone), prepared mechanically to show parts of the ethmoid, otic and occipital regions figures 6, plate 9; 22, 23, plate 15).

Leptolepis sp.; Charmouth, Dorset.

P.51685–7, three fragmentary acid-prepared fishes, showing parts of the braincase. This is an unnamed species which is to be described by Professor Orvar Nybelin, Göteborg, and is referred to here as 'the Sinemurian *Leptolepis*'. This leptolepid does not appear to occur in the shales from the lower part of the Lyme Regis succession which have yielded the bulk of the Lower Lias pholidophorids (beds 50 and 51 of Lang (1924) according to Rayner (1958, p. 141), which lie in the *scipionianum* subzone). All the available specimens are from the 'Woodstones' and 'Flatstones' (bed 83 of Lang, *obtusum* subzone): the fishes in these limestones are less crushed and more amenable to acid treatment than those of the *scipionianum* shales.

(ii) *Toarcian (Upper Lias)*

Pholidophorus cf. *germanicus* Quenstedt; Ilminster, Somerset.

P.3704, head and anterior part of the trunk of a rather large fish, head length *ca.* 45 mm, acid-prepared (figure 15, plate 12). Woodward referred to this specimen (1895, p. 460) as 'probably of this species' (i.e. *P. germanicus*) or (1896, p. 242) 'may even pertain to a variety of this species'. I am unable to give any more definite determination and the specimen will be referred to as *P. germanicus.*

Leptolepis coryphaenoides (Bronn).

Most of the mechanically prepared braincases described by Rayner (1937) were available. In addition:

P.51714, an isolated, acid-prepared braincase, locality unknown.

P.51689–P.51704, a series of isolated bones, acid-prepared, mostly somewhat rolled, from a bone-bed in the *exaratum* subzone at Iron Cross Quarry, Byfield, Northants.

P.51705–P.51713, a series of isolated bones, acid-prepared, from a bone-bed at Dumbleton, Gloucs.

P.51715–P.51718, isolated bones, remains of at least two individuals, from the stomach contents of P.3704, *P. germanicus*, Ilminster, Somerset.

(iii) *Bathonian (Stonesfield Slate,* progracilis *zone)*

Pholidophorus minor Agassiz; Stonesfield, Oxon.

P.1072, an incomplete, isolated braincase (Woodward 1895, p. 475), acid-prepared (figures 36–38).

(iv) *Callovian* (*Oxford Clay*, athleta *zone*)

Pholidophorus sp.; Dives, Calvados, France.

32579, anterior part of a large fish, estimated head length 75 mm, lacking the snout (Woodward 1895, p. 475), acid-prepared (figures 10–14). The specimen is rolled and was obviously not collected *in situ*. The original label reads 'Dives, Vaches noires': according to Wenz (1968, p. 16) the fish horizon here is of Upper Callovian age, zone of *Peltoceras athleta*. This specimen is not determinable to species and will be referred to as 'the Callovian *Pholidophorus* sp.'.

Leptolepis sp.; Dives, Calvados, France.

P.51719–P.51755, numerous dissociated bones comprising parts of at least eleven individuals, estimated standard length 5–7 cm, apparently all of the same species, found within the body cavity of 32579, *Pholidophorus* sp., during acid preparation and presumably stomach contents of that fish. It is not possible adequately to compare these dissociated bones with known *Leptolepis* species, and they are referred to as 'the Callovian *Leptolepis* sp.'.

(v) *Kimmeridgian* (*Lithographic Stone*), *Bavaria*

Pholidophorus macrocephalus Agassiz.

P.1066/P.3582 (Woodward 1895, p. 469), Solenhofen (figure 16); P.12070, Solenhofen (figure 18); P.52518, locality unknown (figure 19): three large (30–40 cm standard length), partially disarticulated fishes, in counterpart, acid-prepared.

P.1085 (Woodward 1895, p. 469), Moritzbrunn, Eichstadt (figure 20), a smaller disarticulated fish, not certainly of this species, acid-prepared.

Leptolepis dubia (Blainville).

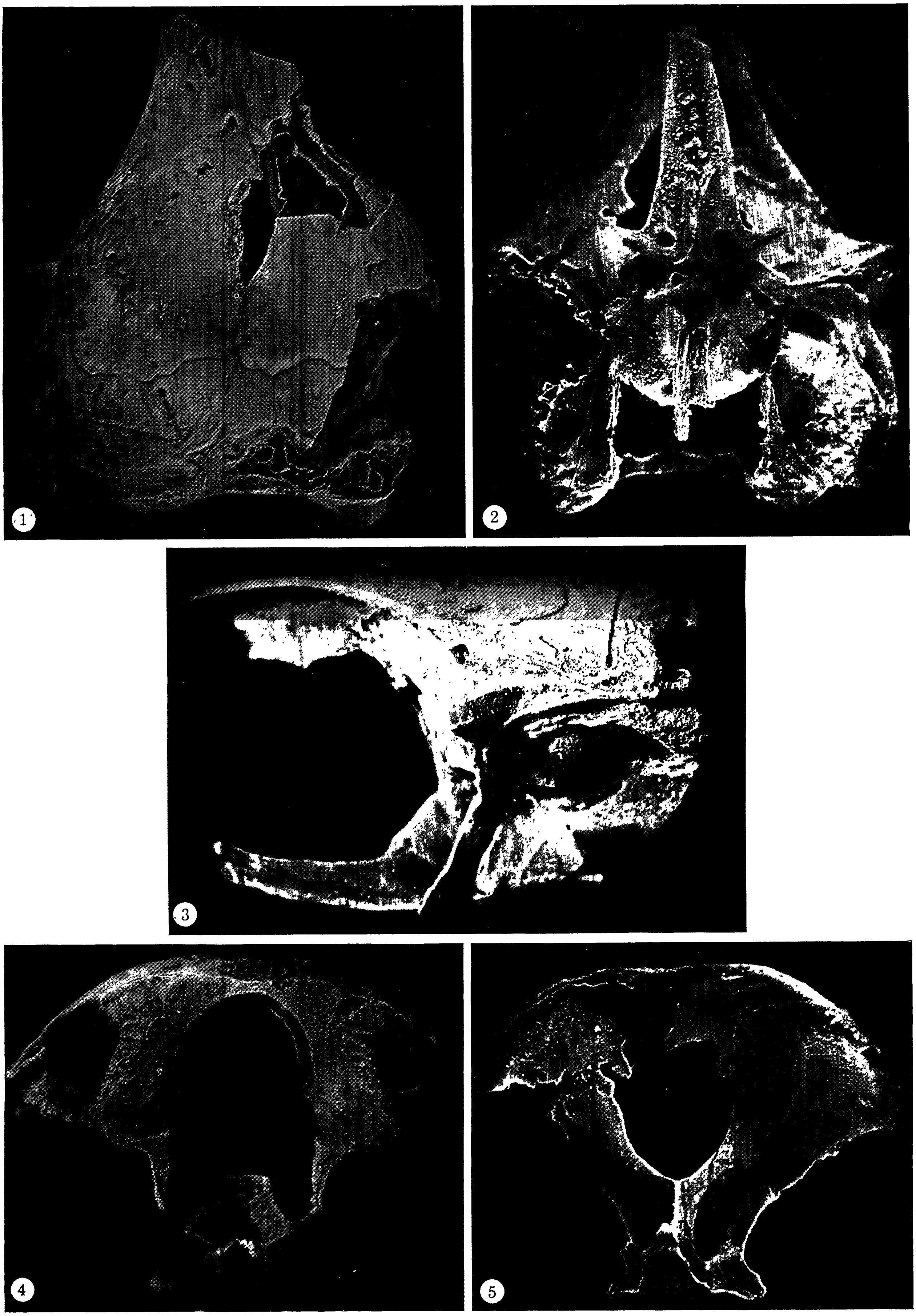
P.51759, a complete head, locality unknown; P.919 (figure 21) a disarticulated fish, Kelheim; and P.3582*a*, an isolated braincase, Solenhofen: these three acid-prepared specimens are all large fish, 15–20 cm in standard length.

P.51761–4, P.55450–5, dissociated bones comprising parts of at least three small individuals, about 7 cm in standard length, from the stomach contents of P.12070, *P. macrocephalus*, Solenhofen.

(vi) *Preparation methods*

The isolated braincases from the Upper Lias and Stonesfield Slate were prepared as free-standing objects by solution of the matrix with dilute acetic acid. The bone-bed materials were obtained by sorting the washed and dried residues after acid treatment of blocks of bone-bed.

The Lithographic Stone specimens of *Pholidophorus macrocephalus* and *Leptolepis dubia* were prepared by the transfer method (Toombs & Rixon 1959). The specimens of *P. germanicus* and the Callovian *Pholidophorus* were prepared by the variation of the transfer technique described by Rixon (1968): the surfaces to be protected from acid attack are first coated with latex and then encased in a shell of fibreglass resin. This method gives very good results with moderately large, uncrushed skulls, and has the advantage over the normal transfer technique that the bones do not adhere to the supporting medium after the matrix has been removed, and can usually be lifted free. The main disadvantage of the method is that the supporting medium is opaque, so that the original exposed surface of the fossil cannot be seen. The limited area exposed to acid attack makes the preparation of large specimens a lengthy business, and sometimes results in decalcification or charring of bones exposed to acid for long periods: this was a problem with the specimen of *P. germanicus*. The specimens of the Sinemurian *Leptolepis*



FIGURES 1–5. *Pholidophorus bechei* Agassiz. Isolated, incomplete braincase, P.51682, in dorsal (figure 1), ventral (figure 2), left lateral (figure 3), posterior (figure 4) and anterior views (magn. × 7 approx.). Specimen whitened with ammonium chloride.

(*Facing p.* 284)

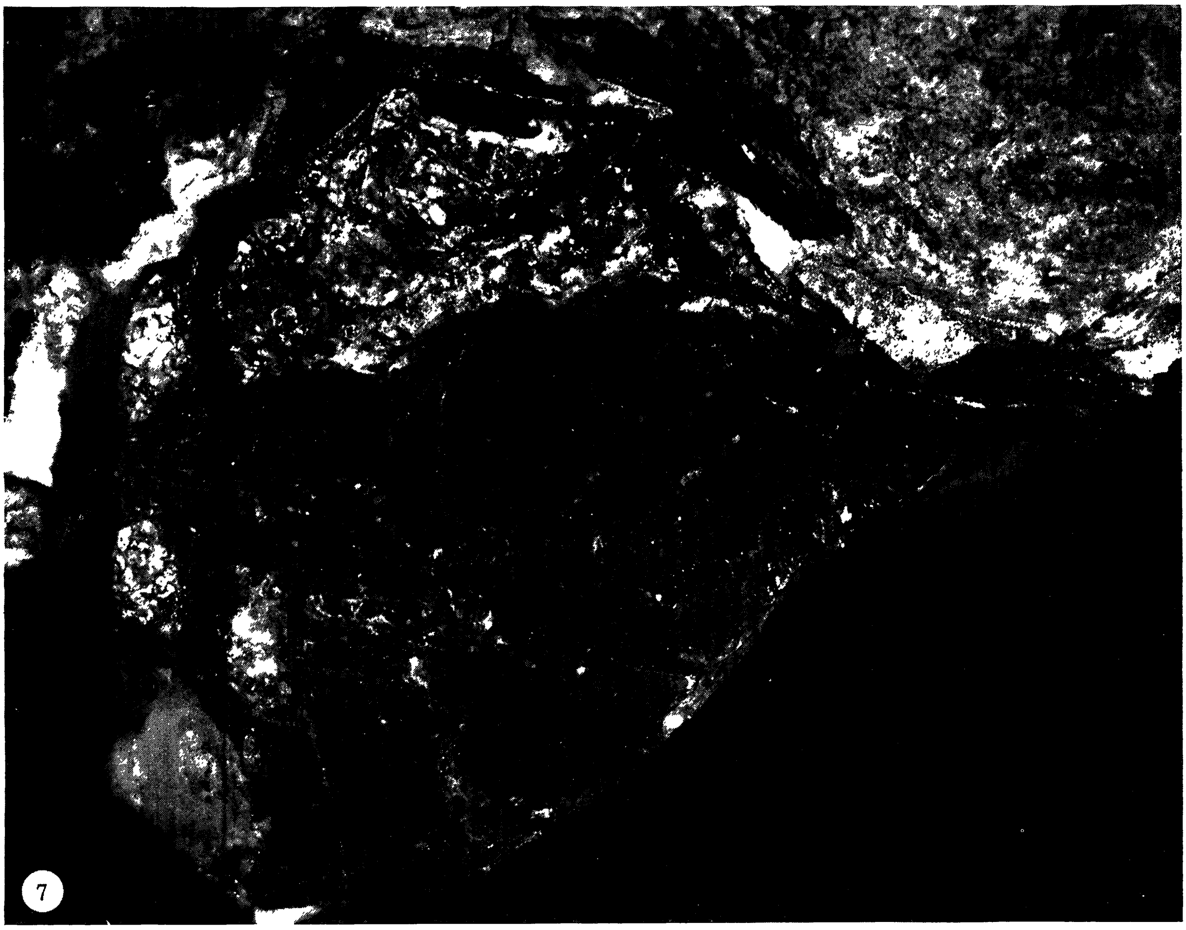
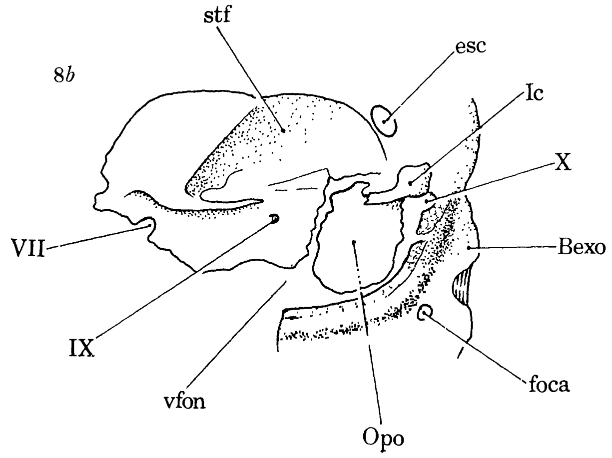


FIGURE 6. *Pholidophoroides limbata* (Agassiz). Skull roof of P.40588, mechanically prepared to show the fossa bridgei of the right side (magn. × 4). See also figures 22, 23.

FIGURE 7. *Pholidophorus bechei* Agassiz. Skull roof of 19010, mechanically prepared to show the fossa bridgei of the left side (magn. × 7.5). See also figure 9.



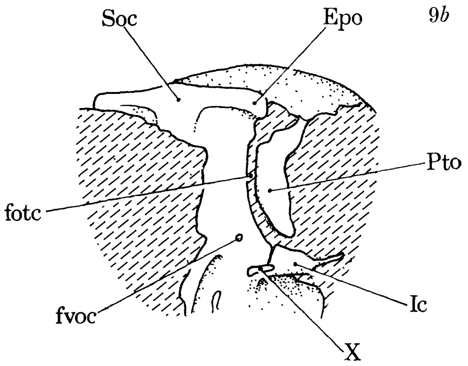


FIGURE 8(*a*, *b*). *Pholidophorus bechei* Agassiz. Postero-ventral part of imperfect neurocranium, SM J4851, in left lateral view to show the opisthotic. (Photograph, magn. × 10; key diagram, magn. × 7 approx.)

FIGURE 9(*a*, *b*). *Pholidophorus bechei* Agassiz. Right side of braincase of 19010 (figure 7) in oblique posterior view to show the dorso-lateral part of the cranial fissure. (Photograph, magn. × 8; key diagram, magn. × 5 approx.)

FIGURE 10. Callovian *Pholidophorus* sp. Isolated, incomplete braincase, 32579, in left lateral view (magn. × 4). Specimen lit from below to illuminate the subtemporal fossa. See also figures 11–14.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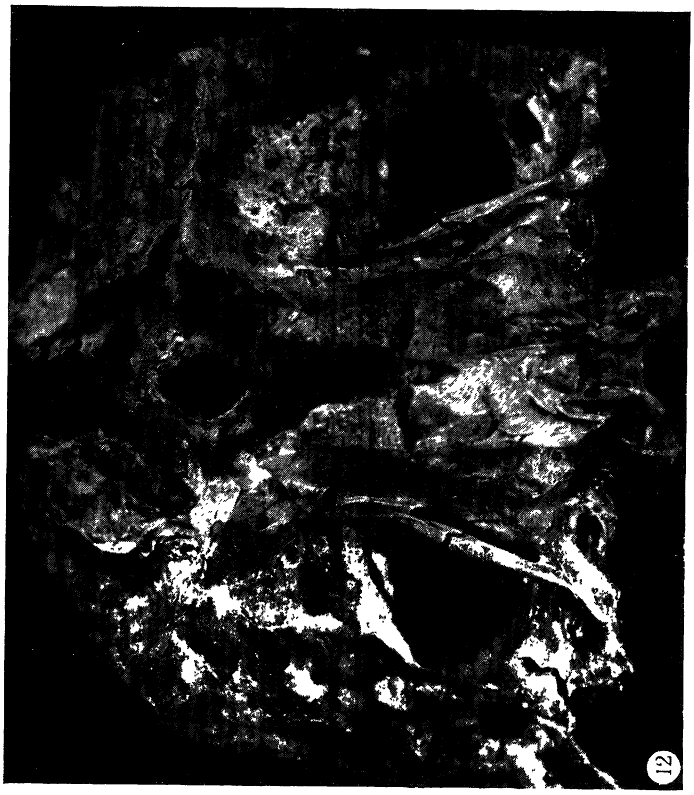
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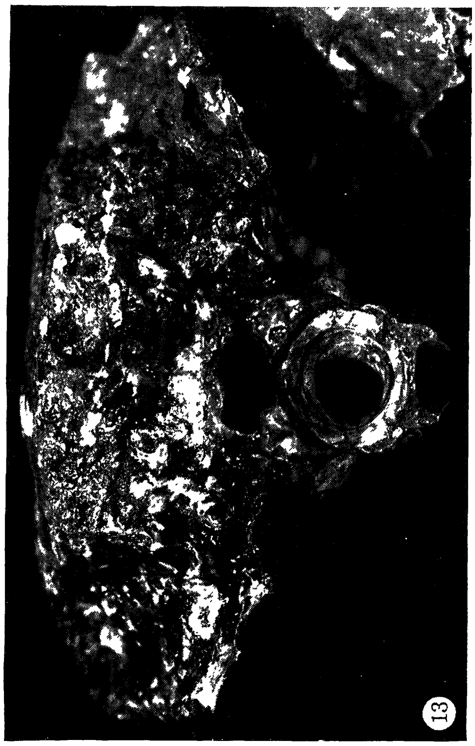
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FIGURES 11–14. Callovian *Pholidophorus* sp. Isolated, incomplete braincase, 32579, in dorsal (figure 11), ventral (figure 12), posterior (figure 13) and anterior (figure 14) views (magn. × 3 approx.). See also figure 10.

⑮

Figure 15. *Pholidophorus germanicus* Quenstedt. Head and anterior part of trunk, P.3704, seen from the left side after removal of most of the bones of the left cheek and palate, exposing the braincase in ventro-lateral view (magn. ×3 approx). The left lachrymal is at the edge of the photograph, and the basal sclerotic bone is conspicuous in the orbit behind it.

FIGURE 16. *Pholidophorus macrocephalus* Agassiz. Partially disarticulated head, P.3582, seen from the right side (magn. × 2¼). The braincase is exposed in ventro-lateral view, with the displaced right hyomandibular covering much of the orbit. The gill-arch skeleton of the left side is exposed in medial view below the braincase.


17


18


19

FIGURE 17. *Pachycormus curtus* Agassiz. Mechanically prepared braincase, 32434, in left lateral view (magn. × 3). See also figure 29.

FIGURES 18, 19. *Pholidophorus macrocephalus* Agassiz. Two isolated braincases in ventral view, P.12070 (figure 18) and P.52518 (figure 19), both magnified × 2 approx.

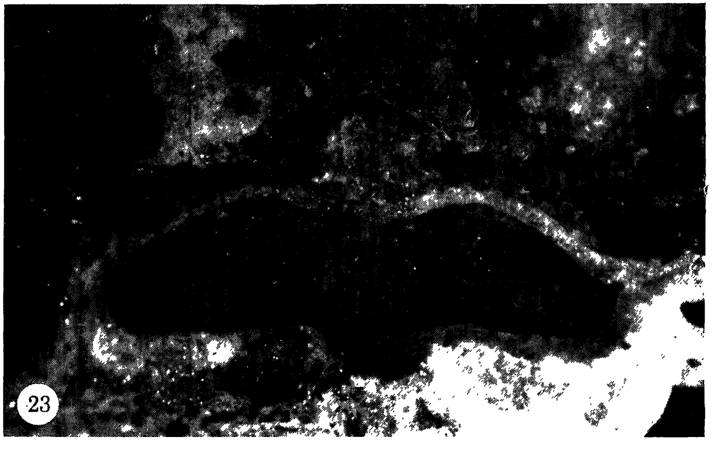
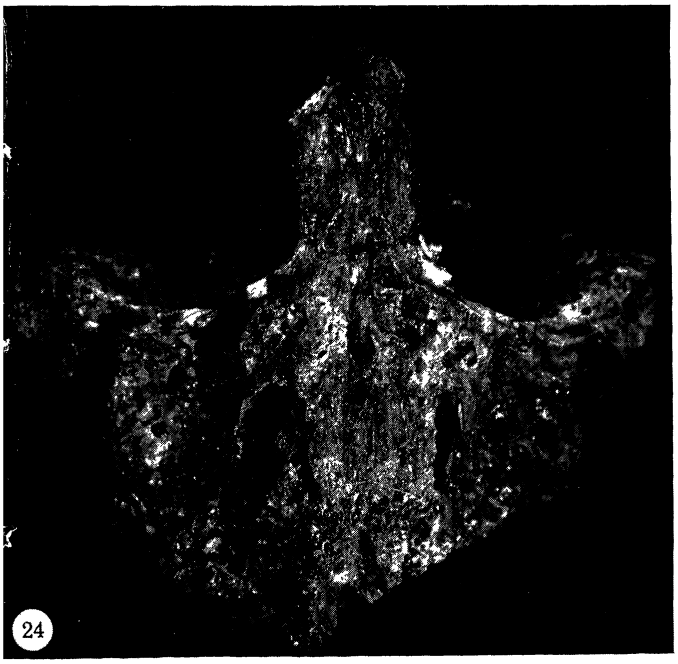


FIGURE 20. *Pholidophorus* cf. *macrocephalus* Agassiz. Braincase of P.1085 in left lateral view (magn. × 4 approx.).

FIGURE 21. *Leptolepis dubia* (Blainville). Isolated braincase, P.919, in ventral view (magn. × 4.5). Most of the parasphenoid is missing.

FIGURES 22, 23. *Pholidophoroides limbata* (Agassiz). Dorsal view of ethmoid region (figure 22) and occiput (figure 23, to show the uninterrupted dorsal portion of the cranial fissure) of P.40588, the skull shown in figure 6. (Both magnified × 8.5)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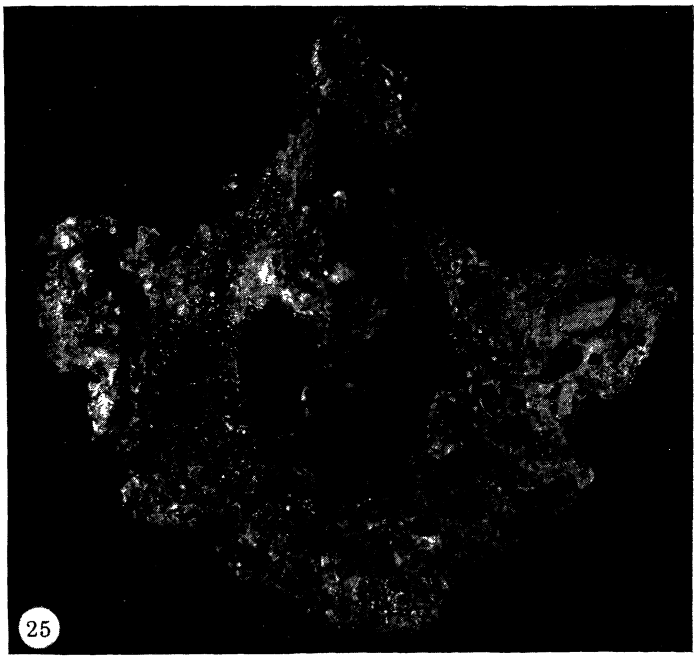
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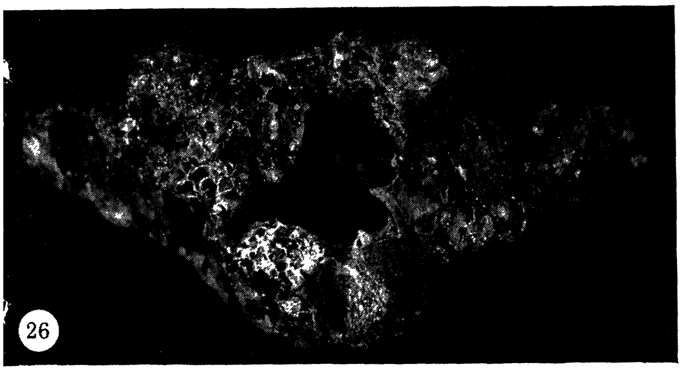
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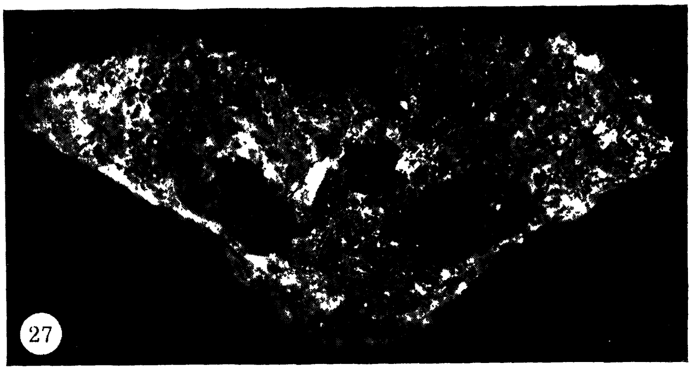
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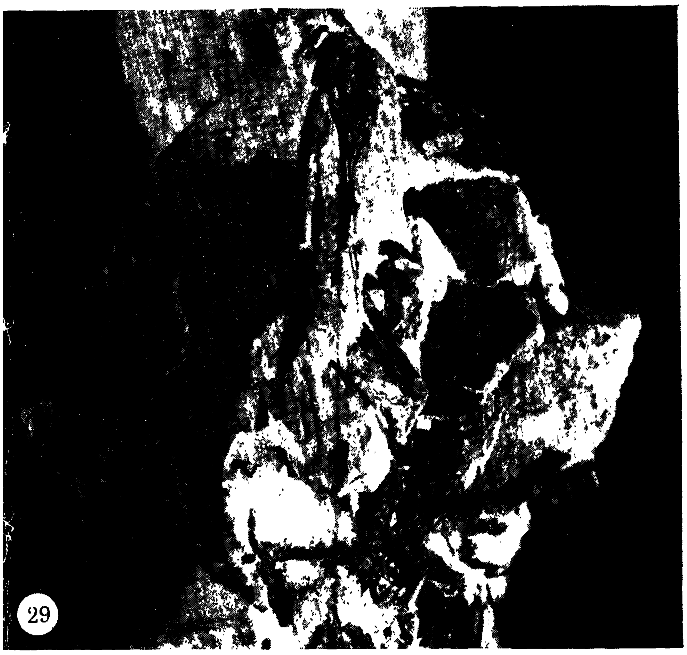
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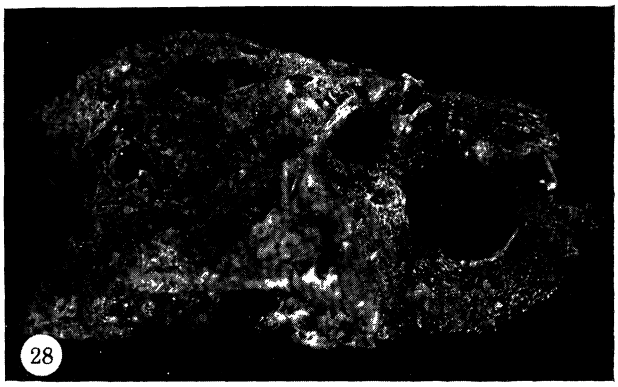
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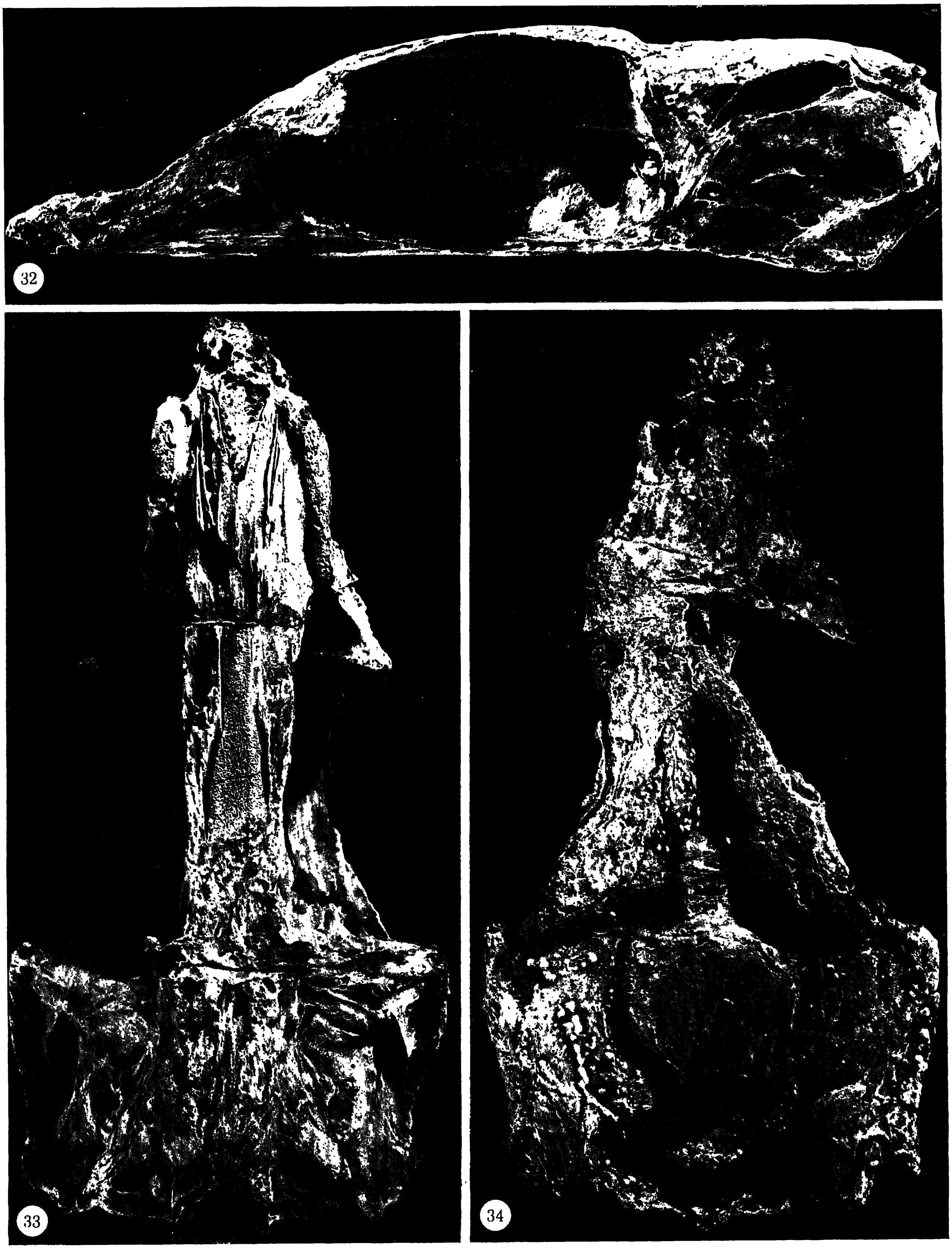
FIGURES 24–28. Undetermined parasemionotid. Isolated, incomplete braincase, MMK 492, in ventral (figure 24), dorsal (figure 25), posterior (figure 26), anterior (figure 27) and right lateral (figure 28) views, all magnified × 4 approx.

FIGURE 29. *Pachycormus curtus* Agassiz. Mechanically prepared braincase, 32434, in posterior view (magn. × 4 approx.). See also figure 17.

Figure 30. Undetermined parasemionotid. Part of disarticulated head, MMK 491A, showing the braincase in ventral view (magn. × 5 approx.). See also stereo-pair, figure 41, plate 20.

Figure 31. *Caturus furcatus* Agassiz. Part of disarticulated head, P.904*a*, showing the braincase in ventral view (magn. × 3 approx.).



FIGURES 32–34. *Heterolepidotus* sp. Isolated braincase, P.13260, in left lateral (figure 32), ventral (figure 33) and dorsal (figure 34) views (magn. × 1.5 approx.). Specimen whitened with ammonium chloride. See also figure 35, plate 19.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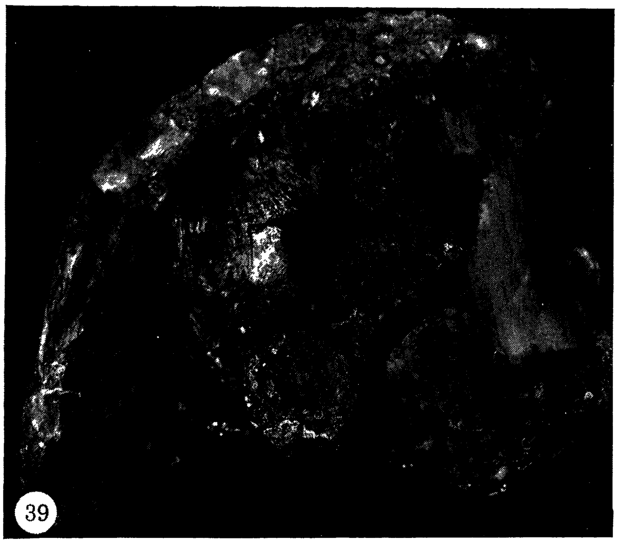
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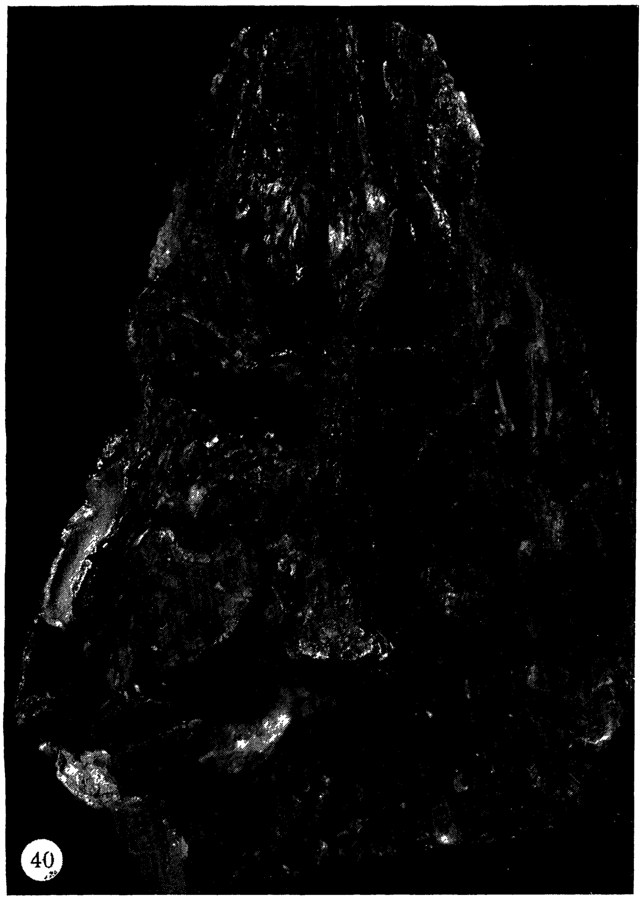
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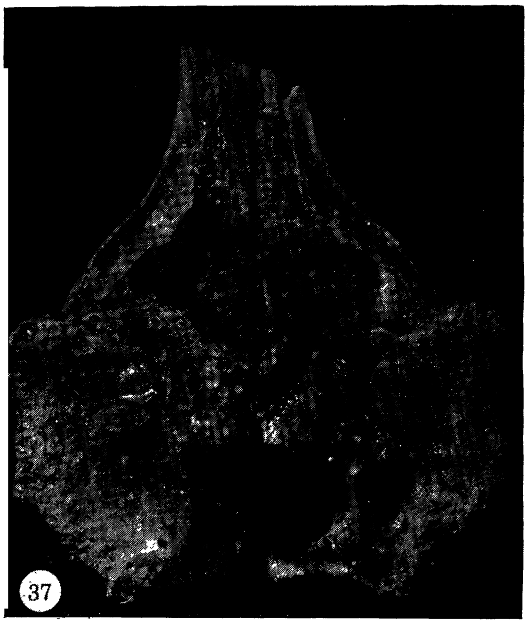
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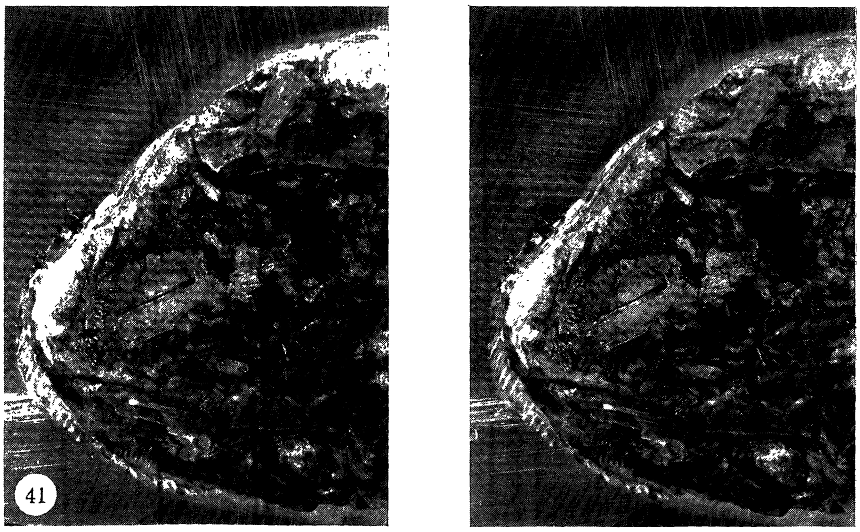
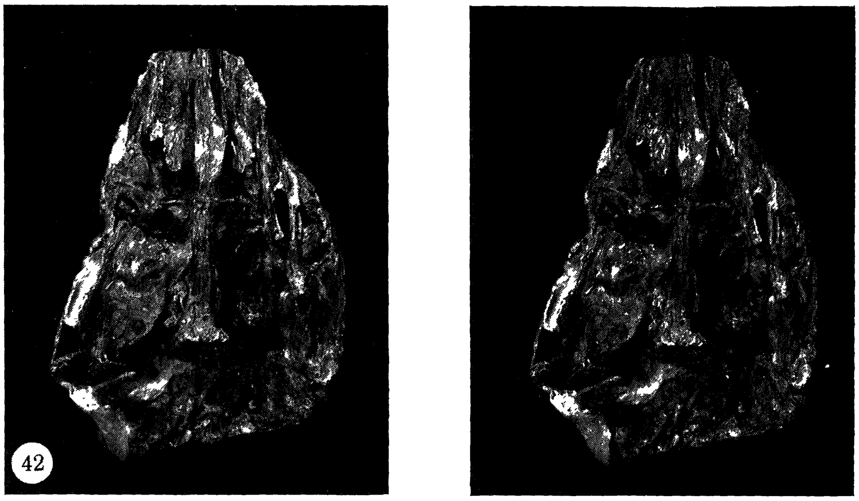
FIGURE 35. *Heterolepidotus* sp. Isolated braincase, P.13260, in posterior view (magn. × 1.5 approx.). See also figures 32–34.

FIGURES 36–38. *Pholidophorus minor* Agassiz. Isolated, incomplete braincase in dorsal (figure 36), ventral (figure 37) and posterior (figure 38) views (magn. × 10 approx.).

FIGURES 39, 40. *Lepidotes toombsi* Jain & Robinson. Imperfect skull, P.34511, showing the braincase in posterior (figure 39) and ventral (figure 40) views (magn. × 1 approx.). See also stereo-pairs, figures 42, 43.





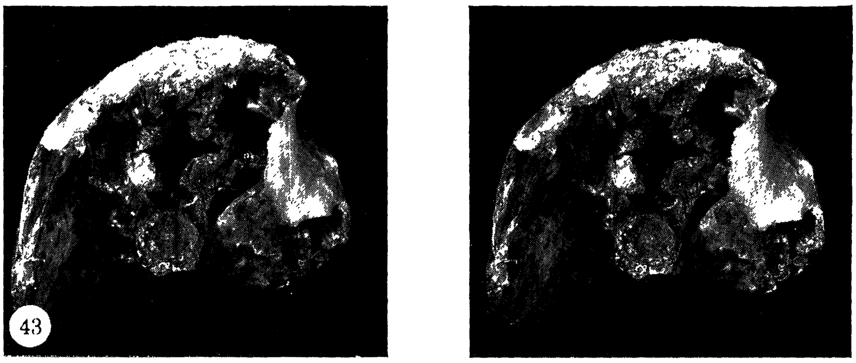


Figure 41. Stereo-pair of the head of the undetermined parasemionotid, MMK 491A, shown in figure 30 (magn. × 0.9).

Figures 42, 43. Stereo-pairs of the skull of *Lepidotes toombsi*, P.34511, shown in figures 39 and 40 in ventral (figure 42, magn. × 0.4) and posterior (figure 43, magn. × 0.5) views.

and the fragmentary specimens of *P. bechei* were prepared without prior embedding as free-standing objects and isolated bones, since the Lower Lias limestones contain too high a proportion of clay to give good results in transfer preparations.

(*b*) *Other material*

In addition to the pholidophorid and leptolepid material listed above, it has been necessary to prepare a number of new specimens and to undertake further preparation of previously described specimens of other Mesozoic actinopterygians, since the available material (principally that described by Rayner (1948) and Gardiner (1960)) was insufficient for detailed comparisons with pholidophorids and leptolepids. This material is listed below.

PERLEIDIDAE: *Perleidus* cf. *stoschiensis* Stensiö. Two specimens from the Lower Trias of Kap Stosch, East Greenland, MMK 495, 496A, acid-prepared by the transfer technique. According to Nielsen (1936, p. 46) there may be 'two or more' species of *Perleidus* in the Greenland basal Trias, but these two specimens appear to be conspecific and show nothing to distinguish them from *P. stoschiensis*. These two specimens were selected as being small (496, the larger fish, has a head length of *ca.* 38 mm and a predorsal length of 10.5 cm, compared with 42 mm and 11.5 cm in the holotype of *P. stoschiensis*) and therefore possibly incompletely ossified, so that the ossification pattern of the braincase would be evident. This proved to be the case, but the combination of a lightly ossified braincase with large, calcite-filled medullary spaces within the bones, and a high clay content in both nodules made these rather unsatisfactory preparations, and both braincases are partially disintegrated.

Perleidus sp. Rubber moulds of the braincase of P.19589–90 (Lehman 1952, pl. 19B, text-fig. 84), Lower Trias, Anaborano, Madagascar, were valuable controls in restoring the lightly ossified and imperfect Greenland braincases.

PARASEMIONOTIDAE: Undetermined parasemionotids. Two specimens from the Lower Trias of Kap Stosch, East Greenland, MMK 492, an isolated, fully ossified braincase, acid-prepared as a free-standing object (figures 24–28, plate 16), and MMK 491A, a transfer preparation of a smaller fish, head length *ca.* 43 mm (figures 30, 41, plates 17 and 20). In MMK 491A the braincase is much less thoroughly ossified than in the Greenland *Perleidus* specimens, but this was a successful preparation because the matrix is a purer limestone and because the endochondral bone has smaller medullary spaces and greater cohesion. The determination of parasemionotids, even to genus, has by now become almost impossible. According to Nielsen (1936, p. 49), *Ospia*, *Broughia*, *Parasemionotus*, *Watsonulus* and 'one or more new genera' occur in the basal Trias of east Greenland. Since then, six more parasemionotid genera have been described from Madagascar (Lehman 1952; Beltan 1968), and the two Greenland genera *Ospia* and *Broughia* have also been reported from Madagascar by Beltan. It will only be possible to evaluate these various forms after a thorough comparative study of the Greenland and Madagascar faunas, but it appears that the characters used to differentiate some of the Madagascar genera (fragmentation of the preopercular, variations in the braincase) are in part individual variations and in part ontogenetic stages.

CATURIDAE: *Heterolepidotus* sp. P.13260, a large, isolated braincase, total length *ca.* 11 cm, from the Lower Lias (Sinemurian, probably *obtusum* subzone) of Lyme Regis, Dorset, acid-prepared as a free-standing object (figures 32–35, plates 18 and 19). This specimen has been determined by comparison with complete specimens of *Heterolepidotus*, but the braincase is virtually identical with that of the acid-prepared specimen of *Caturus chirotes* (GSM 97417) described by Gardiner (1960), and the determination is therefore provisional.

'Aspidorhynchus'. Mr Keith Mitchell, who is working on aspidorhynchids, has pointed out to me that P.9843–4, the two isolated braincases from the Great Oolite (Bathonian) of Kingsthorpe, Northants., described by Rayner (1948) as *Aspidorhynchus* sp., are quite different in structure from all other aspidorhynchid braincases. Comparison of these two specimens with the *Heterolepidotus* braincase mentioned above and with *Caturus* and *Macrepistius* (Schaeffer 1971) leaves no doubt that these are caturid braincases. Both specimens have been further prepared, mechanically and with acid. What to call these specimens is another problem, since they do not fall readily into any known caturid genus. I have chosen to call them *'Aspidorhynchus'*, so that Rayner's complete description of the two specimens will be drawn to the reader's attention.

Caturus furcatus Agassiz. P.904*a* (Woodward 1895, p. 334), a disarticulated skull, estimated total length *ca.* 7 cm, Lithographic Stone (Kimmeridgian), Solenhofen, transfer preparation (figure 31, plate 17).

SEMIONOTIDAE (*sensu lato*): *Dapedium* sp. Two isolated braincases from the Lower Lias, Charmouth, Dorset: P.11189 (Gardiner 1960, figures 37–40), a small braincase, total length 33 mm, from the *davoei* zone (Pliensbachian), has been further prepared with acid, and P.11177 (Frost 1913), a larger braincase, total length 73 mm, probably from the *semicostatum* zone (Sinemurian), has been completely cleared of matrix with acid so that the cranial cavity and fossa bridgei are visible.

Lepidotes toombsi Jain & Robinson. P.34511 (Jain & Robinson 1963, pl. 4), a large head (estimated head length *ca.* 12 cm) from the Kimmeridge Clay, Stretham, Cambs. The dermal bones of this specimen, illustrated by Jain & Robinson, had been previously coated with plastic and it proved possible to remove the matrix within this shell by means of acid to expose an uncrushed braincase (figures 39, 40, 42, 43, plates 19 and 20).

Lepidotes minor Agassiz. P.44914, a crushed skull (estimated head length *ca.* 11 cm) from the Purbeckian of Swanage, Dorset. Acid-prepared without embedding.

PACHYCORMIDAE: *Pachycormus curtus* Agassiz. Mechanical preparation of the left side of 32434 (Wenz 1968, pl. 25, fig. A), an incomplete skull (estimated head length *ca.* 6 cm) from the Upper Lias (Toarcian, *Harpoceras falciferum* zone) of Curcy, Normandy, has produced a complete, undistorted braincase (figures 17, 29, plates 14 and 16). The 'rostral' of 32425, a disarticulated fish from the same locality, has been removed from the block and cleaned with acetic acid.

Pachycormus sp. P.24410 (Wenz 1968, p. 110), also from Curcy is a fragmentary skull of a large individual, about twice the size of 32434. This has been partially prepared mechanically and with acid and shows the posterior part of the braincase.

(*c*) *Descriptive methods*

In the descriptive sections which follow, the comparative method is used, the occipital region of all species being described, followed by the otic and orbitotemporal regions, and so on. The boundaries between these regions are not those of classical embryology but are rough-and-ready ones applicable to the fully ossified braincase. Thus the occipital region is taken to be the territory occupied by those bones ossifying in the occipital arch, and therefore includes part of the saccular recess and myodome, and, in the more advanced species in which the cranial fissure has been obliterated, parts of the labyrinth cavity. The otic and orbitotemporal regions are treated together, since no practical demarcation between them can be drawn in the ossified skull.

3. General features of the neurocranium of pholidophorids and leptolepids

In shape and proportions, all the pholidophorid and leptolepid neurocrania under consideration here are broadly similar. In all, the neurocranium is more or less completely ossified, its external relief is strong, and the course of the external and posterior semicircular canals is visible externally, as in palaeoniscoids and primitive living teleosts (cf. Watson 1925, p. 833; Rayner 1948, p. 327). Few neurocrania are complete enough for sets of comparative measurements to be made, and unless the specimens are entirely uncrushed such measurements are very subjective. Where such measurements can be made or estimated, all the braincases have the maximum breadth (between the postorbital processes) about half the total length (tip of ethmoid to tip of supraoccipital), the maximum depth (at the level of the basipterygoid process of the parasphenoid) about 40 % of the total length, and the length of the orbit and the postorbital length about equal, each approximately 40 % of the total length. The occipital region is always very short, occupying 10 % or less of the length of the braincase. The depth decreases regularly forwards from the hind edge of the orbit, and there is a flexure of the parasphenoid at this level. In the Lower Lias pholidophorids and in all leptolepids the dermal roof of the braincase is quite strongly convex in the transverse plane. In the larger pholidophorids. *P. germanicus*, *P. macrocephalus* and the Callovian *Pholidophorus*, the skull roof is broader and flatter and the relief of the otic region is modified by the extremely large subtemporal fossae. Apart from these minor differences in shape and proportions, pholidophorid and leptolepid neurocrania exhibit important variations in two particulars: the degree of development of the dorsal and lateral parts of the cranial fissure (fissura otico-occipitalis; Nielsen 1949, p. 27); and the mode of ossification of the braincase, principally the number of separate bones of which it is composed in mature and immature individuals, but also the thickness of the endochondral bone and the proportion of cartilage bone to membrane bone.

The cranial fissure, not previously reported in pholidophorids, is complete in *P. bechei* and *P. minor*, and almost complete in *P. germanicus*, dissociated neurocrania of these three species making it relatively easy to observe. The fissure is also probably complete in *Pholidophoroides limbata*, and is partially open in the Callovian *Pholidophorus* and in *P. macrocephalus*. In the Sinemurian *Leptolepis* the cranial fissure is also partially open, but in later leptolepids it has been obliterated and the braincase is of normal teleostean type.

In all pholidophorids and leptolepids the ethmoid region appears to contain paired lateral ethmoids and a median mesethmoid which remain separate throughout life. The remainder of the braincase is known to be most completely ossified in *P. bechei* and *L. coryphaenoides*: in some fully grown individuals of these species a single ossification, without traces of sutures or radiation, occupies the whole of the orbitotemporal, otic and occipital regions, although in *P. bechei* the otic and occipital regions are still separated laterally and dorsally by the perichondrally lined fissura otico-occipitalis and in *L. coryphaenoides* the intercalar is always a separate, superficial bone. Less completely ossified individuals of both these species show that the orbitotemporal, otic and occipital regions ossified from centres corresponding to the median orbitosphenoid, basisphenoid, supraoccipital and basioccipital and the paired pterosphenoids, sphenotics, prootics, pterotics, 'epiotics', intercalars and exoccipitals of teleosts. In *P. bechei* there is also a small opisthotic. Oddly enough, the degree of ossification of the braincase in *P. bechei* and *L. coryphaenoides* is not closely correlated with absolute size, since in both species fully fused braincases, incapable of further growth (cf. Nielsen 1942, p. 92), are known which are only two-thirds the size of others in which some (*P. bechei*) or most (*L. coryphaenoides*) of the ossifications are still separated by sutures. This suggests that ossification set in relatively early in ontogeny and that in some individuals growth was terminated rapidly by fusion of the bones, while in others persistent sutures allowed persistent growth, as in living teleosts.

In the single available braincase of *P. minor* the otic and orbitotemporal regions are occupied by a single ossification, without sutures; the ethmoid and occipital regions are unknown in *P. minor*. In other pholidophorids (*P. germanicus*, the Callovian species and *P. macrocephalus*) the full teleostean complement of separate bones is present except that the basi- and exoccipitals are co-ossified, in the Callovian braincase the pterotic and prootic are partially fused, and in *P. germanicus* and *P. macrocephalus* there is also a small opisthotic and one or two minor independent ossifications around the pterotic. Although these three species are represented by large individuals, the majority of the sutures between the neurocranial bones are still open, and in the individual of *P. germanicus* most of the bones were separated in life by zones of cartilage. In these pholidophorids it is therefore likely that the sutures did not close, and that growth was continuous. The Sinemurian *Leptolepis*, like the pholidophorids, has the basi- and exoccipitals co-ossified, but otherwise has the normal teleost pattern of separate ossifications in the available specimens. Later leptolepids (excluding *L. coryphaenoides*) have the typical teleostean set of neurocranial bones and were probably capable of continuous growth.

In *P. bechei* the endocranial bone is similar in structure to that of palaeoniscoids, perleidids, pholidopleurids, parasemionotids and other primitive actinopterygians (Nielsen 1942, p. 16); thick and massive, without radial structure, with the endochondral portions containing large medullary spaces surrounded by delicate laminae, and with the external and internal surfaces and the canals passing through the bones lined with thin perichondral bone. In other pholidophorids the bone is similar in structure, but becomes slightly less massive in the Upper Jurassic species. The leptolepids show a more obvious thinning of the endochondral bone, starting from the Sinemurian species, in which the bone resembles that of *P. bechei* but is a little thinner. In later leptolepids considerable areas of the braincase cease to ossify in cartilage and consist of membrane bone, as in teleosts, the endochondral bone becomes more compact, and radial structure is normally developed in the superficial perichondral and membranous layers.

4. Occipital region

The most perfectly preserved occipital ossifications available are in *Pholidophorus germanicus* and the Sinemurian and Callovian *Leptolepis* spp., these three forms having the cranial fissure respectively almost complete, partially developed, and completely closed. These three species will be described in detail in sequence, with the inclusion of the Callovian *Pholidophorus* sp. as a complement to *P. germanicus*. The other, less well-known species will then be compared with them.

(*a*) Pholidophorus germanicus *and the Callovian* Pholidophorus *sp.*

These two species will be described together since they are rather similar, and the heavily ossified, intact braincase of the Callovian species, though damaged, forms a useful complement to the dissociated bones of *P. germanicus*. The occipital region of the Callovian species is shown in lateral, ventral, dorsal, posterior, oblique postero-ventral and sagittal view in figures 67–71, 73. In both species the occipital ossifications comprise the co-ossified basi- and exoccipitals, referred to as a basi-exoccipital, as in *Polypterus* (Allis 1922), separate, paired intercalars and epioccipitals†, and a median supraoccipital. In *P. germanicus* there is also a small opisthotic, which is described with the occipital bones since it appears to fuse with the basi-exoccipital during ontogeny.

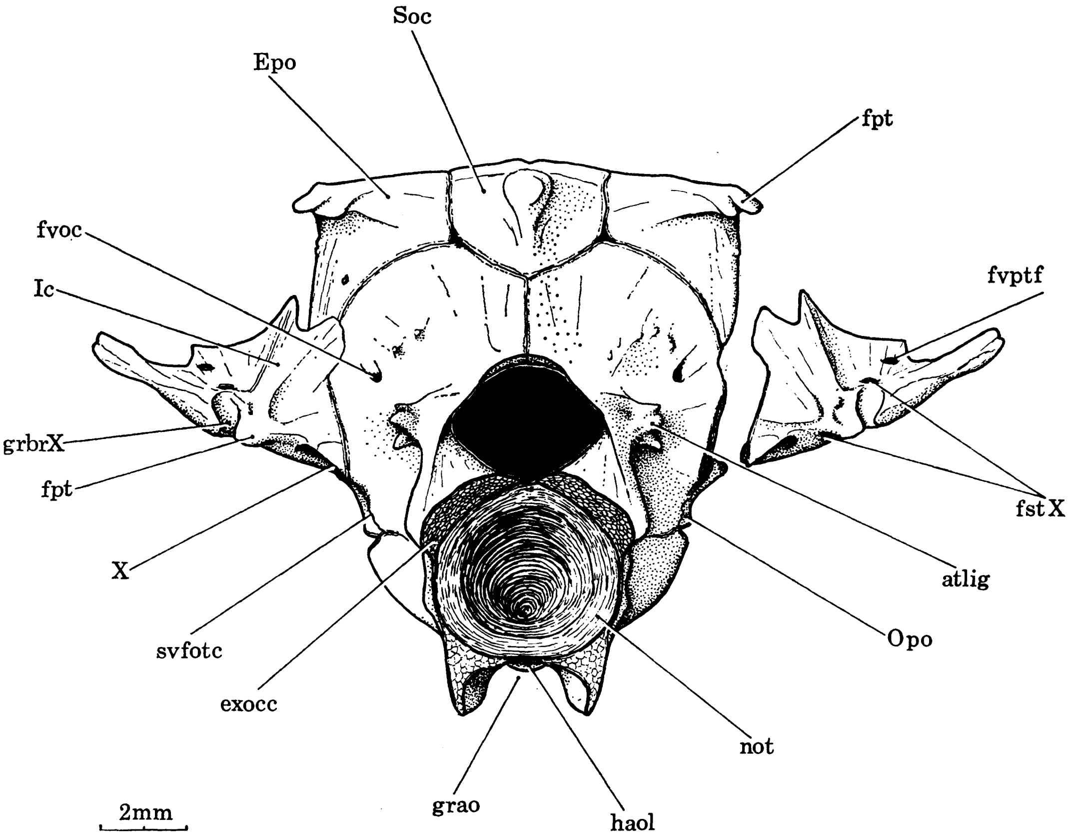


FIGURE 44. *Pholidophorus germanicus* Quenstedt. Occipital ossifications and opisthotic in posterior view, the right intercalar displaced to the right. Based on P.3704.

The *basi-exoccipital* (Bexo) of *P. germanicus* is shown in posterior, anterior, lateral and ventral views in figures 44–47. In both species this bone forms the occipital condyle, encloses the foramen magnum, lines the posterior and ventral margins of the vagus canal, and encloses the posterior part of the otolith chamber and myodome. It consists of thick, very cancellous endochondral bone, lined with perichondral bone except where indicated in the figures. There are residual sutures in the ossification showing that it incorporates paired exoccipitals and a median basioccipital. In *P. germanicus* a median suture above the foramen magnum corresponds to the suture between the upper parts of the exoccipitals in teleosts, and a partial horizontal suture in the floor and wall of the otolith chamber corresponds to the anterior part of the basioccipital/exoccipital suture of teleosts. In the Callovian species the median suture above the foramen magnum is partially obliterated, and the horizontal suture in the wall of the otolith chamber is also less extensive, although it extends further on the internal surface than on the

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† The name 'epioccipital' is introduced here to replace 'epiotic' in pholidophorids, leptolepids, teleosts and some fossil holosteans. This regrettable change follows from the recognition that the 'epiotic' in these fishes is, or is an enlargement of, a bone which has no connexion with the otic capsule, while the name epiotic has also been used for the pterotic in some fossil holosteans, and for a bone of uncertain homologies in living holosteans. The change is justified in full on p. 425.

external. On both sides of the specimen of *P. germanicus* there is also a sinuous, slightly digitate suture running through the floor of the vagus canal and down through the outer layer of perichondral bone to join the basioccipital/exoccipital suture (svfotc, figure 46). This suture cuts through the endochondral bone and through the inner layer of perichondral bone for a short distance below the vagus canal, but opposite the lower part of the suture on the external surface, the inner perichondral bone is uninterrupted. This suture can only mean that in *P. germanicus* the antero-dorsal part of the occipital portion of the wall of the otolith chamber is formed by a separate ossification, the ***opisthotic*** (Opo, figures 44–47), which tends to fuse with the basi-exoccipital during ontogeny. On the broad upper surface of this separate ossification there is a small saucer-like area of perichondral bone which forms part of the ventral wall of the ampullary chamber of the posterior semicircular canal: this small area is the only impression of the semicircular canals on the occipital ossifications. The small opisthotic just described lies in the postero-ventral part of the otic region, anterior to the vagus canal, ventral to the ampullary chamber of the posterior semicircular canal, and lateral to the otolith chamber. It is compared below (§6(*b*)) with the opisthotic of other actinopterygians. Comparison with *Pholidophorus bechei* (p. 322), palaeoniscoids, parasemionotids and pachycormids (p. 447) indicates that the vertical suture behind the opisthotic is the lowermost part of the fissura otico-occipitalis, here without a perichondral lining and tending to close during ontogeny. In the Callovian species there is no sign of a separate opisthotic, the homologous portion of the braincase being an integral part of the basi-exoccipital, with no indication on either the external or internal surface of the bone that there was an independent opisthotic in early ontogeny. In the Callovian

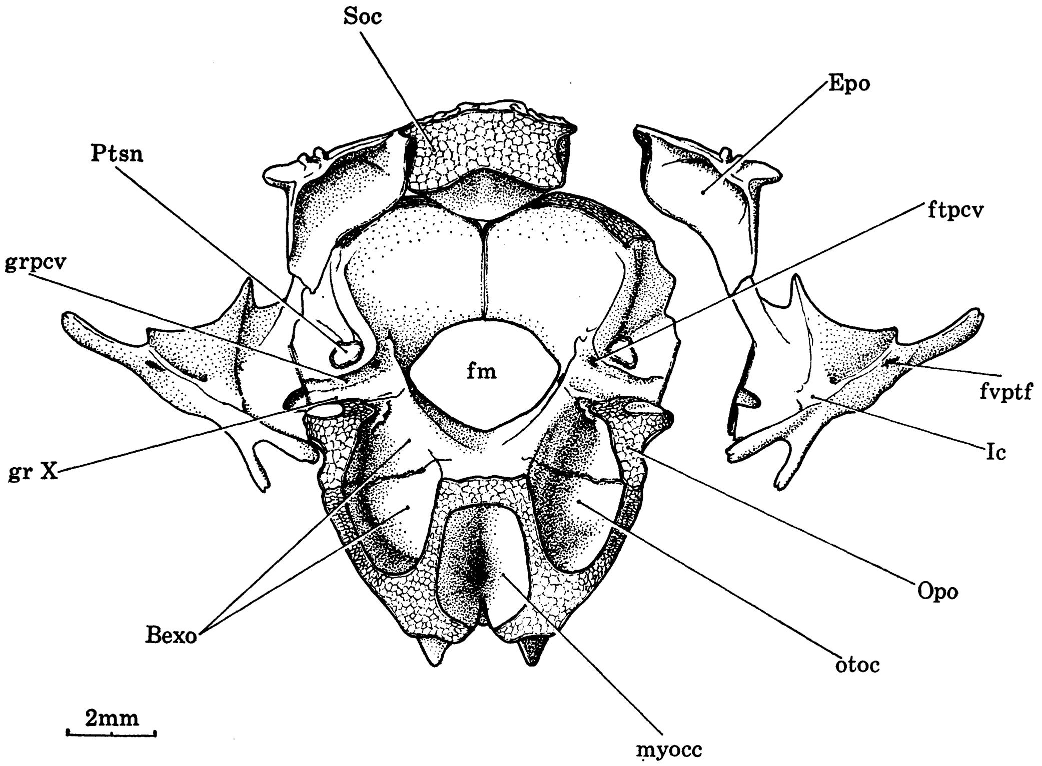


FIGURE 45. *Pholidophorus germanicus* Quenstedt. Occipital ossifications and opisthotic in anterior view, the left epioccipital and intercalar displaced to the left. Based on P.3704.

species, therefore, the lowermost part of the fissura otico-occipitalis, below the vagus foramen, has been obliterated, apparently by forward extension of the exoccipital (see further §6(*a*)).

The occipital condyle (figures 44, 70, 71, 73) is mainly occupied by a hollow cone of calcified notochordal tissue (Patterson 1968, p. 208) which forms a plug in a conical cavity in the endochondral bone. This cavity is directed antero-ventrally, and occupies a little more than half the length of the ossification, ending close behind the most posterior part of the myodome (figure 73). Above the notochordal plug there is a pair of projecting knobs (exocc, figures 44, 70), homologous with the exoccipital condyles of teleosts, whose flat ventro-medial faces are without perichondral bone and were capped by cartilage articulating with the intercalaries (and possibly also the neural arch) of the first vertebra. Below the notochordal plug there is a pair of longitudinal ventral crests, deepest posteriorly, whose hind faces are without perichondral bone and articulated with the basiventrals of the first vertebra. These ventral crests form the walls of a median groove (grao) for the dorsal aorta, and although they do not meet below it to form an aortic canal, they are without perichondral bone ventrally in *P. germanicus* and a short canal may have been formed in cartilage. The wall of the aortic groove is perforated by a rather large, dorso-laterally directed canal (foca, figures 46, 47, 67, 71) corresponding to a similarly placed canal in *Pteronisculus*, *Australosomus*, the Kansas palaeoniscids, parasemionotids, etc. This canal was at first identified by Watson, Stensiö and others as an efferent arterial canal, but Nielsen (1942, p. 34) decided that it transmitted a minor dorsal artery (Bjerring 1971, fig. 6). The canal appears to be homologous with the canal in *Amia* which transmits a 'spinal' artery up towards the exoccipital (Allis 1897, p. 706; Aldinger 1932, p. 27). A similar, dorso-laterally directed foramen or canal is invariably present in primitive actinopterygians (p. 319), and also occurs in rhipidistians (Bjerring 1971, fig. 8B) and dipnoans (Säve-Söderbergh 1952, figs 1, 8) and it will be referred to as the foramen of the occipital artery. Just in front of this foramen there is a small, median cup-like structure (haol, figures 44, 47, 68, 70, 71, 73) of thin membrane or perichondral bone, open posteriorly and partially filled by spicules of endochondral bone. This cup-like structure is part of the basi-exoccipital, but in *P. germanicus* gives the appearance of an independent ossification which has fused with the neurocranium during ontogeny. A similar cup-like structure is a conspicuous feature of all the pholidophorids and leptolepids described here, but I can find no such structure in any living teleost, nor has one been described in any fossil actinopterygian, although it is present in some forms, as will be shown in the discussion. Among living fishes, the only comparable structure is in larval *Polypterus*, where Allis (1922, p. 212) has described a median cartilaginous postero-ventral projection fitting into the notch formed by the bifurcation of the dorsal aorta in a 75 mm specimen. Allis called this the median subaortic process and referred to Pollard's (1892) description of it in a 21 cm specimen as 'a small oval block of cartilage curiously surrounded by a thin shell of bone', which would be a fairly accurate description of the structure in *P. germanicus* and the Callovian species. As to the function of this cup-like structure in pholidophorids, it must lie, as in *Polypterus*, close in front of the bifurcation of the dorsal aorta, and from its form, a hollow cone open posteriorly, it evidently served as the point of origin of some structure passing backwards in the mid-line. This can only have been the median ligament within the aorta. In *Acipenser* and *Polyodon* (Bridge 1878, p. 714) there is a very large, curtain-like ligament running the whole length of the dorsal aorta, and a similar but less massive ligament is recorded in various primitive teleosts (clupeoids, salmonoids, cyprinoids: Burne 1909; de Kock & Symmons 1959; Dornesco & Santa 1963). In clupeoids the ligament emerges from the aorta anteriorly and inserts on the underside of the basioccipital, but it leaves little or no trace on the bone. Presumably, the very conspicuous housing for the ligament on the basioccipital in pholidophorids and leptolepids indicates that the ligament was more massive than it is in living teleosts. The cup-like structure in pholidophorids resembles the conical plug of notochordal calcification filling the occipital condyle, and it is interesting to find that the aortic ligament in salmonids and sturgeons develops around the hypochordal rod (Franz 1897; Jollie 1962, p. 162). Anterior to the insertion of the aortic ligament, the walls of the aortal groove diverge and decrease in height, disappearing at the anterior edge of the basi-exoccipital.

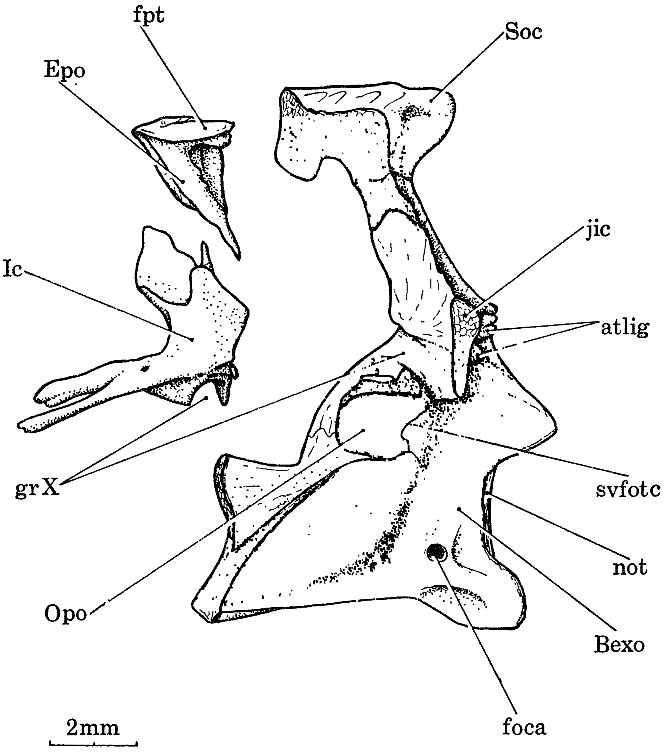


Figure 46. *Pholidophorus germanicus* Quenstedt. Occipital ossifications and opisthotic in left lateral view, the left epioccipital and intercalar displaced forwards. Based on P.3704.

Above the occipital condyle is the large, ovoid foramen magnum (fm, figures 44, 45, 70, 71). In the inner wall of the foramen magnum there are two foramina in *P. germanicus* and one in the Callovian species. The latter foramen (focn, figure 73) and the more posterior and larger of the two in *P. germanicus* transmitted an occipital nerve through a postero-laterally directed canal opening just in front of a projection (atlig, figures 44, 46, 70, 71) which lies lateral to the foramen magnum. This nerve corresponds to the single occipital nerve described by Nielsen (1942, p. 34) in *Pteroniscuius* and to the first occipital nerve of living chondrosteans and holosteans, which has a ventral root only and is said by Bjerring (1970, 1971) to be the ventral root of the vagus nerve. In the Callovian species the exit foramen of the occipital nerve is double. The canal leading from the more anterior foramen in the inner wall of the foramen magnum of *P. germanicus* cannot be followed with certainty throughout its course, but it certainly passes dorso-laterally and anastomoses with a posteriorly directed canal originating in the upper part of the vagus canal (ftpcv, figure 45). After this anastomosis, the common canal appears to run dorso-laterally and open on the posterior face of the basi-exoccipital (fvoc, figure 44). In the Callovian species the opening in the hind wall of the vagus canal and on the posterior surface of the bone are also present, the latter lying on the suture between the basi-exoccipital and the intercalar (fvoc, figures 70, 71).

In *P. germanicus* the posterior wall of the vagus canal (figure 45) is divided by a low ridge into a narrow upper division (grpcv) and a broader lower division (gr X): as is usual in primitive actinopterygians, the upper division contained the posterior cerebral vein, the lower division the vagus nerve (cf. Stensiö 1925, p. 21). The narrow canal originating in the posterior wall of the vagus canal in *P. germanicus* lies in the dorsal division of the canal on both sides of the specimen, and must therefore be interpreted as vascular. The dorso-laterally directed canal originating in front of the internal opening of the occipital nerve canal is on the same horizontal level as the latter, and was therefore probably nervous, transmitting a branch of the occipital nerve to the dorso-lateral surface of the basi-exoccipital, together with a tributary of the posterior cerebral vein.

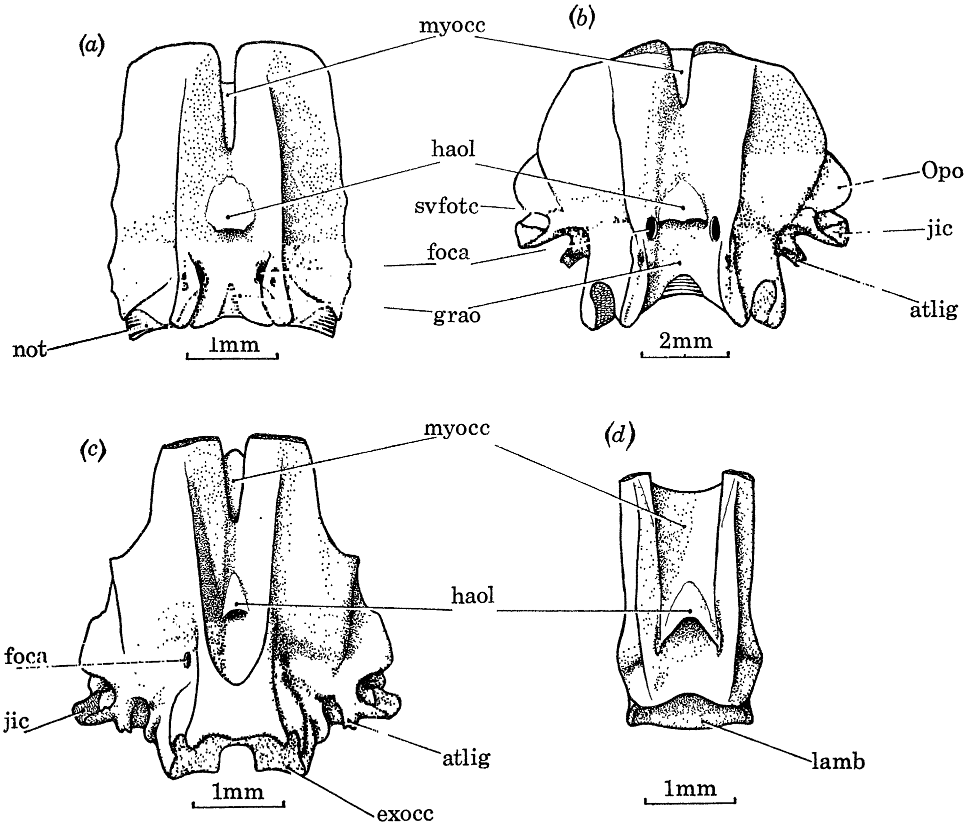


FIGURE 47. (*a*) *Pholidophorus bechei* Agassiz, basioccipital in ventral view, from P.51684; (*b*) *Pholidophorus germanicus* Quenstedt, basi-exoccipital and opisthotic in ventral view, from P.3704; (*c*) Sinemurian *Leptolepis* sp., basi-exoccipital in ventral view, from P.51685; (*d*) Callovian *Leptolepis* sp., basioccipital in ventral view, from P.51719.

In *Pteronisculus* there is also a canal running from the hind wall of the vagus canal. It opens into the cranial cavity close in front of the occipital nerve canal (Nielsen 1942, p. 38, fig. 5). As in *P. germanicus*, this canal opens into the dorsal part of the vagus canal, or (on one side of Nielsen's specimen) into the cranial fissure above the vagus canal: this canal in *Pteronisculus* is therefore also likely to have been vascular. In view of the variability of this canal in *Pteronisculus*, the likelihood that it is vascular, and its evident homology with a similar canal in pholidophorids, it is highly improbable that Bjerring (1971, fig. 6) is right in proposing that it transmitted a hypothetical 'branch of the abducens nerve innervating the basicranial muscle of the third metamere'. Examination of a series of braincases of *Amia*, *Lepisosteus* and various Mesozoic actinopterygians convinces me that in such fishes, where the endocranial wall is still rather thick, the area between the vagus canal and the occipital nerve canal is one in which a variety of small, sometimes azygous or blind-ending canals occur, and that it is fruitless in fossils to attempt to interpret every such canal.

As mentioned above, between the foramen magnum and the external opening of the occipital nerve canal there is a projection which occupies a similar position to the epineurals on the anterior vertebrae. In *P. germanicus* this projection is large and trifid (atlig, figures 44, 46), in the Callovian species it is smaller (atlig, figures 70, 71). Presumably these projections mark the origin of the second intermuscular septum (cf. *Amia*, Allis 1897; *Scomber*, Allis 1903).

The dorsal surface of the basi-exoccipital is without perichondral bone and adjoins the supraoccipital medially and the epioccipitals laterally (figures 44, 45, 70, 73). In *P. germanicus* the most lateral part of the area of contact with the epioccipital is covered by perichondral bone (figure 45), and from this point down to the front edge of the vagus groove, the anterior face of the basi-exoccipital is entirely lined with perichondral bone. This perichondrally lined area is the persisting part of the *fissura otico-occipitalis*, and as figures 45 and 46 show, it occupied about 40% of the height of the basi-exoccipital. The upper margin of the vagus groove in *P. germanicus* is formed by a strong horizontal crest which turns through a right angle at the medial edge of the groove, and continues dorsally, separating the cranial cavity from a dorso-lateral depression. This depression was occupied in life by the posterior part of the pterotic region, mainly cartilaginous in this specimen, and a very small separate endo- and perichondral ossification (Ptsn, figure 45) from the surface of the cartilage remains in position in the depression on both sides of the basi-exoccipital. Postero-lateral to the depression and to the vagus groove below it there is an elliptic, laterally directed, almost vertical area without perichondral bone (jic, figure 46) which meets the intercalar. In the Callovian species, the perichondrally lined fissura otico-occipitalis is slightly less extensive, ending ventrally just above the vagus canal. As a result, the vagus canal lies entirely within the basi-exoccipital, and this bone extends anterior to it to form the postero-ventral part of the wall of the chamber for the ampulla of the posterior semicircular canal (figure 73), an area lined in *P. germanicus* by the opisthotic.

In both species, the endochondral bone of the anterior face of the basi-exoccipital below the vagus canal met the prootic, and there was a triangular interspace of cartilage in the wall of the otolith chamber at the junction of the prootic with the opisthotic and basioccipital in *P. germanicus* (figure 96) and with the notch in the basi-exoccipital at the suture between the two components of the latter in the Callovian species (vfon, figures 67, 71). This cartilaginous interspace is the homologue of the vestibular fontanelle of palaeoniscoids, *Australosomus* and parasemionotids. The antero-ventral part of the basi-exoccipital consists of thick endochondral bone forming the walls of the occipital part of the myodome and otolith chambers (figures 45, 68, 73). The anterior face of this bone surrounding the myodome is without perichondral lining (figure 45) and met the prootic in synchondrosis: this junction is the homologue of the fissura oticalis ventralis of palaeoniscoids, *Australosomus*, etc., on the one hand, and of the basioccipital/prootic suture of teleosts on the other.

The occipital portion of the myodome (myocc, figures 45, 68, 73) occupies a little more than one-third of the length of the basioccipital. The floor of this part of the myodome is incomplete since there is a median notch in the anterior edge of the bone (figures 47, 68). The posterior parts of the otolith chamber (otoc, figures 45, 73) are similar to those of recent teleosts, but there is no differentiation of the saccular and lagenar chambers.

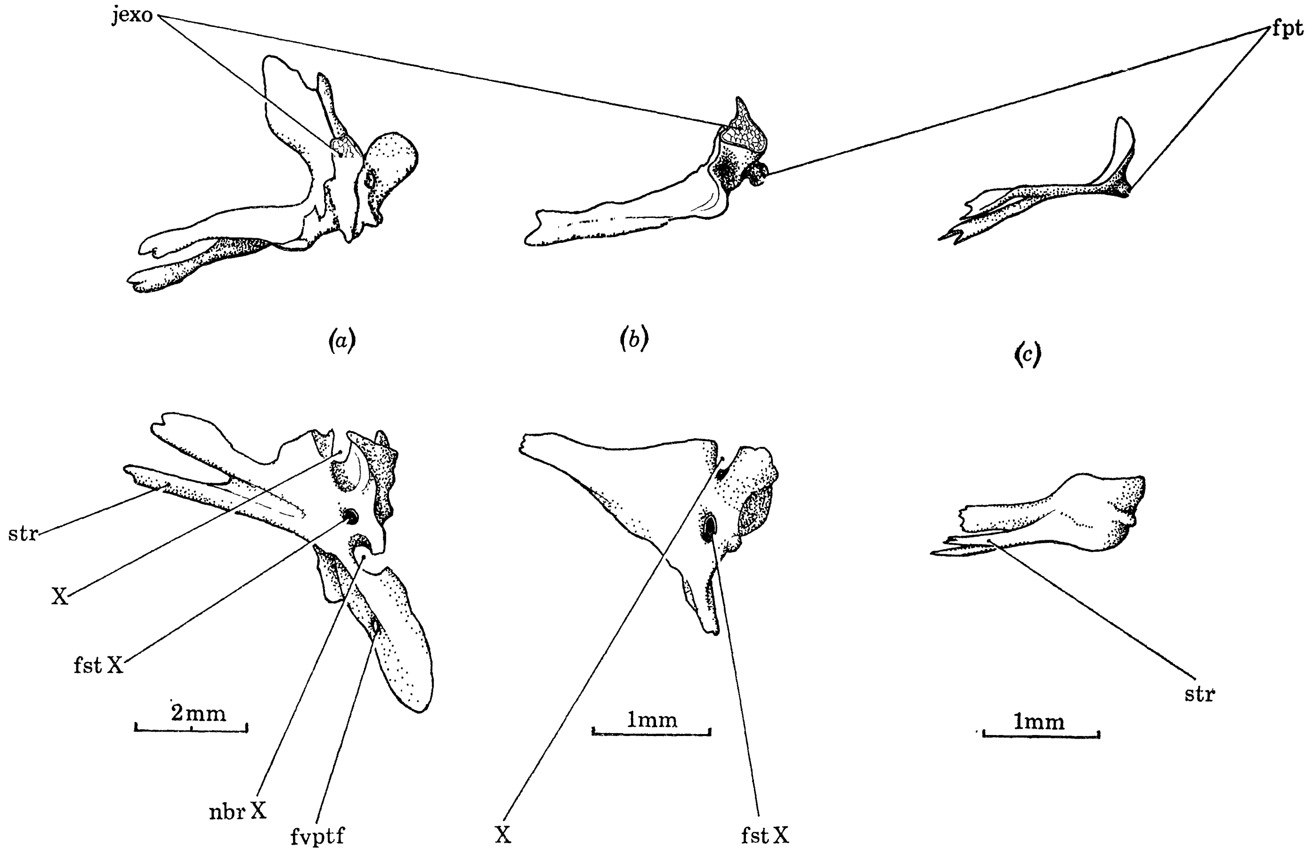


FIGURE 48. Right intercalar in medial view (above) and ventral view (below) of (*a*) *Pholidophorus germanicus* Quenstedt, from P.3704; (*b*) Sinemurian *Leptolepis* sp., from P.51685; (*c*) Callovian *Leptolepis* sp., from P.51723.

The *intercalar* (Ic) is a large and complex bone. The intercalar of *P. germanicus* is shown in posterior, anterior, lateral, medial and ventral view in figures 44, 45, 46, 48 and 96; that of the Callovian species in figures 67, 68, 70 and 71. Although in *Amia* and teleosts (the only living fishes with an intercalar) the intercalar is a membrane bone, without endochondral components, there is no doubt that in pholidophorids it consists of an endochondral core from which expansive sheets of membrane bone have grown (cf. Sagemehl 1891; Schaeffer 1971, p. 23). The endochondral part of the bone is a small, vertical plate, meeting the basi-exoccipital in synchondrosis (jexo) immediately behind the vagus canal (X). This plate carries a facet (fpt) on its posterior surface receiving the ventral (internal) limb of the post-temporal. From the plate of endochondral bone, there are dorsal, lateral and anterior outgrowths of membrane bone. In *P. germanicus* the dorsal outgrowth is a broad, somewhat antero-medially directed sheet ending in two processes, the medial one fitting against a similar ventral outgrowth from the epioccipital, the lateral one fitting over the outer face of the pterotic. The lateral outgrowth consists of a sheet of thick bone which buttresses the ledge formed by the pterotic between the floor of the post-temporal fossa and the ventro-lateral surface of the braincase. This lateral strut and the dorsal outgrowth of the intercalar are joined by a broad sweep of membrane bone which lines the postero-medial part of the floor of the post-temporal fossa. This sheet is perforated by a small foramen, probably vascular, transmitting vessels to the muscles in the fossa (fvptf, figure 44). The anterior outgrowth of the intercalar is a ventro-medially directed strut of membrane bone which bifurcates anteriorly into a broad medial strut fitting against the prootic in the angle between the subtemporal fossa above and the jugular groove below; and a narrow lateral strut (str) which meets a corresponding strut passing back from the prootic lateral to the jugular groove (figure 96). The junction of these lateral struts forms a bridge across the subtemporal fossa, as in *Elops* and osteoglossids amongst living teleosts. At the base of this anterior outgrowth of the intercalar there is a medial flange of membrane bone which forms the antero-lateral boundary of the vagus foramen. On both sides of the specimen of *P. germanicus* there is a large notch in the anterior wall of the vagus foramen suggesting that some structure passed anteriorly into the crevice between the pterotic and the superficial flange of the intercalar. A similar notch is present in the Callovian species (see below), but it is occluded on one side by a flange from the basi-exoccipital, indicating that whatever passed through the notch was not a constant feature. Lateral to the vagus foramen, and in front of the facet for the post-temporal on the hind face of the intercalar, there is a narrow canal through the bone with a large notch in the edge of the bone lateral to it (fst X, nbr X, figure 48). These mark the passage of two branches of the vagus trunk passing up towards the skull roof, probably the supratemporal branches of the vagus and of the lateral line nerve (auricular branch of Norris), as in *Amia* and *Scomber* (Allis 1897, 1903; Norris 1925).

The intercalar is particularly well shown in the Callovian *Pholidophorus* sp., where the intact braincase gives a very clear idea of the way in which the membranous outgrowths of the bone enwrap the surrounding cartilage bones (figures 70, 71). The intercalar has the same dorsal, lateral and anterior outgrowths as in *P. germanicus*. The dorsal outgrowth extends up to the epioccipital and is curved to house the ventral part of the posterior semicircular canal, which emerged from the pterotic and was surrounded only by cartilage in this region. The lateral outgrowth consists of a broad, horizontal wing which is a single sheet of bone posteriorly but opens out anteriorly into upper and lower sheets, the two sheets enclosing the posterior part of the external semicircular canal which, like the posterior canal, emerged from the pterotic and was only surrounded by cartilage in this region. The solid, posterior part of the lateral outgrowth forms the posterior margin of the post-temporal fossa, and is perforated by a rather large foramen (fvptf, figures 68, 69, 70), probably transmitting vessels to the musculature in the fossa. The bifid anterior outgrowth of the intercalar is as in *P. germanicus*. On the right side of the specimen a notch in the intercalar forms a foramen in the anterior wall of the vagus foramen, as in *P. germanicus*, but on the left side this notch is filled by a flange of the exoccipital, suggesting that no structure passed through the foramen where it is present. The notch (nbr X, figures 68, 70) and canal (fst X, figures 68, 69, 70) for the auricular and supratemporal branches of the vagus are as in *P. germanicus*.

The *epioccipital* (Epo) of *P. germanicus* is shown in posterior, anterior, lateral and ventral views in figures 44, 45, 46 and 49; that of the Callovian species in figures 67, 69, 70, 71 and 73. In comparison with the epioccipital (epiotic) of teleosts it is a small and very simple bone, consisting only of a sheet of thick endochondral bone with small membrane bone outgrowths from its dorsal and lateral margins. The ventral and medial surfaces of the bone met the basi-exoccipital and supraoccipital in synchondrosis. The anterior face of the bone is entirely lined with perichondral bone forming the dorso-lateral part of the cranial fissure. From the lateral and dorsal margins of this anterior face there are sheets of membrane bone projecting forwards, wrapping over the postero-dorsal part of the pterotic, in the same way as the membranous flanges of the intercalar enfold the postero-lateral part of the pterotic. Ventro-laterally the membranous outgrowth of the epioccipital extends below the body of the bone and meets the dorsal outgrowth of the intercalar. On the dorsal surface of the epioccipital there is a lateral knob (fpt) which is the site of insertion of the ligament from the dorsal limb of the post-temporal.

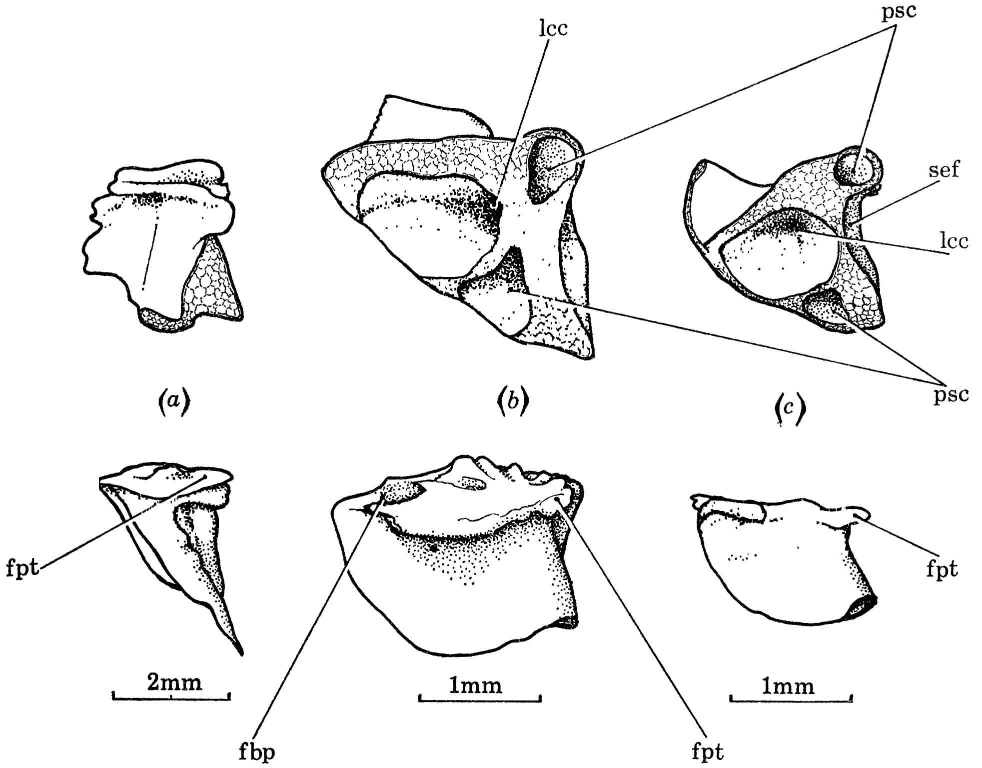


FIGURE 49. Left epioccipital in ventral view (above) and lateral view (below) of (*a*) *Pholidophorus germanicus* Quenstedt, from P.3704; (*b*) Sinemurian *Leptolepis* sp., from P.51685–6; (*c*) Callovian *Leptolepis* sp., from P.51724.

Below and behind this knob there is in *P. germanicus* a shelf of membrane bone projecting posteriorly, whose digitate hind margin was the point of origin of the first intermuscular septum, as in *Amia* and *Scomber*. In the Callovian species the epioccipital extends further forwards on the skull roof than it does in *P. germanicus*, covering the upper surface of the pterotic with membranous splints (figure 69). It is to be noted that the epioccipital has no relation with the semicircular canals in these species.

The *supraoccipital* (Soc) of *P. germanicus* is shown in posterior, anterior, lateral and dorsal view in figures 44, 45, 46 and 50; that of the Callovian species in figures 67, 69, 70, 71 and 73. In both species it is a thick mass of endochondral bone whose lateral and ventral faces met the epioccipitals and basi-exoccipital in synchondrosis. The supraoccipital extends forwards well beyond the epioccipitals and its anterior face met the cartilage between the pterotics (figure 69), obliterating the mid-dorsal part of the cranial fissure (cf. *Pholidophoroides limbata*, figure 82). On the dorsal surface of the supraoccipital in *P. germanicus* there are irregular paired depressions which housed the parietals.

In the Callovian species the supraoccipital is much more completely ossified than in *P. germanicus*. It ends anteriorly in a deep, transverse bolster of bone (figures 72, 73). The antero-ventral face of this bolster is covered by perichondral bone and bears a pair of depressions (lmt, figure 72) referred to below (p. 356) in the description of the cranial cavity. In *P. bechei*, where the cranial fissure is complete, these depressions are found in the otic ossifications, in front of the fissure. Lateral to these depressions, the supraoccipital ended in cartilage joining it with the pterotic in the medial wall of the lateral cranial canal (see p. 342), and the supraoccipital has a small strip of perichondral bone contributing to the channel for the uppermost part of the posterior semicircular canal. The dorsal surface of the supraoccipital bears ridges and splints of membrane bone which contact the parietals and extend on to the pterotic (figure 69).

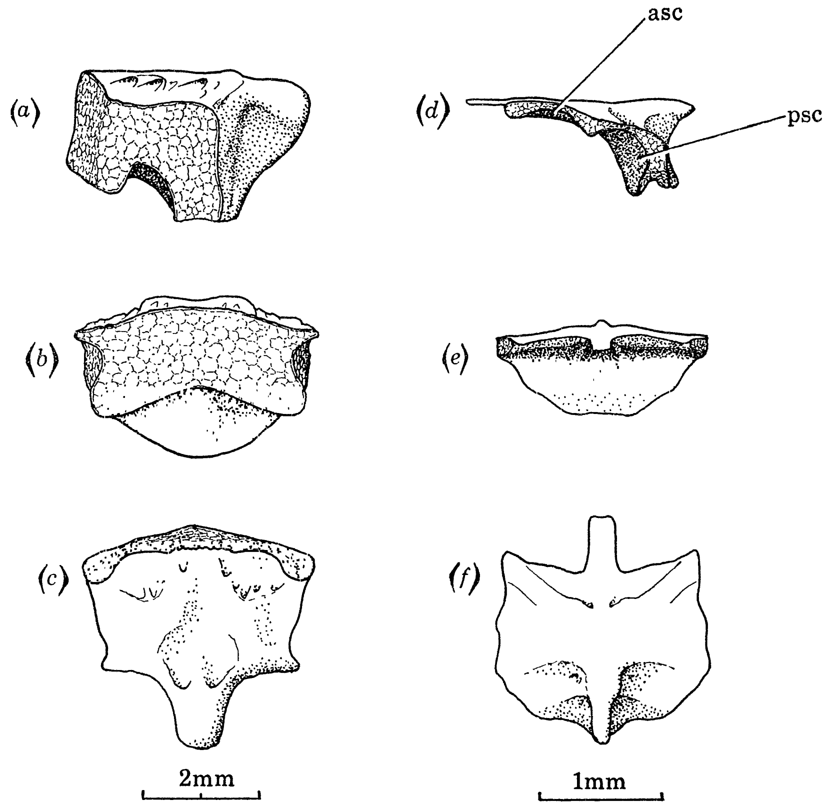


FIGURE 50. Supraoccipital of *Pholidophorus germanicus* Quenstedt (*a–c*), from P.3704, and Callovian *Leptolepis* sp. (*d–f*), from P.51725, in left lateral (*a*, *d*), anterior (*b*, *e*) and dorsal (*c*, *f*) views.

(*b*) *Sinemurian* Leptolepis *sp.*

The occipital ossifications comprise, as in *Pholidophorus germanicus* and the Callovian *Pholidophorus*, a basi-exoccipital, paired intercalars and epioccipitals and a median supraoccipital.

The *basi-exoccipital* of P.51685 is shown in ventral, lateral, anterior and posterior view in figures 47, 51 and 52. Although the bone is broadly similar to that of *P. germanicus* it differs in proportions, having a relatively longer ventral (basioccipital) portion and a steeper posterior profile, with the exoccipital condyles less prominent (cf. figures 46, 47*b* with figures 51, 47*c*).

Also, in contrast to *P. germanicus* and the Callovian *Pholidophorus*, and despite the small size of the fish (head length *ca.* 25 mm), there is no trace of sutures within the ossification and the basi- and exoccipital portions are completely co-ossified. However, in the more lightly ossified P.51686 the basi- and exoccipitals are still separate. The endochondral bone is thinner than in the pholidophorids, especially in the lateral wall of the otolith chamber and above the foramen magnum.

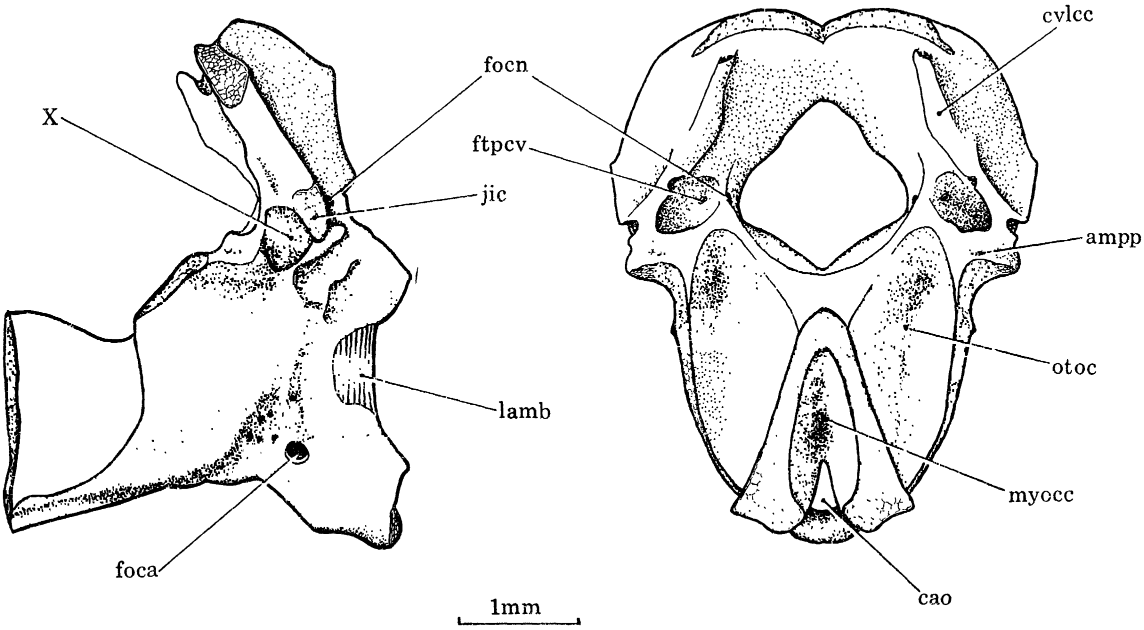


FIGURE 51. Sinemurian *Leptolepis* sp. Basi-exoccipital in left lateral (left) and anterior (right) views. Based on P.51685.

As in the pholidophorids, the occipital condyle (figures 51, 52) is filled by a deep, hollow cone of dense calcified tissue (lamb), occupying about half the length of the ventral part of the bone. This tissue is thinner, smoother and more regular in texture than in the pholidophorids, and in contrast to the latter it resembles the surrounding bone in colour. This tissue in the occipital condyle has not been investigated histologically, but it resembles that in the vertebral centra, which have been sectioned. As will be shown in the third paper in this series, the centra of *P. germanicus* and the Callovian *Pholidophorus* are crescentic hemichordacentra, those of the Sinemurian *Leptolepis* are annular, and mainly of perichordal origin. As in the centra, the bulk of the tissue forming the occipital condyle of the Sinemurian *Leptolepis* appears to be dense, acellular laminar bone (osteoid tissue, François 1966, p. 318), as in the first formed part of the autocentra of teleosts. However, lining the cavity of the occipital condyle there is a layer of paler, fibrous tissue, variable in extent from one specimen to another but thickest around the rim of the cavity: this tissue appears to be notochordal. The upper part of the occipital condyle is formed by a pair of projecting exoccipital condyles (exocc, figure 52), cartilage covered in life. The aortic canal, below the occipital condyle, is complete for a short distance (cao, figures 47*c*, 51, 52). The dorso-laterally directed foramen of the occipital artery (foca, figures 47*c*, 51) leaves the aortic groove just in front of the closed canal, and in front of this foramen there is a median conical structure (haol, figures 47*c*, 52), deeper and narrower than that of *P. germanicus* and the Callovian *Pholidophorus*, but occluded with endochondral bone as in these species, which received the aortic ligament.

The foramen magnum (fm, figures 51, 52) is higher than that of *P. germanicus*, and in the floor of the foramen magnum there is a shallow median depression, absent in *P. germanicus* and the Callovian *Pholidophorus*, corresponding to the cavum sinus imparis of teleosts. In the inner wall of the foramen magnum there is a single foramen (focn, figure 51) transmitting an occipital nerve to an exit foramen (focn, figure 52) lying just behind the vagus foramen, above the more lateral of two projections giving origin to intermuscular septa (figure 52). In the hind wall of the vagus canal there is a very small foramen (ftpcv, figure 51) which appears to have communicated with the occipital nerve canal, but no dorsal opening corresponding to that in *P. germanicus* and the Callovian *Pholidophorus* can be seen. On the dorsal surface of the basi-exoccipital the area without perichondral bone, meeting the supraoccipital and epioccipitals, is smaller than it is in *P. germanicus* (cf. figures 45, 51). From the lateral margin of this area down to the vagus canal the anterior face of the ossification is lined with perichondral bone. This area represents the persisting part of the fissura otico-occipitalis, and occupies about the same proportion of the basi-exoccipital as in *P. germanicus*. The vagus groove (X, figures 51, 52) is more ventrally directed than in *P. germanicus*, and in contrast to the latter there is a slender bridge of membrane bone which converts the outer part of the groove into a canal. From this bridge a crest (cvlcc, figure 51) passes dorso-medially almost to the upper edge of the ossification. This crest, like the bridge across the vagus canal, is formed of thin membrane bone and covers a fairly wide canal. The lower opening of this canal lies in the uppermost part of the external opening of the vagus canal, while its upper opening lies immediately below the lateral cranial canal in the epioccipital (see below). In *P. bechei* there is evidence that the posterior cerebral vein, which occupied the upper part of the vagus canal, received a tributary from the lateral cranial canal (p. 338), and the canal on the anterior face of the basi-exoccipital in the Sinemurian *Leptolepis* is interpreted as having contained a similar vein. The crest covering this canal seems to correspond to the similarly placed ridge in *P. germanicus* (figure 45) which separates the cranial cavity from the depression housing the posterior part of the pterotic. Behind the external opening of the vagus canal there is a laterally directed area without perichondral bone (jic, figures 47*c*, 51) which met the intercalar. This area is smaller than it is in *P. germanicus* (figure 46). In front of the vagus groove the horizontal, perichondrally lined upper surface of the basi-exoccipital is rather broad and shallowly concave. This concavity formed the floor of the recess housing the ampulla of the posterior semicircular canal, an area formed in *P. germanicus* by the opisthotic. As in the Callovian *Pholidophorus* this is the only impression of the semicircular canals on the basi-exoccipital. In front of this area the thin bone in the lateral wall of the otolith chamber is without perichondral lining anteriorly and met the prootic and pterotic in synchondrosis. There is no notch in the anterior margin of the basioccipital to suggest a vestibular fontanelle. The occipital division of the otolith chamber (otoc, figure 51) is higher and a little deeper than in *P. germanicus* but otherwise similar. The occipital division of the myodome (myocc, figure 51) is also higher than in *P. germanicus*, but occupies about one-third of the length of the ossification, as in the latter. The median notch in the floor of the myodome is larger than in *P. germanicus* (figure 47*b*, *c*).

The *intercalar* of the Sinemurian *Leptolepis* is shown in ventral and medial view in figure 48. Although the bone resembles the intercalar of *P. germanicus* and the Callovian *Pholidophorus* rather than those of living teleosts in retaining a small endochondral component, it is otherwise smaller, simpler and more teleost-like than that of the pholidophorids. The endochondral component consists of a small triangular wedge at the postero-medial corner of the bone, meeting the basi-exoccipital in synchondrosis (jexo). The endochondral component is smaller than in the pholidophorids, and the facet for the ventral limb of the post-temporal (fpt) lies on the membranous part of the bone rather than on the endochondral part as it does in pholidophorids. The dorsal and lateral membranous outgrowths of the intercalar, respectively sheathing the postero-medial wall and hind margin of the post-temporal fossa, are smaller than in the pholidophorids, the dorsal outgrowth hardly projecting above the endochondral component, and the flange of bone joining the two outgrowths is not pierced by a foramen. The anterior outgrowth of the intercalar is not bifid but projects laterally in a shelf above the jugular groove, and there was no separate bridge across the subtemporal fossa. The medial edge of the intercalar is excavated to form the dorsal margin of the vagus foramen (X), and there is a notch in the anterior wall of this excavation, as in *P. germanicus*. In the lateral wall of this excavation there is a small foramen (figure 48*b*), but this appears to end blindly and not to have transmitted any structure. Lateral to the vagus foramen there is a foramen on the underside of the intercalar (fst X) leading into a dorso-laterally directed canal which opens on the posterior face of the bone, lateral to the facet for the post-temporal. This passage transmitted the supratemporal branch of the vagus.

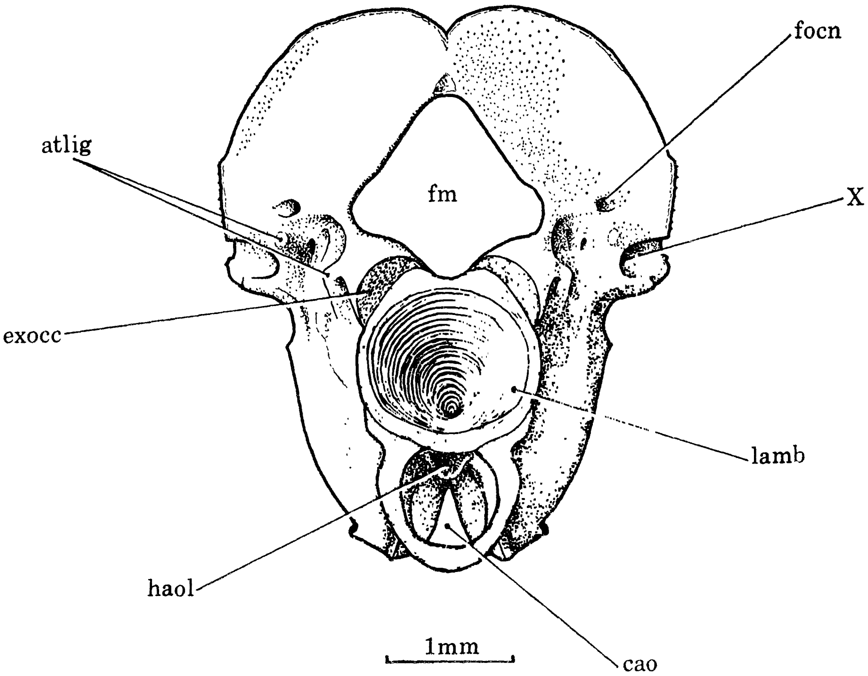


FIGURE 52. Sinemurian *Leptolepis* sp. Basi-exoccipital in posterior view. Based on P.51685.

The *epioccipital* of the Sinemurian *Leptolepis* is shown in ventral and lateral view in figure 49. The bone differs profoundly from those of *P. germanicus* and the Callovian *Pholidophorus* and resembles the teleostean 'epiotic', since it extends forwards to enclose the posterior semicircular canal and the lateral cranial canal (see below), and its anterior face is without perichondral bone, the dorso-lateral part of the cranial fissure having been obliterated. The posterior wall of the bone, which corresponds to the body of the epioccipital in pholidophorids, consists of slightly thinner endochondral bone than in the latter. The dorsal surface of the bone bears a small knob (fpt) for the insertion of the ligament from the dorsal limb of the post-temporal, and projects posteriorly in a shelf for the insertion of the first intermuscular septum, as in *P. germanicus*. The dorsal surface of the bone bears irregular projections of membrane bone which meet the overlying parietals, but anteriorly there is a small depression, not in contact with the roofing bones (fbp). This depression is the homologue of the shallow, postero-medial portion of the fossa bridgei of pholidophorids, which is there found on the pterotic (p. 341). There is no sign of a foramen for the supratemporal branch of the glossopharyngeal nerve in this depression, as there is in pholidophorids. The lateral wall of the epioccipital consists of rather thick endochondral bone and forms the medial wall of the post-temporal fossa, meeting the pterotic in synchondrosis ventrally. In the roof of the fossa there is a triangular shelf of membrane bone projecting laterally from the epioccipital. On the internal surface of the epioccipital there is a deep depression which ends in a blind pocket (lcc) lateral to the middle part of the tube which housed the upper part of the posterior semicircular canal (psc). This depression is the homologue of the lateral cranial canal of pholidophorids (p. 337).

An isolated supraoccipital of the Sinemurian *Leptolepis* has not yet been found, and this bone is not visible in any of the intact skulls. The bone was presumably similar to those of *P. germanicus* and the Callovian *Leptolepis* in shape (figure 50), but intermediate between these in the thickness of the endochondral bone.

(*c*) *Callovian* Leptolepis *sp.*

In this species, as in living teleosts, the basi- and exoccipitals do not co-ossify, and there is the normal teleostean complement of bones.

The *basioccipital* is shown in ventral, lateral, anterior and posterior view in figures 47*d* and 53. Although easily compared with the ventral part of the basi-exoccipital in pholidophorids and the Sinemurian *Leptolepis*, it is essentially of normal teleostean type. The basioccipital condyle is formed by a deep, conical plug of dense, smooth tissue (lamb, figure 53*e*), thinner and shorter than in pholidophorids and the Sinemurian *Leptolepis*, and occupying about one-third of the length of the bone. This tissue appears to be laminar bone, as in living teleosts. One or two specimens have a ring of pale, fibrous tissue lining the rim of the conical cavity and this is probably the remnant of the notochordal calcification. Below the occipital condyle the aortic groove is almost obliterated, and there is no foramen for the occipital artery, which must have passed lateral to the bone. The conical housing of the aortic ligament (haol, figure 47*d*) is larger and closer to the posterior edge of the bone than it is in pholidophorids and the Sinemurian *Leptolepis*, and is not occluded by endochondral bone. The ventral surface of the housing of the aortic ligament is continuous anteriorly with the roof of the myodome (figure 53*f*) which occupies more than half the length of the bone and has no floor whatever. The anterior opening of the occipital division of the myodome is a compressed triangle, as in the Sinemurian *Leptolepis*, but the endochondral bone of its walls is much thinner than in the latter, as is the bone forming the postero-ventral wall of the otolith chamber. Above the myodome, the otolith chambers (otoc) are separated only by a thin median crest, apparently of membrane bone, which is digitate postero-dorsally (figure 53*d*) where it received processes from the exoccipitals.

The *exoccipital* is shown in posterior, anterior and lateral view in figure 54. It differs profoundly from the exoccipital region of the basi-exoccipital in pholidophorids and the Sinemurian *Leptolepis* since the cranial fissure has been obliterated and the bone extends forwards to enclose the vagus and glossopharyngeal foramina, the ampulla and ventral part of the posterior semicircular canal, and the posterior part of the subtemporal fossa. Posteriorly the bone has a thick, projecting exoccipital condyle (exocc, figure 54*d*), without perichondral covering, which buttresses the plug of laminar bone in the basioccipital condyle below and presents an articular surface for the first vertebra. Above the condyle, the exoccipital forms the wall of one half of the broad foramen magnum (fm), meeting its fellow for a short distance above the foramen. There is a single occipital nerve foramen (focn), very close to, or (in some individuals) notching

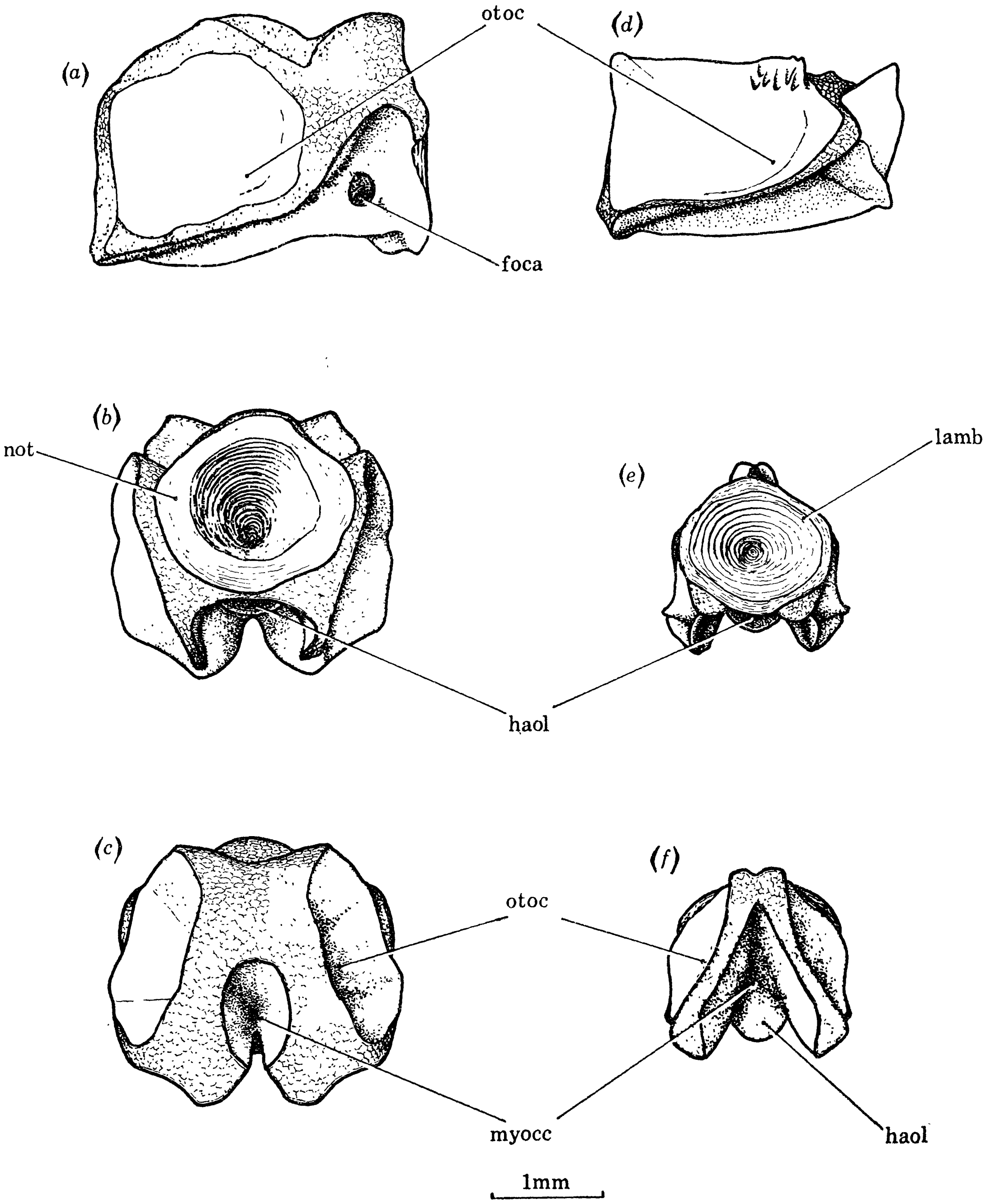


FIGURE 53. Basioccipital of *Pholidophorus bechei* Agassiz (*a–c*), from P.51683, and Callovian *Leptolepis* sp. (*d–f*), from P.51719, in left lateral (*a*, *d*), posterior (*b*, *e*) and anterior (*c*, *f*) views.

the edge of, the foramen magnum. The internal opening of the vagus canal (X) lies close in front of the occipital nerve foramen, and the vagus canal passes postero-ventrally to open directly below the occipital nerve. Behind the external opening of the vagus canal there is a group of pits and a short process (atlig) for the insertion of the second intermuscular septum. From the internal opening of the vagus canal a strong crest extends antero-medially (figure 54*e*), separating the cranial cavity from the otolith chamber (otoc) and ending in a digitate process which meets its fellow and interlocks with the digitations on the upper edge of the basioccipital. There was probably a large tributary of the posterior cerebral vein from the lateral cranial canal, as in the Sinemurian species, since in most specimens there is a groove (gvlcc, figure 54*e*) running dorsally from the internal opening of the vagus canal almost to the dorsal edge of the bone. Lateral to this groove and the internal opening of the vagus canal there is a deep excavation, open laterally, on the inner face of the bone (ampp, figure 54*e*, *f*). This housed the ampulla of the posterior semicircular canal, and in large individuals the ventral part of the semicircular canal was also enclosed within the bone (psc, figure 54*f*). Lateral to the posterior ampullary recess the exoccipital contained the posterior part of the external semicircular canal, and its external surface forms the medial part of the posterior horizontal buttress of the neurocranium, being covered in life by the intercalar, which leaves an impression on the exoccipital (acic, figure 54*d*). The postero-dorsal part of the otolith chamber (otoc), enclosed by the exoccipital below the vagus canal, is similar in form to those of *P. germanicus*, the Callovian *Pholidophorus* and the Sinemurian *Leptolepis*. Near the anterior edge of the exoccipital the lateral wall of the otolith chamber is penetrated by a small, antero-laterally directed foramen for the glossopharyngeal nerve (IX, figure 54*f*). Close in front of the

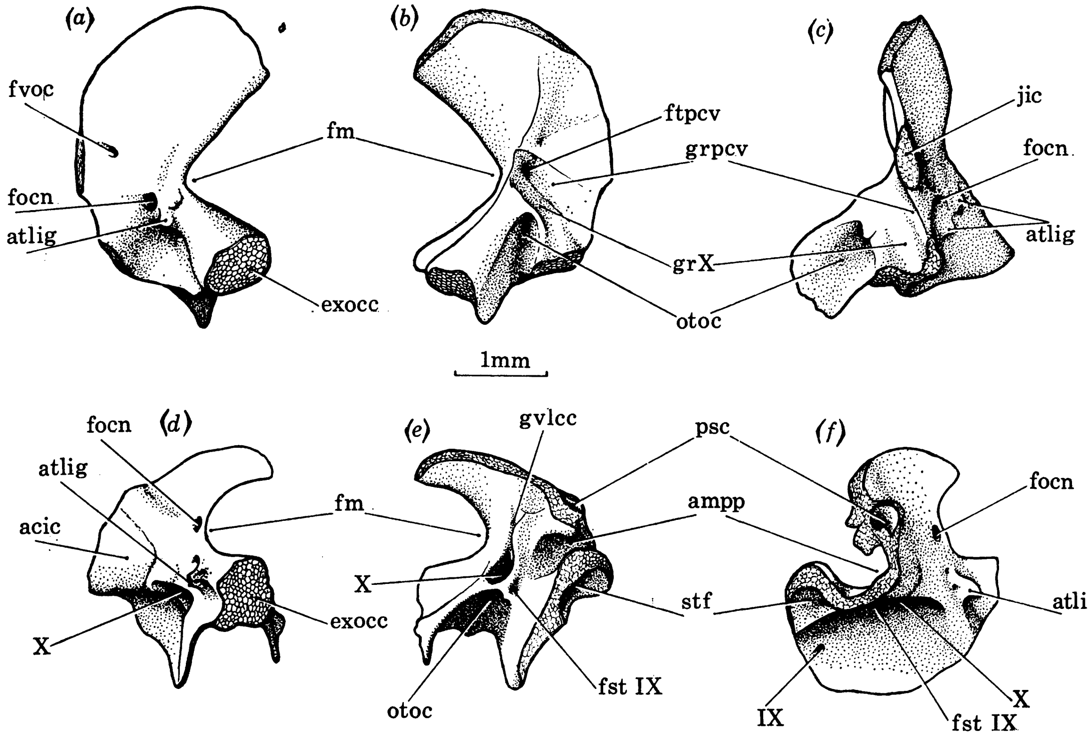


FIGURE 54. Left exoccipital of *Pholidophorus bechei* Agassiz (*a*–*c*), mainly based on P.51683, and Callovian *Leptolepis* sp. (*d*–*f*), from P.51720, in posterior (*a*, *d*), anterior (*b*, *e*) and left lateral (*c*, *f*) views.

vagus foramen the wall of the otolith chamber is penetrated by a second foramen (fst IX, figures 54*e*, *f*), similar in size to the glossopharyngeal, which probably transmitted the supratemporal branch of the glossopharyngeal. Above the glossopharyngeal foramen the exoccipital forms the posterior part of the subtemporal fossa (stf), a sharply bounded depression facing ventro-laterally.

The *intercalar* is shown in medial and ventral view in figure 48. In contrast to the intercalars of pholidophorids and the Sinemurian *Leptolepis* the bone is of normal teleostean type, small, simple and without an endochondral component. The posterior part of the intercalar is a lamina of membrane bone, curved to fit around the postero-ventral buttress of the braincase, covering the junction of the pterotic and exoccipital. A small postero-ventral projection (fpt) marks the articulation of the ventral limb of the post-temporal. The medial edge of the bone does not border the vagus foramen. Anteriorly the bone becomes narrower and thicker, and extends forwards as a pair of splints, the upper, medial one fitting against the exoccipital and prootic above the jugular vein, the lower one (str) meeting a similar membranous splint projecting back from the prootic, forming a bridge across the subtemporal fossa.

The *epioccipital* is shown in ventral and lateral view in figure 49. It is similar to that of the Sinemurian *Leptolepis* but has thinner endochondral walls, a plane dorsal surface with no remnant of the fossa bridgei, and has the shelf in the roof of the post-temporal fossa continued forwards to the anterior edge of the bone. There is a shallow excavation (sef) on the lower part of the posterior face of the bone which is the upper part of a small sub-epiotic fossa (Phillips 1942, p. 464). Among eight available epioccipitals, four have the perichondral lining of the inner face of the bone either undeveloped or unpreserved. The other four examples, which are large and well ossified, fall into two pairs, each probably from a single individual. In one pair of bones the only perichondral lining on the cranial surface is a small, weakly concave disk, evidently forming the postero-dorsal corner of the cranial cavity. In the other pair (figure 49) there is a deep, perichondrally lined excavation on the cranial surface of the bone (lcc), with a slight dilatation at its tip, where it is only separated from the dorsal surface of the bone by a thin membrane. This excavation is the homologue of the lateral cranial canal in the Sinemurian species, from which it differs only in being slightly reduced, so that it no longer extends lateral to the tube containing the posterior semicircular canal (psc). These two pairs of epioccipitals seem to show that the presence or absence of a lateral cranial canal in the Callovian *Leptolepis* is subject to individual variation. Because all the braincases of this species are dissociated, it is not possible to correlate the presence or absence of the lateral cranial canal with presence or absence of the vertical groove on the inner face of the exoccipital which is interpreted above as having housed a vein draining the canal.

The *supraoccipital* is shown in lateral, dorsal and anterior view in figure 50. It is of normal primitive teleostean type, differing from those of *P. germanicus* and the Callovian *Pholidophorus* in having much thinner endochondral walls and in having its anterior margin formed of thin membrane bone, with a median membranous projection extending forwards below the parietals. On the internal surface of the dorsal part of the bone there is a pair of V-shaped depressions, open laterally, which mark the position of the uppermost parts of the anterior and posterior semicircular canals (asc, psc).

(*d*) Pholidophorus bechei

No complete set of acid-prepared occipital ossifications is yet available in this species, but a fairly complete description can be compiled from the mechanically prepared specimens used by

Rayner (1948), especially P.1052, from the two fragmentary acid-prepared specimens (P.51160, P.51683), and from the structure of the well preserved otic region of P.51682. The restorations of the occipital region in posterior, lateral and sagittal view in figures 55, 56 and 65 are based on these specimens. P.51682 shows that the cranial fissure was complete in *P. bechei*, that the posterior surface of the otic region (the anterior wall of the cranial fissure) was completely lined with perichondral bone from the vestibular fontanelle upwards, and that the semicircular canals and their ampullae were entirely contained within the otic ossification. It follows that in this individual the epioccipital and supraoccipital must have been lined anteriorly with perichondral bone, that the epioccipital must have been similar to that of *P. germanicus* (figure 49) and the Callovian *Pholidophorus*, a simple plate of bone having no relation to the posterior semicircular canal, and that the supraoccipital must have lacked the forward endochondral extension present in *P. germanicus* and the Callovian species.

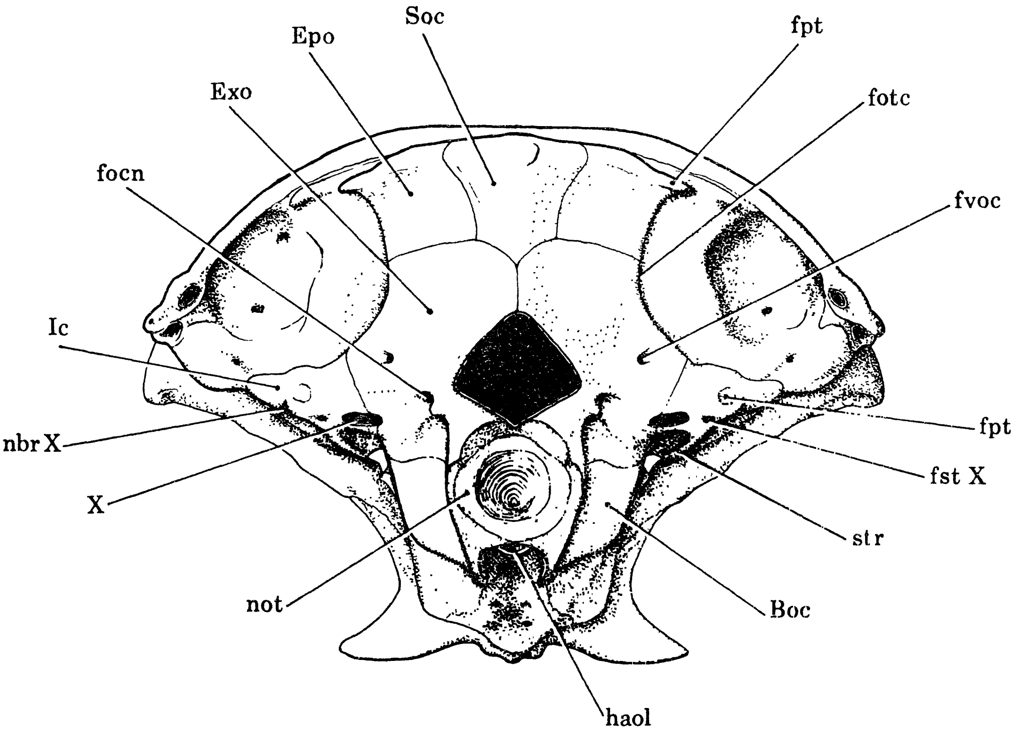


FIGURE 55. *Pholidophorus bechei* Agassiz. Restoration of braincase in posterior view, to show the details and ossification pattern of the occipital region (for the otic region see figure 59). Composite, based on several specimens. (Magn. × 9 approx.)

The *supraoccipital* and *epioccipital* (figures 55–57) are visible only in P.1052, 19010 and SM J4851, in superficial aspect. In 19010 (figure 57*b*) the epi- and supraoccipitals are co-ossified, although there is a trace of a suture between this compound ossification and the exoccipitals below. In P.1052 (figure 57*a*) and SM J4851 (figure 57*c*) there are sutures between the epioccipitals and supraoccipital, and between these bones and the exoccipitals. As figure 57 shows, the dorsal portion of the fissura otico-occipitalis (fotc) is variable in *P. bechei*. In 19010 the fissure ends about midway across the epioccipital on the left side, but on the right side the fissure disappears beneath the parietal and cannot be followed further. In P.1052 conditions are similar except that the suture disappears on the left side, and on both sides the epioccipital/

supraoccipital suture ends anteriorly in an imperfectly ossified area suggesting the remains of a small, paired posterior dorsal fontanelle. In SM J4851 the fissure extends to the medial edge of the epioccipital on the right side, but is hidden beneath the parietal on the left side. In all three specimens the supraoccipital has a median anterior extension passing forwards beneath the parietals, but this is clearly formed of fibrous membrane bone, not of endochondral bone, and is analogous with the anterior membranous outgrowths of the intercalar rather than with the endochondral extension of the supraoccipital present in *P. germanicus* and the Callovian *Pholidophorus*. Beneath this membranous outgrowth, the mid-dorsal part of the fissura otico-occipitalis may have been open and perichondrally lined, as in P.51682, or closed by fusion between the supraoccipital and otic ossifications, as it appears to be in 19010 and P.1052. P.51682 (figures 59, 60) shows that the membranous outgrowth of the supraoccipital fitted in a shallow median depression (rsoc) on the otic ossifications, beneath the parietals.

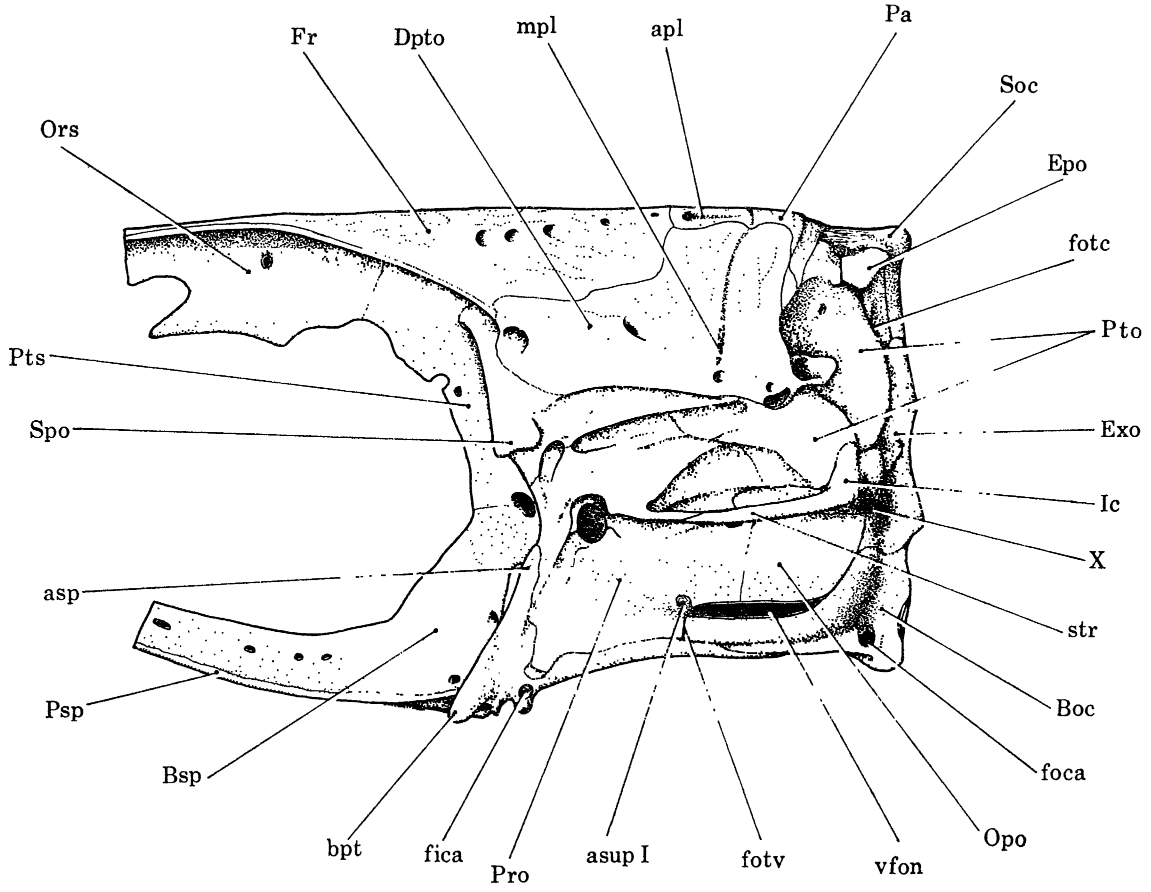


FIGURE 56. *Pholidophorus bechei* Agassiz. Restoration of post-ethmoid parts of neurocranium and attached dermal bones in lateral view. Composite, based on several specimens: the otic and orbitotemporal regions from P.51682 (see figure 61 for details), with the approximate position of sutures added from other specimens. (Magn. × 9 approx.)

The exoccipitals, basioccipital and intercalars are co-ossified in P.1052, while in 19010 and SM J4851 the basi- and exoccipitals are co-ossified but the intercalars are independent, and in P.51160 and P.51683 all three bones are separate. In P.1052 the basioccipital is also fused anteriorly with the otic ossification, the fissura oticalis ventralis having closed during ontogeny.

An isolated *basioccipital* is shown in lateral, posterior, anterior and ventral views in figures 53 and 47. The bone is very similar to the basioccipital region of *P. germanicus*, but the occipital portion of the myodome (myocc, figures 53, 65) is smaller, occupying one-third or less of the length of the bone and having thicker endochondral walls. The dorsal surface of the basioccipital is without perichondral bone and the lateral wall of the otolith chamber (otoc) is very incomplete in comparison with *P. germanicus* and the Callovian *Pholidophorus*; it is slightly more extensive in the fully ossified P.1052. Although Rayner (1948, p. 322) described a short aortic canal in *P. bechei*, in every specimen there appears to have been only a pair of crests, as in *P. germanicus*, which may have carried a short canal formed in cartilage.

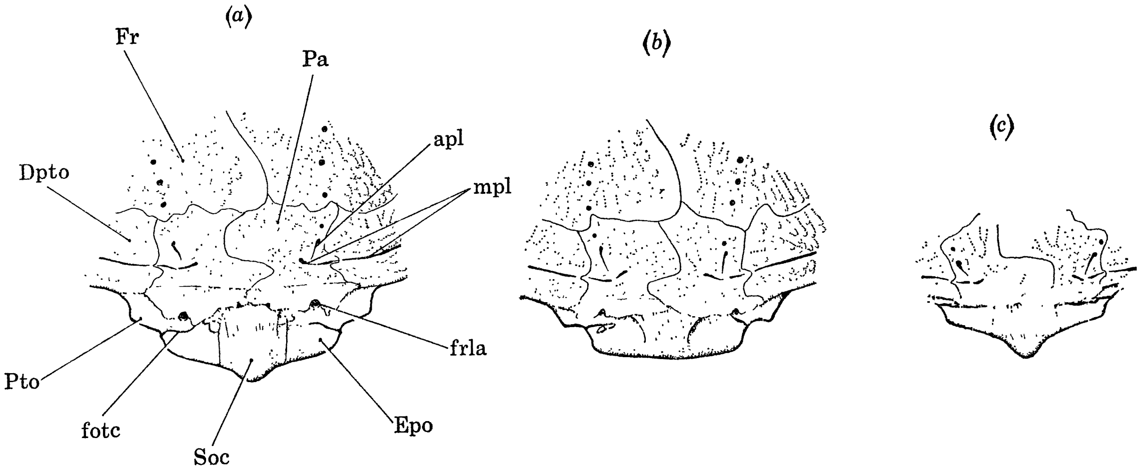


FIGURE 57. *Pholidophorus bechei* Agassiz. Posterior part of skull roof and occipital ossifications in dorsal view of (*a*) P.1052, (*b*) 19010, and (*c*) SM J4851. (*a*), (*b*) magn. × 3 approx.; (*c*) magn. × 4 approx.

The *exoccipital* is known in P.1052, 19010 and SM J4851 (mechanically prepared) and in the incomplete acid prepared specimens, P.51160 and P.51683, on which the restoration shown in posterior, anterior and lateral view in figure 54 is based. It is basically similar to the exoccipital region of the basi-exoccipital in *P. germanicus* (figures 44–46), but has the anterior surface completely covered by perichondral bone and lacks the region antero-ventral to the vagus groove which in *P. germanicus* is occupied by a small, partially independent opisthotic (cf. figures 54*c*, 46). As is shown below (p. 322), there is an opisthotic in *P. bechei*, but here it fuses with the otic region during ontogeny. As in *P. germanicus*, there are two foramina in the inner wall of the foramen magnum, the more posterior (focn, figure 65) transmitting an occipital nerve directly through the bone, the more anterior (fdoc, figure 65) joining an antero-dorsally directed canal which originates in the hind wall of the upper part of the vagus groove (ftpcv, figure 54*b*) and emerges about halfway between the occipital nerve foramen and the dorsolateral margin of the bone (fvoc, figure 54*a*). Between the occipital nerve foramen and the foramen magnum there is a group of projections marking the insertion of the second intermuscular septum. The crest forming the upper margin of the vagus groove and the medial margin of the area occupied by the pterotic is developed as in *P. germanicus*, but the vagus groove itself (gr X) is more ventrally directed than in the latter. In front of the vagus groove the exoccipital forms only the most postero-medial part of the wall of the otolith chamber and its anterior surface is lined with perichondral bone throughout. In the medial wall of the otolith chamber the exoccipital extends forwards and was applied to the upper surface of the basioccipital.

The *intercalar* of *P. bechei* (figures 55, 56) is known only in the mechanically prepared P.1052, 19010 and SM J4951. In P.1052 it is co-ossified with the exoccipital so that its precise limits are not clear, but in 19010 and SM J4851 it is distinct and appears to have only a small endochondral component, if anything smaller than that of *P. germanicus.* The membranous outgrowths of the intercalar are damaged in all three specimens, but the bone seems to differ from that of *P. germanicus* and the Callovian *Pholidophorus* primarily in lacking a dorsal outgrowth, and in this it resembles the Sinemurian *Leptolepis.* Anteriorly the intercalar sends forwards a pair of splints, a very long lateral one (str, figure 56) meeting a similar posterior outgrowth from the prootic and forming a bridge across the subtemporal fossa, and a shorter, laminar medial splint applied to the lateral face of the otic region. The lateral outgrowth of the intercalar enwraps the hind edge of the pterotic region, as in *P. germanicus* and the Callovian *Pholidophorus.* The intercalar forms the antero-lateral margin of the vagus foramen, as in *P. germanicus,* and lateral to the vagus foramen there is a small foramen (fst X, figure 55) and a notch (nbr X, figure 55) in the hind margin of the bone marking the passage of the supratemporal and auricular branches of the vagus.

(*e*) Pholidophoroides limbata

In this species the upper part of the occipital region is visible in the mechanically prepared P.40588 (figures 23, 82). This region is more primitive in *P. limbata* than in any other pholidophorid. The supra- and epioccipitals are co-ossified and the dorsal part of the fissura oticooccipitalis (fotc, figure 82) is uninterrupted and perichondrally lined throughout. There is no mid-dorsal expansion of the fissure (posterior dorsal fontanelle) as there is in palaeoniscoids. The supraoccipital lacks the anterior membranous extension present in *P. bechei,* having only a mid-dorsal hump. But this hump is truncated anteriorly and its upper surface is fibrous in appearance, while in front of it there is a well marked median depression (rsoc) in the otic ossifications, beneath the parietals, as in *P. bechei.* This suggests that in *P. limbata* there was a dense band of connective tissue running from the hump on the supraoccipital into the depression on the roof of the otic region, and that the anterior extension of the supraoccipital in *P. bechei* arose by ossification of such connective tissue.

(*f*) Pholidophorus minor

The occipital ossifications of this species are unknown, but the posterior face of the otic ossification (figure 83) is so like that of *P. bechei* (figure 62) and *Pholidophoroides limbata* (figure 82) that it is probable that the occipital ossifications were also similar, except that the intercalar may not have formed a strut across the subtemporal fossa (see p. 363).

(*g*) Pholidophorus macrocephalus

The occipital ossifications are partially visible, in external view only, in P.3582, P.52518 and P.12070, and are reconstructed in dorsal and ventral view in figures 84 and 145. The bones are crushed in all specimens and the epioccipital and supraoccipital are incompletely exposed, but in general the occipital region seems to be very similar to that of *P. germanicus* and especially to the Callovian *Pholidophorus* sp.

There is a co-ossified basi-exoccipital (Bexo) in all three specimens, but as in *P. germanicus* and the Callovian species there is a partial suture above the foramen magnum, and another running back from the large vestibular fontanelle (vfon). The occipital condyle is filled by a hollow cone of notochordal calcification, and the aortic groove, foramen for the occipital artery (foca) and cup for the aortic ligament (haol) are all as in *P. germanicus* and the Callovian species, except that the walls of the aortic groove are perichondrally lined ventrally, as in the Callovian species, so that no aortic canal could have developed. As in the latter, there are also two exit foramina for the occipital nerve, lying midway between the foramen magnum and the vagus foramen, just lateral to an oblique row of projections marking the insertion of the second intermuscular septum. There is a canal leading upwards from the posterior face of the vagus groove, and a foramen near the upper margin of the posterior face of the exoccipital, so a dorsal occipito-vascular canal was probably developed as in *P. bechei*, *P. germanicus* and the Callovian species. Because of dislocation of the bones on the right side of P.12070, the anterior face of the exoccipital component of the basi-exoccipital is exposed. This is without perichondral bone up to the lower margin of the vagus groove, but above the groove it is lined with perichondral bone as in *P. germanicus* and the Callovian species, indicating persistence of a part of the cranial fissure. The exoccipital forms no part of the cavity for the ampulla of the posterior semicircular canal, and the vagus canal is not enclosed within the basi-exoccipital as it is in the Callovian species. The anterior wall of the vagus canal is probably formed by a small opisthotic (p. 365), but this bone does not fuse with the basi-exoccipital as it does in *P. germanicus*, and it is described with the otic region. The saccular chamber appears to be very like that of *P. germanicus* but the occipital part of the myodome cannot be seen since the parasphenoid is still in position in all three specimens.

The intercalar (Ic) is even larger and more complex than in *P. germanicus* and the Callovian species. It has a small endochondral component, behind the vagus foramen, and in P.12070 a ring of membrane bone forms the external opening of the vagus canal (X). The facet for the post-temporal, bifid anterior outgrowth with the lateral portion forming a strut across the subtemporal fossa, and the foramina for vessels (fvptf) and the supratemporal branch of the vagus (fst X) are as in the Callovian *Pholidophorus*, but the medial portion of the anterior outgrowth is more extensive than in that species, reaching the glossopharyngeal foramen (IX) and containing a notch or foramen for the supratemporal branch of that nerve. The ventral sheet of the lateral outgrowth of the intercalar is less extensive than in the Callovian species, so that the cartilage enclosing the posterior part of the external semicircular canal was partially exposed in life (figure 84). The upper lamina of the lateral outgrowth of the intercalar is particularly large, sweeping dorso-laterally and making contact with the posterior end of the descending lamina of the dermopterotic. The dorsal outgrowth of the intercalar stretches up to contact the epioccipital, as in *P. germanicus* and the Callovian species.

The epioccipital (Epo, figure 145) is only partially visible. It has strong anterior and lateral shelves of membrane bone extending from its dorsal surface, the anterior one suturing with the parietal, the lateral one meeting a similar shelf from the pterotic. But the endochondral part of the pterotic extends back below the membranous outgrowth of the epioccipital, and the endochondral portion of the latter appears to be small, as in *P. germanicus* and the Callovian species, so the dorso-lateral section of the cranial fissure was evidently persistent, though it is not perichondrally lined where its surfaces are visible in P.3582.

All that can be seen of the supraoccipital is its dorsal surface (Soc, figure 145). The supraoccipital crest is larger than in other pholidophorids. At its base there is a pair of flat facets which articulated with the post-temporal, and between them a median groove runs back along the supraoccipital crest, passing through a canal in its tip in P.12070. This groove must have transmitted branches of the vagus or ramus lateralis accessorius nerves (more probably the latter) to the skin in the mid-line in front of the dorsal fin. Anteriorly, the dorsal surface of the supraoccipital bears membrane bone outgrowths which suture with the parietals.

(*h*) Leptolepis coryphaenoides

The occipital region of this species has been figured and described by Rayner (1937), and Wenz (1968) has commented further on the epioccipital and supraoccipital. The occipital bones are shown in ventral view in figure 89 and in sagittal view in figure 90, and the epioccipital and supraoccipital are shown in ventral view in figure 58.

It has already been found that the dermal bones of the skull and the caudal skeleton are very variable in *L. coryphaenoides* (Wenz 1968; Patterson 1968; it is assumed here that Wenz is correct in her opinion that *L. normandica* Nybelin is merely part of the range of variation of *L. coryphaenoides*). The braincase is similarly variable, but most of the differences encountered seem to be reflections of inconsistency in the degree of ossification. Rayner remarked that in most braincases 'the thoroughness of the ossification has obscured the sutures', and this is true of most intact examples, including the acid-prepared specimen restored in figures 89 and 90: apart from the intercalar, which is always surrounded by a suture, the orbitotemporal, otic and occipital regions are occupied by a single ossification, without traces of sutures or radiation, and the cranial fissure has been completely closed. Amongst the bone-bed material of *L. coryphaenoides*, the individual bones are always distinct except for occasional co-ossification of the basi- and exoccipitals, as in the Sinemurian *Leptolepis* and pholidophorids. Apart from these fusions between the bones, the occipital ossifications of *L. coryphaenoides* are closely comparable with those of the Callovian *Leptolepis*, but exhibit a few primitive features reminiscent of the Sinemurian species.

In the basioccipital, the short aortic canal described by Rayner is only present exceptionally (P.7038*c*) and is extremely delicate, with much thinner walls than in the Sinemurian species (figures 51, 52). Other individuals show only a pair of crests alongside the cup for the aortic ligament (haol, figure 89), with either a notch or a foramen for the occipital artery, while in some specimens, including that shown in figures 89 and 90, these crests are so small that they are not even notched by the artery, as in the Callovian *Leptolepis*. Where an aortic canal is present, the two efferent arterial foramina described by Rayner do not appear to exist. As in the Callovian *Leptolepis*, the cup housing the aortic ligament is large, close to the hind end of the bone, delicate and not occluded with endochondral bone. The floor of the occipital division of the myodome may be ossified for a short distance in front of the cup for the ligament, or may be completely unossified (figure 89) as in the Callovian *Leptolepis*. The cone of laminar bone filling the occipital condyle is generally intermediate between the Sinemurian and the Callovian species in thickness and depth. No remnant of notochordal calcification has been seen.

The exoccipital shows a somewhat more primitive condition than that of the Callovian *Leptolepis* since it does not extend forwards far enough to enclose the glossopharyngeal foramen, which always lies in the prootic (IX, figure 86). The small foramen in front of the vagus (fst IX, figures 89, 90) which Rayner described as the glossopharyngeal must have transmitted the supratemporal branch of the glossopharyngeal, as in the Callovian species (figure 54). The single occipital nerve pierced or notched the wall of the foramen magnum (focn, figure 90), as in the Callovian species, and there is a deep cavum sinus imparis between the exoccipitals in the floor of the foramen magnum (csim, figure 90).

The intercalar (Ic, figure 89) has no endochondral component and is entirely superficial, overlying the junction of the exoccipital and pterotic, as in the Callovian species. The anterior process of the intercalar (which was not illustrated by Rayner) is undivided, so that there is no strut across the subtemporal fossa, and in this and in its width lateral to the vagus foramen the intercalar is more like that of the Sinemurian *Leptolepis* than the Callovian species (cf. figures 89, 48).

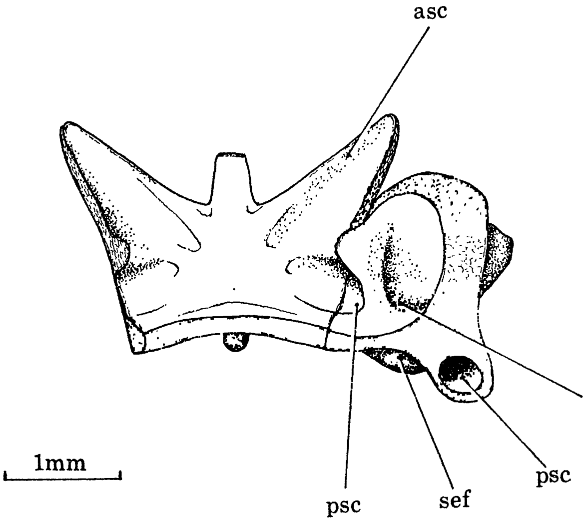


FIGURE 58. *Leptolepis coryphaenoides* (Bronn). Supraoccipital and left epioccipital in ventral view, from P.51708.

The epioccipital (Epo; figure 58) rarely extends so far ventrally as in Rayner's reconstruction (1937, fig. 8), but this is a more consistent picture than Wenz's drawing (1968, fig. 79*b*), which must be from an excessively lightly ossified specimen in which only the uppermost part of the posterior semicircular canal was bone-enclosed. The epioccipital is similar in shape to those of the Sinemurian and Callovian species (figure 49), but resembles the former in having a fairly extensive depression, not in contact with the roofing bones, on the anterior part of its dorsal surface, and in having the lateral process in the roof of the post-temporal fossa formed in finished bone, so that it is shorter than in the Callovian species and does not reach the anterior margin of the bone. The depression on the dorsal surface of the epioccipital is the remains of the shallow, postero-medial division of the fossa bridgei in pholidophorids and underlies the middle pit-line, but as in the Sinemurian species no foramen for the supratemporal branch of the glossopharyngeal nerve is visible in its floor. Wenz has described the depression in the lateral surface of the epioccipital, behind the process in the roof of the post-temporal fossa, as the pre-epiotic fossa, comparing it with Ridewood's descriptions of clupeoids, but the clupeoid pre-epiotic fossa lies at the junction of the epioccipital, pterotic and parietal, in quite a different position. In most specimens there is a small foramen in the epioccipital in the upper part of the medial wall of the post-temporal fossa, perhaps homologous with the foramen for a branch of the supratemporal nerve in the pterotic of pholidophorids (fst IX, figures 61, 74), but it is variable in position and not always present. On the posterior face of the epioccipital there is a well marked sub-epiotic fossa (sef, figure 58), as in the Callovian species. On the cranial surface of the epioccipital there is always a deep excavation, the lateral cranial canal (lcc, figure 58). As in those individuals of the Callovian *Leptolepis* which retain this structure, it does not extend lateral to the tube for the posterior semicircular canal (psc, figure 58) as it does in the Sinemurian species. In fully ossified braincases (figure 90) there may be a bony strut separating the anterior (alcc) and posterior (plcc) openings of the lateral cranial canal: the upper part of this strut must ossify from the epioccipital, but it is not developed in any of the isolated examples of the bone.

The supraoccipital (Soc; figure 58) resembles that of the Callovian species, consisting of rather thin endochondral bone and bearing traces of the anterior and posterior semicircular canals on its internal surface (asc, psc, figure 58). However, the replacement of cartilage bone by membrane bone is less complete than in the Callovian species and the median anterior process of the bone is still endochondral. In some specimens (figure 58) a pair of antero-lateral wings of the supraoccipital ossified perichondrally around the upper surface of the anterior semicircular canal.

(*j*) Leptolepis dubia

The occipital ossifications of this species are restored in ventral view in figure 92. In the large, complete braincases the basi- and exoccipitals appear to be co-ossified, but in the small specimens from the stomach contents of *Pholidophorus macrocephalus* they are separate. Otherwise there is the normal complement of separate bones.

The hollow cone of dense laminar bone filling the occipital condyle is very thin, and occupied only about one-quarter of the length of the basioccipital (Boc, figure 92). There is a narrow ring of whitish tissue lining the inner surface of the rim of the cone, and this is probably a remnant of calcified notochordal tissue.

The cup-like housing for the aortic ligament (haol) lies at the extreme posterior end of the ventral face of the basioccipital, directly below the occipital condyle, and there is no trace of an aortic groove. The basioccipital portion of the myodome has no floor, and opens posteriorly (pmyo) between the divergent hind ends of the parasphenoid.

The exoccipital (Exo) resembles that of the Callovian *Leptolepis*, extending forwards to enclose the glossopharyngeal foramen and the ventral part of the posterior semicircular canal and its ampulla, and forming the roof of the posterior part of the subtemporal fossa (stf). But in the larger specimens the exoccipital is more completely ossified than in the Callovian species so that it also envelops the posterior part of the external semicircular canal and forms the floor of the posterior part of the post-temporal fossa. As in *L. coryphaenoides* and the Callovian species, there is a separate foramen (fst IX) for the supratemporal branch of the glossopharyngeal just in front of the vagus foramen. The single occipital nerve notched the lateral border of the foramen magnum. There is a groove running dorsally from the vagus foramen on the inner face of the bone, but this groove is narrower than in the Callovian species.

The intercalar is a superficial membrane bone, as in *L. coryphaenoides* and the Callovian species. The intercalar (Ic, figure 92) borders the vagus foramen and the supratemporal branch of the glossopharyngeal must have passed internal to this part of the bone. The extreme postero-lateral corner of the bone, lateral to the facet for the post-temporal, is perforated in large individuals by a small foramen for the supratemporal branch of the vagus (fst X). The anterior part of the intercalar is bifid, as in the Callovian *Leptolepis*, but the medial strut is much shorter than the lateral strut, which forms a massive bridge across the subtemporal fossa. The medial strut does not extend as far forwards as the glossopharyngeal foramen, and altogether the intercalar appears very similar to that of *Elops*.

The epioccipital is similar to that of the Callovian *Leptolepis*, but extends further ventrally so that it surrounds the upper part of the ampullary chamber of the posterior semicircular canal. The depression on the inner face of the epioccipital, which when well developed is the homologue of the lateral cranial canal of pholidophorids, is variable, as in the Callovian species. Among five available epioccipitals, three have only a shallow cup on the inner surface, as in some Callovian specimens, one has a larger, hemispherical depression, and one has a fairly deep excavation.

The supraoccipital is very like that of the Callovian *Leptolepis*, but the thumb-like supraoccipital crest is longer.

(*k*) *Occipital region: summary and discussion*

(i) *Summary of conditions in pholidophorids and leptolepids*

Facts relating to the cranial fissure, its closure, and the consequent framing by the occipital bones of structures which are found in the otic ossifications of primitive pholidophorids, are summarized and discussed in § 6, after the description of the otic region, and the occipital region of the myodome is summarized and discussed in § 9, after the description of the parasphenoid. Other points in the structure of the pholidophorid and leptolepid occipital region are as follows.

(1) In some individuals of *Pholidophorus bechei* and *Leptolepis coryphaenoides* the occipital bones may fuse completely, so that the region is occupied by a single ossification, with no visible radiation centres or sutures except those around the intercalar in *L. coryphaenoides* and its membranous outgrowths in *P. bechei*. In *P. bechei* the fissura oticalis ventralis may also be closed by bone, so that the occipital and otic ossifications are fused ventrally. In *L. coryphaenoides*, where the cranial fissure is obliterated, the occipital and otic ossifications may fuse throughout. In other species, a median supraoccipital and paired epioccipitals and intercalars are usually distinct. In pholidophorids the basi- and exoccipitals co-ossify, but residual sutures show that this basi-exoccipital ossified from three centres. In the Sinemurian *Leptolepis* the basi- and exoccipitals also co-ossify, but in other leptolepids the basi- and exoccipitals are usually distinct.

(2) Despite these various fusions or co-ossifications, all pholidophorids and leptolepids evidently ossified the occipital region from eight centres: median supra- and basioccipital, paired epioccipitals, intercalars and exoccipitals. The only addition to this pattern is the small opisthotic in *P. germanicus*, an otic bone which fuses with the basi-exoccipital during ontogeny.

(3) The supraoccipital ossified from the centre of the upper margin of the occipital arch. It is primitively a vertical plate of cartilage bone, separated from the otic region by the cranial fissure, which does not expand in pholidophorids into a median posterior dorsal fontanelle. This primitive type of supraoccipital is found in *Pholidophoroides limbata* and probably also in *Pholidophorus minor*. In *P. bechei* the supraoccipital develops membrane bone outgrowths overlapping the otic region in the mid-line, and in some individuals it may fuse with the otic ossifications, closing the mid-dorsal part of the cranial fissure. In other pholidophorids and in all leptolepids the supraoccipital extends forwards in cartilage bone, as it does in teleosts. The supraoccipital crest is small and confined to the posterior face of the bone in all pholidophorids and leptolepids.

(4) The epioccipital (= 'epiotic', see p. 425) ossifies from the dorso-lateral corner of the occipital arch, where the ligament to the upper limb of the post-temporal originates. Like the

supraoccipital, the pholidophorid epioccipital is primitively a vertical plate of cartilage bone, separated from the otic region by the cranial fissure, and an epioccipital of this type is found in all pholidophorids, although in the more advanced forms the bone develops considerable outgrowths of membrane bone overlapping the pterotic, and in *P. macrocephalus* the anterior face of the epioccipital is not perichondrally lined. In leptolepids the epioccipital encloses the upper part of the posterior semicircular canal and resembles the 'epiotic' of teleosts. A shallow subepiotic fossa develops on the posterior face of the epioccipital in leptolepids.

(5) The pholidophorid intercalar is an endochondral ossification developing in a lateral process of the occipital arch immediately postero-dorsal to the vagus foramen: this process is the homologue of the cranio-spinal process of chondrosteans and receives the ligament from the ventral limb of the post-temporal. From this endochondral core, extensive outgrowths of membrane bone develop, covering the adjacent otic bones and the lower part of the fissura otico-occipitalis. In the Sinemurian *Leptolepis* the intercalar still has a small endochondral component, but in later leptolepids this is lost and the intercalar becomes a superficial membrane bone, as it is in all living teleosts. Loss of the endochondral portion of the intercalar and its consequent superficial position, overlying the junction of the pterotic and exoccipital, appear to be due to the anterior and lateral extension of the exoccipital which follows closure of this portion of the cranial fissure (p. 420).

(6) The membrane bone outgrowths of the intercalar are best developed in *P. germanicus*, the Callovian *Pholidophorus* and *P. macrocephalus*. There is a dorsal outgrowth, sheathing the medial side of the opening of the post-temporal fossa, a lateral outgrowth, sheathing the horizontal buttress below the post-temporal fossa, and an anterior outgrowth extending forwards between the subtemporal fossa and the jugular groove. The membrane bone portions of the intercalar may completely surround the vagus foramen in pholidophorids, and in *P. macrocephalus* the lateral outgrowth of the bone contacts the descending lamina of the dermopterotic. In *P. bechei* the dorsal outgrowth is lacking, as it is in leptolepids, and in leptolepids the lateral outgrowth is also much smaller. The anterior outgrowth is bifid in all pholidophorids and in the Callovian *Leptolepis* and *L. dubia*, the lateral portion meeting a strut from the prootic and forming a bridge across the subtemporal fossa. The levator muscles of the branchial arches must have taken their origin on this bridge, as they do in *Elops*. In the Sinemurian *Leptolepis* and *L. coryphaenoides* the anterior outgrowth of the intercalar is broad and undivided, forming a ledge projecting horizontally above the jugular groove. Postero-lateral to the vagus foramen, the intercalar is usually perforated or notched by the supratemporal branch of the vagus and a dorsal (auricular) branch of the lateral line nerve.

(7) In pholidophorids the lateral outgrowth of the intercalar enwraps that portion of the otic region containing the external semicircular canal, and in *P. germanicus*, the Callovian *Pholidophorus* and *P. macrocephalus* this part of the otic region was incompletely ossified, so that in the fossil skulls the intercalar has a groove on its inner face which lines the cavity for the canal. This shows that a groove for a semicircular canal on a part of the intercalar is not necessarily evidence that the bone is a primary component of the cranial wall, as Beltan (1957) and Schaeffer (1971, p. 23) have suggested it is in *Caturus*.

(8) The exoccipital ossifies from a centre lateral to the floor of the foramen magnum, growing round the latter, forming part of the occipital condyle below it, and surrounding the postero-dorsal portion of the otolith chamber. In some pholidophorids (*P. bechei*, *P. germanicus*, *P. macrocephalus*) the exoccipital is limited anteriorly by the cranial fissure, meeting the pterotic

above the vagus canal and the opisthotic below it; in the Callovian *Pholidophorus* and the Sinemurian *Leptolepis* the exoccipital extends forwards below the vagus canal, occupying the territory of the opisthotic, and in other leptolepids the cranial fissure has been completely obliterated and the exoccipital resembles those of teleosts, containing the vagus canal, the posterior ampullary chamber and, in advanced leptolepids, the glossopharyngeal foramen. These changes are discussed in detail in § 6*a*.

(9) The basioccipital ossifies around the tip of the notochord and comes to form the bulk of the occipital condyle, and to enclose the notochord pit, the postero-ventral part of the otolith chamber, and the occipital part of the myodome. Extension of the myodome (discussed in detail in § 9) into the basioccipital is an exclusively teleostean specialization. The anterior face of the basioccipital always lacks perichondral lining, and the cartilage between this surface and the otic ossifications is the homologue of the fissura oticalis ventralis of palaeoniscoids (§ 6*a*).

(10) The notochordal pit is filled by a hollow cone of calcified notochordal tissue in pholidophorids. In leptolepids the bulk of this tissue is replaced by dense, acellular bone ('osteoid tissue'), but a thin layer of notochordal calcification often remains lining the notochordal pit, especially around the rim of the cavity. The notochordal pit ends directly behind the myodome. In *P. bechei* the notochord occupied about two-thirds of the length of the basioccipital, the myodome about one-third. In the Callovian *Leptolepis* these proportions are reversed, while in *L. dubia* the notochord only occupies about a quarter of the length of the basioccipital, having retreated as the myodome increases in size. Intermediate conditions between these extremes are found in later pholidophorids and earlier leptolepids.

(11) A closed aortic canal has been found only in the Sinemurian *Leptolepis* and in a few individuals of *L. coryphaenoides*. In Lower Jurassic pholidophorids the crests forming the walls of the aortic groove are without perichondral bone ventrally, and a short canal could have ossified late in life. The only foramen in the wall of the aortic canal or groove is that for the occipital artery. In some individuals of *L. coryphaenoides*, in the Callovian *Leptolepis* and in *L. dubia* the wall of the aortic groove is reduced and this artery no longer perforated it.

(12) In the roof of the aortic groove, immediately in front of the point at which the aorta bifurcated, there is a median, cup-like housing for the anterior end of the aortic ligament (which develops in the hypochordal rod) in all pholidophorids and leptolepids. In pholidophorids this structure is moderately large, lies close in front of the foramen of the occipital artery, is often partially occluded by spicules of bone, and sometimes appears to be an independent structure, fused with the basioccipital. In the Sinemurian *Leptolepis* the structure is smaller, placed farther forwards, and similarly occluded. In later leptolepids it increases in size, is never occluded, and appears to migrate backwards, until in *L. dubia* it is very large and placed below the occipital condyle.

(13) The floor of the occipital division of the myodome contains a small, elongate median fenestra in pholidophorids and in the Sinemurian *Leptolepis*. In later leptolepids this fenestra increases in size until the myodome has no endocranial floor at all, and is closed ventrally only by the parasphenoid. This reduction in the floor of the myodome is probably responsible for the backward migration of the housing of the aortic ligament (§ 9).

(14) The cavum sinus imparis, a depression in the floor of the foramen magnum which penetrates down into the basioccipital and in living teleosts contains a vascular plexus, is not recognizable in pholidophorids but is present in leptolepids. There is a similar depression in the floor of the foramen magnum in the palaeoniscoid *Pteronisculus* (Nielsen 1942, fig. 5).

(15) There is no evidence in pholidophorids and leptolepids of more than one occipital nerve. In pholidophorids the exit foramen of this nerve is sometimes double, and in advanced leptolepids the nerve may only notch the border of the foramen magnum. In pholidophorids a dorso-laterally directed canal originates in front of the occipital nerve canal, receives a posteriorly directed canal from the dorsal part of the vagus canal (which carried the posterior cerebral vein), and opens on the dorso-lateral surface of the exoccipital. In the Sinemurian *Leptolepis* the opening in the hind wall of the vagus canal is present, but it must open into the occipital nerve canal.

(ii) *Comparison of pholidophorids and leptolepids with other groups*

The ossification pattern of the occipital region is compared with that of other groups in §6*b*, and only a few anatomical points are considered here.

1. *Intercalar.* The bifid anterior outgrowth of the intercalar in pholidophorids, the Callovian *Leptolepis* and *L. dubia*, with the lateral strut meeting a strut from the prootic to form a bridge across the subtemporal fossa, is a unique specialization linking pholidophorids and leptolepids with primitive teleosts. The distribution and function of this bridge are discussed in §5*k* (ii), with the subtemporal fossa.

2. *Notochord pit and occipital condyle.* In pholidophorids the deep notochordal pit in the basioccipital is partially occluded by a hollow cone of thick notochordal calcification. In leptolepids this tissue is replaced by perichordal osteoid tissue, thinner and more regular in texture, although a thin layer of chordal tissue may remain around the rim of the cavity. As will be shown in the third paper in this series, this change from notochordal tissue to perichordal tissue in the notochord pit is coincident with a change in the composition of the vertebral centra. Viewed as a phylogenetic sequence, the change in the tissue lining the notochordal pit in pholidophorids and leptolepids mirrors the change in the composition of the vertebral centra during early ontogeny of primitive living teleosts (*Salmo, Clupea, Esox*; François 1967), where the centrum first calcifies as a delicate chordacentrum which regresses later after it becomes surrounded by a perichordal, osteoid autocentrum. This sequence of development is unique to teleosts and relates them to pholidophorids and leptolepids.

The very thick notochordal calcification lining the notochordal pit in pholidophorids is unique to that group. The only other fish in which a cone of notochordal calcification has been described in the occipital condyle is the pholidopleurid *Australosomus* (Nielsen 1949, fig. 1) and here the tissue is thin. This is probably found in all pholidopleurids, since chordacentra are characteristic of that group. I have also observed such a lining in GSM 97417, the specimen of *Caturus chirotes* described by Gardiner (1960), in which the occipital condyle is lined by a very thin sheet of dense tissue which might be chordal in origin.

A close association between the tip of the notochordal pit and the hind end of the myodome is characteristic of pholidophorids and leptolepids. Such an association is evidently a primitive actinopterygian character, since in palaeoniscoids the long notochordal space is only separated from the myodome (*Pteronisculus*, Kansas palaeoniscid A) or its fore-runner, the space containing the pituitary vein (*Kentuckia*, the Gogo palaeoniscoids) by a thin sheet of bone (Nielsen 1942, fig. 9; Rayner 1951, figs. 9, 10; Gardiner 1973, fig. 4). In all actinopterygian groups the notochordal space becomes occluded in the ossified braincase of the more advanced members, and only in teleosts, where the myodome extends back into the occipital region, does the approximation between the tip of the notochordal space and the myodome persist.

The occipital condyle of pholidophorids and leptolepids is formed by the plug of notochordal (pholidophorids) or perichordal osteoid tissue lining the notochordal pit, with a dorsal contribution from a pair of cartilage-faced exoccipital condyles. The extent to which the exoccipital facets contribute to the condyle seems to depend only on the degree of development of the notochordal or osteoid plug: in fully ossified individuals the plug covers the exoccipital facets almost completely. In leptolepids, where the sutures between the basi- and exoccipitals usually persist in the adult, removal of this osteoid plug would expose a tripartite occipital condyle such as is found in *Salmo*, *Megalops*, *Hiodon*, *Heterotis*, *Denticeps* and many scopelomorphs, paracanthopterygians and acanthopterygians (Greenwood 1968, p. 233; Rosen & Patterson 1969, figs. 10, 61). Greenwood (1968, p. 233) assumed that this tripartite occipital condyle is primitive for teleosts, and, following Ridewood (1904*a*), that those teleosts with the occipital condyle formed only by the basioccipital have incorporated a 'half-centrum' into the braincase. I have mentioned that pholidophorids and leptolepids do not support this hypothesis (Patterson 1970*a*, p. 179), but could not present any cogent alternative. It now appears to me that the primitive teleost occipital condyle is lined, as in pholidophorids, leptolepids and many living forms, by a cone of notochordal (pholidophorids) or perichordal tissue which develops around the notochord in the same way as the first formed part of the vertebral centra, and subsequently fuses with the braincase. Where sutures between the basi- and exoccipitals persist in the adult braincase, as in living teleosts, this cone of osteoid tissue fuses with the basioccipital, not the exoccipitals, and in full-grown individuals it may extend upwards to cover the exoccipital condyles, giving the impression, especially in lateral view, that a centrum or part centrum is fused with the basioccipital, as in many of the primitive teleostean braincases illustrated by Ridewood (1904*a*,*b*,*c*, 1905: *Elops*, *Albula*, *Mormyrops*, *Osteoglossum*, *Chatoessus*, *Dussumieria*, *Engraulis*, *Chanos*) and the Cretaceous clupeomorph *Spratticeps* (Patterson 1970*a*, fig. 2). In all these fishes, as in pholidophorids and leptolepids, the surface of the occipital condyle does not differ essentially from that of a centrum, consisting of a cone of osteoid tissue. In those teleosts with a tripartite occipital condyle this cone of osteoid tissue is reduced or absent both on the occipital condyle and on the anterior face of the first vertebra, which is modified to fit the occipital condyle closely. This condition, which results in decreased mobility of the occipital joint, is a specialization relative to the simple, intervertebral-like occipital joint of pholidophorids, leptolepids, *Elops*, *Albula*, etc.

In summary, there is no evidence that primitive teleosts have incorporated a centrum or 'half-centrum' into the braincase. The only centrum-like tissue incorporated is the zone of perichordal osteoid tissue which lines the notochordal pit. In this, teleosts are more primitive than other living actinopterygians, all of which have incorporated one or more centra into the braincase (*Polypterus*, 1; *Acipenser* up to 8; *Lepisosteus*, 3; *Amia*, 2).

3. *Occipital nerves.* The single occipital nerve canal of pholidophorids and leptolepids is presumed to be homologous with the single canal of palaeoniscoids, *Australosomus* and parasemionotids, and this probably represents the primitive actinopterygian condition. If it is assumed that this canal carried a single occipital nerve, represented by a ventral root only, I do not think that it is justifiable to homologize that nerve with any one of those known in living fishes. Allis's (1898*b*) objections to Fürbringer's scheme of occipital nerves in actinopterygians seem never to have been answered, and too little is known of variations of the occipital nerves in primitive teleosts. In *Salmo*, for example, the single occipital nerve canal in the exoccipital transmits three ventral roots (Daget 1964, p. 253), while in *Scomber* the exoccipital may contain

five occipital nerve canals transmitting three occipital nerves, the first with a ventral root only (Allis 1903, p. 292), but there is no evidence that the exoccipital of *Scomber* differs in composition from that of *Salmo*.

Among fossil actinopterygians, a single occipital nerve canal, as in pholidophorids and leptolepids, is also found in palaeoniscoids, *Australosomus* and parasemionotids. A second occipital nerve, with separate dorsal and ventral roots, sometimes notches the border of the foramen magnum (parasemionotids, figure 97; *Perleidus*, figure 115) and may become enclosed within the bone only by increased ossification, as in *Heterolepidotus* (figure 102) and Stensiö's specimen of *Perleidus stoschiensis* (1932, fig. 59). Most other non-teleostean actinoptergygians have incorporated neural arches and spino-occipital nerve canals in the braincase and so are more specialized than pholidophorids and leptolepids (*Saurichthys*, living chondrosteans and holosteans, semionotids (figures 108, 110, 113)).

In pholidophorids there is a dorso-laterally directed canal originating in the cranial cavity immediately in front of the occipital nerve canal and opening on the dorso-lateral part of the posterior surface of the exoccipital. A similar canal (fvoc) is present in parasemionotids (figure 97), *Caturus chirotes* (GSM 97417), '*Aspidorhynchus*' (figure 100) and *Heterolepidotus* (figure 104). The only living fish in which I have found such a canal is the osteoglossid *Scleropages*, where in the skull figured by Ridewood (1905; BM(NH) 1905.3.20.6) there is a canal leading dorso-laterally from the internal opening of the foremost occipital nerve canal, and opening near the dorso-lateral margin of the exoccipital. Dissection of a small individual of *Scleropages* has failed to disclose such a canal, but shows that in this region a dorsal branch of the vagus nerve passes over the surface of the exoccipital accompanied by a large tributary of the posterior cerebral vein from the skull roof and anterior trunk musculature. I assume that where the dorso-laterally directed canal occurs in *Scleropages* it carried this vein, and its function may have been the same in pholidophorids, parasemionotids and caturids.

In pholidophorids and the Sinemurian *Leptolepis* a narrow canal originates in the upper, vascular part of the vagus canal and passes back into the dorso-laterally directed canal discussed above (pholidophorids) or into the occipital nerve canal (Sinemurian *Leptolepis*). This also presumably carried a tributary of the posterior cerebral vein. I have not observed such a canal elsewhere. In *Pteronisculus* a similar canal (Nielsen 1942, p. 38) leads from the vagus canal into the cranial cavity in front of the internal opening of the occipital nerve canal. As pointed out above (p. 294) this canal was also probably vascular, and not nervous as Bjerring (1971, fig. 6) supposes.

4. *Aortic canal and ligament.* Among pholidophorids and leptolepids, a closed aortic canal has only been found in the Sinemurian *Leptolepis* and a few individuals of *L. coryphaenoides*. But in *Pholidophorus bechei* and *P. germanicus* the walls of the aortic groove are without perichondral lining so that a canal might have formed in cartilage and ossified late in life. It is worth emphasizing that closure of the aortic canal in bone may only be an ontogenetic feature: the lightly ossified parasemionotid from East Greenland shown in figures 97 and 98 lacks an aortic canal, whereas fully ossified individuals of *Broughia* (Stensiö 1932) have a closed canal.

The only living fish with an aortic canal is *Polypterus*. Here the canal is long and bifurcates anteriorly, the lateral dorsal aortae arising within the canal. Allis (1922, p. 207) described a blind canal in the basi-exoccipital in the position of the external opening of the occipital artery canal of pholidophorids and *Amia*, but could find no artery in this position in his 75 mm specimen. Possibly the occipital artery atrophies early in ontogeny in *Polypterus*. In palaeoniscoids the aortic canal is frequently long and bifurcates anteriorly, as in *Polypterus*, but there is also often a median or paired opening in the floor of the canal through which the second efferent arteries joined the aorta. There is always a dorso-laterally directed canal for the occipital artery, as in pholidophorids, which is sometimes double. *Perleidus* (figures 115, 116) shows essentially the palaeoniscoid condition except that the aortic canal is somewhat shorter and there is no aperture for efferent arteries. In all these forms with an aortic canal which bifurcates anteriorly, the aortic ligament, if present, must have originated on the pillar which divides the canal (subaortic process of Allis in *Polypterus*).

In *Australosomus* the aortic canal is short, as in the Sinemurian *Leptolepis*, and has the usual paired, dorso-laterally directed canal for the occipital artery. In front of the canal, at the point where the aorta bifurcates, there is a well marked median process (Nielsen 1949, figs. 5, 6) which must mark the origin of the aortic ligament.

Among the parasemionotids, Stensiö (1932, p. 270) described a short aortic canal in *Broughia*, but Lehman (1952) found only an aortic groove in *Watsonulus* and *Parasemionotus*, with a dorso-laterally directed canal for the occipital artery which may be double. The Greenland parasemionotid illustrated here (figures 97, 98) has a short aortic groove which contains a cup-like recess (haol), partially occluded by spicules of bone, which is clearly homologous with the housing of the aortic ligament in pholidophorids and leptolepids, although it lies behind the openings of the paired canals for the occipital artery (foca), not in front of them as it does in pholidophorids and leptolepids. Beltan (1968) has described and illustrated a long aortic canal of palaeoniscoid type in the parasemionotids *Thomasinotus* and *Lehmanotus*. The parasphenoid is unknown in these two forms, but it is unlikely that a long parasphenoid of parasemionotid type could coexist with such an aortic canal. If *Thomasinotus* and *Lehmanotus* are really parasemionotids, it is more likely that the aortic canal has been misinterpreted, its supposed posterior opening being the cavity housing the aortic ligament. In *Broughia* the short aortic canal restored by Beltan (1968, fig. 24) seems far too narrow to be a true aortic canal, and in the specimen (pl. 28B) there appears to be a foramen for the occipital artery just in front of the supposed aortic canal, suggesting that the latter is the housing of the aortic ligament, as in the Greenland specimen illustrated in figure 98.

In the semionotid *Dapedium* there is a short endoskeletal aortic canal (Frost 1913, fig. 1; figure 113, cao) which is covered laterally and continued forwards by paired posterior processes of the parasphenoid. In the roof of the aortic canal there is a small, conical housing for the aortic ligament (P.11177) which lies behind the internal opening of the canal for the occipital artery, as in parasemionotids. In *Lepidotes* (figure 109) there is an aortic groove formed by paired posterior processes of the parasphenoid resembling those in *Dapedium*, and immediately behind the opening of the canal for the occipital artery (foca) there is a median area on the basioccipital without perichondral lining (aol, figure 109) which probably marks the origin of the aortic ligament.

In *Pachycormus* (figures 106, 107) there is an aortic groove formed by the basioccipital posteriorly and the parasphenoid anteriorly. Near the posterior margin of the roof of this groove there is a conical housing for the aortic ligament (32443). This lies just in front of the canal for the occipital artery, as in pholidophorids and leptolepids.

In caturids there is no aortic groove or canal, but the canal for the occipital artery is always present (foca, figures 99, 103). Behind the lower opening of the canal and at the extreme posterior end of the basioccipital there may be a cup-like structure filled with endochondral bone (*Caturus chirotes*, '*Aspidorhynchus*') or an area without perichondral lining (*Caturus furcatus*, *Heterolepidotus*, figures 103, 104) marking the origin of the ligament.

In *Amia* and *Lepisosteus* the canal for the occipital artery still penetrates the basioccipital, but the aortic ligament is reduced. In living teleosts the occipital artery never passes through the basioccipital, but in some forms (*Elops* and *Albula*, for example) there is an area without perichondral lining at the extreme posterior end of the underside of the basioccipital, between the divergent hind ends of the parasphenoid. In *Elops* this marks the origin of the aortic ligament. In other primitive teleosts (*Salmo* and *Argentina*, for example) the aortic ligament originates in a pit in the roof of the posterior opening of the myodome.

In summary, during actinopterygian evolution the point at which the dorsal aorta bifurcates and the aortic ligament originates on the braincase has migrated backwards, presumably in connexion with enlargement of the circulus cephalicus (Ridewood 1899). In some forms (semionotids, parasemionotids, caturids) the origin of the ligament comes to lie behind the foramen of the occipital artery. In *Pachycormus*, pholidophorids and primitive leptolepids the ligament still originated in front of the occipital artery foramen, but in advanced leptolepids and teleosts the artery no longer passes through the basioccipital and the ligament originates at the extreme posterior end of the basioccipital. In living holosteans the ligament is reduced. The development of a cup-like housing for the aortic ligament is confined to the 'holostean' grade (parasemionotids, some caturids, semionotids, *Pachycormus*, pholidophorids and leptolepids).

5. Otic and orbitotemporal regions

These regions will be described in detail in *P. bechei*, *P. germanicus* and the Callovian *Leptolepis*, with the inclusion of the Callovian *Pholidophorus* as a supplement to *P. germanicus*. The other species will be compared with these three.

(*a*) Pholidophorus bechei

The description which follows is based mainly on P.51682 (figures 1–5, plate 8), restored in lateral, ventral, dorsal, posterior, anterior and sagittal view in figures 59–65. The dermal bones (parietals, dermopterotics and frontals above, parasphenoid below) are very intimately associated or fused with the endocranium, so that sutures between the two are difficult to observe in this specimen, especially around the posterior margins of the parietals, the ascending process of the parasphenoid and above the postorbital process, and the sutures illustrated in these regions are in part speculative.

In P.51682 the otic and orbitotemporal regions of the endocranium consist of a single undivided ossification, without traces of sutures or radiation. In P.1052 (Rayner 1948, p. 322) there is a single suture in the rear of the orbit, in the position of the teleostean suture between the pterosphenoid above and the prootic and basisphenoid below, and there is a trace of a vertical continuation of this suture, in the position of the pterosphenoid/sphenotic junction. In this specimen the fissura oticalis ventralis has closed during ontogeny so that the otic and occipital ossifications are fused ventrally. In 19010 the pterosphenoid/prootic suture is visible in the orbit and in the fossa bridgei, and there is also a separate basisphenoid. In SM J4851 most of the bones of the orbital surface are not preserved, but there are separate pterosphenoids and sphenotics. The prootics are fused with the pterotics. Running through the lateral wall of the otolith chamber in this specimen (figure 8) there is a vertical suture which passes behind the glossopharyngeal foramen (IX) and turns posteriorly in the jugular groove: this suture delimits a small bone (Opo) which forms the posterior part of the lateral wall of the otolith chamber, meeting the prootic anteriorly, the pterotic dorsally and the basi-exoccipital (Bexo) posteriorly, and lying antero-ventral to the vagus foramen (X). Although SMJ4851 is the only specimen in which such a bone is individualized (this region is fused with the remaining otic ossifications in P.51682 and 19010, and with both the otic and occipital ossifications in P.1052), it is regarded as sufficient evidence of the presence of an *opisthotic* during the ontogeny of *P. bechei*: the bone closely resembles the opisthotic of *P. germanicus* (figures 44–46).

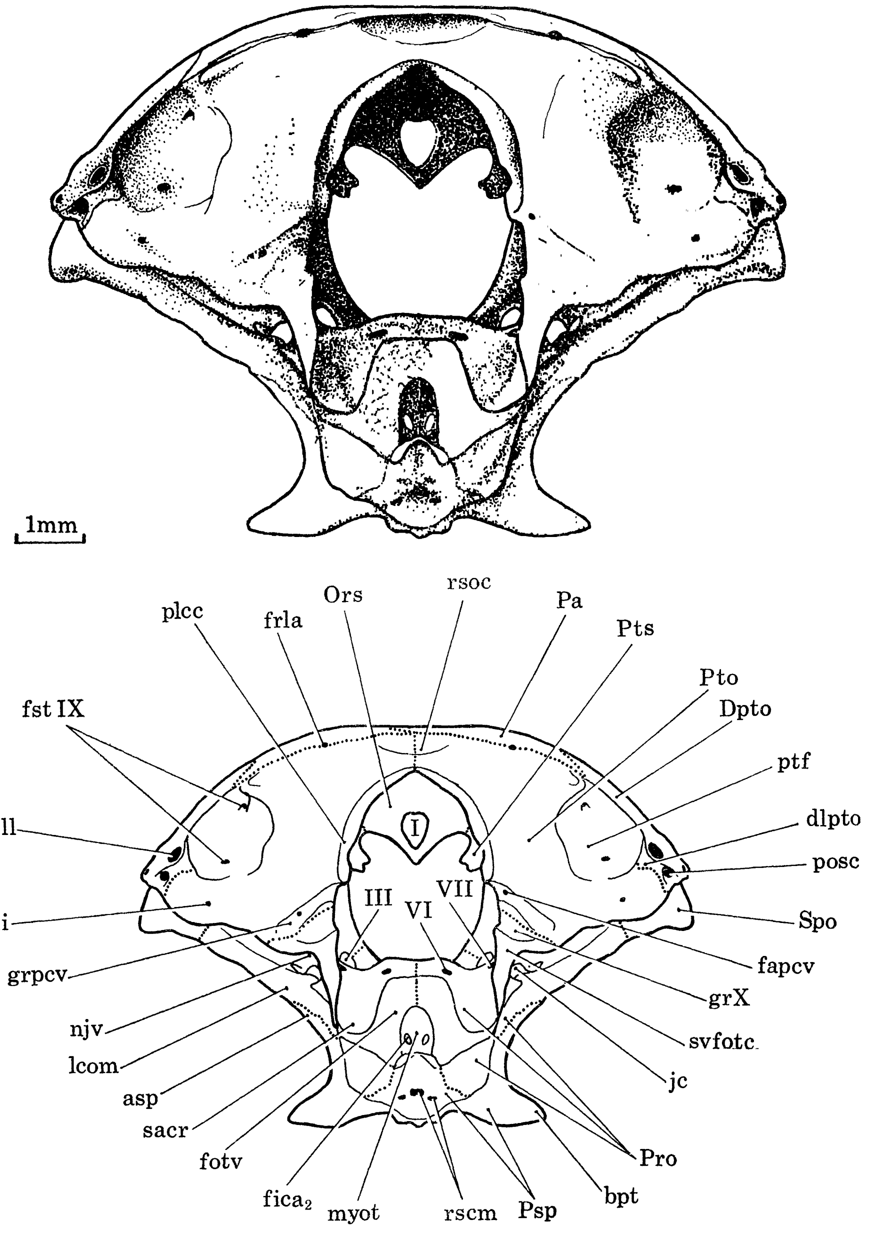


FIGURE 59. *Pholidophorus bechei* Agassiz. Otic and orbitotemporal regions of neurocranium and attached dermal bones in posterior view, from P.51682. In the key diagram the sutures are represented by dotted lines, those between the neurocranial bones restored from other specimens.

In the acid-prepared P.51160 there is a separate prootic and therefore, by inference, separate pterotics, sphenotics, pterosphenoids and a basisphenoid were also present, although the remaining orbitotemporal and otic bones are too heavily pyritized to be recognizable. The ventral part of the prootic of this specimen is short rostro-caudally, and does not appear to include the glossopharyngeal foramen, suggesting that there was a considerable space between it and the occipital bones which was occupied by the opisthotic.

The otic region of the neurocranium is separated from the occipital ossifications by the cranial fissure, comprising the fissura oticalis ventralis below and the fissura otico-occipitalis (Nielsen 1949, p. 27) laterally and dorsally. As shown in figure 59, the posterior face of the otic region of P.51682 is lined with perichondral bone from the floor of the saccular recess (sacr) upwards. This perichondrally lined area, representing the persisting part of the fissura otico-occipitalis, was evidently slightly less extensive in some individuals of *P. bechei* since in P.1052 the otic and occipital regions are fused up to the lower margin of the vagus foramen, and in others the mid-dorsal part of the fissure is closed (figure 57). The sub-vagal portion of the fissura otico-occipitalis is open in the other mechanically prepared braincases.

The cranial cavity opens widely through the posterior face of the otic region (figure 59), but much of this large opening was occluded in life by the occipital ossifications, which fitted into the opening like a plug (figures 9, plate 10, 55). A notch midway down the margin of the opening of the cranial cavity leads into a shallow, ventro-laterally directed groove, the anterior wall of the vagus canal. This groove is divided by a low ridge into an upper portion (grpcv) and a broader, more horizontal lower portion (gr X). The upper division of the vagus canal contained the posterior cerebral vein (cf. Stensiö 1925: p. 21), and the lower division was occupied by the vagus nerve. There is a small foramen in the upper, vascular division of the groove, asymmetrical on the right and left sides of the specimen (fapcv), leading forwards into the cavity occupied by the ampulla of the posterior semicircular canal, and presumably transmitting a small vein. Below the vagus groove there is a perichondrally lined area (svfotc), the sub-vagal portion of the fissura otico-occipitalis, forming the lateral wall of the otic division of the saccular recess (sacr), and below this the posterior face of the otic region turns forwards horizontally and its narrow margin is no longer lined with perichondral bone. This horizontal surface was joined to the horizontal margin of the basioccipital (figure 53) by an area of cartilage, represented in the fossil braincases by a space. This cartilage filled space (vfon, figure 56) is the homologue of the vestibular fontanelle of palaeoniscoids, *Australosomus* and some parasemionotids. The vestibular fontanelle was variably developed in *P. bechei*: in 19010 it appears to have been as in figure 56, in SM J4851 it was more elongate, with a notch in its upper margin at the junction of the prootic and opisthotic, while in P.1052 the whole wall of the saccular recess is covered with perichondral bone and the fontanelle has been obliterated (Rayner 1948, fig. 45). At the antero-dorsal corner of the vestibular fontanelle there is in P.51682 a small area without perichondral bone on the lateral face of the wall of the saccular recess. This area (asup I, figures 56, 61, 62) appears to represent the point of articulation with the braincase of the suprapharyngobranchial of the first branchial arch (cf. Nielsen 1949, p. 41): it is not recognizable in the mechanically prepared specimens, except perhaps SM J4851. Below the vestibular fontanelle the posterior face of the otic region is represented by the massive endochondral bone surrounding the opening of the otic division of the myodome (myot, figure 59), meeting the corresponding surface of the basioccipital in synchondrosis in the fissura oticalis ventralis: in P.1052 this is closed by bone.

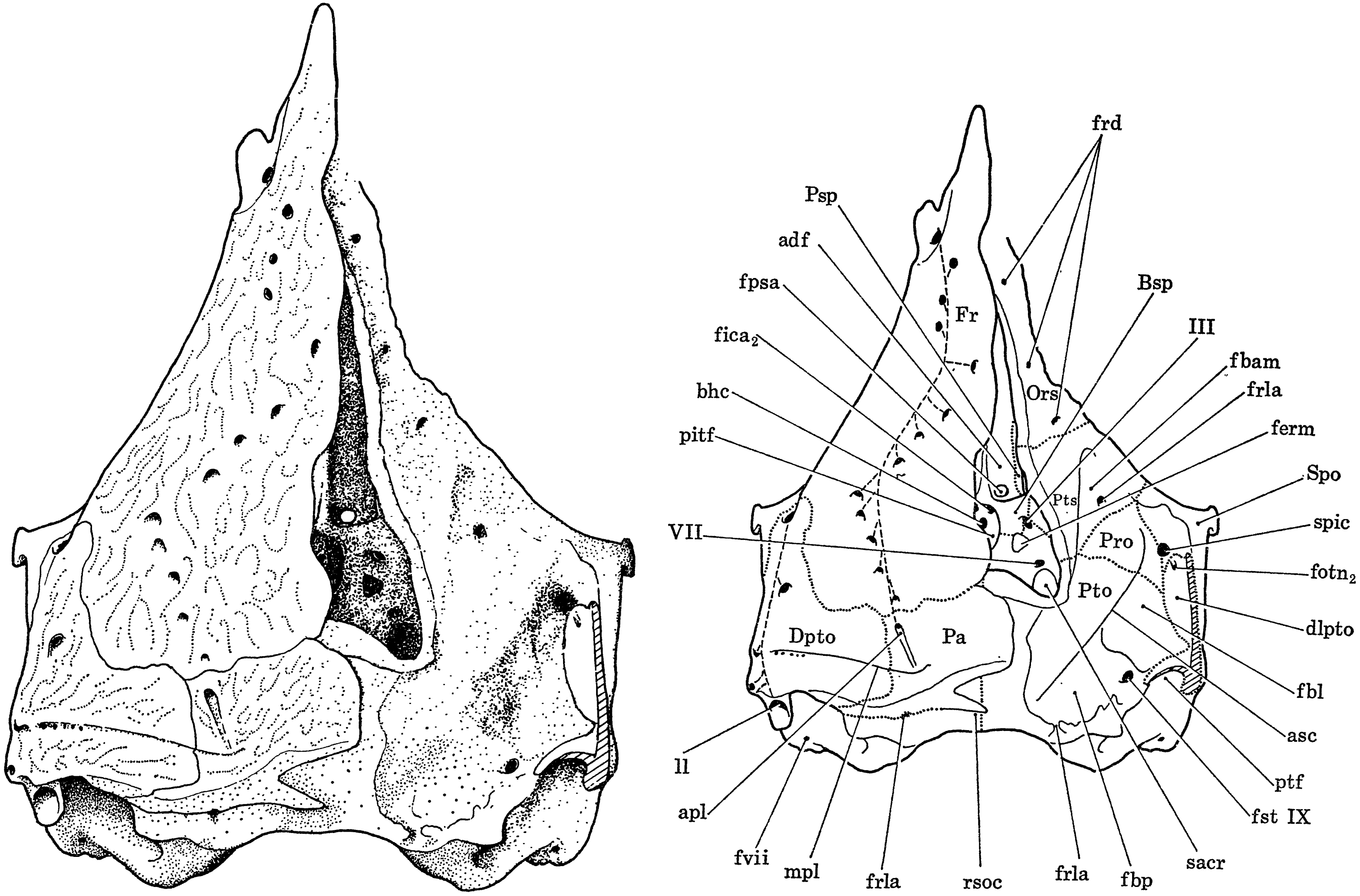


FIGURE 60. *Pholidophorus bechei* Agassiz. Otic and orbitotemporal regions of neurocranium and attached dermal bones in dorsal view, based on P.51682 and 19010 (magn. × 9 approx.). The dermal roofing bones are removed on the right side except for the descending lamina of the dermopterotic, which is drawn as if cut away from the main portion of the bone, the cut surface cross-hatched. In the key diagram the course of the sensory canals is indicated by broken lines, and sutures are represented by dotted lines, those between the neurocranial bones restored from 19010 and other specimens.

The dorsal surface of the otic and orbitotemporal regions is shown in figure 60. This is based mainly on 19010 (figure 7), which has been prepared mechanically, and partly on P.51682, where the dermal bones are broken away on the incomplete right side (figure 1, plate 8).

The dorsal surface of the otic and orbitotemporal regions contains a large, triangular *anterior dorsal fontanelle* (adf, figure 60), extending from the middle of the orbit back to the level of the anterior part of the saccular recess, behind the pituitary fossa. The anterior dorsal fontanelle is about as large as it is in *Pteroniscülus* (Nielsen 1942, fig. 7). The fontanelle is surrounded by a narrow brim, without perichondral bone, which met the underside of the frontals; cartilage presumably extended inwards from this brim and constricted the fontanelle to some extent. Between this brim and the antero-lateral margin of the orbitotemporal region, which also contacts the roofing bones, there is a shallow longitudinal groove (the supraorbital fossa) lying below and medial to the supraorbital canal in the frontal, with two or three foramina in its floor (frd, figure 60) transmitting branches of the superficial ophthalmic nerves to the neuromasts of the canal. At the level of the postorbital process the supraorbital fossa turns postero-medially, following the course of the supraorbital canal, and dies out near the postero-lateral corner of the anterior dorsal fontanelle. Lateral to the posterior part of the fossa there is a longitudinal ridge which ends at the postero-lateral corner of the fontanelle. The *fossa bridgei* lies lateral to and behind this ridge. The fossa bridgei consists of three portions, a shallow, antero-medial portion (fbam) lying medial to the oblique ridge (asc) over the anterior semicircular canal, a deep lateral portion (fbl), lateral to the anterior semicircular canal, and a shallow posterior portion (fbp), behind the semicircular canal. Laterally the fossa bridgei is bounded by the margin of the neurocranial roof, which meets the dermopterotic. The descending lamina of the dermopterotic (dlpto) lines the lateral wall of the fossa. Posteriorly the fossa is bounded by an almost transverse wall which contacts the parietal (Pa) medially and the dermopterotic (Dpto) laterally, where it separates the fossa bridgei from the post-temporal fossa.

The shallow antero-medial portion of the fossa bridgei contains one or two foramina (frla) which may have transmitted the recurrent lateralis branch of the facial nerve. In 19010 this part of the fossa is crossed by an oblique suture which separates the pterosphenoid from the prootic and sphenotic. The deep lateral division of the fossa bridgei contains the upper opening of the spiracular canal (spic). This opening lies at the anterior edge of the descending lamina of the dermopterotic, and presumably marks the junction of the prootic and sphenotic (cf. figure 69). The otic nerve emerged through the spiracular canal (see below) and gave off two rami, one passing antero-laterally through a canal below the frontal/dermopterotic suture (fotn_1, figure 63) and one passing postero-laterally through the descending lamina of the dermopterotic (fotn_2, figure 60) to emerge in the dilatator fossa (fotn_2, figure 61). The shallow posterior division of the fossa bridgei contains a foramen (fst IX, figure 60) which lies directly below the middle pit-line and must have transmitted the supratemporal branch of the glossopharyngeal nerve. A notch or canal in the hind wall of the fossa (frla, figures 57, 59, 60) is assumed to have transmitted the recurrent lateralis nerve back to the trunk. The fossa bridgei does not communicate with the cranial cavity.

The *post-temporal fossa* (ptf, figures 59, 60, 61) lies at the extreme postero-lateral corner of the neurocranial roof. It is a deep depression, open posteriorly, which is roofed by the dermopterotic, bounded medially by the buttress housing the posterior semicircular canal (psc, figure 61), and anteriorly by the ridge forming the hind wall of the fossa bridgei, with which it has no communication. The post-temporal fossa has no endochondral roof, and its antero-lateral corner is lined by a transverse portion of the descending lamina of the dermopterotic (dlpto, figures 59, 60). The post-temporal fossa was traversed by the supratemporal branch of the glossopharyngeal nerve, which entered through a foramen in its floor and left through a foramen in its antero-medial wall, leading through into the fossa bridgei (fst IX, figure 59). On the posterior face of the buttress below the post-temporal fossa there is a small foramen (fvii, figure 59) leading into the cavity occupied by the external semicircular canal. A shallow groove leads ventro-medially from this foramen towards the notch (njv, figure 59) on the posterior face of the otic ossification through which the jugular vein passed, indicating that the foramen is venous.

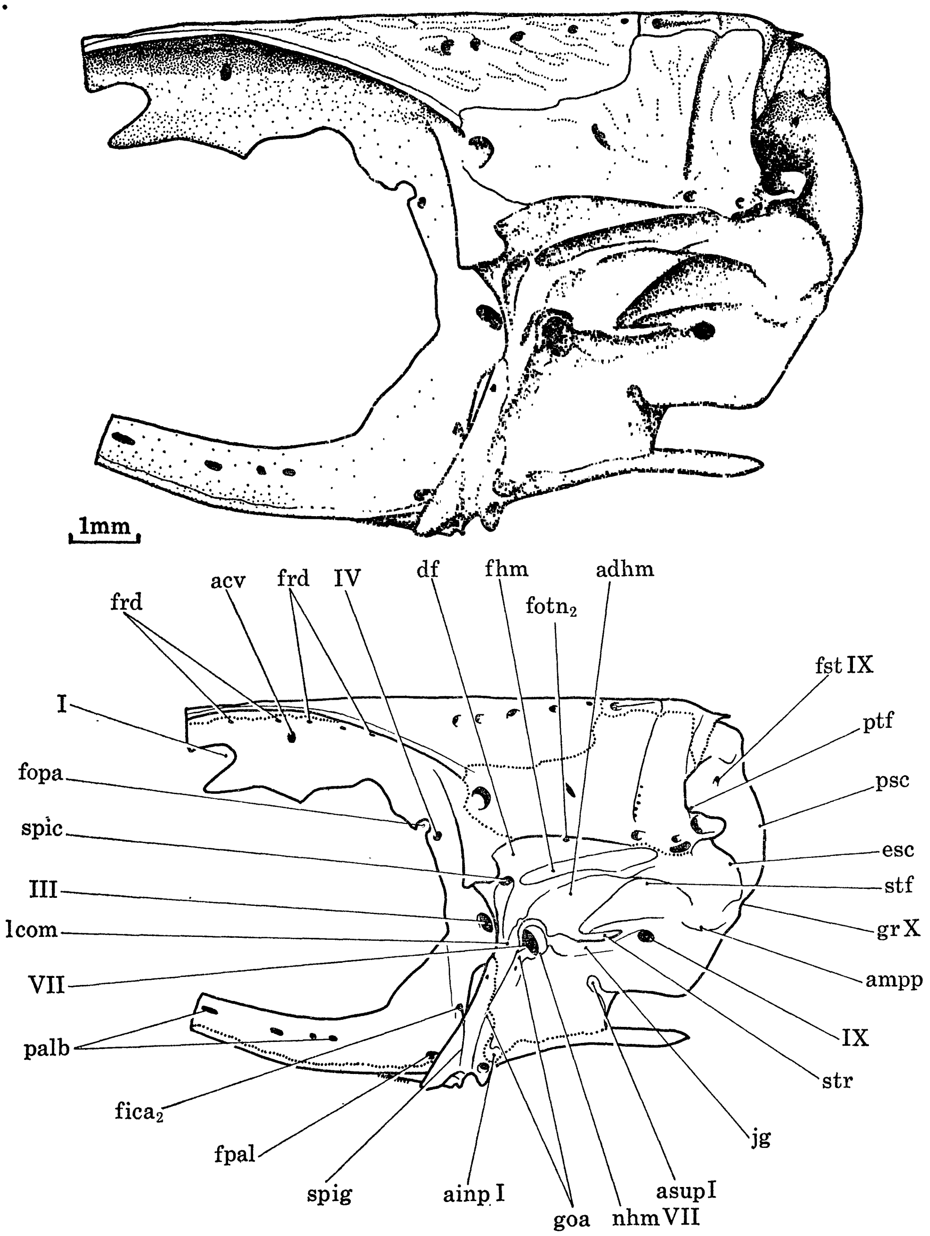


FIGURE 61. *Pholidophorus bechei* Agassiz. Otic and orbitotemporal regions of neurocranium and attached dermal bones in left lateral view, from P.51682. In the key diagram sutures are represented by dotted lines. For sutures between the neurocranial bones, see figure 56.

The lateral face of the otic region has a complex relief (figures 61, 62). Dorsally there is a shallow *dilatator fossa* (df) limited anteriorly by the postorbital process and dorsally by the dermopterotic, with a small foramen for a branch of the otic nerve (fotn$_2$, figure 61) at its upper margin. A narrow longitudinal crest separates the dilatator fossa from the articular facet for the hyomandibular. The *hyomandibular facet* (fhm) is almost horizontal, but its rear end is a little higher and more laterally placed than its front end. The facet is lined with perichondral bone in P.51682, showing that growth had terminated.

Directly in front of the hyomandibular facet is the lower opening of the *spiracular canal* (spic, figures 61, 62), which passes up into the fossa bridgei (see above). From the lower opening of the canal a spiracular groove passes ventro-medially across the lateral face of the braincase, becoming less strongly incised and fading out just above the tip of the ascending process of the parasphenoid (figure 62). The groove can be picked up again just behind the basipterygoid process of the parasphenoid (spig, figures 61, 62). A spiracular canal has not previously been observed in any pholidophoroid.

Below and medial to the posterior part of the hyomandibular facet lies the *subtemporal fossa* (stf) housing the adductor muscle of the operculum. The subtemporal fossa is shallower than in most pholidophorids and is separated from the post-temporal fossa above by a thick layer of endochondral bone within the arch of the external semicircular canal (esc, figures 61, 62). In the roof of the lateral part of the subtemporal fossa there is a foramen (fst IX, figure 62) which transmitted the supratemporal branch of the glossopharyngeal nerve up into the post-temporal fossa. Ventro-medial to the anterior part of the hyomandibular facet there is a rounded depression (adhm), much less obvious than the subtemporal fossa, which was the site of origin of the adductor muscle of the hyomandibular. This depression is separated from the subtemporal fossa by a swelling caused by the recessus utriculus. Below the subtemporal fossa the otic region narrows abruptly (figure 59), and contains only the myodome and the saccular recesses. The wall of the saccular recess is slightly inflated, the swelling dying out below and in front of the facet for the first suprapharyngobranchial. The jugular groove (jg) runs horizontally in the angle formed by this sudden narrowing. Posteriorly the jugular groove is indistinct, but it can be seen to turn dorso-laterally in front of the vagus canal (figure 61), the vein passing lateral to a swelling caused by the ampulla of the posterior semicircular canal and leaving the otic region through a slight notch lateral to the vagus canal (njv, figure 59) and then receiving the posterior cerebral vein from the upper division of that canal. A small vascular foramen (fvii, figure 62) leads into the cavity for the ampulla of the posterior semicircular canal, just medial to the jugular groove. Below the subtemporal fossa the jugular groove contains the glossopharyngeal foramen (IX, figure 61), from which a groove leads antero-ventrally across the wall of the saccular recess. At the anterior edge of the subtemporal fossa the upper margin of the jugular groove becomes strongly marked and bears a strut of membrane bone (str) which projects posteriorly and sutures with the anterior limb of the intercalar (figure 56). The lower margin of the jugular groove becomes prominent a little further forwards, where it forms two projecting spurs with a notch (nhm VII, figures 61, 62) between them. Directly above this notch, the large facial foramen (VII) opens into the jugular groove, and the notch marks the passage of the hyomandibular trunk of the facial nerve. The lateral commissure (lcom), forming the lateral wall of the jugular canal, is very short but broad, and consists of a dorso-laterally directed crest, triangular in section, overlain ventrally by the ascending process of the parasphenoid. Immediately behind the lateral commissure there is a well marked groove for

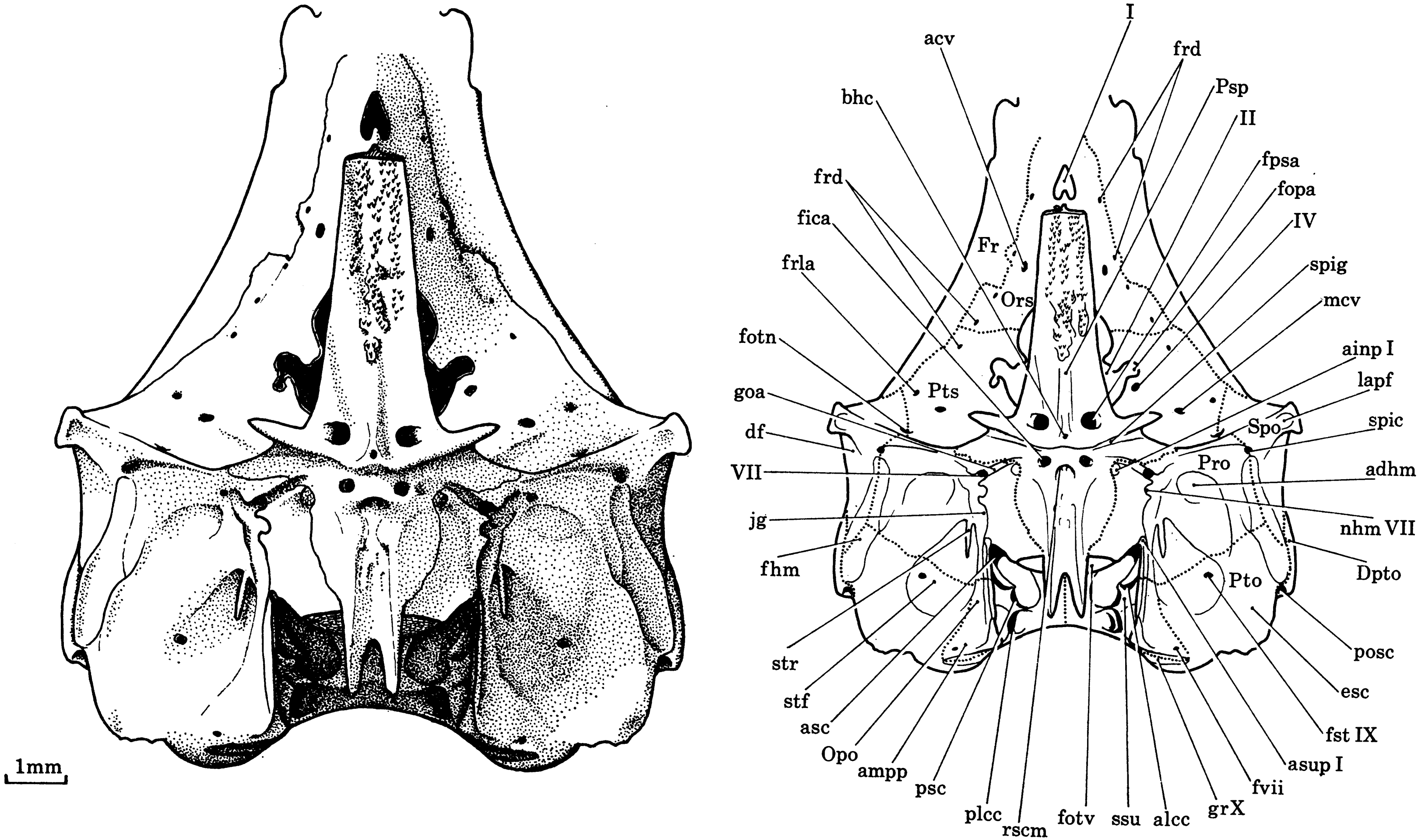


Figure 62. *Pholidophorus bechei* Agassiz. Otic and orbitotemporal regions of neurocranium and attached dermal bones in ventral view, from P.51682. In the key diagram sutures are represented by dotted lines, those between the neurocranial bones restored from other specimens.

the orbital artery (goa, figures 61, 62), passing dorso-laterally from the internal carotid foramen (fica) in the parasphenoid across the ascending process of the parasphenoid and up into the jugular canal through a notch just in front of the notch for the hyomandibular nerve. A minute foramen in the upper part of the arterial groove transmitted an artery into the thickness of the wall of the myodome.

At the extreme antero-ventral corner of the lateral face of the otic region, just above the internal carotid foramen in the parasphenoid and in the angle between the ascending process

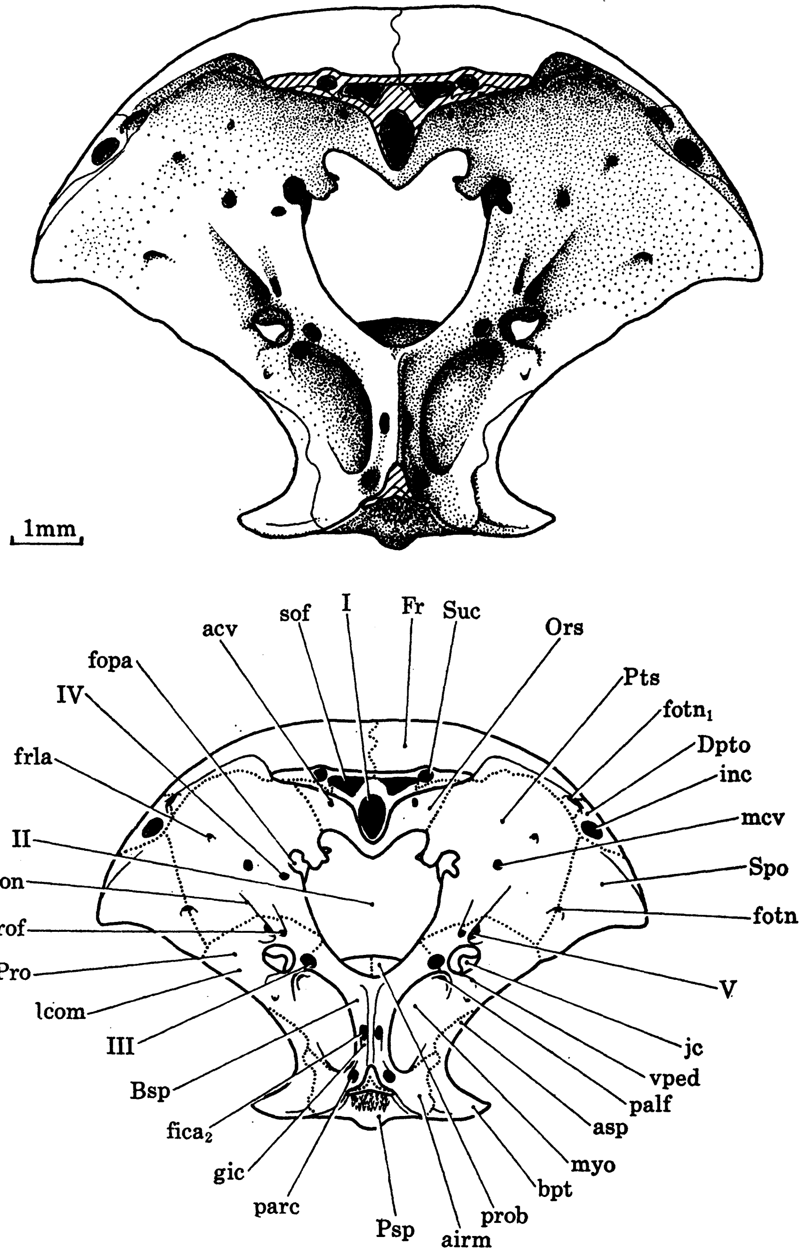


FIGURE 63. *Pholidophorus bechei* Agassiz. Otic and orbitotemporal regions of neurocranium and attached dermal bones in anterior view, as if cut through the middle of the orbit, from P.51682. Cut surfaces cross-hatched. In the key diagram sutures are represented by dotted lines, those between the neurocranial bones restored from other specimens.

and the body of the parasphenoid, there is an antero-laterally directed area without perichondral bone (ainp I, figures 61, 62), the point of articulation of the infrapharyngobranchial of the first gill-arch.

The anterior, orbital face of the orbitotemporal region (figure 63) is separated from the lateral surface by a sharp crest formed by the postorbital process, the lateral commissure and the ascending process of the parasphenoid. This anterior face is occupied ventrally by the basisphenoid region and the paired openings of the myodome, and dorsally by a pair of smoothly curved walls of bone, separated medially by the optic fenestra (II), and joined to the basisphenoid region antero-ventrally, in front of the orbital opening of the trigeminofacial chamber.

The *trigeminofacial chamber* (see Schaeffer 1971, p. 6, for a discussion of the usage of this term) is reduced to a short longitudinal canal, leading forwards from the jugular groove beneath the lateral commissure and having a wide, funnel-like opening into the orbit. As is shown below, the trigeminal and facial ganglia probably lay in this extramural chamber, and the term trigeminofacial chamber is appropriate.

The external opening of the facial canal (VII, figure 61) is low in the jugular groove behind the lateral commissure, and this opening is partially confluent with a large opening in the floor of the groove, the palatine fenestra (palf, figures 63, 64), communicating with the myodome below. The facial nerve therefore emerged into a space lying partly in the floor of the jugular groove and partly in the dorso-lateral corner of the myodome. The internal opening of the facial canal (VII, figure 65), which lies just below the utricular recess, is smaller than the external opening and is not recessed in the bone, so the geniculate ganglion probably lay in the space in the floor of the jugular groove. From the ganglion, the palatine nerve passed down into the myodome through the palatine fenestra and the hyomandibular trunk passed laterally through the notch in the lower margin of the jugular groove. The opercular branch of the facial nerve passed postero-dorsally towards the adductor muscles of the hyomandibular and operculum through a notch in the upper margin of the jugular groove above the facial foramen. In the posterior face of the lateral commissure, above and just in front of the facial foramen, there is a small foramen which appears to end blindly in the thickness of the bone, and must have been vascular.

The external opening of the trigeminal canal (V, figure 63) lies antero-dorsal to the facial foramen. In lateral view (figure 61) it is covered by the lateral commissure, but it is anteriorly directed and opens into the upper part of the orbital opening of the trigeminofacial chamber rather than into the jugular canal. The internal, cerebral opening of the trigeminal canal (V, figure 65), which lies close in front of the antero-ventral margin of the utricular recess, is more than twice as large as the inner opening of the facial canal, but is hardly recessed in the bone and the gasserian and lateralis ganglia probably lay just outside the canal, where there is a marked recess (figure 63). The lateralis branches of the facial nerve issued through the trigeminal foramen, and a groove (gson) leading dorso-laterally across the orbital surface from the trigeminal foramen marks the course of the superficial ophthalmic nerves. There is a separate canal for the profundus nerve which originates immediately in front of the trigeminal canal (prof, figure 65) and opens medial to the trigeminal foramen (prof, figure 63). A short groove leads antero-dorsally from the profundus foramen, diverging slightly from the groove for the superficial ophthalmic nerves.

In the ventro-lateral corner of the orbital opening of the trigeminofacial chamber there is an inconspicuous ridge or knob (vped, figures 63, 64). This structure is insignificant in *P. bechei*, but in early leptolepids, especially the Sinemurian species, there is a process in this position which is the homologue of the lower portion of the pterosphenoid pedicle of *Amia* and some teleosts.

The large oculomotor foramen (III, figures 61, 63, 64, 65) lies at the level of the orbital opening of the jugular canal, midway between the latter and the margin of the optic fenestra.

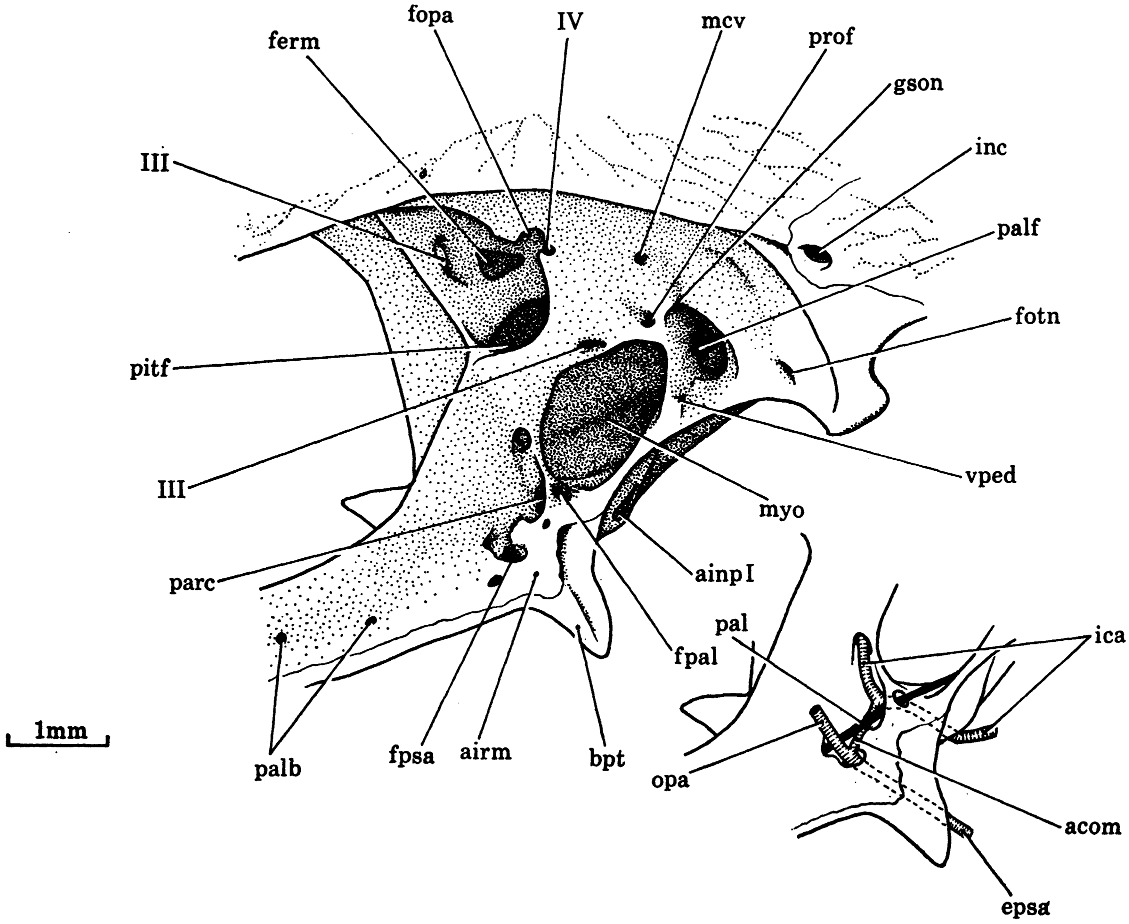


FIGURE 64. *Pholidophorus bechei* Agassiz. Braincase in antero-dorso-lateral view, looking into the rear of the orbit from the left side, from P.51682. Inset at lower right is an outline of the foot of the basisphenoid and the parasphenoid, with the nerves and arteries restored.

The *basisphenoid region* (figure 64) consists of a vertical pillar which flares dorsally into a pair of dorso-laterally directed arms joining the orbital surface of the braincase at the level of the oculomotor foramen, and which is continuous ventrally with endochondral bone forming the floor of the myodome and orbit. The pillar divides the opening of the myodome into right and left halves, while the dorso-lateral arms form the upper margin of the opening of the myodome and separate the optic fenestra (II) from the pituitary fossa (pitf). This vertical pillar is slender and keeled anteriorly, but broader posteriorly, and is longest (rostro-caudally) ventrally, where its anterior edge runs out into the median keel below the orbit on which the interorbital septum inserted. Lateral to this keel the endochondral bone which floors the orbit is little more than a thin skin on the upper surface of the parasphenoid. In P.51682 the preserved portion of the parasphenoid is coated with substitution bone throughout its length below the orbit, but 19010 shows that this coat did not extend below the anterior part of the orbit, so that the ethmoid and orbitotemporal ossifications were discontinuous ventrally.

Lateral to the foot of the basisphenoid pillar the endochondral bone is thicker and forms a transverse bolster which is perforated by canals for the palatine nerve and the internal carotid and efferent pseudobranchial arteries, as described below. This transverse bolster is the homologue of the cartilaginous presphenoid bolster of *Amia*, which contains the small paired bones which are the only basisphenoid ossifications in that fish. In *P. bechei* lateral expansions of the perichondral bone of this transverse bolster are applied to the anterior face of the basipterygoid process of the parasphenoid (figure 64). There is a narrow vertical crevice between this perichondral bone and the parasphenoid, and a thin layer of cartilage must have extended through this space on to the groove in the anterior face of the lateral part of the basipterygoid process, but it can hardly have contributed to the articulation between the process and the palate.

The internal carotid arteries (ica, figure 64), after passing through the parasphenoid (fica, figures 56, 62), ran through a short parabasal canal in the foot of the basisphenoid which is directed antero-dorsally and somewhat medially, and emerged close to the mid-line in the floor of the orbit (parc, figures 63, 64). In this canal, the artery was joined by the palatine nerve (pal, figure 65), which entered through an antero-ventrally directed foramen (fpal, figure 64) in the floor of the myodome. A very slender canal passes back from the carotid canal and opens in the floor of the myodome, presumably transmitting a small vessel.

The efferent pseudobranchial arteries (epsa, figure 64) passed through a pair of foramina in the parasphenoid (fpsa, figure 62) and then through a short, dorso-medially directed canal in the foot of the basisphenoid to emerge in the floor of the orbit (fpsa, figures 60, 64), just in front of the opening of the parabasal canal. A groove links the efferent pseudobranchial and carotid foramina in the floor of the orbit, and there was evidently a communicating branch between the two arteries in this groove (acom, figure 64). There can have been no transverse commissure between either the efferent pseudobranchials, as there is in most living teleosts, or the carotids, for an uninterrupted median septum of bone separated the vessels of each side. After its anastomosis with the internal carotid, the efferent pseudobranchial turned upwards and forwards into the orbit as the ophthalmic artery (opa, figure 64). The internal carotid, after anastomosing with the efferent pseudobranchial, turned upwards and ran in a groove (gic, figure 63) on the anterior face of the broad posterior part of the basisphenoid pillar. Halfway up the pillar, the artery entered a foramen ($fica_2$, figure 63) and passed through a short vertical canal in the pillar, emerging on its posterior face ($fica_2$, figures 60, 65) to enter the cranial cavity through the pituitary fossa.

The palatine nerve, emerging in the floor of the orbit with the internal carotid, passed forwards (presumably accompanied by the palatine artery) medial to the efferent pseudobranchial artery and entered the palatine canal through a foramen (figure 64; fpal, figure 61) in the lateral face of the foot of the basisphenoid pillar. The palatine canal leads forwards horizontally between the parasphenoid and the endochondral bone forming the floor of the orbit. The lateral wall of the palatine canal is fenestrated (palb, figure 61), but these openings may be due to incomplete ossification rather than branches of the nerve or artery.

At the foot of the posterior face of the basisphenoid pillar a narrow bucco-hypophysial canal originates in the floor of the myodome (bhc, figures 60, 65). This canal passes antero-ventrally through the transverse basisphenoid bolster and through the parasphenoid to open in the roof of the mouth on a slight eminence just behind the efferent pseudobranchial foramina (bhc, figure 62).

The *myodome* is long, extending back into the anterior third of the basioccipital, as described in §4 (*d*). The portion of the myodome enclosed within the otic ossification (which is equivalent to the whole myodome of all non-teleostean actinopterygians) is deeper than it is wide, approximately triangular in section anteriorly (figure 63), tapering to an elliptic section posteriorly (figure 59). The endocranial side walls of this cavity are thick posteriorly, thin anteriorly,

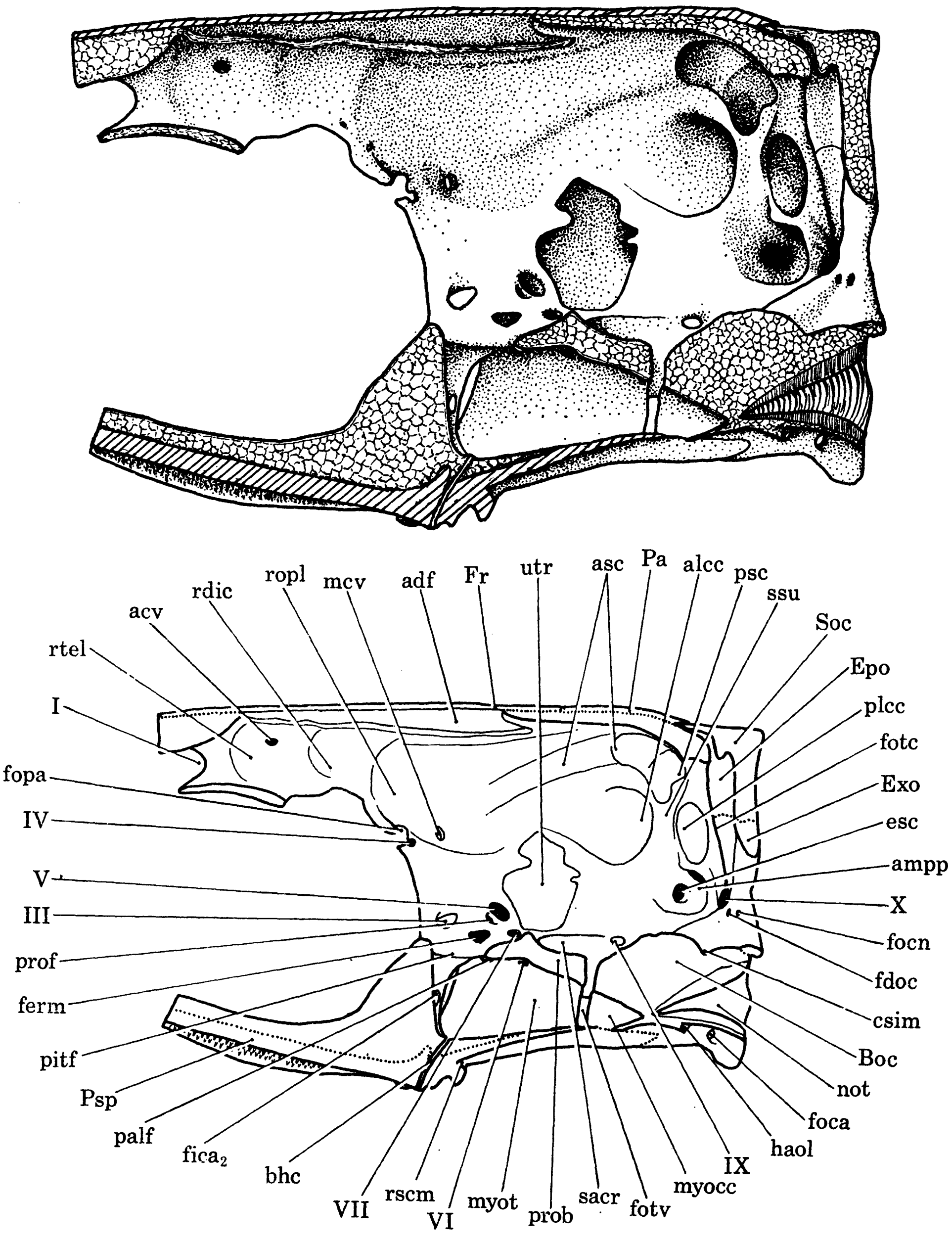


FIGURE 65. *Pholidophorus bechei* Agassiz. Restoration of the post-ethmoid parts of the neurocranium and attached dermal bones in sagittal section, from the left side. Composite, the otic and orbitotemporal regions based on P.51682, the occipital region on several other specimens. Sectioned dermal bones cross-hatched, sectioned endochondral bone reticulated. In the key diagram sutures are represented by dotted lines. (Magn. × 9 approx.)

where they are braced externally by the ascending process of the parasphenoid. The roof of the cavity is also thicker posteriorly than anteriorly. The endochondral floor is only complete anteriorly, where it grades into the foot of the basisphenoid pillar; posteriorly there is an elongate fenestra adjoining the notch in the floor of the occipital portion, forming an elliptic fenestra, covered ventrally by the parasphenoid (figure 65). The roof of the myodome is weakly concave in the longitudinal plane, and is perforated by a pair of antero-ventrally directed canals for the abducens nerves (VI, figures 59, 63, 65), and by a median, ovoid pituitary fossa (pitf, figures 60, 64, 65). Lateral to the pituitary fossa, midway between its margin and the cerebral opening of the facial canal, the thin bone of the roof of the myodome is perforated by a pair of triangular apertures (ferm, figures 60, 64, 65) through which the cranial cavity communicates with the myodome. The margins of these apertures are thin and flimsy, and the apertures are slightly asymmetrical on the two sides of the specimen: these facts suggest that the apertures were closed in life by membrane, and are fenestrae, not foramina. Such paired fenestrae in the roof of the myodome are not present in other pholidophorids (but see *P. minor*, p. 363, and the Sinemurian *Leptolepis*, p. 370) nor have they been described in other fossil actinopterygians, but comparison with other pholidophorids and with caturids and parasemionotids shows that these fenestrae lie in a depression in the floor of the cranial cavity which housed the lateral part of the saccus vasculosus.

The walls of the myodome are perfectly smooth, and there is no sign of a line of attachment for either a vertical or horizontal myodomic membrane, nor of the point of origin of any eye muscle. The external rectus muscles must have passed back to the posterior end of the myodome, as usual, and originated on its hind wall, in the basioccipital. In most living teleosts the anterior rectus muscles also enter the myodome, in a separate ventral compartment beneath the horizontal myodomic membrane, but it is unlikely that this ventral myodome was developed in *P. bechei*. Allis (1919) speculated on the origin of the ventral compartment of the teleostean myodome and concluded that it arose by the anterior rectus muscles penetrating into the palatine canal following regression of the presphenoid bolster, the horizontal myodomic membrane being the homologue of the original floor of the myodome in forms like *Amia*. In *P. bechei* the morphology of the 'presphenoid bolster' is so like that in *Amia* that one would expect the origin of the anterior and inferior recti muscles to be similar, on the anterior or antero-lateral face of the bolster, where indeed there is an area which could have accomodated them (airm, figures 63, 64). It is shown below that in *P. macrocephalus* (figure 85) the openings of the palatine canal and ascending canal for the internal carotid are confluent, producing a ventro-medial opening into the myodome, while in advanced leptolepids (figures 141, 142) the parasphenoid is modified in a way which shows that a ventral compartment of the myodome was developed. These facts are summarized in §9, and it is concluded that *P. bechei* had no ventral posterior myodome.

Above the basisphenoid, myodome and trigeminofacial chamber, just described, the orbital face of the orbitotemporal region consists of a pair of smoothly curved walls of bone, which are separated by the median optic fenestra (II, figures 62, 63, 64), flare out to the postorbital processes laterally, and meet the frontals dorsally. The optic fenestra is very large, extending from the upper margin of the basisphenoid pillar up to the middle of the dorsal wall of the orbit. The fenestra is partially divided into anterior and posterior portions by a constriction (figure 63) which corresponds to the constriction of the cranial cavity between the recesses for the diencephalon and optic lobes (see below), and there is a small spur projecting into the cranial cavity at this constriction (figures 63, 65). The optic nerves and accompanying vessels therefore passed into the orbit through the posterior division of the optic fenestra, while the anterior division must have been closed by membrane. Just behind the constriction of the optic fenestra, in the antero-lateral part of the portion transmitting the optic nerves, there is in P.51682 a large notch in the thin bone forming the wall of the fenestra, and on the right side of the specimen this notch (fopa, figures 63, 64, 65) is subdivided so that there is a foramen (IV, figures 63, 64, 65) below it. This separate foramen is also present in the mechanically prepared P.1052 and 19010, lying further from the margin of the optic fenestra in both: in all three specimens this foramen is in line with the shallow groove running antero-dorsally from the profundus foramen. On the same horizontal level as this foramen there is in all three specimens a second foramen (mcv, figures 63, 64, 65), more laterally placed, which lies just medial to the groove for the superficial ophthalmic nerves and in front of a low ridge which limits this groove medially. In P.1052 and 19010 this second foramen is much closer to the first than it is in P.51682. The ridge medial to the groove for the superficial ophthalmic nerves, which ends just behind the second foramen (mcv), is produced ventrally as the pterosphenoid pedicle in other polidophorids (*P. germanicus*, *P. macrocephalus* and the Callovian *Pholidophorus*; figures 68, 72, 79) and in them the foramen opens in the antero-lateral face of the base of the pedicle. These two foramina are found side by side in the pterosphenoid of all pholidophorids and leptolepids: their interpretation is discussed in detail on p. 409, and it is concluded that the more medial and anterior foramen (IV) transmitted the trochlear nerve, the more lateral and posterior (mcv), the middle cerebral vein. The notch in the margin of the optic fenestra (fopa), which is confluent with the trochlear foramen on one side of P.51682, probably transmitted the optic artery, which passes through a foramen close to the antero-dorsal margin of the optic fenestra or through a notch in this margin in primitive actinopterygians.

Lateral to the foramen for the middle cerebral vein there are two smaller foramina. One of these (frla, figures 62, 63, 65) lies dorso-lateral to the vascular foramen and in line with the groove for the superficial ophthalmic nerves. This foramen leads into a narrow canal which passes almost directly dorsally and opens into the anterior part of the fossa bridgei, medial to the postorbital process (figure 60): it must have transmitted the first branch of the superficial ophthalmic nerves, including branches to the neuromasts of the posterior part of the supraorbital sensory canal, but also the recurrent branch of the facial, the ramus lateralis accessorius (Freihofer 1963), and for this reason the foramen is referred to as the ramus lateralis accessorius foramen. Ventro-lateral to this foramen and lateral to the groove for the superficial ophthalmic nerves is the foramen for the otic nerve (fotn, figures 62, 63). This is ventro-medially directed and linked by an inconspicuous groove with the groove for the superficial ophthalmics. The otic foramen lies directly anterior to the lower opening of the spiracular canal, and the two are only separated by the crest between the lateral and orbital faces of the braincase: the dorsolaterally directed canal for the otic nerve leads into the spiracular canal.

Anterior to the ramus lateralis accessorius foramen there is a series of three or four small foramina (frd, figures 61, 62), asymmetrical on the two sides of the specimen, transmitting branches of the superficial ophthalmic nerves to the skull roof and supraorbital sensory canal. The uppermost part of the orbital surface of the endocranium, which contains these small foramina, is spongy in texture and bears a series of projecting flanges of membrane bone below the frontals.

The foramen for the anterior cerebral vein (acv, figures 61, 62, 63) opens just in front of the anterior margin of the optic fenestra, passes dorso-medially and originates high in the wall of the cranial cavity (figure 65). The olfactory nerves emerged through a median foramen (I, figures 61, 62, 63, 65) at the anterior end of the cranial cavity and ran forwards to the ethmoid region through the orbit. In the available material it is impossible to tell whether the orbitotemporal and ethmoid ossifications were continuous above the orbit, but if they were joined it can only have been by a thin skin of substitution bone on the underside of the frontals.

The otic and orbitotemporal regions of the *cranial cavity* are shown in the reconstructed sagittal section (figure 65). The brain was closely enveloped by bone, as in palaeoniscoids and other primitive fossil actinopterygians, and much of its relief can be deduced from the shape of the cavity in the bone, although in the otic region the openings for the labyrinth cavity and lateral cranial canal (see below) obscure the relief of the brain. Anteriorly, the cranial cavity decreases rapidly in height in front of the anterior dorsal fontanelle, and this most anterior part of the cranial cavity contained the olfactory bulbs and the proximal parts of the olfactory tracts. At the level of the front end of the anterior dorsal fontanelle the cranial cavity increases in breadth and the telencephalon was accomodated in this swelling (rtel), which gave off the anterior cerebral vein (acv). A further slight swelling above the anterior part of the optic fenestra must have housed the anterior part of the diencephalon (rdic). Above the central part of the optic fenestra, just in front of the trochlear notch or foramen (IV), there is another marked increase in the breadth of the cranial cavity, a large, rounded depression occupying the dorso-lateral part of the orbitotemporal region, medial to the postorbital process and in front of the anterior semicircular canal. These paired depressions (ropl) contained the large optic lobes, and the optic nerves left antero-ventrally through the optic fenestra, while the trochlear nerve traversed the ventro-lateral part of the depression to emerge close to the optic nerves. The middle cerebral vein (mcv) left the lateral part of the depression for the optic lobe. Below the optic lobes, the ventral part of the cranial cavity decreases rapidly in breadth. Its walls are perforated by the foramina of the oculomotor (III), profundus (prof), trigeminal and facial nerves (V, VII), and its floor by the median pituitary fossa (pitf) and the paired fenestrae (ferm) leading into the myodome. The trigeminal and facial nerves passed out in front of the recess for the utriculus (utr), not through it. The position of the cerebellum is not indicated by any strong depression in the wall of the cranial cavity: evidently the cerebellum lay below the posterior part of the anterior dorsal fontanelle, medial to the anterior semicircular canal and above the utricular recess. Behind the cerebellar region the walls of the cranial cavity are occupied by the openings of the labyrinth and the lateral cranial canal, so that the relief of the hindbrain cannot be deduced. The height of the cranial cavity decreases slightly in this region, and the abducens (VI), glossopharyngeal (IX) and vagus (X) nerves left the cranial cavity successively, the last through the cranial fissure at the transition to the occipital region.

The *labyrinth cavity* is mostly enclosed within the walls of the otic region of the braincase, and its structure can be deduced with some confidence (figure 66). The saccular recess (sacr, figures 65, 66) is rather short and shallow in comparison with those of living teleosts. As noted above (§ 4) there is no differentiated recess for the lagenalith in the occipital division of the saccular recess, and if the sacculith conformed to the shape of the recess it would have been about twice as long as deep, as are some of the Jurassic sacculiths referred to *Pholidophorus* (Stinton & Torrens 1968). The glossopharyngeal nerve passed through the upper part of the saccular recess in the usual way, and the recess is in wide communication with the cranial cavity above. The utriculus occupied a very deep chamber (utr) in the side wall of the otic region, communicating with the cranial cavity by a constricted opening, with projections on its anterior and posterior margins. The ampulla of the anterior semicircular canal (ampa, figure 66) lay in an antero-dorsal diverticulum of the utricular recess, and the ampulla of the external semicircular canal (ampe) lay in a posterior diverticulum of the recess, behind the projections on the posterior margin of the entrance to the recess. The sinus superior, the common, vertical portion of the anterior and posterior semicircular canals, lay on the concave medial face of a vertical strut of bone (ssu, figure 65) medial to the lateral cranial canal, and at the upper end of this strut the two semicircular canals entered the cranial wall, the posterior (psc) passing ventrally and the anterior passing antero-laterally, its course shown by a ridge on both the external (asc, figure 60) and internal (figure 65) surfaces of the braincase. The anterior semicircular canal is remarkably long in comparison with the posterior and external canals; anteriorly it loops sharply postero-ventrally and enters its ampulla in front of the utricular recess. The ampulla of the posterior semicircular canal (ampp) lay in a deep recess just below the posterior opening of the lateral cranial canal (figure 65). The external semicircular canal passed laterally through the anterior part of this recess, as in Kansas palaeoniscid A (Rayner 1951, fig. 10), *Perleidus*, *Ospia* (Stensiö 1932, fig. 61) and *Caturus* (Rayner 1948, fig. 8), not through a separate opening in the cranial wall as it does in *Kentuckia*, *Pteronisculus* and *Boreosomus*. The external semicircular canal (esc) is extremely short, looping round the subtemporal fossa to enter its ampulla in the posterior wall of the utricular recess.

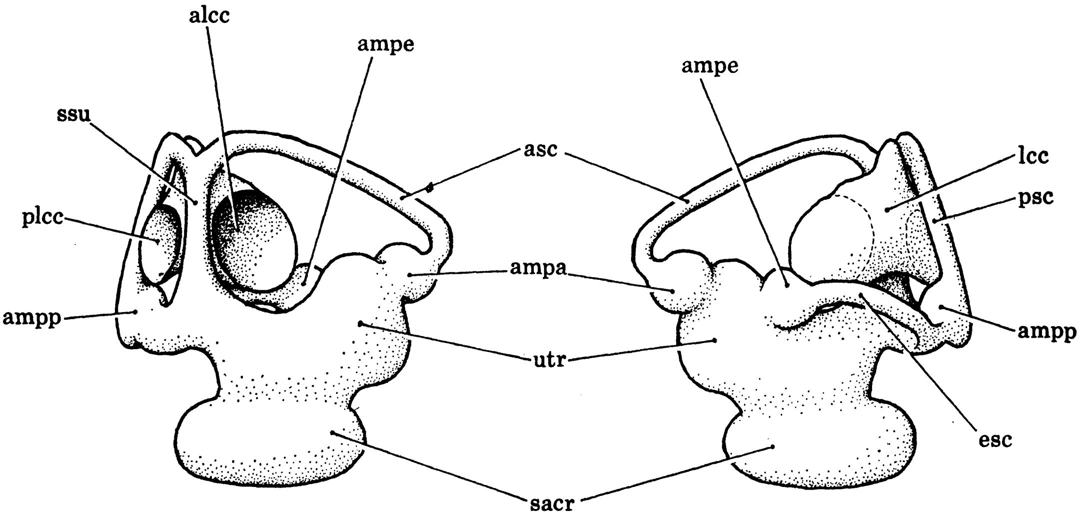


FIGURE 66. *Pholidophorus bechei* Agassiz. Reconstruction of the labyrinth cavity and lateral cranial canal of the left side in medial view (left) and lateral view (right), based mainly on P.51682 (magn. × 9 approx.). In the right hand drawing the openings of the lateral cranial canal are indicated by broken lines.

The *lateral cranial canal* is the name given by Rayner (1948) to an intramural canal in the otic region of the braincase of *Caturus* and *Dapedium*. In *Pholidophorus bechei* the canal (lcc, figure 66) is identical in position with that of *Caturus*, opening into the cranial cavity anteriorly through a large opening (alcc, figures 62, 65, 66) below the anterior semicircular canal and postero-dorsal to the utricular recess, passing lateral to the strut supporting the sinus superior (ssu, figure 65) and medial to the posterior semicircular canal, and re-entering the cranial cavity through a smaller, oval opening (plcc, figures 59, 62, 65, 66) above the recess for the ampulla of the posterior semicircular canal, close in front of the cranial fissure. On one side of P.51682 the posterior opening of the lateral cranial canal is smaller than on the other, and its upper portion is replaced by a circular foramen opening into the cavity for the posterior semicircular canal. In Rayner's *Caturus* sp. the lateral cranial canal is 'rounded but irregular, with a distinct ventral expansion in the middle of its length' (Rayner 1948, p. 299), but in *C. groenlandica* (Aldinger 1932, fig. 2) the canal has a dorsal diverticulum. In *P. bechei* there is also a prominent dorsal diverticulum (figure 66) which rises towards the roof of the neurocranium at the hind margin of the postero-medial, shallow portion of the fossa bridgei, coming closest to the surface just medial to the foramen of the supratemporal branch of the glossopharyngeal nerve (fst IX, figure 60), where the canal is only separated from the fossa bridgei by a very thin layer of bone. Perforation of this wall would result in a condition like that in *Polyodon, Pteronisculus* and *Boreosomus*, where the fossa bridgei communicates with the cranial cavity by a canal passing through the arch of the posterior semicircular canal, but as Rayner (1951, p. 78) notes, there is no obvious homologue of the anterior opening of the lateral cranial canal in any palaeoniscoid. Aldinger's hypothesis that the lateral cranial canal contained an electric organ is highly improbable, as Nielsen and Rayner have already said, but no other explanation of its function has been offered. In *P. bechei* the ventral part of the posterior opening of the canal is almost confluent with the upper part of the groove for the posterior cerebral vein on the posterior face of the otic region (figures 59, 65), and there is every indication that a major tributary of this vein, which itself seems to have been very large, emerged from the lateral cranial canal. In *Caturus* there is also a sulcus running from the inner opening of the vagus canal up to the posterior opening of the lateral cranial canal (Rayner 1948, fig. 8). This suggests that the canal was occupied by a vascular plexus, but does not help much in deciding on its function.

The *sclerotic* of *P. bechei* is nowhere well preserved. The sclerotic ring consisted of four broad segments (P.9652), each containing more than one layer of bone: presumably there were dermal and perichondral layers, as in *P. germanicus* (see below). In several specimens (e.g. 36473, P.1049*c*) there are indications of a basal sclerotic bone, as in *P. germanicus* (figure 81), but the preservation is never sufficiently good for an unequivocal interpretation.

(*b*) Pholidophorus germanicus *and the Callovian* Pholidophorus *sp.*

In these species the otic and orbitotemporal regions of the braincase contain independent pterotic, prootic, sphenotic, basisphenoid, pterosphenoid and orbitosphenoid ossifications. In *P. germanicus* there is also a small opisthotic (Opo, figures 44–46), described above with the occipital ossifications; a small ossification behind the lower part of the posterior semicircular canal (Ptsn, figure 45) which presumably fused with the pterotic in full-grown individuals; and a small ossification applied to the outer face of the descending lamina of the frontal, just behind the centre of ossification of that bone (Ptso, figure 146). This ossification is present on both sides of the specimen; it lies above the pterosphenoid, but could not have fused with that bone in full-grown individuals since its exposed (lower) surface is perichondrally lined. No other fish is known to have such a bone, and it may only be an individual anomaly.

In the specimen of *P. germanicus* the bones in the otic and orbitotemporal regions were separated by considerable areas of cartilage, so that there are few points of contact between them (figure 96). The Callovian species is much more thoroughly ossified, with little or no cartilage between the bones, the pterotic and prootic partially fused superficially, and the cranial and labyrinth cavities more completely enveloped in bone: these differences may only be a consequence of the larger size of the Callovian fish (about two-thirds as large again as the individual of *P. germanicus*). In *P. germanicus* there is a large basal sclerotic ossification in the orbit: this bone was probably also present in the Callovian species, but this region is missing from the fossil. Because of the more complete ossification and the intact condition of the braincase, the Callovian species complements *P. germanicus* by giving a clearer picture of the cavities and fossae in the braincase. The Callovian braincase is restored in lateral, ventral, dorsal, posterior, oblique postero-ventral, anterior and sagittal views in figures 67–73.

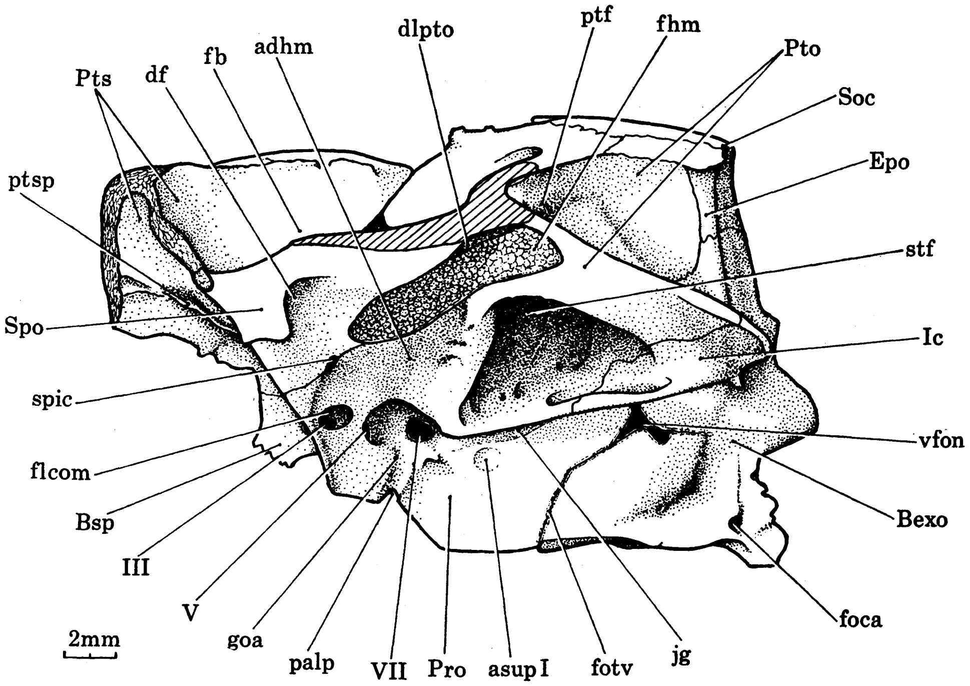


FIGURE 67. Callovian *Pholidophorus* sp. Preserved parts of neurocranium in left lateral view, from 32579. The descending lamina of the dermopterotic is shown in position, as if cut away from the body of the bone, the cut surface cross-hatched. The postorbital process is restored on the basis of P.3704, *P. germanicus*.

The *pterotic* (Pto) of *P. germanicus* is shown in lateral, ventral and posterior view in figure 74, and in dorsal view in figure 75. In both species the pterotic contains the greater part of the subtemporal and post-temporal fossae, the posterior part of the fossa bridgei, and the lateral cranial canal. It also enclosed most of the posterior and external semicircular canals, and the major part of the articular facet for the hyomandibular lay in cartilage lateral to the pterotic: as preserved the hyomandibular facet (fhm, figures 67, 68, 71) is a deep pit whose walls are formed by the pterotic, prootic and sphenotic, and which is roofed by the outer face of the descending lamina of the dermopterotic.

The entire ventral surface of the pterotic is occupied by the *subtemporal fossa* (stf), housing the adductor muscle of the operculum. The surface of the bone in this fossa exhibits several subsidiary depressions and is pitted and ridged for muscle attachment. The subtemporal fossa is much deeper than in *P. bechei*, and in the Callovian species it is deeper than in *P. germanicus*, so that it produces a hump in the floor of the post-temporal fossa. The postero-dorsal wall separating the subtemporal fossa from the post-temporal fossa is thin and translucent, and the antero-dorsal wall is even thinner, forming a delicate, fenestrated (flcc, figure 74) membrane between the subtemporal fossa and the lateral cranial canal. At the apex of the subtemporal fossa there is a small foramen (fst IX, figures 68, 74*b*) leading into a vertical canal which passes up in the medial wall of the post-temporal fossa and branches near the dorsal surface of the pterotic, one branch opening into the fossa bridgei (fst IX, figures 69, 74*a*, 75), in the normal position of the supratemporal branch of the glossopharyngeal nerve, and one branch opening into the post-temporal fossa (fst IX, figures 69, 74*c*). This canal evidently transmitted the supratemporal nerve to the skull roof, and the difference in its course from that of *P. bechei*, where the nerve traversed the post-temporal fossa, must be due to the greater depth of the subtemporal fossa in these species, which results in its apex lying medial to the post-temporal fossa. In *P. germanicus* the opening in the fossa bridgei is the larger of the two exit foramina but in the Callovian species it is the smaller, suggesting a reduction in the importance of the sense organs of the middle pit-line in the latter species.

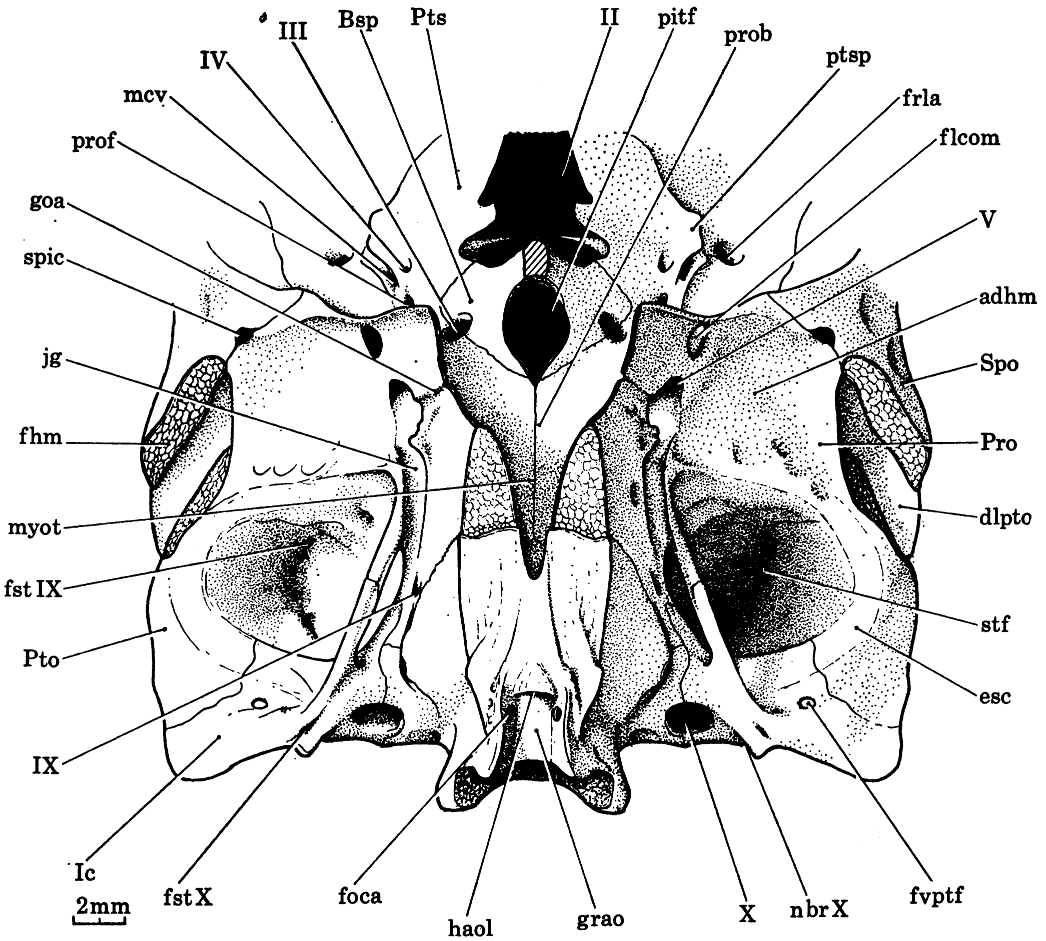


Figure 68. Callovian *Pholidophorus* sp. Preserved parts of neurocranium in ventral view, from 32579.

The posterior face of the pterotic forms the floor and medial wall of the post-temporal fossa. In *P. germanicus* this fossa (ptf, figures 74, 75) is hardly deeper (dorso-ventrally) than that of *P. bechei* (figures 59, 60) but rostro-caudally it is considerably longer, extending forwards lateral to and below the posterior part of the fossa bridgei. In *P. germanicus* the post-temporal fossa and fossa bridgei are still completely separated by an oblique wall of endochondral bone (figures 74*a*, 75) which ended laterally in cartilage lying on the anterior face of the small transverse descending lamina of the dermopterotic (figure 146).

The most significant structural difference between the Callovian species and *P. germanicus* is that the former has developed a communication between the post-temporal fossa and the fossa bridgei. In the Callovian species the transverse wall which separates these cavities in *P. germanicus* has been reduced to a slender bar, formed medially by the pterotic and laterally by the descending lamina of the dermopterotic (figures 69, 70), and this bar arches over a large oval opening through which the post-temporal fossa communicates with the fossa bridgei. Through this opening, trunk musculature passed into the fossa bridgei, inserting on the dermopterotic and frontal in the roof of the fossa, the large descending lamina of the dermopterotic (dlpto) in its lateral wall, and on the pterotic, sphenotic, prootic and pterosphenoid in its floor. This is the condition of the post-temporal fossa in the living *Elops* (Ridewood 1904*a*, p. 38; Forey 1973*a*), except that the bar between the post-temporal and fossa bridgei divisions is lacking, so that they are entirely confluent.

The dorsal face of the pterotic (figures 69, 75) forms the posterior part of the fossa bridgei. As in *P. bechei*, the posterior part of the fossa bridgei consists of a deep lateral portion (fbl), communicating with the post-temporal fossa in the Callovian species, and a shallow medial

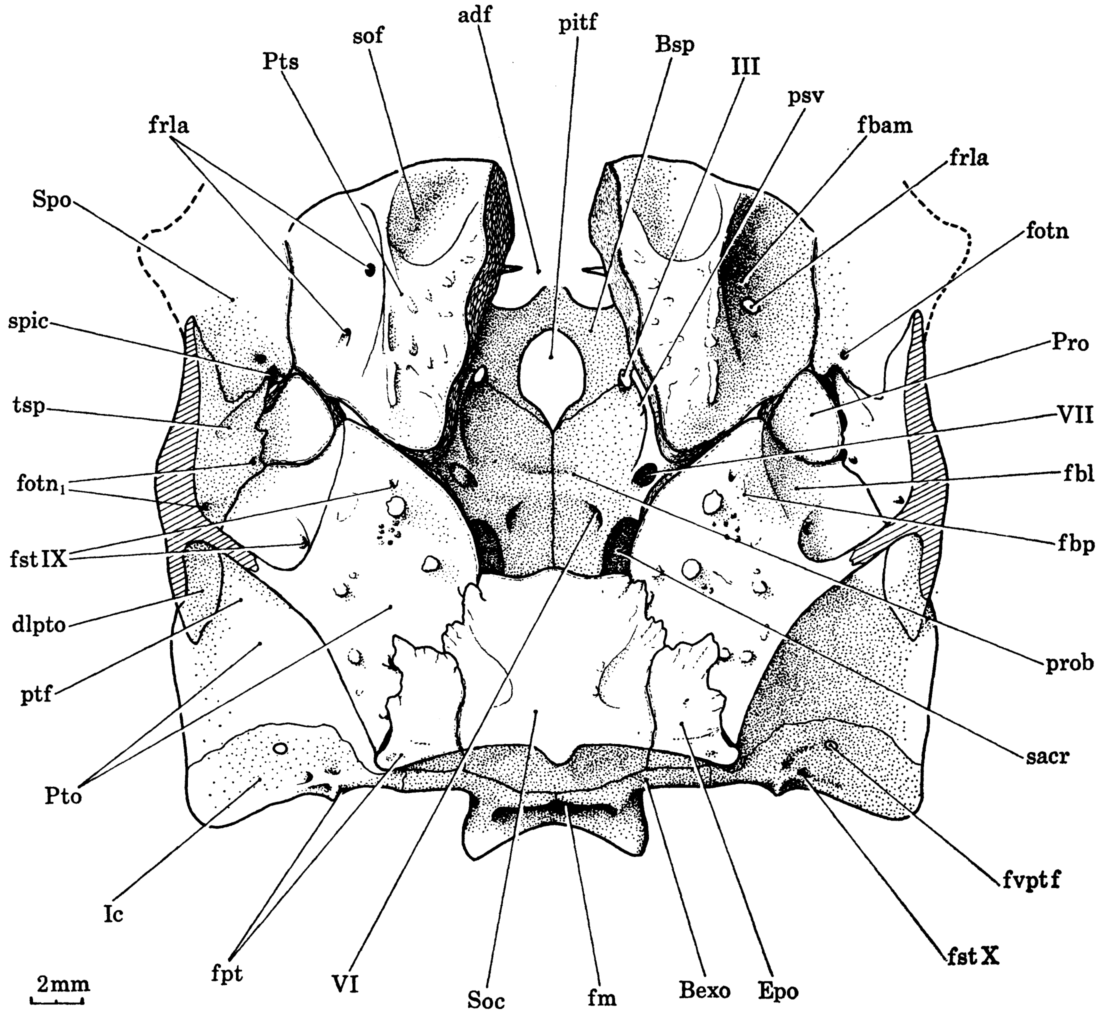


FIGURE 69. Callovian *Pholidophorus* sp. Preserved parts of neurocranium in dorsal view, from 32579. The descending lamina of the dermopterotic is shown in position, as if cut away from the body of the bone, the cut surface cross-hatched.

portion (fbp) containing the foramen of the supratemporal nerve (fst IX). Medial to the fossa bridgei and post-temporal fossa the dorsal surface of the pterotic has a plane area bearing ridges and splints of membrane bone which meet the overlying dermopterotic and parietal. This part of the bone projects postero-laterally over the post-temporal fossa in a shelf which meets a similar shelf on the epioccipital, and in the Callovian species the medial edge of this dorsal part of the pterotic is overlapped by membranous splints from the supraoccipital and epioccipital (figure 69).

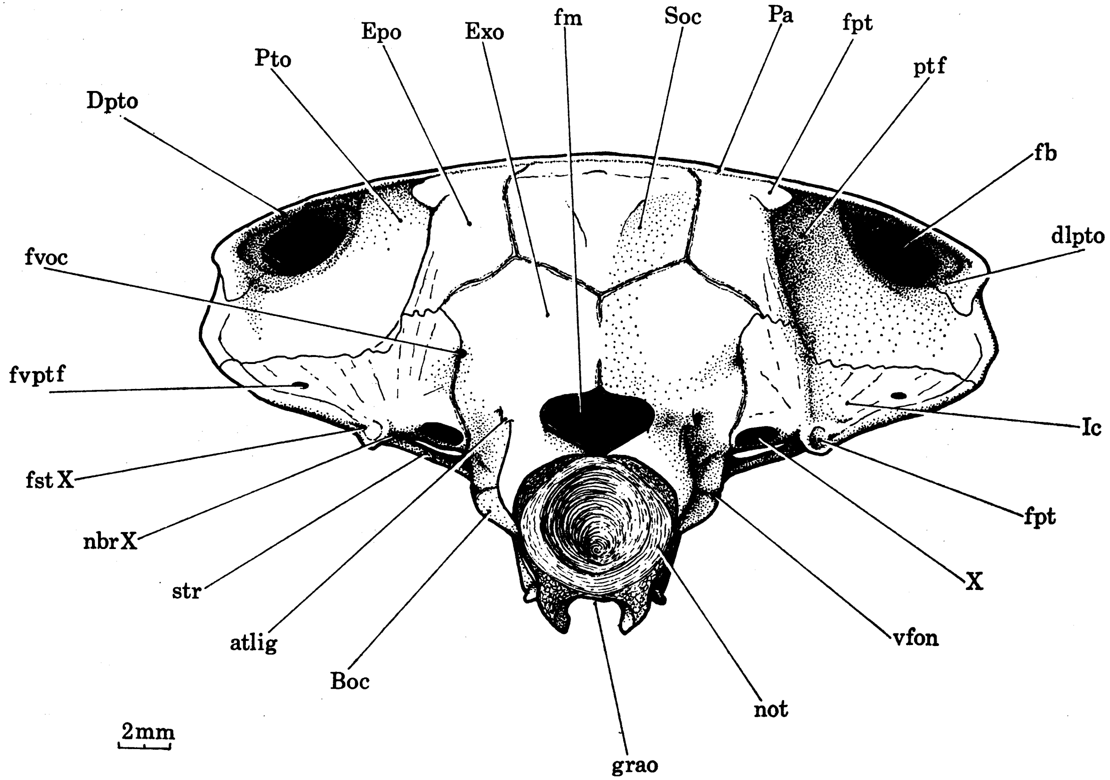


Figure 70. Callovian *Pholidophorus* sp. Neurocranium and attached roofing bones in posterior view, from 32579.

The medial face of the pterotic (figure 73) is occupied by a deep cavity, the lateral cranial canal (lcc), whose outline in *P. germanicus* is shown in figures 74*c* and 75. The floor of this cavity has a slight central hump caused by the subtemporal fossa below. Above this hump, there is an expansion in the roof of the cavity which almost reaches the dorsal surface of the bone, close behind the shallow, medial part of the fossa bridgei. This cavity closely resembles the lateral cranial of *P. bechei* (p. 337) in shape and position, but in *P. germanicus* it lacks an ossified medial wall. In the more completely ossified Callovian species the lateral cranial canal has a thick medial wall (ssu, figure 73), more extensive than in *P. bechei*, ending medially in cartilage which supported the sinus communis, the common vertical portion of the anterior and posterior semicircular canals. The lateral cranial canal of the Callovian species also appears to be longer rostro-caudally than that of *P. bechei* (cf. figures 65, 73). In *P. germanicus* the sinus communis lay in cartilage medial to the pterotic, and the anterior semicircular canal also lacks an ossified wall. In the Callovian species, the anterior semicircular canal ran in a channel on the medial face of the pterotic (asc, figure 73). The posterior semicircular canal, turning down postero-lateral to the lateral cranial canal, was partially enclosed in the pterotic in *P. germanicus* (psc, figure 74*c*), more completely enclosed in the Callovian species (figure 73). The external semicircular canal ran round the circumference of the pterotic, encircling the subtemporal fossa, and again was more completely bone-enclosed in the Callovian species than in *P. germanicus* (esc, figures 68, 71, 73, 74).

The *prootic* (Pro) of *P. germanicus* is shown in dorsal view in figure 75 and in lateral, medial and anterior views in figure 76. In both species it is an extremely complex bone, containing the trigeminofacial chamber, and contributing to the walls of the myodome, subtemporal fossa, fossa bridgei, saccular and utricular recesses, and ampullary chambers of the posterior, anterior and external semicircular canals. The lateral surface of the prootic (figures 67, 76*a*) has an almost vertical ventral part forming the outer wall of the myodome anteriorly and of the saccular recess posteriorly. The horizontal jugular groove (jg) runs along the upper edge of this ventral part. Just below the middle part of the jugular groove there is a shallow depression (asup I) which appears to be the homologue of the articular area for the first suprapharyngobranchial in *P. bechei* (figure 61). The lower margin of the jugular groove is weakly defined except anteriorly, where there is a spur, lateral to the facial foramen (VII), dividing the groove for the orbital artery (goa) from the hyomandibular nerve: there is a similar spur in *P. bechei*. The upper margin of the jugular groove is more strongly marked, and below the anterior part of the subtemporal fossa a long rod of membrane bone projects horizontally from it, lateral to the jugular groove. This rod met the antero-lateral process of the intercalar (figures 67, 68, 70, 71, 96), forming a bridge (str) across the subtemporal fossa. The glossopharyngeal foramen

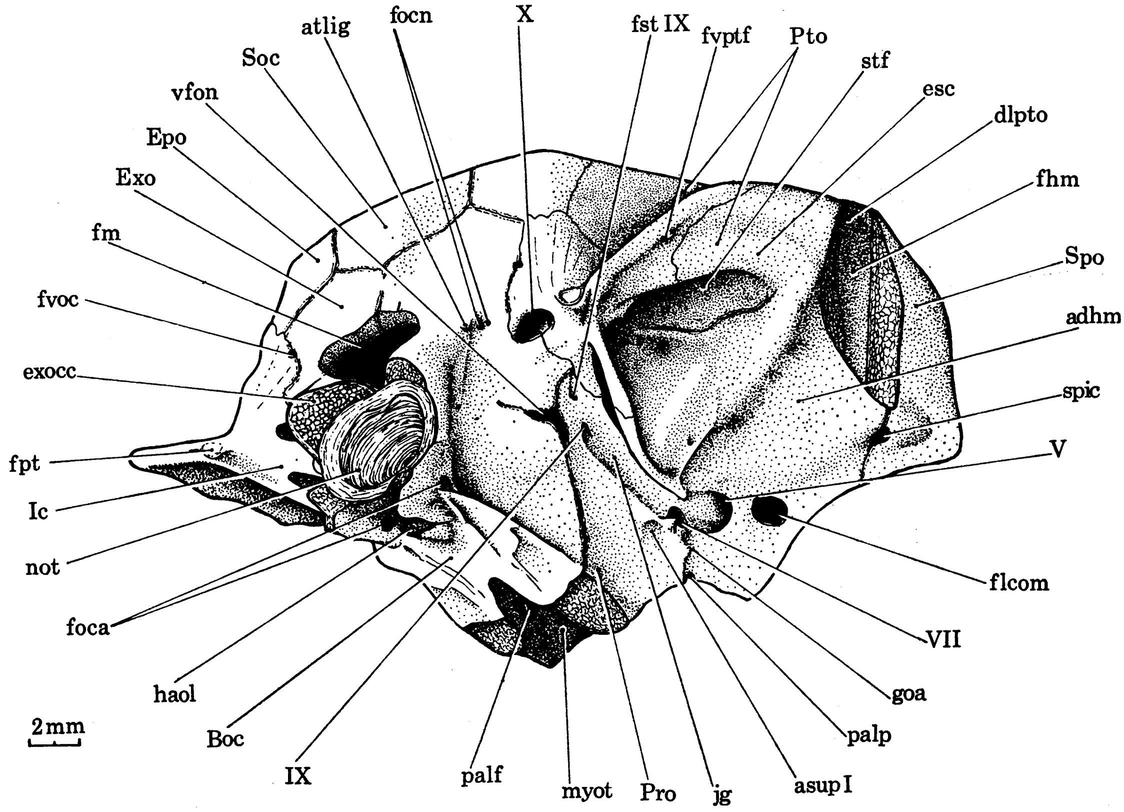


FIGURE 71. Callovian *Pholidophorus* sp. Preserved parts of neurocranium in postero-ventro-lateral view, from the right side. From 32579.

(IX, figures 68, 71, 76) lies in the posterior part of the jugular groove, as in *P. bechei.* In the Callovian species there is a separate foramen for the supratemporal branch of the glossopharyngeal (fst IX, figure 71) near the posterior margin of the prootic. The groove for the orbital artery (goa) runs up into the jugular groove just in front of the facial foramen, as in *P. bechei*, but most of the groove lay on the ascending process of the parasphenoid (figure 141). In *P. germanicus* the membranous wall of the short prootic portion of the groove is perforated by a foramen leading into the myodome (palp, figure 76) and probably transmitting the posterior branch of the palatine nerve. In the Callovian species this foramen notches the lower border of the prootic. The *lateral commissure* (lcom), bridging the jugular groove anteriorly, is short and thick in *P. germanicus*, as in *P. bechei.* In the Callovian species the lateral commissure is much less massive than in *P. germanicus*, consisting mainly of thin membrane bone, and contains a large opening (flcom, figures 67, 68, 71, 72). There seems to be no structure which could have passed through this aperture, and it may well be only a fenestration of the thin membrane bone. The foramina of the facial and trigeminal nerves are described below.

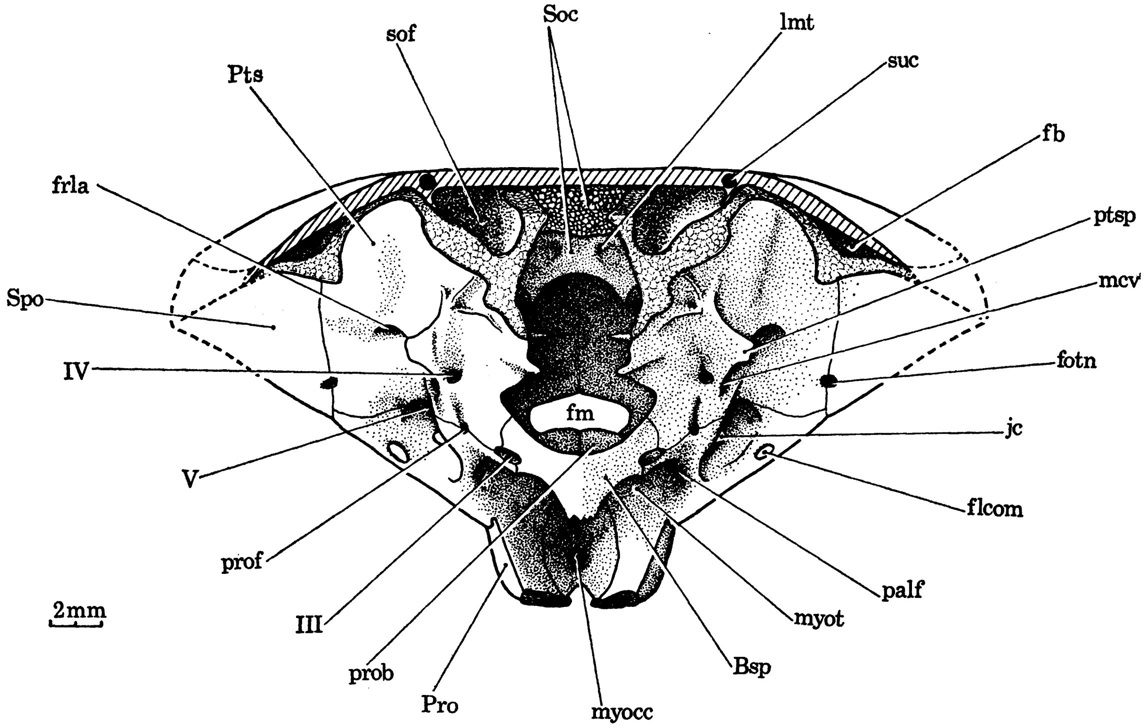


FIGURE 72. Callovian *Pholidophorus* sp. Preserved parts of neurocranium and attached roofing bones in anterior view, from 32579. Cut surfaces of dermal bones cross-hatched.

Above the jugular groove, the lateral face of the prootic contains two large depressions separated by an oblique crest. The anterior depression (adhm, figures 67, 68, 71, 76) is relatively shallow and housed the adductor muscle of the hyomandibular. The posterior depression (stf) is the anterior part of the subtemporal fossa. The crest separating these two depressions is irregular and pitted, as is the bone on either side of it, and several nutritive foramina lead into the thickness of the bone. Near the anterior margin of the lateral face of the prootic, in front of the adductor hyomandibulae fossa, there is a shallow spiracular groove (spig, figures 67, 68, 76) which turns somewhat posteriorly at the upper edge of the bone. The anterior part of the articular facet for the hyomandibular lay in cartilage lateral to the upper part of the prootic. The ventral face of the prootic consists of thin membrane bone anteriorly, especially in the Callovian species (figure 68), and posteriorly of thick endochondral bone ending in cartilage which met the parasphenoid.

The posterior face of the prootic is occupied by the openings of the otic part of the myodome and saccular recess (sacr) ventrally, the subtemporal fossa in the middle of the bone, and the recess for the ampullae of the posterior (Callovian species) or external (*P. germanicus*) semicircular canals (ampp, ampe) dorsally. The posterior margins of the prootic are without perichondral bone, and in the Callovian species they suture with the basi-exoccipital ventrally and fuse with the pterotic dorsally while in *P. germanicus* they ended in cartilage passing back to the basi-exoccipital ventrally (fissura oticalis ventralis) and to the opisthotic and pterotic dorsally (figure 96).

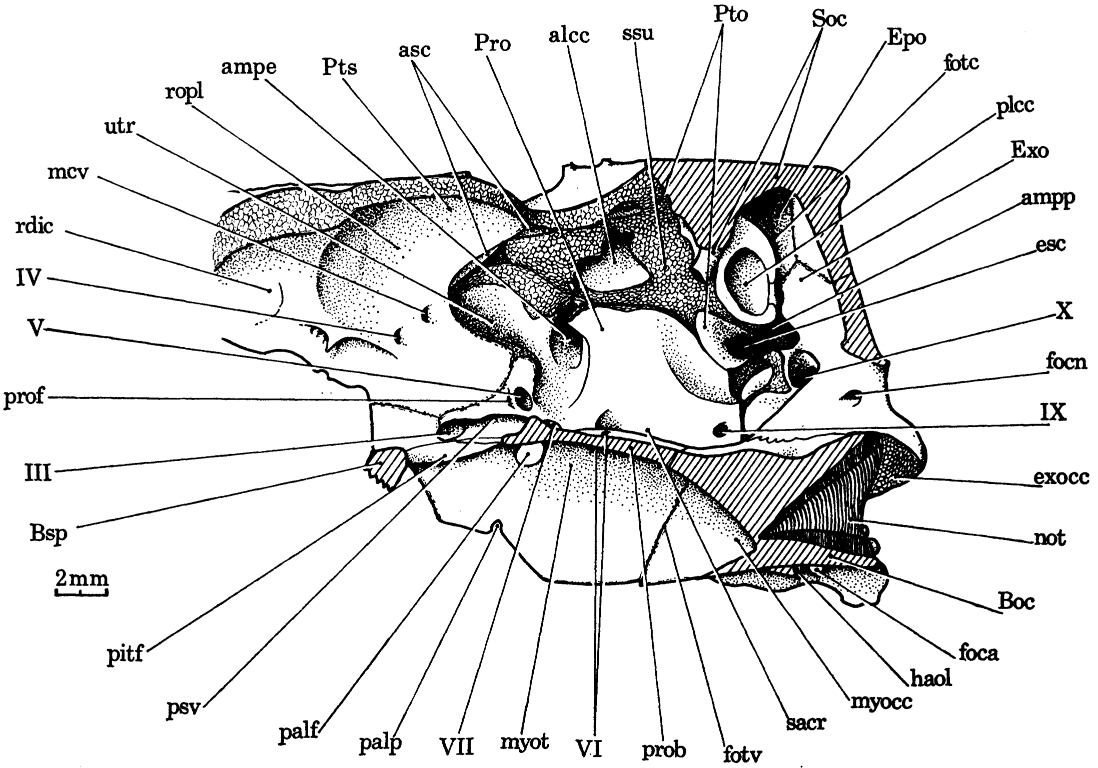


FIGURE 73. Callovian *Pholidophorus* sp. Reconstruction of preserved parts of neurocranium in sagittal section, from the left side, based on 32579. Sectioned surfaces cross-hatched.

The dorsal surface of the prootic (figures 69, 75) has a small concave area lined with perichondral bone which contributes to the floor of the fossa bridgei, but it is otherwise without perichondral lining. In *P. germanicus* the upper surface of the prootic was separated from the neighbouring bones by cartilage, but in the Callovian species it meets the pterosphenoid and sphenotic anteriorly and the pterotic posteriorly. The part of the fossa bridgei floored by the prootic is proportionally larger in *P. germanicus* (figure 75) than in the Callovian species (figure 69).

The anterior face of the prootic (figures 72, 76*c*) surrounds the orbital opening of the myodome (myot) ventrally, contains the anterior opening of the trigeminofacial chamber dorsolateral to the myodome, and above this surrounds the ampullary chamber of the anterior

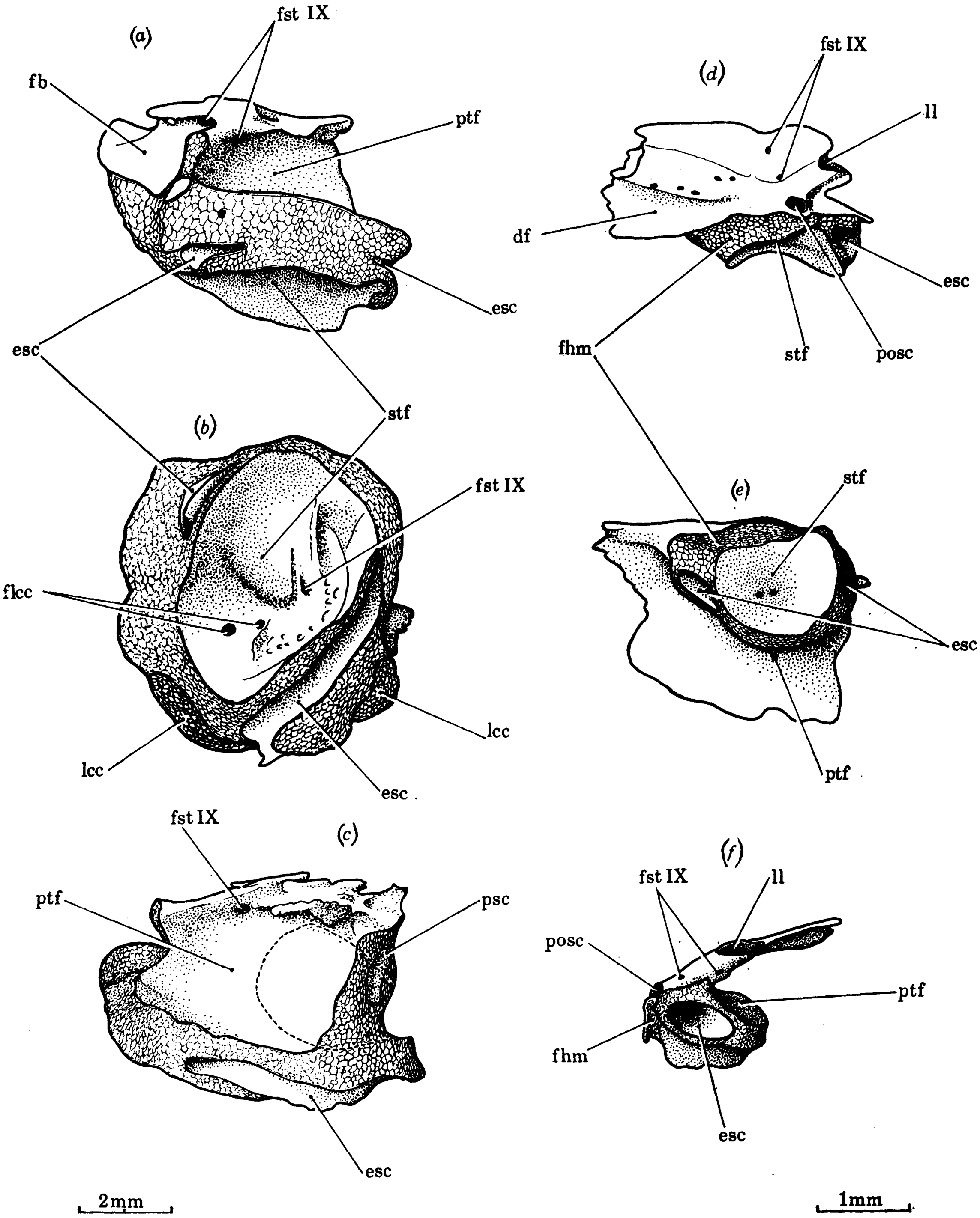


FIGURE 74. (*a–c*) Left pterotic of *Pholidophorus germanicus* Quenstedt, from P.3704, in lateral (*a*), ventral (*b*, anterior to left) and posterior (*c*) views. In (*c*) the outline of the lateral cranial canal is indicated by a broken line. (*d–f*) Left pterotic (incorporating dermopterotic) of Callovian *Leptolepis* sp. in lateral (*d*), ventral (*e*) and posterior (*f*) views, from P.51727.

semicircular canal (figure 73; ampa, figure 76). In the Callovian species the anterior face of the prootic meets the pterosphenoid and sphenotic dorsally in the wall of the orbit; in *P. germanicus* narrow zones of cartilage separated these bones.

The medial face of the prootic (figures 73, 76*b*) is occupied by the myodome ventrally and the cranial cavity and labyrinth dorsally. The myodome is separated from the cranial cavity by the prootic bridge (prob), which is perforated by a foramen for the abducens nerve (VI, figures 69, 73, 76*b*). There is no fenestra in the prootic bridge such as there is in *P. bechei.* The antero-lateral edge of the prootic bridge meets the basisphenoid, and in *P. germanicus* the posterior margin of the pituitary fossa was formed by the cartilage covering the front of the prootic bridge. In the Callovian species the basisphenoid is more completely ossified and almost encloses the pituitary fossa (pitf, figures 68, 69). The oculomotor foramen (III, figures 67, 68, 69, 72, 73, 76) lies between the prootic and basisphenoid, notching both bones. From the oculomotor notch in the prootic a groove runs postero-laterally across the upper surface of the prootic bridge and ends in a deep, blind recess (psv, figures 69, 73, 75, 76*b*) just in front of the internal opening of the facial canal: this recess contained the lateral part of the saccus vasculosus. Lateral to the prootic bridge, the saccular recess (sacr, figures 69, 73, 75, 76*b*) communicates widely with the cranial cavity. The saccular recess ends anteriorly close behind the facial foramen. The internal opening of the glossopharyngeal foramen (IX, figures 73, 76*b*) lies close

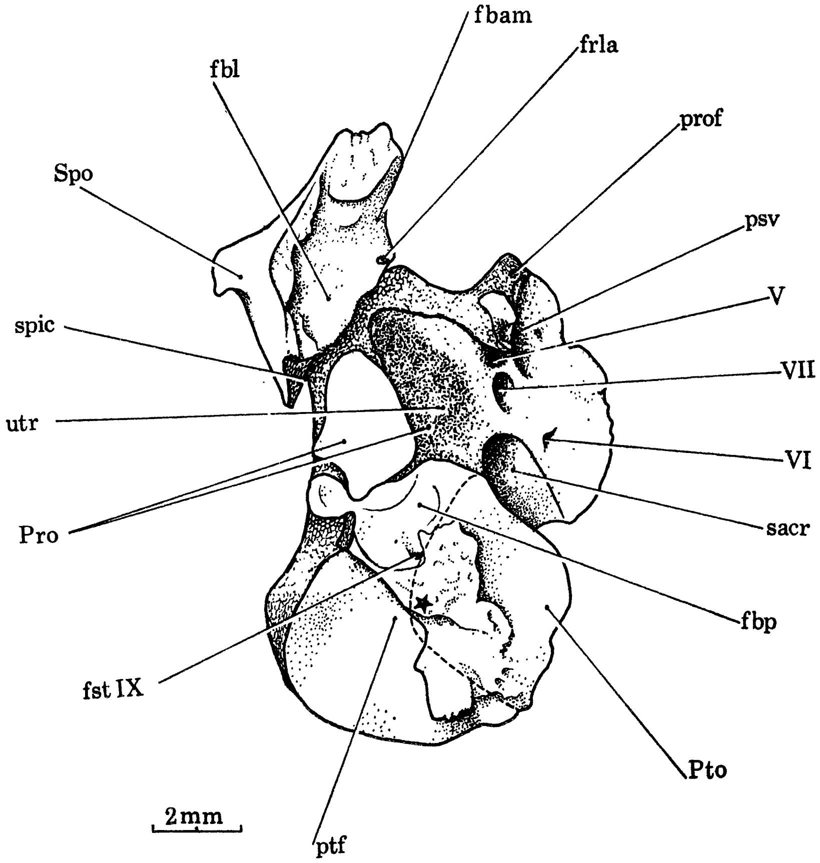


FIGURE 75. *Pholidophorus germanicus* Quenstedt. Left sphenotic, prootic and pterotic in dorsal view, from P.3704. The outline of the lateral cranial canal in the pterotic is indicated by a broken line; an asterisk marks the ossification centre of the pterotic.

to the posterior margin of the prootic, in the lateral wall of the saccular recess. Above the saccular recess the anterior part of the internal face of the prootic is occupied by a large, rounded depression (utr, figures 73, 75, 76*b*) which housed the utriculus. The ampullae of the anterior and external semicircular canals lay in antero-dorsal and postero-lateral extensions of this depression (ampa, ampe, figures 73, 76), and the anterior part of the external canal ran out to the pterotic through a notch in the dorsal edge of the prootic. In the more completely ossified Callovian species the internal surface of the prootic contributes to the chamber for the ampulla of the posterior semicircular canal (ampp, figure 73) above the glossopharyngeal foramen.

The canal for the facial nerve originates in an oval foramen (VII, figures 69, 73, 75) which is ventro-laterally directed and not recessed in the prootic. This foramen leads into a cavity in the prootic which communicates with the myodome by a large palatine fenestra (palf, figures 71, 72, 73, 76 *b*, *c*) and with the jugular groove by a smaller, laterally directed foramen (VII, figures 67, 71, 76*a*) which is about equal in size to the internal opening of the passage. The geniculate ganglion evidently lay in this cavity in the prootic, as in *P. bechei*, and from it the palatine nerve passed down into the myodome and the hyomandibular trunk passed laterally. The canal for the trigeminal nerve originates antero-dorsal to the facial canal in an antero-laterally directed foramen (V, figures 73, 75, 76*b*), somewhat recessed in the bone and about half as large again as the facial foramen. As in *P. bechei*, the trigeminal canal opens into the dorso-medial wall of the orbital opening of the trigeminofacial chamber (V, figures 67, 72, 76*c*), where there is a recess which probably housed the gasserian and lateralis ganglia, and the superficial ophthalmic nerves ran upwards in a groove across the orbital surface of the prootic and pterosphenoid. The profundus nerve passed through a narrow canal which originates just in front of the trigeminal canal (prof, figures 73, 76*b*) and opens into the orbit above the oculomotor foramen. On one side of the specimen of *P. germanicus* the profundus canal lies mainly within the prootic but opened into the orbit through the cartilage between the prootic and pterosphenoid (figure 76), while on the other side of the specimen the canal originated in that cartilage and ran mainly through the pterosphenoid (figure 79). In the Callovian species the profundus canal originates in the prootic and emerges on the pterosphenoid/prootic suture (figure 72). On the most anterior part of the internal face of the prootic, above the internal opening of the profundus canal, there is a depression (ropl, figures 73, 76*b*) separated from the rest of this surface by a crest: this is the lowermost part of the recess housing the optic lobes.

The *sphenotic* (Spo) of *P. germanicus* is shown in dorsal view in figure 75 and in lateral and medial view in figure 77. In both species the sphenotic is relatively small and does not extend far enough medially to enter the wall of the cranial or labyrinth cavities, so that its inner face is without perichondral bone (figures 73, 77*b*). The postorbital process (damaged in the Callovian species) lies in the centre of the lateral surface of the bone. In front of the postorbital process the orbital surface of the sphenotic is smoothly concave. Behind the postorbital process there are two shallow depressions, the upper (df) being the anterior part of the dilatator fossa, the lower, which lies antero-dorsal to the front end of the hyomandibular facet, having contained the origin of the levator arcus palatini muscle (lapf).

The dorsal surface of the sphenotic (figures 69, 75) contains the antero-lateral part of the fossa bridgei. This is limited antero- and postero-laterally by raised shelves of bone, the anterior one meeting the frontal, the lateral one overhanging the most lateral part of the fossa and meeting the dermopterotic, with the anterior part of the descending lamina of the

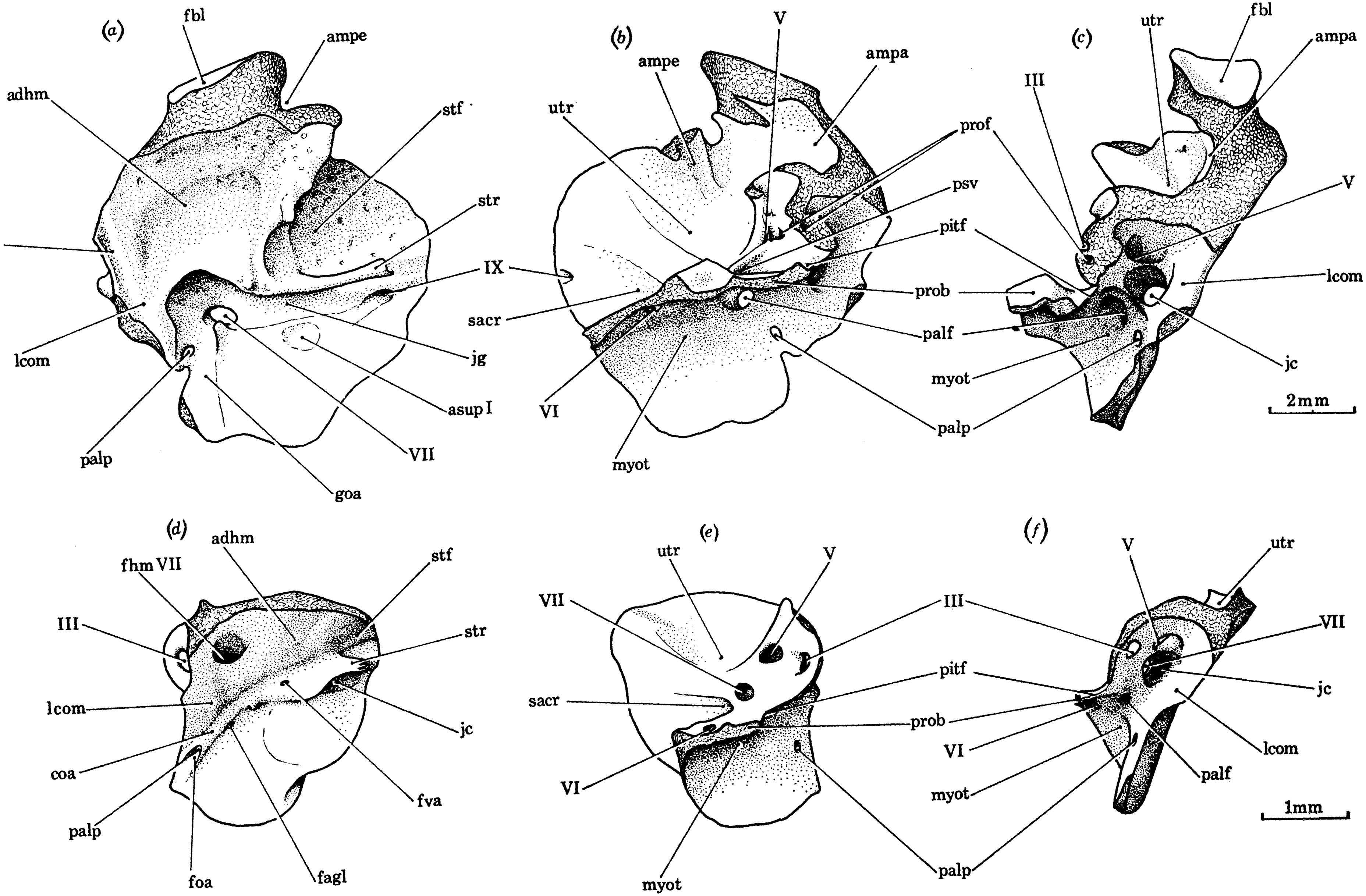


FIGURE 76. Left prootic of *Pholidophorus germanicus* Quenstedt (*a–c*), from P.3704, and Callovian *Leptolepis* sp. (*d–f*), from P.51729, in lateral (*a*, *d*), medial (*b*, *e*) and anterior (*c*, *f*) views.

dermopterotic (dlpto, figure 69) applied to its inner face. The sphenotic part of the fossa bridgei consists of a deep posterior portion (fbl)and a shallower anterior portion (fbam), separated by a low transverse ridge which is continuous postero-medially with the ridge over the anterior semicircular canal. In *P. germanicus* the sphenotic is broader on the right side of the specimen than on the left, and at the medial edge of this transverse ridge on the right side there is the opening of a canal (frla, figures 75, 77*b*) which passed up from the orbit through the pterosphenoid (see below). This canal transmitted the recurrent branch of the facial nerve (ramus lateralis accessorius): in the Callovian species this nerve passed through the pterosphenoid (see below).

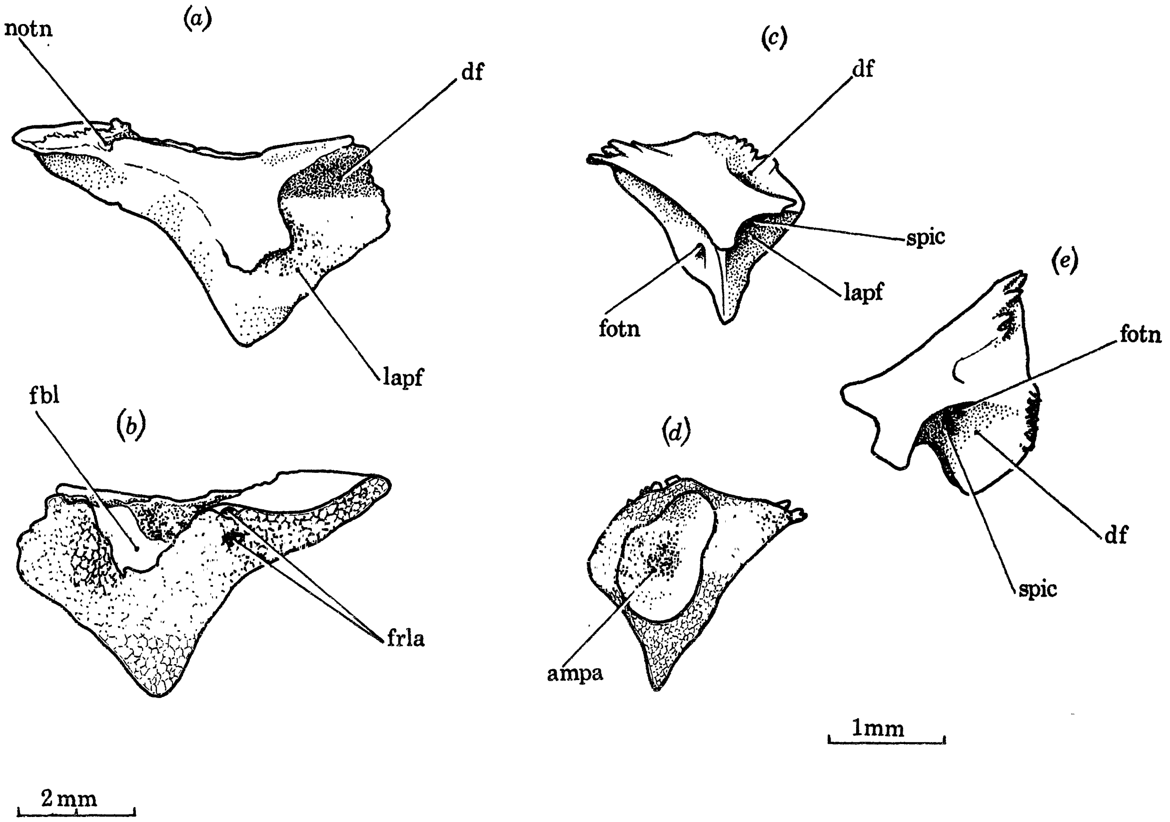


FIGURE 77. Left sphenotic of *Pholidophorus germanicus* Quenstedt (*a*, *b*), from P.3704, and Callovian *Leptolepis* sp. (*c*–*e*), from P.51730, in lateral (*a*, *c*), medial (*b*, *d*) and dorsal (*e*) views. Both reversed.

In *P. germanicus* the otic nerve and spiracular canal passed through the cartilage medial to the sphenotic and left no impression on the bone. In the more completely ossified Callovian species the orbital opening of the otic nerve canal (fotn, figure 72) lies on the suture between the sphenotic and pterosphenoid, while the lower opening of the spiracular canal (spic, figures 67, 68, 71) lies on the lateral surface of the braincase, on the suture between the sphenotic and prootic, immediately in front of the hyomandibular facet and close behind the foramen for the otic nerve. The otic nerve canal leads into the spiracular canal on the medial face of the sphenotic. The spiracular canal is dilated at this junction and was only separated from the foremost loop of the anterior semicircular canal by a thin layer of cartilage. The spiracular sense organ probably lay in this dilated portion of the canal. Dorsally, the canal opens into the fossa bridgei through a notch in the posterior margin of the sphenotic (spic, figure 69). A tapering process of the descending lamina of the dermopterotic fits into this notch, and there is a groove on the inner face of this process which leads postero-dorsally and ends in a shallow depression (tsp, figure 69). I assume that the spiracular tube lay in this groove and ended in the depression.

In the fossa bridgei, the otic nerve appears to have branched, the anterior branch, which in the Callovian species emerged into the fossa through a separate canal leading antero-dorsally from the spiracular canal (fotn, figure 69), passing out through a notch (notn, figure 77) on the sphenotic between the areas of contact with the frontal and dermopterotic, and the posterior branch passing into the dilatator fossa through one or two foramina in the descending lamina of the dermopterotic (fotn_1, figure 69).

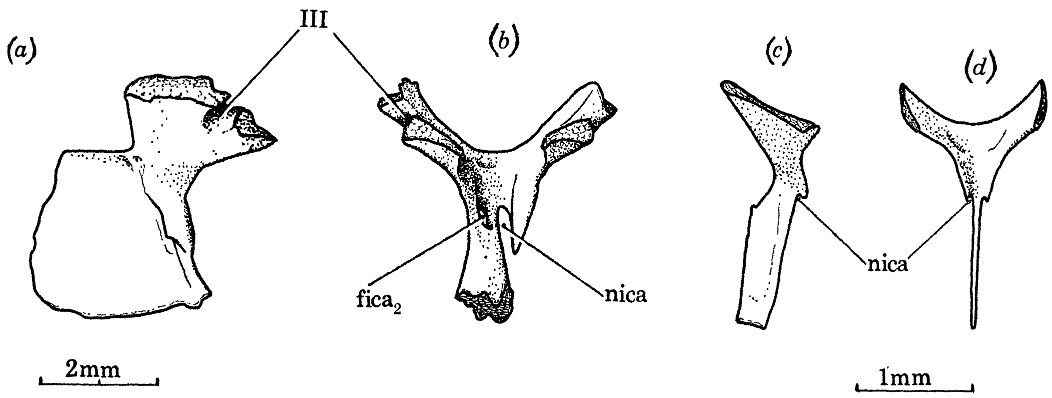


FIGURE 78. Basisphenoid of *Pholidophorus germanicus* Quenstedt (*a*, *b*), from P.3704, and Callovian *Leptolepis* sp. (*c*, *d*), from P.51731, in left lateral (*a*, *c*) and posterior (*b*, *d*) views.

The *basisphenoid* of *P. germanicus* is shown in lateral and posterior views in figure 78. It is comparable with the corresponding part of the braincase in *P. bechei* but is much less completely ossified ventrally. The pedicel of the basisphenoid, forming the postero-ventral part of the interorbital septum and separating the left and right openings of the myodome, is much longer rostro-caudally than in *P. bechei*, but anteriorly it consists only of thin membrane bone. The broad posterior part of the pedicel is grooved and penetrated by the internal carotid (fica_2) in just the same way as in *P. bechei* except that on one side of the fish the foramen for the artery is incompletely ossified (nica). The dorso-lateral arms of the basisphenoid, separating the optic fenestra and pituitary fossa, were joined by cartilage to the pterosphenoids laterally and the prootics posteriorly. The anterior margin of the oculomotor foramen is formed by a notch (III) in the basisphenoid.

In the Callovian species the basisphenoid pedicel is badly damaged and its foot is embedded in a mass of pyrite, but the upper part of the bone (Bsp, figures 68, 72) is more completely ossified than that of *P. germanicus* so that it enclosed the pituitary fossa (pitf) and is sutured to the pterosphenoid and prootic. The foot of the basisphenoid pedicel, cartilaginous in *P. germanicus*, appears to be ossified much as in *P. bechei* in the Callovian species, with a pair of parabasal canals for the palatine nerves and internal carotids. But the basisphenoid makes no contribution to the basipterygoid process, does not surround the upper opening of the bucco-hypophysial canal, and does not meet the prootic, so that the foremost part of the myodome has no endochondral wall or floor and is lined only by the parasphenoid.

The *pterosphenoid* (Pts) of *P. germanicus* is shown in lateral, medial and dorso-lateral view in figure 79. It is a thick wedge of cartilage bone, broadest dorsally and narrow ventrally, where it borders the optic fenestra. The dorsal surface of the bone (figure 79*b*) was mostly covered by cartilage and there is only a small, concave area of perichondral bone contributing to the roof of the braincase. In the Callovian species the pterosphenoid is incomplete anteriorly but is much more thoroughly ossified than in *P. germanicus*: together with the pterotic and prootic it is one of the largest bones in the braincase The ventral part of the bone is closely comparable with that of *P. germanicus*, but the entire dorsal surface (Pts, figure 69) is perichondrally lined and is very extensive. This dorsal surface consists of three portions, a postero-medial raised area which is flat (except for grooves containing nerves and vessels) and which met the overlying frontal, an antero-medial depression (sof) which is homologous with the posterior part of the paired, longitudinal depressions above the orbit (supraorbital fossae) in *P. bechei* (figure 60), and a very deep lateral depression (fbam), separated from the supraorbital fossa by a longitudinal crest, which is the foremost part of the fossa bridgei. The fossa bridgei and post-temporal fossa are

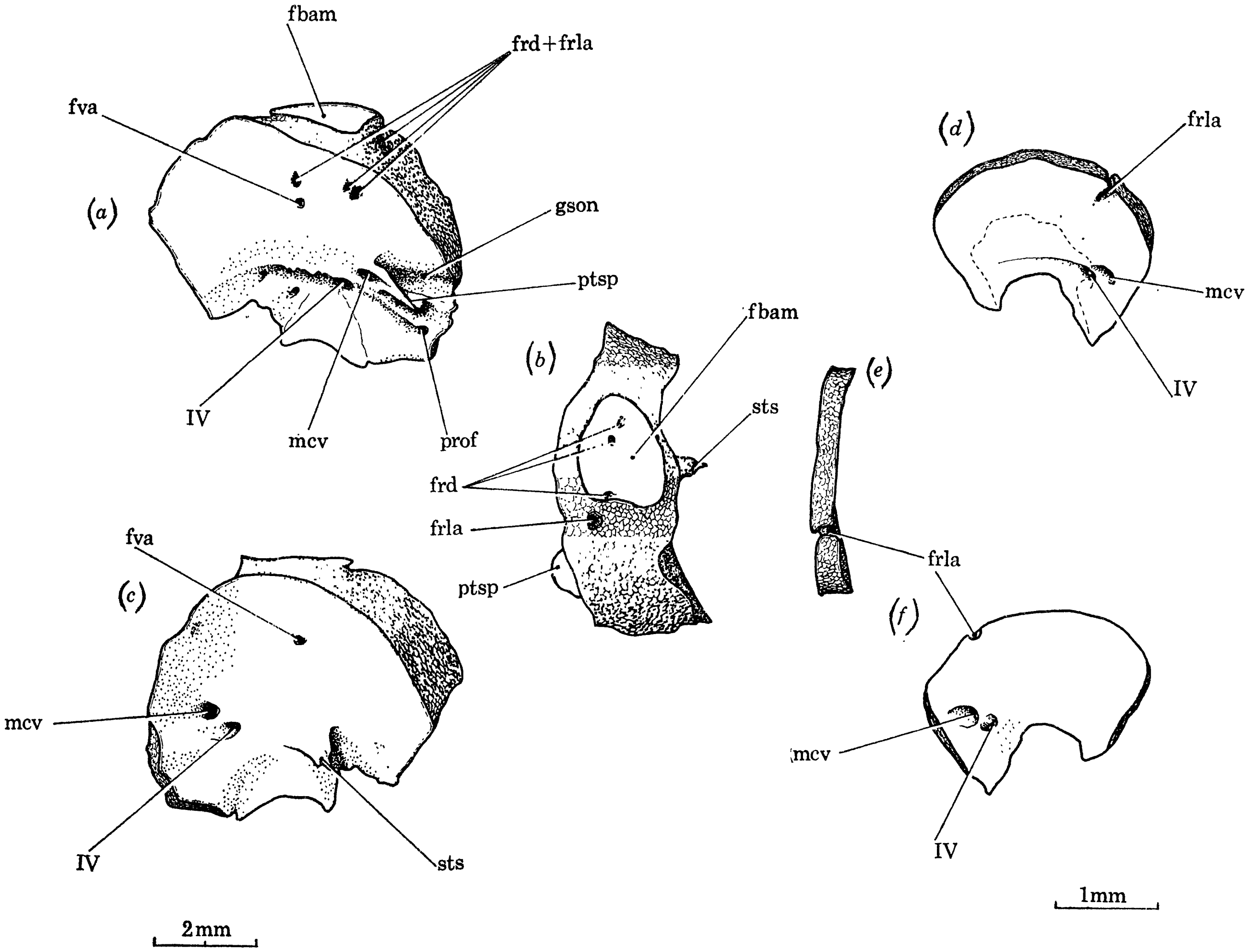


FIGURE 79. Left pterosphenoid of *Pholidophorus germanicus* Quenstedt (*a–c*), from P.3704, and Callovian *Leptolepis* sp. (*d–f*), from P.51733, in lateral (*a*, *d*), dorso-lateral (*b*, *e*) and medial (*c*, *f*) views. In (*d*) the broken line indicates the limit of the endochondral portion of the bone.

confluent in this species, and this depression in the pterosphenoid presumably served for trunk muscle insertion. The small perichondrally lined area on the dorsal surface of the pterosphenoid of *P. germanicus* (fbam, figure 79) is the homologue of the deepest part of the pterosphenoid portion of the fossa bridgei in the Callovian species.

In the Callovian species the pterosphenoid meets the basisphenoid and prootic ventrally in the orbit (figure 72), the sphenotic laterally and the prootic and pterotic posteriorly in the neurocranial roof (figure 69). It is separated from its fellow by the anterior dorsal fontanelle (adf, figure 69) dorsally and the optic fenestra ventrally, and presumably met the orbitosphenoid, missing in this specimen, anteriorly. In *P. germanicus* the pterosphenoid had similar relationships but the bones were separated by zones of cartilage, which must have been very extensive in the roof of the braincase.

The upper part of the inner, cerebral surface of the pterosphenoid is smoothly concave in *P. germanicus* (figure 79*b*), this concavity corresponding to the portion of the cranial cavity in *P. bechei* which housed the optic lobe. In the Callovian species there is a second depression anteriorly (rdic, figure 73) on the inner face of the pterosphenoid, homologous with the part of the cranial cavity housing the anterior part of the diencephalon in *P. bechei*. Below the depression for the optic lobe there is in both species a spur of membrane bone (sts, figure 79), more extensive in the Callovian species (figure 72), projecting almost horizontally into the cranial cavity, with a projection on the ventral margin of the bone below it. This projection corresponds to the constriction separating the true optic fenestra from the anterior, membrane-closed portion of the fenestra in *P. bechei*. The spur projecting into the cranial cavity is also present in rudimentary form in *P. bechei* (figures 62, 65). This spur must have lain below the brain, and the membrane closing the anterior portion of the optic fenestra must have been inserted on it.

On the inner face of the pterosphenoid there are three foramina in *P. germanicus*, two in the Callovian species. The smallest of the three foramina in *P. germanicus* (fva, figure 79) is absent in the Callovian species and passes horizontally through the thick upper part of the bone: presumably it transmitted a small vessel. The other two foramina lie close together in the lower part of the depression for the optic lobe and pass antero-laterally through the bone. The more anterior foramen transmitted the trochlear nerve (IV, figures 73, 79), the more posterior the middle cerebral vein (mcv). The external opening of the trochlear foramen (IV, figures 67, 68, 72, 79) is in line with a groove leading up from the profundus foramen, as in *P. bechei*, while the external opening of the vascular foramen (mcv) is in line with the groove for the superficial ophthalmic nerves, as in *P. bechei*, and passes through the foot of a large wing of membrane bone, projecting ventro-laterally. This wing (ptsp), represented in *P. bechei* only by a weak ridge, is short rostro-caudally but wide in *P. germanicus*, longer and more irregular in the Callovian species but broken off distally on both sides of the specimen (figures 67, 68, 72). This wing is the homologue of the pterosphenoid pedicle of *Amia*, some teleosts (Allis 1909, p. 40), and *Pteronisculus magnus* (Nielsen 1942, p. 90). It is smaller than the pedicle in *Amia*, which extends ventrally to join the ascending process of the parasphenoid and is endochondrally ossified distally. In *Pteronisculus magnus* the pedicle is shorter rostro-caudally than in the pholidophorids and consists of endochondral bone. In teleosts the pedicle seems always to consist of membrane bone and is comparable with that of pholidophorids. Behind the pedicle there is a more or less well marked recess, connected with the groove for the superficial ophthalmic nerves, but it is unlikely that any structure lay in this recess. The superficial ophthalmic nerves passed lateral to the pedicle, and in the upper part of the lateral surface of the pterosphenoid there are several foramina leading to dorsally directed canals which transmitted branches of the nerves to the skull roof. In *P. germanicus* there are three or four of these foramina (frd, frla, figure 79), in the Callovian species there are two small foramina on the left side, one very large one on the right side (frla, figures 68, 69). The most posterior of the several foramina in *P. germanicus* and the more posterior of the two on the left side of the Callovian species, which lead into the fossa bridgei (through the sphenotic on one side of *P. germanicus*, figure 79), transmitted the ramus lateralis accessorius of the facial nerve, and on the right side of the Callovian species this nerve and the succeeding branch of the superficial ophthalmics passed together through the single large canal.

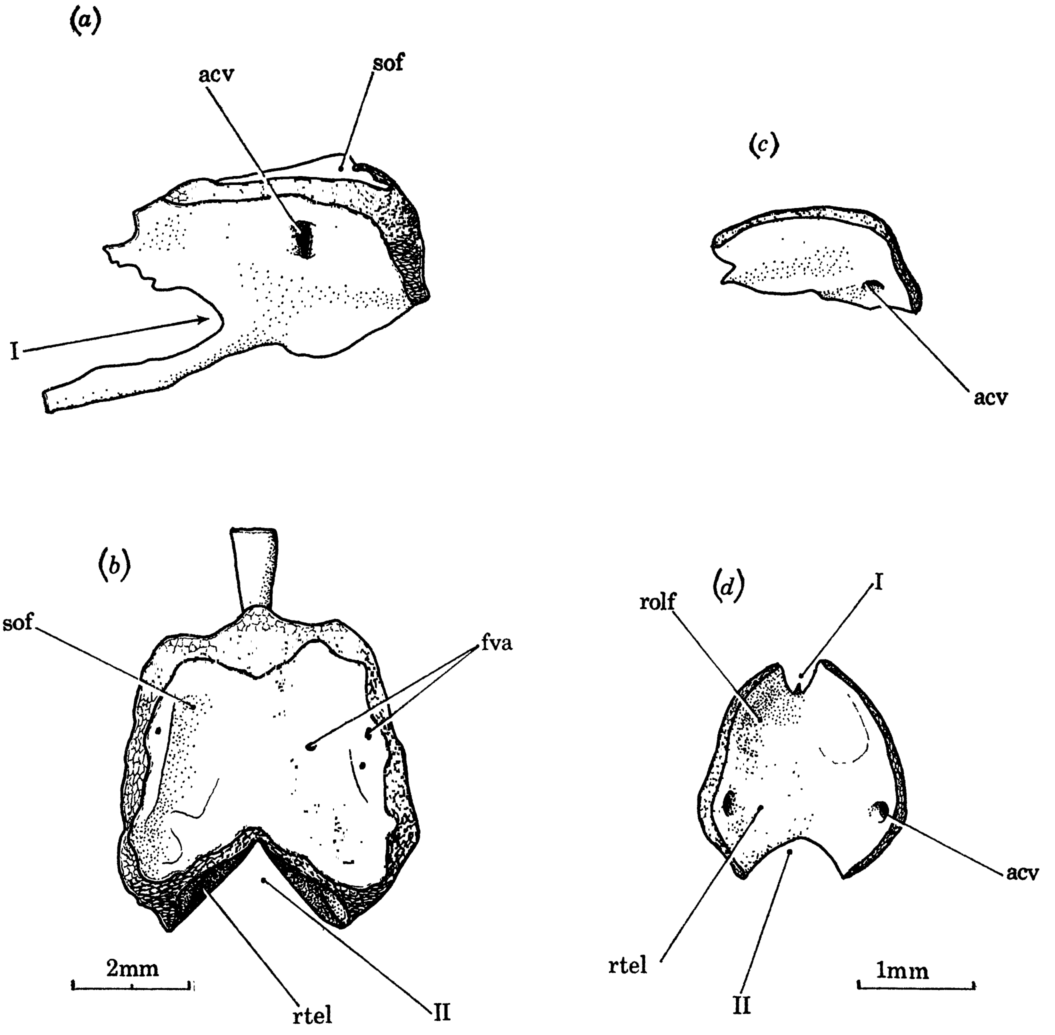


Figure 80. Orbitosphenoid of *Pholidophorus germanicus* Quenstedt (*a*, *b*), from P.3704, and Callovian *Leptolepis* sp. (*c*, *d*), from P.51734, in left lateral (*a*, *c*) and dorsal (*b*, *d*) views.

The *orbitosphenoid* of *P. germanicus* is shown in lateral and dorsal view in figure 80: in the Callovian species this bone is not preserved. It is a median bone, and the only indication that it might have had a paired origin in ontogeny is a slight seam or crease in the mid-line on the posterior part of its ventral margin. The bone is triangular in section and completely surrounds the most anterior part of the cranial cavity. The olfactory nerves left through a median opening

(I) in its anterior edge, and below this opening there is a long, antero-ventrally directed process, capped in life with cartilage extending forwards into the ethmoid cartilage. The anterior cerebral vein passed through a long canal in the lateral wall of the bone (acv). The anterior part of the cranial cavity, enclosed within the orbitosphenoid, is narrow anteriorly, where the olfactory bulbs were housed, and shows a pair of expansions for the telencephalon (rtel) just below the internal opening of the anterior cerebral vein, as in *P. bechei*. Posteriorly, the ventral edge of the orbitosphenoid forms the anterior margin of the optic fenestra (II). The dorsal surface of the orbitosphenoid is mainly covered by perichondral bone, and forms a pair of longitudinal depressions separated by a median crest: these depressions, the supraorbital fossae (sof) were continued posteriorly on the pterosphenoids in the Callovian species. The median crest and the most lateral part of the dorsal surface contact the frontals. The small, irregular foramina on the upper surface of the orbitosphenoid (figure 80*b*) are vascular, the superficial ophthalmic nerves having passed lateral to the bone.

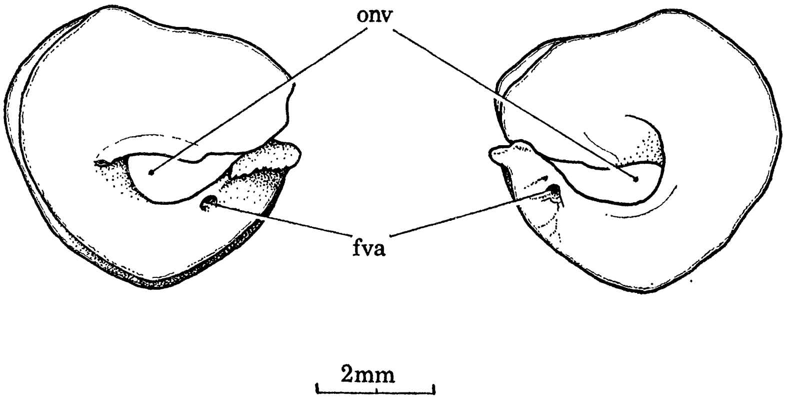


FIGURE 81. *Pholidophorus germanicus* Quenstedt. Left basal sclerotic bone in lateral (left) and medial (right) views, from P.3704.

In the Callovian species no *sclerotic ossifications* are preserved. In *P. germanicus* the circumcorneal area of the sclerotic is ossified in a ring containing four segments. Each of these consists of three separate plates: an inner and outer layer of very thin perichondral bone, developed on the surfaces of the sclerotic cartilage, and a superficial layer of thicker dermal bone which is thickest around the margin of the cornea. The outer face of this dermal bone bears a few delicate, reticulate grooves radiating from its centre of ossification, which is the mid-point of the corneal margin. These three plates are closely applied to one another, but are nowhere fused.

The innermost part of the sclerotic of *P. germanicus*, around the entry of the optic nerve and vessels, is ossified as a *basal sclerotic bone*, shown in medial and lateral view in figure 81. The bone is discoid, only slightly dished, and consists of inner and outer layers of perichondral bone with very little endochondral bone between them. The disk is interrupted posteriorly by a notch which extends to the centre of the bone, where it is widest. The walls of this notch are offset so that it forms a canal running antero-ventrally into the eyeball, and this canal (onv) contained the optic nerve and the veins and arteries of the eye. On the lateral face of the bone, close to the postero-ventral margin of the canal, there is a small foramen (fva, figure 81) which leads through the bone and ramifies on its inner face. This foramen must have transmitted a vessel supplying or draining the tissue on the outer surface of the sclerotic. A basal sclerotic bone does not seem to have been described in any living actinopterygian, and the only fossil forms in which it is described are the Cretaceous ichthyodectids, where Bardack (1965, pp. 44, 56, fig. 16) illustrates it in *Ichthyodectes* and mentions its presence in *Xiphactinus*. Amongst pholidophorids, a basal sclerotic also occurs in *P. macrocephalus* (p. 368), and probably in *P. bechei*.

The *cranial cavity* is similar in *P. germanicus* and the Callovian species, but is more easily interpreted in the intact braincase of the latter (figure 73). The most anterior part of the cranial cavity, where the olfactory bulbs and telencephalon were housed in the orbitosphenoid, is not preserved in the Callovian species, but has been described above in *P. germanicus*. The optic lobes lay in a large depression (ropl, figure 73) on the inner face of the pterosphenoid, with a small postero-ventral contribution from the prootic. This depression is not so clearly separated from the utricular recess and the ampullary chamber of the anterior semicircular canal as it is in *P. bechei* (figure 65). The internal openings of the canals for the trochlear nerve and middle cerebral vein (IV, mcv) lie in this depression, and its antero-ventral border is marked by the spur of membrane bone projecting into the cranial cavity and by a crest behind this spur. Below the depression for the optic lobe lies the median pituitary fossa (pitf), enclosed within the basisphenoid. The oculomotor foramen (III) lies lateral to the pituitary fossa, and behind the oculomotor foramen there is the groove and pit (psv) in the prootic housing the lateral part of the saccus vasculosus. The utricular recess (utr) is much less sharply separated from the cranial cavity than it is in *P. bechei*, and the floor of the recess is continuous with the part of the floor of the cranial cavity containing the facial foramen. Above the trigeminal foramen, a vertical crest on the prootic separates the utricular recess from the depression for the optic lobe. This crest was continued upwards in cartilage covering the junction of the prootic and pterosphenoid. Posteriorly, the utricular recess is limited by a crest on the upper part of the prootic, and this crest was continued upwards in cartilage covering the junction of the prootic, pterotic and pterosphenoid. The relief of the posterior part of the cranial cavity is obscured by the openings of the labyrinth cavity and lateral cranial canal, but on the anterior face of the supraoccipital there is a pair of depressions (lmt, figure 72), medial to the uppermost part of the sinus communis, which may be the impressions of a pair of metencephalic lobes, as in *Boreosomus* (Nielsen 1942, fig. 66) and some Kansas palaeoniscoids (Stensiö 1963, fig. 37*a*).

The anterior dorsal fontanelle in the fossil skull is an irregular opening extending from the supraoccipital to the hind end of the orbitosphenoid (adf, figure 69). The walls of the fontanelle are of thick endochondral bone, without perichondral lining (figure 73), and in life the fontanelle must have been largely occluded by cartilage, so that it was smaller than in *P. bechei* (figure 60).

The labyrinth cavity of the Callovian species is less completely enveloped in bone than it is in *P. bechei*. The otolith chamber (sacr), enclosed within the prootic and basi-exoccipital and communicating widely with the cranial cavity above, shows some signs of division into an anterior saccular division and a posterior lagenar division, behind the glossopharyngeal foramen. The sinus communis, rising above the saccular recess, was separated from the lateral cranial canal by an ossified wall, as in *P. bechei*. This wall, part of the pterotic, lacks a perichondral inner lining and so was covered by cartilage, but the bone alone is thicker and longer (rostro-caudally) than its homologue in *P. bechei*. The uppermost part of the posterior semicircular canal lay between the supraoccipital and pterotic, and a small area of perichondral bone on the antero-lateral face of the supraoccipital contributes to the wall of this cavity. Further postero-laterally, the posterior semicircular canal was almost surrounded by the pterotic, with a small strip of cartilage on its hind face separating it from the perichondrally lined anterior face of the epioccipital (the cranial fissure). Below this, the canal emerged from the pterotic and lay in cartilage anterior to the intercalar before curving antero-ventrally into its ampulla (ampp), which was enclosed by the exoccipital, prootic and pterotic. From the upper end of the sinus communis the anterior semicircular canal ran forwards through a perichondrally lined channel in the pterotic (asc), then through a similar channel in the hind face of the pterosphenoid, and then looped down between the sphenotic, pterosphenoid and prootic to enter its ampulla, which lay in an anterior diverticulum of the utricular recess in the prootic. The external semicircular canal passed through the anterior part of the chamber for the ampulla of the posterior semicircular canal (esc), as in *P. bechei*, and looped around the subtemporal fossa through the pterotic to enter its ampullary chamber (ampe) in the prootic behind the utricular recess.

The lateral cranial canal (alcc, plcc, figure 73) has been described above (p. 342), with the pterotic.

(*c*) *Callovian* Leptolepis *sp.*

The otic and orbitotemporal regions of this species are typically teleostean except for one or two retained primitive characters. There are separate pterotic, prootic, sphenotic, pterosphenoid, basisphenoid and orbitosphenoid bones, and the endochondral pterotic is fused with the dermopterotic into a compound pterotic of normal teleostean type. The bones were separated by interspaces of cartilage which probably persisted throughout the life of the fish, since among the available material there is considerable variation in size but little in the extent of the bones (except for the pterotic).

The compound *pterotic* is shown in lateral, ventral and posterior view in figure 74 and in dorsal view in figure 147. The endochondral portion of the bone is small and very different from the complex pterotics of pholidophorids. In the most completely ossified examples it is a simple, almost disk-like bone, its concave dorsal and ventral surfaces respectively forming the floor of the posterior part of the post-temporal fossa (ptf) and the roof of the deepest part of the subtemporal fossa (stf), its ventro-lateral face forming the posterior part of the hyomandibular facet (fhm) and its lateral part containing a conduit for the external semicircular canal (esc). There is much variation in the extent of the endochondral portion of the pterotic; most specimens are so poorly ossified that the tube for the semicircular canal is incomplete ventrally, and the most lightly ossified specimens show that ossification began on the ventro-lateral (outer) surface of the descending lamina of the dermopterotic, above the middle part of the semicircular canal. Even at the earliest stages, the dermal and endochondral components are fused. Medially, the pterotic never extends far enough to form part of the wall of the cranial cavity: this marked difference from the pholidophorid pterotic is in part due to reduction in ossification, but is mainly a result of forward extension of the epioccipital (figure 49), which has come to occupy much of the territory of the pholidophorid pterotic and caused a shift in the ossification centre of the bone (p. 422).

The descending lamina of the dermopterotic is developed as in pholidophorids (figures 60, 69, 82, 146), below the sensory canal along the lateral margin of the bone. The lamina projects ventro-medially, forming the outer part of the floor of the post-temporal fossa and fusing with the autopterotic. The lamina is developed only on the posterior part of the pterotic, fading away anteriorly and projecting posteriorly beyond the body of the dermopterotic. In well ossified individuals this posterior projecting flange is fused into the endochondral part of the bone and only its tip is recognizable, projecting above the opening of the tube for the semicircular canal. The main dermal portion of the pterotic is the usual curved lamina roofing the post-temporal fossa, meeting the parietal medially and the frontal anteriorly (figure 147), and carrying the otic and temporal divisions of the main lateral line in a raised tube laterally. The tube for the sensory canal is sharply angled, with a short posterior portion, almost transverse, which received the canal from the supratemporal (ll), and a longitudinal anterior portion transmitting the canal to the dermosphenotic through a terminal opening. The preopercular canal joined the main canal through a lateral opening (posc) at the angle in the canal. There is a series of pores along the medial edge of the longitudinal portion of the canal, interspersed with and grading into small foramina, so that it is a matter of opinion how many pores there are. The illustrated specimen (figures 74*b*, 147) shows six or seven pores, but others have as few as three or four. The otic division of the canal was innervated by a branch of the otic nerve, entering the tube through a foramen medial to the anterior part of the descending lamina, the temporal division by a branch of the supratemporal ramus of the glossopharyngeal, entering through a foramen in the hind edge of the bone (fst IX, figure 74). Lateral to the anterior part of the sensory canal there is a projecting lamina of dermal bone which forms the upper border of the dilatator fossa (df) The middle pit-line, deeply incised on the bone in pholidophorids, is indicated in this *Leptolepis* only by a transverse alignment of two or (rarely) three minute foramina (figures 74, 147), transmitting branches of the glossopharyngeal nerve to the sense organs (the same foramina are recognizable in *Elops*), and by a slight notch in the medial edge of the bone.

The *prootic* is shown in lateral, medial and anterior view in figure 76. Like the endochondral part of the pterotic, it is less complex than its homologue in pholidophorids. It lacks the whole of the dorsal portion which in pholidophorids forms part of the floor of the fossa bridgei, and its contribution to the cranial cavity is correspondingly smaller. Posteriorly, the prootic is also less extensive than in pholidophorids, since most of the ventral part of the subtemporal fossa and the glossopharyngeal foramen are here contained in the exoccipital (figure 54). In general, the endochondral bone is also much thinner than in the pholidophorid prootic and its relief is less emphatic, so that the impression of various structures on the bone is less evident or absent. Thus there is no sign of the articulation of the first suprapharyngobranchial, the crest between the subtemporal fossa (stf) and the area of origin of the adductor muscle of the hyomandibular (adhm) is hardly recognizable, there is no sign of the spiracular groove (although a spiracular canal is still represented in the sphenotic, see below), and there is no recess for the saccus vasculosus behind the internal opening of the oculomotor foramen. On the other hand, the anterior part of the saccular recess is visible externally as a slight swelling or inflation of the prootic. This slight otic bulla is partially a consequence of the thinness of the bone, but the saccular recess is more extensive anteriorly than in pholidophorids, extending forwards as a pocket below the facial foramen.

As in pholidophorids and teleosts, the prootic surrounds the anterior part of the saccular recess (sacr, figure 76*e*) and myodome (myot, figures 76*e*,*f*), and contains the foramina of the oculomotor, trigeminal, facial and abducens nerves (III, V, VII, VI). The oculomotor foramen lies entirely within the prootic, not between it and the basisphenoid as it does in pholidophorids, but otherwise the passages for the nerves are much as in pholidophorids except that they are foramina, not canals, because of the much thinner bone they penetrate. The facial foramen is about as large as the trigeminal, not much smaller as it is in pholidophorids, suggesting that the geniculate ganglion lay partly in this opening in the cranial wall. This is also indicated by the position of the small palatine foramen (palf, figure 76*f*), which leads down into the myodome immediately outside the opening. There is no separate profundus foramen, and this nerve probably entered the orbit with the oculomotor, as it does in most teleosts, since the upper margin of the internal opening of the oculomotor foramen shows a slight groove running back towards the trigeminal foramen. The position of the pituitary fossa (pitf) is only indicated by a slight excavation of the medial edge of the prootic bridge (prob), between the areas of contact with the basisphenoid anteriorly and with its fellow posteriorly.

The most significant difference from the pholidophorid prootic concerns the structure of the jugular canal. In pholidophorids the jugular groove is only covered over as a canal for a short distance anteriorly: in other words, the lateral commissure is very short, hardly more than a strut across the foremost part of the jugular groove. In the Callovian *Leptolepis* the jugular groove is roofed almost from end to end of the prootic, forming a long jugular canal (jc) whose outer wall projects posteriorly in a jagged splint (str) which sutures with the intercalar. The groove for the orbital artery is also roofed over as a tube (coa) running up into the jugular canal. In the lateral wall of the jugular canal, between the trigeminal and facial foramina, there is a large dorso-laterally directed foramen (fhm VII) which transmitted the hyomandibular trunk of the facial nerve. This type of trigeminofacial chamber – a long jugular canal with its lateral wall perforated by the hyomandibular trunk and with a long canal for the orbital artery leading into its floor – is typical of palaeoniscoids (Nielsen 1942) and also of primitive teleosts (Patterson 1964). However, there is an important difference between the palaeoniscoid or chondrostean condition and the teleostean: in chondrosteans the lateral wall of the jugular and orbital artery canals consists of thick endochondral bone, the primitive lateral commissure, while in *Leptolepis* and teleosts it consists of thin membrane bone. In the Callovian *Leptolepis* the only endochondral bone in the lateral wall of the jugular canal is a narrow zone anteriorly (lcom), at the level of the trigeminal foramen, and this narrow zone alone represents the lateral commissure, just as in pholidophorids. The enclosed jugular and orbital artery canals in *Leptolepis* and teleosts are not a resemblance to chondrosteans, but are derived from the pholidophorid condition, where the lateral commissure is greatly reduced (this is confirmed by comparisons with more primitive leptolepids, p. 370 and figure 86). The re-enclosure of the jugular vein and orbital artery is due to the development of membrane bone outgrowths from the endochondral body of the prootic. This process, *the development of membrane bone as outgrowths from or replacement for cartilage bone*, has already been shown to be important in the pholidophorid intercalar and supraoccipital and will be referred to again below: it is responsible for many of the differences between the pholidophorid and leptolepid braincases.

In the lateral wall of the jugular and orbital artery canals of the Callovian *Leptolepis* there are two small foramina in addition to the large opening for the hyomandibular trunk. One (fagl) lies in the posterior wall of the canal for the artery and is ventrally directed – possibly it transmitted the branch of the glossopharyngeal nerve which accompanies the artery into the jugular canal. The second foramen (fva) lies in the lateral wall of the middle part of the jugular canal and may have transmitted a vessel to or from the muscles originating in this region. Just behind the entry of the arterial canal into the jugular canal there is always a small spur projecting from the ventral edge of the jugular canal. This is obviously the homologue of the spur in the same position in pholidophorids (figures 61, 67, 76*a*). At the lower opening of the arterial canal there is a small foramen (palp) leading through into the myodome, as in pholidophorids, and probably transmitting a posterior branch of the palatine nerve.

The *sphenotic* is shown in lateral, dorsal and medial view in figure 77. In contrast to the pholidophorid sphenotic, the bone forms part of the wall of the labyrinth cavity, a deep recess (ampa) in its medial face housing the anteriormost part of the anterior semicircular canal and its ampulla. Laterally, the sphenotic bears a prominent, elongate postorbital process overhanging a recess (lapf) in which the levator arcus palatini muscle originated. This recess is limited anteriorly and postero-dorsally by crests, the anterior one separating it from the smoothly concave orbital surface and the postero-dorsal from the dilatator fossa (df). The anterior part of the hyomandibular facet lay in cartilage between the postero-ventral margin of the sphenotic and the prootic below. The dorsal surface of the sphenotic is small and almost plane: the antero-lateral part of the fossa bridgei, which is deeply excavated in the dorsal surface of the sphenotic in pholidophorids, has evidently been entirely reduced. Splints of membrane bone at the anterior and posterior edges of the dorsal surface of the bone suture with the frontal and dermopterotic respectively.

The otic nerve entered a rather large foramen (fotn, figure 77*c*) in the centre of the orbital surface of the sphenotic and passed through a postero-dorsally directed canal which opens in the most anterior part of the dilatator fossa (fotn, figure 77*e*). In the posterior part of the levator arcus palatini fossa there is the opening of a narrow canal (spic, figure 77*c*) which leads through the crest separating this fossa from the dilatator fossa and opens just behind the otic nerve canal (spic, figure 77*e*). Comparison with pholidophorids and earlier leptolepids (figure 88) shows that this can only be the greatly reduced spiracular canal.

The sphenotic of the Callovian *Leptolepis* clearly forms a larger proportion of the braincase than in pholidophorids, since it extends far enough medially to house part of the anterior semicircular canal and its ampulla, extends ventrally well beyond the orbital opening of the canal for the otic nerve, and posteriorly well beyond the spiracular canal.

The *basisphenoid* is shown in lateral and posterior view in figure 78. It is of normal teleostean type, with a slender pedicel and a pair of dorso-lateral arms which met the prootic, forming the anterior margin of the pituitary fossa and the lower margin of the optic fenestra. A pair of small processes on the posterior surface of the pedicel mark the passage of the internal carotids (nica) into the pituitary fossa. Most of the bone is membranous: the only endochondral portions are the lateral parts of the arms and the foot of the pedicel.

The *pterosphenoid* is shown in lateral, dorso-lateral and medial view in figure 79. It is a simple, axehead-shaped bone, proportionally much thinner than its homologue in pholidophorids (cf. figures 79*b*, *e*). The central portion is thin and membranous, and there is endochondral bone only around the anterior, dorsal and posterior edges. As in pholidophorids, the trochlear nerve and middle cerebral vein (IV, mcv) passed into the orbit through the posterior part of the bone. The dorsal edge of the bone is notched by a canal (frla) for the first branch of the superficial ophthalmic nerves. In contrast to the pholidophorid pterosphenoid, there is no trace of a pterosphenoid pedicle, no perichondral bone on the dorsal surface, and no medial spur above the optic fenestra.

The *orbitosphenoid* is shown in lateral and dorsal view in figure 80. It is a median bone, with no indication of a paired origin in ontogeny. In contrast to the pholidophorid orbitosphenoid, the bone lies entirely below the cranial cavity, the portion which roofs the cranial cavity in pholidophorids being absent or unossified. The endochondral bone is much thinner than in pholidophorids, and the bone bordering the optic fenestra (II) and the exit foramen of the olfactory nerves (I) is membranous. The long anterior process of the orbitosphenoid in pholidophorids is reduced to a short spur. The anterior cerebral vein passed through an almost vertical, slit-like passage (acv) in the postero-dorsal part of the bone. The portion of the cranial cavity enclosed within the orbitosphenoid shows an anterior swelling for the olfactory lobes (rolf), and a larger posterior swelling (rtel) for the telencephalon.

No intact sclerotic ossifications have been recognized in the Callovian *Leptolepis* material.

The cranial cavity of the Callovian *Leptolepis* differs from those of pholidophorids in being much less closely and completely enclosed by bone. The posterior dorsal fontanelle is obliterated, as in *P. germanicus* and the Callovian *Pholidophorus*, by forward extension of the supraoccipital. The anterior dorsal fontanelle would be very large in the braincase as preserved, extending from the supraoccipital to the ethmoid region, since it is not closed anteriorly by ossification of the dorsal part of the orbitosphenoid. Laterally, this fontanelle communicates widely with the post-temporal fossa between the sphenotic, pterotic and epioccipital, though this opening must have been at least partially closed by cartilage in life. The dilatations of the cranial cavity for the olfactory lobes and telencephalon (in the orbitosphenoid) and the optic lobes (in the pterosphenoid) are as in pholidophorids. As noted above, the saccular chamber is larger than in pholidophorids, and the utricular recess in the prootic is less sharply marked off from the cranial cavity. The posterior semicircular canal was enclosed within the epioccipital dorsally and the exoccipital ventrally; the external semicircular canal was enclosed within the pterotic, and the anterior semicircular canal lay free in the cranial cavity, with its most anterior part lying in a recess in the sphenotic. The sinus communis also lay free in the cranial cavity, so that there is no bony partition separating the anterior and posterior openings of the lateral cranial canal, which appears merely as a deep cavity in the epioccipital (figure 49).

(*d*) Pholidophoroides limbata

The dorsal surface of the otic and orbitotemporal regions is visible in the mechanically prepared P.40588 (figures 6, 82), showing the fossa bridgei, post-temporal fossa and anterior dorsal fontanelle. These structures are similar to their counterparts in *P. bechei* (figure 61).

The anterior dorsal fontanelle (adf) is about as large as in *P. bechei*. The fossa bridgei consists of the same three regions as in *P. bechei*, a shallow antero-medial portion (fbam), separated from the supraorbital fossa (sof) by a longitudinal crest and lying in front of the ridge over the anterior semicircular canal (asc), a deep lateral portion (fbl) and a shallow postero-medial portion (fbp). In the antero-medial part of the fossa there are two foramina (frla) for the ramus lateralis accessorius and a branch of the superficial ophthalmic nerves. In the postero-medial part of the fossa there is a foramen for the supratemporal branch of the glossopharyngeal nerve (fst IX), as in *P. bechei*, and two presumed exit canals for the ramus lateralis accessorius (frla), one in the posterior wall and one in the medial. The floor of the groove leading to the posterior canal contains a small foramen (? fst IX) which may represent an anastomosing branch from the supratemporal branch of the glossopharyngeal or from an intracranial branch of the vagus (cf. Norris 1925, pp. 385, 398).

The spiracular canal opens in the deep anterior part of the lateral division of the fossa bridgei (spic). The canal appears to be much wider than in *P. bechei* or the Callovian *Pholidophorus* (figures 60, 69), and the descending lamina of the dermopterotic (dlpto), which lines the medial wall of the fossa bridgei, does not extend forwards towards the spiracular canal as it does in other pholidophorids. The main otic nerve must have passed through the spiracular canal, as in other pholidophorids, but a posterior ramus passed through the floor of the fossa and emerged

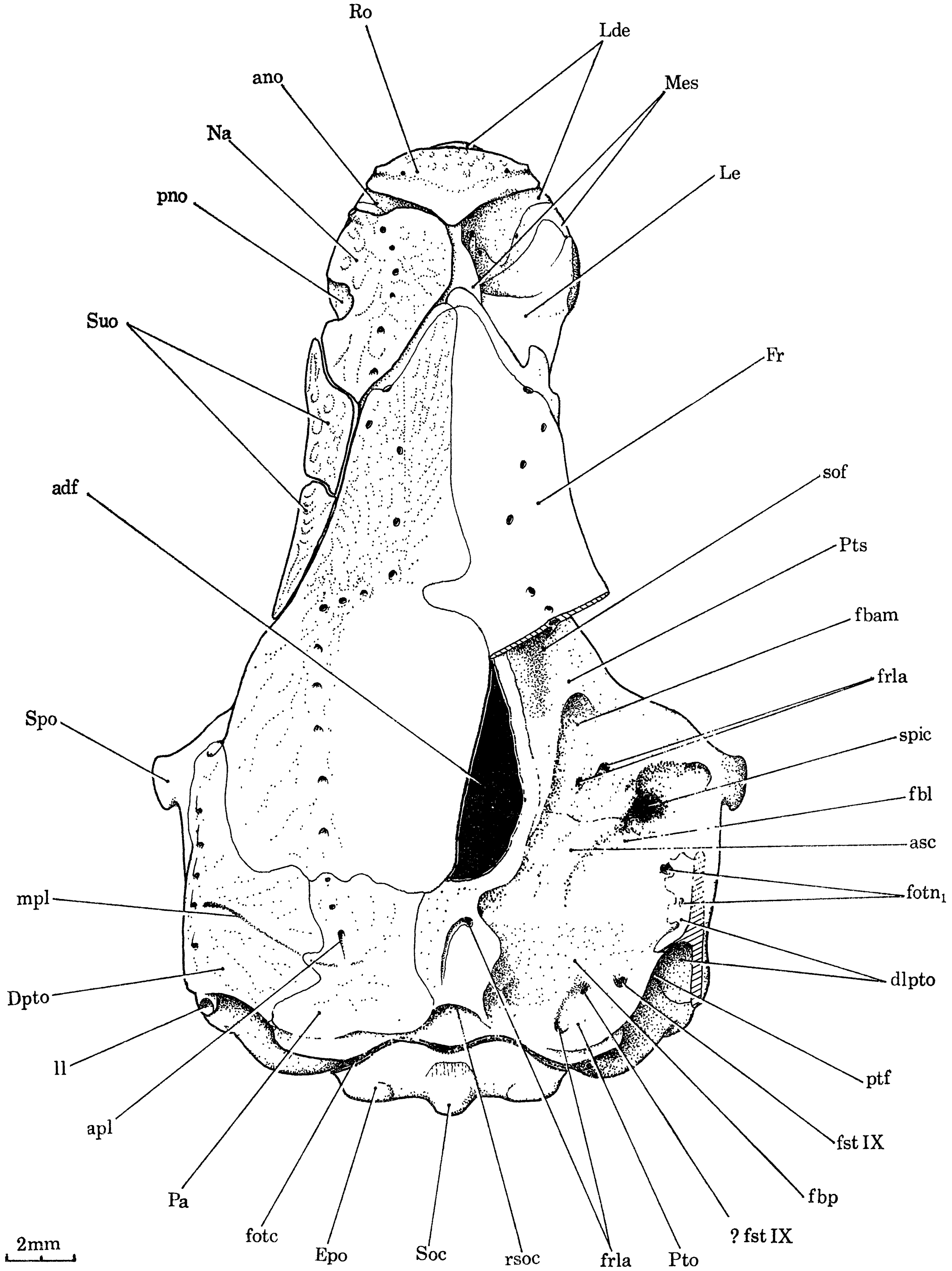


FIGURE 82. *Pholidophoroides limbata* (Agassiz). Restoration of braincase and associated dermal bones in dorsal view, drawn as if the right parietal were removed, the right dermopterotic cut away from its descending lamina, and the posterior part of the right frontal cut away, based on P.40588. Cut surfaces cross-hatched. For details of the snout see figure 124.

($fotn_1$) in a notch in the margin of the descending lamina of the dermopterotic before penetrating the latter.

The small post-temporal fossa (ptf) is separated from the fossa bridgei by an oblique wall of cartilage bone, as in *P. bechei* and *P. germanicus* (figures 60, 69). An extensive posterior portion of the descending lamina of the dermopterotic lines the lateral part of the post-temporal fossa.

The only suture visible in P.40588 runs transversely across the floor of the fossa bridgei, close behind the level of the spiracular canal (figure 82). Comparison with the Callovian *Pholidophorus* (figure 69) indicates that the medial part of this suture must separate the pterosphenoid (Pts) and pterotic (Pto), and the lateral part must pass between the sphenotic and prootic.

(*e*) Pholidophorus minor

The otic and orbitotemporal regions of this braincase (figures 36–38) are restored in ventral view in figure 83. The only available specimen is considerably crushed and damaged: this and its very small size make it impossible to elucidate many details, but in general the braincase appears to be closely comparable with that of *P. bechei* and it will be described very briefly.

As in fully ossified individuals of *P. bechei*, the otic and orbitotemporal regions consist of a single ossification, without sutures, which is very intimately associated or fused with the dermal roofing bones. The cranial fissure is complete, since the posterior face of the otic region is lined with perichondral bone from the level of the saccular recess upwards (svfotc, fotc). As in *P. bechei* the vagus canal is represented by a shallow groove (grX) on the posterior face of the otic region and the myodome (myot) opens posteriorly through the ventral part of the cranial fissure (fotv). The myodome is without an ossified floor in this specimen, but this thin layer of bone is probably broken away with the parasphenoid, as is the ventral part of the basisphenoid region. Little can be said of the dorsal surface of the neurocranium since the dermal roofing bones are still in place, but one striking difference from *P. bechei* is the very small anterior dorsal fontanelle (adf), a triangular opening directly above the pituitary fossa (pitf), comparable in size with the anterior dorsal fontanelle of *Boreosomus* (Nielsen 1942, fig. 59). The post-temporal fossa appears to be separated from the fossa bridgei by a wall of endoskeletal bone, as in *P. bechei*, *P. germanicus* and *Pholidophoroides limbata.*

The subtemporal fossa (stf) is hardly as deep as in *P. bechei*, not hypertrophied as it is in *P. germanicus* and the Callovian species. As in *P. bechei* the jugular groove (jg) is only distinct anteriorly and the ascending process of the parasphenoid ended in a notch (npsp) just below the lateral commissure. The latter (lcom) is reduced to a slender splint. In all other pholidophorids in which the prootic region is known there is a posteriorly directed process of membrane bone above the jugular groove which sutured with the antero-lateral process of the intercalar, forming the bridge across the subtemporal fossa (figures 62, 68, 76, 84). In *P. minor* this process is not developed on the prootic, implying that there was no bridge across the subtemporal fossa, an important difference from other pholidophorids. The facial foramen (VII) opens into the jugular groove behind the lateral commissure. The facial canal communicates with the myodome, as in other pholidophorids, but in *P. minor* this palatine fenestra in the roof of the myodome is so large that it probably incorporates the fenestra in the roof of the myodome which is present in *P. bechei* (ferm, figure 60). The groove (goa) for the orbital artery, passing up into the jugular canal, is hardly recognizable. As in other pholidophorids, the trigeminal foramen (V) opens into the upper part of the orbital opening of the jugular canal, and there is a separate

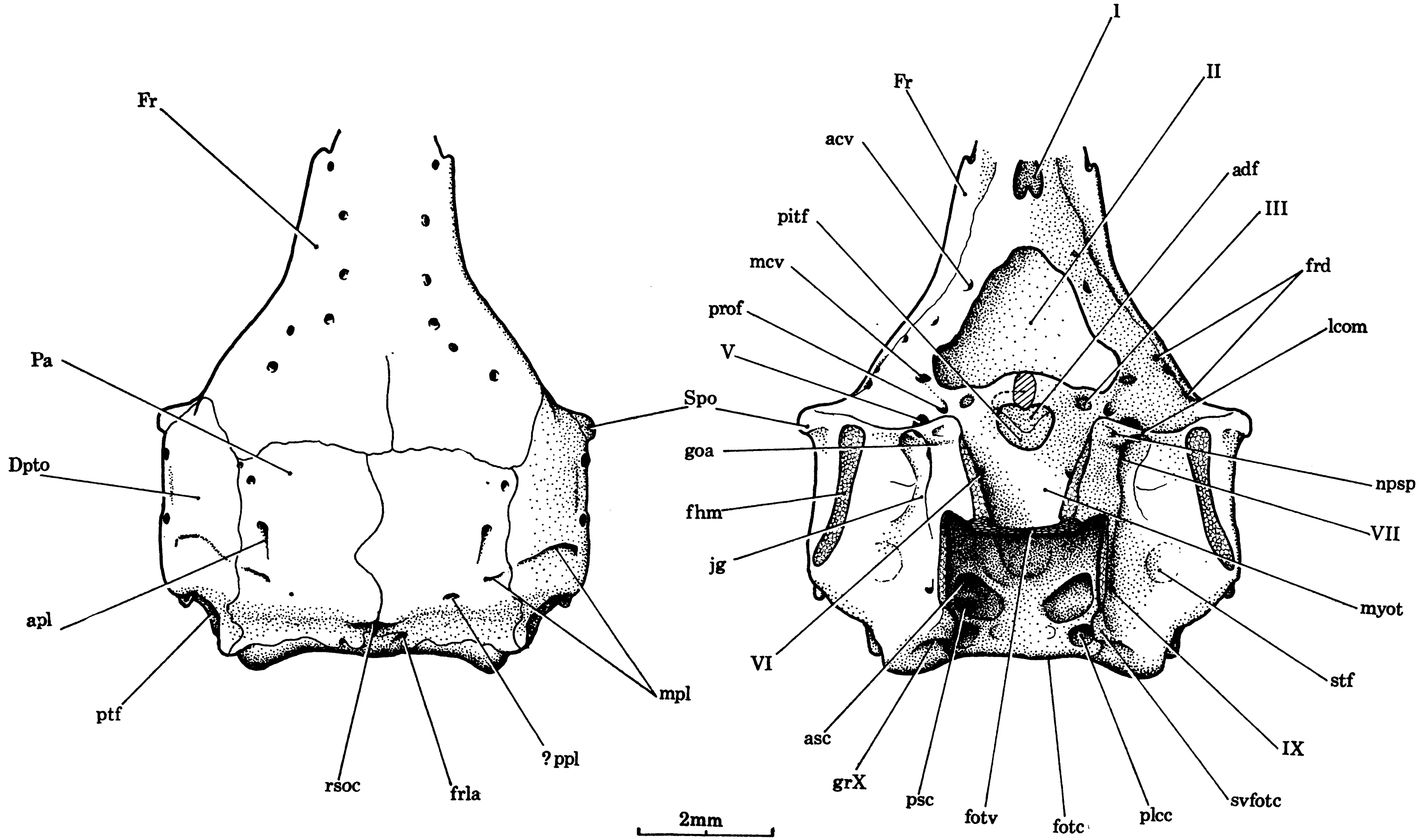


Figure 83. *Pholidophorus minor* Agassiz. Restoration of otic and orbitotemporal regions of neurocranium and attached roofing bones in dorsal (left) and ventral view, based on P.1072. In the right hand drawing the broken basisphenoid pedicel is cross-hatched, and the outline of the concealed portion of the anterior dorsal fontanelle is indicated by a broken line on the left side.

profundus foramen (prof) midway between the trigeminal and oculomotor foramina. The foramen of the otic nerve is not recognizable, nor is a spiracular groove or canal.

The optic fenestra (II) is very large, far larger than in *P. bechei*, and the trochlear nerve must have passed through it. Anteriorly, the orbitotemporal ossification of the braincase tapers and appears to end in front of the foramen for the olfactory nerves (I), indicating that the ethmoid region, missing from the specimen, was a separate ossification.

So far as they can be observed, the cranial and labyrinth cavities agree with those of *P. bechei*, with the utricular recess sharply separated from the cranial cavity, the anterior semicircular canal bone-enclosed throughout its length, a lateral cranial canal with an ossified medial wall, and a common opening into the cranial cavity for the external semicircular canal and the ampulla of the posterior semicircular canal.

(*f*) Pholidophorus macrocephalus

The otic and orbitotemporal regions of this braincase (figures 84, 85) are, so far as they can be seen, almost identical with those of the Callovian *Pholidophorus* sp., except that there is probably a small opisthotic. In all three available specimens the braincase is ossified about as completely as in the Callovian species, but there appears to be no fusion between the pterotic and prootic as there is in the latter. The pterotic (Pto) is crushed and broken in the subtemporal fossa in all three specimens, but where it is best preserved, in P.12070, it seems to end in the medial wall of the fossa dorsal to the anterior extension of the intercalar, and below it there appears to be a small opisthotic (Opo) which forms the anterior wall of the vagus canal and the ventral part of the posterior ampullary chamber. The opisthotic is therefore similar in size to that of *P. germanicus*, but it does not fuse with the basi-exoccipital as in the latter, the subvagal portion of the fissura otico-occipitalis persisting as a cartilage-filled suture.

In *P. macrocephalus* the communication between the post-temporal fossa and the fossa bridgei is more extensive than in the Callovian species, since the transverse portion of the descending lamina of the dermopterotic is reduced, and only a medial endochondral remnant of the bar separating the two cavities remains. The anterior part of the fossa bridgei cannot be seen, but as in the Callovian species the pterosphenoid is very extensive and must have contributed to it and to paired supraorbital fossae on the roof of the neurocranium over the orbit. Whether these depressions were separated from the fossa bridgei, as they are in *P. bechei* and the Callovian species, or were confluent with it cannot be seen.

The descending lamina of the dermopterotic (dlpto) is very large, forming the floor of the lateral part of the post-temporal fossa and appearing in the roof of the hyomandibular facet (fhm) in the fossil skulls, as it does in the Callovian species. The descending lamina extends posteriorly to make contact with the intercalar (Ic), and in all three specimens there is a small independent endo- and perichondral ossification (Ptsl) on the posterior part of the lateral surface of the lamina, postero-lateral to the external semicircular canal. In P.3582 and P.12070 this small ossification is separated from the pterotic by a gap, cartilage filled in life, but in P.52518 (inset, figure 84) the bone is larger and sutures with the pterotic, although it is unlikely that it formed any part of the wall of the cavity for the external semicircular canal.

There is a spiracular groove on the prootic, and the spiracular canal (spic) passes through the sphenotic (Spo). The medial wall of the spiracular canal is ossified, not cartilaginous as it is in the Callovian species, and the lower opening of the canal for the otic nerve lies just within the sphenotic, not on the sphenotic/pterosphenoid suture as it does in the Callovian

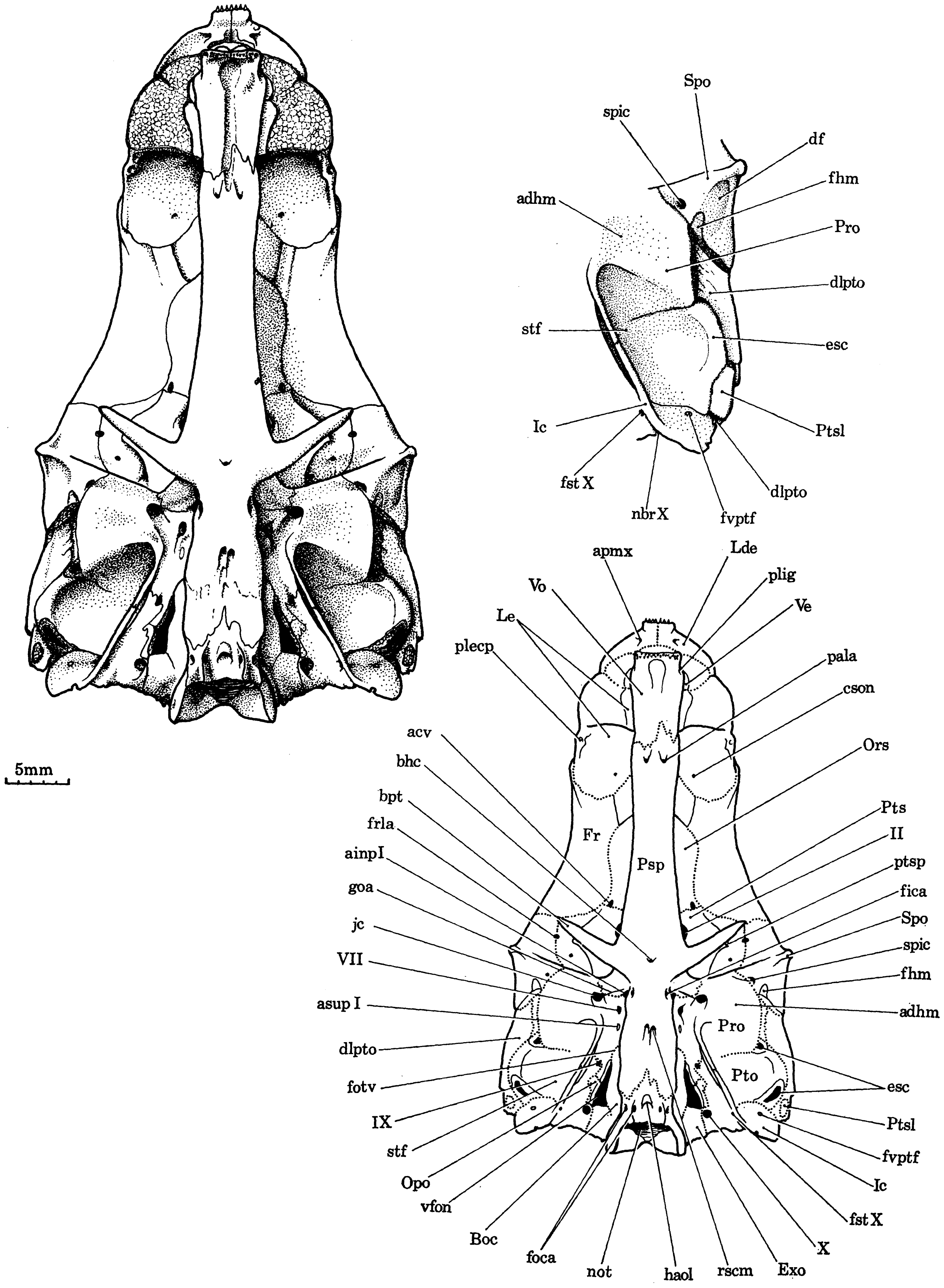


FIGURE 84. *Pholidophorus macrocephalus* Agassiz. Restoration of neurocranium and attached dermal bones in ventral view, based mainly on P.12070. Inset at upper right is an enlarged sketch of the region of the left hyomandibular facet, based on the more thoroughly ossified P.52518, to show the separate bone (Ptsl) lateral to the pterotic. In the key diagram sutures are indicated by dotted lines.

species. Although the sphenotic appears to be more extensive than it is in *P. germanicus* and the Callovian species, it does not extend medially far enough to form part of the wall of the cavity for the anterior semicircular canal.

As in *P. germanicus* and the Callovian species, the subtemporal fossa (stf) is very deep, and its flimsy walls are always more or less crushed in the fossils. The myodome, jugular groove and trigeminofacial chamber are as in the Callovian species, except that the lateral commissure, which is always crushed and broken, may be further reduced (lcom). The oculomotor and profundus foramina lie on the basisphenoid/prootic and pterosphenotic/prootic sutures respectively (III, prof, figure 85). The upper part of the basisphenoid is crushed or damaged in all the specimens, but P.52518 (figure 85) shows that the pedicel of the bone reached the parasphenoid and is about as long (rostro-caudally) as in *P. germanicus*. There are no anterior or posterior extensions of the pedicel in the floor of the myodome or orbit, and there can have been no transverse anastomosis between the efferent pseudobranchial arteries. Processes marking the passage of the internal carotids up into the pituitary fossa are present on the basisphenoid pedicel as on the right side of *P. germanicus* (figure 78), but they differ from the latter in extending down to the parasphenoid, and are endochondrally ossified ventrally and linked with the foot of the pedicel, enclosing a triangular opening (myom) through which passed the palatine nerve and the connecting vessel between the internal carotid and efferent pseudobranchial arteries. Comparison with *P. bechei* (figures 63, 64) shows that this opening is produced by loss of the wall between the parabasal canal and the ascending canal for the internal carotid. The paired, ventro-laterally directed struts of the basisphenoid so formed recall the conditions in Kansas palaeoniscid 'A' (Watson 1925, p. 838) and *Perleidus* (Stensiö 1932, p. 203). In *Kentuckia* the lateral struts of the basisphenoid (Rayner 1951, fig. 8) are not

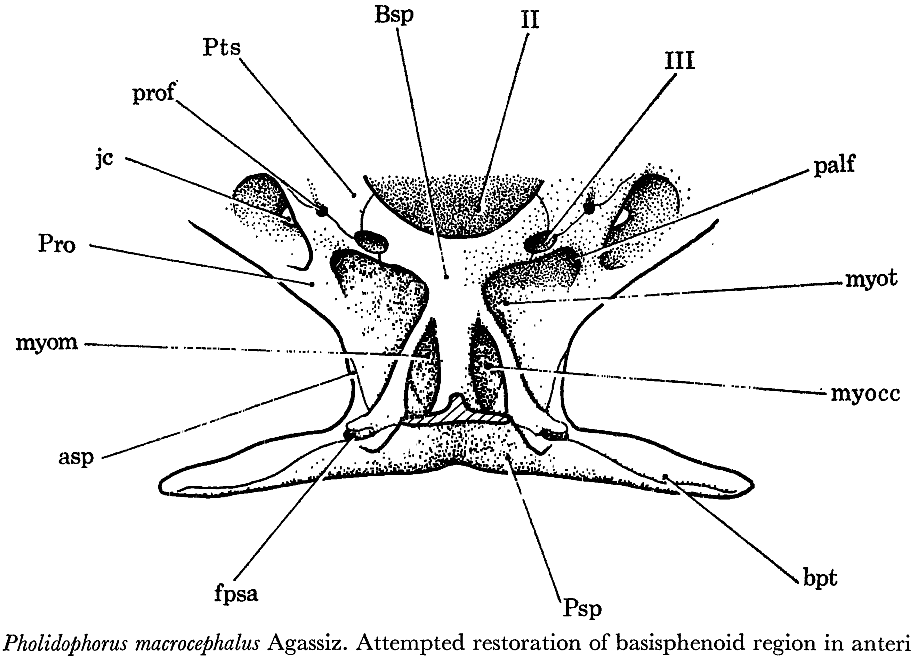


FIGURE 85. *Pholidophorus macrocephalus* Agassiz. Attempted restoration of basisphenoid region in anterior view, the parasphenoid cut through beneath the orbit (cut surface cross-hatched). Basisphenoid and parasphenoid from P.52518, proportions of the prootic, etc., adapted from the Callovian *Pholidophorus* sp. (Magn. × 4 approx.)

precisely homologous with those just mentioned since they lie in part anterior to the efferent pseudobranchial arteries. Nielsen (1942, p. 64) suggested that the internal rectus muscle passed into the myodome through this triangular opening formed by confluence of the parabasal and ascending carotid canals (see further p. 542).

There is a long (rostro-caudally) but narrow pedicel on the pterosphenoid (ptsp), as in the Callovian species, and the foramina of the trochlear nerve and middle cerebral vein are as in the latter. The medial spur projecting into the cranial cavity above the optic fenestra is particularly large in *P. macrocephalus*. The orbitosphenoid (Ors), missing in the Callovian species, has a long anterior process, as in *P. germanicus*, and also has a rather large plate of membrane bone ventrally, forming the upper part of the interorbital septum. As in *P. germanicus*, the orbitosphenoid completely encloses the anterior part of the cranial cavity, having an ossified dorsal portion which forms the floor of the supraorbital fossae. The foramen of the anterior cerebral vein (acv) appears to lie in the postero-dorsal corner of the orbitosphenoid, much further back than in *P. germanicus* but as in leptolepids.

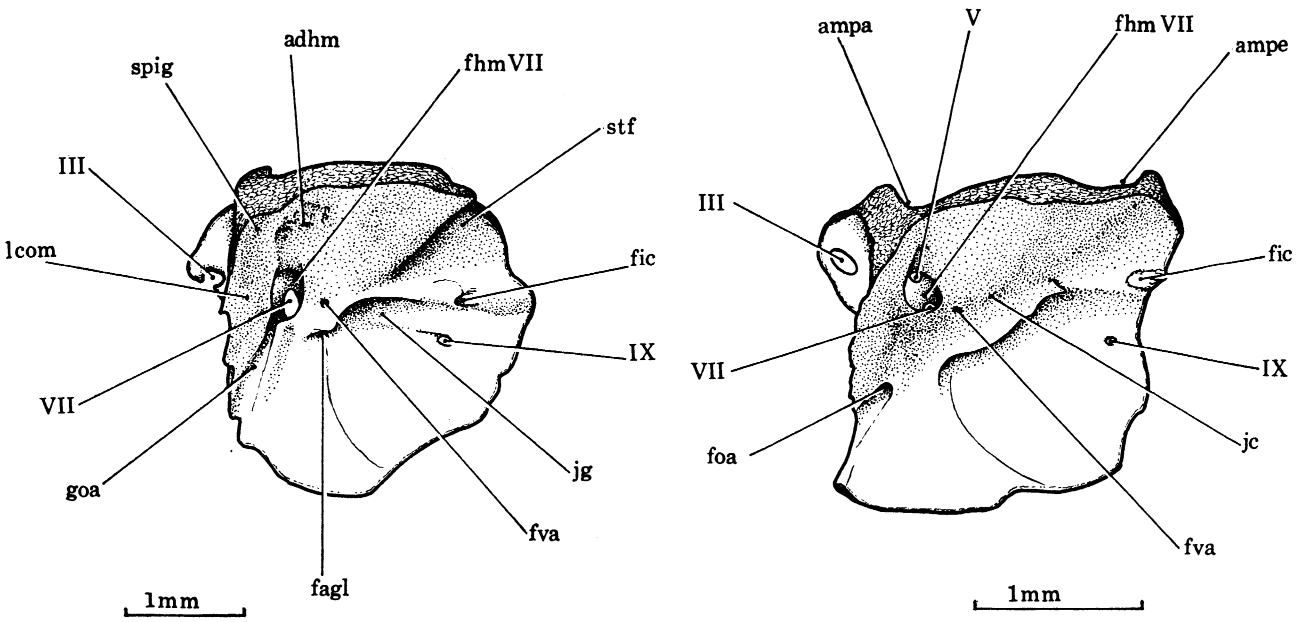


FIGURE 86. Left prootic, in lateral view, of Sinemurian *Leptolepis* sp. (left), based on P.51685–6 (reversed), and *Leptolepis coryphaenoides* (Bronn) (right), from P.51715.

In *P. macrocephalus* the circumcorneal area of the sclerotic is ossified as a sclerotic ring which consists of only two segments, as in teleosts. In the base of the orbit there is also a large basal sclerotic bone, closely resembling that of *P. germanicus* (figure 81) but more thoroughly ossified, so that it is relatively larger and the upper and lower margins of the notch in the hind margin meet, enclosing a foramen rather than a notch, and this foramen is partly divided into a larger anterior and a smaller posterior portion, as it is in *Caturus chirotes* (figure 94): presumably, the optic nerve passed through the posterior opening and the optic vessels through the anterior.

(*g*) *Sinemurian* Leptolepis *sp.*

The otic and orbitotemporal regions are still incompletely known in this species. The pterotic is visible only in one crushed and poorly ossified specimen (P.51685). So far as can be seen it is similar to that of the Callovian *Leptolepis*, but whether it is fused with the dermopterotic is unknown: the post-temporal fossa and fossa bridgei were certainly confluent.

The prootic is shown in lateral view in figure 86 and in anterior view in figure 87. This bone and the prootic of *L. coryphaenoides* (figure 86) form an almost perfect morphological series linking the pholidophorid prootic, as exemplified by *P. germanicus* and the Callovian *Pholidophorus*, with the primitive teleostean type already present in the Callovian *Leptolepis* (figure 76).

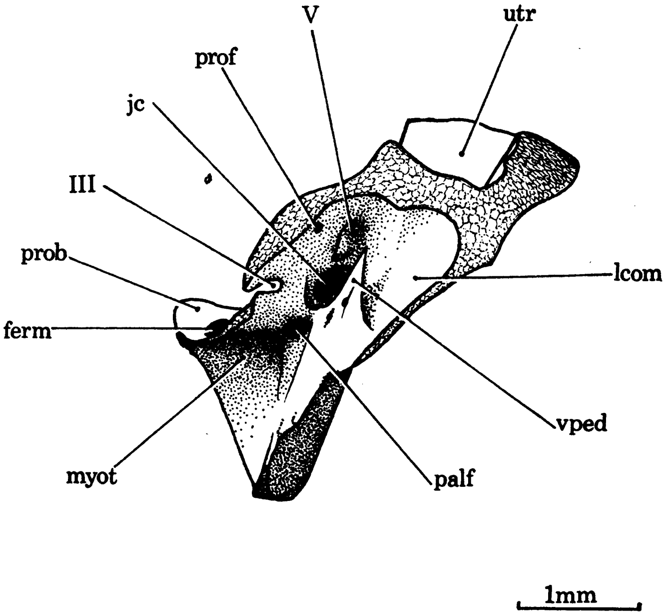


FIGURE 87. Sinemurian *Leptolepis* sp. Left prootic in anterior view, based on P.51685–6 (reversed).

As in the Callovian *Leptolepis*, the dorsal portion of the prootic which occurs in pholidophorids is lacking, and the bone does not contribute to the floor of the fossa bridgei. In thickness of the endochondral bone, the Sinemurian species is intermediate between the massive bone of the pholidophorids and the thin bone of later leptolepids, and the surface relief of the prootic is also intermediate between these two: as in pholidophorids the crest between the subtemporal fossa (stf) and the area of origin of the adductor muscle of the hyomandibular (adhm) is still quite prominent, there is still a recess for the saccus vasculosus behind the oculomotor foramen on the inner face of the bone, the spiracular groove (spig) is still just recognizable on the prootic, and the saccular recess is not much inflated; as in leptolepids, the articular area of the first suprapharyngobranchial is not recognizable. The anterior process of the intercalar is not bifid (figure 48) and there is no strut projecting back from the prootic to bridge the subtemporal fossa; the anterior end of the intercalar fitted against a facet (fic) above the jugular groove at the posterior end of the prootic. As in pholidophorids, the glossopharyngeal foramen (IX) still lies well within the prootic. The oculomotor foramen (III) lies on the suture between the prootic and basisphenoid, as in pholidophorids, not within the prootic as it does in later leptolepids, but it is deeply incised within the margin of the prootic, tending towards the leptolepid condition. As in pholidophorids, there is a separate profundus foramen (prof, figure 87). The internal opening of the facial foramen is equal in size to the trigeminal, as in the Callovian *Leptolepis*, not smaller as it is in pholidophorids, and the palatine foramen (palf) between the floor of the jugular canal and the roof of the myodome is about the same size as the facial foramen. In one of the two available prootics there is a fenestra (ferm, figure 87) in the prootic bridge behind the oculomotor foramen, as in *P. bechei*: in the other specimen the prootic bridge is broken in this region, but the bone is paper thin, and could well have been fenestrated or deeply emarginate.

The structure of the jugular canal forms a perfect intermediate between the pholidophorids and *L. coryphaenoides*. The endochondral part of the lateral commissure is a narrow band (lcom) anteriorly, as in pholidophorids and leptolepids. The groove for the orbital artery (goa), leading up into the jugular canal, is deeply incised on the prootic but not roofed over by membrane bone as it is in *L. coryphaenoides* and the Callovian *Leptolepis*. Behind the facial foramen the jugular groove (jg) is roofed over by membrane bone, as in later leptolepids, but the extent of this membranous wall is less than in *L. coryphaenoides* and much less than in the Callovian *Leptolepis*. Between the endochondral lateral commissure and this membranous wall there is a large foramen (fhm VII) which transmitted the hyomandibular trunk dorsally and received the orbital artery ventrally. As in the Callovian *Leptolepis*, there is a small foramen (fva) behind this in the wall of the jugular canal, and another small, ventrally directed foramen (fagl) in its floor, immediately below the projecting spur which is also present in pholidophorids.

In the orbital opening of the trigeminofacial chamber there is a vertical process (vped, figure 87), mainly consisting of membrane bone, which arises from the ridge separating the myodome from the jugular canal and projects antero-dorsally to end in a point in front of the trigeminal foramen. There is a small knob in this position in *P. bechei* (figures 63, 64) and a rudimentary process in some specimens of *L. coryphaenoides* (p. 374). Allis has described a similar process on the prootic of *Trigla* (1909, p. 123) and I have observed one in *Coregonus*, *Salmo* and *Argentina*. In *Trigla* the process opposes the pterosphenoid pedicle and is bound to it by ligaments, and in many teleosts an ossified pedicle is formed by junction of the pterosphenoid with a similar process on the prootic, but in the Sinemurian *Leptolepis* there is no pterosphenoid pedicle (see below). This process must be the homologue of the lowermost, endochondrally ossified part of the pterosphenoid pedicle of *Amia* (cf. Allis 1897, p. 495), and, as in *Amia*, must lie lateral to the jugular vein and superficial ophthalmic, profundus, oculomotor and abducens nerves, and medial to the orbital artery and mandibular, maxillary and buccal nerves. In both available prootics of the Sinemurian *Leptolepis* the foot of the process is penetrated by a small foramen (figure 87), but there are several other equally minute foramina in the orbital surface of the prootic, some of them ending blindly within the bone, and it seems fruitless to try to interpret them all.

An isolated sphenotic of the Sinemurian *Leptolepis* is shown in dorsal and lateral view in figure 88. Like the prootic, this bone is intermediate in structure between the sphenotics of pholidophorids and those of later leptolepids. Internally, the bone lines a very small part of the cavity for the anterior semicircular canal (figure 88*b*), much less than in *L. coryphaenoides* (figure 88*d*), while in pholidophorids it does not reach this cavity. The medial part of the dorsal surface of the bone is excavated by the anterior part of the fossa bridgei (fb), here confluent with the post-temporal fossa, and notched by the upper opening of the spiracular canal (spic), as in pholidophorids. The anterior part of the hyomandibular facet (fhm) lies on the postero-ventral part of the lateral surface of the bone, and above this is the deep anterior part of the dilatator fossa (df). As in *P. macrocephalus*, the spiracular groove (spig) runs up in front of the hyomandibular facet, and the spiracular canal passes through the bone to emerge in the fossa bridgei. The lower opening of the canal for the otic nerve (fotn) lies close to the lower margin of the orbital surface of the bone, as in *P. macrocephalus*. The canal for the otic nerve leads postero-dorsally into the spiracular canal, and there is a fairly large chamber within the bone where the two canals meet, presumably housing a spiracular sense organ. A branch of the otic nerve must have accompanied the spiracular diverticulum into the fossa bridgei, and another branch passed dorso-laterally and emerged through a foramen (fotn) in the anteriormost part of the dilatator fossa.

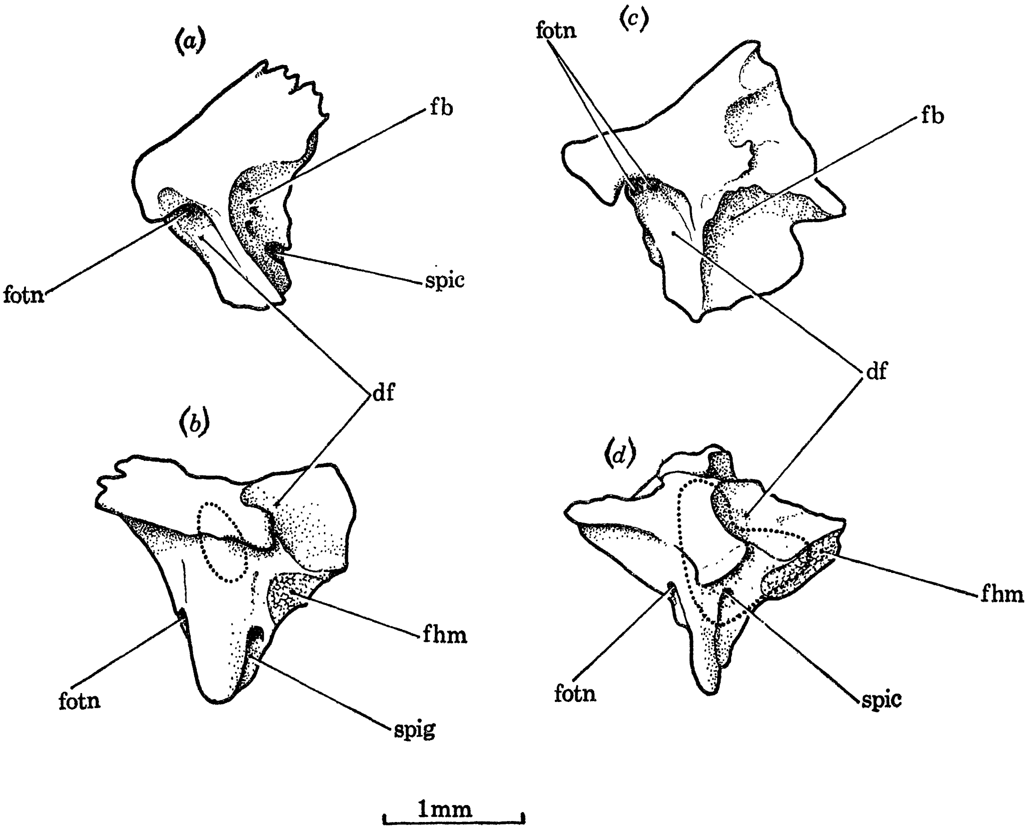


FIGURE 88. Left sphenotic of Sinemurian *Leptolepis* sp. (*a*, *b*), from P.51685, and *Leptolepis coryphaenoides* (Bronn) (*c*, *d*), from P.51696, in dorsal (*a*, *c*) and lateral (*b*, *d*) views. In (*b*) and (*d*) a dotted line marks the outline of the recess for the anterior semicircular canal on the inner face of the bone.

The basisphenoid of the Sinemurian *Leptolepis* is partially visible in the intact skull of P.7801. The pedicel of the bone reaches the parasphenoid and is intermediate between those of *P. germanicus* and the Callovian *Leptolepis* in rostro-caudal length (figure 78). No canals or notches for the internal carotids are visible.

The pterosphenoid is known from a single broken example (P.51686). It is of leptolepid type, resembling those of *L. coryphaenoides* and the Callovian *Leptolepis* (figures 79, 90) in making no contribution to the roof of the neurocranium and having no pterosphenoid pedicle or spur on the medial face, and the endochondral bone is hardly thicker than in the Callovian *Leptolepis*. The foramina of the trochlear nerve and middle cerebral vein are as in other leptolepids, and the foramen for the ramus lateralis accessorius lies within the upper part of the bone, as in pholidophorids. The orbitosphenoid of the Sinemurian *Leptolepis* is partially visible in one intact skull, P.7801: it appears similar to that of *L. coryphaenoides* in shape, but has the foramen of the anterior cerebral vein in the centre of its upper border, as in *P. germanicus* (figure 80).

The sclerotic ring of the Sinemurian *Leptolepis* consists of two segments, arranged fore and aft of the eyeball, as in teleosts, other leptolepids and *P. macrocephalus*. There is no sign of a basal sclerotic bone, although the retinal pigment is exceptionally well preserved in several specimens.

(*h*) Leptolepis coryphaenoides

The otic and orbitotemporal regions of this species have been described and illustrated by Rayner (1937), and are restored in ventral and sagittal view in figures 89 and 90. As in the occipital region of this species (see above), there is considerable variation in the degree of ossification. Some specimens, like that shown in figures 89 and 90, have a single ossification, without sutures, occupying the whole of the orbitotemporal, otic and occipital regions, while others have the normal teleostean complement of separate bones. Amongst the bone-bed and stomach contents material of this species, the individual otic and orbitotemporal bones are always found separate, without fusion. As in the occipital ossifications, these isolated bones are closely comparable with those of the Callovian *Leptolepis* but retain a few primitive features reminiscent of the Sinemurian *Leptolepis*. In fully fused braincases, like that in figures 89 and 90, the limits of some of the bones are still indicated by scalloping around the margin of the anterior dorsal fontanelle (adf). The latter extends from the anterior edge of the supraoccipital to the ethmoid region in some individuals, to the middle of the orbitosphenoid in others (figure 91), and is very wide (figure 90), but it was presumably constricted by cartilage to some extent in life.

The dermal and endochondral portions of the pterotic are fused in all my material. Rayner (1937, p. 325) describes separate auto- and dermopterotics in one specimen, 'perhaps slightly immature', in Professor D. M. S. Watson's collection: I have been unable to find this specimen among the Watson collection, now in the University Museum of Zoology, Cambridge. The autopterotic is more completely ossified than in the Callovian *Leptolepis*, surrounding the lateral part of the ampullary chamber of the posterior semicircular canal and in fully ossified individuals (figure 90) forming a portion of the wall of the cranial cavity between the anterior and posterior ampullary chambers. On the dorsal surface of the autopterotic, which forms the floor of the post-temporal fossa, there is a hump over the ampullary chamber of the external semicircular canal which divides the fossa into deep anterior and posterior portions. The posterior division is the homologue of the original post-temporal fossa of *P. bechei* and *P. germanicus*; the anterior division, which is deepest laterally and is continued forwards on to the posterior half of the sphenotic, is the homologue of the deep lateral portion of the fossa bridgei of pholidophorids. The shallow postero-medial division of the fossa bridgei is still represented on the epioccipital (p. 312). The post-temporal fossa of *L. coryphaenoides* ends over the sphenotic (figure 88*c*) at the level of the postorbital process, and does not extend forwards on to the pterosphenoid. The precise medial extent of the fossa cannot be made out since the upper portion of its medial wall is unossified, and in the fossils it communicates with the cranial cavity (ptf, figure 90), but it is likely that the fossa ended lateral to the supraorbital sensory canal in the frontal.

The dermal portion of the pterotic is described and illustrated by Rayner (1937), Nybelin (1962) and Wenz (1968). The middle pit-line extends on to the dermopterotic in some individuals but not in others.

The subtemporal fossa (stf) is rather shallow, as in the Callovian species, and is separated from the post-temporal fossa above by a substantial layer of bone within the arch of the external semicircular canal.

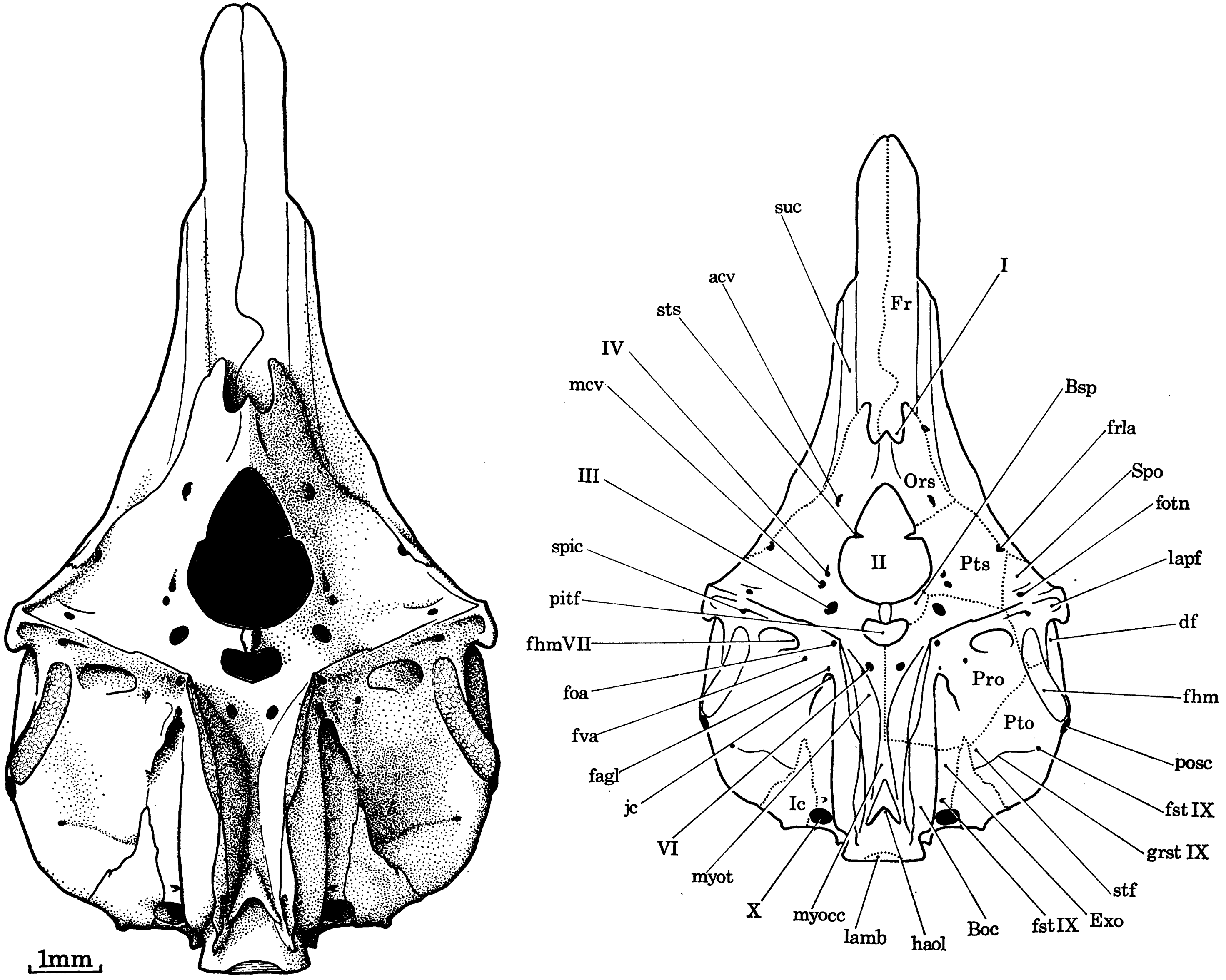


Figure 89. *Leptolepis coryphaenoides* (Bronn). Restoration of post-ethmoid portions of neurocranium and attached roofing bones in ventral view, mainly based on P.51714. On the right side of the key diagram the sutures (indicated by dotted lines) between the neurocranial bones are added from other specimens.

The prootic, shown in lateral view in figure 86, is intermediate in structure between those o the Sinemurian and Callovian species (figures 76, 86). Even in fully ossified braincases, the prootic does not contribute to the floor of the post-temporal fossa, ending against the sphenotic and pterotic at the level of the anterior and external ampullary chambers. The relief of the external surface of the prootic is less emphatic than in the Sinemurian *Leptolepis* and resembles the Callovian species. The recess for the saccus vasculosus behind the oculomotor foramen on the inner surface of the bone is still just recognizable in some specimens (psv, figure 90), but in others it is lost, as in the Callovian species. There is no spiracular groove on the prootic. As in the Sinemurian species, the anterior process of the intercalar is not bifid (figure 89) so there is no strut from the prootic passing back across the subtemporal fossa, only a facet (fic) for the intercalar above the posterior part of the jugular groove. The glossopharyngeal foramen (IX) still lies within the prootic, as in pholidophorids and the Sinemurian *Leptolepis*, but it is close to the posterior edge of the bone. As in the Callovian *Leptolepis* the oculomotor foramen (III) lies within the prootic and there is no separate profundus foramen. There is a deep, irregular emargination in the medial edge of the prootic bridge at the level of the facial foramen; this results in the pituitary fossa being drawn out transversely (pitf, figure 89) and it appears that the fenestrae present in the prootic bridge of *P. bechei* and the Sinemurian *Leptolepis* have become confluent with the pituitary fossa. The trigeminal and facial foramina (V, VII, figure 90) are about equal in size while the palatine foramen in the roof of the myodome (palf, figure 90) is much smaller, as in the Callovian *Leptolepis*. The post-facial part of the jugular canal (jc) is more completely roofed over by membrane bone than it is in the Sinemurian *Leptolepis*, less so than in the Callovian species. The groove for the orbital artery is roofed over (coa) as in the Callovian *Leptolepis*, but there is no foramen between this groove and the myodome as there is in the latter and *P. germanicus*. In the post-facial wall of the jugular canal there are the same two small foramina (fva, fagl, figure 89) as in the Sinemurian and Callovian *Leptolepis*. The spur above the lower of these, present in pholidophorids and the Sinemurian and Callovian *Leptolepis*, is hardly recognizable.

In the ventro-lateral corner of the orbital opening of the jugular canal there is in some specimens a small spur projecting dorso-medially, with a minute foramen through its base. This is a rudimentary homologue of the well developed process in this position in the Sinemurian *Leptolepis* (figure 87). In other specimens there is no trace of this rudiment, as in the Callovian species (figure 76*f*).

The foramina for nerves and vessels just described in the prootic are in some ways different from those described by Rayner (1937; 1948, p. 325). The foramen and groove for the palatine nerve ('facial branch') which she described are in fact for the orbital artery. The foramen leading from the cranial cavity into the ventral part of the orbital opening of the jugular canal, which Rayner assigned to the profundus nerve, is absent in my specimens, although the much larger oculomotor foramen lies very close to this position: Rayner described the oculomotor foramen as lying in the basisphenoid, whereas it is well within the prootic in all my specimens.

An isolated sphenotic of *L. coryphaenoides* is shown in figure 88. Internally (figure 90) the sphenotic surrounds the whole of the anterior loop of the anterior semicircular canal and the upper part of its ampulla, meeting the pterotic posteriorly and the pterosphenoid anteriorly. The dorsal surface of the sphenotic contains two depressions separated by a transverse ridge, which overlies the anterior semicircular canal. The anterior depression is shallow and does not appear to continue medially on to the pterosphenoid. The posterior depression (fb), which is deeper and ends anteriorly in a blind crevice within the bone, is the foremost part of the post-temporal fossa: as in the Callovian *Leptolepis*, and in contrast to pholidophorids and the Sinemurian species, the spiracular canal no longer opens into this depression.

The orbital and lateral surfaces of the sphenotic resemble those in the Callovian *Leptolepis* (figure 77), except that the anterior part of the hyomandibular facet (fhm) lies on the sphenotic, because of the more complete ossification of the braincase. The canal for the otic nerve (fotn) originates in the centre of the orbital face of the bone and opens into the anteriormost part of the dilatator fossa (df), as in the Callovian *Leptolepis*, but in *L. coryphaenoides* there are two or, more often, three upper openings, usually with posteriorly directed grooves leading from them. There may also be one or two minute passages leading through into the foremost, crevice-like part of the post-temporal fossa. In front of the hyomandibular facet there is a short spiracular groove, as in pholidophorids and the Sinemurian *Leptolepis*, leading into a narrow spiracular

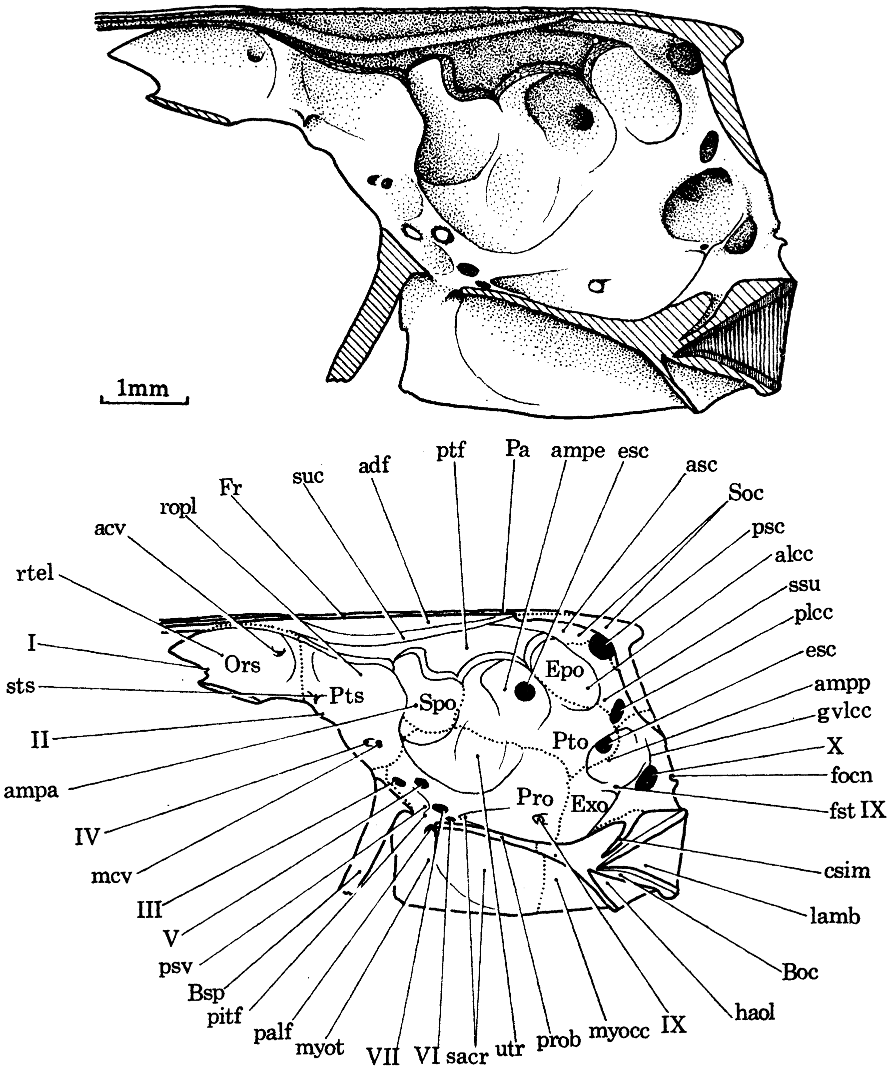


FIGURE 90. *Leptolepis coryphaenoides* (Bronn). Restoration of post-ethmoid portions of neurocranium and attached roofing bones in sagittal section, from the left side. Based mainly on P.51714. Sectioned surfaces cross-hatched. In the key diagram the sutures (indicated by dotted lines) between the neurocranial bones are added from other specimens.

canal (spic). The spiracular canal joins the canal for the otic nerve within the bone, as it does in pholidophorids, but here their roles are reversed since the spiracular canal is much narrower than the otic canal, and does not lead through into the fossa bridgei (now confluent with the post-temporal fossa) except for the minute openings in the foremost part of the fossa, which are in quite a different position from the normal position of the spiracular canal. The spiracular diverticulum must have ended blindly within the bone, while some structure accompanying it opened into the dilatator fossa, as in the Callovian *Leptolepis*.

The basisphenoid of *L. coryphaenoides* (figure 90) has a slender pedicel of membrane bone, as in the Callovian species (figure 78), but there is a pair of grooves for the internal carotids on its posterior face.

The pterosphenoid (figures 89, 90) also resembles that of the Callovian *Leptolepis* (figure 79), and appears to make no contribution to the roof of the neurocranium, although in well ossified specimens it is quite broad postero-dorsally where it meets the sphenotic. The central part of the bone is membranous and there is no pterosphenoid pedicle, but there is a spur projecting medially into the optic fenestra (sts, figures 89, 90), as in pholidophorids. The foramina of the trochlear nerve (IV) and middle cerebral vein (mcv) are as in the Callovian species, and as in the latter the foramen of the ramus lateralis accessorius notches the upper border of the bone, passing between it and the frontal (frla, figure 89).

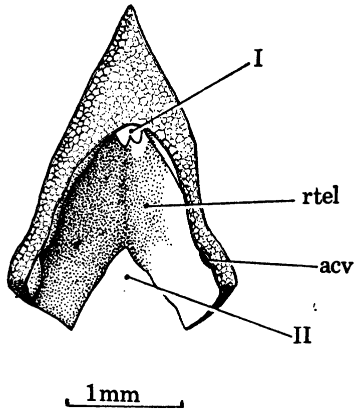


FIGURE 91. *Leptolepis coryphaenoides* (Bronn). Orbitosphenoid in dorsal view, from P.51717.

An isolated orbitosphenoid is shown in dorsal view in figure 91. In this well ossified example the orbitosphenoid roofs the anteriormost part of the cranial cavity, closing the anterior dorsal fontanelle, but in other specimens (figure 90) this dorsal portion is absent and the bone then resembles that of the Callovian species (figure 80) in every way.

A sclerotic ring ossified in two pieces has been illustrated by Rayner (1937, fig. 1) and Wenz (1968, figs 88, 91, 93, 96). There is no basal sclerotic bone.

The cranial cavity of *L. coryphaenoides* (figure 90) is a little more closely bone-invested than that of the Callovian *Leptolepis* but is otherwise similar, with dilatations for the telencephalon (rtel) in the orbitosphenoid and for the optic lobes (ropl) in the pterosphenoid and prootic. The utricular recess (utr) is entirely confluent with the cranial cavity, but the ampullary chamber of the anterior semicircular canal (ampa) is marked off anteriorly by a crest on the hind edge of the pterosphenoid. The posterior semicircular canal (psc) was contained within the epioccipital and exoccipital, the external (esc) within the pterotic, and the anterior was sometimes partly surrounded by the supraoccipital posteriorly (figure 58) and was embedded in the sphenotic anteriorly. Rayner's statement (1937, p. 65) that a feature of *L. coryphaenoides* is 'the entire absence of any bony laminae surrounding the semicircular canals' is untrue. In fully ossified individuals (figure 90) the upper part of the sinus communis was supported by a bony wall (ssu) which separates the anterior and posterior openings of the lateral cranial canal (alcc, plcc). This wall, which presumably ossifies partly from the epioccipital and partly from the pterotic, is much shorter both rostro-caudally and dorso-ventrally than its homologue in pholidophorids (figures 65, 73) and is more posteriorly placed, lying obliquely across the narrow gap between the point of entry of the posterior semicircular canal (psc) into the epioccipital and the upper edge of the posterior ampullary chamber (ampp). As mentioned above (p. 313), the lateral cranial canal is a pocket within the epioccipital and it does not extend lateral to the posterior semicircular canal as it does in the Sinemurian *Leptolepis*. A groove (gvlcc) on the exoccipital leads ventrally from the posterior opening of the lateral cranial canal towards the vagus canal, as in the Callovian *Leptolepis* (figure 54*e*).

(*j*) Leptolepis dubia

The otic and orbitotemporal regions of this species are restored in ventral view in figure 92. There is the normal teleostean complement of bones, and the braincase is fully ossified, with little or no cartilage between the bones.

The dermal and endochondral components of the compound pterotic (Pto) are completely fused. The subtemporal fossa (stf) is deeper than in other leptolepids, but it is separated from the post-temporal fossa by a substantial layer of bone, and is not so large as in *P. germanicus* and the Callovian *Pholidophorus*. The subtemporal fossa is lined mainly by the pterotic, but although the pterotic is more completely ossified than in the Callovian *Leptolepis* the prootic and exoccipital meet in the medial part of the fossa and it is unlikely that the pterotic lined much, if any, of the cranial cavity. In the dermal portion of the pterotic (Patterson 1967, fig. 4), the tube for the sensory canal is angled, as in the Callovian *Leptolepis*, and medial to the point of entry of the sensory canal there is an emargination in the posterior edge of the bone which housed the supratemporal. The middle pit-line does not extend on to the pterotic. There are one or two pores on the posterior, transverse portion of the sensory canal, and four or five pores, each at the end of a medially directed tube, along the anterior portion, in front of the anastomosis with the preopercular canal. The tip of the descending lamina of the dermopterotic projects posteriorly in a splint, as in the Callovian species.

The post-temporal fossa is partially visible in P.51759, and in that specimen it apears to be very spacious, extending forwards to the level of the postorbital process and inwards towards the mid-line, much as in *Elops*. But the endochondral bone forming the floor and medial wall of the fossa is badly crushed so that bone junctions cannot be recognized, and it is possible that the large size of the fossa in this specimen is itself an artefact due to crushing, since other specimens show that the sphenotic did not form part of the floor of the fossa, even in large individuals. It is possible that in large individuals the prootic and pterosphenoid contributed to the fossa, as in *Elops*: if so, the prootic and pterosphenoid would be more extensive than in the other leptolepids described here. But in the small, stomach content specimens these bones resemble those of the Callovian *Leptolepis*, and are without a perichondrally lined dorsal portion.

In the prootic (Pro) the jugular canal (jc) and orbital artery canal (foa) are roofed by membrane bone, as in the Callovian species, and the foramina of the oculomotor, trigeminal, facial, hyomandibular, abducens and palatine nerves are the same size and in the same positions as in the latter. The pituitary fossa is more deeply excavated in the margin of the prootic bridge than it is in the Callovian species, and as in *L. coryphaenoides* there is no foramen between the groove for the orbital artery and the myodome.

The sphenotic (Spo) bears the anterior part of the hyomandibular facet (fhm) and contains a large cavity for the foremost part of the anterior semicircular canal. The dorsal surface of

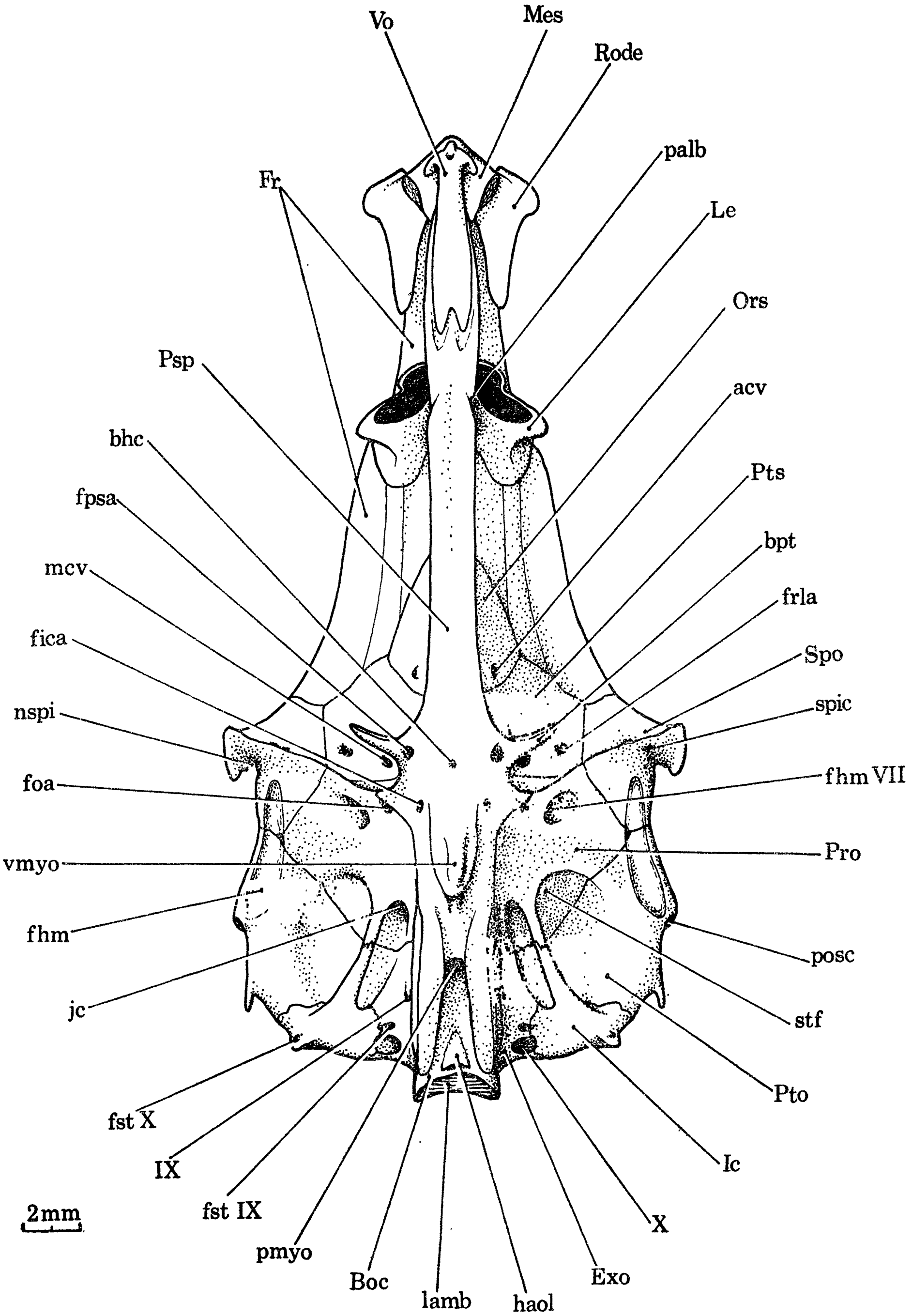


FIGURE 92. *Leptolepis dubia* (Blainville). Restoration of braincase in ventral view, based mainly on P.919. For details of the snout see figure 130.

the sphenotic is mostly occupied by the large dilatator fossa, and the bone does not appear to have contributed to the floor of the post-temporal fossa. There is a deep excavation for the origin of the levator arcus palatini muscle on the underside of the overhanging postorbital process. The canal for the otic nerve originates in the centre of the orbital face of the sphenotic and emerges in the dilatator fossa. In five specimens where the lateral face of the sphenotic is visible, two have a vestigial spiracular canal (spic, figure 92) passing through the ridge limiting the dilatator fossa, as in the Callovian species, two merely have a notch (nspi, figure 92) in this position, and P.919 (figure 92) exhibits both conditions.

The basisphenoid is identical with that of the Callovian species (figure 78) except that the pedicel is longer dorso-ventrally.

In the small specimens from the stomach contents of *P. macrocephalus* the pterosphenoid is almost identical with that of the Callovian species, but it is possible that in large individuals the bone was more extensive and contributed to the floor of the post-temporal fossa. The foramina of the trochlear nerve and middle cerebral vein (mcv) are as in the Callovian species (these foramina were misidentified in Patterson 1967, fig. 5), and there is no pterosphenoid pedicle. In small individuals the foramen of the first branch of the superficial ophthalmic nerves notches the upper margin of the pterosphenoid, as in the Callovian species, but in large individuals it lies within the bone (frla, figure 92).

The orbitosphenoid resembles that of the Callovian species (figure 80), and in small individuals the bone does not extend above the cranial cavity, but it is not possible to tell whether it did so in large ones. The foramen of the anterior cerebral vein (acv) is in the same position as in the Callovian species.

The sclerotic is ossified in two segments and there is no basal sclerotic bone.

(*k*) *Otic and orbitotemporal regions: summary and discussion*

(i) *Summary of conditions in pholidophorids and leptolepids*

Facts relating to the cranial fissure, its closure, and the consequent framing by the occipital bones of structures which are found in the otic ossifications of primitive pholidophorids are summarized and discussed in §6(*a*). The myodome and basipterygoid process are discussed in §§9 and 8. Other points in the structure of the pholidophorid and leptolepid otic and orbitotemporal regions are as follows.

(1) In full-grown individuals of *Pholidophorus bechei*, *P. minor*, in some *Leptolepis coryphaenoides* and probably in *Pholidophoroides limbata* the otic and orbitotemporal regions are occupied by a single ossification, without sutures or visible radiation centres, and this single bone may also fuse with the occipital ossification in *P. bechei* and *L. coryphaenoides* (see point 1, p. 314). In other pholidophorids and leptolepids, including some individuals of *L. coryphaenoides*, sutures between the neurocranial bones persist, probably throughout life. In all leptolepids, the normal teleostean complement of bones is present: median orbitosphenoid and basisphenoid, paired pterosphenoids, sphenotics, prootics, and pterotics. Among pholidophorids, the ossification pattern is unknown in *P. minor* and *Pholidophoroides limbata*, while the Callovian *Pholidophorus* shows the same ossifications as leptolepids and teleosts. In *P. germanicus*, *P. macrocephalus* and incompletely ossified individuals of *P. bechei* these same bones are present, but in addition there is a small opisthotic. In all pholidophorids the pterotic is much more extensive than in leptolepids. In *P. germanicus* and *P. macrocephalus* there are additional small ossifications, in *P. germanicus* behind the lower part of the posterior semicircular canal and beneath the ossification centre of

the frontal, in *P. macrocephalus* lateral to the posterior part of the external semicircular canal, on the outer face of the descending lamina of the dermopterotic. The small ossification behind the posterior semicircular canal in *P. germanicus* probably fused with the pterotic in full-grown individuals while that beneath the frontal remained independent. The small ossification in *P. macrocephalus* may become quite large and probably remained distinct throughout life.

(2) The pholidophorid opisthotic, known in *P. bechei*, *P. germanicus* and *P. macrocephalus*, is a small bone lying behind the glossopharyngeal canal (in the prootic) and in front of the vagus canal. It forms part of the outer wall of the saccular recess, part of the floor of the ampullary chamber of the posterior semicircular canal, and the antero-ventral wall of the vagus canal. In *P. bechei* the opisthotic is limited posteriorly by the cranial fissure and fuses with the otic ossifications during ontogeny, in *P. germanicus* it fuses with the occipital ossifications during ontogeny, and in *P. macrocephalus* it appears to remain independent.

(3) The pholidophorid pterotic is a large bone, forming the walls of the post-temporal fossa and the posterior parts of the fossa bridgei and subtemporal fossa, surrounding the lateral cranial canal, and containing the greater part of the posterior and external semicircular canals and part of the anterior canal. The position of the ossification centre of this large bone is not known with certainty, but in *P. germanicus*, since the rather lightly ossified pterotic does not impinge upon the anterior semicircular canal and only reaches the external and posterior canals peripherally (at its ventral and posterior margins), it is clear that the ossification centre cannot have been associated with a semicircular canal, as it is in the pterotic of teleosts. The inferred position of the ossification (growth) centre is indicated by a star in figure 75. This point is the postero-lateral shoulder of the otic capsule and is medial to the post-temporal fossa, behind the fossa bridgei, above the apex of the subtemporal fossa and the lateral cranial canal, and below the suture between the parietal and dermopterotic. The small outlier of the pterotic behind the lower part of the posterior semicircular canal is probably an outer perichondral lamella induced by encroachment of the main ossification on the inner surface of the canal (cf. de Beer 1937, p. 127). The larger subsidiary ossification in *P. macrocephalus*, postero-lateral to the external semicircular canal, on the lateral surface of the posterior part of the descending lamina of the dermopterotic, has endochondral components and appears to retain its individuality throughout life. No other fish is known to have such a bone.

The endochondral pterotic does not fuse with the dermopterotic in pholidophorids, except perhaps in full-grown *P. bechei* and *P. minor*, where all the dermal roofing bones seem to fuse with the endocranium to some extent.

In leptolepids the pterotic is much smaller than in pholidophorids. It forms the wall of the posterior part of the subtemporal fossa, the floor of the posterior part of the post-temporal fossa, encloses the external semicircular canal, and in fully ossified individuals of *L. coryphaenoides* forms a small part of the lining of the cranial cavity between the anterior and posterior ampullary chambers, and the lower part of the strut medial to the lateral cranial canal. These differences from the pholidophorid pterotic are a consequence of closure of the cranial fissure, and are discussed in §6(*a*). The auto- and dermopterotics are fused early in ontogeny in all leptolepids, except perhaps in the Sinemurian species. In the Callovian species the centre of ossification of the autopterotic is known to have lain on the outer face of the descending lamina of the dermopterotic, over the middle part of the external semicircular canal: the bone ossifies from the same point in living teleosts.

(4) The prootic is broadly similar in pholidophorids and leptolepids, enclosing the

trigeminofacial chamber and contributing to the walls of the myodome, subtemporal fossa, saccular and utricular recesses, and anterior and external ampullary chambers. In pholidophorids the prootic also has a dorsal portion forming the floor of the middle part of the fossa bridgei (or post-temporal fossa, where this becomes confluent with the fossa bridgei in the Callovian species and *P. macrocephalus*, see point 13 below). A similar dorsal portion of the prootic is not definitely known in any leptolepid: it is certainly not present in fully ossified *L. coryphaenoides* but might occur in large *L. dubia*. The prootic extends far enough posteriorly to enclose the glossopharyngeal foramen in pholidophorids and in the Sinemurian *Leptolepis* and *L. coryphaenoides*, but in Upper Jurassic leptolepids this foramen lies in the exoccipital. The ossification centre of the prootic is not known with certainty in any pholidophorid or leptolepid, but in all the bone presumably ossified from a centre close to the facial canal.

In all pholidophorids and leptolepids the prootic bridge is developed in the same way as in generalized teleosts, meeting its fellow in the mid-line to separate the cranial cavity and myodome, bordering the pituitary fossa anteriorly, and being penetrated by a canal for the abducens nerve.

In the Sinemurian *Leptolepis* there is a vertical spur in the orbital opening of the trigeminofacial chamber which is the homologue of the lower part of the pterosphenoid pedicle of *Amia* and some teleosts. This spur is also present in rudimentary form in *P. bechei* and some individuals of *L. coryphaenoides*.

(5) The pholidophorid sphenotic must ossify from the tip of the postorbital process, and the bone forms no part of the wall of the cranial or labyrinth cavities. In pholidophorids the sphenotic forms part of the floor of the anterior part of the fossa bridgei, and the otic nerve canal and spiracular canal passed through the cartilage medial to the sphenotic (*P. germanicus*, Callovian species) or enter the bone near its lower margin (*P. macrocephalus*).

In leptolepids the sphenotic is more extensive since the upper part of the prootic is reduced, and it comes to line (but not enclose) the cavity for the foremost loop of the anterior semicircular canal and its ampulla: a larger part of this cavity is lined by the sphenotic in later leptolepids than in early ones. The leptolepid sphenotic also carries the antero-dorsal part of the hyomandibular facet, and the lower openings of the otic nerve canal and spiracular canal come to lie in the centre of the anterior and lateral faces of the bone.

(6) In *Pholidophorus bechei* the basisphenoid is heavily ossified and resembles this region in palaeoniscoids, extending ventrally to form the endochondral floor of the myodome and orbit, and having a transverse bolster at its foot which encloses canals for the palatine nerves, internal carotid and efferent pseudobranchial arteries, and the bucco-hypophysial canal, and contributes to the basipterygoid process. The pedicel of the basisphenoid also contains a pair of vertical canals for the internal carotids. In later pholidophorids the ventral part of the basisphenoid is less thoroughly ossified: the myodome and orbit no longer have cartilage-bone extensions of the basisphenoid in their floors, while the parabasal canal in the foot of the basisphenoid persists in the Callovian species, fails to ossify in *P. germanicus*, and is confluent with the vertical canal for the internal carotid in *P. macrocephalus*, so that in the latter species there is a large triangular opening between the orbit and myodome, bordered laterally by a strut of the basisphenoid, as in Kansas palaeoniscid 'A' and *Perleidus*.

In leptolepids the basisphenoid is of normal teleostean type, with a slender pedicel which consists mainly of membrane bone and is notched or grooved posteriorly by the internal carotids.

In pholidophorids the rostro-caudal length of the foot of the basisphenoid pedicel is such that there can have been no transverse anastomosis between the efferent pseudobranchial arteries. Such an anastomosis, which occurs in most living teleosts, could have developed in leptolepids, where the foot of the pedicel is reduced.

(7) The pholidophorid pterosphenoid is very large, its dorsal part consisting of massive endochondral bone whose upper perichondral lining forms the floor of the anteriormost part of the fossa bridgei and of the posterior part of a supraorbital fossa in the roof of the endocranium, separated from the fossa bridgei by a longitudinal crest. When fully ossified, as in the Callovian *Pholidophorus*, the pterosphenoid contributes to the cavity for the anterior semicircular canal and meets the pterotic posteriorly. In *P. bechei*, although the precise limits of the pterosphenoid are not known, it is likely that the anterior part of the anterior semicircular canal was contained within the pterosphenoid.

In *Pholidophorus germanicus*, *P. macrocephalus* and the Callovian species there is a well developed pterosphenoid pedicle: this consists mainly, if not entirely, of membrane bone, as it does in those teleosts with an ossified pterosphenoid pedicle, not of endochondral bone as it does in *Amia* and *Pteronisculus magnus*. In *P. bechei* the pedicle is represented only by a low ridge.

On the inner surface of the pterosphenoid of pholidophorids there is a medially directed spur of membrane bone which lay beneath the brain and marks the division between the posterior part of the optic fenestra, transmitting the optic nerves and vessels, and the anterior portion which was closed by membrane, inserting on this spur. The spur is smallest in *P. bechei*, largest in the Callovian species and *P. macrocephalus*.

In leptolepids the pterosphenoid is much less massive than in pholidophorids: it contains a good deal of membrane bone, has no connexion with the anterior semicircular canal, and is not known to contribute to the roof of the endocranium, although it is possible that there was such a contribution in large *L. dubia*. There is no pterosphenoid pedicle in leptolepids (the Sinemurian species has the lower part of such a pedicle developed on the prootic), and the medial spur on the inner face of the pterosphenoid is only present in some individuals of *L. coryphaenoides*.

(8) In all pholidophorids and leptolepids the orbitosphenoid is a median bone with no sign of having had a paired origin, although presumably, as in teleosts, it ossified from paired centres. In pholidophorids the orbitosphenoid encloses the foremost part of the cranial cavity, having an ossified dorsal wall which floors the anterior portion of the supraorbital fossae on the roof of the orbitotemporal part of the braincase. There is also often a long, median anterior process passing forwards towards the ethmoid region, below the olfactory nerves, and ending in cartilage. In leptolepids, the dorsal surface of the orbitosphenoid only ossifies in some individuals of *L. coryphaenoides* and the bone is normally V-shaped in section, as it is in non-elopiform teleosts. The anterior process of the orbitosphenoid is never more than a short spur in leptolepids, and most of the bone is membranous.

(9) In *Pholidophorus germanicus*, *P. macrocephalus* and probably in other pholidophorid species there is a large, discoid, perichondrally ossified basal sclerotic bone, surrounding the optic nerves and vessels where they entered the eyeball. Such an ossification has not been found in any leptolepid.

(10) The sclerotic ring is known in detail only in *Pholidophorus germanicus*. In this species it consists of four segments, each containing three distinct portions, a superficial dermal plate and inner and outer perichondral ossifications, which are nowhere fused. The sclerotic ring also

contains four segments in *P. bechei*, while in *P. macrocephalus* and in leptolepids it contains two, arranged fore and aft of the eyeball.

(11) The anterior dorsal fontanelle is very small in *Pholidophorus minor*, larger in *P. bechei* and the Callovian *Pholidophorus*, in both of which it is about equal in size to that of *Pteronisculus* and *Perleidus*, and even larger in the lightly ossified *P. germanicus*. In leptolepids the fontanelle becomes so large that it is hardly recognizable, extending forwards to the ethmoid region (except in those individuals of *L. coryphaenoides* in which the dorsal surface of the orbitosphenoid ossifies) and becoming confluent with the post-temporal fossa laterally.

(12) The fossa bridgei is only individualized in the Lower Jurassic pholidophorids, *P. bechei*, *P. minor*, *P. germanicus* and *Pholidophoroides limbata*. In Upper Jurassic pholidophorids and in leptolepids the fossa bridgei is confluent with the post-temporal fossa.

In *P. bechei*, *P. germanicus* and *Pholidophoroides limbata* the fossa bridgei is an elongate depression on the lateral part of the dorsal surface of the otic and orbitotemporal regions, roofed by the frontal and dermopterotic, and with its lateral wall formed by the descending lamina of the dermopterotic, which projects into the fossa medial to the lateral crest of the endocranial roof. In all three species the fossa is partially divided into antero-medial, lateral and postero-medial portions by the ridge over the anterior semicircular canal, but this division is more obvious in *P. bechei* and *P. limbata*, where the ridge over the semicircular canal is more prominent and extends closer to the lateral wall of the fossa, since the braincase is narrower. The spiracular canal opens into the deep lateral part of the fossa immediately lateral to the foremost part of the ridge over the semicircular canal, at the junction of the sphenotic, prootic and pterosphenoid. The antero-medial portion of the fossa, medial to the semicircular canal, is floored mainly by the pterosphenoid and contains the opening of the canal for the ramus lateralis accessorius. The deep lateral portion of the fossa, containing the opening of the spiracular canal, is floored by the sphenotic, prootic and pterotic. The shallow posterior portion of the fossa is floored by the pterotic, is only separated from the underlying lateral cranial canal by a thin layer of bone, and contains the opening of the canal for the supratemporal branch of the glossopharyngeal nerve.

(13) The post-temporal fossa in *P. bechei*, *P. minor* and *Pholidophoroides limbata* is a small depression or groove on the posterior face of the pterotic, lateral to the ridge over the posterior semicircular canal, which lies between it and the cranial fissure. The post-temporal fossa is roofed by the dermopterotic and is separated from the fossa bridgei in front by a transverse wall of the pterotic, with a small, transverse portion of the descending lamina of the dermopterotic applied to its dorso-lateral surface. The supratemporal branch of the glossopharyngeal nerve traversed the fossa, entering through its floor and leaving through its antero-medial wall.

In *Pholidophorus germanicus* the post-temporal fossa only differs from that of *P. bechei* in being a little larger, so that the wall separating it from the fossa bridgei is thin and oblique, and the supratemporal nerve passes up through the bone medial to the fossa, because of hypertrophy of the subtemporal fossa. In the Callovian *Pholidophorus* the post-temporal fossa and fossa bridgei are each exactly comparable with those of *P. germanicus* (apart from minor differences due to incomplete ossification in the latter), but the wall separating the two has become perforated, so that the post-temporal fossa communicates with the deep postero-lateral portion of the fossa bridgei beneath an arched strut formed by the pterotic medially and the transverse portion of the descending lamina of the dermopterotic laterally. Through this opening, trunk muscles must have entered the fossa bridgei, inserting on the dermopterotic, prootic, sphenotic and pterosphenoid, and functionally the fossa bridgei has become an extension of the post-temporal fossa. In *P. macrocephalus* the dermopterotic portion of the strut between the post-temporal fossa and fossa bridgei is reduced and only the pterotic portion remains.

In all leptolepids the post-temporal fossa communicates widely with the fossa bridgei, and as in *P. macrocephalus* only the endochondral portion of the division between the two remains as a short process or shelf on the epioccipital. Because of the closure of the cranial fissure, discussed in full in §6(*a*), the medial wall of the leptolepid post-temporal fossa is formed by the epioccipital, not the pterotic, and this is a fundamental difference from pholidophorids. In the Sinemurian *Leptolepis* the anterior part of the fossa bridgei (now part of the post-temporal fossa) still contains the opening of the spiracular canal, but in later leptolepids this is lost and the anterior part of the fossa bridgei is reduced. No leptolepid is known to have contributions to the floor of the post-temporal fossa from either the prootic or the pterosphenoid. The canal for the supratemporal nerve, which opens into the shallow, postero-medial portion of the fossa bridgei in pholidophorids, is no longer recognizable in leptolepids. But this portion of the fossa bridgei still persists in early leptolepids as a shallow depression on the dorsal surface of the epioccipital. In Upper Jurassic leptolepids this too is lost. In leptolepid braincases the post-temporal fossa communicates with the cranial cavity through an opening in front of the epioccipital, above the pterotic and behind the sphenotic: this opening was presumably closed in life by cartilage or membrane.

(14) The subtemporal fossa, which in living teleosts houses the adductor muscle of the operculum and sometimes branchial levator muscles, is similarly developed in *Pholidophorus bechei*, *P. minor*, the Sinemurian *Leptolepis*, *L. coryphaenoides* and the Callovian *Leptolepis*. In all it is conspicuous, but is separated from the post-temporal fossa or fossa bridgei above by a substantial layer of bone within the arch of the external semicircular canal. In *L. dubia* the fossa is a little deeper. In *P. germanicus*, the Callovian *Pholidophorus* and *P. macrocephalus* the subtemporal fossa is extremely deep, and there is only a thin, translucent layer of bone between its apex and the lateral cranial canal. In pholidophorids the subtemporal fossa lies mainly in the pterotic, with a small anterior contribution from the prootic, but in leptolepids, after closure of the cranial fissure, the exoccipital replaces the pterotic in the posterior part of the fossa.

In pholidophorids there is a less conspicuous fossa on the prootic, in front of the subtemporal fossa, which contained the origin of the adductor muscle of the hyomandibular. Among leptolepids, this fossa is only well defined in the Sinemurian *Leptolepis*, although the muscle must have originated in the same place in later leptolepids, as it does in living teleosts.

In pholidophorids (except *P. minor*) and in Upper Jurassic leptolepids there is a bridge across the subtemporal fossa formed by struts of membrane bone from the prootic and intercalar. In Lower Jurassic leptolepids the intercalar extends forwards over the prootic in the medial wall of the fossa, but only forms a ledge with a pocket above it. The bridge across the fossa is formed slightly differently in pholidophorids and in Upper Jurassic leptolepids, since in the former the prootic portion is a rod above the jugular groove, while in the leptolepids it is an outgrowth of the membranous wall of the jugular canal, which is absent in pholidophorids (point 20 below). It is therefore likely that the bridge is independently developed in the two groups, the leptolepid type arising from the ledge present in Lower Jurassic leptolepids.

(15) The articular facet for the hyomandibular is long and inclined somewhat antero-ventrally in pholidophorids and leptolepids, so that it is less horizontal than in generalized living teleosts. It is similarly inclined in *Amia*, parasemionotids (figure 97) and holosteans such as

Heterolepidotus (figure 102) and *Pachycormus* (figure 106) while in palaeoniscoids (figure 117) and 'subholosteans' (figure 115) it is much more steeply inclined.

In the larger pholidophorids, *P. germanicus*, *P. macrocephalus* and the Callovian species, the hyomandibular facet lay between the prootic and pterotic medially and the sphenotic laterally, and probably remained cartilaginous throughout life, appearing in the fossil skulls as a deep groove which is roofed by the descending lamina of the dermopterotic: the facet appears similar in parasemionotids (figure 98) and various fossil holosteans (figures 99, 103, 106, 108, 112). In *P. bechei* and *P. minor* the facet ossifies, becoming lined with perichondral bone in fully grown individuals: it is not known what proportions of the facet are formed by the prootic, pterotic and sphenotic in these species, but the facet presumably marks the junction of the prootic and pterotic with the sphenotic. In leptolepids the facet is also ossified, and lies mainly on the pterotic, as in teleosts, with a small anterior contribution from the sphenotic. The prootic may form a small part of the lower margin of the facet in leptolepids, but it is notable that the foremost part of the facet lies entirely on the sphenotic, not on the sphenotic/prootic suture as it does in living teleosts.

(16) There is a dilatator fossa in all pholidophorids and leptolepids. In pholidophorids it lies entirely upon the lateral surface of the sphenotic, but in leptolepids the pterotic (dermal and endochondral components) forms the posterior part of the fossa, as in living teleosts. On the underside of the postorbital process, below the anterior part of the dilatator fossa and above the lower opening of the spiracular canal, there is also an area on the sphenotic for the origin of the levator arcus palatini muscle. In pholidophorids this area is not sharply separated from the dilatator fossa, but in leptolepids the two are separated by a crest which is better developed in Upper Jurassic forms than in Lower Jurassic.

(17) The articular facet for the first suprapharyngobranchial in *Pholidophorus bechei* is a small area, sometimes without perichondral lining, at the antero-dorsal margin of the vestibular fontanelle. In *P. germanicus*, *P. macrocephalus* and the Callovian *Pholidophorus* the facet is a small perichondrally lined depression on the prootic, just below the jugular groove. In leptolepids the facet is no longer recognizable.

(18) The articular facet for the first infrapharyngobranchial in *Pholidophorus bechei* is an area without perichondral lining, facing antero-ventro-laterally, and lying at the antero-ventral corner of the prootic, in the notch between the ascending process and the posterior portion of the parasphenoid, immediately above the internal carotid foramen and behind the groove for the orbital artery. In other pholidophorids the facet must have occupied the same position, but it is not even ossified endochondrally and its presence is only indicated by an incisure in the parasphenoid (figures 84, 141). In Lower Jurassic leptolepids this incisure in the parasphenoid is also usually present (figures 143, 144), but in some individuals of *L. coryphaenoides* and in Upper Jurassic leptolepids it becomes shallower (figures 92, 141, 144*b*) and the infrapharyngobranchial must have articulated with the parasphenoid, as it does in living teleosts.

(19) There is a spiracular groove and canal in all pholidophorids, and in all but the most advanced leptolepids (Callovian species, *L. dubia*), where the groove is greatly reduced and the canal may be only represented by a notch.

In pholidophorids the ascending process of the parasphenoid extends up to the lateral commissure, and the spiracular groove runs from its upper end to the lower opening of the spiracular canal, which lies immediately in front of the hyomandibular facet. In all pholidophorids the upper opening of the spiracular canal lies in the lateral part of the fossa bridgei, lateral to the foremost part of the ridge over the anterior semicircular canal, at the junction of the sphenotic, pterosphenoid and prootic. Except in *Pholidophoroides limbata*, a process of the descending lamina of the dermopterotic fits into the upper opening of the canal, and in the Callovian species the spiracular diverticulum ended in a groove on the inner face of this process. In *P. germanicus* and the Callovian species the spiracular groove lies on the prootic, the lower opening of the spiracular canal lies on the suture between the prootic and sphenotic, and the canal passed medial to the sphenotic. In *P. macrocephalus* the lower opening of the canal lies on the sphenotic, so the canal must have passed through the bone. In all pholidophorids the canal for the otic nerve runs into the spiracular canal, and in the Callovian species there is a dilatation of the canal at this junction which probably contained a spiracular sense organ.

In the Sinemurian *Leptolepis* the spiracular groove is still just recognizable on the prootic, but in later leptolepids it is confined to the sphenotic, the latter bone expanding relative to the prootic until the lower opening of the spiracular canal lies in the centre of its lateral surface (point 5 above). In the Sinemurian *Leptolepis* the spiracular canal opens into the fossa bridgei at the posterior edge of the sphenotic, as in pholidophorids, and is dilated where it is joined by the otic nerve canal, suggesting that there was a spiracular sense organ. But in later leptolepids the canal no longer opens into the fossa bridgei, and only in *L. coryphaenoides* is it joined by the otic nerve canal. In this species the spiracular canal is much narrower than the nerve canal, and there is no obvious dilatation where the canals meet, suggesting that the spiracular sense organ had been lost. In the Callovian *Leptolepis* and in *L. dubia* the spiracular canal is only indicated by a very short canal through the crest separating the dilatator fossa from the fossa for the levator arcus palatini, and in some *L. dubia* there is only a notch in this position. In these Upper Jurassic leptolepids the vestigial spiracular canal can hardly have transmitted a spiracular diverticulum, for the canal leads into the dilatator fossa, a site of muscle origin. The only comparable condition seems to be in *Saurichthys* (Stensiö 1925, pp. 28, 73), where the spiracular canal opens not in the fossa bridgei but on the lateral surface of the otic region, lateral to the hyomandibular facet, in much the same position as the dilatator fossa. Stensiö deduced that this canal must have transmitted a branch of the orbital artery ('external carotid') comparable to branches described in *Polyodon* by Allis (1911, p. 285) as being associated with the spiracular canal. One of these passes through the otic nerve canal into the fossa bridgei, the other enters the protractor hyomandibularis, which is the undifferentiated mandibular constrictor dorsalis, homologous with the levator arcus palatini and dilatator operculi of higher actinopterygians. The vestigial spiracular canal of Upper Jurassic leptolepids may have transmitted an artery to the dilatator operculi, an artery which in more primitive leptolepids accompanied the spiracular diverticulum into the fossa bridgei and thence into the dilatator fossa, but I can find no description of a similar artery in living teleosts. In *Scorpaena* a vein perforates the floor of the dilatator fossa and accompanies the ramus lateralis accessorius (Allis 1909, p. 87).

The pholidophorids and leptolepids described here provide a very clear illustration of a trend towards reduction of the spiracular diverticulum from the palaeoniscoid or primitive holostean type of spiracular canal, found in pholidophorids, to the Recent teleostean condition, where the diverticulum is lost.

(20) In pholidophorids the lateral commissure, forming the lateral wall of the trigeminofacial chamber, is short and consists of endochondral bone. The hyomandibular trunk passed

out behind the lateral commissure and the jugular vein and orbital artery ran across the lateral surface of the prootic in open grooves. In Upper Jurassic leptolepids these grooves are roofed over as long canals, and the hyomandibular trunk passed out through a laterally directed foramen in the wall of the jugular canal. It has been pointed out above (p. 359) that although the advanced leptolepid type of trigeminofacial chamber, which also occurs in primitive living teleosts, resembles the trigeminofacial chamber of palaeoniscoids and other primitive actinopterygians, this resemblance is secondary and is due to the development of membrane bone extensions from a short primary lateral commissure of pholidophorid type. These changes are demonstrated with exceptional clarity in early leptolepids.

In the Sinemurian *Leptolepis* the jugular groove is roofed over for a short distance behind the exit of the hyomandibular trunk, enclosing a foramen for the latter, but the groove for the orbital artery is still open so that the artery ran into the jugular canal through the lower part of the hyomandibular nerve foramen. In the Toarcian *L. coryphaenoides* the jugular groove is roofed to a greater extent posteriorly and the upper part of the groove for the orbital artery is also roofed over, so that the artery entered the floor of the jugular canal through a separate foramen. In the Callovian *Leptolepis* the wall of the jugular canal extends almost to the posterior margin of the prootic and its rear end is produced into a group of splints which interdigitate with the tip of the antero-lateral spur of the intercalar, bridging the subtemporal fossa. The groove for the orbital artery is also roofed over almost to the ventral margin of the prootic. This is essentially the condition in living *Elops*, except that there the strut meeting the intercalar is even longer and the orbital artery canal is shorter. Other primitive living teleosts such as *Megalops*, *Albula*, *Coregonus*, *Argentina* and *Osteoglossum* show variations which seem to be derivable from the advanced leptolepid condition by some reduction of the bony cover over the jugular vein and orbital artery.

(21) The trigeminofacial chamber is basically similar in all pholidophorids and leptolepids apart from the development in leptolepids of membrane bone outgrowths converting the jugular groove and orbital artery groove into canals (point 20 above). The endochondral portion of the lateral commissure is slender in all pholidophorids and leptolepids. The jugular groove is rather deeply incised on the neurocranium in pholidophorids, and in *P. bechei* it can be traced back to the vagus foramen, but in leptolepids the groove becomes inconspicuous posteriorly.

In all pholidophorids and leptolepids there are only two foramina, the facial and trigeminal, leading from the cranial cavity into the trigeminofacial chamber. The facial foramen is laterally directed, originates antero-ventral to the utricular recess, and opens into the jugular groove or canal close behind the endochondral lateral commissure. In pholidophorids this passage is a canal, because of the thickness of the endochondral bone, but in advanced leptolepids this part of the cranial wall is paper thin and membranous, so that there is only a foramen. In pholidophorids the external opening of the facial canal is confluent with the palatine fenestra, a rather large opening in the floor of the jugular groove, leading into the dorso-lateral corner of the myodome. The palatine nerve passed into the myodome through this opening and the geniculate ganglion evidently lay in this extramural space in the floor of the jugular groove. In leptolepids the opening in the floor of the jugular canal decreases in size so that only a palatine foramen remains, as in living teleosts, and the facial foramen increases in size until it is equal in size to the trigeminal: in the Sinemurian *Leptolepis* the palatine foramen and facial foramen are equal in size and the facial foramen is only a little smaller than the trigeminal, in *L. coryphaenoides* the palatine foramen is much smaller. These facts suggest that in leptolepids the geniculate ganglion retreated from its position in the floor of the jugular canal until it lay within the enlarged facial foramen.

The trigeminal foramen of pholidophorids and leptolepids is antero-laterally directed' originates in front of the utricular recess, and opens into the dorso-medial part of the orbital opening of the trigeminofacial chamber, not into the jugular canal itself. As with the facial nerve, there is a trigeminal canal in pholidophorids, a foramen in the thinner bone of advanced leptolepids. In pholidophorids the trigeminal canal opens into a well marked recess in the orbital wall, and the gasserian ganglion probably lay in this recess. In leptolepids, this recess becomes inconspicuous, and the ganglion may have retreated into the foramen.

In all pholidophorids and leptolepids the buccal, otic and superficial ophthalmic nerves accompanied the trigeminal trunk through the trigeminal foramen, and the lateralis ganglion probably lay beside the gasserian. The superficial ophthalmic nerves passed antero-dorsally across the orbital wall in a more or less well marked groove which passes lateral to the pterosphenoid pedicle, where this is developed. A series of canals in the pterosphenoid portion of the roof of the orbit transmitted branches of the nerves to the roofing bones. The first (most posterior) of these canals opens into the foremost part of the fossa bridgei (or post-temporal fossa where this is confluent with the fossa bridgei) and is interpreted as having transmitted the ramus lateralis accessorius.

The otic nerve ran dorso-laterally across the wall of the orbit, diverging from the superficial ophthalmics, and entered the otic nerve canal which leads through the postorbital process into the spiracular canal in pholidophorids and the Sinemurian *Leptolepis*, passing with the latter into the fossa bridgei (or post-temporal fossa where these are confluent). In *L. coryphaenoides* the otic nerve canal opens into the foremost part of the dilatator fossa, but is still joined by the much reduced spiracular canal, while in Upper Jurassic leptolepids the otic canal opens into the dilatator fossa in front of the remnant of the spiracular canal. The position of the lower opening of the otic nerve canal, which lies on or just above the sphenotic/pterosphenoid suture in pholidophorids and in the centre of the orbital face of the sphenotic in Upper Jurassic leptolepids, is summarized above (point 5).

Schaeffer (1971, p. 6) has pointed out the error of Goodrich's (1930) statement, frequently quoted or paraphrased, that the trigeminofacial chamber of teleosts is secondarily divided by a wall of membrane bone into a pars jugularis and a pars ganglionaris. As Schaeffer says, the medial wall of the jugular canal in teleosts is part of the primordial lateral wall of the neurocranium. The fact that it ossifies in membrane in some teleosts (and in advanced leptolepids) seems to be only a consequence of the thinning of endochondral bone and replacement of endochondral bone by membrane bone which is so widespread in the braincases of Upper Jurassic leptolepids compared with those of primitive pholidophorids. Schaeffer recommends that the term trigeminofacial chamber should be applied to 'the extramural cavity between the lateral cranial wall and the lateral commissure', whether the ganglia of the trigeminal and facial nerves lie in this cavity or within the cranial wall, so making the terms 'pars jugularis' and 'pars ganglionaris' redundant, and this usage is adopted here. The apparent retreat of the gasserian and geniculate ganglia from the chamber into their foramina in leptolepids is a trend from the condition in palaeoniscoids, where the ganglia are extracranial, towards the condition in teleosts, where they are partly or wholly intracranial, but these comparisons will be made in more detail below (p. 401).

(22) There is a separate profundus canal in all pholidophorids and in the Sinemurian *Leptolepis*. In *P. bechei* this canal originates very close to the internal opening of the trigeminal canal, diverges from the latter as it passes through the bone, and opens midway between the trigeminal foramen and the oculomotor; in *P. minor* the canal opens in the same position. In *P. germanicus*, the Callovian *Pholidophorus* and the Sinemurian *Leptolepis* the internal opening of the canal lies further from that of the trigeminal, and in these species and *P. macrocephalus* the external opening lies above the oculomotor foramen, on or near the pterosphenoid/prootic suture.

In all leptolepids, except the Sinemurian species, there is no separate profundus foramen and the nerve entered the orbit through the oculomotor foramen, as it does in many living teleosts (cf. Allis 1909, p. 82).

(23) In all pholidophorids and leptolepids the oculomotor foramen is large, approximately equal in size to the trigeminal. In those pholidophorids where bone junctions can be recognized, the oculomotor foramen lies on the basisphenoid/prootic suture, notching both bones. In the Sinemurian *Leptolepis* the foramen also lies on this suture, but is deeply incised in the prootic, while in all other leptolepids it lies entirely within the prootic, as in living teleosts.

(24) The trochlear foramen lies within the pterosphenoid in all pholidophorids and leptolepids. The foramen originates in the recess which housed the optic lobe, passes through the bone antero-laterally, and emerges close to the margin of the optic fenestra. In pholidophorids, where there is a separate profundus foramen, the external opening of the trochlear foramen is in line with a groove leading up from the profundus foramen.

A constant feature of all pholidophorids and leptolepids is the presence of a second foramen which originates close behind the trochlear foramen, passes through the pterosphenoid more transversely than the latter and emerges in the orbit postero-lateral to it, separated from it by the pterosphenoid pedicle where this is developed, and in line with the groove for the superficial ophthalmic nerves. A similar foramen has been interpreted as the foramen of the anterior cerebral vein in several fossil actinopterygians (see p. 411). But in all pholidophorids and leptolepids the foramen of the anterior cerebral vein lies further forwards, in the orbitosphenoid. This foramen or canal originates high in the lateral wall of the recess for the telencephalon and passes transversely through the bone: it is sometimes slit-like and directed almost vertically. The foramen lies in the centre of the orbitosphenoid (*P. germanicus*, Sinemurian *Leptolepis*) or in the posterior part of the bone (*P. macrocephalus*, other leptolepids).

The foramen accompanying the trochlear foramen has been referred to throughout the descriptive sections as the foramen of the middle cerebral vein. This interpretation is justified in the comparative section on p. 409.

(25) In all pholidophorids and leptolepids there is a very large interorbital fenestra, and the interorbital septum was membranous, as in most teleosts. Only in fully ossified individuals of *P. bechei* is there endocranial bone over the parasphenoid below the orbit, and here it is only a thin skin.

The optic fenestra, transmitting the optic nerves and accompanying vessels, is a relatively large, median opening in all pholidophorids and leptolepids. In *P. bechei* the optic artery still perforated or notched the margin of the fenestra, as it does in palaeoniscoids, but in other forms this vessel leaves no trace on the braincase. Where ossification patterns are known, the optic fenestra is limited by the orbitosphenoid anteriorly, the pterosphenoids laterally and the basisphenoid posteriorly, as in generalized teleosts.

(26) The olfactory tracts left the cranial cavity through a median opening in the front of the orbitosphenoid in all pholidophorids and leptolepids.

(27) In *P. bechei* the cranial cavity is closely invested by bone so that the contour of much of the brain can be recognized, as in palaeoniscoids. In other pholidophorids and especially in leptolepids the bony lining of the cranial cavity becomes less close and complete, partly through thinning of the bone and partly through reduction in ossification. In pholidophorids and leptolepids recesses for the olfactory bulbs and telencephalon (in the orbitosphenoid) and optic lobes (in the pterosphenoid) can be recognized. In the Callovian *Pholidophorus* there is a pair of depressions on the anterior face of the supraoccipital which appear to be the impressions of a pair of metencephalic lobes, as in some palaeoniscoids. In *P. bechei* and *P. minor* these depressions are just recognizable, but here they lie on the pterotic.

The pituitary fossa, in the floor of the cranial cavity, lies between the basisphenoid and the prootic bridge, as in teleosts. In most pholidophorids, in the Sinemurian *Leptolepis* and some *L. coryphaenoides* there is a small recess in the floor of the cranial cavity lateral to the pituitary fossa and behind the oculomotor foramen. In *P. bechei* and the Sinemurian *Leptolepis* there is an irregular fenestra in the prootic bridge medial to the site of this recess, while in *P. minor* the palatine fenestra is so large that it probably incorporates this fenestra and in some *L. coryphaenoides* the pituitary fossa is emarginate as if it incorporates the fenestra. These recesses or fenestrae appear to have housed the saccus vasculosus. In palaeoniscoids such as *Kentuckia* (Rayner 1951, fig. 9) and *Pteroniscus* (Nielsen 1942, fig. 9) there is a recess in the hind wall of the pituitary fossa, below the dorsum sellae, interpreted by Nielsen as having housed the posterior part of the saccus vasculosus. This recess resembles the so-called cavum sacci vasculosi (Lehn) of *Polypterus* (de Beer 1926*a*, fig. 69; Hansen 1971, fig. 9), and the corresponding cavity in *Acipenser* (Hansen 1971, fig. 2). In parasemionotids (MMK 492), '*Aspidorhynchus*' (P.9844; psv, figure 101) and *Lepidotes* (P.9998, P.34511) there is a similar recess in the hind wall of the pituitary fossa, but here the recess is drawn out laterally, like the 'cross-canal' (Allis) which houses the saccus vasculosus in *Lepisosteus* (Holmgren & Stensiö 1936, p. 472), and it has only a partial dorsal wall, so that it is more or less open towards the cranial cavity: these forms are intermediate in the structure of this recess between the palaeoniscoid type and the pholidophorid type, where only the lateral portions of the recess are still recognizable. It appears, therefore, that in pholidophorids and leptolepids the saccus vasculosus lay on the upper surface of the prootic bridge, as in living teleosts (de Beer 1926*b*, p. 57), not in the myodome as it does in *Amia* (Hansen 1971, fig. 15). The only other fossil holostean in which I have been able to observe this region is *Dapedium* (P.11177, P.11189), where there is no obvious recess for the saccus vasculosus, and it may have been housed in the myodome, as in *Amia*.

(28) The labyrinth cavity, like the cranial cavity, is much more completely invested by bone in primitive pholidophorids than in leptolepids. In *P. bechei* all the semicircular canals (except the sinus communis) are bone-enclosed throughout their length, and the utricular recess is separated from the cranial cavity by a constricted opening. In later pholidophorids such as the Callovian species the posterior and external semicircular canals were partially enclosed by cartilage, the anterior canal lay partially free in the cranial cavity, and the utricular recess is less sharply separated from the cranial cavity. In leptolepids, the posterior and external semicircular canals are completely enclosed, as they are in teleosts, in consequence of the changed ossification pattern after closure of the cranial fissure (§6(*a*)), but the anterior canal

lay free in the cranial cavity, there is no strut supporting the sinus communis except in some *L. coryphaenoides*, and the utricular recess is continuous with the cranial cavity.

The saccular recess is a little larger in leptolepids than in pholidophorids, extending forwards below the facial foramen and being more inflated laterally.

In all pholidophorids and leptolepids the external semicircular canal ran through the recess housing the posterior ampulla, not through a separate opening in the cranial wall.

(29) A lateral cranial canal is present in all pholidophorids and in all leptolepids except some individuals of *L. dubia* and the Callovian species. In pholidophorids the lateral cranial canal is a spacious cavity in the pterotic, lateral to the sinus communis and antero-medial to the posterior semicircular canal, which communicates with the cranial cavity by two openings, an anterior one above the external ampulla and a posterior one above the posterior ampulla. The anterior opening is always larger than the posterior, and the canal has a dorsal diverticulum which is only separated from the shallow, postero-medial portion of the fossa bridgei by a thin partition. In pholidophorids (except the lightly ossified *P. germanicus*) the openings of the canal are separated by a vertical strut which carried the sinus communis on its inner face. In *P. bechei* and *P. minor* this strut is narrow, but in the Callovian species it is rather massive, and the lateral cranial canal is correspondingly longer rostro-caudally.

In leptolepids, the strut separating the anterior and posterior openings of the lateral cranial canal only ossifies in some individuals of *L. coryphaenoides*, and the canal usually appears only as a diverticulum of the postero-dorsal part of the cranial cavity. Because of changes in the ossification pattern consequent upon closure of the cranial fissure (§6(*a*)), this diverticulum lies in the epioccipital, not in the pterotic as in pholidophorids. In primitive leptolepids such as the Sinemurian species, this depression on the inner face of the epioccipital extends lateral to the upper part of the posterior semicircular canal in a blind pocket which is the homologue of the dorsal diverticulum of the canal in pholidophorids. In later leptolepids this pocket is reduced, and the canal is only recognizable as a rounded depression on the inner face of the epioccipital. In *L. dubia* and the Callovian species the presence or absence of this depression is subject to individual variation, some having only a weakly concave area of perichondral bone on the inner face of the epioccipital, as in most living teleosts.

As to the function of the lateral cranial canal, a groove on the exoccipital below its posterior opening suggests that the canal was drained by a large vein, falling into the posterior cerebral vein, and it therefore probably contained vascular tissue. But the variability in the canal in Upper Jurassic leptolepids suggests that it can have had no essential role. I suggest, therefore, that the canal was filled with fatty tissue, like the fossa bridgei of living chondrosteans, which appears to include the homologue of the canal (p. 414), and that this tissue was richly supplied with blood.

(ii) *Comparison of pholidophorids and leptolepids with other groups*

The ossification pattern of the otic and orbitotemporal regions is compared with that in other groups in §6(*b*), and only anatomical points are considered here.

1. *Fossa bridgei and post-temporal fossa.* The fossa bridgei is only individualized in Lower Jurassic pholidophorids: in later pholidophorids and in leptolepids it becomes confluent the post-temporal fossa.

The fossa bridgei is typically developed in fossil and living chondrosteans, although it is poorly defined in the primitive *Kentuckia* (Rayner 1951, fig. 6). Among chondrosteans, the closest resemblance to the type of fossa bridgei found in pholidophorids is in the palaeoniscoid *Boreosomus* (Nielsen 1942, fig. 59; Lehman 1952, fig. 45), where the same three regions can be recognized. The only differences are that in *B. piveteaui* the shallow, postero-medial part of the fossa sometimes communicates, through an irregular fenestra, with an intramural space which appears to be the homologue of the lateral cranial canal (p. 414), and the supratemporal branch of the glossopharyngeal nerve enters the fossa laterally. In pholidophorids, a communication between the fossa bridgei and lateral cranial canal resembling that in *B. piveteaui* would appear if the thin partition separating the fossa from the underlying lateral cranial canal were to ossify incompletely. Among holosteans, the parasemionotids (Lehman 1952, fig. 104) and caturids (e.g. *Caturus* sp., Rayner 1948, fig. 5; *C. chirotes*, GSM 97417) seem to have essentially the same type of fossa bridgei as pholidophorids.

In those pholidophorids with a discrete fossa bridgei, the post-temporal fossa is small, especially in *P. bechei* and *Pholidophoroides limbata*. This primitive type of pholidophorid post-temporal fossa, which undoubtedly contained trunk musculature, has no homologue in palaeoniscids and *Australosomus*, where the occipital ossification is as wide as the posterior part of the otic region, leaving almost no space for trunk muscle insertion on the posterior face of the otic ossifications. A post-temporal fossa seems to be represented in *Birgeria* by a postero-dorsal depression on the 'prootico-opisthotic' (Nielsen 1949, fig. 60) which has the same relationship to the supratemporal nerve, and a similar depression is less obvious in *Saurichthys* and sturgeons (Stensiö 1932, figs 33, 34). In *Perleidus* (Stensiö 1932, fig. 59; Lehman 1952, fig. 84) there is a depression on the dorso-lateral surface of the otic region which is traversed by a groove for the supratemporal nerve and is probably a rudimentary post-temporal fossa, as suggested by Griffith & Patterson (1963, p. 36), although, like the corresponding depression in *Birgeria*, *Saurichthys* and sturgeons, it is open laterally rather than posteriorly. In parasemionotids (Stensiö 1932, figs 72, 73; figure 97) there is a post-temporal fossa which is closely comparable with that of primitive pholidophorids.

In Upper Jurassic pholidophorids the post-temporal fossa and fossa bridgei become confluent, by breakdown of the wall (formed by the pterotic and dermopterotic) which separates them in more primitive forms. In Upper Jurassic pholidophorids trunk musculature extended forwards through this opening into the spacious fossa bridgei, floored by the prootic, sphenotic and pterosphenoid. In leptolepids, the extent of the post-temporal fossa shows that it also incorporates the fossa bridgei, but the prootic and pterosphenoid do not contribute to its floor, and its medial wall is formed by the epioccipital, not the pterotic, as a consequence of closure of the cranial fissure.

The evolution of the fossa bridgei and post-temporal fossa was discussed by Griffith & Patterson (1963), who concluded that the post-temporal fossa might have become confluent with the fossa bridgei as it enlarged, or might have overgrown and enclosed the fossa bridgei, so producing the lateral cranial canal: the first of these interpretations is now seen to be correct. Griffith & Patterson's discussion was based on the premise that neither a fossa bridgei nor a spiracular canal occurred in pholidophorids, and this is now known to be false. Concerning the function of the fossa bridgei (Griffith & Patterson 1963, p. 35; Lehman 1966, p. 19), the fact that the fossa is apparently identical in structure in *Pholidophorus germanicus* and the Callovian *Pholidophorus* and contained trunk muscles in the latter but not in the former, supports Rayner's opinion (1951, p. 79) that the fossa bridgei had no function in primitive actinopterygians, for if the fossa had contained any structure of importance it would hardly have been so readily available for invasion by trunk musculature.

In all living teleosts the medial wall of the post-temporal fossa is formed by the epioccipital, as in leptolepids, and (except where it is secondarily reduced) the fossa extends far enough forwards to show that it incorporates the fossa bridgei, as in leptolepids and advanced pholidophorids. In osteoglossomorphs, clupeomorphs and euteleosteans the post-temporal fossa seems never to extend forwards beyond the sphenotic, and is floored by the exoccipital, pterotic and sphenotic (except for some characins, where the prootic may enter anteriorly (Allis 1909, p. 10), and a minute prootic contribution seen on one side of a large skull of *Chanos*), and often communicates with the cranial cavity in dried skulls: in all these features these groups resemble leptolepids. In elopiform teleosts the post-temporal fossa is of normal teleostean type in having the medial wall formed by the epioccipital, but in extent it is more like that of advanced pholidophorids. In *Elops* (Ridewood 1904*a*, p. 38; Allis 1909, p. 9) and the Cretaceous *Notelops* (Dunkle 1940, p. 186) the fossa is floored by the exoccipital, pterotic, prootic, sphenotic and pterosphenoid, just as in the Callovian *Pholidophorus*. In *Pterothrissus* the fossa is somewhat smaller, ending against the pterosphenoid without the latter making any real contribution to it, and having no relationship with the sphenotic, which is occupied by the large dilatator fossa. In *Albula* (Ridewood 1904*a*, p. 47) the post-temporal fossa does not reach the pterosphenoid, probably because the dilatator fossa is greatly enlarged and extends across the sphenotic on to the pterosphenoid. In *Megalops* (Shufeldt 1884, p. 815, fig. 34; Ridewood 1904*a*, p. 44) the post-temporal fossa is a hypertrophied version of that in *Elops*: it extends forwards on to the orbitosphenoid, ending there in a pair of deep pockets, and communicates widely with its fellow through a large median fenestra whose floor is formed by the pterosphenoids and supraoccipital, which meet and completely close the anterior dorsal fontanelle. In pholidophorids the foremost part of the fossa bridgei is separated by a longitudinal crest from paired supraorbital fossae on the pterosphenoid and orbitosphenoid, and a post-temporal fossa of the type seen in *Megalops* could develop from the pholidophorid (or elopid) type by breakdown of this longitudinal crest, allowing the trunk muscles to pass forwards into the paired grooves above the orbit.

In elopiform teleosts there is an extensive medially directed 'pre-epiotic pocket' (Allis 1909, p. 10) just within the post-temporal fossa. This pocket extends into the supraoccipital in *Elops*, *Notelops*, *Megalops* and *Albula*, and in all elopiforms the epioccipital is compressed into a vertical lamina which does not contribute to the lining of the cranial cavity. In clupeoids the epioccipital has the same form and the pre-epiotic pocket is developed as the pre-epiotic fossa (Ridewood), which often opens on the skull roof between the epioccipital, parietal and supraoccipital. In generalized characins the post-temporal fossa also has an extensive pre-epiotic pocket which opens on the skull roof between the epioccipital, parietal and supraoccipital (Roberts 1969, p. 412), and the epioccipital has the same laminar form as in elopiforms and clupeoids: the pre-epiotic pocket of characins seems to be exactly homologous with the pre-epiotic fossa of clupeoids. In *Chanos* and the osteoglossoid *Arapaima* the form of the epioccipital and the pre-epiotic pocket of the post-temporal fossa are just as in *Elops*, and in *Scleropages* and *Osteoglossum*, although the pocket does not extend into the supraoccipital, the epioccipital has the same laminar form.

The widespread occurrence of this pre-epiotic pocket in the most primitive living teleosts suggests that it may be a primitive feature. The laminar epioccipital of all these fishes, which does not contribute to the lining of the cranial cavity, recalls the epioccipital of pholidophorids, which has much the same shape, but this resemblance is certainly spurious since in teleosts the epioccipital houses the posterior semicircular canal, while in pholidophorids the epioccipital lies behind the cranial fissure, and the posterior semicircular canal is still enclosed within the pterotic. The pre-epiotic pocket appears to be the topographic homologue of the shallow, postero-medial portion of the fossa bridgei of pholidophorids and primitive leptolepids, a structure which is reduced or lost in Upper Jurassic leptolepids.

In summary, the spacious post-temporal fossa of primitive living teleosts, especially the elopiforms, contains homologues of the post-temporal fossa and fossa bridgei of pholidophorids. Although the post-temporal fossa of elopiforms resembles that of pholidophorids, not leptolepids, in its extent forwards and medially, it must be derived from a post-temporal fossa of leptolepid type since its medial wall is formed by the epioccipital, not by the pterotic as it is in pholidophorids.

In *Amia* the functional portion of the post-temporal fossa (containing trunk musculature; Allis 1897, pl. 24, fig. 21) appears to be very long and comparable in size with that of many teleosts, but the fossa ends anteriorly at the level of the ampulla of the external semicircular canal, as in *Pholidophorus germanicus*, and the length of the fossa in *Amia* is mainly a consequence of the greater length of the occipital and posterior otic regions in comparison with pholidophorids. The functional post-temporal fossa of *Amia* has an antero-lateral pocket or diverticulum which extends forwards to the opening of the spiracular canal and contains no musculature (Allis 1889, p. 501; 1909, p. 9). This diverticulum appears to be the remains of the fossa bridgei. In the caturids *Heterolepidotus* (P.13260), *Caturus chirotes* (GSM 97417) and Rayner's Toarcian *Caturus* (1948, fig. 5), the post-temporal fossa and fossa bridgei are separated by an oblique wall of bone, as in *P. germanicus*. In these forms, especially *Heterolepidotus* (figure 104), the fossa appears to be much larger than in *P. germanicus*, but as in *Amia* this is mainly a consequence of the greater length of the posterior otic region. In other caturids, *Macrepistius* (Schaeffer 1971) and '*Aspidorhynchus*' (Rayner 1948, fig. 19), the post-temporal fossa appears even larger, but excavation of it in '*Aspidorhynchus*' (figure 100) shows that it is somewhat antero-medially directed, as in *Amia*, and it ends blindly against an oblique wall of endochondral bone at the level of the ampulla of the external semicircular canal. Thus in *Amia* and caturids there is no evidence that trunk musculature ever entered the fossa bridgei, or that the post-temporal fossa ever became broadly confluent with the fossa bridgei, and this is a fundamental difference from pholidophorids and teleosts. The large post-temporal fossa of *Amia* and caturids has arisen merely by enlargement of the small, primitive type of fossa seen in *P. bechei* and parasemionotids.

In *Lepisosteus* there is no functional post-temporal fossa (Allis 1920, p. 251). There is an elongate 'supraotic depression' (Allis), which is described as the temporal groove (= post-temporal fossa) by Holmgren & Stensiö (1936, p. 471), but this does not contain musculature and must be the fossa bridgei.

In *Lepidotes* (figures 108, 110) there is a large post-temporal fossa, whose medial wall and floor are formed posteriorly by the 'epiotic' (Epi). The anterior parts of the floor and medial wall of the fossa are not ossified so that it is impossible to be certain how far it extended forwards or whether it communicated with the fossa bridgei, but the post-temporal fossa appears to end blindly anteriorly in a pocket in the descending lamina of the dermopterotic. The fossa bridgei, if present, lay in cartilage medial to the sphenotic and above the prootic.

In *Dapedium* (P.11177; figures 112, 113) the post-temporal fossa has a rather small posterior opening, but anteriorly it is in open communication with the lateral part of an extremely spacious fossa bridgei, and trunk muscles must have entered the fossa bridgei as in advanced pholidophorids and teleosts.

In *Pachycormus* (32434, figures 106, 107) the post-temporal fossa is also in open communication with the fossa bridgei, as in *Dapedium* and advanced pholidophorids. As in pholidophorids, the medial wall of the fossa is formed by the pterotic.

In summary, among holosteans *Lepisosteus* has no post-temporal fossa and a rudimentary fossa bridgei; *Amia* has a large post-temporal fossa which is homologous with that of primitive pholidophorids, and trunk muscles do not enter the rudimentary fossa bridgei; caturids have a large post-temporal fossa of the same type as *Amia*, which never became confluent with the fossa bridgei; *Lepidotes* has a large post-temporal fossa which appears to end blindly in the dermopterotic, but the fossa bridgei is unknown; and in *Dapedium* and *Pachycormus* the post-temporal fossa is in open communication with the fossa bridgei and trunk muscles entered the latter, as in advanced pholidophorids and teleosts.

2. *Subtemporal fossa.* In Devonian palaeoniscoids (Gardiner 1973, fig. 3; Miles 1971, fig. 5. 6) there is a conspicuous 'subtemporal fossa', but it is likely that this gave origin to an undifferentiated dorsal hyoid constrictor muscle inserting on the hyomandibular and operculum, as in living chondrosteans (Edgeworth 1935, p. 99), and it is therefore homologous with both the subtemporal fossa and the adductor hyomandibulae fossa in pholidophorids. In later palaeoniscoids (Rayner 1951, fig. 7; Watson 1925, figs 10, 14, 15; Nielsen 1942, figs 11, 62, 63) this area of muscle origin seems to be more diffuse and is not a single, clearly defined fossa. There is no obvious subtemporal fossa in living chondrosteans or holosteans, but in most fossil holosteans there is a recognizable depression within the arch of the external semicircular canal which is the homologue of the pholidophorid subtemporal fossa, and a less well-marked depression anteriorly for the origin of the adductor hyomandibulae (*Heterolepidotus* figures 102, 103; *Macrepistius*, Schaeffer 1971, fig. 5; '*Aspidorhynchus*', figure 99; *Dapedium*, figure 112; *Lepidotes*, figures 108, 109; *Pachycormus*, figure 106). In all these fishes, as in living holosteans, the dorsal hyoid constrictor must have been subdivided.

In parasemionotids (Stensiö 1932, fig. 73; Beltan 1968, figs 25, 31; figures 97, 98) there is a well defined subtemporal fossa, and in some forms there is a clear division between an anterior portion for the adductor hyomandibulae and a posterior portion, within the arch of the external semicircular canal, for the adductor operculi, as in pholidophorids and the holosteans mentioned above. In *Australosomus* (Nielsen 1949, fig. 2) and *Perleidus* (Stensiö 1932, fig. 73; figures 115, 116), two fishes in which the neurocranium is still very similar to those of palaeoniscoids in shape, as it is in pholidophorids, there is a large subtemporal fossa but it shows no real division into anterior and posterior portions, and the dorsal hyoid constrictor may have been still undivided. In *Australosomus*, however, it is clear that the deep posterior part of the fossa lay posterior to the hyomandibular, opposite the upper part of the opercular (Nielsen 1949, figs 25, 29), and must have housed muscles inserting on the operculum.

In teleosts, a well developed subtemporal fossa is found only in osteoglossids, elopiforms, some characins and cyprinoids (Ridewood 1904*a*, p. 62), and the Cretaceous ichthyodectids (Bardack 1965) and saurodontids (Bardack & Sprinkle 1969). In *Elops*, *Notelops*, *Megalops* and *Albula* the subtemporal fossa resembles those of *P. germanicus*, *P. macrocephalus* and the Callovian *Pholidophorus* in being extremely deep, so that it forms a hump in the floor of the post-temporal fossa (Allis 1909, p. 9) and has a very thin roof, but the fossa is lined by the prootic, pterotic and exoccipital, as in leptolepids, with a small contribution from the supraoccipital in the uppermost part of the fossa in *Elops* and *Albula*. In *Pterothrissus* the fossa is shallower. In *Megalops* and *Tarpon* the ventro-medial part of the subtemporal fossa is much altered by modifications of the intercalar associated with the swimbladder diverticulum (Greenwood 1970*a*), and in these fishes the jugular vein passes through this part of the fossa, leaving posteriorly through a canal between the intercalar and exoccipital (Greenwood 1970*a*, pl. 2). In the Cretaceous ichthyodectids and saurodontids there is a similar canal for the jugular vein. This is said by Bardack (1965) and Bardack & Sprinkle (1969) to run through the exoccipital, but in the ichthyodectid material that I have seen it passes between the intercalar and exoccipital, as in *Megalops*, although it is deeply excavated in the exoccipital. In ichthyodectids and saurodontids the subtemporal fossa is very deep, as in elopiforms and advanced pholidophorids, but it is lined by the pterotic, prootic and exoccipital, as in leptolepids.

In osteoglossids the subtemporal fossa is lined by the prootic, pterotic and exoccipital, and is separated from the post-temporal fossa by a substantial layer of bone, as in leptolepids. According to Weitzman (1962, p. 26) the subtemporal fossa of characins is largest in *Hoplias malabaricus*: Roberts (1969, p. 413) reports a similar fossa in other generalized characins. Here it is also of leptolepid type, not excessively deep and lined by the prootic, pterotic and exoccipital.

In cyprinoids the subtemporal fossa contains the enlarged levator muscles of the posterior branchial arches (Ridewood 1904*a*, p. 62; Allis 1909, p. 38), and is therefore probably a specialization associated with the pharyngeal dentition, not a primary feature.

In all pholidophorids and in Upper Jurassic leptolepids the subtemporal fossa is bridged by struts of membrane bone from the prootic and intercalar: in pholidophorids the prootic portion of this bridge is a rod above the jugular groove, in leptolepids it is an outgrowth from the wall of the jugular canal. There is also a bridge across the subtemporal fossa in the teleosts *Elops*, *Osteoglossum*, *Scleropages* and the Mesozoic ichthyodectids and saurodontids. In all these fishes the prootic portion of the bridge is developed as an outgrowth from the membranous wall of the jugular canal, and is therefore of leptolepid type: in ichthyodectids and osteoglossids the prootic portion of the bridge actually lies ventral to the posterior opening of the jugular canal.

In *Elops* the levator muscles of the branchial arches take their origin in sequence on the bridge across the subtemporal fossa, and this must have been its function in pholidophorids and leptolepids.

In pholidophorids the prootic portion of the bridge across the subtemporal fossa arises just above the jugular groove, at the base of the ridge separating the subtemporal fossa from the adductor hyomandibulae fossa. In caturids there is a well marked process in this position (*Caturus*, Aldinger 1932, fig. 9; *Macrepistius*, Schaeffer 1971, fig. 5; '*Aspidorhynchus*', figure 99, prlm; *Heterolepidotus*, Gardiner 1960, fig. 29; figures 102, 103, prlm), often without perichondral lining at the tip. Schaeffer (1971, p. 9) accepted a suggestion of mine that this process might mark the articulation of the first suprapharyngobranchial, but I now believe that this articulation lay below the jugular groove (p. 397). Aldinger (1932, p. 35) interpreted this process as marking the origin of the levator muscles of the anterior branchial arches; this interpretation agrees with the function deduced for the homologous strut in pholidophorids. In caturids the process lies just above the glossopharyngeal foramen, much further back than the point of origin of the process in pholidophorids. In pholidophorids the process has clearly been displaced forwards by hypertrophy of the subtemporal fossa; this displacement of the process may account for the development of the bridge across the subtemporal fossa as a supplementary site of origin for the levator muscles of the gill arches. It is notable that such a strut is only developed among teleosts in forms with a hypertrophied subtemporal fossa.

3. *Dilatator fossa.* In all pholidophorids and leptolepids there is a dilatator fossa. In pholidophorids it is confined to the sphenotic and includes an anterior area for the levator arcus palatini muscle, but in leptolepids it extends posteriorly on to the pterotic, and the anterior portion becomes separated by a crest.

The dilatator operculi and levator arcus palatini muscles are differentiated in living holosteans but not in chondrosteans (*Polypterus* excepted) (Edgeworth 1935, p. 48). In fossils, an area of attachment for these muscles is first evident on the braincase in *Perleidus* (figure 115) and parasemionotids (figure 97), but there is no evidence of separate areas for the two muscles. In fossil holosteans the two areas appear to be differentiated to about the same extent as in pholidophorids.

The leptolepid type of dilatator fossa, which extends on to the pterotic and is separated by a crest from the area of origin of the levator arcus palatini muscle, is found only in teleosts.

4. *Articulation of the first suprapharyngobranchial.* In pholidophorids this is represented by a facet, which may lack perichondral lining in *P. bechei*, below the jugular groove on the prootic. In leptolepids this area is no longer recognizable. In those teleosts which retain an ossified first suprapharyngobranchial (elopoids and *Alepocephalus*; Nelson 1968*b*, p. 137) there is no indication in dried skulls of its articulation with the prootic, as in leptolepids.

In palaeoniscoids (Nielsen 1942, p. 196) and *Australosomus* (Nielsen 1949, p. 122) the first suprapharyngobranchial articulates with a large and prominent facet, without perichondral lining, which lies immediately below the glossopharyngeal foramen and postero-dorsal to the vestibular fontanelle. The articulation is in a similar position in sturgeons (van Wijhe 1882, pl. 15, fig. 3). In pholidophorids the articulation lies further forwards, midway between the glossopharyngeal and facial foramina and antero-dorsal to the vestibular fontanelle: this change in position may be partly due to backward migration of the vestibular fontanelle, but forward migration of the gill arches is probably also involved.

In *Lepisosteus* the cartilaginous first suprapharyngobranchial does not articulate with the braincase, and in *Amia* there is no suprapharyngobranchial. An articular area for the first suprapharyngobranchial has not yet been recognized in any fossil holostean (for Schaeffer's (1971, p. 9) interpretation of the articulation in caturids see above, p. 396). In caturids there is usually an area without perichondral lining just below the glossopharyngeal foramen (*Caturus*, Aldinger 1932, p. 12, pl. 1, fig. 1; Gardiner 1960, fig. 36: '*Aspidorhynchus*', Rayner 1948, fig. 20; figure 99, asup I: *Heterolepidotus*, figure 102, asup I: *Osteorachis*, P.3648*a*). This area is partially surrounded by the anterior outgrowth of the intercalar, and lies in a deep notch in the latter. In these caturids, this area appears to mark the articulation of the first suprapharyngobranchial. The other possible interpretation of an incompletely ossified area in this position is that it is the remains of the vestibular fontanelle, but in that case one would expect the intercalar to overgrow it, not surround it. The notch in the intercalar around the facet can be compared with the deep notch in the parasphenoid which surrounds the articular facet for the first infrapharyngobranchial in pholidophorids and many other fossil actinopterygians (see below).

In *Pachycormus* the first suprapharyngobranchial probably articulated with the anterior part of the vestibular fontanelle (figure 106, vfon), since in well ossified individuals (P.24410) this persists as a circular area, without perichondral lining, directed antero-laterally. In *Perleidus* and parasemionotids the articulation was also probably with some part of the vestibular fontanelle. In *Dapedium* and *Lepidotes* there is no recognizable articular area for the first suprapharyngobranchial.

5. *Articulation of the first infrapharyngobranchial.* In pholidophorids and Lower Jurassic leptolepids this is represented by an area without perichondral lining at the antero-ventral corner of the prootic, in a notch between the ascending and posterior processes of the parasphenoid. In Upper Jurassic leptolepids the first infrapharyngobranchial articulated with the parasphenoid, as it does in living teleosts.

In *Amia* and *Lepisosteus* the first infrapharyngobranchial articulates with the parasphenoid, as in teleosts, but in most fossil holosteans there is an area without perichondral lining in a notch in the parasphenoid, as in pholidophorids. This facet is present in *Caturus* (visible in GSM 97417, *C. chirotes*; *C. porteri*; and Aldinger's 1932, pl. 3, fig. 1), *Heterolepidotus* (ainp I, figures 102, 103), '*Aspidorhynchus*' (perichondrally lined, figure 99), *Pachycormus* (Rayner 1948, fig. 18; figure 106) and *Dapedium* (figure 112). In *Lepidotes* (figure 108) this area is unossified, while in *Macrepistius* (Schaeffer 1971, fig. 5) the notch in the parasphenoid is apparently lost, and the infrapharyngobranchial may have articulated with the parasphenoid, as in living holosteans.

An exactly similar facet is also present in parasemionotids (MMK 492) and *Perleidus* (P.19590), though not previously described or illustrated in these forms.

In *Acipenser* the first infrapharyngobranchial articulates with the parasphenoid (van Wijhe 1882, pl. 15, fig. 3), but in *Polyodon* it articulates in the notch between the ascending process and the body of the parasphenoid (Bridge 1878, p. 708), as in pholidophorids and fossil holosteans. In *Pteronisculus* the articulation is with the parasphenoid (Nielsen 1942, fig. 45). In *Australosomus* the first infrapharyngobranchial is applied to the underside of the neurocranium, articulating with it both in front of and behind the fissura oticalis ventralis, but ending anteriorly in the notch between the ascending process and the body of the parasphenoid, in the usual way (Nielsen 1949, p. 122). In *Eusthenopteron* the first infrapharyngobranchial articulates with the otico-occipital ossification, posterior to the fissura oticalis ventralis (the ventral part of the intracranial joint, Gardiner 1970; Miles 1971, p. 113), and it appears that the articulation was also posterior to the fissura oticalis ventralis in the earliest actinopterygians (Gardiner 1973, figs 1, 5), where there is a facet immediately behind the groove for the orbital artery. This change in position of the articulation relative to the fissura oticalis ventralis during actinopterygian evolution is due to posterior migration of the fissure (p. 416).

6. *Spiracular groove and canal.* In all living teleosts the spiracular tube is obliterated, and this condition is achieved in Upper Jurassic leptolepids. Pholidophorids and Lower Jurassic leptolepids have a spiracular groove on the parasphenoid and braincase, and a spiracular canal passing through the postorbital process and opening into the fossa bridgei (except in *L. coryphaenoides*). Presumably this tube carried a spiracular diverticulum, like the spiracular canal of living holosteans and chondrosteans.

Among fossil holosteans, a spiracular canal has been described or restored in the amiids *Sinamia* (Stensiö 1935) and *Enneles* (Santos 1960), the caturids *Caturus groenlandicus* (Aldinger 1932) and *Caturus* sp. (Rayner 1948, fig. 5), in *Pachycormus* (Lehman 1949; spic, figure 106) and parasemionotids (Stensiö 1932; Lehman 1952; Beltan 1968). A spiracular canal also occurs in the caturids *Heterolepidotus* (spic, figures 102, 103), *Caturus chirotes* (GSM 97417) and '*Aspidorhynchus*' (figure 99). The canal is probably also present in *Macrepistius*, since the ascending process extends up to the sphenotic immediately in front of the hyomandibular facet (Schaeffer 1971, fig. 3) in the same way as in other caturids. There is also a spiracular canal in *Dapedium* (P.11177, P.11189; figure 112) and *Lepidotes* (*L. latifrons*, P.9998; *L. toombsi*, spic, figures 108, 109; *L. minor*, P.44914), so that a spiracular canal appears to be a feature of all non-teleostean actinopterygians, and the loss of the canal in advanced leptolepids is another unique specialization relating them to teleosts.

In living chondrosteans, the spiracular canal passes through the (cartilaginous) postorbital process and opens into the fossa bridgei, and this is true also of *Birgeria*, *Perleidus*, *Australosomus*, *Pteronisculus*, *Boreosomus* and the Kansas palaeoniscids, except that in all the postorbital process is ossified. But in *Pteronisculus* and the Carboniferous palaeoniscids the spiracular canal is very short, and in *Kentuckia* its dorsal opening is close to the lateral margin of the cranial roof and there is no discrete fossa bridgei. In the Devonian palaeoniscoids from Western Australia the spiracular groove is very long and the spiracular canal is only enclosed by a loop of bone immediately below the dermal roof (Gardiner 1970, fig. 3; Miles 1971, fig. 5. 6) which resembles a similar loop in *Eusthenopteron* (Jarvik 1954, fig. 1). These facts indicate that during actinopterygian evolution there has been a trend towards elongation of the bone- or cartilage-enclosed spiracular canal at the expense of the spiracular groove, and that the upper opening of the canal has moved medially.

In pholidophorids, amiids, *Pachycormus* and those caturids where the ossification pattern is known the lower opening of the spiracular canal lies at the junction of the sphenotic and prootic. This is probably also its position in *Dapedium* and parasemionotids (figures 112, 97, 98). In *Lepisosteus* the canal also originates in this position, but in large individuals it becomes deeply incised in the prootic. In *Lepidotes* the lower opening of the canal lies entirely within the prootic (figures 108, 109): this is a unique specialization. In P.44914 (*Lepidotes minor*) there is a large fenestra in the underside of the tube for the sensory canal in the dermopterotic above the upper opening of the spiracular canal, as in *Eusthenopteron* (Jarvik 1954, fig. 5).

In *Perleidus* (figures 115, 116) and palaeoniscoids (figure 117) the spiracular canal passed posterior to the postorbital process (sphenotic) rather than medial to it, and the small loop of bone which surrounds the short spiracular canal of primitive palaeoniscoids can hardly mark the junction of the sphenotic and prootic as it does in holosteans and pholidophorids.

7. *The inner face of the sphenotic and the pons moultoni.* Allis (1909, p. 9) proposed that the sphenotic of teleosts was originally an ossification of the postorbital process, 'wholly independent of the anterior semicircular canal'. He based this upon the conditions in *Amia*, *Elops* and *Esox*, in none of which does the sphenotic contain any part of the anterior semicircular canal. This is also true of pholidophorids, *Lepisosteus*, *Lepidotes*, *Pachycormus*, *Caturus*, '*Aspidorhynchus*', and presumably of all non-teleostean actinopterygians, so that the relationship between the sphenotic and the anterior semicircular canal which develops in leptolepids is another unique specialization relating them to teleosts. In teleosts it seems that the absence of any relationship between the sphenotic and the semicircular canal can only be characterized as primitive when the bone is separated from the labyrinth cavity by junction of the pterotic and pterosphenoid medial to it, as in pholidophorids. Such a junction occurs in *Elops*, *Megalops* and *Albula*, but not in *Esox* or *Pterothrissus*. In the latter genera, and in other teleosts such as *Salmo* in which the

sphenotic does not contact the semicircular canal, the condition is probably not strictly primitive, but due to reduction in ossification.

The fact that the generalized elopomorphs *Elops*, *Megalops* and *Albula* retain a pholidophorid type of sphenotic, while leptolepids agree with non-elopomorph teleosts in having a cavity for the anterior semicircular canal on the inner face of the sphenotic, might be taken as evidence that leptolepids are more closely related to non-elopomorph teleosts than to elopomorphs. But it would be premature to draw such conclusions from the retention of a single primitive character in elopiforms (see further p. 562).

Haedrich (1971) has given the name pons moultoni to a bridge of bone on the inner surface of the teleostean sphenotic which encloses part of the anterior semicircular canal. He finds this to be present in almost all the perciform families assigned by Freihofer (1963) to the 'pattern 10' type of ramus lateralis accessorius, in a few other perciform families, in the beryciform *Trachichthys* and in *Polymixia*. Haedrich regarded this structure as of potential phylogenetic importance, but in a postscript to his paper, added after discussion with me, he stressed that it might only be a retained, primitive feature. The point I had made with Dr Haedrich was that in primitive actinopterygians such as palaeoniscoids all the semicircular canals are bone enclosed throughout their length, and that any such bony casing in teleosts was likely to be a remnant of the palaeoniscoid condition. At that time I did not have the material for a detailed study of the pholidophorid and leptolepid sphenotic, but it is now clear that the presence of a pons moultoni on the sphenotic must be regarded as an advanced character, as Haedrich proposed. In *Elops* there is a similar bridge around the anterior semicircular canal, but here it is formed by the pterosphenoid (Allis 1909, p. 9 and personal observations) or prootic (Allis 1920, p. 252), while in *Megalops* a similar bridge is formed by the prootic. Neither of these structures is a true pons moultoni; they are homologous with structures found in fully ossified pholidophorids and are primitive features. Since a true pons moultoni, formed by the sphenotic, is an advanced character, it may prove to be of value in establishing relationships within the acanthopterygians, and its distribution would probably repay further study. Re-examination of the Cretaceous acanthopterygian and ctenothrissiform braincases which I described in 1964 shows that the pons moultoni is present in the polymixiids *Berycopsis* and *Homonotichthys*, the holocentrid *Caproberyx*, where it is particularly large, and the trachichthyid *Hoplopteryx simus*. It appears to be absent in the less thoroughly ossified *Hoplopteryx lewesiensis*, and in the ctenothrissiforms *Ctenothrissa* and *Aulolepis*. In the ctenothrissiforms the sphenotic plays a smaller part in the lining of the cranial cavity than in the Cretaceous acanthopterygians, providing another example of the trend towards enlargement of the sphenotic which is evident in leptolepids.

8. *The lateral commissure.* Pholidophorids have a short lateral commissure and the jugular vein, orbital artery and hyomandibular trunk all entered the trigeminofacial chamber behind it. In leptolepids membrane bone outgrowths from the lateral commissure roof over the grooves for the jugular vein and orbital artery so that there is a long jugular canal and separate foramina for the hyomandibular trunk and orbital artery. Similar outgrowths from the lateral commissure are present in generalized members of all teleostean cohorts except the clupeomorphs, where the trigeminofacial chamber is modified by the large prootic bulla, and the development of these long canals, roofed by membrane bone, is another unique specialization relating leptolepids to teleosts.

The primitive condition of the lateral commissure in actinopterygians is exemplified in palaeoniscoids and *Polyodon*, where the commissure is a massive structure of cartilage or substitution bone, penetrated by a long jugular canal which receives an ascending canal for the orbital artery. In palaeoniscoids the lateral wall of the jugular canal is usually penetrated by one or more narrow canals interpreted as having transmitted the hyomandibular trunk or branches of the latter. A lateral commissure of essentially this type is also present in *Acipenser*, *Perleidus* (figure 115) and *Australosomus*, but in living holosteans, parasemionotids, caturids *Pachycormus* and semionotids the lateral commissure is reduced to about the same extent as in pholidophorids, so that the jugular canal is short and the orbital artery enters its posterior opening (except in *Amia*).

9. *The trigeminofacial chamber, the nerves and vessels passing through it, and the profundus and oculomotor nerves.* In primitive living teleosts (Allis 1909, 1919; Stensiö 1925; de Beer 1926*a*, 1927; Dunkle 1940; Daget & d'Aubenton 1957; Patterson 1964; Goody 1969; Forey 1973*a*) the trigeminofacial chamber agrees very well with that of Upper Jurassic leptolepids, having the same three posterior openings (for the jugular vein, hyomandibular trunk and orbital artery) in the membrane bone wall of the jugular canal, the geniculate and gasserian ganglia partly or wholly intracranial, the oculomotor, trigeminal and facial foramina similarly placed, and the same distribution of the branches of the trigeminal and facial nerves. In living teleosts the course of the palatine nerve is variable: it may pass through a foramen in the floor of the trigeminofacial chamber, as in leptolepids, it may leave the orbital opening of the chamber, or it may leave through the floor of the cranial cavity. There may also be a separate profundus foramen in teleosts, and the nerves which pass through the trigeminal foramen in leptolepids (trigeminal nerve, buccal and superficial ophthalmic branches of facial) may pass through separate passages in some teleosts. These variations are a consequence of the intracranial position of the ganglia.

In primitive pholidophorids the trigeminofacial chamber differs from that of Upper Jurassic leptolepids and living teleosts in having a short lateral commissure which does not cover the facial foramen, so that the jugular vein, hyomandibular trunk and orbital artery enter through a single posterior opening; a larger communication with the myodome (palatine fenestra) and a reduced pre-palatine floor to the chamber; the ganglia lying in the trigeminofacial chamber; a thicker, endochondrally ossified wall between the cranial cavity and the chamber; the otic nerve canal running into the spiracular canal; a separate profundus foramen on the prootic/pterosphenoid suture; and the oculomotor foramen on the prootic/basisphenoid suture. In almost all these features, pholidophorids resemble primitive fossil holosteans and some chondrosteans.

In *Amia* (Allis 1897; de Beer 1926*a*) the medial wall of the trigeminofacial chamber (prefacial commissure and pila antotica) and the floor of the chamber do not ossify, so that it communicates widely with the cranial cavity and myodome, and there are no separate oculomotor, profundus, trigeminal, facial or palatine foramina. The chamber is enlarged anteriorly by the space enclosed by the pterosphenoid pedicle, and a short intramural canal for the superficial ophthalmic nerves is formed secondarily by a strut at the root of the pterosphenoid pedicle, so that these nerves appear to leave through a separate foramen in the pterosphenoid. There is a separate foramen for the orbital artery in the lateral commissure. The otic nerve canal originates in the cartilaginous roof of the chamber and does not join the spiracular canal. There is little similarity here to the pholidophorids.

In *Lepisosteus* (Allis 1909; de Beer 1926*a*, 1937) there is no myodome and for this reason the trigeminofacial chamber is rather different from those of *Amia* and pholidophorids. As in *Amia*, the prefacial commissure does not ossify so that the chamber is confluent with the cranial cavity through the large opening that transmits the trigeminal and facial nerves. In contrast to *Amia*, the pila antotica ossifies (secondarily according to de Beer 1937, but see Rayner 1951, p. 80) and there is a separate profundus foramen between the prootic and pterosphenoid, as in pholidophorids. There is no ossified basisphenoid and the oculomotor foramen lies in the pterosphenoid. The orbital artery enters the posterior opening of the trigeminofacial chamber, as in pholidophorids, but it is very small (de Beer 1927, p. 302), and is apparently replaced functionally by an orbito-nasal artery (external carotid of Allis) which leaves the internal carotid within the prootic and enters the chamber through the palatine foramen. This palatine foramen in *Lepisosteus* is the homologue of the foramen in the ventro-lateral corner of the myodome of *Amia* and pholidophorids, through which the palatine nerve enters the parabasal canal: it is not homologous with the palatine foramen or fenestra in the floor of the trigeminofacial chamber of pholidophorids and leptolepids, and as in *Amia*, the chamber of *Lepisosteus* has no pre-palatine floor. The otic nerve canal originates in the roof of the trigeminofacial chamber, and passes up without joining the spiracular canal. Once again, there is little similarity to pholidophorids here.

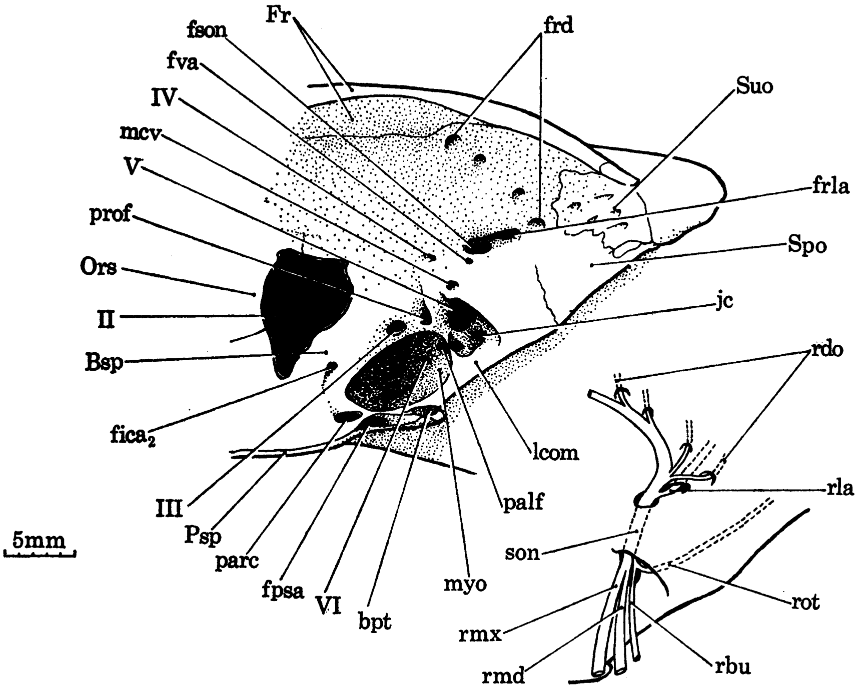


FIGURE 93. *Heterolepidotus* sp. Sketch of the rear of the left orbit of P.13260 (see figures 102–104) in oblique antero-lateral view. Inset at lower right is an attempted restoration of the nerves leaving the trigeminal foramen, intramural passages indicated by broken lines.

In caturids (*Caturus*, *Heterolepidotus*, '*Aspidorhynchus*', *Macrepistius*: Aldinger 1932; Rayner 1948; Gardiner 1960; Schaeffer 1971; figures 93, 99, 101, 102) the trigeminofacial chamber is more pholidophorid-like, but also shows some resemblance to *Amia*. The lateral commissure is very short and is even interrupted in Rayner's Toarcian *Caturus* (1948, fig. 5), and the chamber has a single posterior opening. The orbital artery does not leave a conspicuous groove on the lateral surface of the braincase as it does in pholidophorids, but a notch in the lower margin of the posterior opening of the jugular canal suggests that the artery pursued a similar course, leaving the internal carotid just before the latter entered its foramen, looping round in front of the articulation of the first infrapharyngobranchial, and running up into the posterior opening of the jugular canal. In lacking a separate foramen for the orbital artery the caturids appear to be more advanced than *Amia*. As in pholidophorids, the medial wall of the trigeminofacial chamber (prefacial commissure and pila antotica) is ossified, and there are separate facial, trigeminal and profundus foramina, although in '*Aspidorhynchus*' (and probably also in *Macrepistius*) the facial and trigeminal canals are only separate distally, and the prefacial commissure was certainly under reduction. Where known (*Caturus chirotes*, Rayner's *C.* sp.) the facial and trigeminal canals originate in the utricular recess. In *Caturus* Rayner (1948) interpreted the trigeminal foramen as for the buccal and superficial ophthalmic branches of the facial, the profundus as the oculomotor and the oculomotor as the trigeminal, and Gardiner (1960, fig. 27) used similar interpretations in *Osteorachis*, although the specimen in question (P.3648*a*) is too imperfect for confident identifications. Where bone junctions can be recognized ('*Aspidorhynchus*', figure 101; *Macrepistius*), the profundus foramen (prof) lies in the pterosphenoid (identified as the oculomotor by Rayner 1948, figs 22, 23) and the oculomotor (III) lies between the basi- and pterosphenoid ('*Aspidorhynchus*', identified as the internal carotid by Rayner) or between the pterosphenoid, basisphenoid and prootic (*Macrepistius*). As in pholidophorids, the external opening of the facial foramen is confluent with a palatine fenestra (palf, figures 93, 101) through which the trigeminofacial chamber communicates with the myodome and which transmitted the palatine nerve and probably contained the geniculate ganglion. In *Caturus chirotes*, *Heterolepidotus* and '*Aspidorhynchus*' the floor of the chamber in front of the palatine fenestra is only represented by a slender strut. In Rayner's Toarcian *Caturus* the pre-palatine floor of the chamber is more complete, as in pholidophorids. In *Caturus groenlandicus*, Aldinger (1932, p. 20, pl. 2, fig. 1) found a small foramen in the roof of the myodome, midway between the palatine fenestra (f.fr in Aldinger's figure) and the abducens foramen, which is linked by a groove or canal with the palatine foramen in the floor of the myodome. This foramen opens directly into the cranial cavity, not into the trigeminofacial chamber, and Aldinger interpreted it as having transmitted the palatine nerve, so indicating that the geniculate ganglion was intracranial. However, no other caturid has such a foramen, and in other respects the palatine fenestra of *C. groenlandicus* agrees exactly with other caturids.

In all caturids there is an intramural canal in the pterosphenoid for the superficial ophthalmic nerves (fson, figures 93, 101), as in *Amia*. This canal originates in the roof of the trigeminofacial chamber and passes antero-medially through a portion of the pterosphenoid which must be the homologue of the root of the pedicle in *Amia*. In '*Aspidorhynchus*' there is a well developed pedicle on the pterosphenoid (ptsp, figure 101), while *Macrepistius* appears to have a true pterosphenoid pedicle (pila lateralis), as in *Amia*, formed by the pterosphenoid above and the prootic below. The course of the otic nerve is not known fully in any caturid (Rayner (1948, fig. 6; *Caturus*) and Gardiner (1960, fig. 30; *Heterolepidotus*) assign the otic nerve to the canal carrying the first branch of the superficial ophthalmics). In *Heterolepidotus* the otic nerve canal (rot, figure 93) originates in the foremost part of the roof of the trigeminofacial chamber, as in *Amia*, and it probably had the same origin in other caturids, but its further course is unknown.

In general, caturids resemble pholidophorids and differ from *Amia* in having a short pre-palatine floor to the trigeminofacial chamber and in having no separate foramen for the orbital artery, but they resemble *Amia* in having an intramural canal for the superficial ophthalmic nerves and probably in the course of the otic nerve. '*Aspidorhynchus*' and *Macrepistius* are particularly *Amia*-like in having a reduced prefacial commissure and a pterosphenoid pedicle. The pterosphenoid forms more of the wall of the trigeminofacial chamber in caturids than it does in pholidophorids.

In *Pachycormus* (figure 106) no complete account of the trigeminofacial chamber has been published, although Rayner (1948) and Lehman (1949) have described and figured the lateral surface of the prootic and pterosphenoid. The lateral commissure is short, ending in front of the facial foramen, as in pholidophorids and caturids, and the chamber has only one posterior opening. Lehman (1949, p. 27) identified a foramen for the orbital artery in the floor of the jugular groove behind the lateral commissure, but comparison with 32434, 32443 and P.24410 shows that this is the facial foramen (VII, figure 106). There is a groove for the orbital artery on the lateral surface of the prootic (goa, figure 106), passing postero-dorsally from the internal carotid foramen, in front of the facet for the first infrapharyngobranchial, and entering the posterior opening of the trigeminofacial chamber in front of a small spur, as in pholidophorids. There is a large palatine fenestra between the myodome and trigeminofacial chamber, limited anteriorly by a pre-palatine strut which is about as broad as in pholidophorids. The trigeminal foramen (identified by Rayner as the superficial ophthalmic foramen) leads into a prominent groove for the superficial ophthalmic nerves. There is a separate profundus foramen which lies just within the prootic (P.24410) or on the prootic/pterosphenoid suture (32443), as in pholidophorids. The large oculomotor foramen (III, figure 106) lies at the junction of the prootic, pterosphenoid and basisphenoid, notching all three bones. The otic nerve canal originates on the sphenotic/pterosphenoid suture and probably leads into the spiracular canal, as in pholidophorids. Altogether, the trigeminofacial chamber of *Pachycormus* is very similar to that of pholidophorids. It differs from that of caturids in having no intramural canal for the superficial ophthalmics, in the position of the otic canal, and in having the profundus foramen within the prootic.

In *Lepidotes* (Rayner 1948; Beltan 1957; Gardiner 1960; figure 108) the lateral commissure is short and the orbital artery presumably entered the posterior opening of the trigeminofacial chamber, although it has left no trace on the bone. The facial and trigeminal canals originate in the utricular recess. The palatine foramen, leading from the floor of the chamber into the myodome, is not enlarged into a fenestra as it is in pholidophorids, caturids and *Pachycormus*, and the geniculate ganglion lay in the chamber rather than in a fenestra in its floor. The pre-palatine floor of the chamber is developed to about the same extent as in pholidophorids. The foramina in the prootic appear to be correctly determined by Gardiner in *L. mantelli* and *L. latifrons* (1960, figs 45, 46), while Rayner assigns the oculomotor foramen to the trigeminal in *L. semiserratus* and Beltan assigns the trigeminal foramen to branches of the facial and the entry foramen of the otic canal to the superficial ophthalmics. In *L. mantelli* and *L. latifrons* both the oculomotor and profundus foramina lie within the prootic, but in *L. semiserratus* and *L. toombsi* the profundus appears to be represented by a rather large, slit-like foramen which lies between the prootic and pterosphenoid, as in pholidophorids. The otic canal originates on the orbital surface of the prootic (fotn, figures 108, 109), and in *L. toombsi* it joins the spiracular canal in the sphenotic. There is no separate foramen for the superficial ophthalmics, the large, transversely directed foramen identified as such in *L. mantelli* by Beltan and Gardiner being for the middle cerebral vein (p. 412; mcv, figures 108, 109). In general, the trigeminofacial chamber of *Lepidotes* resembles those of pholidophorids and *Pachycormus*, but the prootic is more extensive and there is no palatine fenestra, only a foramen.

In *Dapedium* (Rayner 1948; Gardiner 1960; figure 112) no bone junctions are recognizable, but otherwise conditions are much as in *Lepidotes*. As in the latter, the orbital artery leaves no trace on the braincase, the facial and trigeminal canals originate in the utricular recess, and there is a palatine foramen, not a fenestra, between the floor of the trigeminofacial chamber and the myodome. The abducens foramen is very close to the palatine foramen in *Dapedium*, and on the right side of P.11189 the two are partially confluent, this 8-shaped foramen leading into the trigeminofacial chamber, not the cranial cavity, and indicating that on one side of this specimen the abducens nerve emerged through the facial foramen. The superficial ophthalmic nerves emerged through the trigeminal foramen in *Dapedium*, as in *Lepidotes*, *Pachycormus* and pholidophorids: the groove for the superficial ophthalmics on the orbital surface is interpreted as vascular by Gardiner, and these nerves are assigned to the foramen of the middle cerebral vein (p. 412), while Rayner assigns the superficial ophthalmics to the oculomotor foramen. There is an independent profundus foramen ventro-lateral to the oculomotor foramen on the right side of P.11177, but the two are confluent on the left side of this specimen and in P.11189, where the foramen is assigned by Gardiner to the internal carotid. The otic canal originates on the orbital surface of the postorbital process, and opens into the fossa bridgei separate from the spiracular canal (P.11177). *Dapedium* resembles *Lepidotes* in many ways, but differs in the course of the otic nerve and in tending to amalgamate the oculomotor and profundus foramina.

In parasemionotids (Stensiö 1932; Lehman 1952; Beltan 1968; figures 97, 98) the lateral commissure is more massive than in pholidophorids and other fossil holosteans, but the trigeminofacial chamber still has only a single posterior opening. In all previous accounts of the parasemionotid braincase, following Stensiö, the orbital artery is said to have reached the chamber through the myodome, branching off the internal carotid within the parabasal canal and passing up into the myodome through the palatine foramen. But in the Greenland parasemionotids there is a well marked groove for the orbital artery on the lateral face of the prootic (goa, figures 97, 98), exactly as in pholidophorids and *Pachycormus*. The passage from the parabasal canal into the floor of the myodome must have transmitted only the palatine nerve, as in pholidophorids. The facial and trigeminal canals originate in the recess for the utriculus, as in *Caturus*, *Lepidotes* and *Dapedium*. In previous accounts, the facial and trigeminal canals are described and illustrated as opening very close together (Stensiö, *Ospia*) or as being confluent (Lehman, *Parasemionotus*, *Watsonulus*; Beltan, several genera). In the Greenland specimens that I have prepared, the facial canal, which is relatively narrow, opens in the ventro-medial corner of the orbital opening of the jugular canal, and the wide trigeminal canal opens dorso-medial to it. In MMK 491A the trigeminal canal is divided by a horizontal partition, and the resulting double opening is very similar to the two foramina in *Ospia* which Stensiö interpreted as the trigeminal and facial foramina: possibly the facial foramen, further back in the opening of the jugular canal, was not exposed in Stensiö's specimen. In the Madagascar parasemionotids a small canal opening into the ventro-medial part of the anterior end of the jugular canal is illustrated in *Parasemionotus* by Lehman (1952, fig. 112) and in *Devillersia* and *Piveteaunotus* by Beltan (1968, figs 38, 41). This canal, interpreted by Lehman and Beltan as having transmitted an unnamed branch of the facial nerve, resembles the facial canal in MMK 491 and 492 and should be interpreted as such. There is no pre-palatine floor to the trigeminofacial chamber, but in the fully ossified MMK 492 the rudiments of a pre-palatine strut are indicated by projections from the inner and outer walls of the chamber, partially delimiting a palatine foramen.

Similar projections are illustrated in *Parasemionotus* by Lehman, and the channel enclosed by them is interpreted as having contained the pituitary vein.

In the Greenland parasemionotids the anterior opening of the jugular canal is divided by a bar of bone into a large ventro-medial portion and a small dorso-lateral portion (coa, figure 97). The latter is in line with the groove for the orbital artery in the posterior opening of the canal, and probably carried that artery. A similar opening is illustrated in *Parasemionotus* and described in *Watsonulus* by Lehman, who interpreted it as having transmitted the hyomandibular trunk back into the jugular canal. The same opening seems to be indicated in some of Beltan's illustrations. The superficial ophthalmic nerves passed through the trigeminal foramen, or through a separate dorsal part of this foramen in *Ospia* and MMK 491. There are separate profundus and oculomotor foramina (both assigned to the oculomotor by Lehman and Beltan), but their position with respect to the separate ossifications making up the wall of the orbit is unknown. The otic nerve canal originates in the wall of the orbit just above the trigeminofacial chamber, within the prootic (fotn, figures 97, 98), and passes up into the fossa bridgei without joining the spiracular canal.

The trigeminofacial chamber of parasemionotids differs from that of pholidophorids in several ways. The anterior position of the facial foramen and the lack of a prefacial floor to the chamber are probably primitive features (see below). The origin of the trigeminal and facial canals in the utricular recess is a resemblance to non-pholidophorid fossil holosteans. The otic nerve resembles that of caturids and *Dapedium*.

In *Perleidus* (Stensiö 1932; Lehman 1952, 1954; figures 115, 116) the lateral commissure is longer than in pholidophorids, holosteans and parasemionotids and the chamber has more than one posterior opening. In the two Greenland specimens that I have prepared the chamber has three posterior openings in addition to the main one for the jugular vein, as in Lehman's (1954) Madagascar specimen, and the jugular canal is subdivided longitudinally in the same way as in the latter. Of these three openings, one (coa, figures 115, 116) is directed ventrally, and two (fhmv+VII, figures 115, 116) are directed laterally. The more anterior of the two lateral openings leaves the jugular canal postero-laterally while the more posterior is transversely directed. Lehman interpreted the anterior one (fhm VII) as having transmitted the hyomandibular trunk and the posterior one as having contained the hyomandibular vein: these interpretations seem reasonable. Lehman interpreted the ventrally directed opening (coa) as having transmitted the hyo-opercularis artery, and followed Stensiö in assigning the orbital artery ('external carotid') to a canal passing up into the floor of the myodome from the anterior end of the groove for the lateral dorsal aorta. As in parasemionotids, it is more reasonable to assign this ascending canal to the internal carotids, the orbital artery having passed up across the lateral surface of the prootic and entered the trigeminofacial chamber through the canal (coa) in its floor. The facial and trigeminal canals originate in the recess for the utriculus and are separated by a prefacial commissure. I find it difficult to accept either Stensiö's or Lehman's account of the trigeminal and facial nerves, although the Greenland specimens that I have prepared are too imperfect for a definitive account. In my opinion, Stensiö's 'trigeminus fontanelle' is the lateral part of an expanded pituitary fossa, and the notch in its lateral margin which he interpreted as having transmitted the roots of the trigeminus carried the oculomotor nerve: these are the conditions in MMK 495. If the facial canal is correctly named in Stensiö's description, the canals 't' and 'tv', which Stensiö (1932, fig. 65) interpreted as vascular, would be the profundus and trigeminal canals, but I think it more likely that the small facial foramen was not visible in Stensiö's specimen, that his facial foramen is the trigeminal, the canal 'tv' is the profundus, and 't' is for the middle cerebral vein (p. 412): this would give a better agreement with MMK 495. In Lehman's (1954) account, I would interpret the canal 'V' as the oculomotor, 'tv' as the profundus, the facial canal as the trigeminal, and the canal 'VII_2' as the facial: with these reinterpretations Lehman's specimen seems to agree with MMK 495. The chamber has no pre-palatine floor, as in parasemionotids. The superficial ophthalmic nerves emerged through the trigeminal foramen, and their course is indicated by a groove running up from this opening. As interpreted here, there are separate profundus and oculomotor foramina, the latter close to or on the margin of the pituitary fossa. The otic nerve canal originates in the wall of the orbit above the trigeminofacial chamber and opens into the fossa bridgei without joining the spiracular canal.

The trigeminofacial chamber of *Perleidus* resembles those of parasemionotids, but is more primitive in the long lateral commissure and separate openings for the jugular vein, hyomandibular trunk and orbital artery. The position of the oculomotor foramen, close to or within the margin of an enlarged pituitary fossa, is a unique specialization, but appears to be due only to transverse expansion of the fossa, not to any change in position of the nerve.

In *Acipenser* and *Polyodon* the lateral commissure is massive. In *Acipenser* the trigeminofacial chamber has only a single posterior opening, but in *Polyodon* the orbital artery enters by a separate vertical canal. In *Polyodon* the trigeminal and facial ganglia are intracranial, in *Acipenser* they are partly or wholly extracranial (Stensiö 1925, p. 76). In *Polyodon* the facial canal opens into the jugular canal while in *Acipenser* the hyomandibular trunk emerges in the orbit and turns posteriorly to traverse the jugular canal. In both genera the palatine nerve passes ventrally within the cranial wall, dividing as it does so; since the nerve does not enter the chamber there is no pre-palatine floor. In both genera the trigeminal nerve and lateralis branches of the facial emerge in the orbit, in front of the jugular canal, and their passage is considerably subdivided so that there are separate exit foramina for the superficial ophthalmics, otic, maxillary and mandibular nerves. In *Acipenser* there is no prefacial commissure according to de Beer (1937), and the subdivision of the passages for the trigeminal and associated nerves is probably due to continuing growth of cartilage. There is a separate oculomotor foramen but no profundus. The otic nerve passes through the postorbital process and opens into the fossa bridgei antero-medial to the spiracular canal.

In palaeoniscoids, *Saurichthys* and *Australosomus* the trigeminofacial chamber seems to be based on a common plan (Stensiö 1925; Nielsen 1942, 1949; Rayner 1951; Lehman 1952). The lateral commissure is long and thick, and the trigeminofacial chamber may open posteriorly by a single foramen transmitting the jugular vein and hyomandibular trunk (Kansas palaeoniscids B, C, *Boreosomus*, *Australosomus*, *Saurichthys*, *Pteronisculus cicatrosus*), or these structures may leave through separate foramina (*Kentuckia*, Kansas palaeoniscid A, *Pteronisculus stensioei*). It is not easy to decide which of these conditions is more primitive: the separate openings might be mainly a consequence of heavier ossification, generally held to be a primitive feature, or of a less oblique hyomandibular, held to be advanced. Comparison of the angle of the hyomandibular in the various forms shows that the second of these explanations is inadmissible, suggesting that the double posterior opening of the chamber is primitive. In all these fishes there is a vertical canal transmitting the orbital artery up into the trigeminofacial chamber. This artery passed lateral to the lower part of the wall of the myodome, as in pholidophorids and holosteans, but whether or not it always passed anterior to the articulation of the first infrapharyngobranchial (as in pholidophorids and the earliest known actinopterygians) is a point which requires further investigation. The gasserian and geniculate ganglia lay in the trigeminofacial chamber, and the trigeminal and facial canals originate immediately in front of the utricular recess (*Pteronisculus*, *Australosomus*, Kansas palaeoniscid A) or the facial canal may originate within the utricular recess (*Kentuckia*, *Boreosomus*). The facial canal opens into the orbital opening of the jugular canal, and the hyomandibular trunk turned postero-laterally to traverse the canal. There is no prefacial floor to the trigeminofacial chamber and the palatine nerve passed down into the myodome through the orbital part of the chamber. There is a separate profundus foramen in *Kentuckia*, the Kansas palaeoniscids and *Pteronisculus*, but none in *Boreosomus*, *Saurichthys* or *Australosomus*. In the latter genera the profundus may have passed out with the oculomotor nerve, as in *Polypterus*, or with the trigeminal (Nielsen 1949, p. 58). The superficial ophthalmic nerves usually pass out through the trigeminal foramen, but in *Kentuckia* and Kansas palaeoniscid A the trigeminal canal becomes subdivided during its passage through the cranial wall, so that there is a separate superficial ophthalmic foramen above the orbital opening of the trigeminal canal, as in *Amia* and caturids. The otic nerve canal originates in the roof of the foremost part of the trigeminofacial chamber, and does not join the spiracular canal except in *Boreosomus* and *Australosomus*.

From this survey, I conclude that the trigeminofacial chamber of the actinopterygian morphotype would show the following features: a long, massive lateral commissure, with separate posterior openings for the jugular vein and hyomandibular trunk and a vertical canal for the orbital artery; the gasserian and geniculate ganglia extracranial; the trigeminal and facial canals originating in front of the recess for the utriculus; a narrow facial canal emerging low in the orbital opening of the jugular canal, the hyomandibular trunk turning posteriorly to traverse the jugular canal and the palatine nerve passing down into the parabasal canal, with no prefacial floor to the chamber; a wide trigeminal canal opening in the orbit dorsomedial to the facial canal, the otic nerve canal originating in the roof of the chamber and passing up into the fossa bridgei without joining the spiracular canal; a large oculomotor foramen antero-medial to the trigeminal foramen. Whether or not a separate profundus foramen and an intramural canal for the superficial ophthalmics are primitive cannot yet be decided. Pholidophorids agree with this morphotype in having the ganglia extracranial, and the facial and trigeminal canals in front of the utricular recess, and in the position of the oculomotor foramen, which has varied little in actinopterygian history.

Pholidophorids, *Lepisosteus* and fossil holosteans (parasemionotids included) are united by reduction of the lateral commissure into a narrow pillar, so that the orbital artery enters the jugular canal through its posterior opening. *Amia* is more primitive in retaining a separate canal for the orbital artery. Pholidophorids and living and fossil holosteans (parasemionotids excluded) are united by having the facial foramen within or behind the jugular canal, and pholidophorids are united with fossil holosteans by having a palatine foramen or fenestra in the floor of the chamber, limited by a pre-palatine strut or partition. This pre-palatine floor is foreshadowed in parasemionotids, but is absent in *Amia* and *Lepisosteus*. Fossil and living holosteans, parasemionotids and *Perleidus* agree in having the origin of the facial and trigeminal canals within the utricular recess: probably this is merely a consequence of a looser bony envelope around the brain and labyrinth. Pholidophorids are specialized in having the otic nerve and spiracular canals joined, but this also occurs in *Lepidotes*, *Boreosomus*, *Australosomus* and probably in *Pachycormus*. The intramural canal or chamber for the superficial ophthalmic nerves in *Amia* and caturids may well be a specialization, but a similar chamber exists in some palaeoniscoids. In living holosteans the facial and trigeminal foramina are confluent: this is hardly evidence of relationship since the same condition occurs in many advanced teleosts. In *Lepidotes* and *Dapedium* there is a palatine foramen between the trigeminofacial chamber and myodome, as in teleosts and advanced leptolepids, not a fenestra as in other fossil holosteans. In general, the closest approach to the pholidophorid trigeminofacial chamber seems to be in *Pachycormus*.

10. *The pterosphenoid pedicle.* Among living fishes, a pterosphenoid pedicle is developed in *Amia* and various teleosts. In *Amia* (and also in the fossil amiids *Sinamia* and *Enneles*: Stensiö 1935; Santos 1960) the pedicle is formed entirely by the pterosphenoid, is endochondrally ossified throughout its length, and meets the ascending process of the parasphenoid ventrally. In teleosts the pedicle ossifies mainly in membrane and may be formed by the pterosphenoid alone or by the prootic and pterosphenoid. Amongst pholidophorids and leptolepids, the upper, pterosphenoid portion of the pedicle is developed in the larger pholidophorids, *P. germanicus*, *P. macrocephalus* and the Callovian species, and the lower, prootic portion is developed in the Sinemurian *Leptolepis*, but the pedicle is never present as a complete bony septum. In all caturids there appears to be a homologue of the upper part of the pedicle in the chamber within the pterosphenoid which encloses the superficial ophthalmic nerves. In '*Aspidorhynchus*' there is a well developed, endochondrally ossified pterosphenoid pedicle (ptsp, figure 101) which was presumably attached to the parasphenoid (pasp) by ligament. In *Macrepistius* there is a complete pedicle (Schaeffer 1971, fig. 4), but its lower part is formed by the prootic, not the parasphenoid.

A pterosphenoid pedicle is also partially developed in *Pteronisculus magnus* (Nielsen 1942, p. 90) and probably in Kansas palaeoniscid B (Watson 1925, p. 843), while the intramural chamber for the superficial ophthalmic nerves in *Kentuckia* and Kansas palaeoniscid A (Rayner 1951) is presumably homologous with the upper part of the pedicle, as in caturids. It is therefore likely that a pterosphenoid pedicle of some sort, or at least the potentiality to develop such a structure, is a primitive actinopterygian feature.

11. *The anterior and middle cerebral veins and trochlear nerve.* A constant feature of pholidophorids and leptolepids is a transversely directed canal in the pterosphenoid close behind the canal for the trochlear nerve. This is referred to throughout the descriptive sections as the canal for the middle cerebral vein. Justification of this identification, and the consequent reinterpretation of the corresponding foramen in various fossil actinopterygians, necessitates a short account of the cerebral veins in living actinopterygians.

In embryonic living fishes the blood from the brain is typically drained through three veins, the anterior, middle and posterior cerebral veins, whose development and evolution are discussed by Bertmar (1965). The posterior cerebral vein drains the mid- and hindbrain or the hindbrain alone, leaves the cranium with the vagus nerve, and falls into the jugular vein. The middle cerebral vein drains the fore- and midbrain or the midbrain alone, leaves the cranium in front of the trigeminal nerve (true middle cerebral vein) or between the trigeminal and facial nerves (secondary middle cerebral vein), and falls into the jugular vein or supraorbital vein. The anterior cerebral vein drains the forebrain, especially the epiphysial plexus, and leaves the cranium through a separate foramen in the orbital wall, falling into the supraorbital (orbitonasal) vein.

In *Acipenser* (Grodzinski 1949) the middle cerebral vein leaves the cranial cavity through the trigeminal foramen, but this is a secondary vein and the primitive vein, which lies further forwards, atrophies during ontogeny (Bertmar 1965). The anterior cerebral vein leaves the cranium well in front of the trochlear nerve, in the region of the olfactory nerve.

In adult *Lepisosteus* there is no anterior cerebral vein foramen and the trochlear foramen is described (Allis 1909, p. 187) and illustrated (Holmgren & Stensiö 1936, fig. 36) as being single, but in a large dried skull (the specimen illustrated by Rayner 1948, figs 33, 34) I find that a single internal opening leads into a canal which bifurcates and has two external openings, a smaller, anteriorly directed one which must have transmitted the trochlear nerve, and a larger, antero-ventrally directed one, lying postero-ventral to the trochlear foramen. In an 80 mm *Lepisosteus* larva Allis (1909, p. 187) found two canals in this position, the anterior transmitting the trochlear nerve, the posterior a branch of the orbitonasal (supraorbital) vein. In 33 and 65 mm larvae, Hammarberg (1937, figs 22, 25–27) shows this venous foramen, labelling it as the vena cerebralis intermedia (= middle cerebral vein), and he also found an anterior cerebral vein foramen, further forwards in the wall of the orbit. Holmgren (1943, fig. 65) reconstructed the veins in Hammarberg's 33 mm larva, and shows the anterior and middle cerebral veins joining the supraorbital vein. The anterior cerebral vein appears to atrophy in adult *Lepisosteus*, its function presumably being taken over by the middle cerebral vein.

In *Amia* the middle cerebral vein does not develop (Bertmar 1965). In adult *Amia* the trochlear nerve enters the orbit through the optic fenestra, unaccompanied by any vessel, and the anterior cerebral vein passes through an almost vertical canal in the foremost part of the pterosphenoid. This canal originates in front of the epiphysial crest and emerges just medial to the foremost part of the pterosphenoid pedicle.

In adult *Polypterus* no veins leave the cranial cavity in the immediate vicinity of the trigeminal nerve but there are two venous canals in the sphenoid, one above the trigeminal foramen and one antero-dorsal to the trochlear foramen (Allis 1922, p. 228). In a 75 mm larva both these foramina transmit 'meningeal veins from the dorsal surface of the brain' falling into the supraorbital vein (Allis) and it is reasonable to interpret these as the anterior and middle cerebral veins.

In most teleosts the middle cerebral vein (which is not secondary, Bertmar 1965) leaves the cranium with the trigeminal nerve and falls into the jugular vein (Allis 1909, p. 44; Grodzinsky 1947), the trochlear nerve enters the orbit, unaccompanied by any vessel, through the optic fenestra or through a foramen in the pterosphenoid close to the margin of the optic fenestra, and the anterior cerebral vein passes through the optic fenestra or through a transversely directed canal in the pterosphenoid close in front of the trochlear foramen (Allis 1909, p. 39). In *Elops*, for example, the external openings of the canals for the trochlear nerve and anterior cerebral vein lie close together in the centre of the pterosphenoid, but their internal openings are far apart since the venous canal passes medially to open into the cranial cavity in front of the epiphysial crest, while the nerve canal passes posteriorly and opens into the recess housing the optic lobe. But in adults of the osteoglossomorph *Hiodon* there is a large foramen for the anterior cerebral vein in the anterior part of the pterosphenoid, opening into the cranial cavity high up in front of the epiphysial crest, the trochlear foramen originates in the floor of the recess for the optic lobe, as usual, and close behind it there is a larger foramen, more laterally directed, which transmits a vessel. In sections through the head of a 25 mm *Hiodon*, this vessel can be identified as the middle cerebral vein, falling into the supraorbital vein. In adult *Hiodon*, the two foramina in the pterosphenoid are arranged as in pholidophorids and leptolepids. In the osteoglossomorph *Heterotis* the middle cerebral vein also leaves the cranial cavity through a separate foramen midway between the trigeminal and trochlear foramina, and falls into the supraorbital vein (Daget & d'Aubenton 1957, figs 13, 14). The trochlear and middle cerebral vein foramina of *Hiodon* and *Heterotis* are arranged as in *Lepisosteus*. On this evidence, the foramen behind the trochlear foramen of pholidophorids and leptolepids is interpreted as having transmitted the middle cerebral vein.

Bertmar (1965, p. 123) notes that in teleosts the anterior cerebral vein migrates posteriorly during ontogeny: that a similar migration has occurred in phylogeny is indicated by the fact that the anterior cerebral vein foramen lies well forward in the orbitosphenoid in *Pholidophorus germanicus* and the Sinemurian *Leptolepis*, in the posterior part of the orbitosphenoid in *P. macrocephalus* and later leptolepids, and in the pterosphenoid in living teleosts. The middle cerebral vein of *Salmo* and *Hepsetus* also migrates caudally during ontogeny (Bertmar 1965, p. 122), falling into the supraorbital vein in early stages, the jugular vein in later stages. Evidence of a similar migration in phylogeny is provided by the fact that in adult pholidophorids, leptolepids, *Hiodon* and *Heterotis* the middle cerebral vein passes through a canal well in front of the trigeminal foramen, close behind the trochlear foramen, while in other teleosts it passes through the trigeminal foramen.

Summarizing this review, the anterior cerebral vein leaves the forebrain portion of the cranial cavity, in front of the epiphysial crest, through a transversely directed canal originating high in the cranial cavity. The anterior cerebral vein always runs into the supraorbital vein, lies in front of the trochlear foramen, and is absent in adult *Lepisosteus*. The anterior cerebral vein migrates posteriorly in the ontogeny and phylogeny of teleosts.

The middle cerebral vein leaves the cranial cavity in the recess for the optic lobe, and always lies behind the trochlear foramen. It is absent in *Amia* at all stages, and is replaced by a secondary vein during ontogeny in *Acipenser*. Primitively (*Lepisosteus*, pholidophorids and leptolepids, some osteoglossomorphs) the middle cerebral vein passes through a separate, antero-ventrally directed foramen close behind the trochlear foramen and runs into the supraorbital vein, but the vein migrates posteriorly during the ontogeny and phylogeny of teleosts, and in most teleosts it leaves the cranial cavity with the trigeminal nerve and falls into the jugular vein.

These conclusions can now be used to reinterpret the canals in the upper part of the orbital wall in fossil actinopterygians: a useful pointer to the identification of the foramina of the trochlear nerve and middle cerebral vein is that the former usually lies in line with the profundus foramen, the latter in the groove for the superficial ophthalmic nerves. In *Saurichthys* there are two foramina in the upper part of the wall of the orbit, above the optic foramen, which are the external openings of a canal which originates in the recess for the optic lobe and bifurcates during its passage through the cranial wall (Stensiö 1925, fig. 10: v. cerebr. ant., IV). Stensiö (p. 38) interpreted these as having transmitted the trochlear nerve (posterior branch) and anterior cerebral vein, and interpreted two similar foramina in the same way in *Birgeria mougeoti* (Stensiö 1921, p. 169) and Kansas palaeoniscid B (Stensiö 1932, figs 66B, 75A: re-interpreted from Watson, who allocated the anterior foramen to the profundus). In all these fishes it would be better to interpret the anterior of the two foramina as the trochlear, the posterior as the middle cerebral vein, although in *Birgeria* caution is necessary since the foramina in the sphenoid are different in *B. groenlandica* (Nielsen 1949). In *Saurichthys*, *Birgeria*, the Kansas palaeoniscids, *Kentuckia* and *Boreosomus* there is no sign of an anterior cerebral vein canal, but in *Pteronisculus* and *Australosomus* there is such a canal, originating in the recess for the telencephalon. In *Kentuckia*, Kansas palaeoniscid A, *Boreosomus* and *Australosomus* the trochlear canal is single and there is no evidence of a middle cerebral vein, although one might suspect that the large foramen assigned to the trochlear nerve in *Boreosomus* (Nielsen 1942, fig. 64; Lehman 1952, fig. 46) also contained this vessel. In *Pteronisculus* there is a vascular canal (Nielsen 1942, p. 78, figs 13–15; Lehman 1952, fig. 18) which has the same relations as that of the middle cerebral vein in pholidophorids, and should be so interpreted (see also Bjerring 1971, fig. 6).

In *Perleidus* no canal for the anterior cerebral vein has yet been observed, but there is a canal for the middle cerebral vein (mcv, figure 116; Stensiö 1932, fig. 65, 't'; Lehman 1954, fig. 4, 't') with the usual relationship to the canal for the trochlear nerve.

In parasemionotids there is an anterior cerebral vein canal (Stensiö 1932, fig. 73; Lehman 1952, fig. 105; Beltan 1968, fig. 28), and in MMK 491 the trochlear and middle cerebral vein canals are as in pholidophorids and *Perleidus*: these two canals seem also to be present in *Parasemionotus* (Lehman 1952, figs 112, 114).

In *Pachycormus* there is a foramen in the orbitosphenoid for the anterior cerebral vein (acv, figure 106; Rayner 1948, fig. 18, the lower of the two foramina; Lehman 1949, labelled '?'), and there are two foramina in the pterosphenoid, unlabelled by Rayner and interpreted by Lehman as having transmitted the oculomotor and superficial ophthalmic nerves. But the oculomotor foramen lies further back, between the basisphenoid, pterosphenoid and prootic, and the superficial ophthalmics emerged from the trigeminal foramen; these two foramina in the pterosphenoid must have transmitted the trochlear nerve and middle cerebral vein, as in pholidophorids. The same two foramina can be seen in Rayner's Toarcian *Caturus* (1948, figs 7, 8; the medial one interpreted as the profundus), but here there is apparently no anterior cerebral vein foramen. In *Caturus chirotes* (GSM 97417), *Heterolepidotus* and '*Aspidorhynchus*' the same two foramina are present, their internal openings visible in GSM 97417, their external in *Heterolepidotus* (mcv, IV, figure 93) and '*Aspidorhynchus*' (figure 101). *Macrepistius* also seems to have these two foramina in the pterosphenoid (Schaeffer 1971, fig. 4), but in all these caturids the orbital surface of the pterosphenoid is complicated by the development of the chamber enclosing the superficial ophthalmic nerves, and the middle cerebral vein opened close to or within this chamber. In *Heterolepidotus* there is a small, transverse canal for the anterior cerebral vein (acv, figure 102), and a similar canal is probably present in *Caturus chirotes* and '*Aspidorhynchus*' (P.9844) but not, apparently, in *Macrepistius*.

In *Dapedium* there is a transverse canal for the middle cerebral vein which originates close to the internal opening of trochlear canal (whose external opening is labelled as the oculomotor foramen by Gardiner (1960, fig. 40)) and opens close to the ascending canal for the first branch of the superficial ophthalmic nerves. Rayner (1948, p. 310) describes this canal and interprets it as vascular, while Gardiner (1960, p. 304, fig. 40) interprets it as the exit foramen of the superficial ophthalmics, and the adjoining vertical nervous canal as vascular. There is a transverse canal for the anterior cerebral vein high in the orbital wall, above the middle of the orbit.

In *Lepidotes* (figures 108, 109) the canals for the middle and anterior cerebral veins are arranged as in *Dapedium*: the middle cerebral vein passed through the pterosphenoid (mcv), the anterior cerebral vein (acv) through the orbitosphenoid. The canal for the middle cerebral vein is interpreted as for the superficial ophthalmic nerves by Beltan (1957, fig. 3) and Gardiner (1960, fig. 45).

The primitive condition of the venous drainage of the anterior part of the actinopterygian brain is presumably to have both the anterior and middle cerebral veins developed, but *Pteroniscutus* is the only palaeoniscoid in which there is evidence of both veins. Both veins were present, however, in fossil holosteans (parasemionotids included), as in pholidophorids. Living chondrosteans and holosteans deviate from this condition, but I can see no significant pattern in these changes.

12. *The cranial and labyrinth cavities.* Here it seems only necessary to say that in primitive pholidophorids the brain and labyrinth were closely invested with bone to about the same extent as in palaeoniscoids, while in leptolepids the teleost condition is achieved, where the labyrinth and cranial cavities become largely confluent. The contribution of the sphenotic, pterosphenoid and prootic to the lining of the anterior semicircular canal is discussed above (point 7). In fossil holosteans, parasemionotids and *Perleidus* the cranial and labyrinth cavities seem to have been less closely invested than in pholidophorids: this is suggested by the origin of the facial and trigeminal canals in the recess for the utriculus, showing that the latter has become partially confluent with the cranial cavity. The recess housing the saccus vasculosus is discussed above (p. 390).

13. *The lateral cranial canal.* The lateral cranial canal, first described in *Caturus* by Aldinger (1932) and Rayner (1948), is present in pholidophorids as a spacious cavity within the pterotic with anterior and posterior openings into the cranial cavity. In leptolepids the canal loses the wall separating the openings into the cranial cavity so that it appears only as a diverticulum of the postero-dorsal part of the cranial cavity, and because of changes in the ossification pattern following closure of the cranial fissure (see next section) it lies in the epioccipital, not the pterotic. In advanced leptolepids this diverticulum disappears, and it does not occur in any other teleost.

Aldinger and Rayner described and illustrated the lateral cranial canal in *Caturus groenlandicus* and a Toarcian *Caturus* sp. An exactly similar canal is present in *C. chirotes* (GSM 97417) and *Heterolepidotus* (P.13260). This region is not accessible in other caturid braincases, but presumably the canal is present in all caturids. The caturid lateral cranial canal differs from that of pholidophorids in having the posterior opening larger than the anterior, and in having a ventral diverticulum within the arch of the external semicircular canal, an area which is occupied by the subtemporal fossa in pholidophorids.

In *Dapedium*, Rayner (1948) suggested that a lateral cranial canal was present, though she was unable to investigate it in detail: P.11177 shows that the canal is present, and that it has the anterior opening larger than the posterior, as in pholidophorids, has a ventral diverticulum, as in caturids, and a dorsal diverticulum which is only separated from the postero-medial part of the fossa bridgei by a thin partition, as in caturids and pholidophorids. Between the paired lateral cranial canals of *Dapedium* and behind the fossa bridgei there is a large, median intramural chamber whose outline is indicated in figure 113. This chamber communicates with the cranial cavity below by a pair of foramina in its floor, close to the mid-line, but does not communicate with the lateral cranial canal or fossa bridgei. No other actinopterygian is known to have such a chamber.

In *Lepidotes* there is a deep, pocket-like excavation in the 'epiotic', ending blindly lateral to the posterior semicircular canal; there is an exactly similar excavation in the 'epiotic' of *Lepisosteus* (figure 111). This excavation represents a postero-dorsal diverticulum of the cranial cavity which has the same topographic relations as the lateral cranial canal of leptolepids, and must represent the lateral cranial canal. In *Lepisosteus* it is filled with fat. In *Amia* there is also a postero-dorsal diverticulum of the cranial cavity in dried skulls (Kesteven 1951, fig. 3), but this lies within the intercalar and is not the lateral cranial canal. In *Pachycormus* the cranial cavity and lateral cranial canal are not yet known.

In parasemionotids, MMK 492 shows that there was an intramural chamber in the position of the lateral cranial canal. This has an irregular, fenestrated floor, and a posterior opening into the cranial cavity which is larger than that opening in pholidophorids but not so large as in caturids or *Dapedium*. The specimen is too imperfect to be certain whether this canal communicated with the fossa bridgei or whether it had an anterior opening into the cranial cavity, although the latter was probably present. In *Ospia* Stensiö (1932) described a deep postero-medial portion of the fossa bridgei which is certainly the homologue of the space described above, but in *Watsonulus* Lehman (1952) found no such communication between the fossa bridgei and the lateral cranial canal: these variations recall conditions in *Boreosomus* (see below).

In *Perleidus*, MMK 496, though imperfect, seems to show a wide communication between the deep, postero-medial portion of the fossa bridgei and the cranial cavity. This opening lies anterior to the sinus communis, in the position of the anterior opening of the lateral cranial canal in pholidophorids and holosteans, and there appears to be nothing corresponding to the posterior opening in these fishes. Stensiö (1932, figs 59, 60) found the fossa bridgei of *Perleidus* to have a deep postero-medial portion which extends inwards posterior to the sinus communis, but does not communicate with the cranial cavity: in Lehman's Madagascar specimen there appears to be a similar diverticulum (1954, pl. 1). Nielsen (1942, p. 45) says that undescribed material of *Perleidus* shows a connexion between the deep posterior part of the fossa bridgei and the cranial cavity: these variations recall the parasemionotids and *Boreosomus*.

In *Australosomus* (Nielsen 1949) there is no homologue of the lateral cranial canal.

In palaeoniscoids, Rayner (1951, p. 78) has summarized the various intramural spaces and connexions between the cranial cavity and fossa bridgei which are topographic homologues of parts of the lateral cranial canal. Where there is a connexion between the fossa bridgei and the cranial cavity, as in *Pteronisculus* and *Polyodon*, the opening lies behind the sinus communis and is homologous with the posterior opening of the lateral cranial canal. In palaeoniscoids the lateral cranial canal is represented by a chamber in the wall of the otic region which may remain independent (*Kentuckia*), become confluent with the fossa bridgei and cranial cavity (*Pteronisculus*, some *Boreosomus*), or only with the cranial cavity (some individuals of *Boreosomus*). The fact that in *Boreosomus* the lateral cranial canal is separated from the fossa bridgei in some individuals but communicates with it in others, and the variations in the size of this communication in one individual (Nielsen 1942, fig. 59) indicate that it was of no consequence whether or not the partition between the fossa and the canal developed. These variations in palaeoniscoids, similar variations in *Perleidus* and parasemionotids, the presence or absence of the canal as an individual variation in some leptolepids (p. 391), the large median chamber, resembling the lateral cranial canal, in *Dapedium*, and the fact that the homologue of the canal is filled with fat in *Polyodon* and *Lepisosteus* all go to show that the canal was without function. Nevertheless› the canal became stabilized in holosteans (caturids, pholidophorids, *Dapedium*). It is reduced in the same way in *Lepidotes*, *Lepisosteus* and leptolepids, and is lost in *Amia* and living teleosts.

14. *Sclerotic bones.* Among pholidophorids, the sclerotic ring consists of four segments in *Pholidophorus bechei* and *P. germanicus*, as in palaeoniscoids (Watson 1925, p. 820). In *P. macro-*

cephalus and in leptolepids there are only two segments, arranged fore and aft of the eyeball, as in teleosts and fossil holosteans (Edinger 1929): this reduction in number of sclerotic segments presumably occurred independently in *P. macrocephalus* and leptolepids, as it must have done in holosteans.

In *P. germanicus*, where the sclerotic is best known, each of the four segments consists of three layers, an outer dermal layer and inner and outer perichondral layers. In *Australosomus* (Nielsen 1949, fig. 1) the same three layers appear to be present, but the perichondral layers are more extensive than the dermal, and do not underlie the latter closely. The sclerotic ring is known in detail in few fossil actinopterygians, and this three-layered structure may well be widely distributed.

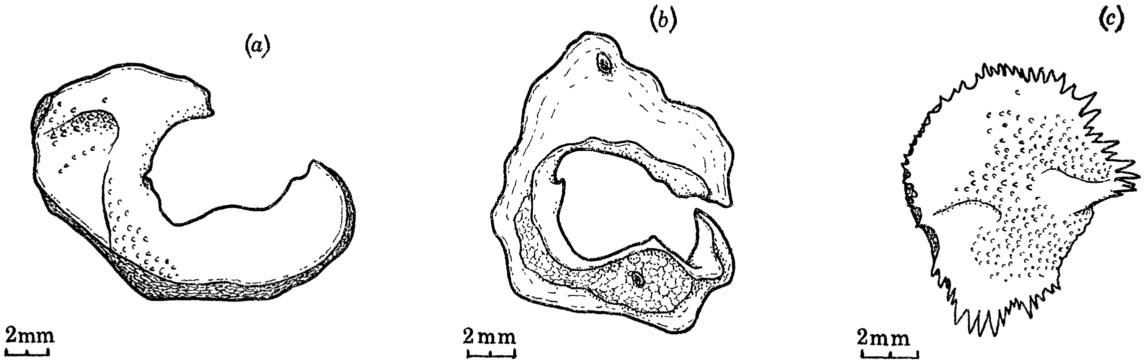


FIGURE 94. Left basal sclerotic bone, in lateral view, of (*a*) *Lepidotes toombsi* Jain & Robinson, from P.34511 (head length *ca.* 12 cm); (*b*) *Caturus chirotes* (Agassiz), from GSM 97417 (head length *ca.* 17 cm); (*c*) *Cladocyclus gardneri* Agassiz, from AMNH 9981 (head length *ca.* 7.5 cm), L. Cretaceous, Santana Fm, Serra do Araripe, Brazil. (*a*) and (*b*) are reversed drawings of right-side bones.

In pholidophorids there is a large, perichondrally ossified basal sclerotic bone surrounding the entrance of the optic nerves and vessels into the eyeball. The only other fishes in which such a structure has been described are the Upper Cretaceous ichthyodectids *Ichthyodectes* and *Xiphactinus* (Bardack 1965, pp. 44, 56, fig. 16): it also occurs in the Upper Jurassic ichthyodectid *Thrissops* (P.917) and the Lower Cretaceous *Cladocyclus* (figure 94). In ichthyodectids the bone is thoroughly ossified but spongy, and has serrated margins. A basal sclerotic also occurs in the caturid *Caturus chirotes* (figure 94) and the semionotid *Lepidotes toombsi* (figure 94): in these two fishes the bone is peri- and endochondrally ossified, and is similar in shape to that of *P. germanicus* (figure 81) but less extensive. The occurrence of such an ossification in pholidophorids, a caturid and a semionotid suggests that it was widely distributed in fossil holosteans, but is only visible under exceptional conditions. In ichthyodectids, retention of the bone is presumably a primitive condition, but its peculiar form, with serrated margins, is a specialization relating those genera which have it.

6. THE CRANIAL FISSURE, ITS CLOSURE, AND OSSIFICATION PATTERNS IN THE OCCIPITAL, OTIC AND ORBITOTEMPORAL REGIONS

(*a*) *The cranial fissure and its closure in pholidophorids and leptolepids: summary and discussion*

The discovery of a complete cranial fissure in primitive pholidophorids and of a morphological sequence explaining its closure in pholidophorids and in leptolepids is perhaps the most important information to have come from this study. This information is summarized and discussed below, and it is shown that closure of the fissure resulted in profound changes in the endocranial bones bordering on the fissure. These changes explain the origin of the teleostean pattern of otic and occipital bones, and throw a new light on the problem of neurocranial bone homologies in other actinopterygian groups.

The term 'cranial fissure' was introduced by Rayner (1951, p. 61) as a replacement for Nielsen's 'fissura otico-occipitalis' and 'fissura oticalis ventralis' (1949, p. 27). Rayner's term is a useful contraction and it is used frequently here, but Nielsen's more cumbersome terms have the advantage of drawing attention to the differences between those parts of the cranial fissure above and below the vestibular fontanelle. The *fissura oticalis ventralis*, below the vestibular fontanelle, is never lined by perichondral bone and represents the cartilage remaining between the ossification originating in the basal plate (basioccipital) posteriorly and in the trabeculae and otic capsule anteriorly. Since the fissura oticalis ventralis was occupied by cartilage in the living animal it could close during ontogeny, as it did in some individuals of *Pholidophorus bechei* (p. 307), *Leptolepis coryphaenoides* (p. 311), *Boreosomus* (Nielsen 1942, p. 287), some parasemionotids and other fossil holosteans. The *fissura otico-occipitalis*, above the vestibular fontanelle, is lined throughout by perichondral bone in primitive forms, and could not close during ontogeny. The fissura otico-occipitalis represents the persistent metotic fissure, between the occipital arch and otic capsule of the embryo.

In Devonian actinopterygians the fissura oticalis ventralis lies well in front of the vestibular fontanelle and passes up into the rear of the orbit. It is in the same position as the ventral portion of the intracranial joint of crossopterygians, and represents the gap between ossifications in the trabecular-polar bar and the basal plate (Gardiner 1970, 1973). In Carboniferous palaeoniscoids the fissura oticalis ventralis lies further back and no longer passes into the orbit, but it is still usually separated from the vestibular fontanelle by a narrow strip of bone (Rayner 1951, p. 70). The fissura oticalis ventralis and the vestibular fontanelle remain separate in some later chondrosteans such as *Boreosomus* and *Pteroniscculus macropterus* (Beltan 1968, fig. 2), but in others such as *Pteronisculus stensioei* and *Australosomus* the two fissures become confluent, as they are in pholidophorids. The fissura otico-occipitalis and the fissura oticalis ventralis are therefore primitively separate, and their confluence, so that the ossified neurocranium consists of two separate blocks, is a specialization consequent upon backward migration of the fissura oticalis ventralis. This migration of the ventral fissure is presumably a consequence of the development of the myodome (§9). As a result, the fissure moves from its original position between the trabecular-polar bar and the parachordals, close behind the pituitary, and comes to lie within the basal plate, derived from the parachordals.

The fissura otico-occipitalis and the fissura oticalis ventralis are thus independent in origin and different in structure. Their subsequent fate is also different. The fissura oticalis ventralis persists in all living teleosts and holosteans as the suture or cartilage between the basioccipital and prootics, and its closure in more primitive, fossil actinopterygians is an ontogenetic process involving simple fusion of the anterior and posterior ossifications at their plane of contact. The fissura otico-occipitalis closes by a more complex, phylogenetic process, which in the ossified skull may result in extension of some bones at the expense of others, and when one speaks of closure of the cranial fissure, it is only the fissura otico-occipitalis which is involved. Facts relating to the cranial fissure and its closure in pholidophorids and leptolepids are as follows (see also figure 95).

(1) In *Pholidophoroides limbata* (Sinemurian), some individuals of *Pholidophorus bechei* (Sinemurian) and in *P. minor* (Bathonian) the cranial fissure is complete, and a perichondrally lined fissura otico-occipitalis extends from the vestibular fontanelle upwards, separating the occipital bones (basi-exoccipital, intercalar, epioccipital and supraoccipital) from the otic (prootic, opisthotic, pterotic), enclosing the vagus canal, and meeting its fellow in the mid-line dorsally. There is no obvious posterior dorsal fontanelle in these forms, but in *P. limbata* the dorsalmost part of the fissure is uninterrupted and the supraoccipital is only a vertical plate of bone with a postero-dorsal median hump. In *P. bechei* the supraoccipital has developed an anterior outgrowth which overlaps the otic ossification. In some individuals this outgrowth must be mainly membranous, but in others the dorsalmost part of the fissure is closed in cartilage-bone (figure 57). Similar variations in the mid-dorsal part of the fissure are known in *Boreosomus piveteaui* (Nielsen 1942, p. 287). In *P. bechei* the portions of the cranial fissure around the vagus canal are covered over by membrane bone outgrowths of the intercalar. In these pholidophorids the labyrinth cavity lies entirely within the otic ossifications, in front of the cranial fissure, except for the posterior part of the otolith chamber, which lies in the basi-exoccipital.

(2) In *Pholidophorus germanicus* (Toarcian) the perichondrally lined cranial fissure extends from the lower margin of the vagus canal up to the medial edge of the epioccipital. The mid-dorsal part of the fissure closed in cartilage in the embryo, and the supraoccipital has grown forwards in this cartilage to join the pterotics in synchondrosis. The sub-vagal portion of the fissura otico-occipitalis was also closed in cartilage, but persisted as a suture separating the exoccipital and opisthotic. In late ontogeny these two bones tended to fuse, so that in a fully ossified individual the basi-exoccipital would appear to extend forwards and form the wall of the lower part of the ampullary chamber of the posterior semicircular canal. Membrane bone outgrowths of the intercalar cover the portion of the cranial fissure around the vagus canal, as in *P. bechei*, and in *P. germanicus* the epioccipital has also developed membranous outgrowths overlapping the dorso-lateral part of the fissure.

(3) In the Callovian *Pholidophorus* sp. the opisthotic is no longer recognizable, and the cranial fissure only extends down to the upper margin of the vagus canal so that the vagus canal is enclosed within the basi-exoccipital and the latter bone forms the hind wall and floor of the ampullary chamber of the posterior semicircular canal. Dorsally the fissure ends at the medial edge of the epioccipital, as in *P. germanicus*, but in the available specimens the supraoccipital is much more completely ossified in the Callovian species than in *P. germanicus* and extends forwards to line depressions housing the hind ends of the metencephalic lobes and a portion of the posterior semicircular canal. The membrane bone outgrowths of the supra- and epioccipital are well developed, binding these bones to the pterotics.

(4) In *P. macrocephalus* (Kimmeridgian) the perichondrally lined cranial fissure does not extend below the vagus canal, but as in *P. germanicus* the fissure is continued beneath the canal as a cartilage-filled suture separating the basi-exoccipital from a small opisthotic. In contrast to *P. germanicus*, this suture appears to remain open throughout life. Dorsally, the supraoccipital portion of the fissure is obliterated, as in *P. germanicus* and the Callovian species, while the epioccipital portion persists as in the latter, but is no longer perichondrally lined so that it must have been bridged by cartilage. There are membrane bone outgrowths of the intercalar, epioccipital and supraoccipital, as in the Callovian species, and the dorsal outgrowth of the intercalar is particularly large.

(5) In the earliest known leptolepid braincase, that of the Sinemurian *Leptolepis* sp., the

cranial fissure extends from the vagus canal up to the lower margin of the epioccipital, and is perichondrally lined. Ventral to the vagus canal, the basi-exoccipital extends forwards below the ampullary chamber of the posterior semicircular canal, and there is no sign of an opisthotic, as in the Callovian *Pholidophorus*. Dorsally, the epioccipital portion of the fissure has closed and the epioccipital extends forwards to enclose the upper part of the posterior semicircular canal, and forms the walls of the lateral cranial canal and the postero-medial part of the fossa bridgei and post-temporal fossa. In pholidophorids, all these structures lie in the pterotic, and the pterotic of leptolepids is greatly reduced in comparison with that of pholidophorids (point 3, §5(*k*)(i)).

(6) In later leptolepids, *L. coryphaenoides* (Toarcian), the Callovian *Leptolepis* sp. and *L. dubia* (Kimmeridgian), the cranial fissure is completely obliterated, and in some individuals of *L. coryphaenoides* the otic and occipital ossifications may fuse throughout. In *L. coryphaenoides* the supraoccipital may extend forwards around the upper surface of the anterior semicircular canal, and the anterior and posterior semicircular canals leave an impression on the bone in all three species. The epioccipital resembles that of the Sinemurian *Leptolepis*, and in *L. coryphaenoides* it still forms the floor of the reduced postero-medial portion of the fossa bridgei. This disappears in the Callovian species and in *L. dubia*, and the lateral cranial canal also regresses in these species. The pterotics of these three species are small, as in the Sinemurian species. The exoccipital of these leptolepids is radically different from the exoccipital portion of the basi-exoccipital in the Sinemurian *Leptolepis* and in pholidophorids, since it extends forwards to enclose the vagus canal, the ampulla and ventral part of the posterior semicircular canal, and the posterior part of the subtemporal fossa. In *L. coryphaenoides* the glossopharyngeal canal still lies in the prootic, but in the Callovian *Leptolepis* and in *L. dubia* this too has become included in the exoccipital. The intercalar, which has an endochondral component in pholidophorids and the Sinemurian *Leptolepis*, is a membrane bone in all later leptolepids.

From the facts summarized above, one can form a clear picture of how the fissura otico-occipitalis became obliterated in teleostean phylogeny, and of the consequences of this on the morphology of the otic and occipital bones. In primitive pholidophorids, where the fissure was complete, any possibility of neurokinesis is excluded by the shape of the fissure, which is not a transverse division but curves forwards ventrally, and is so shaped that the occipital ossification fits into the posterior face of the otic ossification like a plug. Kinesis was further eliminated by the membrane bone outgrowths of the intercalar, which braced the occipital ossification against the prootic and pterotic regions. As pointed out above, confluence of the fissura oticalis ventralis and the fissura otico-occipitalis is a specialization in actinopterygians, and only after this confluence has occurred was there any possibility of neurokinesis (cf. Schaeffer 1968, p. 216; Gardiner 1970). The pholidophorids did not exploit this potentiality, and it is not possible to regard the persistent cranial fissure as adaptive: if kinesis ever occurred at the fissure, pholidophorids seem to have done their best to eliminate such movement. In pholidophorids the cranial fissure can only be regarded as a relict structure, which had already been eliminated partially or completely in all contemporary actinopterygian lineages except the surviving palaeoniscoids.

Closure of the cranial fissure only entails ontogenetic fusion of the occipital arch with the otic capsule in cartilage before ossification begins. This fusion began both at the bottom of the fissure, between the vestibular fontanelle and the vagus canal (basicapsular fenestra of the embryo), and in the mid-line dorsally (taenia tecti medialis of the embryo). In the ossified skull, three processes are involved in closure of the fissure. The first, which is a purely superficial phenomenon, independent of closure of the fissure in cartilage, is *the development of membrane bone outgrowths* from the cartilage bones bordering on the fissure. These membrane bone outgrowths cover the fissure superficially, and bind the occipital and otic ossifications together. In pholidophorids, outgrowths of the intercalar are the most important expression of this phenomenon, but the supraoccipital, epioccipital and pterotic also play a part in various pholidophorids. The other two processes are dependent upon closure of the fissure in cartilage and are to some extent sequential, the first being often a precursor of the second. In the first of these processes, the fissure closes in cartilage, but in the ossified skull it *remains as a suture*, which may fuse in full-grown individuals. In the second, the fissure closes in cartilage and in the ossified skull *it is obliterated by extension of the occipital bones into the otic region*. Examples of the first of these, the fissure remaining as a suture, are found in the upper and lower parts of the fissure. The lower, sub-vagal part of the fissure remains as a suture between the basi-exoccipital and opisthotic in *Pholidophorus germanicus* and *P. macrocephalus*: the upper, dorso-lateral part of the fissure remains as a suture between the epioccipital and pterotic in *P. macrocephalus*. Further examples of this type could probably be found in the supraoccipital region of *P. bechei*, were a range of acid-prepared specimens available (cf. figure 57), but no such example is known among leptolepids. Obliteration of the fissure by forward extension of the occipital bones seems to have been the dominant process in leptolepids, and this process was responsible for the changes in the relative extent of the otic and occipital bones which produced the teleostean pattern of neurocranial ossifications.

Obliteration of the fissure by extension of the occipital bones seems to have proceeded stepwise, from above and below. From above, it appears that the whole of the supraoccipital portion closed at one step (*P. germanicus*, Callovian *Pholidophorus*, *P. macrocephalus*), followed by the whole of the epioccipital portion (Sinemurian *Leptolepis*), since no examples are known of a supra- or epioccipital whose anterior face is partially perichondrally lined. From below, the fissure also closed stepwise, first by the elimination of the sub-vagal portion (Callovian *Pholidophorus*, Sinemurian *Leptolepis*), next by elimination of the supravagal portion (opposite the upper part of the exoccipital; other leptolepids). These two processes, the stepwise obliteration of the fissure from above and below, were evidently not synchronized and proceeded independently, but both in pholidophorids and leptolepids the last part of the fissure to persist is the portion immediately above the vagus canal, opposite the upper part of the exoccipital and the intercalar.

Closure of the cranial fissure in pholidophorids and leptolepids was therefore effected in phylogeny by stepwise extensions of the ontogenetic fusion between the cartilaginous occipital arch and otic capsule, with the result that in the ossified skull the occipital bones bordering on the fissure (supraoccipital, epioccipital, exoccipital) have extended forward into the otic region at the expense of the otic bones bordering on the fissure (pterotic, opisthotic), which appear to be lost (opisthotic) or abbreviated (pterotic) when forms in which the fissure is obliterated are compared with those in which it is fully developed. As a result of this 'capture of territory' by the occipital bones, the supraoccipital has taken over from the pterotic the transverse bolster behind the anterior dorsal fontanelle (tectum synoticum of the embryo), the cavities housing the metencephalic lobes, and the uppermost parts of the anterior and posterior semicircular canals. The epioccipital has taken over from the pterotic the lateral cranial canal, the upper part of the posterior semicircular canal, and the postero-medial parts of the fossa bridgei and post-temporal fossa. The exoccipital has extended into the territory of both the opisthotic and pterotic. From the latter it has taken over the lower part of the posterior semicircular canal and the upper part of its ampullary chamber, and the posterior part of the subtemporal fossa. From the opisthotic, it has taken over the lower part of the posterior ampullary chamber and the wall of the saccular recess behind the glossopharyngeal foramen.

A consequence of closure of the supravagal part of the cranial fissure and forward extension of the exoccipital above the vagus canal was that the intercalar lost its endochondral portion. The exoccipital could not grow forwards around the vagus canal while the intercalar remained as a separate, endochondral growth centre immediately behind the vagus canal, and the exoccipital appears to have 'captured' the territory of the endochondral intercalar, eliminating that part of the bone and leaving the intercalar as a membrane bone, as it is in *Amia* and living teleosts. As is shown below (§6(*b*)) the correlation between an endochondral intercalar and persistence of the portion of the cranial fissure immediately above the vagus canal is also exemplified by caturids, *Pachycormus*, parasemionotids and *Perleidus*, the only other actinopterygians with an undoubted endochondral intercalar.

That the endochondral portion of the intercalar was eliminated as a necessary consequence of forward extension of the exoccipital, following closure of the supravagal portion of the cranial fissure, seems to be a well-founded conclusion, because what is undoubtedly the homologue of the pholidophorid and primitive leptolepid intercalar persists in more advanced leptolepids and in teleosts, because of the existence of other fossil groups (*Pachycormus*, parasemionotids, *Perleidus*) showing the intercalar in its primitive condition, and because of the availability of living actinopterygians (*Amia*, teleosts) in which the ontogeny of the exoccipital and intercalar can be studied. But the changes in the pterotic and opisthotic of pholidophorids and leptolepids which were consequent upon closure of the cranial fissure are only documented in fossil material, and need further discussion.

Among pholidophorids and leptolepids, an opisthotic has only been recognized in *P. bechei*, *P. germanicus* and *P. macrocephalus*. It is a small bone in the postero-ventral part of the otic region, between the glossopharyngeal foramen (in the prootic) and the vagus canal. It forms a small part of the lateral wall of the saccular chamber, part of the floor of the posterior ampullary chamber, and the anterior wall of the vagus canal and subvagal portion of the fissura otico-occipitalis. In *P. bechei* the bone fuses with the otic bones (prootic in front, pterotic above) during ontogeny, and is separated from the occipital bones posteriorly by the perichondrally lined subvagal portion of the cranial fissure. In *P. germanicus* and *P. macrocephalus* the subvagal portion of the fissure is closed in cartilage, and in full-grown individuals of *P. germanicus* the opisthotic fuses with the occipital bones (basioccipital below, exoccipital behind). In the Callovian *Pholidophorus* and in leptolepids the area occupied by the opisthotic in *P. bechei*, *P. germanicus* and *P. macrocephalus* appears to be part of the exoccipital, not a separate ossification, suggesting that the opisthotic has been lost and the exoccipital has extended forwards to take its place. But such 'capture of territory' by one bone from another can always be interpreted in another way, as due to fusion, especially when it appears to be saltatory, as in the case of the opisthotic and exoccipital. Jardine (1970, p. 343) has discussed the meaning of 'loss' and 'fusion' in phylogenetic discussions, and in this case one might hypothesize that the opisthotic, which is known to fuse with the basi- and exoccipital in full-grown *P. germanicus*, fused with the exoccipital at successively earlier ontogenetic stages until only a single ossification centre occurred (Jardine 1970, fig. 4(iii)), and therefore regard the disappearance of the opisthotic as a case of phylogenetic fusion.

Jardine (1970, p. 345) arrived at the following definitions of phylogenetic fusion and loss: '*phylogenetic fusion* would describe cases where fusion of formerly distinct ossificatory centres had occurred in the ontogeny of some member of the fossil sequence, and either had occurred in the ontogeny of subsequent members, or had occurred at successively earlier stages in the ontogeny of subsequent members until eventually only a single ossificatory centre appeared in any stage at ontogeny. *Phylogenetic loss* would describe cases in which an ossificatory centre present in the ontogeny of some member of a sequence did not appear at any stage in the ontogeny of any subsequent member of the sequence.' These definitions were formulated with the dermal skeleton in mind, but to apply them to the neurocranium raises serious difficulties. The only real difference between the two statements is that in the second there is never evidence of ontogenetic fusion of ossifications. But in the primitive actinopterygian braincase, *all* the bones fuse in full-grown individuals, and if Jardine's definitions were rigidly followed one would have to regard all cases of reduction in number of endocranial ossifications as due to phylogenetic fusion, which is nonsensical. The braincase is much less plastic than the dermal skeleton, and to apply a hypothesis of phylogenetic fusion to the opisthotic and exoccipital, for example, would require progressive approximation of the ossification centres of the bones, so that they could meet and fuse at successively earlier ontogenetic stages. The exoccipital of living teleosts and of *Lepisosteus* (which has the same type of exoccipital, growing forwards to enclose the vagus canal and occupy the territory of the opisthotic) arises as inner and outer perichondral lamellae in the occipital arch, behind the vagus foramen, dorso-lateral to the notochord and ventro-lateral to the foramen magnum: so far as one can tell, this is also the position of the exoccipital ossification centre in pholidophorids. In teleosts, the only evidence of an opisthotic is in *Heterotis*, where in a 14 mm embryo Daget & d'Aubenton (1957, p. 896) describe a small perichondral ossification on the internal surface of the braincase in the anterior margin of the vagus foramen. Daget (1964, p. 252) interprets this bone as an opisthotic, and I agree that this is the position in which a much reduced opisthotic might be expected. Unfortunately, nothing is known of the fate of this ossification in *Heterotis*. At the next stage described, 33 mm, the exoccipital has grown forwards and surrounded the vagus foramen entirely, as usual, and it is not known whether the opisthotic is transient (like the prootic of *Polypterus*; Pehrson 1947, p. 405), or whether it persists and fuses with the exoccipital. No other teleost is known to have an opisthotic, and the exoccipital always arises in the occipital arch, behind the vagus foramen. The hypothesis of phylogenetic fusion requires that the exoccipital ossification centre in teleosts also includes the opisthotic ossification centre, which has somehow migrated across the metotic fissure into the occipital arch. This seems to be absurd, and the hypothesis untenable. Further evidence that the teleostean exoccipital developed by extending forwards in phylogeny, eliminating the opisthotic, is provided by a comparison between the exoccipital of a primitive leptolepid like *L. coryphaenoides* with that of the Callovian *Leptolepis* or a living teleost. In *L. coryphaenoides*, as in pholidophorids and *Lepisosteus*, the glossopharyngeal foramen lies within the prootic, but in later leptolepids, as in living teleosts, the exoccipital has grown forwards and enclosed the glossopharyngeal foramen. This seems to be a further continuation of the trend towards anterior expansion of the exoccipital which began with the closure of the subvagal portion of the cranial fissure in pholidophorids. In summary, closure of the parts of the cranial fissure immediately above and below the vagus foramen in the ancestors of teleosts resulted in extension of the exoccipital forwards into the otic region, eliminating the opisthotic and the endochondral portion of the intercalar.

Closure of the dorso-lateral portion of the cranial fissure in the leptolepids resulted in a similar extension of the epioccipital into the otic region, and this had a profound effect on the pterotic. The pholidophorid pterotic is a very large and complex bone whose centre of ossification must lie in the shoulder separating the fossa bridgei and post-temporal fossa, over the partition between the subtemporal fossa and the lateral cranial canal and lateral to the upper parts of the anterior and posterior semicircular canals. In *P. germanicus* there is evidence of a small separate ossification behind the middle part of the posterior semicircular canal (Ptsn, figure 45) and in *P. macrocephalus* there is a larger separate ossification lateral to the posterior part of the external canal, on the ventro-lateral surface of the large posterior expansion of the descending lamina of the dermopterotic (Ptsl, figure 84), but in these forms the pterotic certainly arose from a single primary ossification centre. In leptolepids the area in which the pholidophorid pterotic originates lies in the antero-lateral part of the epioccipital, which has extended forwards to enclose the lateral cranial canal and posterior semicircular canal. The leptolepid pterotic is a comparatively small bone, and it ossifies from a centre over the middle part of the external semicircular canal, on the outer (ventro-lateral) face of the descending lamina of the dermopterotic, medial to the posterior part of the hyomandibular facet and in front of the preopercular sensory canal: the pterotic of living teleosts ossifies from the same centre. This location is at the ventro-lateral margin of the pterotic in pholidophorids, but the structures framed by the leptolepid and teleost pterotic – external semicircular canal, posterior part of hyomandibular facet, floor of post-temporal fossa, roof of subtemporal fossa – are all included within the pholidophorid pterotic.

There seem to be only two possible interpretations of the differences between the pholidophorid and leptolepid pterotic. The first is that the leptolepid bone is homologous with the pholidophorid bone, but that extension of the epioccipital into the vicinity of the original ossification centre of the pterotic has caused this centre to shift ventro-laterally to a position lateral to the post-temporal fossa, above the external semicircular canal. The second is that in leptolepids and teleosts the pholidophorid pterotic has been lost, its upper part being replaced by forward extension of the epioccipital, its lower by expansion of a small ossification on the external semicircular canal.

A third interpretation might be offered, that the pterotic of leptolepids and teleosts is a neoformation, the homologue of the pholidophorid pterotic having been lost. But this hypothesis seems to be logically indistinguishable from the first of the two set out above, and the latter is preferable because the teleost pterotic is the exact topographic homologue of a major part of the pholidophorid bone, and the two bones have essentially the same relationship to the surrounding neurocranial bones.

The second of the two hypotheses under discussion, that the teleost pterotic is derived from a small ossification on the external semicircular canal, requires that such a bone should occur in forms with a pholidophorid type of pterotic. The only known candidates are the opisthotic, and the small independent ossification on the posterior expansion of the descending lamina of the dermopterotic in *Pholidophorus macrocephalus* (Ptsl, figure 84). These must be considered individually.

The opisthotic of pholidophorids lies ventral to the external semicircular canal, plays no part in the support of the latter, and is separated from the location of the ossification centre of the teleost pterotic by the whole width of the subtemporal fossa, which occupies the arch of the external semicircular canal. However, as will be shown in §6(*b*), the opisthotic is larger in some fossil actinopterygians (*Pachycormus*, caturids, parasemionotids, *Perleidus*), and primitively it was probably the largest bone in the braincase. In caturids and *Pachycormus* the opisthotic surrounds all or part of the external semicircular canal, contributes to the hyomandibular facet, and in caturids also floors part of the post-temporal fossa so that it simulates the teleost pterotic quite closely. Despite this similarity, the hypothesis that the teleost pterotic is homologous with the opisthotic appears to be untenable. Pholidophorids are undoubtedly the closest known relatives of leptolepids and teleosts. In pholidophorids the opisthotic, when present, is reduced in comparison with that of *Pachycormus*, caturids and more primitive actinopterygians and has lost all contact with the external semicircular canal, here contained in the pterotic. Within the Pholidophoridae it has been shown above that the opisthotic disappears following closure of the subvagal portion of the cranial fissure and forward extension of the exoccipital: these changes have no effect on the pterotic (e.g. Callovian *Pholidophorus*). In the earliest leptolepid known, these changes have already occurred, and it must be assumed that they had the same result as in pholidophorids, loss of the opisthotic. In all other actinopterygians in which the exoccipital has grown forwards to enclose the vagus canal (*Lepisosteus*, *Lepidotes*, fossil amiids) the opisthotic has also disappeared, suggesting that this is the rule.

In *Pholidophorus macrocephalus* there is a small ossification on the posterior expansion of the descending lamina of the dermopterotic which is a possible precursor of the teleost pterotic. This bone does not form part of the wall of the external semicircular canal, but it ossifies from a centre directly posterior to the ossification centre of the leptolepid pterotic. To transform this bone into a pterotic of teleost type, it is only necessary that the ossification centre should shift forwards along the descending lamina of the dermopterotic until it lies in front of the preopercular sensory canal, over the centre of the external semicircular canal. This change is slight in comparison with the major shift in ossification centre required by the hypothesis that the teleost and pholidophorid pterotics are homologous, and if this small ossification could be shown to be a normal component of the braincase of early pholidophorids or other primitive actinopterygians, this interpretation would be attractive. But although I cannot state categorically that no such minor ossification occurred in *P. bechei* or other primitive actinopterygians, I think the general occurrence of such a bone unlikely. The bone is certainly absent in *P. germanicus* and parasemionotids, where incompletely ossified individuals show the ossification pattern well, and I can find no positive evidence of such a bone in any other fish. In *P. macrocephalus* the small bone in question is closely associated with a large, posterior expansion of the descending lamina of the dermopterotic which lines the floor of the postero-lateral part of the post-temporal fossa and meets the dorso-lateral outgrowth of the intercalar. A similar posterior expansion of the dermopterotic occurs in *Pholidophoroides limbata* (figure 82), but there is no such expansion in *P. bechei* (figure 60), *P. germanicus* (figure 146), *P. minor* (figure 83), the Callovian *Pholidophorus* (figure 69), leptolepids, *Perleidus*, parasemionotids, *Lepidotes*, *Heterolepidotus*, or *Caturus*. In *Amia*, and probably also in '*Aspidorhynchus*', the posterior expansion of the descending lamina of the dermopterotic meets the intercalar, as in *Pholidophorus macrocephalus*, but there is no separate cartilage-bone beneath it. In palaeoniscoids, when a posterior descending lamina is developed on the dermopterotic, as in *Pteronisculus* (Nielsen 1942, p. 120), it covers the lateral surface of the otic region and therefore has no neurocranial bone on its outer face. From this evidence, it appears that the large posterior expansion of the dermopterotic descending lamina in *P. macrocephalus* and *P. limbata* is a specialization peculiar to these pholidophorids, and the small neurocranial ossification on its outer surface in *P. macrocephalus* is also likely to be a specialization, not a general feature of pholidophorids. There is therefore no evidence that generalized pholidophorids, or any other primitive actinopterygians, possessed a small ossification over the external semicircular canal which could have given rise to the teleost pterotic.

A final reason for rejecting the hypothesis that the teleost pterotic arose from a small ossification over the external semicircular canal is that, as shown in §6(*b*), a satisfactory account of the pattern of neurocranial ossifications in all other actinopterygian groups can be given on the basis of the four otic bones occurring in pholidophorids (pterotic, sphenotic, prootic, opisthotic), and parsimony demands that the teleost pattern should be similarly explicable.

The first hypothesis outlined above, that the teleost pterotic is the homologue of the pholidophorid pterotic but owes its different form to a radical shift in the position of the ossification centre, is therefore in harmony with the conditions in other actinopterygian groups. This hypothesis requires that the centre of ossification of the bone should have shifted from a position dorso-medial to the post-temporal fossa to one lateral to the fossa, over the middle of the external semicircular canal. Such a radical shift in the position of the ossification centre may seem improbable in the absence of forms showing the bone ossifying from an intermediate position. But the postero-dorsal part of the otic capsule in pholidophorids and leptolepids contains a complex of spaces (post-temporal fossa, subtemporal fossa, lateral cranial canal, labyrinth) such that growth of the bone from any centre intermediate between the two positions described above would be geometrically impossible, and the shift required must have occurred at one step, as an immediate consequence of forward extension of the epioccipital. Direct evidence of such an event can never be found, of course, although it is unfortunate that the pterotic is so poorly known in the Sinemurian *Leptolepis*, the most primitive leptolepid known. However, an earlier stage in modification of the growth pattern of the pterotic can be demonstrated. It has been shown above that with the closure of the mid-dorsal portion of the cranial fissure in pholidophorids, the supraoccipital grew forwards into the otic region. This extension of the supraoccipital cannot have involved any 'fusion' or 'loss' of ossification centres, for there was no median supraotic bone in pholidophorids, and it took place solely at the expense of the pterotic, which in pholidophorids with a complete cranial fissure met its fellow in the mid-line dorsally. Comparison of dorsal views of the otic region in a pholidophorid with the supraoccipital portion of the cranial fissure open (figures 60, 82) and closed (figure 69) shows that expansion of the supraoccipital must have modified the growth pattern of the pterotic, reducing its medial extent. Forward extension of the epioccipital, following closure of the dorso-lateral portion of the cranial fissure, must have caused much grosser changes in the growth pattern of the pterotic. This extension of the epioccipital seems to have occurred at about the same time as the breakdown of the partition between the fossa bridgei and post-temporal fossa: it will be shown below that this partition is the site of the ossification centre of the pterotic in the parasemionotids, and probably in other primitive holosteans. It is therefore reasonable to suppose that these disturbances in the region of the original pterotic ossification centre caused the centre to shift laterally to the nearest geometrically appropriate location, over the external semicircular canal. I conclude that the teleostean pterotic is the homologue of the pholidophorid bone, and that it is appropriate to use the same name for the two types of bone, as has been done in the preceding descriptions and discussions. The alternative would be to restrict the name 'pterotic' to a bone ossifying from the same centre as the teleostean pterotic, and to use another name (epiotic or some new term) for the bone ossifying from the dorso-medial centre in pholidophorids and other actinopterygian groups. But that usage would obscure the essential unity of plan of the neurocranial ossifications in actinopterygians, and would imply non-homology between the bone in question in teleosts and pholidophorids, which I believe to be untrue.

The other nomenclatorial problem concerns the name to be used for the bone previously called the epiotic in teleosts. As has been demonstrated above, this bone primitively had no connexion with the otic region but was an ossification in the occipital arch, behind the cranial fissure. Only after closure of the dorso-lateral part of the fissure, in early leptolepids, did the bone extend forwards and acquire the association with the posterior semicircular canal which characterizes it in living teleosts. For this reason, the name epiotic is inappropriate. This alone would be insufficient justification for discarding the name, but it will be shown in §6(*b*) that in various fossil holosteans the name epiotic has been used for a true otic bone, the homologue of the pholidophorid pterotic, while in *Amia*, *Lepisosteus* and a few fossil actinopterygians the name epiotic is applied to a bone of uncertain origin, whose phylogenetic homologue can only be guessed. In view of these confused usages, it seems to me wisest to make a fresh start by introducing the name '*epioccipital*' for the dorso-lateral ossification in the occipital arch of primitive actinopterygians and its phylogenetic homologue, the 'epiotic' of teleosts; to use the term pterotic for the postero-dorsal ossification in the otic region and its phylogenetic homologue, the pterotic of teleosts; and to reserve the name epiotic for provisional use in those fishes (such as *Amia*) where the phylogenetic homology of the bone in question is still uncertain.

In the preceding discussion, various occipital bones have been shown to extend forwards into the otic region following closure of the cranial fissure in pholidophorids and leptolepids. This must imply that the occipital ossifications were in some way 'dominant' over the otic bones: such dominance could occur if the occipital bones ossified earlier in ontogeny than the otic bones, so that their growth centres were established before those of the otic region. This situation would arise if there were a neurocranial 'gradient of ossification' which was strongest in the occipital region, or it might be attributable to precocious development of the (cartilaginous) occipital arch with respect to the otic capsule.

This account of the cranial fissure and its closure in pholidophorids and leptolepids, and of the origin of the teleostean pattern of otic and occipital ossifications, can be summarized as follows (see also figure 95).

(1) The cranial fissure consists of two portions, the fissura oticalis ventralis and the fissura otico-occipitalis, which are independent in origin and different in structure and fate. The fissura oticalis ventralis is always closed in cartilage, can close in bone in late ontogeny, and persists in teleosts as the suture between the basioccipital and prootics. The fissura otico-occipitalis, which is complete, perichondrally lined and apparently functionless in early pholidophorids, became obliterated during teleostean phylogeny.

(2) Closure of the fissura otico-occipitalis in phylogeny took place by two distinct and sequential processes. In the first the fissure closed in cartilage by fusion between the occipital arch and otic capsule, but persists in the ossified skull as a suture which may close in late

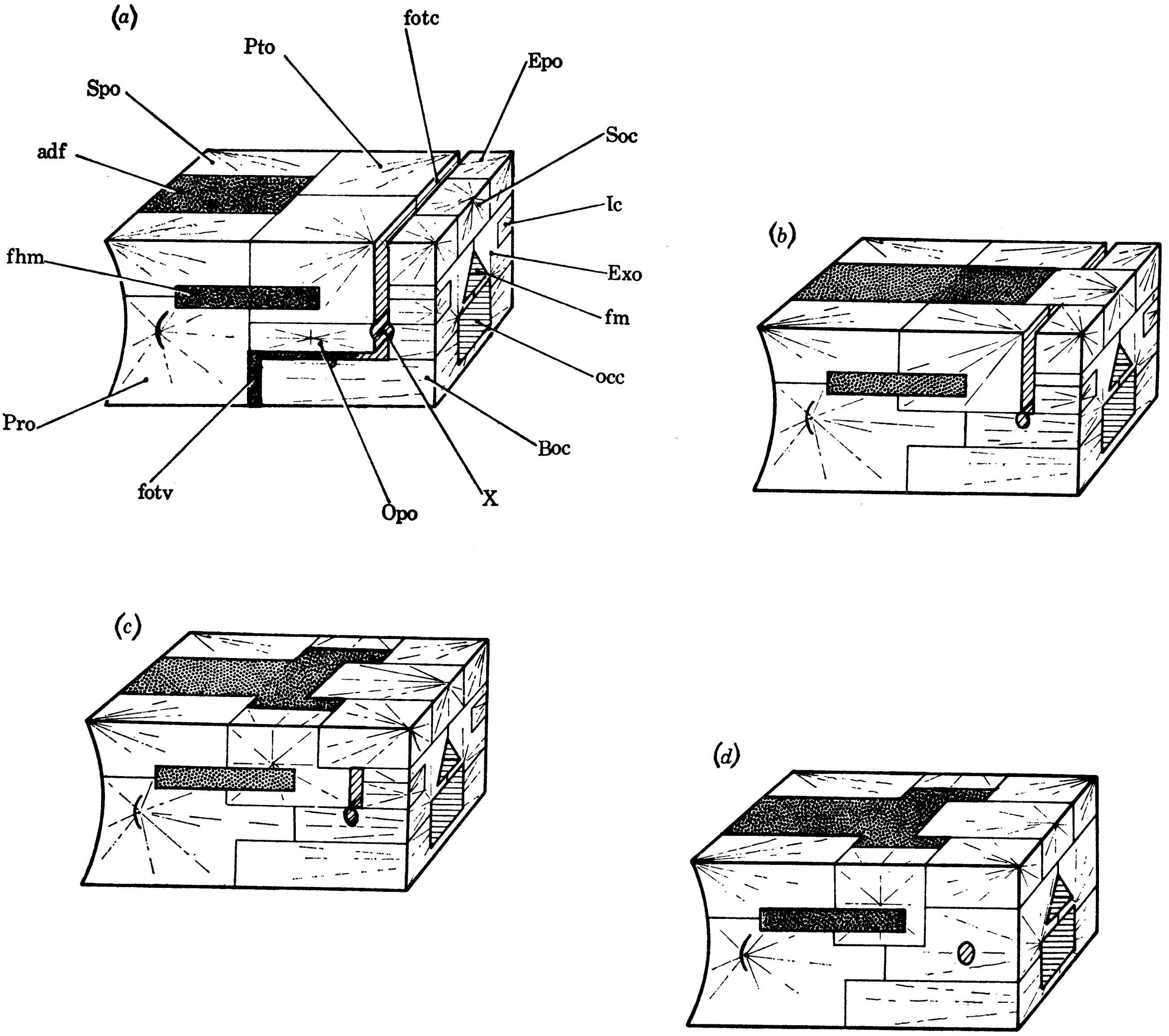


Figure 95. Block diagrams to summarize the cranial fissure and the ossification pattern of the postorbital part of the neurocranium in pholidophorids and leptolepids. The endochondral parts of the neurocrania are drawn as boxes seen in oblique postero-lateral view from the left side, omitting all surface relief and superficial membranous outgrowths, and showing only the ossification centres of the bones, the anterior dorsal fontanelle (as if cartilage-filled), hyomandibular facet, lateral commissure, cranial fissure and vagus canal, foramen magnum and occipital condyle (notochord pit). Stipple indicates cartilage, hatching spaces.

(*a*) A primitive pholidophorid, in which the cranial fissure is uninterrupted (e.g. *Pholidophorus bechei*); (*b*) an advanced pholidophorid in which the supraoccipital and subvagal portions of the fissure have closed, and the opisthotic has been lost (e.g. Callovian *Pholidophorus* sp.); (*c*) a primitive leptolepid in which the epioccipital portion of the fissure has also closed, and the ossification centre of the pterotic has shifted to above the hyomandibular facet (e.g. Sinemurian *Leptolepis* sp.); (*d*) an advanced leptolepid or generalized. Recent teleost, in which the fissure is completely obliterated and the endochondral intercalar is lost (e.g., *Leptolepis coryphaenoides*, Callovian *Leptolepis* sp. or any generalized teleost).

ontogeny. In the second the fissure closed in cartilage and is obliterated in the ossified skull by forward growth of the occipital bones: this implies 'ontogenetic dominance' of the occipital region over the otic. A third phenomenon is also involved, the development of superficial membrane bone outgrowths, bridging the fissure, from the bones bordering it, especially the intercalar. These membrane bone outgrowths often mask the persisting portions of the fissure.

(3) Closure of the fissure proceeded stepwise from above and below, and the two processes were not synchronized. From below, the subvagal portion closed first, resulting in forward growth of the lower part of the exoccipital, which took the place of the opisthotic and eliminated it. From above, the mid-dorsal portion closed first, resulting in forward growth of the supraoccipital which captured territory from the pterotic. Next, the dorso-lateral part of the fissure closed and the epioccipital grew forwards, taking over the lateral cranial canal and posterior semicircular canal from the pterotic and causing a major shift in the ossification centre of the latter, so that both the epioccipital and pterotic acquired the form typical of teleosts. The last part of the fissure to persist was the portion immediately above the vagus canal. When this closed, the resulting forward growth of the upper part of the exoccipital obliterated the endochondral portion of the intercalar, leaving the latter as a membrane bone, as it is in teleosts, and captured territory from the pterotic and, in later leptolepids, from the prootic, so that the glossopharyngeal canal came to lie in the exoccipital, as it does in teleosts. These changes are summarized in diagrammatic form in figure 95.

(4) There is no evidence that the modifications just summarized involved any fusion of ossification centres, but one otic bone, the opisthotic, was lost and the intercalar was lost as an endochondral ossification. The teleost pterotic is considered to be the phylogenetic homologue of the large ossification in the postero-dorsal part of the otic region of pholidophorids and other primitive actinopterygians, and the name pterotic should be used throughout. The name epioccipital is introduced for the ossification in the dorso-lateral part of the occipital arch of primitive actinopterygians, and replaces the name epiotic in teleosts. The name epiotic is reserved for cases like *Amia*, where it is still uncertain whether the bone so named is a pterotic or an epioccipital.

(*b*) *The cranial fissure and ossification patterns in the occipital, otic and orbitotemporal regions in other actinopterygian groups*

(i) *Teleosts*

In all the major groups of living teleosts, the pattern of neurocranial ossifications in the orbitotemporal, otic and occipital regions is identical with that of Upper Jurassic leptolepids. There is a median basioccipital, supraoccipital, basisphenoid and orbitosphenoid, and paired exoccipitals, epioccipitals, pterotics (ossifying over the external semicircular canal), prootics, sphenotics, pterosphenoids and intercalars, the latter ossifying only in membrane, and parts of the otic and orbitotemporal bones are also membranous (see, for example, Dornesco & Soresco 1971*a*, 1973).

Loss of endocranial bones is widespread in the more advanced teleosts: the orbitosphenoid is lost in all non-beryciform acanthopterygians and in many other forms; the pterosphenoid is lost in most pleuronectiforms; the basisphenoid is absent in many groups; the epioccipital is lost in notacanthiforms; and the supraoccipital is lost in some anguilliforms. Such loss of bones may be due to failure in development, the area normally occupied by the bone in question remaining cartilaginous (epioccipital in notacanths, supraoccipital in eels), or the area normally occupied by the bone may no longer chondrify, due to reduction in cartilage (orbitosphenoid of acanthopterygians).

The only additions to the basic teleostean ossification pattern in the orbitotemporal, otic and occipital regions are the opisthotic present in a 14 mm *Heterotis* embryo, possibly a transient ossification (see p. 421), and the rhinosphenoid of characins (see p. 471).

The metotic fissure (= fissura otico-occipitalis) closes in cartilage early in ontogeny in living teleosts: at 14 mm in *Salmo* and *Heterotis*, 13 mm in *Hepsetus*, 11 mm in *Anguilla*, less than 10 mm in *Ictalurus*, 5 mm in *Exocoetus* (de Beer 1937; Daget & d'Aubenton 1957; Bertmar 1959). In the ossified skull the fissura otico-occipitalis is normally obliterated except for the vagus canal (but see below). The fissura oticalis ventralis persists in the ossified skull as the suture between the prootics and basioccipital, and in some teleosts the vestibular fontanelle is also recognizable in the adult skull as an area of membrane or cartilage, in the wall of the saccular chamber, between the prootic, basioccipital and exoccipital. Such a fontanelle remains in clupeomorphs (the auditory fenestra; Greenwood, Rosen, Weitzman & Myers 1966, p. 358), in *Hiodon* and notopterids among osteoglossomorphs (Greenwood 1963), in many beryciforms (Nelson 1955; Patterson 1964) and various perciforms. This fontanelle is closed by membrane in clupeomorphs, osteoglossomorphs and holocentrid beryciforms, by cartilage in trachichthyoid beryciforms and perciforms. In osteoglossomorphs and holocentrids paired cranial diverticula of the swimbladder contact the membrane covering the fontanelle. In morid gadiforms and in anabantoids there is a similar membranous fenestra, in contact with the swimbladder, in the wall of the saccular chamber, but in morids it lies between the basi- and exoccipital, behind the enlarged intercalar (Svetovidov 1948), in anabantoids entirely within the exoccipital and confluent with the glossopharyngeal foramen (Liem 1963, p. 7): neither of these apertures is the exact topographic homologue of the vestibular fontanelle.

In Clupeomorpha, it is possible that the fissura otico-occipitalis is not entirely eliminated. In all clupeomorphs there is a complex otophysic linkage, with paired diverticula of the swimbladder entering the braincase through a canal in the exoccipital, below or in front of the vagus foramen, and expanding in bony bullae within the exoccipital, prootic, and usually also the pterotic. In embryos of *Clupea harengus* this cranial diverticulum of the swimbladder enters the braincase through the basicapsular fenestra (= vestibular fontanelle) according to de Beer (1937, p. 132), since in this species the vagus and glossopharyngeal nerves pass through the same foramen, behind the swimbladder diverticulum. This state of affairs is presumably a specialization of *C. harengus*, however, for in other clupeoids the vagus and glossopharyngeal foramina are separate, and the swimbladder may enter the adult braincase below the vagus, with the exoccipital bulla lying between the vagus and glossopharyngeal foramina (Tracy 1920, fig. 5), or may enter between the two foramina (Tracy 1920, fig. 2), as it does in the most primitive clupeomorph known (Patterson 1970*a*, figs 2, 4). If the swimbladder enters the braincase between the glossopharyngeal and vagus foramina, the canal transmitting it through the bone may represent a persisting subvagal portion of the fissura otico-occipitalis, and in the embryo the diverticulum must pass through the lowermost part of the metotic fissure, not the basicapsular fenestra.

One can only speculate about the earliest stages in the evolution of the clupeomorph otophysic connexion, but certainly it must have arisen from a simpler, extracranial association between the swimbladder and the braincase, perhaps, as Greenwood (1970*a*, p. 132) suggests, of the type found in *Elops*, which develops late in ontogeny. In living clupeomorphs the swimbladder grows forwards into the braincase very early in ontogeny, and this precocious development is surely a specialization made necessary by the extreme complexity of the linkage with the ear. In the ancestral clupeomorphs, it is therefore likely that the swimbladder entered the braincase later in ontogeny, and the fact that it enters through the subvagal portion of the fissura otico-occipitalis implies that this part of the cranial fissure was still open in the ancestral clupeomorph.

A further hint that the fissura otico-occipitalis was not yet obliterated in the earliest clupeomorphs is provided by the Lower Cretaceous *Spratticeps*. This is the most primitive clupeomorph in which the braincase is known, and in this fish (Patterson 1970*a*, p. 172) there is a cavity in the exoccipital above the vagus foramen, between the bony tube containing the posterior semicircular canal and the posterior wall of the braincase: this cavity is the topographic homologue of the supravagal portion of the fissura otico-occipitalis, which is the last part of the fissure to close in pholidophorids and leptolepids. In primitive actinopterygians the supravagal portion of the fissure lies between the exoccipital and pterotic, not within the exoccipital as it does in *Spratticeps*. Unfortunately, there is insufficient material to investigate this cavity in detail in *Spratticeps*, but it does suggest that primitive clupeomorphs retained not only the part of the cranial fissure below the vagus foramen (through which the swimbladder gained access to the ear), but also the portion immediately above the vagus foramen.

The opening above the vagus foramen in the braincase of *Spratticeps* resembles a large foramen in this position in the exoccipital of mormyroids (Taverne 1968, 1969, 1973*a*). This foramen transmits the lateralis and dorsal branches of the vagus, while the remainder of the nerve emerges through a ventro-laterally directed foramen in the normal position. This upper vagus foramen of mormyroids is much larger than the true vagus foramen, and out of all proportion to the nerves it transmits: most of it is filled by a fatty plug (P. H. Greenwood, private communication). In ontogenetic terms, this large opening is a persisting portion of the fissura metotica (Daget & d'Aubenton 1960), like the fissura otico-occipitalis. There is another parallel between mormyroids and clupeomorphs: in mormyroid embryos paired diverticula of the swimbladder grow forwards into the otic capsule, entering in front of the narrow posterior basivestibular commissure and through the same opening as the glossopharyngeal nerve, but behind the latter (Daget & d'Aubenton 1960). This swimbladder diverticulum therefore enters the braincase at the same point as in clupeomorphs; the lowermost part of the metotic fissure, between the glossopharyngeal and vagus nerves. Later in mormyroid ontogeny, the duct linking the intracranial vesicle with the main body of the swimbladder atrophies, and the point of entry of the swimbladder is obliterated in the ossified braincase.

In mormyroids there is therefore some evidence to suggest that both the subvagal and supravagal portions of the fissura otico-occipitalis may have been open in intragroup ancestral forms, as in clupeomorphs. There is one other resemblance between clupeomorphs and mormyroids in the region of the fissura metotica. de Beer (1937, p. 132) noted that in *Clupea* embryos 'the auditory capsule extends backwards laterally to the occipital arch, with the result that the fissura metotica is converted into a tunnel enclosed on the medial side by the occipital arch, and laterally by the medial wall of the posterior extension of the auditory capsule'. In mormyroids, Daget & d'Aubenton (1960, p. 1015) found that 'la taille des capsules otiques est telle que l'arc occipital se trouve presque entièrement caché en vue latérale', so the mormyroid fissura metotica is also tunnel-like. It may be significant that the fissura otico-occipitalis takes

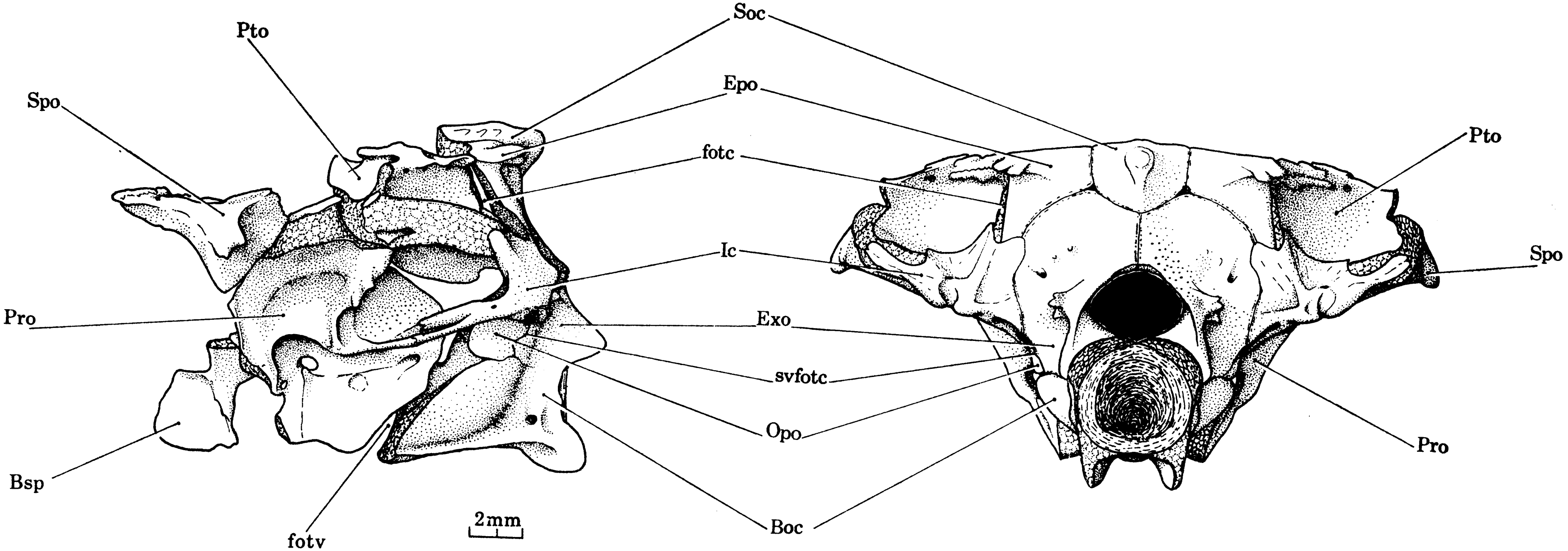


Figure 96. *Pholidophorus germanicus* Quenstedt. Restoration of postorbital portions of neurocranium in left lateral and posterior view, for comparison with the forms illustrated in figures 97–117. Based on P.3704 (for details see figures 44–46, 48–50, 74–78).

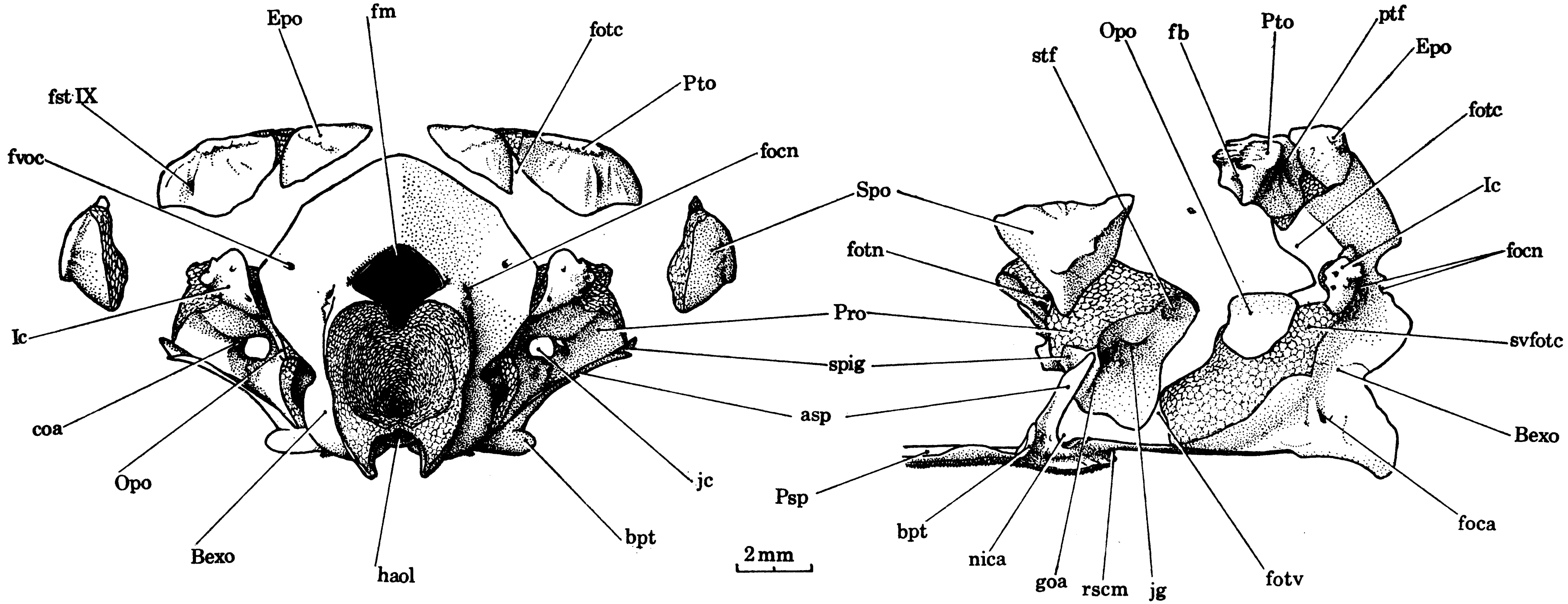


FIGURE 97. Undetermined parasemionotid from East Greenland. Restoration of postorbital portion of neurocranium and parasphenoid of an incompletely ossified individual in posterior and left lateral view. Bones drawn from MMK 491A, proportions of neurocranium from MMK 492.

this form in adult pholidophorids, where the occipital ossifications fit into the posterior opening of the otic region like a plug.

Evaluation of these resemblances between clupeomorphs and mormyroids in the fissura metotica is difficult (see also Greenwood 1973; Taverne 1973*a*). The closest relatives of the mormyroids are either the notopterids and *Hiodon* (Greenwood 1963, 1971; Greenwood *et al.* 1966) or the osteoglossoids (Nelson 1968*a*, 1969*a*, 1972*a*). In the latter group the vagus foramen is normal and there is no otophysic connexion and no vestige of the fissura otico-occipitalis. In *Hiodon* and notopterids the vagus foramen is also normal, and the otophysic connexion is usually simple and extracranial. Where intracranial swimbladder diverticula develop, in the notopterids *Papyrocranus* and *Xenomystus* (Greenwood 1963), they enter through the vestibular fontanelle (both genera) and also in *Papyrocranus* through a foramen dorso-lateral to the vagus foramen which leads not into the cranial cavity or otic capsule, but into an intramural space within the epioccipital, supraoccipital and exoccipital whose ontogenetic development is unknown. Vestiges of the fissura otico-occipitalis are therefore not widely distributed in osteoglossomorphs, but occur only in mormyroids. Such vestiges are a primitive feature, and it is not impossible that the fissure was still partially open in the earliest osteoglossomorphs, and has been lost in all but mormyroids.

In elopomorphs and euteleosteans there is no trace of the fissura otico-occipitalis in the ossified braincase. This could be taken as an advanced character indicating that these two groups form a sister-group pair (cf. Nybelin 1971, p. 47; Forey 1973*b*).

(ii) *Amioids*

The term 'amioids' is here used informally for the Amiiformes of Lehman (1966) and Gardiner (1967), with the addition of the Parasemionotidae and related families (Parasemionotiformes of Gardiner and Lehman), which seem to belong here in a phylogenetic classification. Among the familes included here, the braincase is only known in the Parasemionotidae, Caturidae and Amiidae. This discussion will begin not with *Amia*, in which the braincase is largely cartilaginous, but with the Lower Triassic parasemionotids, in which the braincase ossifies completely from a set of ossification centres which can be closely compared with those of pholidophorids, and which illuminate the condition in caturids.

1. *Parasemionotidae*. In parasemionotids, neurocranial ossification centres have been reported by Lehman (1952, p. 162), who observed sutures in the orbit of *Watsonulus* separating a ventral basisphenoid from a dorsal orbito-pterosphenoid, and Beltan (1968) who found a separate autosphenotic in *Piveteaunotus* (fig. 41) and mentioned, but did not describe or illustrate, prootic and epiotic ossifications in *Watsonulus* (p. 108). A more complete account can be given on the basis of MMK 491 (figures 30, 41, 97, 98). In this specimen the braincase is incompletely ossified and shows the individual ossifications in the orbitotemporal, otic and occipital regions. The majority of these bones were separated in life by broad zones of cartilage. In the occipital region, there is a compound basi-exoccipital, with partial sutures showing that it originated from a median basioccipital and paired exoccipital components; paired intercalars, which are almost entirely composed of cartilage-bone; and paired epioccipitals. There is no supraoccipital. In the otic region there are paired pterotics, opisthotics, prootics and sphenotics, and in the obitotemporal region there are paired pterosphenoids which consist almost entirely of perichondral bone, and a very lightly ossified basisphenoid which appears to be a median bone ossified more completely on one side than the other, and consists of a perichondral shell pene-

trated by a pair of perichondrally lined canals for the palatine nerves and internal carotid arteries. From the degree of ossification of these various bones it is evident that there must have been a gradient of ossification, strongest around the notochord and decreasing rostrally, as was postulated in pholidophorids (p. 425). These parasemionotid neurocranial ossifications can be closely compared with those of incompletely ossified pholidophorids such as *P. germanicus* (figure 96), and will not be described in detail here. The main differences from pholidophorids are the absence of a supraoccipital, reduction of the fissura otico-occipitalis (discussed below), the greater thickness of the cranial wall and the greater breadth of the braincase.

The parasemionotid basi-exoccipital (Bexo, figures 97, 98) is similar to its counterpart in pholidophorids and early leptolepids, except that the myodome does not extend into it and there is no notochordal calcification in the occipital condyle. The anterior face of the exoccipital is perichondrally lined from the vagus canal upwards.

The intercalar (Ic) ossifies lateral to the exoccipital immediately behind the vagus canal, in exactly the same position as in pholidophorids. The endochondral part of the bone is proportionally much larger than in pholidophorids, and the membrane bone outgrowths are restricted to a small, irregular antero-lateral process lapping round the outer margin of the vagus foramen.

The epioccipital (Epo) ossifies from the dorso-lateral corner of the occipital arch, as in pholidophorids, but it is confined to the thickness of the wall of the braincase, and is nowhere perichondrally lined on its anterior or internal surface. The bone met the pterotic in cartilage antero-laterally, and the dorsal part of the fissura otico-occipitalis was certainly closed.

The pterotic (Pto) ossifies antero-lateral to the epioccipital, from a centre below the junction between the parietal and dermopterotic. In this specimen the bone is still confined to the transverse partition between the fossa bridgei (fb) and the posterior face of the otic region, which includes the small post-temporal fossa (ptf; cf. p. 392), and both its anterior and posterior faces are perichondrally lined. A canal for the supratemporal branch of the glossopharyngeal nerve (fst IX) passes through the bone, bifurcating during its passage towards the fossa bridgei, but the bone has not yet grown far enough ventrally to impinge upon the semicircular canals and is much smaller than the pholidophorid pterotic.

In this lightly ossified individual the opisthotic (Opo) is already proportionally larger than its homologue in pholidophorids (cf. figures 96, 97), but is otherwise similar, a discoid bone ossifying from a centre between the vagus and glossopharyngeal nerves and forming the floor of the posterior ampullary chamber and the anterior wall of the vagus canal. In this individual the only other evidence of ossification around the semicircular canals is a delicate crescent of perichondral bone on the right side of the specimen which must have lain on the outer surface of the posterior part of the external semicircular canal. This crescent of bone is isolated but close to the upper margin of the opisthotic, and in fully ossified individuals the opisthotic must have enclosed the major part of the external semicircular canal and posterior ampullary chamber, formed the anterior wall of the vagus canal, and perhaps part of the floor of the fossa bridgei.

The prootic (Pro) ossifies from a centre in, or medial to, the lateral commissure, and has about the same extent as the prootics of pholidophorids and leptolepids. In this lightly ossified individual the bone encloses the facial canal, ends anteriorly just beyond the trigeminal canal (which is double), dorsally at the base of the canal for the otic nerve (fotn), and posteriorly at the beginning of the subtemporal fossa (stf). In fully ossified individuals the bone probably formed the floor of the anterior part of the fossa bridgei.

The sphenotic (Spo) ossifies in the postorbital process, and its medial surface is without perichondral lining. As in pholidophorids, the spiracular canal must have passed upwards between the prootic and sphenotic.

The pterosphenoid is little more than a perichondral shell over the cartilage around the optic fenestra. The basisphenoid is described above.

In this parasemionotid, the ossification pattern is therefore exactly the same as in pholidophorids, except that there is no supraoccipital, the opisthotic is relatively larger and the pterotic relatively smaller. It must be assumed that this pattern is typical of parasemionotids.

In the incompletely ossified parasemionotid just described, the perichondrally lined portion of the cranial fissure (fotc, figures 97, 98) only extends from the floor of the vagus canal up to the dorso-lateral corner of the basi-exoccipital, as in *Pholidophorus macrocephalus* and the Sinemurian *Leptolepis* sp. An isolated parasemionotid braincase from East Greenland, MMK 492 (figures 24–28), is damaged but more thoroughly ossified than the specimen just described. In MMK 492 the fissura oticalis ventralis is obliterated externally, but is still visible as a transverse suture on the internal surface of the bone, below the cranial cavity. This persisting portion of the fissura oticalis ventralis is, of course, without perichondral lining. There is a large vestibular fontanelle, its margins also without perichondral bone, and the lower part of the fissura otico-occipitalis leads back from the vestibular fontanelle to a point just below the vagus canal. Immediately below the vagus canal the fissure is closed for a short distance, and the open portion between this and the vestibular fontanelle is without perichondral lining and could have closed later in ontogeny. From the vagus canal upwards, the fissura otico-occipitalis is open and perichondrally lined to a point just above the external semicircular canal and below the forward curve of the posterior semicircular canal. Above this point the fissure is obliterated. The perichondrally lined portion of the fissure, above the vagus canal, runs almost antero-posteriorly, and the occipital ossifications fit into the posterior face of the otic ossification like a plug, just as in pholidophorids.

The short perichondrally lined portion of the fissura otico-occipitalis in these two Greenland parasemionotids, from the vagus canal up to the upper margin of the basi-exoccipital, is probably all that remains in any parasemionotid. In none of the parasemionotid braincases described previously (Stensiö 1932; Lehman 1952; Beltan 1968) has it been possible to discover how much of the cranial fissure is perichondrally lined. The fissura oticalis ventralis is usually closed, but is still open and confluent with the vestibular fontanelle in individuals described as *Thomasinotus* and *Lehmanotus* by Beltan (1968). The vestibular fontanelle is usually open, but is closed in *Ospia* and some individuals of *Watsonulus*. The subvagal portion of the fissura otico-occipitalis is also usually open, but it is closed in *Ospia*, some *Watsonulus* and *Parasemionotus*, and is partially or unilaterally closed in *Devillersia* and *Piveteaunotus* (Beltan 1968). These variations indicate that the subvagal portion of the fissure must have been without perichondral lining, as in the Greenland specimens, and could close in late ontogeny. Above the vagus canal, the fissura otico-occipitalis seems normally to extend up to the same point as in the Greenland specimens, the upper margin of the basi-exoccipital. But in some individuals of *Watsonulus* and *Parasemionotus*, and in *Piveteaunotus*, even this portion is obliterated, while in *Devillersia* the supravagal portion of the fissure, like the subvagal, was reduced to a series of small nodules of cartilage (Beltan 1968, fig. 38), so that in all these forms the entire fissure must have been without perichondral lining and capable of closure in late ontogeny. In *Broughia*, Stensiö (1932, p. 270) says of the fissura otico-occipitalis 'as in *Perleidus* it was probably present also on the lateral part of the cranial roof', but this part of the braincase is not visible in his specimen, and in none of the Greenland parasemionotids in the Mineralogisk Museum, Copenhagen, have I seen the fissure extending on to the roof of the braincase.

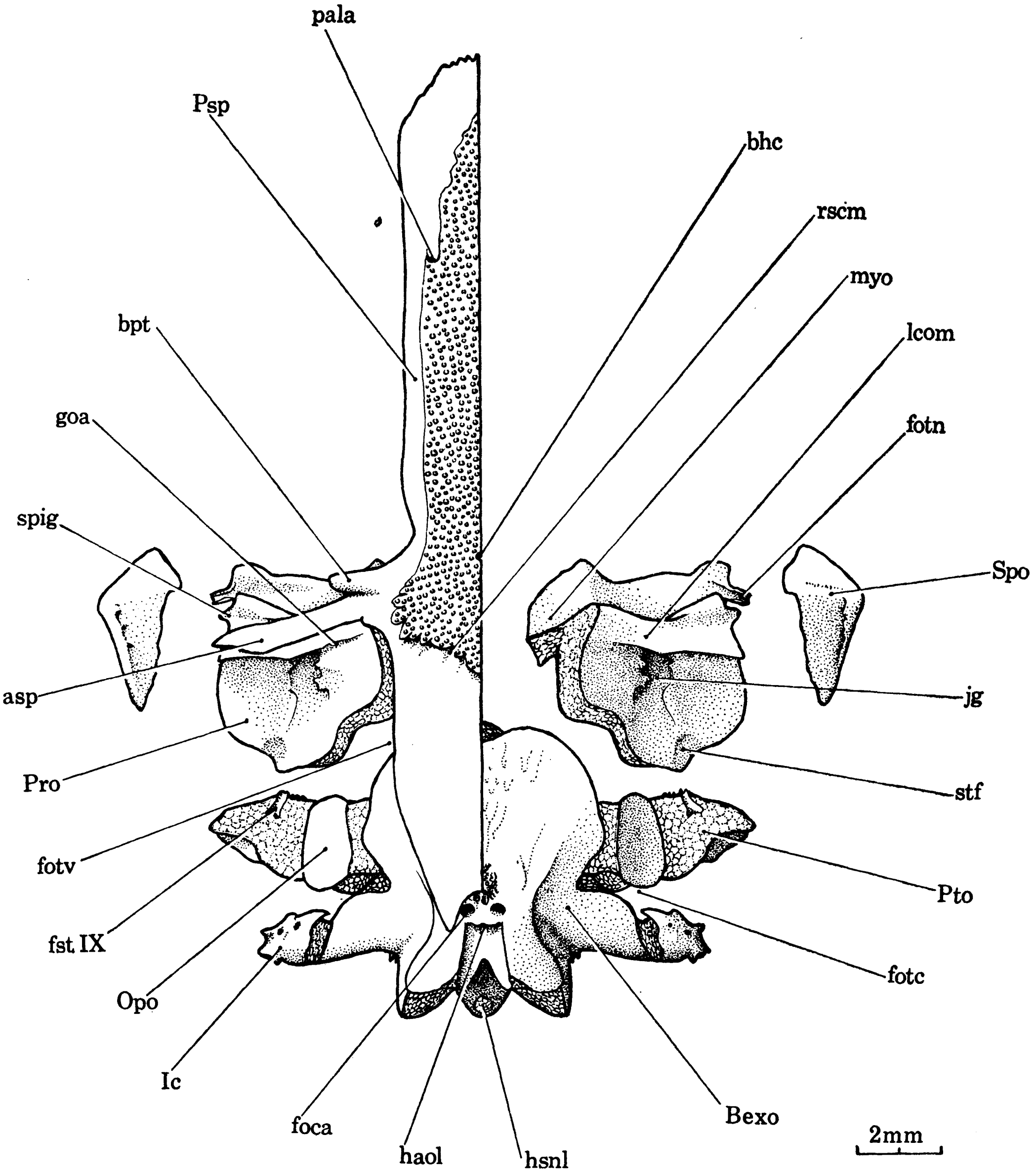


FIGURE 98. Undetermined parasemionotid from East Greenland. Restoration of postorbital portion of neurocranium and right half of parasphenoid of an incompletely ossified individual in ventral view. Bones drawn from MMK 491A, proportions of neurocranium from MMK 492.

In summary, the cranial fissure of parasemionotids differs from that of primitive pholidophorids in having the epioccipital and subvagal portions always closed in cartilage, and in some parasemionotids even the supravagal portion was also closed. Since the cranial fissure was almost or completely closed in parasemionotids, this group cannot include the ancestors of pholidophorids as Gardiner (1960, p. 347) proposed. The parasemionotid braincase is shown diagrammatically in figure 105*a*.

2. *Caturidae*. Among caturids, the braincase is known in several species of *Caturus* ranging from the Sinemurian to the Kimmeridgian (Aldinger 1932; Rayner 1948; Gardiner 1960; P.904*a*), in *Heterolepidotus* (Sinemurian) (Gardiner 1960; figures 102–104), *Osteorachis* (Sinemurian) (Gardiner 1960), '*Aspidorhynchus*' (Bathonian) (Rayner 1948; figures 99–101) and *Macrepistius* (Albian) (Schaeffer 1971). Among these, the neurocranium is completely ossified and more or less sutureless in *Caturus* (except *C. furcatus*, see below), *Heterolepidotus* and *Osteorachis*. But in '*Aspidorhynchus*' and *Macrepistius* all the sutures are persistent and the ossification pattern clear: these two forms are therefore of the greatest importance. In all the caturid braincases without sutures the cranial fissure is completely obliterated and there is no remnant above or below the vagus foramen. In the two genera with persistent sutures, parts of the fissure, though closed in cartilage, may remain as sutures.

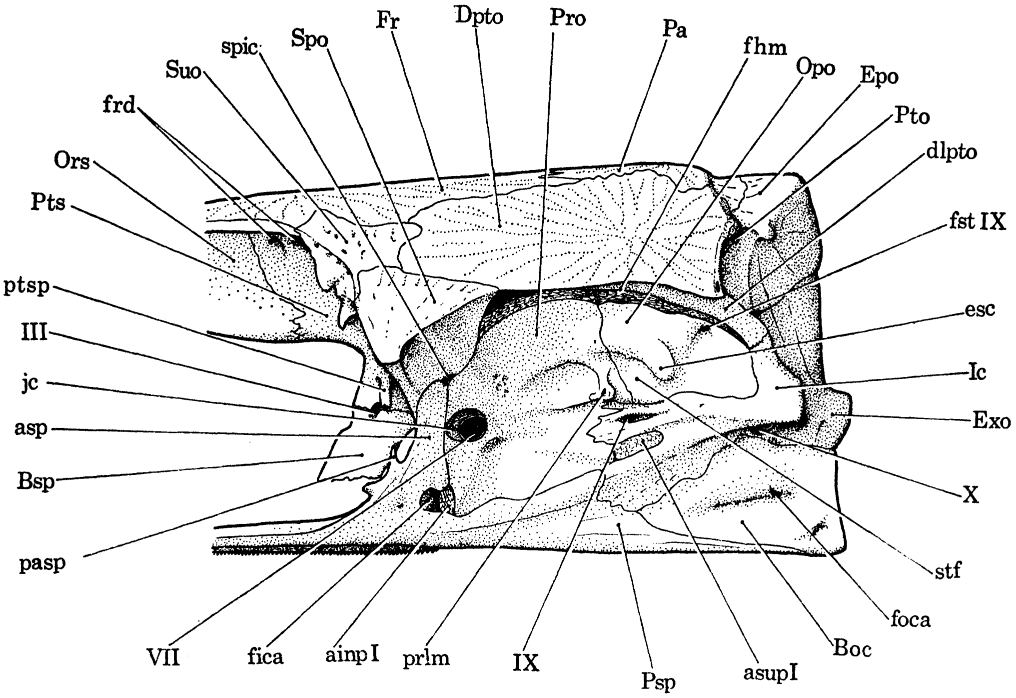


FIGURE 99. '*Aspidorhynchus*' sp. (an undetermined caturid described under this name by Rayner 1948). Restoration of posterior part of braincase in left lateral view. Based on P.9843 and P.9844 (magn. × 2 approx.).

In '*Aspidorhynchus*' (figures 99–101) and *Macrepistius* the ossification pattern is very similar. There is a median basioccipital, basisphenoid and orbitosphenoid (the latter possibly ossifying from paired centres), and paired exoccipitals, intercalars, epioccipitals (the epiotics of Rayner, paired supraoccipitals of Schaeffer), pterotics (undescribed by Rayner, epiotics of Schaeffer), opisthotics (autopterotics of Schaeffer), prootics, sphenotics and pterosphenoids. Rayner (1948, p. 315, fig. 19) described a supraoccipital in one specimen of '*Aspidorhynchus*', P.9843, but this bone (Sot, figure 100) does not appear on the posterior face of the braincase, the normal position of the ossification centre of a supraoccipital, and only intrudes between the anterior extensions of the epioccipitals. The full extent of this bone is hidden by the dermal bones, but it is probably an ossification in the taenia tecti medialis above the otic capsules, and should be called a supraotic. A similar bone occurs in some *Lepidotes* (p. 450).

In '*Aspidorhynchus*' and *Macrepistius* the basioccipital (Boc) has essentially the same relations as in parasemionotids, pholidophorids and teleosts, meeting the prootics anteriorly in the fissura oticalis ventralis. The anterior part of the exoccipital (Exo) is concealed by membranous outgrowths of the intercalar in *Macrepistius*, but in '*Aspidorhynchus*' it is partially visible because of damage to and dislocation of the intercalar: the exoccipital does not extend forwards beyond the vagus foramen, which lies in a notch in its anterior margin, and the bone probably formed no part of the labyrinth cavity.

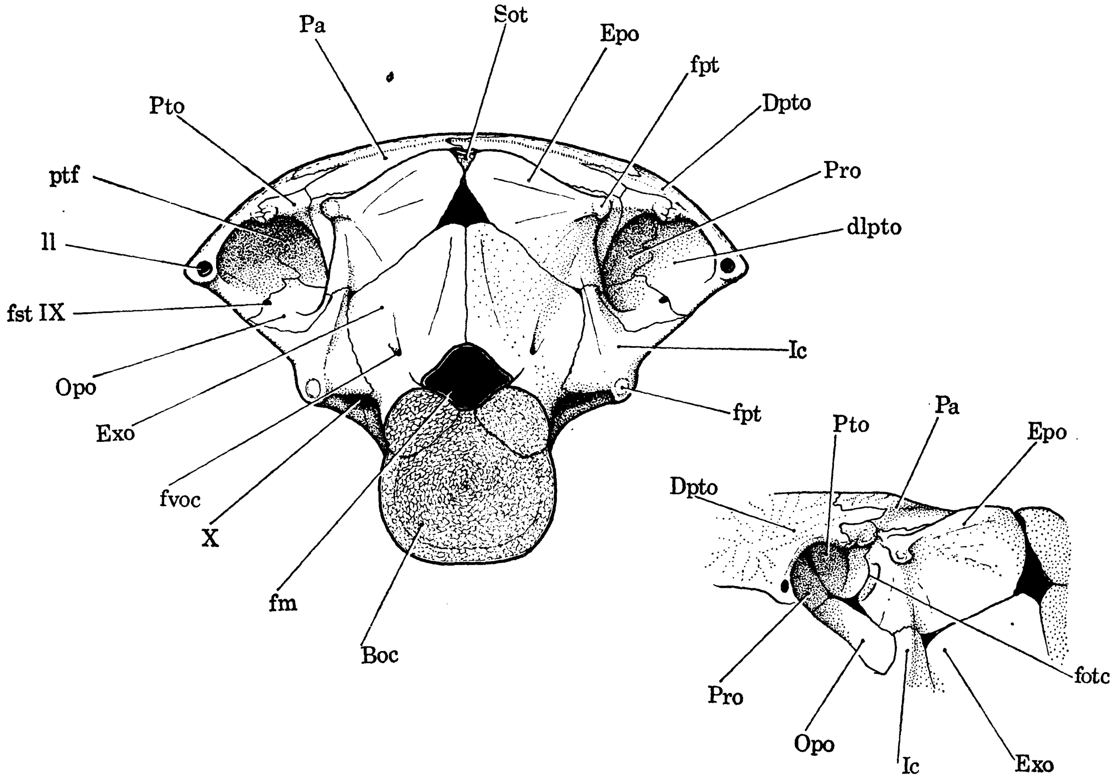


FIGURE 100. '*Aspidorhynchus*' sp. (an undetermined caturid described under this name by Rayner 1948). Restoration of braincase in posterior view. Inset at lower right is an oblique postero-lateral view of the region of the left post-temporal fossa, to show the pterotic and cranial fissure. Based on P.9843 and P.9844 (magn. × 2 approx.).

The intercalar (Ic) has an endochondral component in '*Aspidorhynchus*', and since this is also true of *Heterolepidotus* (figure 104) and *Caturus chirotes* such a component probably exists in *Macrepistius* (cf. Schaeffer 1971, p. 23). The extensive membranous outgrowths of the intercalar are antero-ventrally directed and cover the opisthotic/exoccipital junction and the region of the vestibular fontanelle.

The epioccipitals (Epo) extend forwards some distance between the pterotics on the skull roof, but their precise extent cannot be seen because of the dermal roofing bones. In *Caturus chirotes* (GSM 97417) the anterior parts of the epioccipitals can be seen. They play no part in the support of the semicircular canals or lateral cranial canal, since the pterotics meet in the mid-line above the fork of the anterior and posterior semicircular canals. On the lateral surface of the braincase in '*Aspidorhynchus*' and *Macrepistius* the epioccipital meets the pterotic in a vertical suture medial to the post-temporal fossa. This suture (fotc, figure 100) is in the position of the dorso-lateral part of the fissura otico-occipitalis, and represents the latter closed in cartilage but persisting as a suture, as in *Pholidophorus macrocephalus*.

The pterotic of *Macrepistius* is largely hidden by the overlying dermopterotic, but in '*Aspidorhynchus*' the full extent of the bone can be seen (Pto, figures 99, 100). Its centre of radiation (ossification) lies, as in pholidophorids and parasemionotids, on the postero-lateral shoulder of the braincase, beneath the dermopterotic/parietal suture and a short distance antero-lateral to the centre of the epioccipital. The pterotic forms the medial wall of the post-temporal fossa but does not extend into its floor, nor does it extend anteriorly beyond the level of the anterior end of the intercalar. Internally, the pterotic must enclose the upper part of the posterior semicircular canal and the lateral cranial canal (assuming that the latter was present, as it is in *Caturus chirotes*, where the pterotic has these relations).

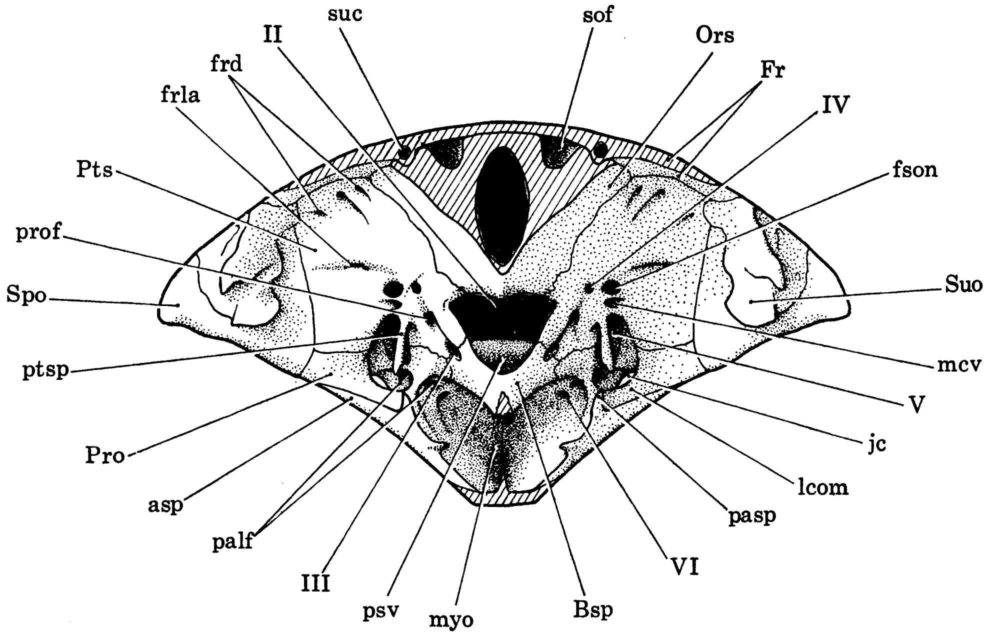


Figure 101. '*Aspidorhynchus*' sp. (an undetermined caturid described under this name by Rayner 1948). Restoration of braincase in anterior view, as if cut through the orbit. Sectioned surfaces cross-hatched. Based on P.9843 and P.9844 (magn. × 2 approx.).

In '*Aspidorhynchus*' the opisthotic is fused to the prootic in P.9844 (Rayner 1948, fig. 20), but in P.9843 it is distinct on both sides of the braincase (Opo, figure 99). The centre of radiation of the opisthotic lies above the glossopharyngeal foramen, close behind the 'knob' (prlm, figure 99) on this surface (in *Macrepistius* this 'knob' lies on the prootic: Schaeffer 1971, fig. 5). The opisthotic extends back beneath the membranous outgrowth of the intercalar and meets the exoccipital above and probably also below the vagus foramen: these sutures are in the position of the sub- and supra-vagal portions of the fissura otico-occipitalis, and like the pterotic/epioccipital suture dorsally, they represent the fissure closed in cartilage but persisting as a suture. Dorsally, the opisthotic forms the floor of the posterior part of the post-temporal fossa, underlying the descending lamina of the dermopterotic laterally, and meeting the pterotic medially (figure 100). Internally, the opisthotic must enclose the lower part of the posterior semicircular canal and its ampulla, and the greater part of the external semicircular canal.

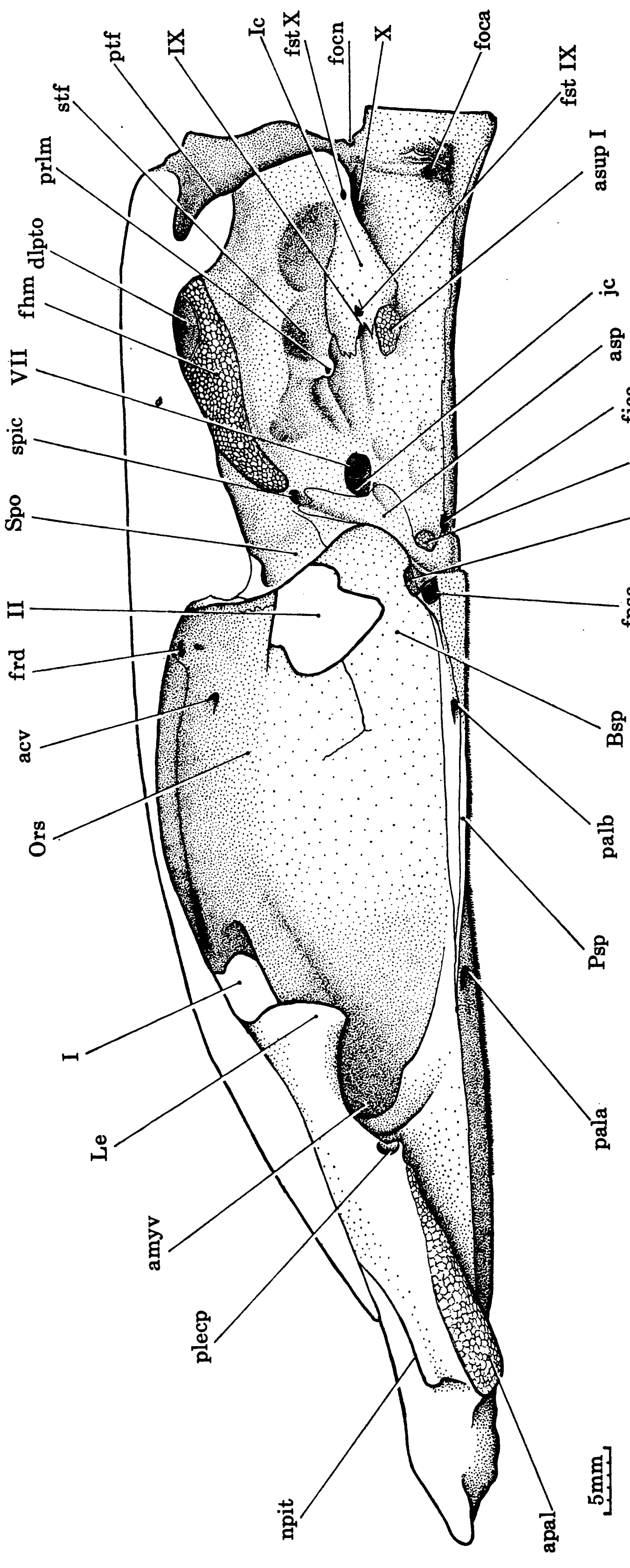


FIGURE 102. *Heterolepidotus* sp. Restoration of braincase in left lateral view (details of roofing bones not shown), based mainly on P.13260.

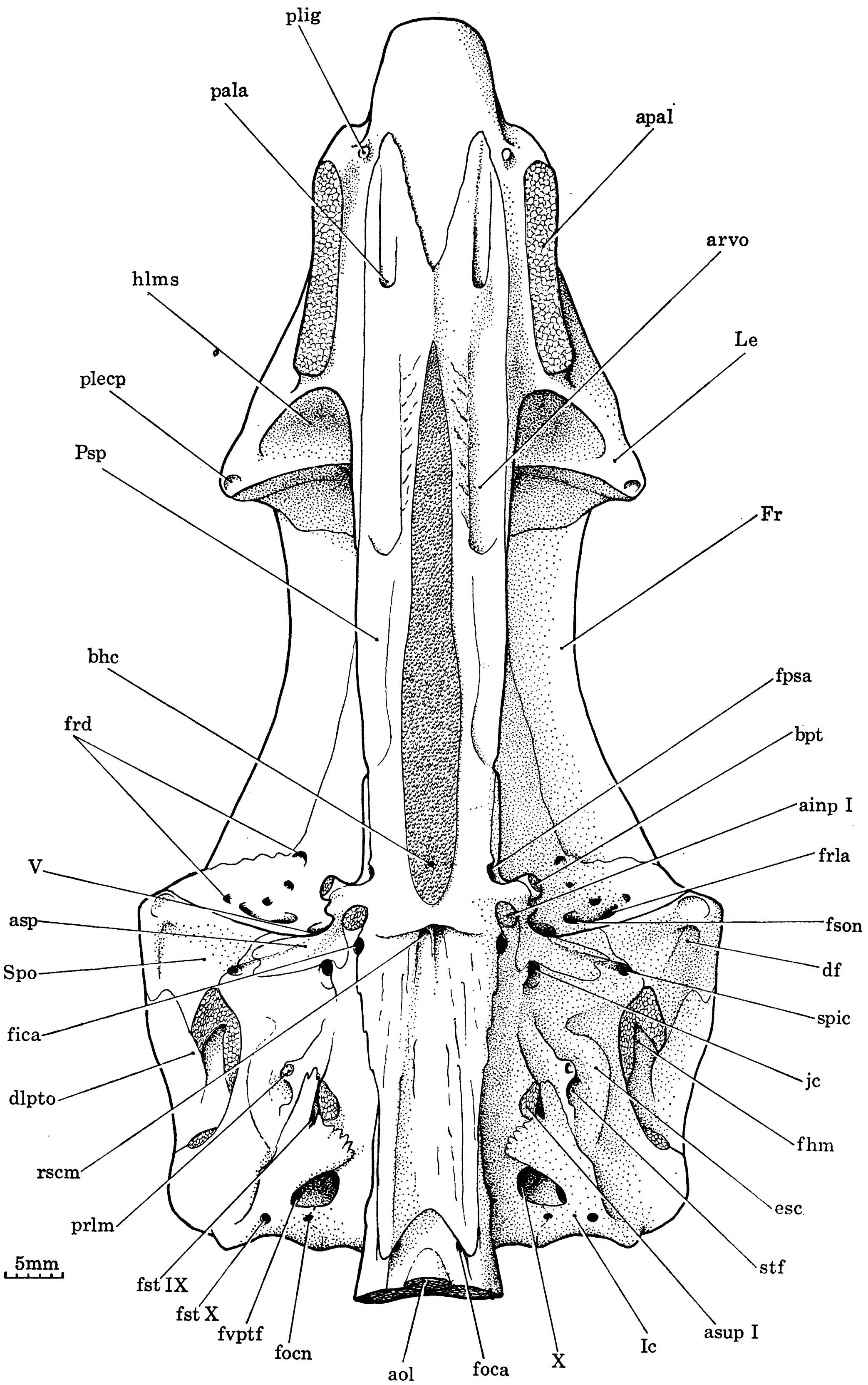


FIGURE 103. *Heterolepidotus* sp. Restoration of braincase in ventral view, based mainly on P.13260.

In *Macrepistius* the opisthotic ossification centre lies dorsal to that of '*Aspidorhynchus*', and the bone extends forwards antero-dorsally above the prootic. Posteriorly, the opisthotic is hidden by the intercalar.

A corollary of the differences in the opisthotic between '*Aspidorhynchus*' and *Macrepistius* is that the prootic also differs in extent in the two. In '*Aspidorhynchus*' the prootic forms the floor of a major part of the post-temporal fossa (Pro, figure 100), but in *Macrepistius*, although the floor of the fossa is obscured, it is likely that the opisthotic formed most of its floor. In '*Aspidorhynchus*' the glossopharyngeal foramen (IX, figure 99) lies in a deep notch in the posterior margin of the prootic, and this is probably its position in *Macrepistius* (Schaeffer 1971, fig. 5).

The sphenotic (Spo) is confined to the thickness of the postorbital process in '*Aspidorhynchus*' and does not surround any part of the anterior semicircular canal. In *Macrepistius* it is probably similar. The pterosphenoid (Pts, figures 99, 101) is large in both genera, and in *Macrepistius* the orbitosphenoid is much larger than in '*Aspidorhynchus*' and forms an almost complete interorbital septum.

In other caturid braincases (with the exception of *Caturus furcatus*, see below), those sutures which can be seen or inferred concur with an ossification pattern like that just described in '*Aspidorhynchus*' and *Macrepistius*. In *Caturus groenlandicus* Aldinger (1932) observed no sutures or radiation centres. In the Toarcian *Caturus* described by Rayner only the sphenotic and prootic are recognizable (1948, fig. 4). In *Caturus porteri* Rayner (1948) recognized epioccipitals, a basiexoccipital, intercalars and pterosphenoids. In *Caturus chirotes*, GSM 97417 shows a partially separate sphenotic, the junction between the fused epioccipitals and the pterotics in the roof of the braincase, and the line of fusion between the intercalar and exoccipital, which shows that the intercalar had an endochondral component. In *Osteorachis*, P.3648*a* shows the sphenotics, pterosphenoids and orbitosphenoid. In *Heterolepidotus*, P.13260 (figures 102–104) shows the lines of fusion between the intercalar and exoccipital (the intercalar again with an endochondral component), between the sphenotic and prootic, and between the pterosphenoid, orbitosphenoid and basisphenoid.

P.904*a*, *Caturus furcatus* (figure 31), shows a crushed, very lightly ossified braincase in which most of the ossifications were separated by broad tracts of cartilage. All the bones present in '*Aspidorhynchus*' and *Macrepistius* can be seen except for the opisthotic. It is impossible to tell whether the intercalar has an endochondral component or not, but the antero-ventral membranous outgrowth of the intercalar is very extensive, ending well in front of the glossopharyngeal foramen. This part of the intercalar covers much of the area normally occupied by the opisthotic, but there is no sign of such a bone projecting dorsally beyond the intercalar, and it appears that the opisthotic has been lost. The exoccipital does not extend anteriorly beyond the vagus foramen, as in other caturids.

In summary (see also figure 105*b*), the braincase of caturids shows the same ossification pattern as in parasemionotids, resembling the latter and differing from pholidophorids in having no supraoccipital, and in having a relatively larger opisthotic and smaller pterotic. In some advanced, lightly ossified caturids (*C. furcatus*) the opisthotic may be lost. Caturids differ from the majority of parasemionotids in having the cranial fissure closed in cartilage throughout its length, but this condition seems already to have been achieved in some parasemionotids. There is nothing in the caturid braincase to oppose the opinion of Brough (1939), Lehman (1952) and Gardiner (1960) that the parasemionotids were ancestral to the caturids.

In parasemionotids and caturids, closure of the cranial fissure has had little effect on the ossification pattern in the otic and occipital regions. In those forms where sutures persist in the fully ossified braincase, the subvagal and supravagal portions of the fissura otico-occipitalis remain as sutures between the prootic and opisthotic and the occipital bones, and the dorsolateral part of the fissure remains as the suture between the pterotic and epioccipital. Dorsally, the epioccipital appears to have grown forwards to some extent, but it does not contact the posterior semicircular canal and does not appear to have caused any modification in the growth pattern of the pterotic. The exoccipital does not grow forwards beyond the vagus canal, and so does not disturb the growth pattern of the intercalar, which remains as a primarily endochondral bone. In pholidophorids and leptolepids, closure of the cranial fissure has been shown to have had profound effects on the ossification pattern in the otic and occipital regions, resulting in loss of the opisthotic and the endochondral portion of the intercalar, and forward extension of the exoccipital, supraoccipital and epioccipital, the latter capturing the posterior semicircular canal from the pterotic and causing a drastic shift in the position of the pterotic ossification centre. The parasemionotid–caturid and pholidophorid–leptolepid lineages can be readily characterized by the different effects of closure of the cranial fissure.

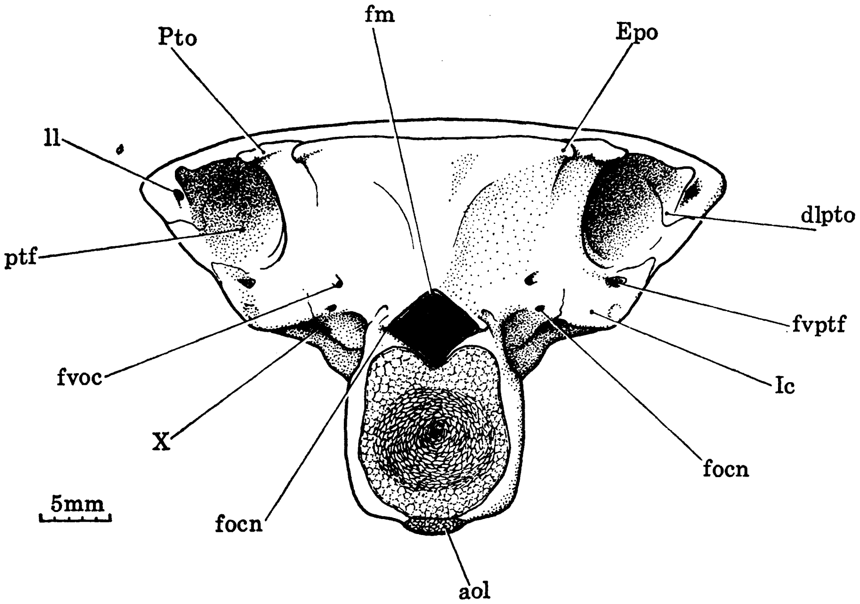


FIGURE 104. *Heterolepidotus* sp. Restoration of braincase in posterior view, based mainly on P.13260. The approximate ossification centres of the pterotic and epioccipital are indicated by the guide-lines, although sutures are not visible around these bones.

3. *Amiidae.* In the Amiidae, the braincase is known in *Amia* and two Lower Cretaceous genera, *Sinamia* (Stensiö 1935) and *Enneles* (Santos 1960). In *Amia* the metotic fissure of the embryo begins to close at 19.5 mm, and by 31.5 mm the cartilaginous roof of the otic and occipital regions is complete and uninterrupted. In the adult braincase of *Amia*, no trace of the cranial fissure remains, except that the broad tract of cartilage between the basioccipital and the prootics could be interpreted as the fissura oticalis ventralis.

In adult *Amia* the ossifications in the orbital and postorbital parts of the braincase comprise a median basioccipital and paired exoccipitals, intercalars, 'epiotics', prootics, sphenotics, pterosphenoids, basisphenoids and orbitosphenoids. In *Sinamia* the same bones are present except that no basisphenoid has been seen and the orbitosphenoid is said to be median (Stensiö

1935, p. 7), while in *Enneles* the same bones are present but the basisphenoid appears to be median. In *Amia* most of the neurocranial bones are separated by extensive tracts of cartilage, but in the fossil amiids the braincase is a little more heavily ossified and there are more contacts between the bones.

The basioccipital of amiids is similar to those of other holosteans and of teleosts. The exoccipital of *Amia* does not extend in front of the vagus foramen, nor does it surround any part of the posterior semicircular canal, so that it does not extend beyond the position of the cranial fissure. But in *Sinamia* (Stensiö 1935, pl. 14, fig. 1) and *Enneles* (Santos 1960, pl. 1, fig. 1) the vagus foramen is entirely enclosed within the exoccipital. In these fossil amiids the exoccipital has therefore extended forwards beyond the position of the cranial fissure, as it does in teleosts. In teleost phylogeny the consequences of forward extension of the exoccipital were loss of the opisthotic and the endochondral portion of the intercalar, and these changes seem also to have occurred in amiids.

The intercalar of amiids is entirely membranous. It overlaps the exoccipital and 'epiotic' postero-medially and the prootic anteriorly, and meets the descending lamina of the dermopterotic dorso-laterally.

The 'epiotic' of amiids never meets its fellow in the mid-line, but in large individuals of *Amia* and in *Sinamia* and *Enneles* it meets the exoccipital postero-ventrally. Even in large individuals, the internal surface of the 'epiotic' of *Amia* is without perichondral bone and does not contribute to the cranial cavity or the tubes for the semicircular canals: this was presumably also true of the fossil amiids. No amiid has both an epioccipital and a pterotic, as do caturids, parasemionotids and pholidophorids, and the amiid 'epiotic' could be interpreted as representing either (but not both: cf. p. 421) of these bones. In *Amia* the bone does not ossify until about the 50 mm stage (de Beer 1937, p. 107; personal observations), after all the other otic and occipital bones have appeared, and long after the coalescence of the occipital arch and otic capsule, so that it cannot be assigned to the otic or occipital region by ontogenetic criteria. The centre of ossification of the 'epiotic' lies posterior to the parietal, and slightly medial to the parietal/dermopterotic suture, in the normal position of an epioccipital, and the facts that the bone meets the exoccipital on the posterior face of the braincase in large *Amia* and in fossil amiids, and that it does not contribute to the support of the posterior semicircular canal, are also suggestive of an epioccipital. But the bone forms a considerable part of the medial wall of the post-temporal fossa and has a dorso-lateral lamina underlying the dermopterotic in the roo of this fossa: these features are suggestive of a pterotic. Although it seems probable that the amiid 'epiotic' is an epioccipital which has extended forwards following loss of the pterotic, it is not impossible that it is a pterotic which has extended postero-medially following loss of the epioccipital, and I do not believe that any conclusive decision on the homology of the bone is possible on present evidence. I therefore propose to continue to refer to the bone as an epiotic until its true nature becomes evident.

The prootic, sphenotic, pterosphenoid and orbitosphenoid of amiids do not differ significantly from those of caturids and parasemionotids. The basisphenoid of *Amia* is a small paired bone ossifying late between the internal carotid and efferent pseudobranchial arteries, in the transverse 'bolster' in front of the floor of the myodome. Although these small paired basisphenoids are not topographically homologous with any part of the basisphenoid of teleosts, which ossifies in the vertical myodomic septum and the floor of the cranial cavity, these bones are certainly phylogenetic homologues (Jardine 1970). In the fossil amiid *Enneles* the basisphenoid is large (Santos 1960, fig. 2) and apparently median, and through this intermediate the basisphenoid of *Amia* can be homologized with those of caturids, parasemionotids, pholidophorids and teleosts.

In summary, the amiid braincase differs from those of caturids and parasemionotids in having the fissura otico-occipitalis obliterated and in lacking opisthotics, endochondral intercalars and (probably) pterotics. These differences in the ossification pattern can be interpreted, by analogy with the pholidophorid-teleost lineage, as a consequence of changes following closure of the fissure in a braincase of caturid or parasemionotid type. The structure of the braincase of parasemionotids, caturids and amiids is summarized diagrammatically in figure 105.

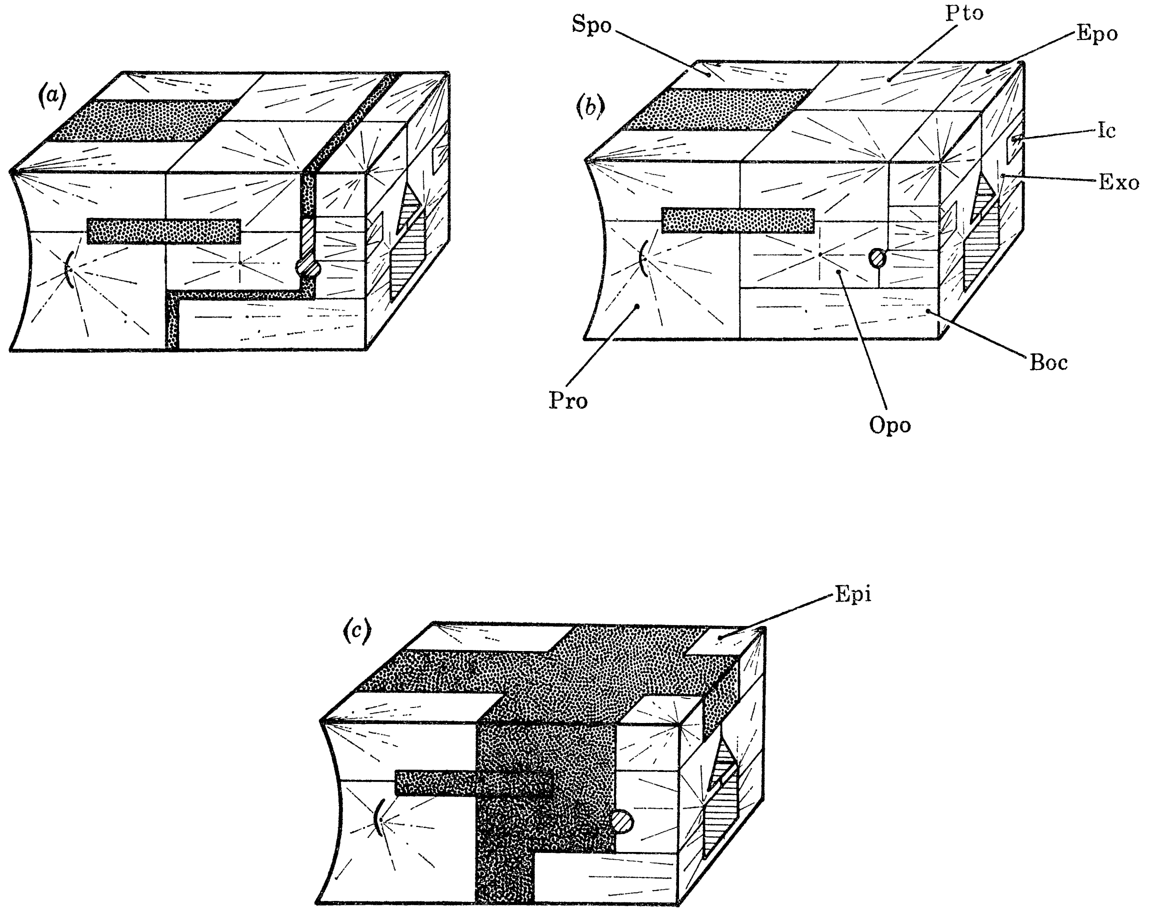


Figure 105. Block diagrams summarizing the cranial fissure and ossification pattern of the postorbital part of the neurocranium in amioids. For conventions adopted see legend of figure 95. (*a*) A parasemionotid, cranial fissure still partially open but mostly cartilage-filled, and obliterated in full-grown individuals, ossification pattern as in primitive pholidophorids but no supraoccipital and opisthotic larger. (*b*) A caturid, cranial fissure obliterated in primitive forms (e.g. *Heterolepidotus*), remaining as a suture in more advanced ones (e.g. *Macrepistius*), ossification pattern as in parasemionotids. (*c*) *Amia*, opisthotic and endochondral intercalar lost, epiotic is probably an epioccipital, pterotic having been lost.

(iii) *Pachycormidae*

Pachycormid braincases have been described in the Upper Cretaceous *Protosphyraena* (Loomis 1900), a Kimmeridgian *Hypsocormus* (Stensiö 1935; Holmgren & Stensiö 1936; Rayner 1948) and the Toarcian *Pachycormus* (Rayner 1948; Lehman 1949; Wenz 1968; Schaeffer 1971).

Protosphyraena and *Hypsocormus* are each known only by a single crushed and incomplete specimen. In *Pachycormus*, three specimens from Curcy, Calvados, have been described, 32443 (Rayner 1948), P.24410 (Wenz 1968, p. 110) and a third by Lehman (1949), but all of these are more or less crushed and damaged. 32434 (Wenz 1968, pl. 25, fig. A; figures 17, 29) has since been mechanically prepared and shows a complete and uncrushed braincase: figures 106 and 107 are based mainly on this specimen.

In *Pachycormus* sufficient sutures persist in the various specimens to show the complete ossification pattern, and some sutures probably persisted throughout life, since no sutureless individuals are known. The orbitotemporal, otic and occipital regions contain a basi-exoccipital, paired intercalars (postopisthotics of Lehman), pterotics (epiotics of Rayner), opisthotics, prootics, sphenotics and pterosphenoids, and a median orbitosphenoid and basisphenoid.

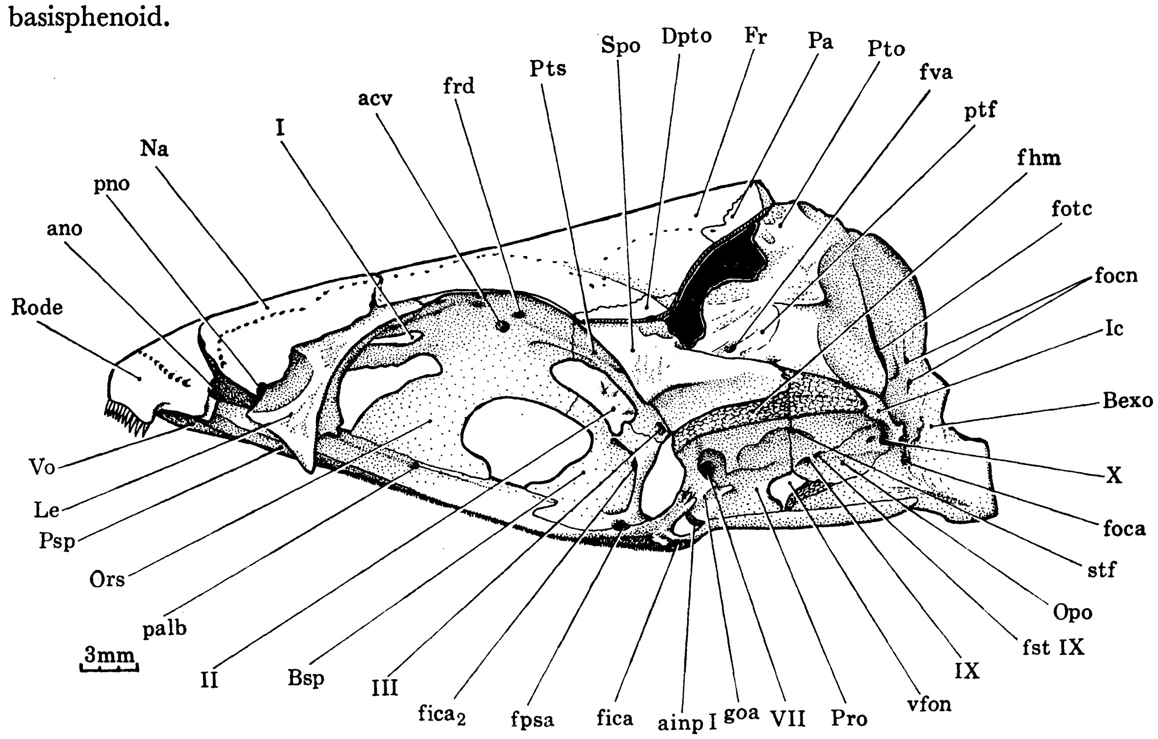


FIGURE 106. *Pachycormus curtus* Agassiz. Neurocranium and associated dermal bones in left lateral view, from 32434. Drawn as if the postero-lateral part of the skull roof were cut away (cut surfaces cross-hatched), exposing the post-temporal fossa and anterior dorsal fontanelle (black).

The basi-exoccipital (Bexo) shows no sign of separate exoccipital (paired) and basioccipital (median) ossification centres, and its shape suggests that it may not ossify from three centres, as does the basi-exoccipital of pholidophorids and other holosteans, but from a pair of centres, like the basi-exoccipital of *Polypterus* (Pehrson 1947), or from four centres. Both Rayner (1948, p. 312) and Lehman (1949, p. 29) believed that they could recognize a separate exoccipital, but Rayner does not illustrate this bone, and the suture which Lehman drew (fig. 13) between his exoccipital and basioccipital does not exist in any of my specimens, while his suture between the intercalar and exoccipital lies well behind the actual position of this suture (figure 107). Dorsally, the basi-exoccipital ended in cartilage, and there is no trace of epioccipitals or a supraoccipital. This, like the ossification pattern of the basi-exoccipital, recalls *Polypterus* (Allis 1922, fig. 14), in which the upper part of the occipital region is similarly unossified.

The intercalar (Ic) is almost entirely a cartilage bone, and its endochondral portion is larger than in other holosteans. It meets the basi-exoccipital postero-medially in a suture which closes in large individuals. The intercalar forms the posterior and lateral margins of the vagus foramen (X) and has a facet for the lower limb of the post-temporal (fpt), as usual, but it also forms the posterior part of the prominent parotic crest, meeting the pterotic and opisthotic respectively on the upper and lower sides of the crest (figures 106, 107). The transverse suture between the intercalar and the pterotic and opisthotic represents the supravagal portion of the fissura otico-occipitalis: this closes laterally, in the shallowest portion of the crest, in 32434, but appears to be perichondrally lined medially.

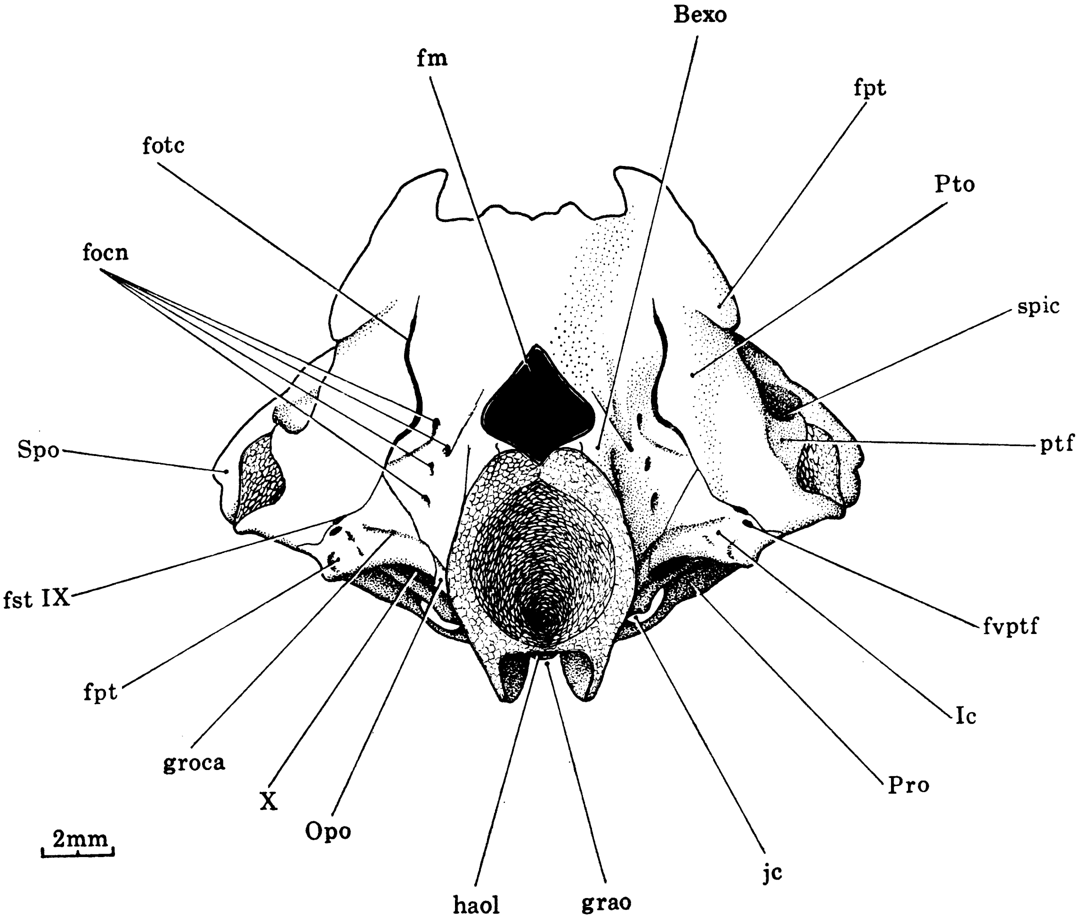


FIGURE 107. *Pachycormus curtus* Agassiz. Restoration of neurocranium in posterior view, based on 32434.

The pterotic (Pto) is a very large bone. It is crushed and displaced in the specimen illustrated by Rayner, and was not exposed in Lehman's specimen. The pterotic forms the floor and medial wall of the greater part of the large post-temporal fossa (ptf, here confluent with the fossa bridgei), meeting the opisthotic ventrally in the parotic crest and the sphenotic antero-laterally. The upper opening of the spiracular canal (spic, figure 107) lies at the junction of the pterotic and sphenotic in the floor of the post-temporal fossa. Posteriorly, the pterotic meets the basi-exoccipital at the fissura otico-occipitalis: in 32443 this part of the fissure is open throughout, but in the large P.24410 it is closed for a short distance ventrally, and in 32434 the most dorsal portion is also closed (fotc, figure 107). Where the wall of this part of the fissure is visible, in 32443, it is without perichondral lining. The pterotic extends dorsal to the basi-exoccipital, and contacts the parietal and dermopterotic. Internally, the pterotic must enclose the greater part of the posterior semicircular canal, the posterior part of the anterior semicircular canal and the lateral cranial canal (if present). The external semicircular canal lay at the horizontal junction between the pterotic and the opisthotic and prootic.

The opisthotic (Opo) extends from the vagus foramen to just in front of the glossopharyngeal foramen, meeting the prootic antero-dorsally in a suture which closes in large individuals, and being separated from the prootic ventrally by the vestibular fontanelle, which is always open (vfon, figure 106). The opisthotic meets the pterotic dorsally in the parotic crest, and is separated from the intercalar and basi-exoccipital behind by the sub- and supravagal portions of the fissura otico-occipitalis; as noted above, the upper part of the junction with the intercalar is closed in 32434, and in P.24410 and 32434 the junction with the basi-exoccipital is also closed. Internally, the opisthotic surrounds the lower part of the posterior ampullary chamber and the underside of the posterior part of the external semicircular canal.

The prootic (Pro) is larger than the opisthotic, and resembles the prootic of parasemionotids and pholidophorids. It meets the basi-exoccipital postero-ventrally in the fissura oticalis ventralis, which is always open. The sphenotic (Spo) is proportionally somewhat larger than in parasemionotids and pholidophorids, but as in those groups it plays no part in the lining of the labyrinth or cranial cavities. The pterosphenoid (Pts), orbitosphenoid (Ors) and basisphenoid (Bsp) will not be commented on, except to note that the orbitosphenoid is misorientated in Lehman's restoration (cf. figure 106).

Hypsocormus and *Protosphyraena* are much less completely known than *Pachycormus*, but as Lehman (1949, p. 30) says, *Hypsocormus* seem to be very like *Pachycormus*, while *Protosphyraena* may differ in having the vagus foramen well within the opisthotic, suggesting either that this bone has undergone a considerable increase in size, or (more probably) that there is fusion between the opisthotic, intercalar and basi-exoccipital.

The pachycormid cranial fissure is only completely known in *Pachycormus*. In young individuals the fissure is open throughout, and parts of it persist as a suture in aged individuals. The fissura oticalis ventralis (between the prootic and basi-exoccipital) and vestibular fontanelle (between the prootic, opisthotic and basi-exoccipital) are open but not perichondrally lined in all specimens. The vestibular fontanelle is comma-shaped (figure 106), and its circular anterior part forms the articular surface for the first suprapharyngobranchial (p. 398). The subvagal portion of the fissura otico-occipitalis (between the opisthotic and basi-exoccipital) closes completely in large individuals. The supravagal portion (between the intercalar and the pterotic and opisthotic) contains the only perichondrally lined part of the fissura otico-occipitalis, in the medial part of the parotic crest. In the lateral part of the parotic crest, the supravagal portion of the fissure closes in some individuals. The dorso-lateral part of the fissura otico-occipitalis, between the pterotic and the basi-exoccipital, is not perichondrally lined and its uppermost and lowermost parts close in some individuals, but the middle part probably persists as a suture. In *Hypsocormus*, the single specimen known only shows the cranial fissure up to the intercalar (Rayner 1948, fig. 16): this part is open throughout, as in young *Pachycormus*.

In summary, the pachycormid braincase is in many ways comparable with those of parasemionotids and caturids on the one hand, and with those of pholidophorids on the other. It resembles pholidophorids in having a very large pterotic, but the size of this bone is partly a consequence of the elevation of the dorsal part of the otic region below the median crest of the skull roof. The opisthotic is larger than in pholidophorids and resembles that bone in caturids, but does not enter the floor of the post-temporal fossa. The large endochondral intercalar, with very slight development of membranous outgrowths, resembles the parasemionotid intercalar. The most important differences from pholidophorids, parasemionotids and caturids are in the occipital region: the apparent absence of a median basioccipital ossification centre and the absence of epioccipital or supraoccipital bones: in these respects pachycormids resemble *Polypterus*. The cranial fissure is recognizable throughout its length in most individuals, but as in parasemionotids and caturids most of the fissure was closed in cartilage, and may be obliterated or persist as a suture. The only perichondrally lined portion is a small area opposite the medial part of the intercalar. The pachycormid ossification pattern is shown diagrammatically in figure 114.

(iv) *Semionotoids*

This term is used informally for the Semionotoidea of Gardiner (1960), a group including the Lepisosteidae and Semionotidae, equivalent to the Semionotiformes + Lepisosteiformes of Lehman (1966) and the Semionotiformes of Gardiner (1967). This usage is not intended to prejudge the question of whether *Lepisosteus* and the semionotids are closely related, but as Rayner (1948, p. 336) found, the braincases of *Lepisosteus* and the semionotid *Lepidotes* are similar, and can usefully be discussed together.

1. *Lepisosteus*. In living *Lepisosteus* the metotic fissure closes in cartilage very early in ontogeny, at 12 mm in *L. platystomus* (Hammarberg 1937), 20 mm in the long-snouted *L. osseus* (de Beer 1937). In *L. platystomus* ossification begins at 33 mm, with the appearance of a pair of exoccipitals and a median basioccipital. In adult *Lepisosteus* the braincase is still largely cartilaginous: in addition to the basi- and exoccipitals, the orbitotemporal, otic and occipital regions include paired 'epiotics', prootics, sphenotics and pterosphenoids, and a median orbitosphenoid. There is no supraoccipital, opisthotic, intercalar or basisphenoid. In the adult braincase, the fissura oticalis ventralis is represented by the wide band of cartilage between the basioccipital and prootics, but otherwise there is no trace of the cranial fissure.

The basioccipital of *Lepisosteus* incorporates two entire vertebral centra and forms the whole of the occipital condyle. The exoccipital includes two neural arches posteriorly, encloses the vagus canal anteriorly, and extends forwards beyond the latter to surround part of the posterior semicircular canal, as in teleosts. This suggests that in the phylogeny of *Lepisosteus*, as in teleosts, closure of the sub- and supravagal portions of the fissura otico-occipitalis was followed by forward extension of the exoccipital, eliminating the opisthotic and intercalar as independent endochondral ossifications. Rayner (1948, p. 330) assumed that the intercalar had been lost in *Lepisosteus* as a consequence of 'the modified mechanics of the shoulder girdle', but her hypothesis seems to depend upon descent of *Lepisosteus* from *Lepidotes*, and on the presence of an intercalar in the latter: neither of these propositions can be substantiated (see below on the intercalar of *Lepidotes*). There are two hypotheses that would account for the absence of an intercalar in *Lepisosteus*: that the bone never existed in the ancestry of this fish, or, as outlined above, that the bone was lost as an endochondral centre when the exoccipital extended forward following closure of the supravagal portion of the fissura otico-occipitalis, and that this occurred before the extensive membranous outgrowths of the intercalar which characterizes caturids, amiids and teleosts had developed. Discrimination between these hypotheses depends upon whether an endochondral intercalar was present in the most primitive actinopterygians.

The 'epiotic' of *Lepisosteus* (figure 111) provides the greatest problem in interpretation since it could be either a pterotic or a hypertrophied epioccipital. The bone ossifies late (at 65 mm in *L. platystomus*), long after the embryonic distinction between otic and occipital cartilage has disappeared, so that its ontogenetic origin cannot be determined. It ossifies over the posterior semicircular canal (as does the pterotic of pholidophorids, parasemionotids, caturids and pachycormids, and the epioccipital of teleosts), and in large individuals surrounds the upper part of this semicircular canal (psc, figure 111). In front of the semicircular canal, the inner surface of the bone contains a deep, blind pit (lcc, figure 111) which is filled with fat and is the topographic homologue of the lateral cranial canal of *Dapedium*, caturids and pholidophorids (p. 413). Anteriorly, the bone meets the prootic and forms the uppermost part of the posterior wall of the orbit, which slopes steeply forwards. On the posterior face of the braincase, the 'epiotic' is widely separated from its fellow and the exoccipitals almost reach the roofing bones between the 'epiotics' (Mayhew 1924, fig. 12). The centre of ossification of the 'epiotic' (estimated from dried skulls) lies in line with the parietal/dermopterotic suture, but well behind the parietal, against a posterior extension of the descending lamina of the dermopterotic. As in the case of the 'epiotic' of *Amia*, there are two hypotheses that might account for this bone. The first is that it is an epioccipital which has extended forwards following closure of the dorsolateral part of the fissura otico-occipitalis, as in teleosts. If so, it has extended much farther than in any teleost, is much more laterally placed, and has caused the pterotic to be eliminated. Secondly, the bone could be a pterotic: it occupies the same position as the pterotic of pholidophorids, parasemionotids and *Pachycormus*, and comparison with the latter is made more exact by the absence of any ossification above the exoccipitals. Discrimination between these two hypotheses depends upon knowledge of the phylogeny of *Lepisosteus*, which is not available. But the 'epiotic' of *Lepidotes* is similar to that of *Lepisosteus*, and the identity of these bones is discussed further in the section on *Lepidotes*.

The remaining otic and orbitotemporal bones of *Lepisosteus* require little comment. The prootic ossifies from a centre just behind the facial foramen. In the adult, the prootic forms a major part of the basipterygoid process and the glossopharyngeal foramen lies well within the bone. The passage of the spiracular canal through the prootic has been mentioned in the discussion of that structure (p. 399). The sphenotic is confined to the postorbital process and does not impinge upon the labyrinth cavity or cranial cavity, as in other holosteans. The pterosphenoid and orbitosphenoid do not differ significantly from those of other holosteans.

2. *Semionotids*. Among semionotids, the braincase is known in *Dapedium* (Rayner 1948; Gardiner 1960; figures 112, 113) and in several species of *Lepidotes* ranging from the Toarcian (*L. semiserratus*) to the Neocomian (*L. mantelli*) (Woodward 1916; Holmgren & Stensiö 1936; Rayner 1948; Beltan 1957; Gardiner 1960; figures 108–110): all are very similar. As Wenz (1968, p. 107) has pointed out, *Dapedium* and *Lepidotes* differ in many ways, and it is difficult to justify their inclusion in the same family. This dissimilarity is especially apparent in the braincase, that of *Dapedium* being very thoroughly ossified and sutureless, that of *Lepidotes* having separate bones bounded by sutures or wide zones of cartilage. Resemblances to *Lepisosteus* are apparent only in *Lepidotes*, and this genus will be discussed first and compared with the living fish.

The orbitotemporal, otic and occipital regions of the braincase of *Lepidotes* comprise a median basioccipital, basisphenoid and orbitosphenoid, and paired exoccipitals, 'epiotics', prootics, sphenotics and pterosphenoids (figures 108–110). There is no supraoccipital or opisthotic. Several authors have reported an intercalar in *Lepidotes*, but this is shown below to be probably an error. In the Purbeckian P.44914, *Lepidotes minor*, there is also a median, rod-like bone below the roofing bones in the otic region. This is evidently an ossification in the taenia tecti medialis and should be called a supraotic. There is no supraotic in the only other specimen of *Lepidotes* which has been prepared with acid, P.34511, *L. toombsi.*

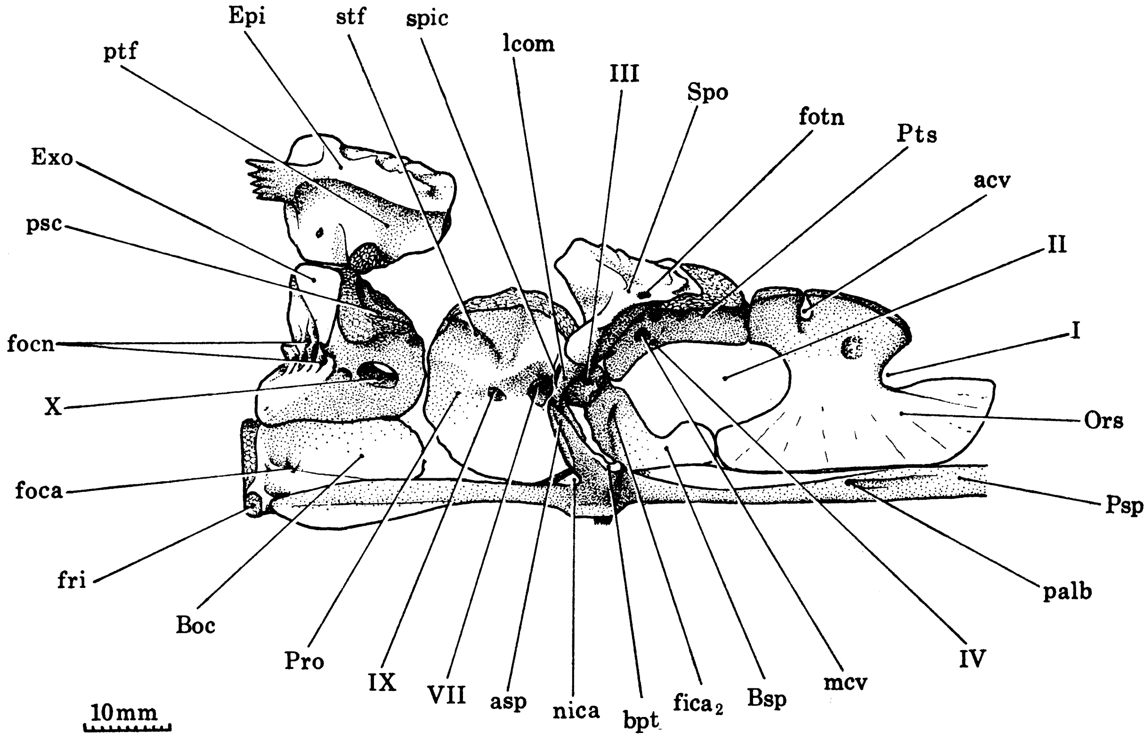


FIGURE 108. *Lepidotes toombsi* Jain & Robinson. Restoration of post-ethmoid portions of neurocranium and parasphenoid in right lateral view, based on P.34511.

The braincase of *Lepidotes* contained a good deal of cartilage, even in large individuals. The fissura oticalis ventralis is represented by the cartilage or suture between the prootics and basioccipital, but the fissura otico-occipitalis is completely obliterated.

The basioccipital (Boc) of *Lepidotes* incorporates one vertebra, as is indicated by a pair of facets for ribs in *L. toombsi* (fri, figures 108, 109) and *L. latifrons* (Woodward 1916, fig. 15), and by a partial suture in *L. semiserratus* (Holmgren & Stensiö 1936, fig. 364). The 'small section of the myodome' which Rayner (1948, p. 307) reported in the basioccipital of P.9998, *L. latifrons*, is the posterior ends of the otolith chambers, while the ventral 'groove for the basicranial canal' (= myodome) described by Woodward (1893, p. 560; 1916, p. 39) and Gardiner (1960, p. 310) is an aortic groove (grao, figures 109, 110), walled by the parasphenoid. In *Lepidotes*, as in other holosteans, the myodome is confined to the prootics.

The exoccipital (Exo) encloses the vagus canal and surrounds the lower part of the posterior semicircular canal (psc, figure 108), as in *Lepisosteus*. Lateral to the foramen magnum, the exoccipital of *L. toombsi* is penetrated by three pairs of foramina (focn, figures 108, 100) for the dorsal and ventral roots of spinal nerves (a–c in Fürbringer's terminology), each pair separated by a vertical crest marking the insertion of an intermuscular septum. In front of these there is a ventral root foramen with a double internal opening transmitting the ventral roots of one or two occipital nerves: this single ventral root canal is normally all that is present in the exoccipital of primitive actinopterygians (p. 318). In *Lepisosteus* this ventral root and the dorsal and ventral roots of a and b pass through the exoccipital, but c and d pass through neural arches fused to the basioccipital, so that the exoccipital of *Lepidotes* includes at least one neural arch which is fused with the basioccipital in *Lepisosteus*. Between the vagus foramen and the occipital nerve foramen, on the ridge separating the lateral and posterior surfaces of the exoccipital, there is a pointed, dorso-laterally directed process (fpt, figures 109, 110). The ventral limb of the post-temporal, which is long and slender in *Lepidotes*, attaches to this small process on the exoccipital. This process is therefore both topographically and functionally homologous with the intercalar of holosteans and teleosts, and in *L. toombsi* there is definitely no intercalar. The absence of this bone can be explained by either of the two hypotheses proposed to account for the absence of an intercalar in *Lepisosteus* (p. 448).

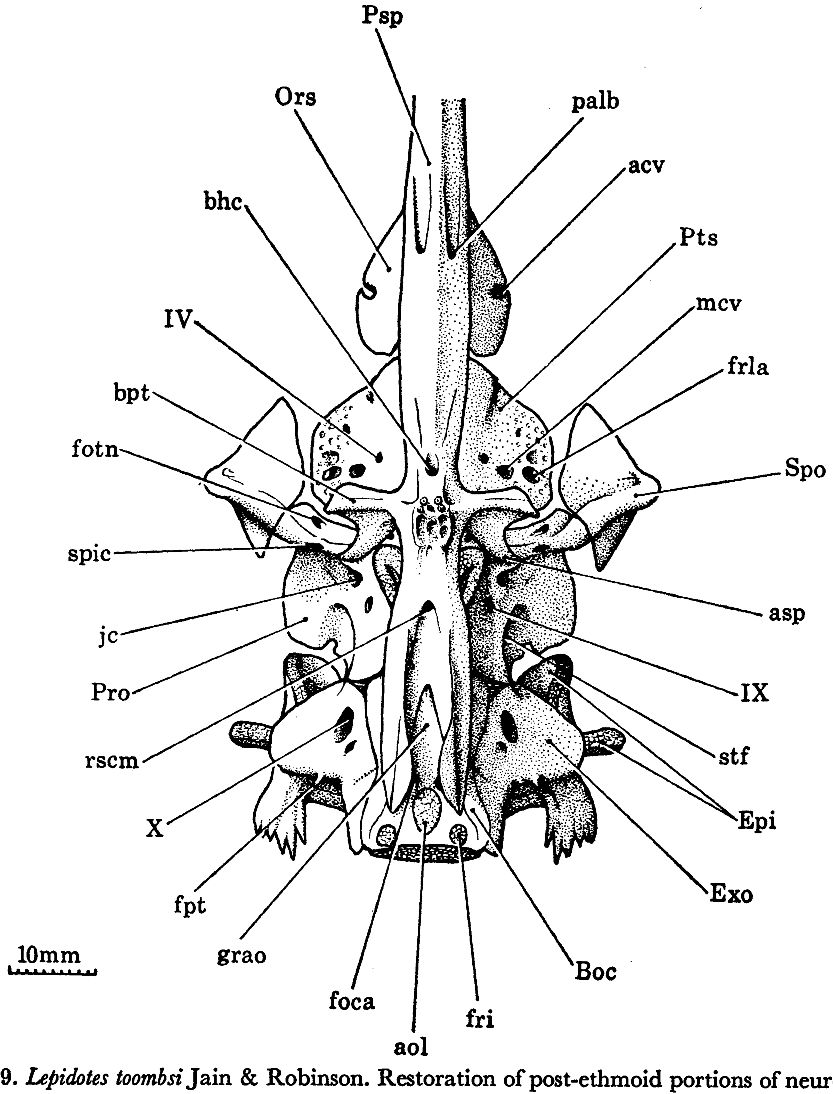


FIGURE 109. *Lepidotes toombsi* Jain & Robinson. Restoration of post-ethmoid portions of neurocranium and parasphenoid in ventral view, based on P.34511.

Other workers have thought that there is an intercalar in *Lepidotes*. Woodward (1916, p. 38) wrote that in P.1124, *L. mantelli*, the exoccipital 'appears to be capped by a small opisthotic' (= intercalar), but there is no evidence of a separate ossification in that specimen (see also Rayner 1948, p. 305). In P.9998, *L. latifrons*, Woodward (1916, p. 39) also surmised that there might have been 'a small opisthotic, which is missing in the fossil', but the exoccipital of this specimen is almost identical with that of the well preserved individual of *L. toombsi* in which there is definitely no such bone. In *L. semiserratus*, Stensiö (1932, fig. 80; 1935, fig. 5), Holmgren & Stensiö (1936, fig. 364) and Rayner (1948, fig. 11) all illustrate a small intercalar between the lateral edges of the 'epiotic' and exoccipital. All these restorations are based on a single specimen in Stockholm, and Rayner (1948, p. 305) writes of the intercalar in this specimen 'it was removed before the specimen was borrowed'. Nevertheless, Rayner included the bone in her restoration of *L. semiserratus* because she had seen 'the remains of a small star-shaped bone in about this position' in a crushed skull of *L. minor*. Gardiner (1960), the last worker to describe a braincase of *Lepidotes*, also found a small intercalar in *L. mantelli*. The explanation of the apparent presence of an intercalar in other specimens of *Lepidotes* seems to be provided by the shape of the 'epiotic' in the specimen of *L. toombsi* illustrated here (Epi, figures 108–110). This bone has a slender lateral process or wing forming a transverse buttress at the back of the floor of the post-temporal fossa. As is shown in the posterior view (figure 110), this process is joined to the body of the bone by a rather narrow isthmus, and were the bone to suffer slight crushing, either dorso-ventrally or laterally, the lateral process would easily become more or less detached and give the impression of a separate intercalar.

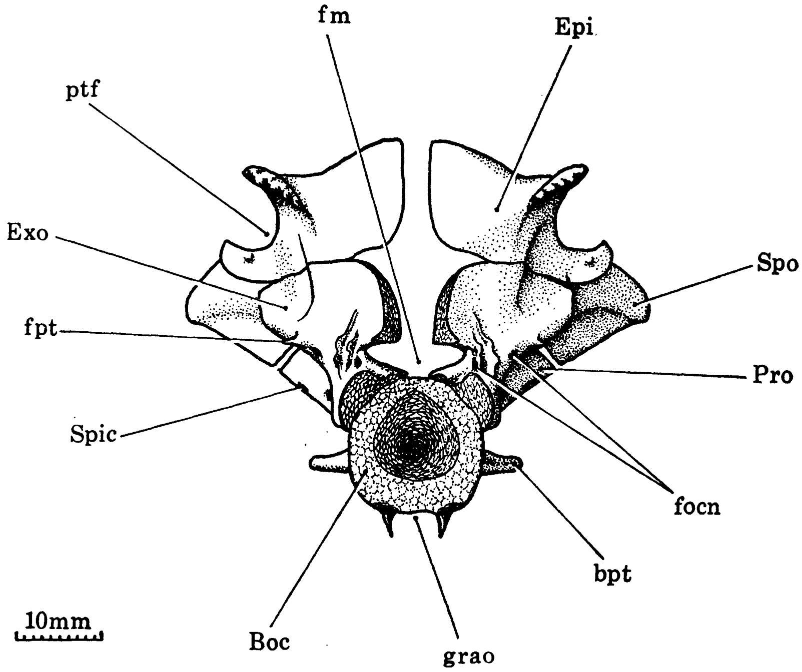


FIGURE 110. *Lepidotes toombsi* Jain & Robinson. Restoration of neurocranium and parasphenoid in posterior view, based on P.34511.

Apart from this lateral process, the 'epiotic' of *Lepidotes* is rather like that of *Lepisosteus* (figure 111). The ossification centre of the bone in *Lepidotes* lies posterior to the parietal/dermopterotic suture, and from this centre a large, digitate, membrane bone outgrowth (mbr) extended back into the trunk musculature. On the internal surface of the bone, there is anteriorly the same deep, blind pit (lcc) as in *Lepisosteus*, the homologue of the lateral cranial canal. Behind this cavity, the bone surrounds the upper part of the posterior semicircular canal (psc), as in *Lepisosteus*, but in the latter this canal lies within the thick posterior wall of the bone, whereas in *Lepidotes* the canal lay in an oblique partition separating the lateral cranial canal from a larger, posterior depression (sup), absent in *Lepisosteus*. This large depression is a conical, blind pit, laterally directed and separated from the lateral cranial canal in front by a thin but uninterrupted partition. This pit closely resembles a paired, dorso-lateral expansion of the cranial cavity in the palaeoniscoid *Boreosomus* ('lobus vagus' of Nielsen, 1942, fig. 66). The other possible interpretation of this pit is that it represents a vestige of the dorso-lateral part of the fissura otico-occipitalis, for in those forms in which this part of the fissure persists (palaeoniscoids, pholidopleurids, pholidophorids) the cranial cavity shows an expansion at this level (e.g. figures 65, 73). But where such an expansion exists it is narrow rostro-caudally and slit-like (see, for example, Nielsen 1942, figs 13, 14, 66; 1949, figs 15, 16), quite unlike the conical cavity in front of it in *Boreosomus*, which resembles that in *Lepidotes*. In retaining this large cavity, the 'epiotic' of *Lepidotes* is probably more primitive than that of *Lepisosteus*. And while the 'epiotic' of *Lepisosteus* can be closely compared with the epioccipital of an early leptolepid where the lateral cranial canal is still represented by a blind pocket in front of the posterior semicircular canal (cf. figures 111, 49*b*), that of *Lepidotes* cannot, for there is no equivalent of the deep posterior pocket in the bone in any epioccipital. Where such a pocket exists, in palaeoniscoids, it lies in the otic region, in front of the cranial fissure, and must have ossified from an otic ossification in the position of a pterotic. This pocket in the 'epiotic' of *Lepidotes* is therefore a feature of the otic region, suggesting that the bone is a pterotic, not an epioccipital. This is also implied by the transverse wing of the bone in the floor of the post-temporal fossa, a structure found in no epioccipital.

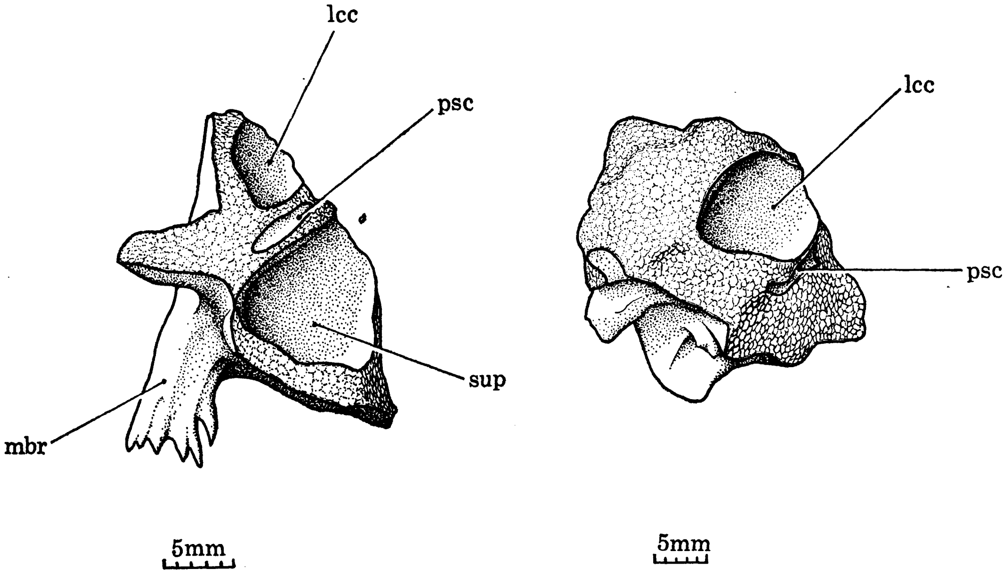


FIGURE 111. Right epiotic, in ventral view, of *Lepidotes toombsi* Jain & Robinson (left), from P.34511, and *Lepisosteus tristoechus* (Bloch & Schneider) (right), from a large dried skeleton (braincase figured by Rayner 1948).

The question of the homology of the 'epiotic' in *Lepisosteus* and *Lepidotes* can be summed up as follows. In both fishes, the bone must be either a pterotic which has extended postero-medially and replaced the epioccipital, or a hypertrophied epioccipital which has extended forward and replaced the pterotic. In both fishes the dorso-lateral part of the fissura otico-occipitalis, the original boundary between epioccipital and pterotic, has completely disappeared, there is no known precursor or close relative of either form which might help in discriminating between the two interpretations, and the topographic relations of the bone can be read either way. But in both fishes the 'epiotic' shows features which are unknown in any epioccipital (in *Lepisosteus* the forward extent of the bone and its position lateral to the exoccipital; in *Lepidotes* the presence of a lateral wing in the floor of the post-temporal fossa and a deep internal excavation behind the posterior semicircular canal), and for this reason it is more probable that the bones are pterotics. This hypothesis implies ancestral conditions in which the pterotic was in some way dominant over the epioccipital (the reverse of conditions in the teleostean lineage), perhaps as in pachycormids and *Polypterus*, where the upper part of the occipital arch did not ossify. This hypothesis, that the bone is a pterotic in *Lepisosteus* and *Lepidotes*, cannot be tested at present and is not supported by decisive evidence. Pending such evidence, I think it wiser to retain the non-committal term epiotic in both fishes.

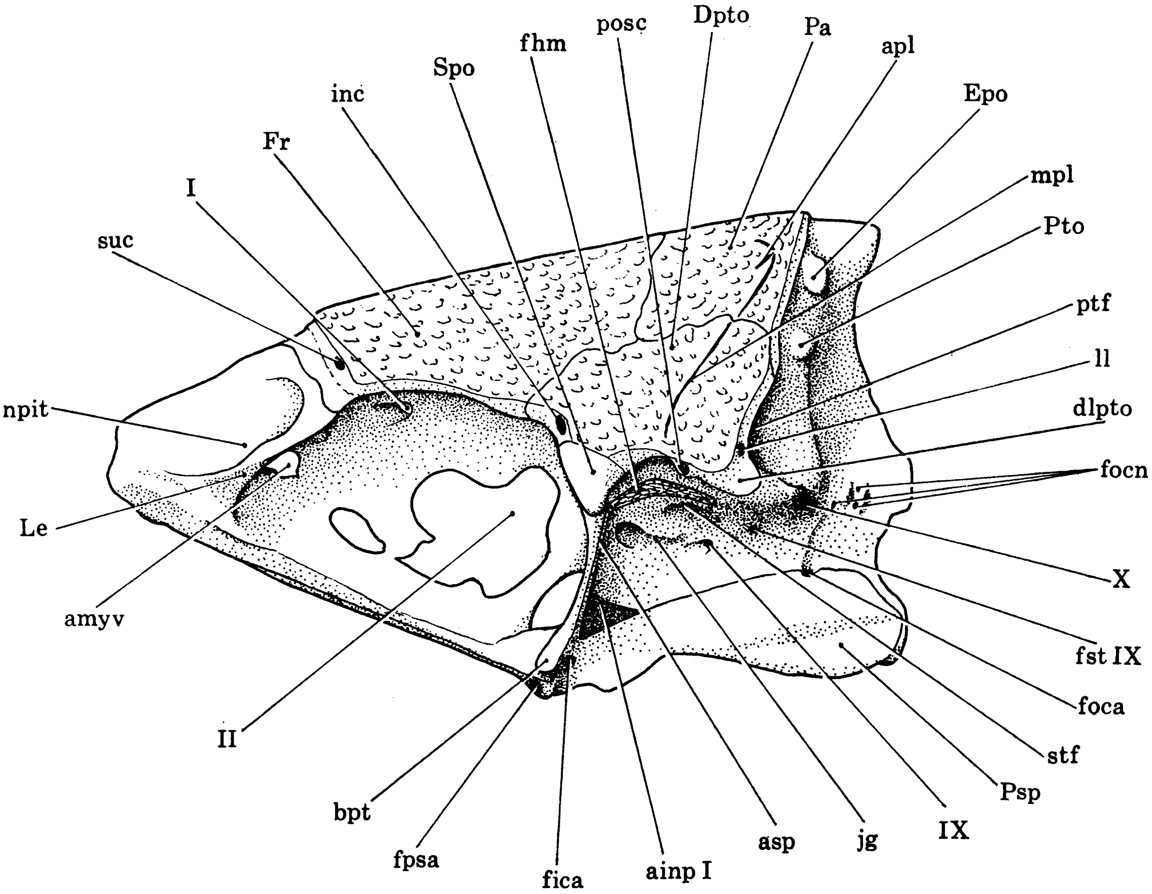


FIGURE 112. *Dapedium* sp. Neurocranium and attached dermal bones in left lateral view, restoration based on P.11177 and P.11189 (magn. × 2 approx.).

The remaining bones of *Lepidotes* raise no problems of homology and require little comment.

The prootic (Pro) has been described by Gardiner (1960). As in *Lepisosteus*, the glossopharyngeal foramen lies well within the bone, and the spiracular canal penetrates it (IX, spic, figures 108, 109). The sphenotic (Spo) is confined to the postorbital process and does not impinge upon the anterior semicircular canal or cranial cavity. The basisphenoid (Bsp), pterosphenoids (Pts) and orbitosphenoid (Ors) are all well ossified and form an almost complete interorbital septum.

Dapedium is the only other semionotid in which the braincase is known (figures 112, 113). Four specimens have been described, P.3541 (Woodward 1893), P.11177 (Frost 1913), P.11189 (Gardiner 1960) and a specimen in Bath Museum (Rayner 1948). All these specimens, including the small P.11189, are very thoroughly ossified, and in the orbitotemporal, otic and occipital regions the only unossified areas are an anterior dorsal fontanelle, the articular areas for the hyomandibular (fhm) and first infrapharyngobranchial (ainp I), and parts of the interorbital septum. There is no trace of any part of the cranial fissure in any specimen, even the fissura oticalis ventralis being obliterated.

Rayner (1948) pointed out that no sutures are visible in any specimen of *Dapedium*, so that the various ossifications named by Woodward (1893) and Frost (1913) cannot be recognized. In P.11189, however, Gardiner (1960) mentions and illustrates sutures delimiting a supraoccipital, basioccipital, intercalar and sphenotic, and a suture between the prootic and exoccipital. Some of these sutures are the margins of dermal bones, and I am unable to find the others either in P.11189 or the larger, less distorted P.11177, in which the internal, cerebral surface of the bone is also visible: no sutures or bone junctions are recognizable on the internal surfaces of the braincase. Any account of ossification centres in *Dapedium* is therefore purely speculative. From the shape of the braincase in posterior view (figure 113) it is likely that separate pterotic and epioccipital ossifications were present, their centres indicated by prominences (Pto, Epo) separated by a small fossa. Whether or not a supraoccipital was present, a point on which there has been some discussion, it is impossible to say. If present, the bone must have been small and confined to the posterior face of the braincase, for in front of the supraoccipital prominence there is the large, median intramural cavity discussed on p. 413.

Similarly, it is impossible to say if there was an intercalar, but if this bone was present (as seems likely from the relief of this part of the braincase; Ic, figure 113) it must have been an endochondral bone. There is no real evidence of separate basi- and exoccipital components, nor any indication of the boundary between these occipital bones and the otic bones. The form of the hyomandibular facet indicates that the sphenotic was distinct (Spo, figure 112), and an unossified area in the antero-ventral wall of the myodome must separate the prootic from the foot of the basisphenoid. In the orbit, there is no evidence of separate orbito- and pterosphenoids.

In summary, the fissura otico-occipitalis is completely obliterated in *Lepisosteus*, *Lepidotes* and *Dapedium*, and in the latter the fissura oticalis ventralis is also obliterated. *Lepisosteus* and *Lepidotes* have a similar ossification pattern, lacking the opisthotic, intercalar, supraoccipital and (probably) epioccipital. *Lepisosteus* also lacks a basisphenoid. In *Dapedium* the pattern can only be inferred, but a pterotic, epioccipital and endochondral intercalar appear to be present, as in pholidophorids, parasemionotids and caturids. The semionotoid braincase is illustrated diagrammatically in figure 114.

(v) *Chondrosteans*

This section will begin with an account of new materal of the Lower Triassic *Perleidus*, where incompletely ossified individuals show an ossification pattern closely comparable with that in parasemionotids and pholidophorids, throwing a new light on the ossification pattern in the palaeoniscoid braincase and clarifying the homologies of the endocranial bones in living chondrosteans.

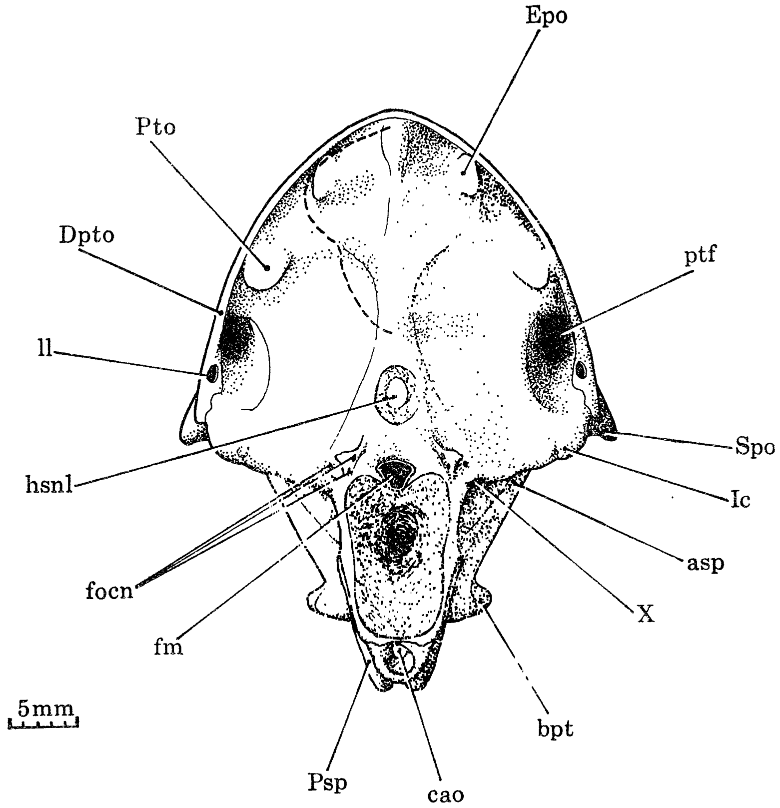


Figure 113. *Dapedium* sp. Neurocranium and attached dermal bones in posterior view, restoration based mainly on P.11177. The outline of the median supracranial cavity is indicated by a broken line on the left side. The probable ossification centres of the epioccipital, pterotic and intercalar are indicated by the guide-lines, although sutures are not visible around these bones.

1. *Perleidus*. The braincase of *Perleidus* has been described by Stensiö (1932; *P. stoschiensis*), Lehman (1952, 1954; *P.* sp., *P. madagascariensis*) and Beltan (1968; *P.* sp.); these authors described fully ossified individuals in which there is no sign of separate ossification centres. The following account is based on MMK 495 and 496, acid-prepared specimens of *P.* cf. *stoschiensis* from East Greenland (figures 115, 116), supplemented by rubber casts of fully ossified specimens of *Perleidus* sp. from the Lower Trias of Madagascar.

In the occipital region, the individual bones are already fused in MMK 496, but residual sutures show that the same bones were present as in MMK 495; a basi-exoccipital ossifying from at least three centres (paired exoccipitals and an apparently median basioccipital), paired intercalars which are mainly endochondrally ossified but have a small anterior membrane bone outgrowth lapping around the outer margin of the vagus foramen, and paired epioccipitals, small, conical bones which have drifted away from the braincase in MMK 495. There is no definite evidence of a supraoccipital in either specimen: in 496 the supraoccipital region is already co-ossified with the exoccipitals but there appears to be a low supraoccipital crest on the posterior face of the occipital region, much as in pholidophorids, while in 495 the supraoccipital area is unossified, but a supraoccipital could have drifted away, like the epioccipitals in that specimen. In figure 115 a supraoccipital has been indicated by broken lines because of the mode of closure of the uppermost part of the fissura otico-occipitalis (see below), and because of the markedly hexagonal outline of the posterior face of the braincase in Madagascar *Perleidus* (P.19589–90).

In the otic and orbitotemporal regions, MMK 496 again has most of the bones already fused, but the sphenotic is still partially distinct and in the roof of the orbit there is a pair of bones, ossified only as perichondral shells, which I tentatively interpret as paired orbitosphenoids, the pterosphenoids having already fused with the prootics and sphenotics. In MMK 495 there are separate, paired pterotics (the right one drifted away), opisthotics, prootics and sphenotics.

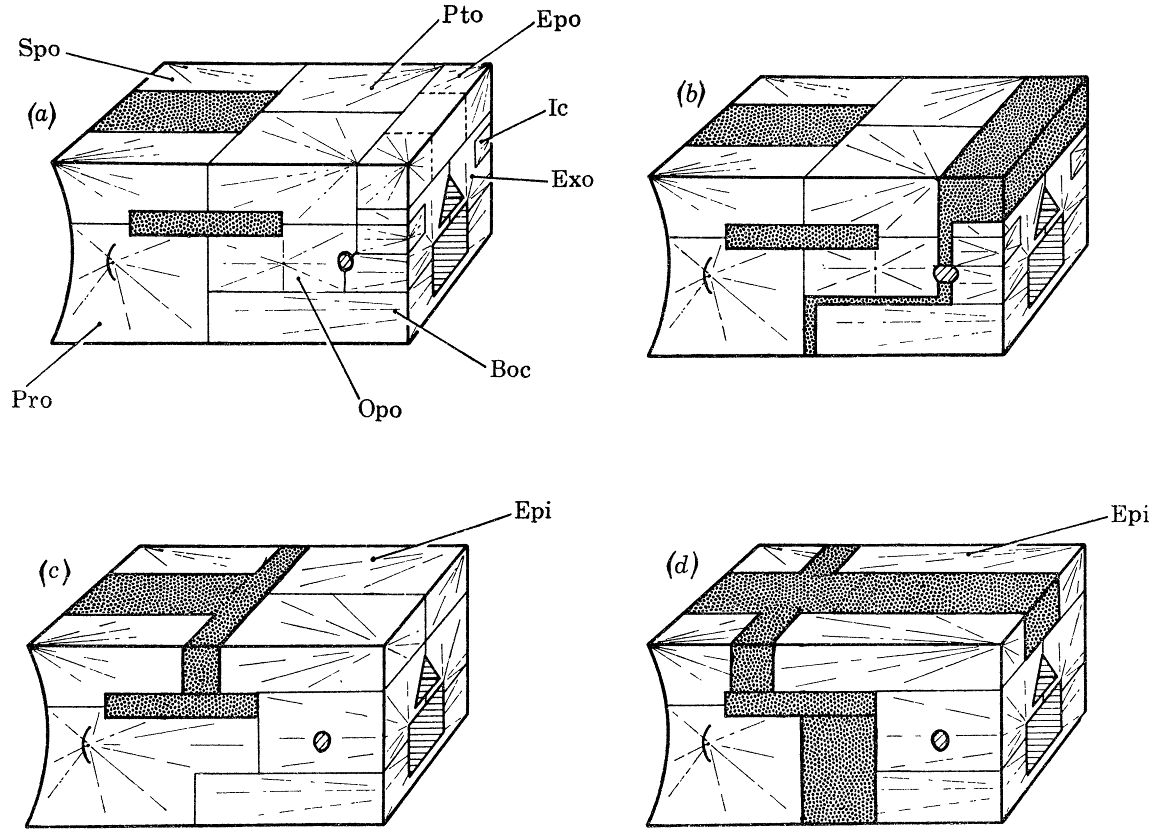


FIGURE 114. Block diagrams summarizing the cranial fissure and ossification pattern of the postorbital part of the neurocranium in semionotoids and *Pachycormus*. For conventions adopted see legend of figure 95. (*a*) Pattern inferred in *Dapedium*, cranial fissure obliterated, but probably remaining as a cartilage-filled suture in incompletely ossified individuals, ossification pattern same as in pholidophorids (if supraoccipital is present) or as in parasemionotids and caturids (if no supraoccipital). (*b*) *Pachycormus*, cranial fissure cartilage-filled (except for very small portion) but persisting as a suture, ossification pattern as in pholidophorids and parasemionotids except that upper part of occipital arch does not ossify. (*c*) *Lepidotes* and (*d*) *Lepisosteus*, cranial fissure obliterated in both, exoccipital extends forwards and opisthotic and intercalar are lost, epiotic occupies the position of both the epioccipital and pterotic: epiotic is probably a pterotic which has extended posteriorly (perhaps through an intermediate stage like *Pachycormus*).

The prootic and opisthotic are already partially fused on the left side of the specimen, but the remaining bones were separated in life by wide tracts of cartilage. The pterosphenoid appears to be represented by a perichondral shell on one side of the specimen, but this might be an orbitosphenoid, or both these bones. There is no sign of the basisphenoid (already fused with the prootics in 496). As in pholidophorids and parasemionotids, there was evidently a rostro-caudal gradient in the ossification of the braincase, strongest around the occipital condyle. The disposition of the various ossifications is indicated in figures 115 and 116. The bones are closely comparable with their homologues in pholidophorids and parasemionotids, and will only be described briefly here. The major difference from parasemionotids is that the opisthotic is proportionally much larger, equalling or surpassing the prootic in size.

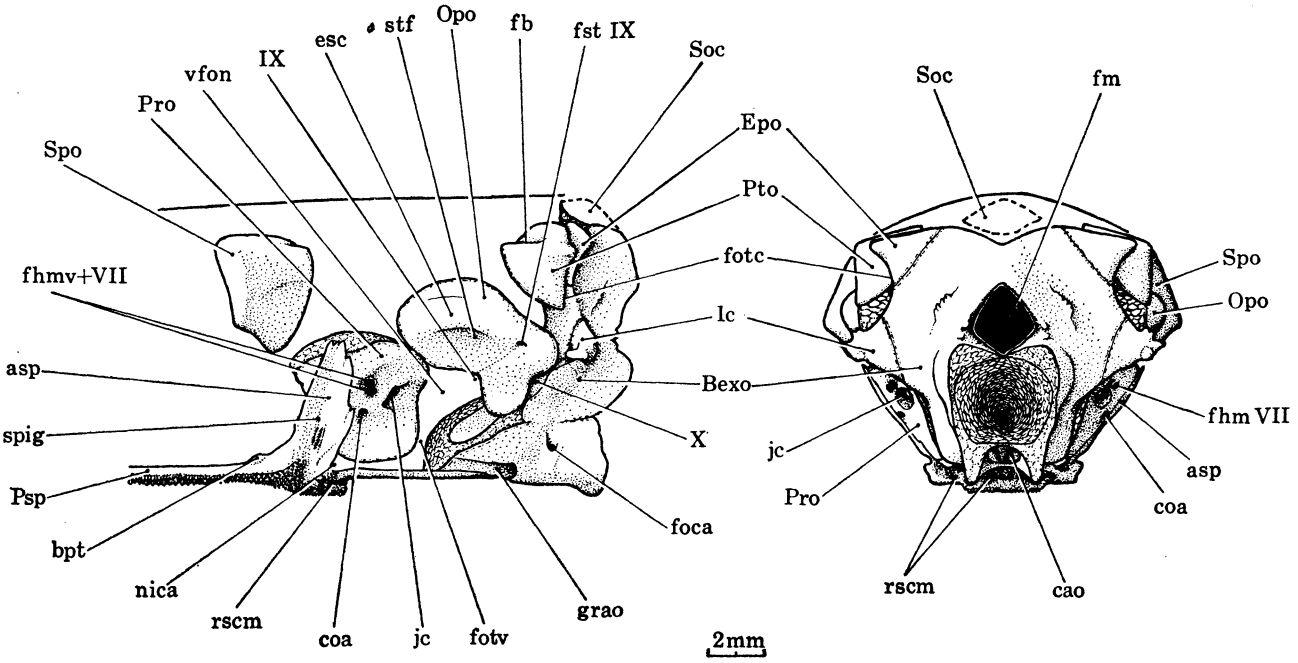


FIGURE 115. *Perleidus* cf. *stoschiensis* Stensiö. Restoration of postorbital portion of neurocranium and parasphenoid of an incompletely ossified individual in left lateral and posterior view. Bones drawn mainly from MMK 495, proportions of neurocranium from MMK 496 and P.19589–90 (*Perleidus* sp.). Contour of roofing bones indicated, and possible supraoccipital suggested by a broken line.

The basi-exoccipital (Bexo) is closely comparable with that of parasemionotids (figures 97, 98), the exoccipital component being particularly large. The anterior face of the exoccipital is perichondrally lined from the lower margin of the vagus canal upwards (fotc). As in parasemionotids, there is no notochordal calcification lining the long notochordal canal. The aortic canal is paired anteriorly (cao, grao, figures 115, 116).

The intercalar (Ic) resembles that of parasemionotids, but its anterior face is perichondrally lined. The epioccipital (Epo) is only as large as the intercalar. It is a rostro-caudally compressed, triangular bone, with the anterior face perichondrally lined, as in pholidophorids. On the left side of MMK 496 the knob-like tip of the epioccipital has fused with the pterotic in front, closing the dorso-lateral corner of the fissura otico-occipitalis for a short distance. This closure appears to be partially in membrane bone but may involve a little cartilage bone internally.

In the otic region, the pterotic (Pto) is about as large as in parasemionotids. It ossifies from the postero-dorsal corner of the otic capsule, lateral to the epioccipital ossification centre and in the transverse partition separating the cranial fissure from the fossa bridgei (fb). In fully ossified individuals it must line the posterior part of the fossa bridgei and the rudimentary post-temporal fossa (p. 392), and enclose the upper part of the posterior semicircular canal.

The opisthotic (Opo) is already very large in the lightly ossified MMK 495 and appears to be the largest bone in the otic region, in sharp contrast to the diminutive opisthotic of pholidophorids and lightly ossified parasemionotids. The bone probably ossifies from a centre lateral to the external semicircular canal (esc), which it encloses. In MMK 495 the vestibular fontanelle is represented by an excavation in the antero-ventral margin of the opisthotic (vfon, figure 115). At this early stage in ossification the glossopharyngeal foramen is still included in the vestibular fontanelle, and is indicated by a notch (IX) in the margin of the opisthotic: from this notch a groove leads postero-dorsally to the opening of the ascending canal for the supratemporal branch of the glossopharyngeal (fst IX). Between the glossopharyngeal notch and the vagus canal (X) the opisthotic extends ventrally in the wall of the saccular recess in a tongue of bone which will be referred to below in the discussion of palaeoniscoids. The posterior face of the opisthotic is perichondrally lined in the region of the vagus canal and forms the anterior

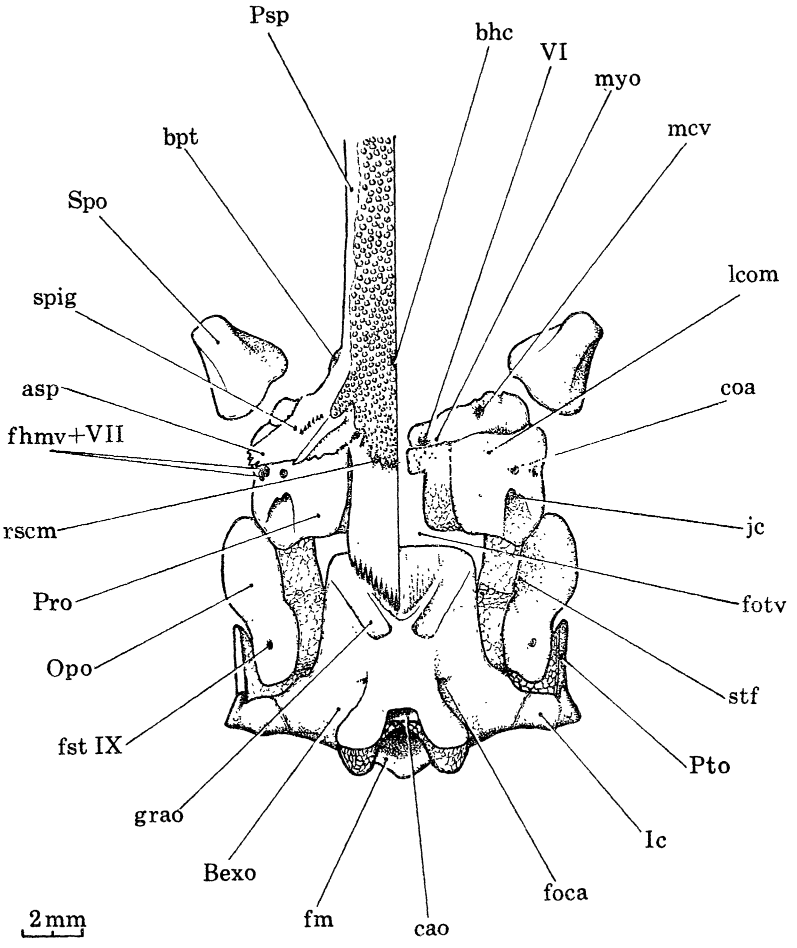


FIGURE 116. *Perleidus* cf. *stoschiensis* Stensiö. Restoration of postorbital portion of neurocranium and right half of parasphenoid of an incompletely ossified individual in ventral view. Bones drawn mainly from MMK 495, proportions of neurocranium from MMK 496.

wall of that canal. The opisthotic lines the subtemporal fossa (stf) and in fully ossified individuals it must have contained the posterior ampulla and the posterior part of the utricular recess, and probably extended dorsally to contribute to the floor of the fossa bridgei and to surround the greater part of the anterior semicircular canal, which is already completely bone enclosed in MMK 496. Antero-dorsally, the hyomandibular facet marks the boundary between the opisthotic and sphenotic.

The prootic (Pro) resembles that of parasemionotids, but is relatively smaller. In fully ossified individuals the sphenotic and opisthotic probably met above it, so that it did not contribute to the floor of the fossa bridgei and enclosed no more of the anterior semicircular canal than the ampulla.

The sphenotic (Spo) ossifies in the postorbital process, as usual, but lies in front of the prootic, not above it as it does in parasemionotids and pholidophorids. In MMK 496 the short spiracular canal is already bone enclosed and passes through the posterior part of the sphenotic. In fully ossified individuals the sphenotic probably lines the anteriormost part of the fossa bridgei, but does not encroach on the anterior semicircular canal.

In MMK 496 the basisphenoid is ossified and represented by a median pedicle with paired dorso-lateral arms which are already fused with the prootic immediately in front of the notch for the oculomotor nerve. In MMK 495 the basisphenoid is not yet ossified. I assume that the junction of the basisphenoid with the prootic also represents the postero-ventral corner of the pterosphenoid, as in pholidophorids, and that the approximate position of the pterosphenoid/prootic suture in the wall of the orbit is indicated by the ascending canal for the first recurrent branch of the facial nerve, as in pholidophorids and parasemionotids. If this is so, the pterosphenoid is already fused with the prootic and sphenotic in MMK 496 and is too lightly ossified to be described in MMK 495. It would form part of the roof of the braincase above the posterior part of the orbit, but would not contact the anterior semicircular canal as it does in pholidophorids.

The orbitosphenoid is possibly represented by a paired perichondral ossification in MMK 496 which forms the dorsal part of the interorbital septum, as usual.

In *Perleidus* the ossification pattern of the braincase is therefore similar to that in pholidophorids and parasemionotids, but the opisthotic is much larger than in either group, the pterotic is about as large as in parasemionotids, not enlarged as it is in pholidophorids, the prootic is relatively smaller than in either group, and there is still doubt as to whether a supraoccipital was present, and whether there were separate ptero- and orbitosphenoids.

In the lightly ossified *Perleidus* specimens just described, the perichondrally lined portion of the cranial fissure (fotc) extends from the lower margin of the vagus canal up to the medial margin of the epioccipital and pterotic, the vestibular fontanelle (vfon) was represented by a large area of cartilage between the prootic, opisthotic and basioccipital, and the fissura oticalis ventralis (fotv) was represented by a broad tract of cartilage between the prootics and the basioccipital. In the fully ossified *Perleidus* braincases described by Stensiö (1932), Lehman (1952, 1954) and Beltan (1968) the fissura oticalis ventralis is obliterated by bone except for a remnant in the specimen described by Lehman in 1954 (figs 4, 8). The vestibular fontanelle is similarly obliterated in Stensiö's Greenland specimen, but in the Madagascar material it is sometimes open and sometimes occluded (Lehman 1952, p. 134). The subvagal portion of the fissura otico-occipitalis, between the vestibular fontanelle and the vagus canal, may be open (Lehman 1954), partially closed (Beltan 1968) or completely closed (Stensiö 1932), and so was presumably without perichondral lining and capable of closing during ontogeny. From the lower margin of the vagus canal up to the lateral part of the roof of the braincase the fissura otico-occipitalis is always open and was presumably perichondrally lined, as in MMK 495–6. In Stensiö's specimen the fissure is closed mid-dorsally over an area which seems to correspond exactly with the extent of the supraoccipital in pholidophorids (cf. figures 44, 55, 57, 69 with Stensiö 1932, fig. 59B and pl. 32, fig. 1). Because of this and because of the presence of a mid-dorsal prominence in the occipital arch, a supraoccipital has been tentatively indicated in figure 115. Closure of the mid-dorsal portion of the fissure is, of course, not conclusive evidence of a supraoccipital, for it is possible that this area represents the gap between the epioccipitals, and was ossified by fusion of the uppermost parts of the exoccipitals with the pterotics.

In summary, the cranial fissure of *Perleidus* differs from that of primitive pholidophorids in having the subvagal portion and a mid-dorsal portion closed in cartilage, the mid-dorsal portion corresponding to the supraoccipital portion in pholidophorids. *Perleidus* differs from parasemionotids in having the epioccipital portion of the fissure still open. These forms are compared diagrammatically in figure 118.

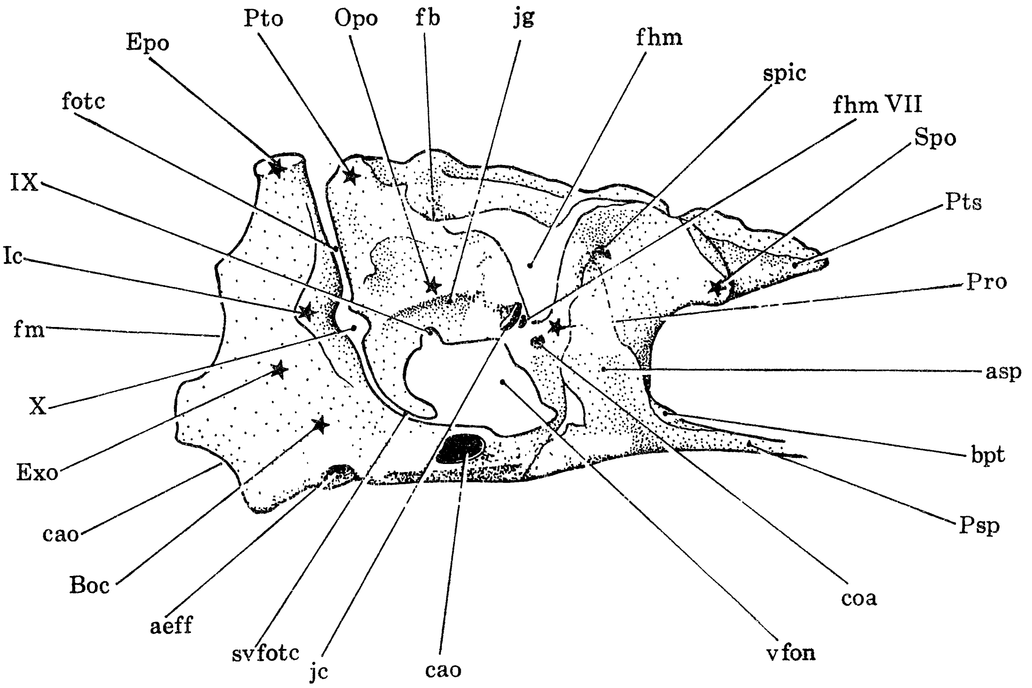


Figure 117. *Pteronisculus magnus* (Nielsen). Post-ethmoid part of neurocranium and parasphenoid of an incompletely ossified individual in right lateral view. Based on Nielsen 1942 (pl. 6, fig. 3), with the addition of asterisks marking the inferred position of the neurocranial ossification centres. (Magn. × 3 approx.)

2. *Palaeoniscoids.* The new information on the ossification pattern of the braincase of *Perleidus* illuminates the question of endocranial ossification centres in palaeoniscoids. The only palaeoniscoids in which anything is known of the ossification pattern are single specimens of *Pteronisculus magnus* and *Cosmoptychius.* In *Pteronisculus magnus* (Nielsen 1942, p. 91, pl. 6, fig. 3, pl. 8, fig. 1; figure 117) there is a pair of bones in the wall of the orbit which are the approximate topographic homologues of the presumed orbitosphenoid of *Perleidus* and the pterosphenoid of pholidophorids, there is a basisphenoid which appears to be paired, and a sphenotic in the post-orbital process. The ventral part of the sphenotic is already fused into the large bone which

occupies the rest of the otic region, and this originally paired ossification is already fused to its antimere posteriorly by a tract of bone separating the anterior and posterior dorsal fontanelles. The occipital region, behind the cranial fissure, is already fully ossified and shows no signs of separate ossifications. Figure 117 is based on a tracing from Nielsen's photograph of this specimen. Comparison with *Perleidus* (figure 115) indicates that the braincase of *Pteroniscúlus* is readily interpreted as showing the same ossification centres and the same rostro-caudal gradient in ossification, strongest around the occipital condyle. In the occipital region, the centres of ossification of the intercalar (Ic) and epioccipital (Epo) are indicated by lateral (craniospinal process of Nielsen) and dorso-lateral prominences. It is impossible to say whether a supraoccipital was present. In the otic region, the centre of the pterotic (Pto) is indicated by a dorso-lateral prominence antero-lateral to the epioccipital. The opisthotic (Opo) has a postero-ventral tongue between the vagus canal (X) and the notch for the glossopharyngeal nerve (IX), as in *Perleidus*, and it must have ossified from a centre lateral to the external semicircular canal. As in *Perleidus*, the hyomandibular facet (fhm) must mark the junction between the opisthotic and sphenotic (Spo), and the short spiracular canal (spic) therefore passes through the posterior part of the sphenotic. The ossification centre of the prootic (Pro) would lie medial to the ascending process of the parasphenoid. In this specimen of *Pteroniscúlus* the prootic evidently formed a smaller part of the braincase than in *Perleidus* while the opisthotic was relatively larger, already forming the floor of the middle part of the fossa bridgei (fb) and surrounding the anterior semicircular canal (Nielsen 1942, pl. 8, fig. 1). This increase in the extent of the opisthotic relative to the prootic is a conspicuous trend in the series *Pholidophorus*-parasemionotid-*Perleidus*-*Pteroniscúlus* (cf. figures 96, 97, 115, 117, 118).

In *Pteroniscúlus stensioei*, although the ossification pattern is unknown, there is in Nielsen's (1942) sectioned specimen a small, independent median ossification in the floor of the cranial cavity, above the anterior end of the notochordal canal (Nielsen 1942, fig. 9; Bjerring 1971, fig. 6D). As Nielsen says, this small bone, which is not perichondrally lined ventrally, must have fused into the occipital ossification in full-grown individuals. No other actinopterygian is known to have a median ossification of this type, but Bjerring (1971) compares the bone with the more numerous 'zygals' of coelacanths and rhipidistians. This comparison seems well founded (though I do not subscribe to the segmental homology Bjerring assigns to the bone in *Pteroniscúlus*) and implies that the presence of zygals is a primitive teleostome character. In non-palaeoniscoid actinopterygians these bones have apparently been lost.

The other incompletely ossified palaeoniscoid is the specimen of *Cosmoptychius* described by Watson (1928) and Schaeffer (1971). This specimen is more lightly ossified than Nielsen's *Pteroniscúlus* but is incomplete, having lost 'much of the upper part of the occiput above the foramen magnum' (Watson 1928, p. 49). The remainder of the occipital region is already fully ossified, but as usual it must include basi- and exoccipital components and an intercalar, the latter clearly visible as a lateral process in Schaeffer's drawing of the specimen in ventral view (1971, fig. 8A). In front of the cranial fissure there is a large, paired otic ossification which forms the anterior wall of the vagus canal, includes the canal for the glossopharyngeal nerve and a groove for its supratemporal branch according to Watson (not confirmed by Schaeffer) and encloses the lower part of the posterior semicircular canal and the external semicircular canal. Schaeffer's drawing of the specimen in ventral view shows a long, tongue-like process at the postero-ventral corner of this bone which is clearly the homologue of the similar process on the opisthotic of *Pteroniscúlus* and *Perleidus* (figures 115, 117). This bone is therefore exactly comparable with the opisthotic in *Pteroniscülus* and *Perleidus*, and Watson was correct in so naming it. The small pterotic, which should ossify in the postero-dorsal corner of the otic capsule immediately in front of the cranial fissure, must have been lost from the specimen with the adjoining upper part of the occipital arch. In addition to the opisthotic, the specimen of *Cosmoptychius* shows an independent sphenotic which lies well in front of the ascending process of the parasphenoid, as in *Pteroniscülus* and *Perleidus*, and a median basisphenoid (Watson) which appears to be homologous with the basisphenoid of *Perleidus*, parasemionotids and pholidophorids since it contains the buccohypophysial canal, canals for the internal carotids and palatine nerves, and lies between the basipterygoid processes. There is no evidence of a prootic in this specimen, but this bone would be expected to be small (see above), and might either be displaced or not yet ossified.

In summary, available information suggests that the ossification pattern of the palaeoniscoid braincase was most like that in *Perleidus*. In the occipital region there were basi- and exoccipitals, intercalars and epioccipitals, and also one or more independent 'zygals'. In the otic region there was a very large opisthotic and a small pterotic and prootic. In the orbitotemporal region there was a basisphenoid (possibly paired), a large sphenotic, and (in *Pteroniscülus*) an ossification in the roof of the orbit which may be an orbitosphenoid, a pterosphenoid, or represent both these bones.

In all known palaeoniscoid braincases the fissura otico-occipitalis is complete and perichondrally lined throughout, except in some individuals of *Boreosomus piveteaui*, where the mid-dorsal part of the fissure may be closed by a narrow bridge of bone (Nielsen 1942, p. 287, fig. 59). The vestibular fontanelle is always open, and its upper part is perichondrally lined in *Pteroniscülus* and *Boreosomus*, like the fissura otico-occipitalis. The fissura oticalis ventralis is not perichondrally lined, and closes in some individuals of *Boreosomus piveteaui*: it is not joined to the fissura otico-occipitalis in the Devonian palaeoniscoids from Western Australia (Gardiner 1970, 1973), the Kansas palaeoniscids (Rayner 1951, p. 70), *Boreosomus* (Nielsen 1942, p. 288) or *Pteroniscülus macropterus* (Beltan 1968, fig. 2), but in *Pteroniscülus stensioei* (Nielsen 1942) and perhaps also in *Kentuckia* (Rayner 1951) the two fissures are confluent. The structure of the palaeoniscoid braincase is summarized diagrammatically in figure 118.

3. *Polypterus*. In *Polypterus* the occipital arch chondrifies while it is still independent of the parachordals. The upper end of the arch fuses with the otic capsule at 9 mm, but its foot does not fuse with the parachordal until 15 mm (Daget, Bauchot, Bauchot & Arnoult, 1964). The vagus foramen, between these two attachments, remains large, and the occipital arch is always much lower than the otic capsule. In the ossified braincase, the fissura oticalis ventralis is represented in the wide tract of cartilage between the basi-exoccipital and the sphenoid. The fissura otico-occipitalis is obliterated, although the suture between the opisthotic and basi-exoccipital lies in the approximate plane of the metotic fissure.

In adult *Polypterus* the orbitotemporal, otic and occipital regions contain a median basi-exoccipital and sphenoid, and paired opisthotics and sphenotics. The basi-exoccipital arises from paired centres above the notochord. It does not extend beyond the vagus canal, which notches its anterior margin, and does not reach any part of the labyrinth cavity. Dorsally, it does not reach the roofing bones, leaving a quadrangular area of cartilage.

The opisthotic ossifies late, at more than 37 mm (Pehrson 1947), from a centre in the postero-lateral angle of the otic capsule, over the middle part of the posterior semicircular canal. In the adult, the bone becomes large and has extensive membrane bone outgrowths. The opisthotic meets the basi-exoccipital above and below the vagus canal, which is incised in its posterior edge. The opisthotic also forms the posterior margin of the facial canal, contains the glossopharyngeal canal, and lodges parts of the posterior and external semicircular canals. This bone could be interpreted as an opisthotic or a pterotic, or as representing both these bones. The centre of ossification of the bone is intermediate between that of a pterotic (above the posterior semicircular canal) and an opisthotic (lateral to the external semicircular canal), but its relations to the ninth and tenth cranial nerves are those of an opisthotic, not a pterotic. Discrimination between the three possible interpretations requires knowledge of the antecedents or closest relatives of *Polypterus*, which is not available, but the fact that the opisthotic is the dominant ossification in the otic region of palaeonisciforms, while the pterotic only becomes large in relatively advanced forms like *Pachycormus* and pholidophorids, favours interpretation of the bone in *Polypterus* as an opisthotic.

The sphenotic ossifies in the postorbital process and fuses almost immediately with the dermosphenotic. In the adult, the bone does not encroach upon the anterior semicircular canal or cranial cavity, as is usual in primitive actinopterygians.

A transient prootic is described by Pehrson (1947, p. 405) as a thickening of the perichondrium in the posterior margin of the trigeminal foramen in 30 and 37 mm embryos.

The sphenoid arises from paired perichondral lamellae between the optic and oculomotor foramina and grows forwards to form a complete interorbital septum. The bone also forms the anterior margin of the trigeminal foramen and prootic bridge, and contains the foramina of the optic, oculomotor and profundus, and trochlear nerves and the pituitary vein. It has been argued by de Beer (1937, p. 87) that the sphenoid represents the product of fusion of the orbitosphenoid, pterosphenoid and basisphenoid of holosteans and teleosts; and by Holmgren & Stensiö (1936, p. 389) that those three bones of teleosts and holosteans are the products of fragmentation of the sphenoid of *Polypterus*: these are two possible phylogenetic interpretations of the topographic homology between these bones. A third hypothesis is that the sphenoid of *Polypterus* is the phylogenetic homologue of one of the three holostean or teleostean bones (preferably the basisphenoid, which ossifies from approximately the same centre) which has extended following loss of the other two. As in the case of the opisthotic of *Polypterus* the information on ancestral conditions which would allow one to choose between these hypotheses is not available.

4. *Acipenseriformes*. In *Acipenser* the occipital arch fuses with three neural arches while the metotic fissure is still open, and then fuses with the upper part of the otic capsule, leaving a large vagus foramen. As in *Polypterus*, the occipital arch is always much lower than the otic capsule. In the adult braincase, the cranial fissure is obliterated by cartilage throughout, but there is no ossification in this region.

In *Acipenser* neurocranial bones only appear in large, aged individuals and are variable in extent and number (Parker 1882; Holmgren & Stensiö 1936). In the orbitotemporal, otic and occipital regions there is a large exoccipital, small opisthotics, prootics and pterosphenoids, and a large orbitosphenoid. The exoccipital lies in the posterior wall of the braincase, dorsal to the medulla. It arises from paired rudiments which may fuse in the mid-line, producing a median bone. The exoccipital is the only bone to ossify throughout the thickness of the cranial cartilage: all the other bones are confined to the outer surface of the braincase. The opisthotic ossifies between the vagus and glossopharyngeal foramina, the normal centre of an opisthotic. The prootic ossifies either in front of or behind the trigeminal foramen. The pterosphenoid lies in the postero-dorsal corner of the orbit, dorsal to the prootic. The orbitosphenoid is paired. In Holmgren & Stensiö's specimen it is a large bone containing the oculomotor and trochlear foramina, but in Parker's specimen this area is occupied by two smaller, separate ossifications: this seems to be a genuine example of fragmentation of neurocranial bones.

Polyodon is even less well ossified than *Acipenser*. The only endocranial ossification recorded is in the large specimen described by Bridge (1878), where there were two small, superficial, scale-like perichondral ossifications lying close together in front of the vagus foramen. Both bones lie behind the plane of the glossopharyngeal foramen and superficial to the ampulla of the posterior semicircular canal. These small ossifications occupy the same position as the opisthotic of *Acipenser* and other fishes: like the double orbitosphenoid of Parker's sturgeon, they appear to be an example of fragmentation of an opisthotic.

5. *Birgeria*. In this Triassic palaeonisciform the neurocranium is incompletely ossified (Stensiö 1921; Nielsen 1949). The otic and occipital ossifications are separated by a complete cranial fissure, but this fissure was probably bridged by cartilage throughout (Nielsen 1949, p. 190). The occipital region is occupied by a single bone in all specimens, solid dorsally but incompletely ossified ventrally (Nielsen 1949, p. 192). There is a prominent cranio-spinal process, implying the presence of an intercalar.

The otic region contains two paired bones, a sphenotic in the postorbital process and a large 'prootico-opisthotic'. This bone meets its fellow in the dorsal mid-line posteriorly in large individuals (Stensiö 1921, p. 153), but ossifies principally in the lateral wall of the otic region. The bone includes the posterior and external semicircular canals, is notched ventrally by the glossopharyngeal canal, carries the articular facet for the first suprapharyngobranchial, and lines the post-temporal fossa and part of the hyomandibular facet. The centre of ossification of this bone (if single) must have lain dorsal to the external semicircular canal, and probably lay lateral to the middle part of the posterior semicircular canal. As in the case of the 'opisthotic' of *Polypterus*, with which Stensiö compared this bone in *Birgeria*, there are three possible interpretations of the 'prootico-opisthotic': that is in an opisthotic, a pterotic, or represents both these bones. The centre of ossification is probably approximately the same as in the opisthotic of *Polypterus*. As in *Polypterus*, discrimination between these three hypotheses requires knowledge of the precursors or closest relatives of *Birgeria*, which we do not have.

The orbitotemporal region of *Birgeria* contains a large, unpaired sphenoid which has about the same relations as the sphenoid of *Polypterus*, with which it has been compared by all who have discussed *Birgeria*. The comments upon the interpretation of the sphenoid of *Polypterus* (p. 464) will apply equally well to that of *Birgeria*.

6. *Saurichthyidae*. In *Saurichthys* (Stensiö 1925, 1932; Beltan 1968) and *Saurorhynchus* (Gardiner 1960) the neurocranium is fully ossified and without sutures in all known specimens. Nothing is known of the ossification pattern, and the cranial fissure is completely obliterated by bone.

7. *Pholidopleuridae*. The pholidopleurid neurocranium is only known in *Australosomus* (Nielsen 1949; Beltan 1968). The cranial fissure is open throughout since the fissura oticalis ventralis and the vestibular fontanelle are confluent. The fissura otico-occipitalis is perichondrally lined throughout, but the vestibular fontanelle was cartilage filled, like the fissura oticalis ventralis. Nothing is known of the ossification pattern, but the braincase is so similar in form to those of palaeoniscoids, *Perleidus* and pholidophorids that it would be surprising if the mode of ossification were different.

(c) *Conclusions*

(i) *The cranial fissure*

The fissura oticalis ventralis is a feature of adult, ossified braincases. Primitively (in Devonian palaeoniscoids, crossopterygians and acanthodians) the fissura oticalis ventralis lies below the rear of the orbit and represents the cartilage remaining between ossifications in the trabeculae and the parachordals: at this stage the fissure can be said to have an embryonic precursor, the gap between the trabeculae and parachordals, and to be a primitive feature. But in most actinopterygians the fissura oticalis ventralis lies further back, as a result of the development of a large myodome and consequent atrophy of the foremost part of the notochord (p. 541), and retention of a fissura oticalis ventralis of this type in the full-grown braincase is not a primitive feature: the fissure tends to persist in those forms with persistent sutures or with incompletely ossified braincases, both derived conditions.

The fissura oticalis ventralis is normally open in palaeoniscoids, but closes in some individuals of *Boreosomus*. It may also close in *Saurichthys*, *Perleidus*, parasemionotids, early caturids, *Dapedium*, and early pholidophorids and leptolepids, all forms in which sutures do not persist in the fully ossified braincase, and in all these fishes the presence or absence of a fissura oticalis ventralis is an ontogenetic feature without phylogenetic significance. The fissure remains as a wide tract of cartilage in *Polypterus*, *Birgeria* and living holosteans, and is not recognizable in sturgeons and *Polyodon*. In *Lepidotes*, pachycormids, teleosts, and those caturids, parasemionotids, pholidophorids and leptolepids in which the fissure persists, it is represented by the suture between the basioccipital and prootics. Except in the pholidophorid–teleost lineage, where the myodome has broken through into the basioccipital, the position of the fissura oticalis ventralis is a rather accurate indication of the position of the hind wall of the myodome (p. 541). Otherwise, the fissura oticalis ventralis is not closely associated with any structure: for example, it may come to lie well behind the glossopharyngeal foramen (*Lepidotes*).

The fissura otico-occipitalis is a feature of adult, ossified braincases and represents the persisting metotic fissure of the embryo: as such, it is undoubtedly a primitive feature. Apart from actinopterygians, a fissura otico-occipitalis is also known in acanthodians (*Acanthodes*, Miles 1971, p. 66), rhipidistians (*Eusthenopteron* and porolepiforms, Jarvik 1954, p. 7; 1972, p. 64; Bjerring 1971, p. 203) and lungfishes (*Griphognathus*, Miles 1971, p. 151), but in these three groups the fissure was evidently bridged by cartilage since the bones bordering it are not perichondrally lined. This, in turn, is undoubtedly an advanced condition relative to the perichondrally lined fissure of primitive actinopterygians.

The vestibular fontanelle, at the antero-ventral corner of the fissura otico-occipitalis and anterior or ventral to the glossopharyngeal foramen, corresponds to the anterior basicapsular fenestra of the embryo. A vestibular fontanelle occurs in rhipidistians (*Eusthenopteron*, Jarvik 1954, fig. 1; Bjerring 1971, fig. 8), and may have been represented within the broad tract of cartilage in the ventro-lateral part of the otic region of *Acanthodes* (Miles 1971, fig. 4.7). The vestibular fontanelle is only known to be perichondrally lined in the palaeoniscoids *Boreosomus* (where it is small and may be completely lined) and *Pteronisculus* (where the uppermost part of the fontanelle may be so lined). A perichondrally lined vestibular fontanelle is presumably primitive and in most other actinopterygians the fontanelle was occluded by cartilage, as in *Eusthenopteron*. But in various teleosts it is closed by membrane, and this condition is associated with an otophysic connexion and may be derived. In those forms where the fontanelle is filled with cartilage, it can close in bone during ontogeny, as it does in *Perleidus* and some parasemionotids and pholidophorids, and is not of phylogenetic significance.

Among actinopterygians, an uninterrupted, perichondrally lined fissura otico-occipitalis is so far known only in palaeoniscoids, *Australosomus* and pholidophorids (*Pholidophoroides limbata*, some *Pholidophorus bechei*, *P. minor*). In pholidophorids, parts of this fissure are covered superficially by membranous outgrowths of the intercalar and (in *P. bechei*) supraoccipital. Portions of the fissure remain perichondrally lined in *Perleidus*, some parasemionotids, pachycormids and early leptolepids, but in all other actinopterygians the fissure is closed in cartilage.

In pholidophorids and leptolepids, the only groups in which there is a closely spaced morphological series illustrating closure of the fissure, the fissure becomes obliterated by three processes, the development of membrane bone outgrowths from bones bordering on the fissure, closure of the fissure in cartilage but persistence as a suture, and obliteration by forward extension of the occipital bones. The first of these processes, the development of membrane bone outgrowths, is a superficial phenomenon, and hides but does not necessarily modify the underlying fissure. The second and third processes are consequent upon ontogenetic closure of the fissure in cartilage, by fusion of the otic capsule and occipital arch in the embryo. The second process, persistence as a suture, may precede the third in phylogeny but cannot follow it.

The first process, development of membrane bone outgrowths bridging the fissure, is known (apart from pholidophorids and leptolepids) in *Perleidus*, parasemionotids and *Pachycormus*, where the intercalar develops a small lateral outgrowth lapping round the lateral margin of the vagus foramen; in caturids and amiids, where the intercalar develops extensive outgrowths ventral to the vagus foramen; and in *Polypterus*, where the opisthotic develops posterior membranous outgrowths covering the site of the dorso-lateral part of the fissure.

The second process, persistence of parts of the fissura otico-occipitalis as a (cartilage-filled) suture, is confined to those groups with persistent sutures, but it may also be inferred as a transient stage in the ontogeny of some forms in which the sutures are obliterated. Persistent sutures along the line of the fissure are found along the lateral part of the fissure in *Polypterus* (basi-exoccipital/opisthotic suture), and in the dorso-lateral and ventro-lateral part of the fissure of *Pachycormus* (pterotic/basi-exoccipital and opisthotic/basi-exoccipital sutures) and caturids (epioccipital/pterotic and exoccipital/opisthotic sutures). Transient sutures along the line of the fissure can be inferred in parasemionotids (epioccipital/pterotic and exoccipital/opisthotic sutures). In the pholidophorid–teleost lineage persistent sutures along the line of the fissure are found only in pholidophorids (basi-exoccipital/opisthotic suture of *P. germanicus* and *P. macrocephalus*, epioccipital/pterotic suture of *P. macrocephalus*.

Obliteration of the fissura otico-occipitalis by forward extension of the occipital bones is the dominant process in pholidophorids and leptolepids, where it proceeded stepwise from above and below (figure 95). From above, two steps are recognizable, obliteration of the supraoccipital and epioccipital portions. From below, two steps are also recognizable, obliteration of the subvagal (opisthotic) and supravagal (intercalar) portions. Similar stepwise closure of the fissure can also be recognized in other groups in which parts of the fissure persist. From above, the thread-like mid-dorsal closure of the fissure in some individuals of *Boreosomus* is probably not significant, but in *Perleidus* a mid-dorsal portion closes which appears to be strictly homologous with the supraoccipital portion in pholidophorids. The epioccipital portion is closed in all parasemionotids. From below, closure of the fissure seems to be more variable; the subvagal portion is closed or partially open in *Perleidus*, and the supravagal portion is partially open in

Pachycormus, and closed, open or partially open in parasemionotids. In terms of the persisting perichondrally lined part of the fissure, in *Perleidus* it extends from the vagus canal to the medial edge of the epioccipital, in parasemionotids from the vagus canal to the upper edge of the exoccipital, and in *Pachycormus* only a small part between the intercalar and the pterotic and opisthotic remains.

In those groups where only parts of the fissure have closed (perleidids, parasemionotids, pachycormids) there is no evidence of forward extension of the occipital bones such as occurs in pholidophorids and leptolepids. This is also true of some forms in which the fissure is completely obliterated by bone (*Saurichthys*, *Dapedium*, some caturids) and of those in which the fissure remains as a suture between the otic and occipital bones (*Polypterus*, some caturids). But in *Lepidotes*, *Lepisosteus* and some amiids the exoccipital has extended forwards into the occipital region, enclosing the vagus canal and sometimes impinging upon the posterior semicircular canal or ampullary chamber. In these forms there is no opisthotic and no endochondral intercalar: in leptolepids the consequence of forward extension of the exoccipital was the loss of these bones, and it must be assumed that the same changes have taken place in *Lepidotes*, *Lepisosteus* and amiids. Whether there has been any extension of dorsal occipital bones (epioccipital) into the otic region, or the reverse, extension of otic bones (pterotic) into the occipital region in these fishes depends upon the homology assigned to the 'epiotic' of *Lepidotes*, *Lepisosteus* and *Amia*. The provisional interpretation adopted here is that in *Lepidotes* and *Lepisosteus* the 'epiotic' is a pterotic which has extended back into the occipital region, and in amiids the 'epiotic' is an epioccipital which has extended forwards.

(ii) *Ossification patterns*

An attempt to give a general account of bone patterns in the actinopterygian braincase necessitates some preliminary discussion of two questions; how endocranial bone homologies are to be recognized between one group and another in the absence of intermediate forms; and whether, in the absence of knowledge of the ossification pattern in the earliest actinopterygians, a hypothesis of increase of ossification centres ('fragmentation') is preferable to one of decrease ('fusion', loss).

One even more general question must first be mentioned. de Beer (1937, p. 503) arrived at the conclusion 'it is not possible to arrive at a satisfactory definition of what constitutes a bone along embryological lines, in terms of separate centres of ossification'. The examples he cites in support of this (multiple ossification centres of tooth-bearing bones, of nasal and frontal in *Amia*, etc.) are mainly drawn from the dermal skeleton. In the endoskeleton, the only difficult cases mentioned by de Beer are the long bones of mammals, with a diaphysis and two epiphyses, and the otic bones of fishes, which arise from internal and external perichondral lamellae. The long bones of mammals are certainly adaptive, and do not concern us here. In the otic bones of fishes, the internal and external lamellae arise opposite one another, and as de Beer says, they can hardly be regarded as separate bones. Some examples have been found in pholidophorids and parasemionotids (pp. 338, 433) of perichondral lamellae which appear to be 'outriders' of a large endo- and perichondral ossification, encroaching upon and doubtless fusing with the perichondral lamellae as it reaches them: these I do not regard as separate bones, realizing that in doing so I am only expressing an arbitrary opinion. But where small, perichondral disks appear, develop no further and are engulfed by an encroaching peri- and endochondral ossification, I think it best to disregard them. Whatever the difficulties of defining 'a bone' in the exoskeleton, I believe that endocranial ossifications can be regarded as single bones, growing from definite ossification centres.

Given that it is possible to recognize 'a bone' in the braincase, how are homologies between such bones to be established from one group to another, in the absence of intermediate forms? de Beer (1937, pp. 491–512) has given the most complete discussion of the general problem of endocranial bone homologies, and Rayner (1948, pp. 332–8) and Schaeffer (1971, pp. 16–29) have discussed the question in relation to fossil actinopterygians: most other authors have restricted themselves to assertions of homology, non-homology or 'partial' homology. In recent years there has been much discussion of the meaning of biological homology (Jardine 1970, and references cited there), and the concept is now a little more explicit. Jardine draws a distinction between 'topographic homology' and 'phylogenetic homology', regarding the latter as a special case of the former. In the braincase, bones which are phylogenetic homologues are not always precise topographic homologues (see the discussion of the basisphenoid of *Amia* and teleosts, p. 443, and of the pterotic of pholidophorids and teleosts, p. 422). It is necessary to break down the concept of topographic homology further, for there are two ways in which topographic homologies are, in practice, established between endocranial bones in different groups. The first is based upon topographic correspondence in adult or fully ossified braincases, the second upon correspondence of the ossification centre in the embryo. In most cases, these two criteria lead to the same conclusion; in the sphenotic and prootic, for example, there is little room for argument about homologies. But there are important examples where the two criteria conflict. Thus Daget (1950, p. 35) proposed that the sphenoid of *Polypterus* is the homologue of the orbitosphenoid and pterosphenoid of *Acipenser*, and Holmgren & Stensiö (1936, p. 389) that it is the homologue of the orbitosphenoid, pterosphenoid and basisphenoid of teleosts, on the grounds of topographic correspondence in the adult. But the sphenoid of *Polypterus* ossifies from a centre between the optic and oculomotor foramina, and by this criterion corresponds to the orbitosphenoid of *Acipenser* and the basisphenoid of teleosts. There is no obvious reason why one of these criteria is preferable to the other, and to discriminate between the alternative topographic homologies it is necessary to translate them into phylogenetic homologies by constructing hypotheses about conditions in a common ancestor. Regarding the bones in the interorbital septum of *Polypterus*, *Acipenser* and teleosts (holosteans show the same pattern as teleosts), the simplest such hypotheses would be the alternatives (*a*) that the ancestral condition was as in *Polypterus*, with a single ossification centre, the extra bones in *Acipenser* and teleosts being new formations: (*b*) that the ancestral condition was as in teleosts, *Acipenser* having lost one bone and *Polypterus* two (the possibility of fusion of these bones is not considered, since it appears that 'phylogenetic fusion' is a concept without meaning when applied to the braincase, see p. 421). Such hypotheses lead on to the second question set out at the head of this section, whether, in the actinopterygian braincase, the hypothesis of increase of ossification centres is preferable to that of decrease (loss).

It has been customary to adopt hypotheses of the first sort (increase, fragmentation), and to regard a neurocranium ossifying from numerous centres as advanced (Stensiö 1932; Holmgren & Stensiö 1936; Daget 1964; Beltan 1968). The alternative hypothesis, that the numerous bones of teleosts and holosteans 'reflect primary ossification sites in the palaeonisciform neurocranium', has been recently proposed by Schaeffer (1971, p. 26), and seems also to be advocated by Westoll (1944, p. 95). Rayner (1948, p. 335) found it impossible to choose between the two hypotheses.

The evidence for the proposition that a subdivided neurocranium is advanced may be summarized as follows. (1) The most highly subdivided neurocranium is that of the teleosts, and these are the most advanced actinopterygians. (2) In those palaeoniscoids where the ossification pattern is known (*Cosmoptychius*, *Birgeria*), it is similar to that in *Polypterus*, and there are fewer bones than in teleosts or most holosteans. (3) The pattern of ossification in these chondrosteans resembles that in *Acanthodes*. The spread of this hypothesis has also been due, in part, to the influence of Stensiö's unjustified assumption (1932, p. 297) that the one or two large ossifications in the braincase of adult palaeoniscoids is evidence that the braincase ossified, during ontogeny, from the same number of centres.

Against the first of the three points listed above, it has now been shown that the braincase of living teleosts actually contains fewer endochondral bones than that of the pholidophorids, which are undoubtedly more primitive, the intercalar and opisthotic having been lost as a consequence of closure of the fissura otico-occipitalis. Among other primitive actinopterygian groups in which the ossification pattern is known, the parasemionotids only lack one bone present in pholidophorids, the supraoccipital, and the latter may or may not be present in *Perleidus*, which otherwise shows the same pattern as pholidophorids and parasemionotids.

Against the second point listed above, it cannot be said that *Polypterus*, though in many ways a very primitive fish, has a primitive braincase. The same is true of *Birgeria*, in which the braincase is constructed very differently from that of the central palaeonisciform type (Nielsen 1949, p. 206). As for *Cosmoptychius*, the braincase is known only from a single incomplete specimen, and alternative interpretations of the parts preserved are possible (p. 462). Against the third point, it is only necessary to point out that *Acanthodes* was the last survivor of the acanthodians, and its braincase is hardly more likely to be indicative of primitive conditions in the group than is that of a living chondrostean or holostean of primitive actinopterygian conditions.

The evidence for the hypothesis of fragmentation or increase in number of neurocranial ossification centres in actinopterygian evolution is therefore questionable. Following the preceding survey of ossification patterns in the orbitotemporal, otic and occipital regions of actinopterygians, it is possible to make a more thorough analysis of evidence for and against the 'fragmentation hypothesis'.

The most primitive actinopterygian braincases known are certainly those of the Devonian palaeoniscoids from Western Australia now being studied by B. G. Gardiner (Gardiner 1970, 1973; Miles 1971, fig. 5.6). These are similar to the 'central palaeonisciform type' as defined by Nielsen (1949, p. 61), differing principally in the anterior position of the fissura oticalis ventralis, the very short spiracular canal, and the absence of a well defined fossa bridgei (cf. Rayner 1951, p. 78). Fishes with a braincase of central palaeonisciform type have been shown above to have an ossification pattern which is most economically interpreted as being essentially the same as in *Perleidus* with the addition of one or more zygals, the only areas of uncertainty being the presence or absence of a supraoccipital, and distinction between an orbitosphenoid and pterosphenoid in the orbit. The major difference between the palaeoniscoid pattern and that of pholidophorids and parasemionotids is the dominance of the opisthotic relative to the prootic and pterotic.

Parasemionotids differ from pholidophorids only in having no supraoccipital, and it is not yet clear whether this is a derived or primitive condition. The parasemionotid pattern is characteristic of all caturids except the Upper Jurassic *Caturus furcatus*, where the braincase is incompletely ossified and the opisthotic apparently lost. In amiids the braincase is also incompletely ossified, and here the opisthotic, intercalar and pterotic (probably) are missing. In pachycormids the upper part of the occipital arch fails to ossify and there is no epioccipital or supraoccipital. In *Lepidotes* and *Lepisosteus* the braincase is also incompletely ossified, and here there is no intercalar, opisthotic, supraoccipital or epioccipital (probably). The basisphenoid is also lost in *Lepisosteus*. Among fossil and living holosteans, the only new bone is the median supraotic recorded in the caturid '*Aspidorhynchus*' and in one specimen of *Lepidotes*: this ossification can hardly be regarded as evidence for the hypothesis of increase in number of ossification centres since it appears in a part of the braincase, the taenia tecti medialis, which was not even chondrified in palaeoniscoids.

In teleosts, the basic pattern of ossification is as in leptolepids, lacking the opisthotic and intercalar of pholidophorids. Examples of loss of neurocranial bones within the teleosts are numerous (p. 427). The only possible example of fragmentation or increase in the occipital, otic and orbitotemporal regions is the rhinosphenoid of characins (Starks 1926; Weitzman 1962; Roberts 1969), a median bone in the foremost part of the interorbital septum, ossifying from paired perichondral lamellae. Yet even here the evidence that this is a new formation is equivocal, for what appears to be the topographic homologue of the rhinosphenoid is present as an independent ossification in the palaeoniscoid *Pteronisculus* (Nielsen 1942, fig. 9, sn), and it is not impossible that such an ossification is widely distributed in fossil actinopterygians in this little-known part of the braincase.

In living chondrosteans, there seem to be two examples of genuine fragmentation, the double orbitosphenoid in Parker's sturgeon and the double opisthotic in Bridge's *Polyodon*. These do not develop beyond the perichondral stage and only appear in aged individuals in an otherwise almost entirely cartilaginous braincase: they cannot be taken as evidence in support of a general hypothesis of bone fragmentation. In other respects, living chondrosteans provide a good example of loss of bones through reduction in ossification.

In *Polypterus*, the ossification pattern differs considerably from the palaeoniscoid type, lacking a basioccipital, intercalar, epioccipital, pterotic and one or two sphenoid bones, and having the prootic represented only by a transient rudiment. If *Polypterus* is an actinopterygian, a link with the palaeoniscoid type may be provided by *Birgeria*, which has essentially the same ossification pattern in the braincase. There is good evidence that *Birgeria* is a somewhat specialized relative of the palaeoniscoids (Nielsen 1949, p. 286), and the ossification pattern of its braincase is most reasonably interpreted as derived from an ancestor of palaeoniscoid type by loss of ossification centres, partly as a result of reduction in ossification and partly as a result of changes in shape. The same interpretation can be applied to *Polypterus*.

From this survey, it is evident that the dominant process in actinopterygian evolution has been reduction in the number of endocranial ossifications, not increase. There is no well documented example of the appearance of a new ossification centre except under special conditions (supraotic of *Lepidotes* and '*Aspidorhynchus*', fragmentation in living chondrosteans). Other possible examples of new ossifications are the supraoccipital of pholidophorids and teleosts and the orbitosphenoid or pterosphenoid of holosteans and teleosts, but in both cases the evidence is still equivocal.

Examples of loss are numerous, especially in the pholidophorids and teleosts, where the evidence is most complete. Such loss may be due to three causes, regression in chondrification (orbitosphenoid of acanthopterygians, for example), regression in ossification (epiotic and supraoccipital in some teleosts, basisphenoid in *Lepisosteus*, epioccipital in *Pachycormus*, opisthotic in *Caturus furcatus*, pterotic in *Amia*, etc.), and changes due to closure of the cranial fissure (intercalar and opisthotic in teleosts and presumably also in living holosteans and *Lepidotes*, and probably the epioccipital in *Lepidotes* and *Lepisosteus*). The loss of zygals in non-palaeoniscoid actinopterygians may be due to posterior migration of the fissura oticalis ventralis caused by enlargement of the myodome (p. 541).

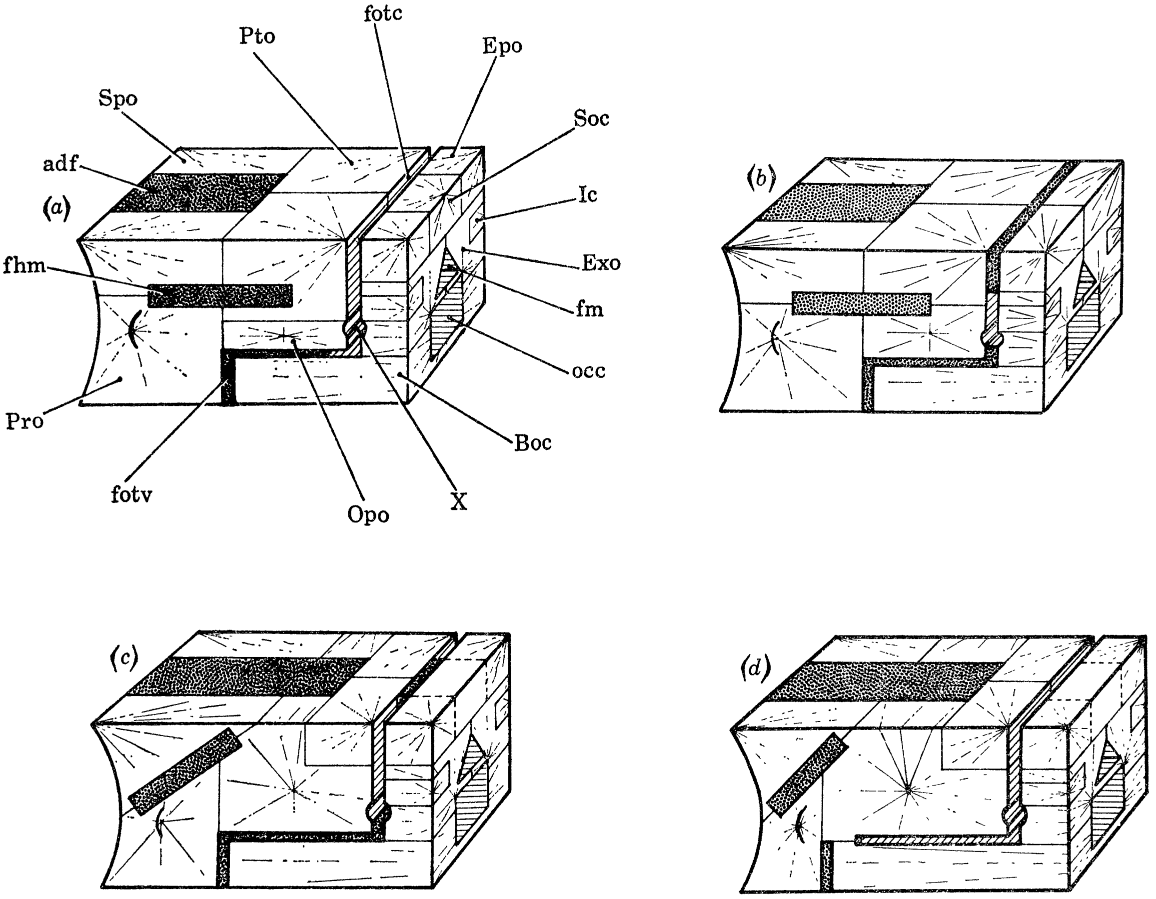


FIGURE 118. Block diagrams summarizing the cranial fissure and ossification pattern of the postorbital part of the neurocranium in primitive actinopterygians. For conventions adopted see legend of figure 95. (*a*) A primitive pholidophorid (e.g. *Pholidophorus bechei*), cranial fissure uninterrupted, supraoccipital present, opisthotic small. (*b*) A parasemionotid, cranial fissure mainly cartilage-filled, no supraoccipital, opisthotic larger. (*c*) *Perleidus*, cranial fissure partially open, supraoccipital may be present, hyomandibular facet inclined, opisthotic very large, pterotic small. (*d*) Inferred condition in primitive palaeoniscoids, fissura oticalis ventralis and fissura otico-occipitalis separate, hyomandibular facet strongly inclined, opisthotic very large, prootic and pterotic small, supraoccipital may be present.

A general hypothesis of bone loss is therefore preferable to one of fragmentation, though caution is still necessary in the region of the interorbital septum. This leads to the hypothesis that the primitive actinopterygian braincase was fully ossified and contained the following ossifications: in the occipital region, a basioccipital (possibly originally paired), large exoccipitals and small intercalars and epioccipitals; in the otic region, large opisthotics, small pterotics and prootics, and one or more zygals; in the orbitotemporal region, a large basisphenoid, probably ossifying from paired centres, large sphenotics, and one or more pairs of bones in the interorbital septum. From this basic pattern, loss of ossification centres through reduction in ossification or changes in the cranial fissure will economically account for all the patterns encountered in actinopterygians (figures 95, 105, 114, 118).

Turning finally to other vertebrate groups, this array of endocranial bones is nowhere found. In acanthodians, which have the most actinopterygian-like braincase of any other group, *Acanthodes* (Miles 1971, fig. 4. 7) has a basioccipital, large, paired exoccipitals with a well developed paroccipital process suggesting an intercalar, a large basisphenoid, and a large dorsal bone which appears to include separate opisthotic and sphenotic centres and may have contained a pterotic and a sphenoid. There is no evidence of epioccipitals or prootics.

In dipnoans, nothing is yet known of the ossification pattern in primitive, fully ossified forms and the living lungfishes have very little neurocranial bone.

In coelacanths, *Latimeria* only has a basisphenoid in the orbitotemporal region, a 'prootic' and three zygals in the otic region, and in the occipital region a supraoccipital, a paired 'exoccipital' which encloses the glossopharyngeal foramen, and upper and lower median 'basioccipitals': though numerous, these bones are not readily comparable with those of actinopterygians (or acanthodians). Almost nothing is known of the ossification pattern in primitive, fully ossified coelacanth braincases. The fissura otico-occipitalis is eliminated in all known coelacanths, and this presumably had some effect on the ossification pattern in the otic and occipital regions.

In tetrapods, there are fewer endocranial ossifications than in primitive actinopterygians. In tetrapods not only is the fissura otico-occipitalis obliterated, but the rhipidistian intracranial joint has also presumably been lost at some stage in phylogeny: these two events must be assumed to have produced a reduction in the number of bones in the braincase. In rhipidistians the ossification pattern remains largely unknown, but Jarvik's (1972) recent interpretation of the otoccipital and posterior part of the ethmosphenoid of *Eusthenopteron* in terms of cranial vertebrae implies numerous ossification centres.

7. Ethmoid region and associated dermal bones

As is usual in fossil fishes, the ethmoid region is much less frequently well preserved than the more posterior parts of the braincase: it is often missing from the fossils, and when preserved it is as a rule less thoroughly ossified. Only in the Callovian *Leptolepis* is a complete set of isolated, uncrushed ethmoid bones available, and in this comparatively advanced species the mesethmoid is apparently unossified. To serve as a basis for comparative descriptions, the ethmoid region will be described in detail in *Pholidophorus germanicus* and the Sinemurian *Leptolepis*: in the first only the lateral ethmoids are well preserved, in the second only the mesethmoid. Together with the endoskeletal ethmoid bones, the investing dermal bones will be described, since in the more advanced leptolepids the roofing bones (rostral and lateral dermethmoids, see p. 481 for the meaning of this new term) become fused with the endoskeleton, and in some leptolepids the vomer is also fused into the ethmoid block.

The terminology employed here mainly follows Weitzman (1967*b*). In the endoskeleton, 'lateral ethmoid' is a term about which there can be little misunderstanding; 'supraethmoid' is a median bone developing on the dorsal surface of the nasal septum; 'ventral ethmoid' is a median bone developing on the underside of the ethmoid cartilage, above and closely associated with the vomer; 'anterior myodome bone' (ethmomyodomal of McDowall 1969) is a median, conical bone ossifying in the hind wall of the nasal septum and lining the foremost part of the anterior myodome. These ossifications may be joined by peri- and endochondral bone into a single ossification in full-grown individuals: the resulting compound ossification is referred to as the mesethmoid. In the dermal skeleton, 'rostral' is the median bone containing the ethmoid commissural sensory canal (or pit-line groove), and the new term 'lateral dermethmoid' is introduced for a paired anamestic bone on the dorsal surface of the snout, underlying the rostral and overlying the supraethmoid (see p. 481 for a fuller account of these bones). The term 'vomer' needs no comment. In some leptolepids, the rostral and lateral dermethmoids fuse with each other and with the underlying mesethmoid: the resulting ossification is called the mesethmoid (see p. 488).

(*a*) Pholidophorus germanicus

The *lateral ethmoid* is shown in lateral, medial, dorsal, posterior and anterior view in figure 119, and in dorsal view in figure 121 (Le). The lateral ethmoids are more lightly ossified than the posterior parts of the braincase and consist only of a shell of thin perichondral bone, with no endochondral bone whatever. As usual in such ossifications, the canals through the bones for nerves and vessels are also surrounded by tubes of perichondral bone.

The left and right lateral ethmoids were separated in life by dorsal and ventral areas of cartilage, and by a wide, bone-lined canal between these. Each lateral ethmoid consists essentially of a transverse wall, ossifying in the orbitonasal lamina, with a postero-dorsal process underlying the frontal and an antero-lateral process lining the postero-lateral part of the nasal pit.

The posterior, orbital surface of the bone is deeply concave and has a wide notch in its medial margin, the posterior opening of the wide, median bone-lined canal (amyo) leading through into the nasal pit. The olfactory nerves presumably passed through this canal into the nasal pits, but the canal is too wide to have contained only these nerves, and its relationship with the anterior myodome bone (see below), embedded in the posterior face of the ethmoid cartilage in front of the canal, shows that the canal is the posterior part of a median anterior myodome. Both the superior and inferior oblique muscles must have passed through the canal into the anterior myodome bone, since there is no other depression on the posterior face of the lateral ethmoid. Lateral to the anterior myodome, the lateral ethmoid is perforated by a narrow longitudinal canal (onc, figures 119*a*, *d*, *e*), which is double throughout its length on the right side of the specimen. This canal must be the homologue of the canal transmitting the orbitonasal vein in sturgeons (Jarvik 1942, p. 269) and *Australosomus* (Nielsen 1949, p. 61). Since the canal is double on the right side, some other structure accompanied the vein, probably the orbitonasal artery (cf. *Polypterus*, Jarvik 1942, p. 260). In the uppermost part of the posterior face of the lateral ethmoid there is the opening of another canal (cson, figures 119*a*–*e*) which leads through the bone and opens in a longitudinal groove on its dorsal surface (gson, figures 119*c*, *e*). This canal and groove lie just medial to the supraorbital sensory canal in the frontal and nasal, and must have carried the superficial ophthalmic nerve innervating that canal. Since the groove turns medially anteriorly it must also have contained the superficial ophthalmic trunk of the trigeminal nerve, and presumably also the profundus, since no other canal is present. The profundus and superficial ophthalmic nerves were therefore united, as in *Australosomus* (Nielsen 1949), *Amia* and most teleosts (Jarvik 1942).

Lateral to the groove for the superficial ophthalmics, the dorsal surface of the lateral

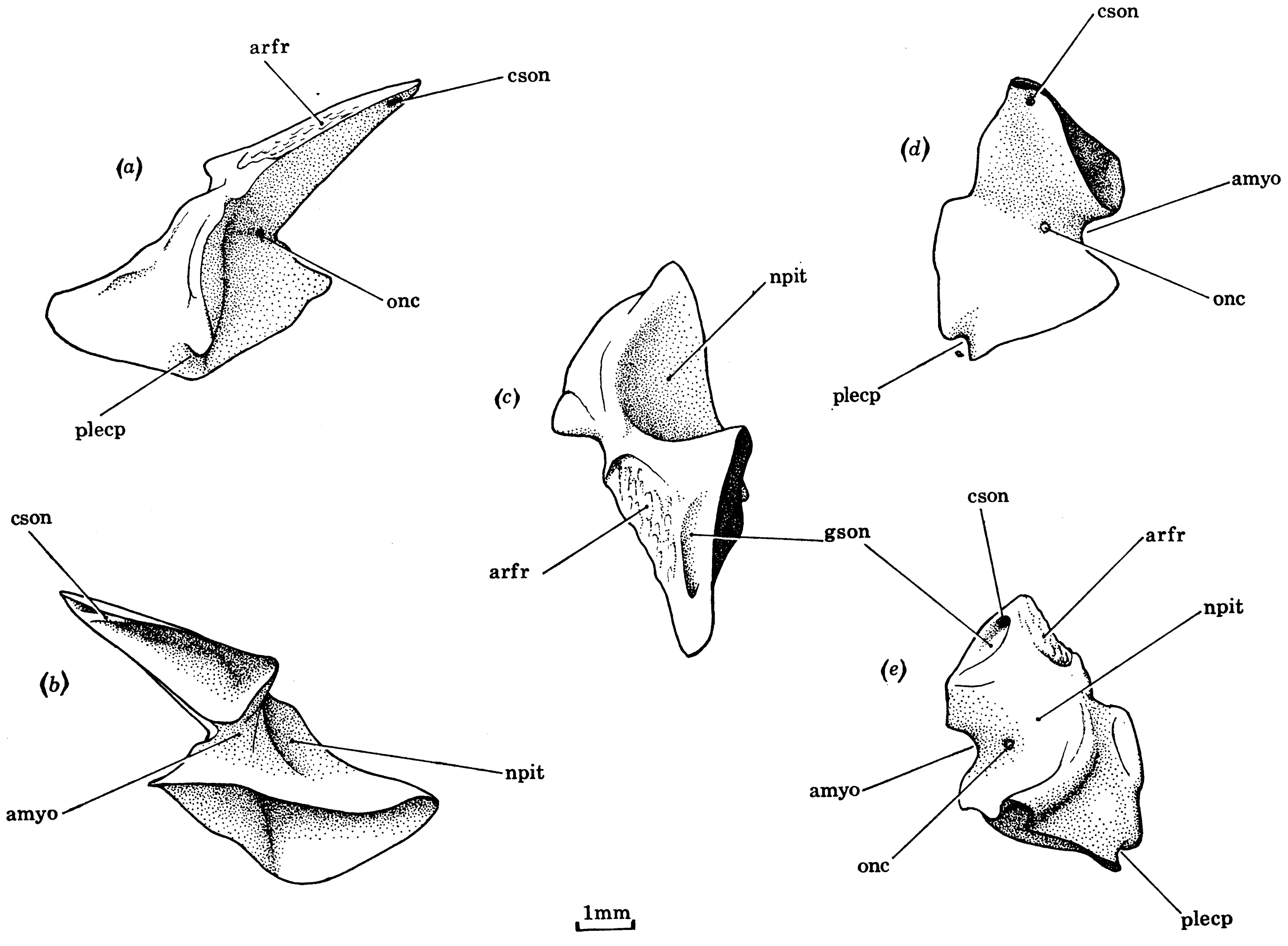


Figure 119. *Pholidophorus germanicus* Quenstedt. Left lateral ethmoid in lateral (*a*), medial (*b*), dorsal (*c*), posterior (*d*) and anterior (*e*) views, from P.3704.

ethmoid is flat and ridged (arfr), and articulated with the antero-lateral lamina of the frontal (figures 121, 146).

Anteriorly, the lateral ethmoid forms the floor, side and hind walls of the posterior and lateral parts of the nasal pit (npit). The canal for the orbitonasal vessels opens in the hind wall of the pit, and its side wall is formed by a curved crest. Lateral to this crest there is a depressed area, probably giving origin to the anterior division of the levator muscles of the palate. This depression is limited posteriorly by a strong vertical ridge, the anterior border of the orbit. The broad lower part of this ridge articulated with the lachrymal. Below the ridge there is a notch (plecp, figures 119*a*, *d*, *e*). A similar notch in the lateral ethmoid of fossil actinopterygians is usually interpreted as having carried the maxillary and buccal nerves, but while these nerves and the accompanying vessels may have passed through the notch, comparison with *P. macrocephalus* (figure 84), leptolepids (figures 128, 130) and living teleosts suggests that the notch was the site of origin of the ligament from the ectopterygoid (cf. Kirchhoff 1958, fig. 18).

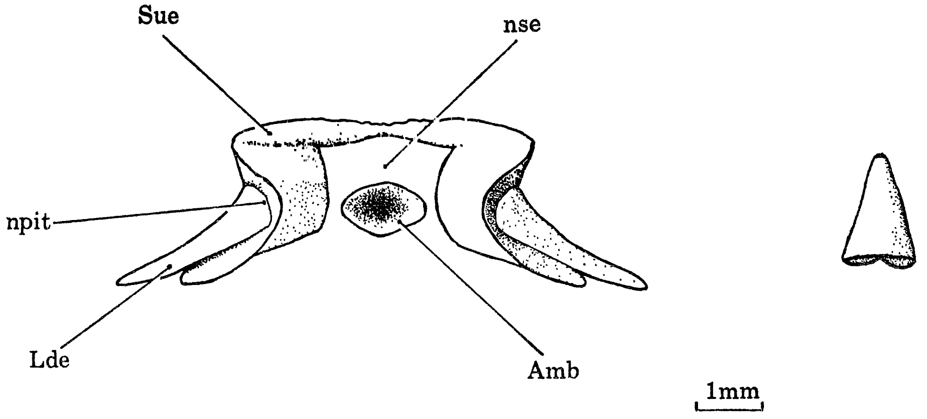


FIGURE 120. *Pholidophorus germanicus* Quenstedt. Left, anterior myodome bone and preserved (posterior) parts of supraethmoid and lateral dermethmoids in posterior view. Right, anterior myodome bone in dorsal view. Based on P.3704.

The ventral surface of the lateral ethmoid was entirely cartilaginous, and the palatine cartilage must have articulated with this surface.

In the acid-prepared specimen of *P. germanicus*, only the most posterior part of the *supraethmoid* is preserved. Like the lateral ethmoid, the supraethmoid is lightly ossified, consisting only of a shell of thin perichondral bone, and the ventral part of the ethmoid cartilage, overlying the vomer, was entirely unossified. The preserved part of the bone (Sue), restored in posterior view in figure 120, closely resembles the corresponding part of the mesethmoid in the Sinemurian *Leptolepis* (figure 123), except that the nasal septum (nse) is broader in *P. germanicus*.

The median *anterior myodome bone* (Amb, figure 120) was embedded in the cartilage of the nasal septum in life. It is an elongate, hollow cone of perichondral bone, open posteriorly, and with its posterior opening broader than high. Both pairs of oblique muscles originated in the cavity of the bone.

In the acid-prepared *P. germanicus* the *rostral* is missing and only the most posterior parts of the *lateral dermethmoids* (Lde, figure 120: see p. 481 for the meaning of this term) are preserved. They are curved laminae of dermal bone lying in the floor of the nasal pit, superficial to the lateral walls of the supraethmoid and quite free from them: the association between the supraethmoid and the lateral dermethmoids appears to have been much less intimate in *P. germanicus* than it is in the Sinemurian *Leptolepis* (see below).

The snout of P.7580, a specimen of *P. germanicus* from the Upper Lias of Ohmden, Germany, has been prepared mechanically and is shown in figure 121. The preservation of this specimen is far from perfect, and it is only possible to interpret the snout by comparison with other pholidophorids (cf. figures 124, 125). The lateral ethmoids (Le) resemble those of the acid-prepared *P. germanicus*, but in the floor of the nasal pit (npit) the surface of the bone is pitted.

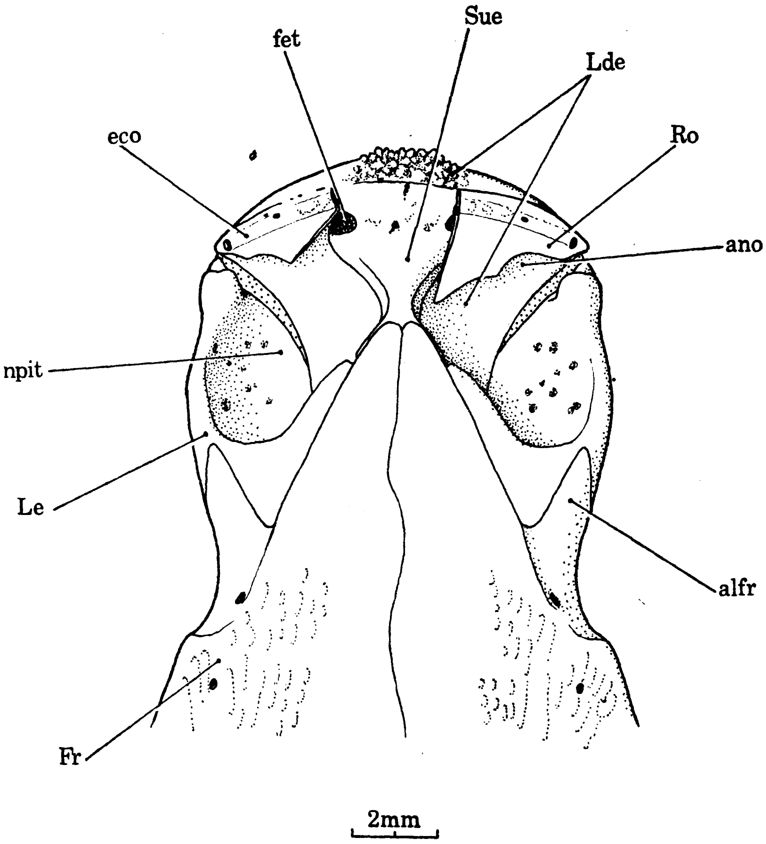


Figure 121. *Pholidophorus germanicus* Quenstedt. Attempted restoration of ethmoid region as preserved in P.7580 (U. Lias, Ohmden, Germany). The middle part of the rostral is missing and the bone beneath it is damaged. Regular stipple in the floor of the nasal pit indicates cartilage.

The posterior parts of the lateral dermethmoids (Lde) line the antero-medial part of the nasal pit, and extend back to the lateral ethmoids. The dorsal surface of the anterior part of the supraethmoid (Sue) is destroyed, and the junction between this bone and the lateral dermethmoids cannot be seen. In the antero-medial corner of each nasal pit there appears to be a large foramen or pit (fet), bordered by the supraethmoid medially and the lateral dermethmoid laterally: no other pholidophorid is known to have such structures, and the preservation of this specimen is such that one can do no more than record them. Anteriorly, the lateral dermethmoids project beyond the rostral in a broad, shallow rostrum which is strongly tuberculated near the mid-line. No median suture between the lateral dermethmoids is visible in this rostrum. The underside of the rostrum has been partially excavated and it is unlikely that the lateral dermethmoids bore teeth (cf. *P. macrocephalus* below). The middle part of the rostral (Ro) is missing, but the preserved parts, overlying the lateral dermethmoids, show that the bone was broad and penetrated throughout its width by the ethmoid commissure (eco). A notch in the posterior margin of the rostral (ano) marks the position of the anterior nostril. On the left side of the specimen the anterior margin of the rostral is partially fused with the lateral dermethmoid, but on the right side the bones are separate.

The *vomer* of *P. germanicus* is shown in dorsal, lateral and ventral view in figure 122. It is an unpaired bone, as in teleosts, and consists of a complex head and a long posterior process. The posterior process is bifid for much of its length and fits in a groove on the underside of the parasphenoid (figure 142). The ventral part of the head of the vomer consists of a massive transverse bar which extends postero-ventrally and bears small teeth. The tooth patch is continuous from side to side, but is partially divided by a constriction in the mid-line. The anterior face of this bar presents a smooth, slightly concave surface without obvious articular facets but with a deep median notch in the upper margin. On the dorsal surface of the head of the vomer there is a pair of ear-like processes directed postero-laterally. The upper surface of these processes was probably only partially covered by the ethmoid cartilage, and the uncovered portion contributed to the articular surface for the head of the maxilla (amx). In the angle between the underside of this process and the head of the vomer there is a recess (plig), open postero-laterally, in which the ethmo-palatine ligament must have originated. There is no ossified autopalatine in *P. germanicus*, but the dermopalatine abutted against the margin of the transverse, tooth-bearing part of the vomer (apal).

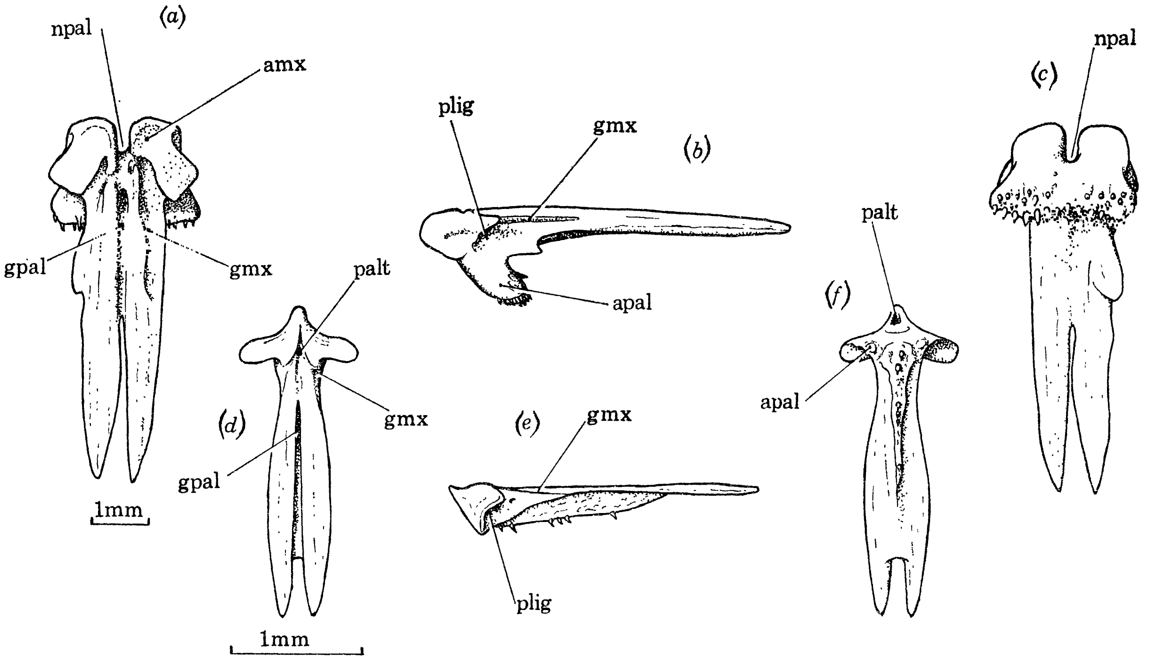


FIGURE 122. Vomer of *Pholidophorus germanicus* Quenstedt (*a–c*), from P.3704, and Callovian *Leptolepis* sp. (*d–f*), from P.51738, in dorsal (*a*, *d*), left lateral (*b*, *e*) and ventral (*c*, *f*) views.

The dorsal surface of the vomer was embedded in the ethmoid cartilage. There is a deep median groove (gpal) on this surface, ending in the median notch (npal) in the head of the bone. This groove contained the anterior branch of the palatine nerves, and branches from the nerves or from the vessels accompanying them passed down into the head of the bone through several minute canals in the floor of the groove. On either side of this groove there is a pair of shallower grooves (gmx) which converge and then pass into the head of the vomer as canals: on the left side of the bone a break in the wall between the lateral groove and the median groove indicates that some structure passed from one groove into the other. These lateral grooves may have carried a terminal branch of the maxillary nerve.

(*b*) *Sinemurian* Leptolepis *sp.*

The *lateral ethmoid* of this species is known by a single incomplete example, from the right side of the individual whose mesethmoid is shown in figure 123. It is ossified perichondrally, without endochondral bone. Only the dorsal part of the bone, above the level of the anterior myodome, is preserved. There is a small facet for the frontal on the dorsal surface of the bone, and the anterior myodome is lined with perichondral bone, as in *P. germanicus*. The lateral ethmoid is much narrower transversely at the level of the anterior myodome than it is in *P. germanicus*. There is no groove for the superficial ophthalmic nerves on the dorsal surface of the bone and no canal for the orbitonasal vessels lateral to the myodome, but there is a slit-like longitudinal canal, lined with perichondral bone, passing through the bone close to its medial margin almost midway between the anterior myodome and the facet for the frontal, a little closer to the latter. This canal may have transmitted either the superficial ophthalmic nerves or the orbitonasal vessels, or possibly both.

The *mesethmoid* of the Sinemurian *Leptolepis* is shown in lateral, dorsal, anterior, ventral and posterior view in figure 123, together with the lateral dermethmoids, with which it is intimately associated. In the single available specimen the mesethmoid consists of rather thick perichondral bone, with little or no endochondral bone. The mesethmoid has a plane dorsal surface bearing a pair of shallow depressions (arfr) which received the anterior ends of the frontals. The area between these depressions and the lateral dermethmoids anteriorly was occupied by the rostral, as indicated in figure 123*b*. An inconspicuous notch in the margin of the mesethmoid immediately behind the rostral (pron, figures 123*b*, *d*, *f*) probably marks the passage of the profundus nerve on to the snout. Anteriorly, the dorsal surface of the mesethmoid ends in a median projection with a pair of feebly developed lateral wings (alpm, figures 123*d*, *e*) underlying the proximal parts of the antero-lateral processes of the lateral dermethmoids (see below). At the extreme tip of the rostral projection of the mesethmoid the perichondral bone appears to be fused with the overlying lateral dermethmoids, but this is the only point at which there is not a distinct suture between the perichondral and dermal bones.

The anterior surface of the mesethmoid presents a pair of weakly concave articular facets (amx), facing antero-dorso-laterally, which articulated with the premaxillae medially and the heads of the maxillae laterally. These facets have a granular surface, differing in texture from the surrounding perichondral bone. In *Heterotis*, Daget & d'Aubenton (1957, p. 899) found that the articulation between the ethmoid cartilage and the premaxilla develops by cleavage of the cartilage, an external lamella becoming incorporated into the premaxilla. The texture of the joint surface in the Sinemurian *Leptolepis* (and in other leptolepids) implies that the same process took place in these fishes. Lateral to the articular facet, the perichondral bone arches forwards, underlying the front edge of the postero-lateral process of the lateral dermethmoid. A slight notch in the mesethmoid at the edge of the articular facet (nbu, figure 123*d*) may mark the passage of the buccal and maxillary nerves.

The lateral surface of the mesethmoid is occupied posteriorly by a deep hollow, the anterior part of the nasal pit (npit). In the lateral part of the floor of the nasal pit the perichondral

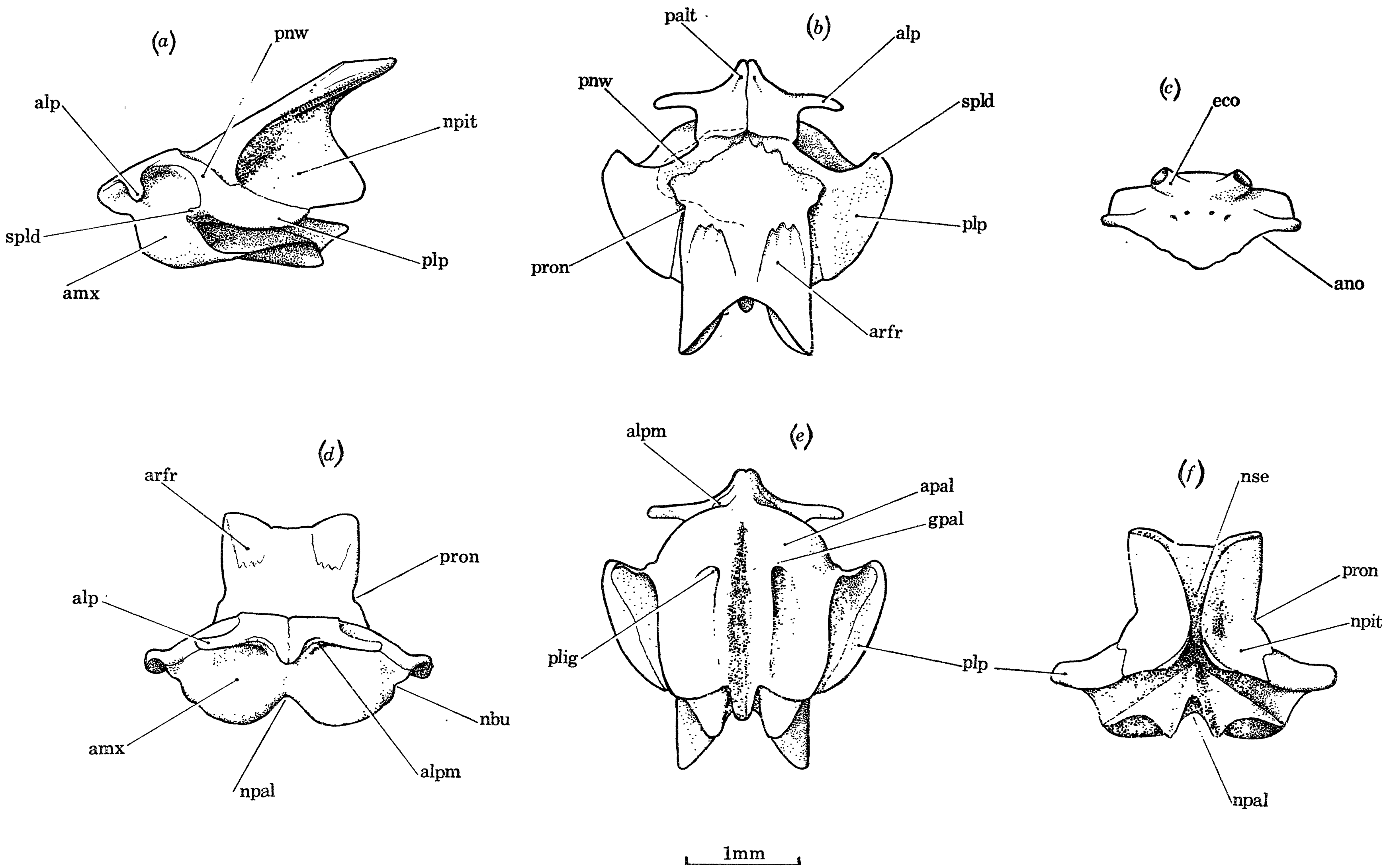


FIGURE 123. Sinemurian *Leptolepis* sp. Mesethmoid and lateral dermethmoids in left lateral (*a*), dorsal (*b*), anterior (*d*), ventral (*e*) and posterior (*f*) views, and rostral (*c*) in dorsal view, from P.51685. In (*b*) the position of the rostral in life is indicated by a broken line on the left side.

bone is overlain by the postero-lateral process of the lateral dermethmoid, which separates the nasal pit from the articular surface anteriorly. Below the nasal pit the ethmoid cartilage was exposed laterally in life.

The ventral surface of the mesethmoid (figure 123*e*) contains a deep median groove and a pair of elongate, dorso-medially directed pits, which are deepest anteriorly. The median groove (gpal), which contains subsidiary grooves and ridges, was occupied by the vomer and by the palatine nerves and accompanying vessels, which passed dorsal to the vomer and emerged anteriorly through a notch (npal) between the articular surfaces for the maxillae. The lateral pit (plig) must have received the ethmo-palatine ligament, and the palatine articulated with the rounded surface (apal) in front of the pit.

The posterior face of the mesethmoid (figure 123*f*) is unossified, the ethmoid cartilage passing back to the lateral ethmoids in the nasal septum (nse) and the floor of the nasal pit. The nasal septum is rather narrow at the posterior margin of the mesethmoid, and there is no sign of an anterior myodome bone, but such a bone could have existed a little further back, in the broader part of the nasal septum, and merely be missing from the specimen.

The name 'lateral dermethmoid' is introduced here for a pair of anamestic dermal bones which underlie the rostral and overlie the mesethmoid in the rostrum and the floor of the nasal pit. These bones occur as independent ossifications in all pholidophorids and in the Sinemurian *Leptolepis*, but fuse with the rostral (and sometimes also with the mesethmoid) in more advanced leptolepids. These bones have not been described before, and none of the names previously given to ossifications in the actinopterygian snout can be applied to them without ambiguity. The term 'lateral dermethmoid', which has not been used before to my knowledge, will serve to distinguish them until their homologies in teleosts and holosteans have been thoroughly investigated (see below, p. 510).

In the Sinemurian *Leptolepis* the *lateral dermethmoids* (figure 123) are closely applied to the dorsal surface of the mesethmoid and it is not possible to remove them. Anteriorly they meet in a median suture and project beyond the mesethmoid in a rostrum which probably received ligaments from the premaxillae. A pair of small foramina (palt, figure 123*b*) close to the mid-line on the dorsal surface of this rostrum must have transmitted the terminal branches of the palatine nerves, as in *Amia* (Jarvik 1942, fig. 100). The median contact between the lateral dermethmoids ends at a transverse ridge which marks the anterior edge of the rostral (figure 123*b*). Behind this ridge the lateral dermethmoids end in a digitate margin between the mesethmoid below and the rostral above.

Each lateral dermethmoid has two lateral processes. The anterior lateral process (alp) is a slender rod, directed laterally and almost horizontally. On the underside of its distal part there is a facet (figure 123*e*) which appears to mark the origin of a ligament or muscle. The posterior lateral process (plp) is narrow proximally, where it is applied to the sloping antero-lateral part of the upper surface of the mesethmoid, forming a low prenasal wall (pnw), and broad distally, where it expands into an axehead-shaped flange extending beyond the perichondral mesethmoid laterally and forming the floor of the anterior part of the nasal pit. Antero-laterally, the thickened anterior margin of the process ends in a slight spur or prominence (spld: cf. *Leptolepis coryphaenoides*, figure 127).

The *rostral* of *L. elongata* (figure 123*c*) is a median, approximately triangular, shield-like bone, much broader than long. Posteriorly it is thin and delicate, but anteriorly, where it fits against the transverse ridge on the lateral dermethmoids and the proximal parts of their posterior lateral processes, it is quite thick. The rostral commissure ran in a raised tube (eco) which occupies only half the breadth of the bone. This tube shows a curvature, concave forwards, which is typical of the rostral commissure in primitive actinopterygians, the median part of the canal passing through the centre of ossification of the bone. Behind the commissure there is a transverse row of four minute pores, but they do not appear to be branches of the canal. At the lateral margin of the rostral there is a weak ridge or process which must mark the anterior border of the anterior nostril (ano).

Nothing is yet known of the vomer in the Sinemurian *Leptolepis*.

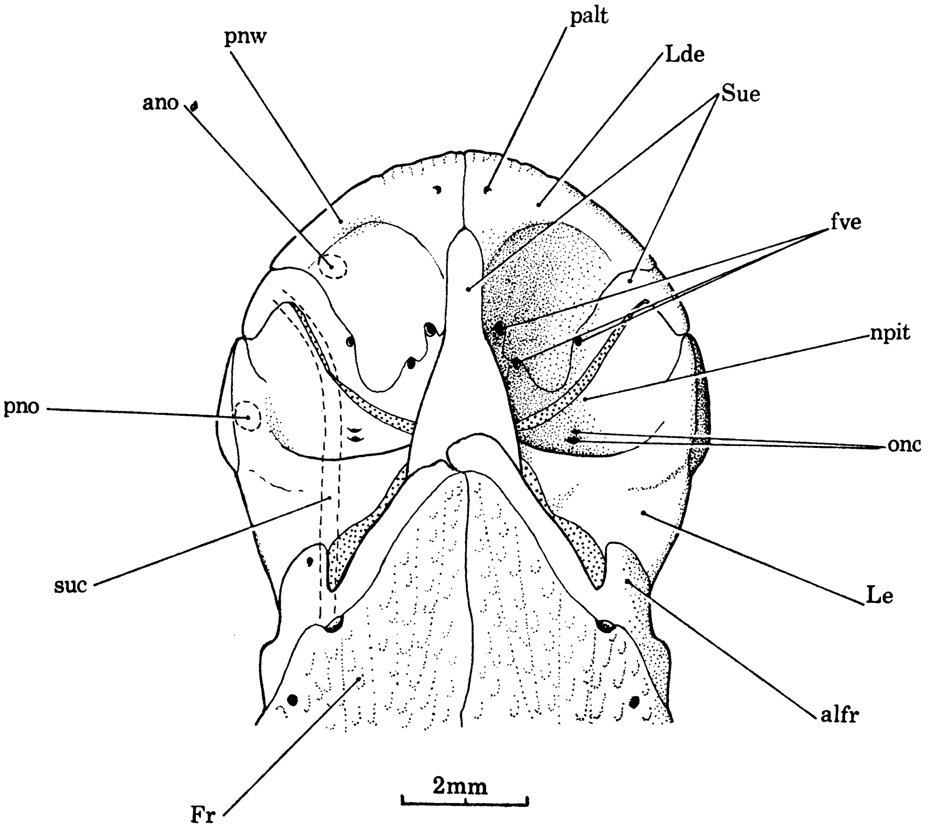


Figure 124. *Pholidophoroides limbata* (Agassiz). Restoration of the ethmoid region in dorsal view, based on P.40588. Heavy dots indicate cartilage, and the position of the anterior and posterior nostrils and of the supraorbital sensory canal in the nasal is indicated by broken lines on the left side.

(*c*) Pholidophoroides limbata

The ethmoid region of the mechanically prepared P.40588–9 is restored in dorsal view in figure 124. The lateral ethmoid (Le) seems to agree with that of *P. germanicus* (figure 119) so far as it is visible, but crushing of the bone prevents any very detailed comparison. Two foramina (onc) in the posterior part of the floor of the nasal pit may be the homologues of the canals for the orbitonasal vessels in *P. germanicus*.

The postero-dorsal part of the supraethmoid (Sue), underlying the anterior ends of the frontals, is narrower and less sharply distinct from the nasal septum below than is the corresponding portion of the mesethmoid in the Sinemurian *Leptolepis* (figure 123), while the lateral parts of the bone, in the floor and side wall of the nasal pit (npit), are much broader than in the latter, extending beyond the lateral dermethmoids. In the side wall of the nasal pit a distinct horn of the supraethmoid extends back to meet the crest on the lateral ethmoid which forms the posterior part of this wall.

The lateral dermethmoids (Lde) overlie the anterior part of the supraethmoid, as in the Sinemurian *Leptolepis*, but they are very different in shape. The main difference between the ethmoid complex in the Sinemurian *Leptolepis* and *P. limbata* is that in the latter the rather elaborate rostrum of the leptolepid is entirely lacking: the nasal pits extend almost to the tip of the snout, and in side view the ethmoid complex of *P. limbata* must have been a simple, low triangle, ending anteriorly in a narrow brim, curved transversely, without the articular facets and anterior lateral processes present in the leptolepid. Though simpler in shape than those of the Sinemurian *Leptolepis*, the lateral dermethmoids of *P. limbata* are more extensive, forming the low prenasal wall (pnw) and lining a major portion of the floor and medial wall of the nasal pit. As in the Sinemurian *Leptolepis*, the lateral dermethmoids meet in a median suture in front of the nasal pits. The greater part of this median contact is overlain by the rostral (Ro, figure 82), but the lateral dermethmoids project in front of the rostral in an insignificant rostrum, as in *P. germanicus* (figure 121). The ventral surface of this rostrum has not been seen, and it is not known whether the lateral dermethmoids bore teeth (cf. *P. macrocephalus* below). This exposed portion of the lateral dermethmoids is ornamented with a few ridges, without enamel, and perforated by a pair of small foramina (palt) for the terminal branches of the palatine nerve, as in *Amia* and the Sinemurian *Leptolepis*. In the medial wall of the nasal pit the posterior margin of the lateral dermethmoid is notched by two foramina (fve) of which the antero-medial is the larger. Under xylene a canal can be seen running antero-laterally from this foramen below the lateral dermethmoid. There is a third foramen in the supraethmoid in the lateral part of the nasal pit. It is unlikely that any nerve passed through these foramina, and they probably transmitted nutritive vessels into the cartilage.

The rostral of *P. limbata* (Ro, figure 82) is broad, shield-like, ornamented with enamelled ridges and tubercles, and penetrated throughout its width by the tube for the rostral commissure, as it is in other pholidophorids (Nybelin 1966, figs 2, 10, 15; figures 121, 145).

In figure 124 the position of the nares (ano, pno) and of the supraorbital sensory canal (suc) in the nasal is indicated (cf. figure 82). It should be pointed out that in this specimen of *P. limbata* the frontals end well behind the rostral and the intervening space was certainly occupied by a median contact between the nasals, contrary to the statement in Nybelin's diagnosis of *Pholidophoroides* (1966, p. 392). This specimen also has two supraorbitals (Suo, figure 82), similar in shape to those of *P. bechei*, another point of difference from Nybelin's generic diagnosis.

(*d*) Pholidophorus bechei

In *Pholidophorus bechei* the single acid-prepared mesethmoid available (P.51160) consists of rather thick perichondral bone with only a little endochondral bone in the foremost part of the bone, but in 39857 a broken surface shows much endochondral bone. In the acid-prepared bone only the ventral surface of the mesethmoid is well preserved. This is exactly as in the Sinemurian *Leptolepis* (figure 123*e*), with a deep median groove housing the vomer and the palatine nerves and vessels, and a pair of elongate, dorso-medially directed grooves or pits for the ethmo-palatine ligaments. 39857 shows the postero-dorsal part of the mesethmoid to have been much as in *P. germanicus* (figure 121), but more heavily ossified and with a broad, plane dorsal surface, clearly differentiated from the nasal septum below, as in the Sinemurian *Leptolepis*. This difference from *P. limbata* (figure 124), where the greater part of the dorsal surface of the supraethmoid is only a narrow crest, is presumably due to the greater length of the frontals in *P. bechei*, which extend forwards between the nasals to the rostral (Nybelin 1966, fig. 2).

The lateral dermethmoids of *P. bechei*, partially visible in several skulls, especially P.1052*d* (Nybelin 1966, pl. 2, fig. 3), appear to resemble those of *P. limbata*. They extend forwards beyond the rostral in a rudimentary rostrum, ornamented with a few ridges, and in P.1052*d* there appears to be a median foramen between them transmitting the terminal branches of the palatine nerve. The posterior extent of the lateral dermethmoids is still unknown in *P. bechei*, but the acid-prepared mesethmoid has part of the right lateral dermethmoid associated with it, and as in the acid-prepared *P. germanicus* the dermethmoid has drifted free, showing that the association between the dermal and perichondral bone was not so intimate as in the Sinemurian *Leptolepis*.

The rostral of *P. bechei* has been illustrated by Nybelin (1966, figs 1, 2). As in *P. limbata*, it is broad, triangular, and penetrated throughout its width by the tube for the rostral commissure, which shows the usual backward curvature in the mid-line, where it passes through the centre of ossification of the bone.

The lateral part of the lateral ethmoid is visible in several skulls, but is always badly crushed. So far as known, it resembles the lateral ethmoids of *P. limbata* and *P. germanicus*.

Nothing is yet known of the vomer in *P. bechei*.

(*e*) Pholidophorus minor *and the Callovian* Pholidophorus *sp.*

The ethmoid region is missing in the available specimens of these species.

(*f*) Pholidophorus macrocephalus

The ethmoid region of this species is shown in ventral view in figure 84 and in dorsal view in figures 125 and 145. In contrast to the otherwise rather similar *P. germanicus*, the ethmoid region is very heavily ossified, almost the whole of the ethmoid cartilage having been replaced by dense endochondral bone.

The lateral ethmoid (Le) resembles that of *P. germanicus*, apart from the more complete ossification. There is a wide, median anterior myodome leading forwards between the lateral ethmoids to the anterior myodome bone, which is here an integral part of the mesethmoid (see below). Lateral to the opening of the myodome there is a canal for the orbitonasal vessels, and the upper part of the lateral ethmoid is penetrated by a canal for the superficial ophthalmic nerves (cson, figures 84, 125). The lateral surface of the lateral ethmoid, above the articular facet for the palatine, is strongly ridged, presumably for muscle attachment, and on the posterior edge of this surface there is a pit facing ventrally (plecp, figure 84) which must have received the ligament from the ectopterygoid (cf. figure 119, *P. germanicus*). Anteriorly, the lateral ethmoid forms the postero-lateral part of the nasal pit (npit), as usual, and meets the lateral dermethmoid in the side wall of the pit and the mesethmoid in its floor.

The mesethmoid (Mes) has a plane dorsal surface, underlying the frontals posteriorly and the rostral and lateral dermethmoids anteriorly (figure 145; in *P. macrocephalus* the frontals extend anteriorly between the nasals and contact the rostral, as in *P. bechei*). There is a pair of foramina for the terminal branches of the palatine nerves (palt, figure 125) in the anterior part of the dorsal surface of the mesethmoid, between the lateral dermethmoids. In the antero-dorsal corner of the nasal pit the mesethmoid projects in a small process which met the overlying rostral. A notch behind this process (pron, figure 125) may have carried the profundus nerve, passing out on to the surface of the snout (cf. Sinemurian *Leptolepis*, figure 123). The mesethmoid forms the broad nasal septum, and embedded in the endochondral bone of its posterior face there is a hollow cone of perichondral bone (Amb, figure 125), open posteriorly, which is the homologue of the independent anterior myodome bone of *P. germanicus* (figure 120), although in *P. macrocephalus* it is an integral part of the mesethmoid. On the underside of the mesethmoid there is a small area of perichondral bone around the vomer (Ve, figure 84). This area, unossified in *P. germanicus*, is the homologue of the median ventral ethmoid bone of some salmoniforms (Weitzman 1967*b*) and leptolepids (see below). The perichondral bone of the underside of the mesethmoid is smooth in *P. macrocephalus* since the paired grooves or pits for ligaments from the palatine, which are a conspicuous feature of the underside of the mesethmoid in *P. bechei* and primitive leptolepids (figures 123, 127), are here found on the lateral surfaces of the head of the vomer.

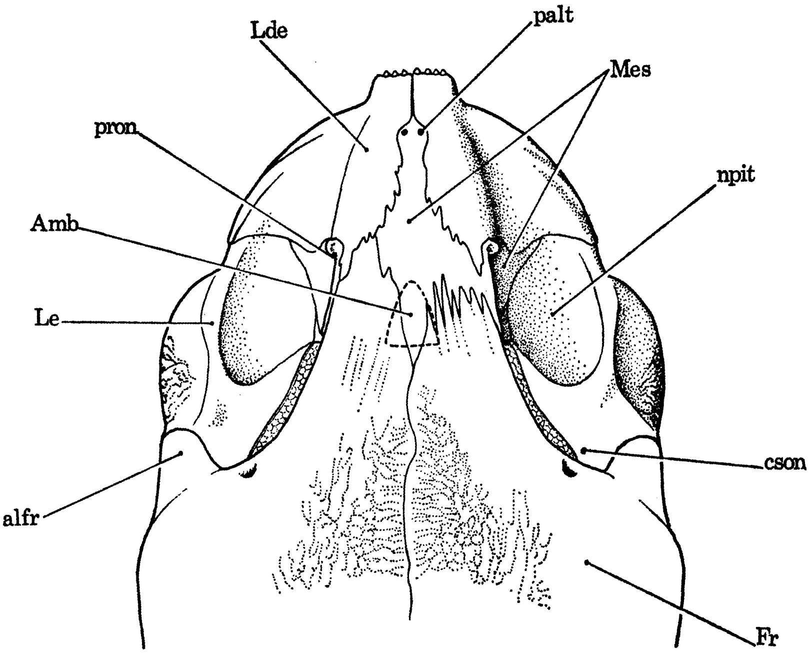


FIGURE 125. *Pholidophorus macrocephalus* Agassiz. Restoration of ethmoid region in dorsal view (cf. figure 145), based mainly on P.12070 and P.52518. Junction between the lateral dermethmoid and frontal on the left side and separation of these bones on the right side are alternative conditions found in the two specimens. The position and shape of the anterior myodome bone is indicated by a broken line. (Magn. × 4 approx.)

The lateral dermethmoids (Lde) are very large, lining most of the anterior part of the nasal pit, extending beyond the mesethmoid to cover the lateral ethmoid postero-laterally, and in some specimens (figure 125) meeting the frontals posteriorly. In the floor of the nasal pit the lateral dermethmoids are only loosely associated with the underlying mesethmoid, but in disarticulated specimens they always remain in position. Anteriorly, the lateral dermethmoids meet in the mid-line and extend beyond the rostral in a rudimentary rostrum. The lateral dermethmoids of *P. macrocephalus* thus resemble those of other pholidophorids (figures 121, 124) in shape and structure, but they exhibit one notable difference, that they bear teeth anteriorly. In P.12070, the best preserved specimen showing these teeth, there is a transverse row of seven teeth, four on the right lateral dermethmoid and three on the left. Lateral to the teeth there is a knob with a pit behind it (apmx, figure 84), marking the articulation with the premaxillae, which were separated in the mid-line by the toothed portion of the lateral dermethmoids.

The rostral of *P. macrocephalus* (Ro, figure 145) is a large, shield-shaped bone covering the mesethmoid and lateral dermethmoids anteriorly and the frontals posteriorly (thus separating the nasals in the mid-line), and bordering the anterior nasal opening (ano, figure 145) postero-laterally. The ethmoid commissural sensory canal penetrates the whole width of the bone, following closely the curve of its anterior margin. Six to eight branches ending in pores arise from the canal, suggesting that it housed 5–7 neuromasts. The rostral is ornamented with ridges and tubercles which radiate from the mid-point of its anterior margin, indicating that the ethmoid commissure runs through the centre of ossification, as usual. The internal surface of the rostral is smooth and contains (P.1070*c*) at least five foramina for branches of the buccal nerve to the neuromasts. The rostral was only loosely attached to the underlying bones, for in disarticulated specimens it has usually drifted away from the braincase, while the lateral dermethmoids remain in place.

The vomer of *P. macrocephalus*, shown in ventral view in figure 84, is a median bone, as in *P. germanicus*, and shows the same regions as in the latter, a bifid posterior process underlying the parasphenoid and a head which includes a transverse, tooth-bearing bar. The teeth are variable in number: in P.12070 there are fewer than in the specimen of *P. germanicus*, in P.52518 there are about twice as many as in the latter, and P.3582 is intermediate between these two specimens. As in *P. germanicus*, there is a median notch for the palatine nerves in the head of the bone, but the head is less distinct from the posterior process and the dorso-lateral processes of the head more weakly developed, so that the paired pits for the ethmo-palatine ligaments (plig) are more elongated.

(*g*) *Reinterpretation of the snout in* Ichthyokentema purbeckensis

The discovery that the lateral dermethmoids bear teeth in *Pholidophorus macrocephalus* (figure 125) makes it desirable to re-examine the composition of the ethmoid region in *Ichthyokentema purbeckensis* (Davies), from the Purbeckian (uppermost Jurassic) of Dorset. Apart from the pholidophorids and leptolepids described here, this species (family Ichthyokentemidae) is the only other pholidophoroid in which the structure of the snout is known in any detail. In *I. purbeckensis*, Griffith & Patterson (1963) found the ethmoid region to consist of a single perichondral and endochondral ossification representing the mesethmoid and lateral ethmoids, and housing the nasal pit, with a broad, heavily toothed median vomer on its underside, and on its dorsal surface a triangular median rostral which contained the ethmoid commissure and projected into the oral margin anteriorly between the premaxillae, bearing a single row of about a dozen teeth. The resemblance between the anterior, toothed portion of this 'rostral' and the anterior part of the lateral dermethmoids in *P. macrocephalus* (cf. figures 84 and 125 with Griffith & Patterson 1963, fig. 3 and pl. 2, fig. 4) and other pholidophorids has led me to re-examine the material of *I. purbeckensis*.

The 'rostral' of *I. purbeckensis* was clearly visible only in three specimens (Griffith & Patterson 1963, p. 11); P.8379, a complete fish (Griffith & Patterson 1963, pl. 2, fig. 5), P.44926, an isolated neurocranium, still in the rock, exposed in dorsal view, and P.44927 (Griffith & Patterson 1963, pl. 2, fig. 4), a free-standing, acid-prepared ethmoid region with the vomer and parasphenoid attached. In the first of these the ethmoid commissure is visible but no rostral teeth can be seen; in the second and third rostral teeth are visible but the ethmoid commissure cannot be seen. On this evidence, and influenced by the expectation that the bone pattern in *Ichthyokentema* would be similar to what was then known in teleosts, pholidophorids and amioids, we described a toothed rostral. In figure 126 the best of these three specimens, P.44927, is restored in dorsal and ventral view as I now interpret it. The 'rostral' of our 1963 description is, in fact, a median rostral, carrying the ethmoid commissure, which has drifted away in this specimen and all other isolated braincases (cf. *P. macrocephalus*, above). This rostral lay above toothed lateral dermethmoids (Lde, figure 126), as in *P. macrocephalus* and other pholidophorids, and the anterior part of the lateral dermethmoids, which is ornamented with ridges, projected beyond the rostral in a rudimentary rostrum, separating the premaxillae. In P.44927 there is a median discontinuity between the left and right halves of the tooth-bearing portion of the lateral dermethmoids, but in P.44926 a similar discontinuity runs just to one side of the mid-line and passes through the centre of a tooth socket: I am therefore inclined to believe that both these discontinuities are merely *post mortem* cracks, and that the lateral dermethmoids were fused anteriorly in *I. purbeckensis* (cf. *P. germanicus* above), since the shape of this median bone suggests that it grew from paired centres of ossification. Immediately behind this median line of fusion there is a median foramen (palt) transmitting the terminal branches of the palatine nerves up to the tissues of the snout. The lateral dermethmoid extends into the anterior part of the floor of the nasal pit (npit), overlying the perichondral ethmoid (Et) there, but it is much less extensive than in pholidophorids (cf. figures 121, 124, 125). These rather small lateral dermethmoids probably represent a primitive condition relative to pholidophorids (cf. below, p. 510 and figures 134, 136, 137, 138). The nasal septum (nse) is narrow, without a differentiated dorsal laminar part of the mesethmoid, as in *Pholidophoroides limbata* (figure 124): in *I. purbeckensis* this area is overlain by a median contact between the nasals (Griffith & Patterson 1963, fig. 1), just as it is in *P. limbata*.

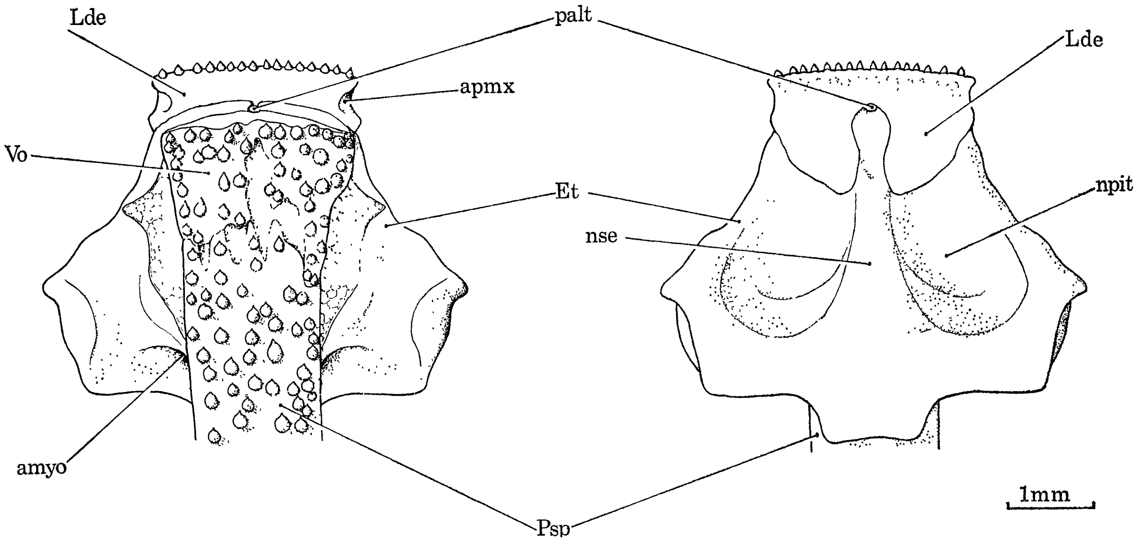


FIGURE 126. *Ichthyokentema purbeckensis* (Davies). Restoration of ethmoid region of neurocranium and attached dermal bones in ventral (left) and dorsal view, based on P.44927.

Seen from below (figure 126), the toothed portion of the lateral dermethmoids extends well in front of the ethmoid, and is separated from the vomer only by a narrow strip of endoskeletal bone, as in *P. macrocephalus* (figure 84). The palatine nerves passed upwards through a median foramen (palt) between the vomer and ethmoid. The vomer of P.44927 (Vo) shows a partially paired tooth patch, the two halves linked anteriorly by a narrow band. P.44929, the isolated bone described by Griffith & Patterson as the vomer, and which formed the basis of that bone in their figures 2 and 3, is a thick, solid bone with its oral face entirely covered by teeth. The aboral surface of this bone does not show the features which are now known to be characteristic of pholidophoroid vomers (figure 122), and I would interpret this specimen as a basihyal tooth-plate.

I. purbeckensis appears to have an anterior myodome (amyo) of the same type as the pholidophorids, a median canal passing forwards between the lateral ethmoids, but it is impossible to see whether an anterior myodome bone was present. The ethmoid ossification contains a good deal of endochondral bone, and is more heavily ossified than any pholidophorid except *P. macrocephalus.*

(*h*) Leptolepis coryphaenoides

A reconstructed mesethmoid complex of this species is shown in dorsal, ventral, lateral, anterior and posterior view in figure 127, and in lateral view in figure 128*a*. This reconstruction is based mainly on bone-bed material from Byfield which has suffered some rolling and abrasion, and it is probable that delicate laminae in the posterior part of the ossification have been destroyed: these have been restored on the basis of complete skulls from Curcy. The mesethmoid complex of *L. coryphaenoides* is deeper and broader than that of the Sinemurian *Leptolepis* (figure 123), but is otherwise similar. The topographic homologues of the dermal rostral and lateral dermethmoid of the Sinemurian species are easily recognized in *L. coryphaenoides*, but they are no longer separate bones. This compound dermal element (rostro-dermethmoid) is fused with the perichondral bone of the mesethmoid to a greater extent than in the Sinemurian species, where there was only fusion at the tip of the rostrum. In *L. coryphaenoides* there is still a distinct suture between the dermal (Rode) and perichondral (Mes) bone on the ventral and posterior surfaces of the ossification (figures 127*b*, *e*), but on the anterior and lateral surfaces fusion is complete, the approximate line of fusion being marked by a slight change in colour and texture of the bone. This ossification in *L. coryphaenoides* therefore incorporates homologues of the rostral, lateral dermethmoids and mesethmoid of pholidophorids and the Sinemurian *Leptolepis*, and it also has the vomer (Vo) fused into its ventral surface. The vomer will be treated as a separate bone, and the remainder of the compound ossification will be called the *rostro-dermethmo-mesethmoid.* As will be shown below, the 'mesethmoid' of most teleosts is almost certainly a rostro-dermethmo-supraethmoid, but I do not advocate usage of this term throughout the teleosts. In *L. coryphaenoides* the limits between the rostral and lateral dermethmoid components cannot be recognized, and the dermal and perichondral components are only distinct posteriorly. In later leptolepids and in teleosts these limits become more obscure, and I do not believe that use of the compound name would serve any useful purpose.

The mesethmoid portion of the rostro-dermethmo-mesethmoid is more heavily ossified than in *L. elongata*, since even in the very small specimens from the bone-bed at Byfield the interior of the anterior part of the bone is occupied by a mass of dense, almost granular endochondral bone. The dorsal surface of the mesethmoid (figure 127*a*) is similar to that of the Sinemurian *Leptolepis* (figure 123 *a*). Posteriorly, the perichondral bone extends beyond the dermal bone for some distance, and the anterior ends of the frontals overlie this perichondral bone (arfr) and suture with the posterior edge of the dermal bone. The ethmoid commissure is represented by an open groove (pit-line: epl) in all the Byfield bone-bed specimens, but it is quite possible that in some specimens this was originally a tube whose upper wall has been abraded *post mortem.* Wenz (1968), with abundant material of *L. coryphaenoides* from Curcy, found that the ethmoid commissure is sometimes represented by a tube, sometimes by a pit-line (groove), and this is also true of the B.M.(N.H.) specimens from Curcy. Wenz also found that the dorsal, commissure-bearing portion of the mesethmoid is frequently divided by a median suture (1968, figs 82, 87, 89). Having made a detailed examination of the B.M.(N.H.) specimens from Curcy, I now agree (cf. Patterson 1970*b*, p. 261) that this is true of almost half the specimens. I have not seen such a paired rostro-dermethmoid in any of the bone-bed specimens from Byfield, however. Anteriorly, the dorsal surface of the mesethmoid ends in a bluntly pointed rostrum. Homologues of the anterior lateral processes of the lateral dermethmoid (alp, figures 127*a*, *c*) are hardly recognizable in the bone-bed material, but they may be abraded off, for in the skulls from Curcy, Dumbleton and Ilminster they may be quite prominent (Rayner 1937, fig. 2), and sometimes fuse with the spur on the posterior lateral process of the lateral dermethmoid (see below).

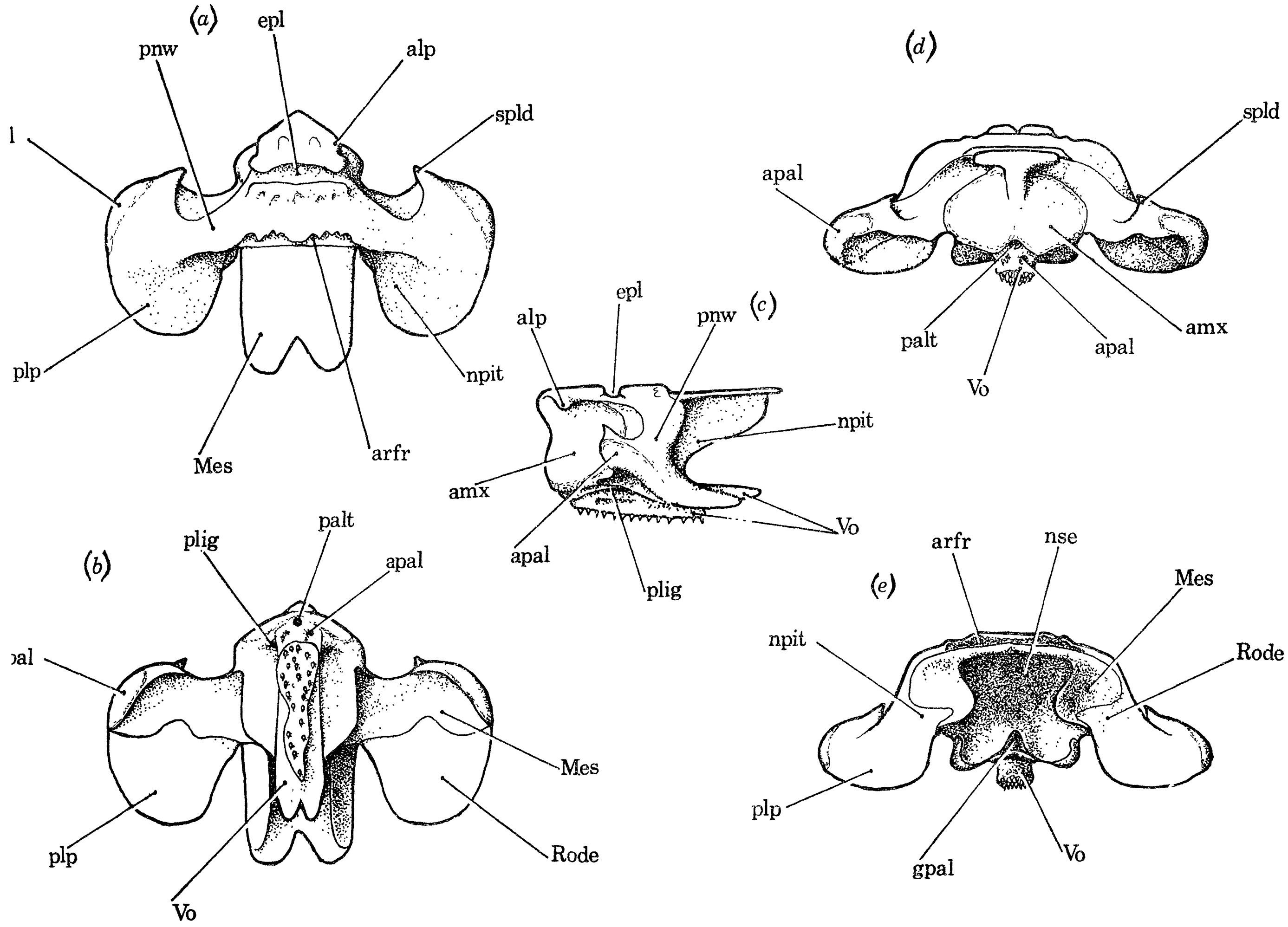


Figure 127. *Leptolepis coryphaenoides* (Bronn). Mesethmoid complex (mesethmoid, rostro-dermethmoid and vomer) in dorsal (*a*), ventral (*b*), left lateral (*c*), anterior (*d*) and posterior (*e*) views. Restoration based on 32454, 32458, P.51699, P.51703 and P.51705. (Magn. × 15 approx.)

The anterior surface of the mesethmoid presents a pair of articular facets (amx) facing antero-dorso-laterally, with a granular surface, as in the Sinemurian species. The lateral part of the rostro-dermethmo-mesethmoid, forming the anterior wall and floor of the nasal pit (npit), is relatively larger than in the Sinemurian species, but as in the latter it consists of a sheet of dermal bone overlying perichondral bone, with a distinct suture between the two on the ventral side and in broken surfaces. The dermal portion of this lateral part (plp), the homologue of the posterior lateral process of the lateral dermethmoid in the Sinemurian species, is relatively longer and broader than in the latter, and is higher anteriorly, so that it forms a clearly defined prenasal wall (pnw). Anteriorly, this dermal bone projects dorso-medially towards the rostrum in a well developed spur (spld): in the Sinemurian species (figure 123) this spur is rudimentary. In *L. coryphaenoides* from Curcy, Wenz found that in many individuals this spur met the anterior lateral process of the lateral dermethmoid, enclosing a circular foramen or fenestra (Wenz 1968, figs 82, 86, 87, 89). Wenz pointed out that these fenestrae could hardly be sensory canal pores or nostrils, but did not speculate further on their function: it seems most probable that this was the attachment of ligaments from the upper jaw on the underside of the medial and lateral portions of the bar enclosing the fenestra. The perichondral portion of the mesethmoid in the floor of the nasal pit is better ossified than in the

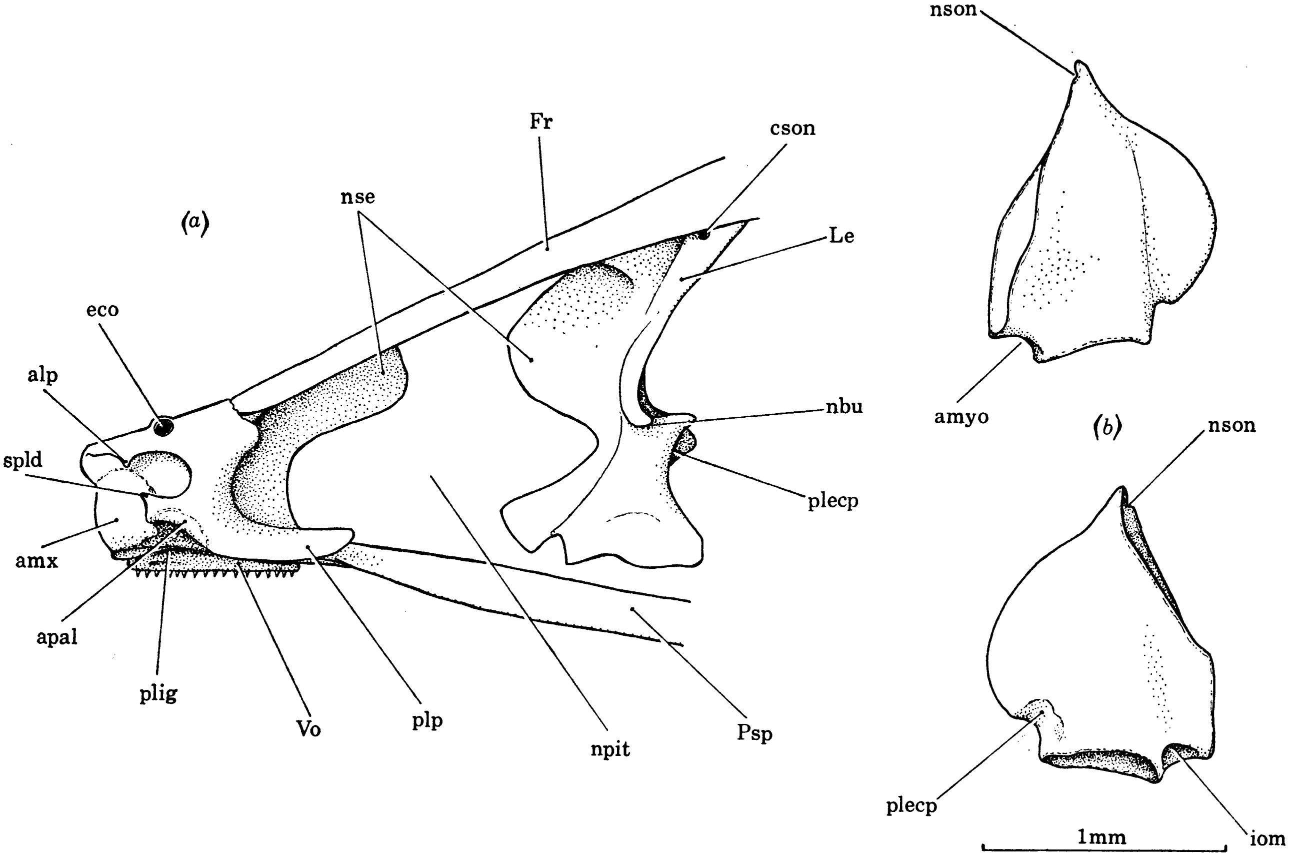


FIGURE 128. (*a*) *Leptolepis coryphaenoides* (Bronn), restoration of ethmoid region in left lateral view, based on 32454, 32458, P.51699 and P.51705 (magn. × 20 approx.). (*b*) Callovian *Leptolepis* sp., left lateral ethmoid in anterior (above) and posterior views, from P.51754.

Sinemurian species, projecting laterally beyond the dermal bone and turning down in a brim which presents a granular articular surface (apal) for the palatine.

Posteriorly (figure 127*e*), the nasal septum (nse) is only ossified perichondrally, as in the Sinemurian species, but it appears to have been much broader than in the latter. There is no sign of an anterior myodome bone, but as in the Sinemurian species such a bone could well have been present, having fallen away from the isolated rostro-dermethmo-mesethmoids, and being obscured by the overlying bones in the complete skulls.

The vomer (Vo, figures 127, 128, 132) is fused with the perichondral bone of the ventral surface of the mesethmoid. Between the vomer and mesethmoid there was the usual median canal for the palatine nerves, which emerged anteriorly through a median foramen (palt, figure 127*b*, *d*) below the facets for the maxillae and premaxillae. Lateral to the vomer, and covered by the latter in ventral view, there is a pair of deep pits (plig, figures 127*b*, *c*; 128*a*) on the underside of the mesethmoid for the ethmo-palatine ligaments, as in the Sinemurian species. The vomer is median, as in pholidophorids and teleosts. It has a posterior process, notched at the tip, which fitted beneath the parasphenoid, and bears teeth on a raised portion which is aligned longitudinally, not transversely as in the vomer of pholidophorids (figures 84, 122). In the single well-preserved specimen, there are about 25 teeth. In front of the tooth patch there is a pair of small facets (apal) which may mark the articulation of the palatines.

The lateral ethmoid of *L. coryphaenoides* (Le, figure 128*a*) is only known from intact, mechanically prepared skulls, especially 32454, 32457 and 32458. The lateral ethmoid is less heavily ossified than the mesethmoid, and consists only of a thin shell of perichondral bone. The bone is shorter rostro-caudally and more vertically aligned than that of *P. germanicus* (figure 119), but is otherwise basically similar in shape. As in *P. germanicus*, the profundus and superficial ophthalmic nerves passed through a canal (cson) in the dorsal part of the bone. There is a median anterior myodome passing forwards through a notch in the medial margin of the bone, as in pholidophorids, but no separate canal for the orbitonasal vessels can be seen, and these vessels may well have passed through the myodomal canal, together with the oblique muscles and olfactory nerves. Lateral to the posterior opening of the myodome there is a horizontal spur (plecp) on the posterior face of the bone, near its lateral margin. This appears to be homologous with the similarly placed pit in *P. macrocephalus* (figure 84), and must have received the ligament from the ectopterygoid. In front of this process the lateral margin of the bone is notched (nbu) for the passage of the buccal and maxillary nerves. Below this notch, there is no clear articular surface for the palatine, which must have articulated with the cartilage capping the ventral surface of the bone. Anteriorly, the lateral ethmoid forms the hind wall of the nasal pit and the posterior part of the nasal septum (nse). It was separated from the mesethmoid by a zone of cartilage.

(*j*) *Callovian* Leptolepis *sp.*

Only one lateral ethmoid of this species has been found: it is shown in anterior and posterior view in figure 128*b*. It is a small, very delicate perichondral ossification, almost laminar in form, which ended in cartilage medially and ventrally. There is no real indication of a contact surface for the frontal, but a minute notch (nson) in the medial margin of the uppermost part of the bone may mark the passage of the superficial ophthalmic nerves. The upper part of the lateral edge of the bone is a curved knife-edge, ending ventrally at a notch with a slight depression (plecp) behind it on the posterior face of the bone. This depression is probably the site of origin of the ligament from the ectopterygoid (cf. figures 84, 128*a*). The medial edge of the bone ends ventrally at a bone-lined notch (amyo), facing ventro-medially, which has a deep pit (iom), open postero-ventrally, in its lining. The notch must be the opening of the anterior myodome, also containing the olfactory nerves, and the pit in its wall suggests that at least one of the oblique muscles, presumably the inferior, originated here, without penetrating into the anterior myodome. The position of the anterior myodome, at the extreme ventral edge of the bone, must indicate that the ventral part of the lamina orbitonasalis was unossified.

No trace of a mesethmoid has been found in the Callovian *Leptolepis* material, either as an isolated bone or attached to the vomer or rostro-dermethmoid: the mesethmoid must have been unossified or nearly so.

Two examples of the compound dermal rostro-dermethmoid have been found, and one has previously been figured in dorsal view (Patterson 1970*b*, fig. 34). Figure 129 shows compound restorations of these two specimens in dorsal, lateral and anterior view. This bone is easily compared with the dermal portion of the rostro-dermethmo-mesethmoid in *L. coryphaenoides* (figures 127, 128) and with the separate rostral and lateral dermethmoids of the Sinemurian *Leptolepis* (figure 123).

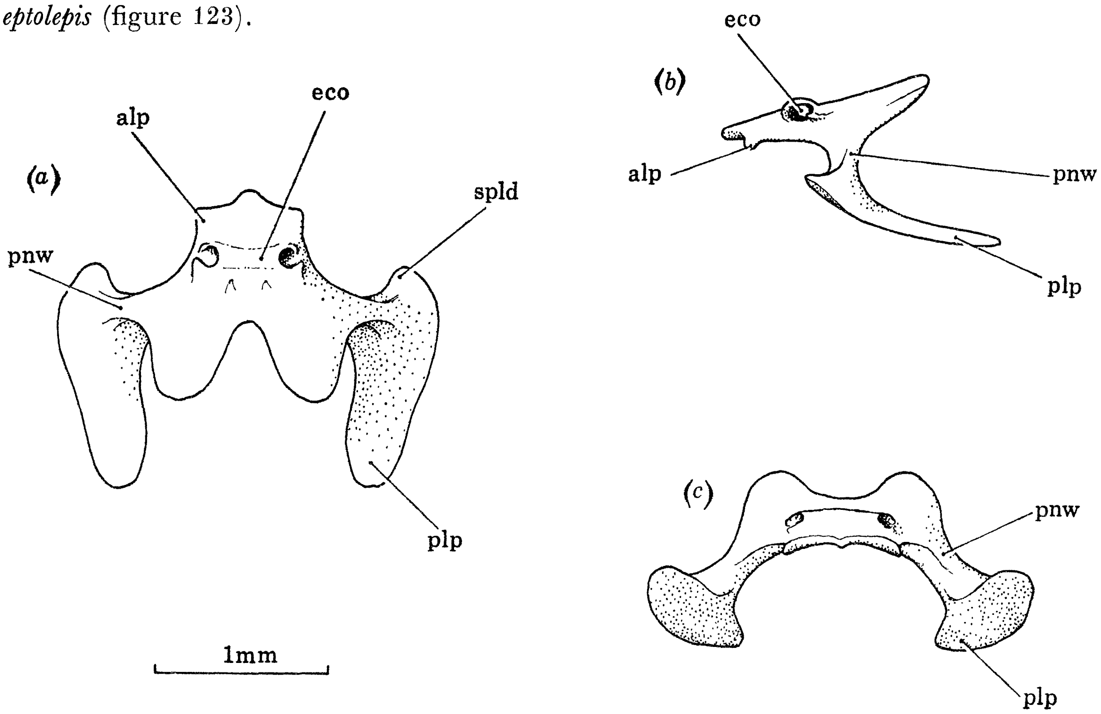


FIGURE 129. Callovian *Leptolepis* sp. Rostro-dermethmoid in dorsal (*a*), left lateral (*b*) and anterior (*c*) views, based on P.51288 and P.51753.

The dorsal surface of the bone is convex in the transverse plane, and ends posteriorly in a pair of processes which appear to have lain on top of the tips of the frontals, not beneath them as they do in pholidophorids and earlier leptolepids. The ethmoid commissure ran in a raised, transverse tube (eco) which occupies about three-quarters of the width of the dorsal surface of the bone. Both specimens show traces of a median suture or seam in front of the tube for the commissure, and in P.51288 this suture (or line of fusion) can be followed to the posterior edge of the bone, but only on its internal surface. This obviously recalls the condition in the Sinemurian *Leptolepis*, where a median rostral overlies the paired lateral dermethmoids. Anteriorly, the dorsal surface of the rostro-dermethmoid ends in a slight median projection, with a pair of lateral projections or knobs (alp) which are the homologues of the anterior lateral processes of the lateral dermethmoid in *L. coryphaenoides* and the Sinemurian species.

The ventro-lateral parts of the rostro-dermethmoid (plp) are homologous with the posterior lateral processes of the lateral dermethmoids in the Sinemurian species, which they closely resemble. There is a stout, ventro-laterally inclined upper portion, forming the medial part of the prenasal wall (pnw), and a curved, rostro-caudally elongate ventral lamina in the floor of the nasal pit. Anteriorly there is a slight prominence (spld) which is the homologue of the antero-medial spur in *L. coryphaenoides*.

The vomer of the Callovian *Leptolepis* is shown in dorsal, lateral and ventral view in figure 122. It resembles that of *L. coryphaenoides* (figures 127, 128, 132), but is, of course, not fused with the mesethmoid since the latter is unossified. In comparison with the vomer of *P. germanicus* (figure 122) the bone is more slender and lightly built. The posterior process of the bone is bifid, as usual, and on its dorsal surface there is a median groove (gpal) for the palatine nerves which sends a canal down into the head of the bone and is joined anteriorly by a pair of converging grooves (gmx), possibly for terminal branches of the maxillary nerves, exactly as in *P. germanicus*. Anteriorly, the terminal branches of the palatine nerves passed through a median canal (palt) in the head of the bone, not through a notch as they did in *P. germanicus*. On the underside of the bone there is an elongate tooth patch, aligned longitudinally, as in *L. coryphaenoides*, not transversely as in pholidophorids (figures 122, 84). In the figured specimen this tooth patch contains six teeth, but in P.51737 there are only three. In front of the tooth patch there is a pair of small facets (apal) which may mark the articulation of the palatines. The head of the bone bears a pair of postero-laterally directed wing-like processes. Comparison with *L. coryphaenoides* suggests that these did not contribute to the articular facets for the upper jaw, being covered by the ethmoid cartilage anteriorly, but their posterior faces formed the anterior wall of the pit (plig) for the ligaments from the palatine.

(*k*) Leptolepis dubia

The ethmoid region of this Kimmeridgian species is restored in dorsal, lateral and ventral view in figure 130. Wenz (1968, fig. 90) has illustrated the ethmoid region of *L. sprattiformis* in dorsal view, and since she follows Saint-Seine's (1949) nomenclature, where *L. dubia* is listed as a synonym of *L. sprattiformis*, her specimens may well be the same species as those in figure 130. I have not seen the distinct median suture through the rostro-dermethmoid which she illustrates (cf. Patterson 1970*b*, p. 261).

The mesethmoid of *L. dubia* contains a good deal of endochondral bone in large individuals, but as in *L. coryphaenoides* the lateral ethmoid (missing in the specimen illustrated in ventral view) appears to be a purely perichondral ossification. The lateral ethmoid (Le) is small and laminar, as in the Callovian *Leptolepis* (figure 128), hardly extending below the level of the anterior myodome.

The mesethmoid (Mes) and rostro-dermethmoid appear to fuse during ontogeny to about the same extent as in *L. coryphaenoides*. In young individuals they are separate (P.51761), and in full-grown individuals (figure 130) they are fused around the rostrum but separate laterally and posteriorly. The vomer also appears to be fused with the mesethmoid rostrally in large individuals, as in *L. coryphaenoides*. The mesethmoid of *L. dubia* resembles that of *L. coryphaenoides*, but is less completely ossified laterally.

The compound rostro-dermethmoid (Rode) differs from that of the Callovian species

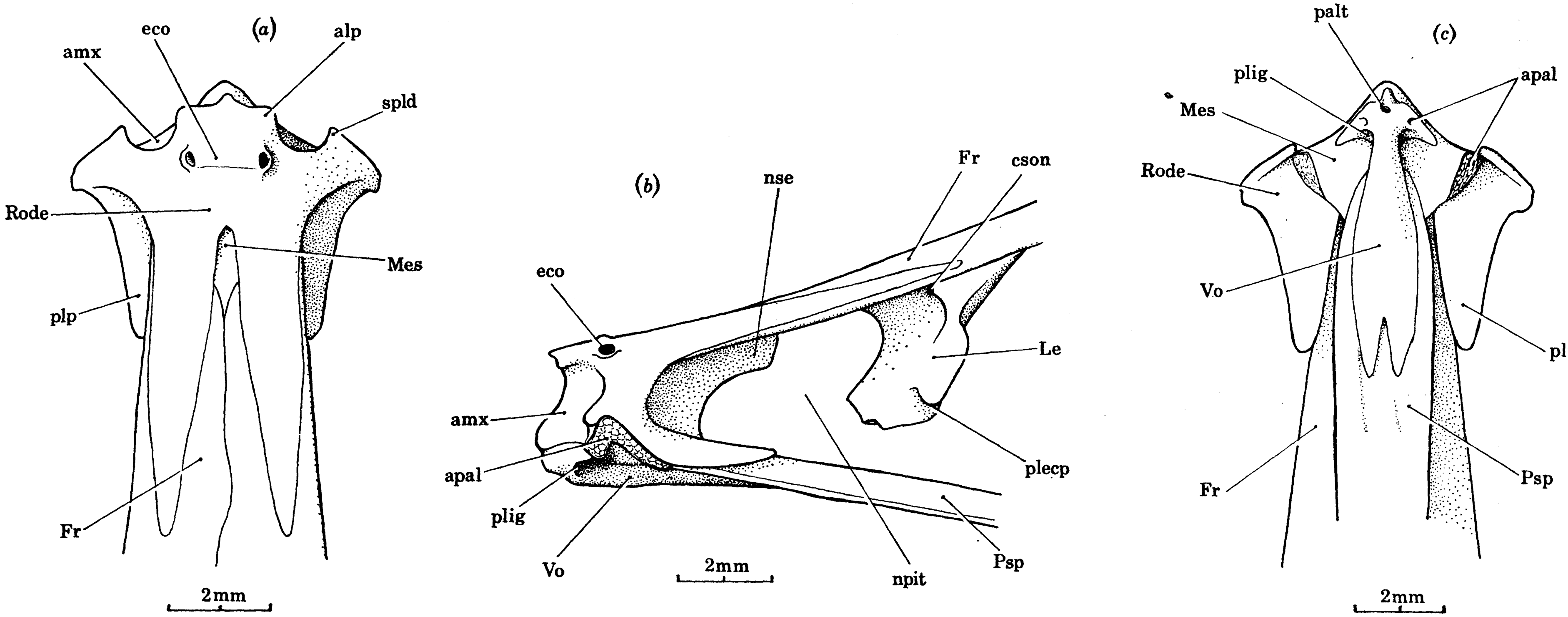


Figure 130. *Leptolepis dubia* (Blainville). Restoration of ethmoid region in dorsal ((*a*) based on P.14491), left lateral ((*b*) based on P.51759) and ventral ((*c*) based on P.919) views. The lateral ethmoid is missing in the specimens shown in (*a*) and (*c*).

(figure 129) principally in having very long posterior processes, overlying the frontals (figure 130*a*). I have not seen a median suture in the rostro-dermethmoid in any of the few specimens showing an uncrushed rostro-dermethmoid (but see Wenz 1968, p. 204).

The vomer (Vo) resembles that of the Callovian species (figure 122), but is toothless. As in the Callovian species, there is a canal for the palatine nerves (palt) through the head of the bone, and the lateral wings of the head form the anterior wall of the pit for the ligaments from the palatine (plig).

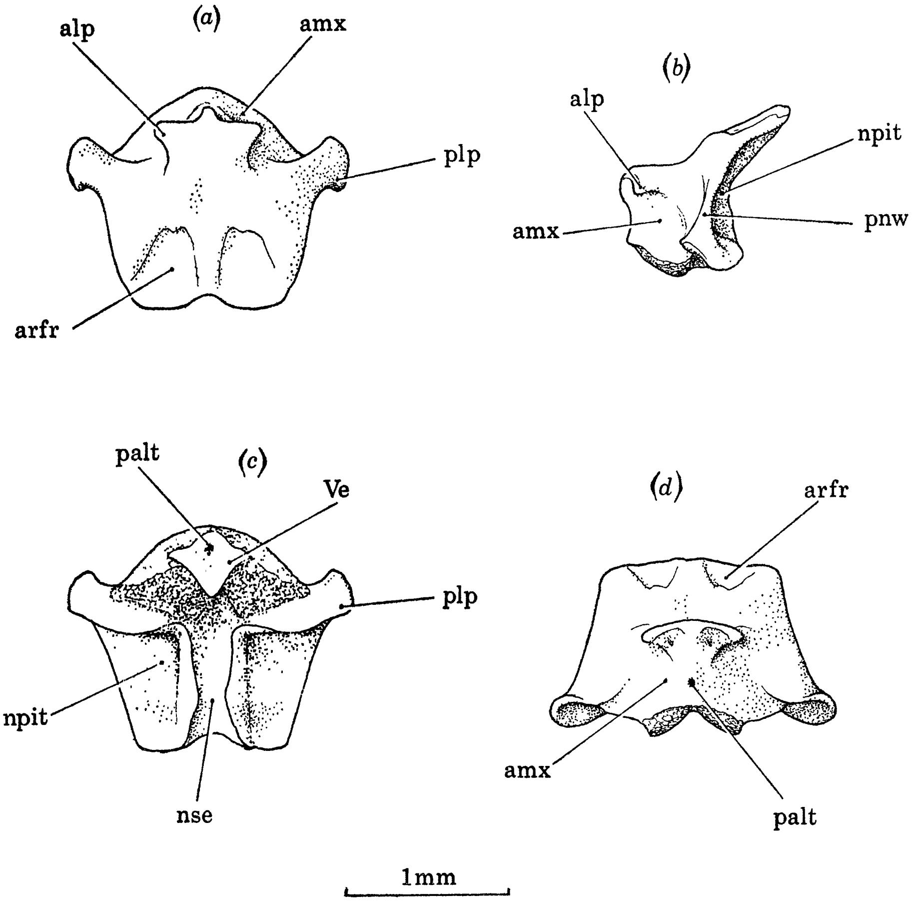


FIGURE 131. Wealden leptolepid. Isolated mesethmoid from the Weald Clay (Barremian) in dorsal (*a*), left lateral (*b*), ventral (*c*) and anterior (*d*) views, from P.54611.

(*l*) *A Wealden leptolepid*

This account is based on two isolated mesethmoid complexes (P.54611–2) from a bone-bed in the middle division of the Weald Clay (Barremian) at Henfield, Sussex (Patterson 1966, p. 286). These bones are among a series previously identified as *Clupavus* sp. (Patterson 1966, p. 287), by comparison with the Purbeckian *Leptolepis brodiei* Agassiz, at that time the type-species of *Clupavus* Arambourg. It now appears that *L. brodiei* is a *Leptolepis sensu lato* (Patterson 1970*b*, p. 283), and the Wealden bones are best referred to as an undetermined leptolepid. This material is included here since it serves to complete the morphological sequence between pholidophorids and primitive leptolepids, in which the rostral, lateral dermethmoids and mesethmoid are separate bones, and the majority of living teleosts, in which there is only a single bone in the mesethmoid region.

One of the Wealden bones is shown in dorsal, ventral, lateral and anterior view in figure 131. In comparison with the other leptolepids described here, the mesethmoid complex is very short and deep but otherwise has the same topography. There is a rostrum with a pair of short lateral processes (alp), the homologues of the anterior lateral processes of the lateral dermethmoid in early leptolepids. Behind the paired facets for the upper jaw (amx) there is a ventrolateral process (plp) whose posterior surface forms the prenasal wall (pnw). This process is the homologue of the posterior lateral process of the lateral dermethmoid in early leptolepids. On the dorsal surface of the bone there is a pair of facets (arfr) for the frontals, which overlapped the mesethmoid, as in *L. coryphaenoides* and the Sinemurian species. On the underside of the bone, there is an isolated area of perichondral bone (Ve) on the surface of the mass of fine-grained endochondral bone which fills the antero-ventral part of the ossification. This piece of perichondral bone includes a median groove which housed the anterior part of the vomer, and a foramen (palt) for the terminal branches of the palatine nerves. It is homologous with the ventral ethmoid (Weitzman 1967*b*) of some living teleosts, and with the central part of the underside of the mesethmoid in *L. coryphaenoides* and the Sinemurian *Leptolepis*. Apart from this isolated piece of perichondral bone, the remainder of the surface of the ossification is a continuous shell of bone, without sutures. Comparison with other leptolepids shows that this shell must include the lateral dermethmoids and the perichondral mesethmoid, here indistinguishably fused. In this Wealden leptolepid the ethmoid commissure, presumably reduced to a superficial pit-line, no longer leaves any trace on the underlying bone. Whether this means that the rostral has been lost, or whether it is also incorporated in the compound mesethmoid must remain an open question.

The compound mesethmoid (dermethmo-mesethmoid) of this Wealden leptolepid seems to be directly comparable with that of those living teleosts which have only one bone in the mesethmoid region.

(*m*) *Ethmoid region: summary and discussion*

(i) *Summary of conditions in pholidophorids and leptolepids*

(1) In all pholidophorids and leptolepids, the endoskeleton of the ethmoid region contains three major ossifications, a median mesethmoid and paired lateral ethmoids. These bones are not known to fuse during ontogeny in any pholidophorid or leptolepid, but do so in the pholidophoroid *Ichthyokentema purbeckensis*.

(2) The lateral ethmoid appears to ossify from a single centre in the lateral margin of the lamina orbitonasalis. The bone is frequently only perichondrally ossified in pholidophorids and leptolepids, but in *Pholidophorus macrocephalus* it is fully ossified endochondrally, and in *I. purbeckensis* there is a good deal of endochondral bone. There is no evidence in pholidophorids and leptolepids that the lateral ethmoid incorporates any dermal element ('prefrontal', 'dermectethmoid': cf. de Beer 1937, p. 498; Daget 1964, p. 240; Dornesco & Soresco 1971*b*).

(3) The mesethmoid appears to have ossified principally from a median dorsal supraethmoid centre in the anterior part of the nasal septum. Except in *P. germanicus* and the Callovian *Leptolepis*, there was also a median ventral centre of ossification on the underside of the ethmoid cartilage which gave rise to a plate of perichondral bone, closely associated with the vomer. This plate of bone, the homologue of the ventral ethmoid of some teleosts (Weitzman 1967*b*), is incorporated in the mesethmoid in *P. bechei*, the Sinemurian *Leptolepis*, *L. coryphaenoides*, *L. dubia*, *P. macrocephalus* and the Wealden leptolepid, but remains distinct in the latter two

species. In the Callovian *Leptolepis* the mesethmoid was apparently unossified; in *P. germanicus* (supraethmoid) and the Sinemurian *Leptolepis* (mesethmoid) it is only ossified perichondrally; in *P. bechei*, *L. coryphaenoides*, *L. dubia* and the Wealden leptolepid the mesethmoid contains some endochondral bone, and in *P. macrocephalus* it is fully ossified endochondrally.

(4) There is an anterior myodome bone in *P. germanicus* and *P. macrocephalus*, ossifying as an independent perichondral cone in the nasal septum. In *P. macrocephalus* it becomes incorporated in the mesethmoid in fully ossified individuals. An anterior myodome bone has not been found in other pholidophorids or in any leptolepid, but in no species is the material sufficiently good to say that the bone was absent.

(5) The ethmoid region of the braincase is invested by four dermal bones: a median rostral containing the ethmoid commissure; paired, anamestic lateral dermethmoids; and a median vomer. In pholidophorids these bones are independent, but in leptolepids the roofing bones tend to fuse with each other and with the mesethmoid, and the vomer may also fuse with the mesethmoid.

(6) In all pholidophorids the rostral is a large, independent shield-like bone which occupies the whole width of the snout, is penetrated throughout its width by the ethmoid commissure, and forms the anterior border of the anterior nostril. In the Sinemurian *Leptolepis* the rostral is much narrower than in pholidophorids and the ethmoid commissure only occupies half its width, but the bone still borders the anterior nostril. In all other leptolepids the rostral is fused with the lateral dermethmoids in a compound rostro-dermethmoid. The ethmoid commissure is still bone enclosed in some individuals of *L. coryphaenoides*, in the Callovian *Leptolepis* and in *L. dubia*; it is represented by a groove (pit-line) in some individuals of *L. coryphaenoides*, and no longer leaves any trace on the bone in the Wealden leptolepid.

(7) The lateral dermethmoids of pholidophorids are plate-like bones which cover the greater part of the dorsal surface of the mesethmoid and line the anterior part of the nasal pit. They may extend on to the lateral ethmoid either laterally (*P. macrocephalus*) or medially (*P. germanicus*) and may suture with the frontals posteriorly (*P. macrocephalus*). They meet each other in the mid-line anteriorly, and project beyond the rostral in a rudimentary, shelf-like rostrum, which may be tuberculated. In *P. macrocephalus* and *Ichthyokentema purbeckensis* the lateral dermethmoids separate the premaxillae and bear teeth. It is possible that the lateral dermethmoids are toothed in some other pholidophorids, but in *P. germanicus* they were probably not toothed. In *I. purbeckensis* the lateral dermethmoids fuse in the mid-line: this may also be true of *P. germanicus*.

In leptolepids the lateral dermethmoids are never toothed. In the Sinemurian *Leptolepis*, the lateral dermethmoids are still independent ossifications and line the anterior part of the nasal pit, but they are much more intimately bound to the mesethmoid than in pholidophorids, and form a complex rostrum, tending to fuse with the mesethmoid at the tip of this rostrum. In all other leptolepids the lateral dermethmoids fuse with the rostral, presumably during ontogeny where there is still a bone-enclosed ethmoid commissure. In some individuals of *L. coryphaenoides* this rostro-dermethmoid has a median suture, and a trace of such a suture remains in the dermethmoid component of the bone in the Callovian species and perhaps also in *L. dubia*. This rostro-dermethmoid also fuses with the mesethmoid during ontogeny. In *L. coryphaenoides* and *L. dubia* the rostro-dermethmoid and mesethmoid remain distinct on the posterior and ventral surfaces of the ossification, but in the Wealden leptolepid fusion is complete.

(8) The vomer of pholidophorids and leptolepids is a median bone. It has a posterior

process which underlies the parasphenoid and may be bifid for much of its length: this bifurcation is probably due to the median passage for the palatine nerves, not to ossification from paired centres. In pholidophorids the head of the vomer has a transverse bar bearing teeth, a plane anterior surface, and a pair of small postero-lateral processes which enclose a pit for the origin of the ethmo-palatine ligament. The palatine nerve passes through a groove on the dorsal surface of the bone. In leptolepids the head of the vomer has a longitudinal bar bearing teeth (except in *L. dubia*, where the bone is toothless), a keeled anterior surface covered by the ethmoid cartilage or mesethmoid, and a pair of lateral processes which form the anterior wall of the pit for the ethmo-palatine ligament, here lying on the mesethmoid (as it does also in *P. bechei*). The palatine nerves pass through a canal in the head of the vomer in leptolepids.

(9) In pholidophorids and leptolepids there is an anterior myodome, represented by a median, perichondrally lined canal between the lateral ethmoids. This canal contained the olfactory nerves and the oblique eye muscles, and in *P. germanicus* and *P. macrocephalus* the muscles originated in the median anterior myodome bone. In the Callovian *Leptolepis* there is a pit in the lateral ethmoid at the opening of the anterior myodome, suggesting that one oblique muscle, presumably the inferior, originated in the pit and did not pass into the anterior myodome. In pholidophorids one or two canals for the orbitonasal vessels pass through the lateral ethmoid lateral to the anterior myodome. In the Sinemurian *Leptolepis* there is a similar canal, but in other leptolepids the orbitonasal vessels probably passed through the anterior myodome into the nasal capsule.

(10) There is no bony articulation between the lateral ethmoid and the palate in pholidophorids and leptolepids. A notch, process or pit on the ventro-lateral part of the lateral ethmoid is interpreted as the site of origin of the ligament from the ectopterygoid.

(11) The most significant difference between the ethmoid regions of pholidophorids and leptolepids is the appearance in the latter of a complex rostrum with large articular surfaces for the premaxilla and maxilla, and processes giving origin to ligaments from these bones. In pholidophorids, the nasal pits extend almost to the tip of the snout and the rostrum is a horizontal keel, formed by the lateral dermethmoids. The dorsal surface of the snout is enclosed by the large, shield-like rostral. In leptolepids narrowing of the rostral (or separation of the bone into a median rostral and paired lateral rostrals: Nybelin 1967*a*) results in fenestration or flexibility in the previously rigid bony cover of the snout, and at the same time the rostrum changes from the simple horizontal keel of pholidophorids into a vertically keeled structure, presenting a pair of antero-laterally directed articular facets for the upper jaw on the mesethmoid, capped by a projecting rostrum, formed by the lateral dermethmoids, which has a pair of lateral processes for ligament attachment. This complex leptolepid rostrum is separated from the nasal pit by a prenasal wall, formed by the differentiated proximal part of the posterior lateral process of the lateral dermethmoid. The distal part of this process presents a ventro-lateral articular surface for the palatine and has an anterior projection for ligament attachment. In some individuals of *L. coryphaenoides* this projection may fuse with the anterior process of the lateral dermethmoid, forming a complete bar for ligament attachment. The articular surfaces for the upper jaw on the mesethmoid have a granular surface, implying that the joint develops in the same way as in living teleosts, by cleavage within the cartilage, an external lamella of cartilage being incorporated in the joint surface of the dermal jaw bones.

This leptolepid type of rostrum appears fully fledged in the Sinemurian species. All those pholidophorids in which the snout is well known show no trends towards it. It is unfortunate that little is yet known of the ethmoid region in *P. bechei* or in *Pholidolepis*, for these forms seem to approach the leptolepids most closely (Nybelin 1966).

(12) In pholidophorids, the frontals overlie the postero-dorsal part of the mesethmoid. Below this there is a well differentiated nasal septum, but anteriorly, where the rostral overlies the mesethmoid, there is only a low crest. In *P. macrocephalus*, the frontals may suture with the lateral dermethmoids anteriorly beneath the rostral. In the Sinemurian *Leptolepis*, the frontals overlie the mesethmoid but do not contact the lateral dermethmoids. In other leptolepids, the frontal meets the rostro-dermethmoid, suturing with its posterior margin in *L. coryphaenoides*. In two more advanced leptolepids, *L. dubia* and the Callovian species, the rostro-dermethmoid overlies the anterior end of the frontals, but in the Wealden leptolepid the frontals overlie the compound mesethmoid. In leptolepids the nasal septum is always well defined throughout its length, presumably as a consequence of the increased height of the rostrum in comparison with pholidophorids.

(ii) *Comparison with other groups*

1. *Ossification patterns in the endoskeleton.* In pholidophorids, the ethmoid region includes paired lateral ethmoids and a median mesethmoid which is principally formed by the supraethmoid but may include minor contributions from a ventral ethmoid and an anterior myodome bone. No leptolepid is yet known to have had an anterior myodome bone, but the pattern of ossification is otherwise similar to that in pholidophorids. This pattern is only known to be duplicated in living teleosts.

Paired lateral ethmoid ossifications are probably a primitive actinopterygian feature. Among living fishes, they occur in *Latimeria*, *Polypterus*, large *Acipenser* (Parker 1882), *Amia* and teleosts. Among fossil actinopterygians, lateral ethmoids are recorded in *Birgeria* (Nielsen 1949), *Caturus* (Rayner 1948), *Macrepistius* (Schaeffer 1971), *Pachycormus* and *Hypsocormus* (Holmgren & Stensiö 1936; Rayner 1948; Lehman 1949; figure 106), and *Sinamia* (Stensiö 1935). In *Perleidus*, MMK 496 shows a pair of perichondrally ossified lateral ethmoids resembling those of pholidophorids. In *Lepidotes*, Rayner (1948, p. 306) has suggested that the lateral ethmoid illustrated in *L. semiserratus* by Stensiö (1932, fig. 80) and Holmgren & Stensiö (1936) is actually the autopalatine. My own observations on *Lepidotes* (especially P.6342, *L. mantelli*, and 32580, *L.* sp.) indicate that there was a single pair of endoskeletal ossifications in the ethmoid region. These extend well forwards beneath the nasal ('ascending') processes of the premaxillae and might represent pre-ethmoids, but they are more economically interpreted as lateral ethmoids, as in other primitive actinopterygians. In fully ossified forms such as *Heterolepidotus* (figures 102, 103), *Dapedium* (figure 112), parasemionotids (Beltan 1968, figs 26, 31) and palaeoniscoids it is evident that lateral ethmoids must also have been present during ontogeny.

The only living fishes with any endoskeletal ossification in the braincase anterior to the lateral ethmoids are *Amia* and teleosts. In *Amia* there is a pair of bones (septomaxillaries of Allis; pre-ethmoids of Holmgren & Stensiö, de Beer, etc.) which ossify late in ontogeny and in the adult are sandwiched between the vomer and the nasal ('ascending') process of the premaxilla. They form the posterior border of the articular surface for the head of the maxilla and encroach on the articular surface of the palatine. Similar pre-ethmoids have been restored in *Lepidotes* and *Hypsocormus* by Stensiö (1935). Rayner (1948, p. 306) considers that the supposed pre-ethmoid of *Lepidotes* is a part of the autopalatine (see above under lateral ethmoid), but confirms the presence of the bone in *Hypsocormus*. Lehman (1949) mentions a pre-ethmoid in *Pachycormus*, but was unable to determine its precise position. I have found no ossifications in front of the lateral ethmoid in *Pachycormus* (the bone which appears to occupy this position in Rayner's (1948, fig. 18) illustration of 32443 is the displaced right lateral ethmoid). In *Hypsocormus*, preparation of the snout of P.10906, *H. tenuirostris*, confirms the presence of a pair of large pre-ethmoids which line the anterior part of the nasal pits and are closely associated with the paired vomers.

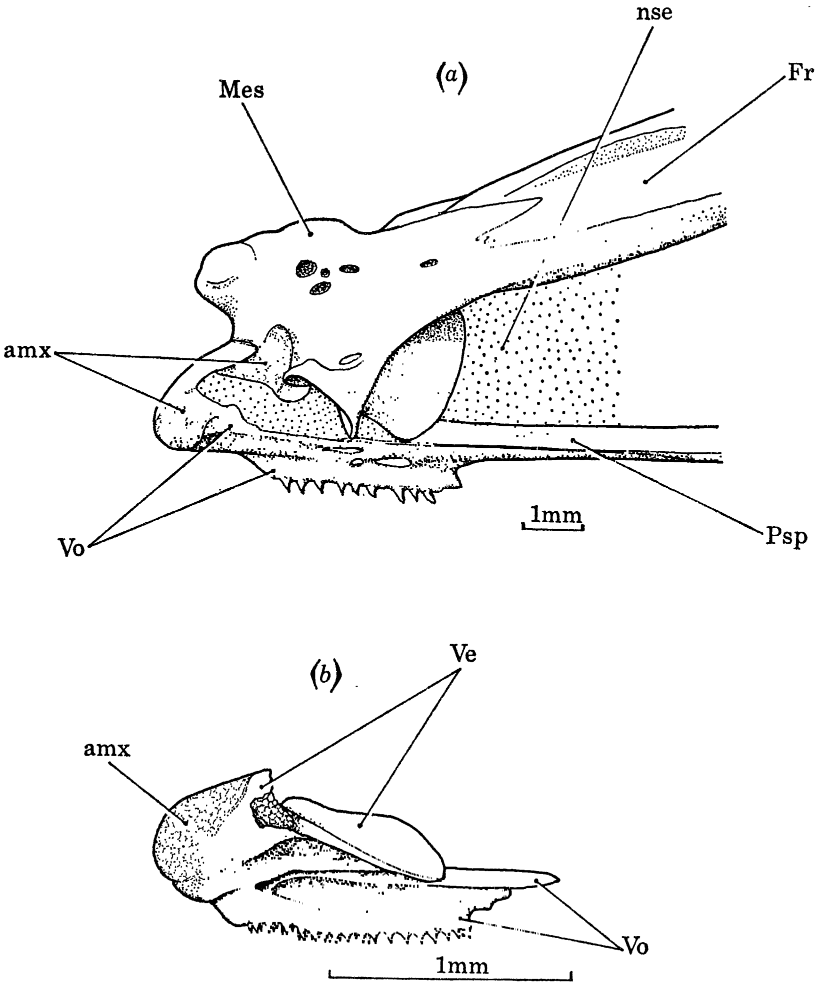


Figure 132. (*a*) *Clupea harengus* L., ethmoid region in left lateral view, from a dried skeleton (heavy stipple indicates cartilage). (*b*) *Leptolepis coryphaenoides* (Bronn), isolated vomer and attached ventral part of mesethmoid in left lateral view, from P.51705.

In teleosts, the ethmoid ossifications are varied and insufficiently studied, especially in early ontogeny. In general, higher euteleosteans have a single ossification in front of the lateral ethmoids, the mesethmoid, which incorporates dermal components (see p. 514). Lower euteleosteans, clupeomorphs, elopomorphs and osteoglossomorphs tend to have the mesethmoid region more lightly ossified, and exhibit a range of ossifications. These are most numerous, so far as is known, in the osmerids *Spirinchus* (Weitzman 1967*b*) and *Thaleichthys* (Chapman 1941). Here there are five perichondral ethmoid ossifications: median supraethmoid, ventral ethmoid and anterior myodome bones, and paired capsular ethmoid bones in the medial wall of the nasal capsule. Capsular ethmoid bones are known as separate ossifications only in osmerids, this area being occupied by ventral flanges of the supraethmoid where ossified in other teleosts. An anterior myodome bone is recorded in osmerids, stomiatoids, *Argentina* (where it is fused into the mesethmoid, Weitzman 1967*b*), galaxioids (McDowall 1969) and myctophiforms (independent or fused with the mesethmoid, Weitzman 1967*b*): further search might well reveal such a bone in other euteleosteans, but it appears to be absent in elopomorphs, clupeomorphs and osteoglossomorphs. A ventral ethmoid occurs as an independent perichondral lamella in osmerids, in the gonostomatid *Polymetme*, and in galaxioids (Weitzman 1967*b*; McDowall 1969). In *Megalops* the mesethmoid (peri- and endochondrally ossified) is 'in rigid union with the vomer, and separates fairly readily from the ectosteal mesethmoid [= rostral]; this gives the vomer the appearance of being in part a cartilage-bone' (Ridewood 1904*a*, p. 44; see also Forey (1973*a*) on *Tarpon*). In megalopids the 'mesethmoid' ossifies late, from a centre on the dorsal surface of the vomer, and is therefore a ventral ethmoid with endochondral extensions. In clupeomorphs the mesethmoid is usually thoroughly ossified. A transverse suture runs across the keeled rostrum (figure 132), passing through the granular articular surface for the maxillae, and separating the mesethmoid from what is normally referred to as the vomer (see, for example, Ridewood 1904*b*; Phillips 1942). But this suture separates two blocks of endochondral bone in the rostrum, the lower block continuous with the dermal bone of the vomer. The 'vomer' of clupeoids (Vo, figure 132), with the block of endochondral bone fused to its antero-dorsal surface, exactly resembles an isolated vomer of *Leptolepis coryphaenoides* with the attached ventral part of the mesethmoid, except that in the leptolepid a distinct layer of perichondral bone (homologue of the ventral ethmoid of teleosts) is visible above the shaft of the vomer (Ve, Vo, figure 132*b*). The ontogeny of the vomer is not known in clupeoids, but in several teleosts the vomer has been found to assume perichondral relations with the underside of the ethmoid cartilage during ontogeny (*Salmo*, de Beer 1937, p. 130; *Exocoetus*, de Beer 1937, p. 131; *Cyclopterus*, de Beer 1937, p. 159; *Solea*, de Beer 1937, p. 164; *Heterotis*, Daget & d'Aubenton, 1957, p. 898), or to include endochondrally ossified portions (*Cyprinus*, Dornesco & Soresco 1971*a*), and I interpret this as evidence that the vomer of these forms is compound, incorporating dermal (vomer) and endoskeletal (ventral ethmoid) components.

In esocoids and many cyprinoids there is a pair of endoskeletal ethmoid ossifications, the so-called pre-ethmoids (Allis 1909, p. 19; Starks 1926; Harrington 1955) or septomaxillae (Dornesco & Soresco 1971*a*). In cyprinoids, these bones lie directly over paired, dorso-lateral processes of the vomer and articulate with the maxilla anteriorly and the palatine laterally. There is a well developed supraethmoid in cyprinoids which may suture with the pre-ethmoids. Cyprinoid pre-ethmoids might be homologous with the ventral ethmoid of *Megalops*, clupeoids, etc., but in *Cyprinus* it seems that the true ventral ethmoid is represented by an endochondral ossification, ventro-medial to the pre-ethmoid, which becomes incorporated in the vomer (Dornesco & Soresco 1971*a*). The pre-ethmoids of cyprinoids are therefore probably new formations, associated with the development of protrusile jaws. In *Esox* the pre-ethmoids lie in the margin of the ethmoid cartilage and contact the lateral corner of the vomer below and the antero-lateral corner of the dermal 'proethmoid' above. The palatine articulates with the pre-ethmoid but the maxilla fails to do so, although it is attached to it by dense connective tissue. There are no other endoskeletal ossifications in front of the lateral ethmoid of *Esox*, so the pre-ethmoids could be regarded as derivatives of the ventral ethmoid, as homologous with the pre-ethmoids of cyprinoids, or as paired derivatives of the supraethmoid. Since the pre-ethmoid of *Esox* is more intimately associated with the dermal proethmoid than with the vomer (Allis

1898*b*, p. 435), and since the most remarkable feature of the snout of *Esox* is the wide separation of the anterior ends of the proethmoids, I think it more likely that the endoskeletal ossifications are paired derivatives of the dorsal supraethmoid, and are not homologous with the 'pre-ethmoids' of cyprinoids.

In addition to the teleostean ethmoid bones discussed above, there are other endoskeletal ossifications of more limited distribution, including the parasphenethmoids of *Astronesthes* and *Borostomias* (Weitzman 1967*a*), on the underside of the lamina orbitonasalis, and the accessory nasals of *Ctenothrissa* (Patterson 1964, p. 223), in the floor of the nasal capsule. In the galaxioid *Retropinna* the lateral ethmoid is double, consisting of separate cup-like perichondral disks on the anterior and posterior faces of the lamina orbitonasalis (McDowall 1969, p. 799).

In teleosts, therefore, the endoskeletal ethmoid ossifications are far more numerous and varied than in other fishes. An analysis of the ossification pattern in the postethmoid parts of the actinopterygian braincase (p. 472) resulted in the conclusion that the dominant process in phylogeny has been reduction in the number of ossification centres, not increase (fragmentation). Application of such a hypothesis to the ethmoid region would result in the conclusion that the teleost ethmoid ossifications represent a primitive pattern. I do not think this is so for two reasons. First, increase in the number of ethmoid ossifications in teleosts is found principally in groups in which the degree of ossification of this region is greatly reduced. Extra bones such as the two lateral ethmoids of *Retropinna* and the capsular ethmoids of some osmeroids do not develop beyond the stage of small perichondral disks over an ethmoid cartilage which never contains any endochondral bone. It is doubtful whether they deserve the name 'bone' (see p. 468), and they seem comparable to the fragmented opisthotic of *Polyodon* and orbitosphenoid of *Acipenser* (p. 465), which occur in similar conditions of greatly reduced ossification.

Secondly, there is good evidence that the area in which the principal variations in ethmoid ossifications of teleosts occurs, the region anterior to the lateral ethmoids, is a new formation in actinopterygians. In all palaeonisciforms the lamina orbitonasalis (= lateral ethmoids) forms the anterior boundary of the braincase, with almost no endoskeletal ossification in front of it (Watson 1925; Nielsen 1942, 1949; Rayner 1951; Gardiner 1970, 1973). In palaeoniscoids the nasal pit is open anteriorly, limited posteriorly by the lamina orbitonasalis, and is otherwise bounded only by crests or processes from the latter which are not suggestive of independent ossification centres. If the palaeoniscoid type of ethmoid region is primitive for actinopterygians, then the development of an endoskeletal rostrum, with a well defined nasal septum and nasal pits which are open dorsally or laterally instead of anteriorly, is a derived condition, probably developed independently in several lineages (saurichthyids, living chondrosteans, higher actinopterygians, etc). Independent ossifications in this rostrum, in front of the lateral ethmoids, are known in pachycormids, *Amia* and teleosts (including pholidophorids), although, of course, they could have existed during ontogeny in fully ossified forms like saurichthyids, pholidopleurids, *Dapedium* and *Heterolepidotus*. There is no good evidence that the rostrum was acquired independently in those groups where there are ossification centres in front of the lateral ethmoids, so that these centres (paired in pachycormids and *Amia*, primitively median in teleosts) can be regarded as phylogenetic homologues. The paired pre-ethmoids of pachycormids and *Amia* probably develop in relation to the paired vomers, which are primitive relative to the median vomer of teleosts, and can therefore be regarded as primitive relative to the median supraethmoid and ventral ethmoid of teleosts. The paired 'pre-ethmoids' of cyprinoids and *Esox* appear to represent a secondary, derived condition, not a primitive one as Daget (1964) supposed.

2. *Ossification patterns in the dermal roofing bones of the snout.* In pholidophorids and leptolepids the ethmoid region is roofed by a median rostral and paired lateral dermethmoids. The primitive condition of these groups is assumed to be as in certain pholidophorids, where the rostral is a broad, shield-like bone, occupying the whole breadth of the snout, penetrated throughout its width by the ethmoid commissure and bordered by the nasals behind, and the lateral dermethmoids lie beneath the rostral, line the anterior part of the nasal pit and project beyond the rostral in a shelf-like rostrum which separates the premaxillae and bears a few teeth near the mid-line (toothed lateral dermethmoids are assumed to be primitive relative to toothless ones in the absence of any indication that the teeth are a secondary development).

According to Gardiner (1963, see also Jessen 1968) the actinopterygian ethmoid region is primitively roofed by a median (anamestic) postrostral which separates the nasals and borders the anterior nostril, and paired rostro-premaxillo-antorbitals which meet in the mid-line below (anterior to) the postrostral, bear teeth, and contain the characteristic triradiate anterior portion of the infraorbital sensory canal, with the ethmoid commissure anteriorly and the antorbital branch postero-dorsally. Gardiner assumed that the latter branch anastomosed with the terminal portion of the supraorbital canal between the nostrils, but this assumption is probably unjustified (Jollie 1969). Wenz (1968, p. 245) felt that 'les phénomènes de fusion-fragmentation se manifestent de façon anarchique' in the snout of primitive actinopterygians so that it is impossible to define a primitive ossification pattern. In Wenz's view, primitive features of the actinopterygian snout are a complete dermal cover, a postrostral, and units corresponding to the rostral, premaxillae and antorbitals which may fuse in a variety of ways. Schaeffer (1973) furnishes the snout of the actinopterygian morphotype with a median rostral and postrostral. My own opinion is that very exceptional material is necessary before a reconstruction of the snout can be made in which one has full confidence, and that many such reconstructions should be treated with caution. There does appear to be a good deal of variation in the roofing bones of the palaeonisciform snout, and I do not think that a sound hypothesis on the primitive condition can yet be set down, although the ensuing analysis of the pattern in fossil groups leads to a hypothesis which accounts for some of this variation.

At the 'holostean' level, the pattern of the snout is more stable. In *Lepisosteus*, amiids (Stensiö 1935) and caturids (*Caturus*, Saint-Seine 1949, fig. 70; GSM 97417; figure 133: *Furo*, Saint-Seine 1949, fig. 69; Wenz 1968, fig. 71: *Heterolepidotus*, Schaeffer 1960) there is a median rostral which is hardly more than a tube around the ethmoid commissure, nasals which meet in the mid-line behind the rostral, antorbitals which contain a triradiate portion of the infraorbital sensory canal, and paired premaxillae with long 'ascending processes' which line the nasal pit. These 'ascending processes' are certainly not homologous with the ascending process of the teleostean premaxilla, and here they will be referred to as 'nasal processes'. Because the process ossifies independently in the ontogeny of *Amia*, Bjerring (1972) interprets it as an originally independent bone (the 'rhinal bone'), but the form of the much smaller process in more primitive actinopterygians (figures 137, 138) indicates that it developed originally as an outgrowth of the premaxilla. In *Lepisosteus* the nasal process of the premaxilla is perforated by the olfactory nerve and forms a large part of the skull roof, where it contains a portion of the supraorbital sensory canal: embryological evidence on the composition of this process is conflicting (Hammarberg 1937; Aumonier 1941). In *Amia* the nasal process is also perforated by the olfactory nerve, and this is true of some caturids (Wenz 1968, fig. 77). In *Heterolepidotus typicus* (Woodward 1895, text-fig. 35), *Caturus furcatus* and *C. porteri* the process is at least notched by the nerve, and may be perforated by it. In *Lepisosteus* and amiids the junction between the anterior limb of the antorbital and the rostral lies below the medial border of the anterior nostril (Stensiö 1935, p. 20). Published restoration of caturids show the rostral as being considerably broader, but the relation between the canal-bearing portions of the antorbital and rostral is probably the same as in living holosteans, since the junction between these bones in caturids is not a simple edge-to-edge joint (figure 133): the rostral (Ro) has a lateral process which overlaps the anterior limb of the antorbital (Ant), and the ethmoid commissure enters the ventral face of the rostral and occupies little more than half the breadth of the latter (seen in GSM 97417, *Caturus chirotes*; P.3633*b*, *Furo orthostomus*; and 32450, holotype of *Furo normandica* Wenz).

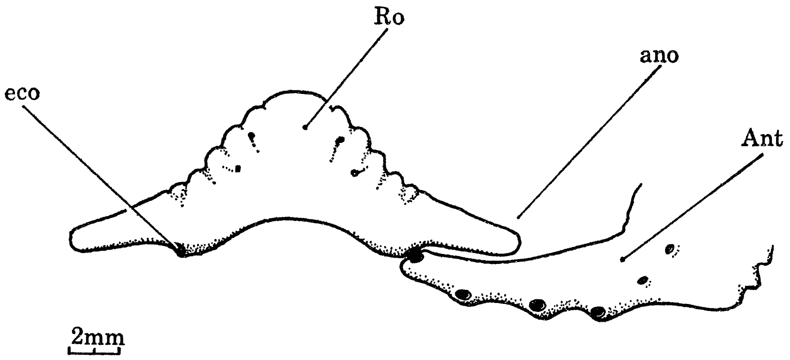


Figure 133. *Caturus chirotes* (Agassiz). Rostral and anterior part of left antorbital in anterior view, based on GSM 97417.

In the snout of *Dapedium* (figure 134) the same dermal bones are present as in amiids and caturids, but the rostral, nasals and antorbitals are more massive and form a complete carapace, only interrupted by the nostrils (ano, pno: note that there are two nostrils with normal relationships to the surrounding bones, despite Gardiner's statement (1963, p. 317) that semionotoids have only one). The premaxillae (Pmx) have an exposed portion which is heavily ornamented in some species (or individuals), and a pair of nasal processes (nprpm) which line the nasal pit beneath the rostral (despite Wenz's statement (1968, pp. 60, 79, 107) that there is no ascending process on the premaxilla). These nasal processes are shorter than in living holosteans and are not perforated by the olfactory nerve.

In *Lepidotes* the snout is not well known, apart from the premaxillae (Woodward 1916, pl. 5, fig. 11; Wenz 1968, figs 39, 44), which have very long nasal processes, perforated by the olfactory nerve. Schematic restorations of the other dermal bones in the snout of *L. semiserratus* have been made by Holmgren & Stensiö (1936, fig. 365), Rayner (1948, fig. 10) and Gardiner (1963, fig. 19), but the only attempt at an accurate reconstruction is Wenz's (1968) of *L. elvensis*, shown with paired rostrals. Rayner (1948, p. 304) mentioned 'what is possibly a rostral' in P.12211 (*L. minor*), and among well over a hundred skulls of *Lepidotes* in the B.M. (N.H.) this specimen (figure 135) is the only one in which the snout is more or less intact. The nasals (Na) and antorbitals (Ant) of this specimen agree closely with the nasal and 'paired rostral' of Wenz's (1968, fig. 44) specimen of *L. elvensis*, and the small median rostral (Ro) must be missing from the latter. In *Lepidotes* the long anterior process of the antorbital appears to pass antero-ventral to the rostral, as in caturids (figure 133). The configuration of the nasal in *Lepidotes* indicates that there were two nostrils, as in *Dapedium*, caturids and *Amia*, not one as Gardiner (1963, p. 317) supposed.

In *Semionotus* the premaxillae have long nasal processes, perforated by the olfactory nerve (Schaeffer & Dunkle 1950, figs 5, 6), as in *Lepidotes*, but the remaining bones of the snout are too poorly known for comment (cf. Lehman 1966, figs 153*b*, *d*).

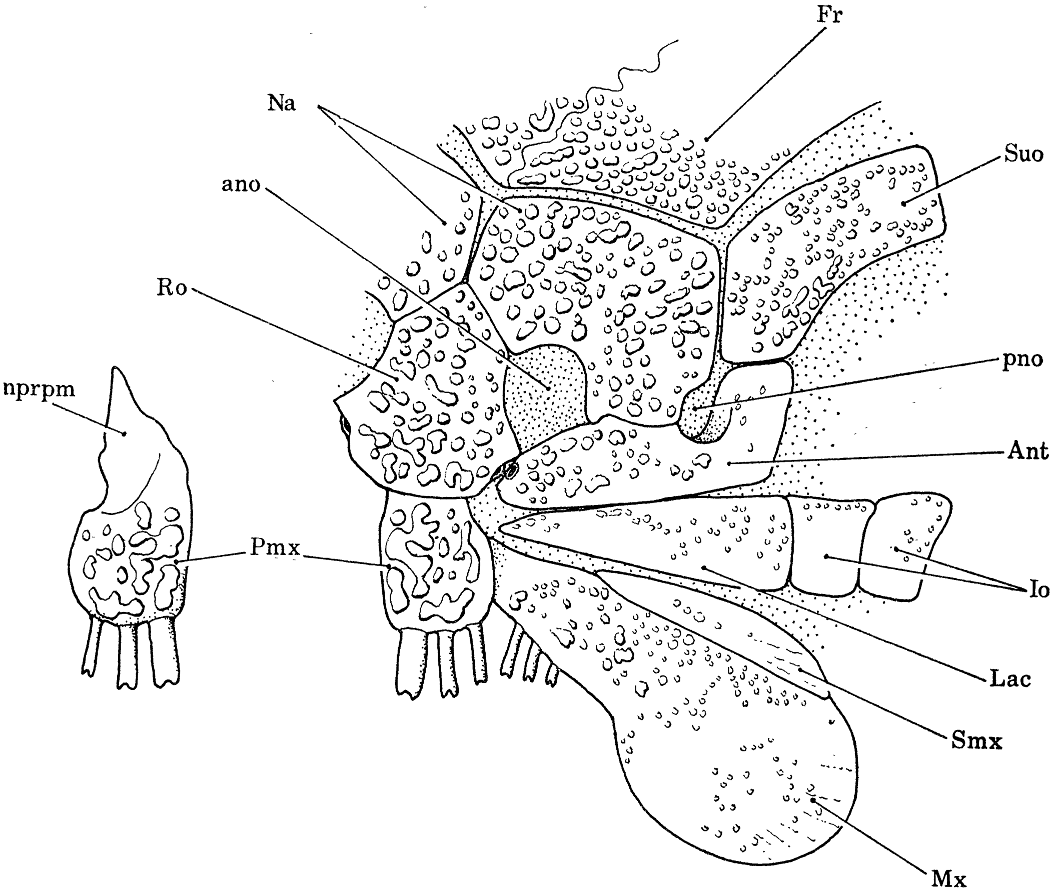


FIGURE 134. *Dapedium* sp. Sketch restoration of snout, drawn as if the dermal bones were folded out in one plane and the right premaxilla displaced to the right. Based on P.1561, P.3538*a* (both *D. colei* Agassiz) and P.3540 (*D. punctatum* Agassiz) (magn. × 2.5 approx.).

In the Permian *Acentrophorus*, placed with *Dapedium* and *Lepidotes* in the Semionotidae (Gardiner 1967) or Semionotiformes (Lehman 1966), Gardiner (1960, figs 69, 70; 1963, fig. 19) restored the snout as containing paired premaxillae, widely separated antorbitals, and nasals separated by a median rostro-postrostral. The ethmoid commissure is shown passing through the anterior part of the nasal and across the rostro-postrostral. Amongst the specimens of *Acentrophorus* that I have seen (including the collection in the Hancock Museum, Newcastle-upon-Tyne, which contains most of the specimens illustrated by Gill 1923), I have found no trace of a median bone between the nasals. It is not possible to produce a satisfactory restoration from these specimens, but the most complete snout is interpreted in figure 136*a*. This seems to show nasals (Na) separated by an unossified area, antorbitals (Ant) with long anterior processes overlying the premaxillae (Pmx), and a small median rostral (Ro), a pattern comparable with that of other holosteans. The premaxillae (figure 136*b*) have short nasal processes which pass back and line the nasal pit, much as in *Dapedium* (figure 134).

In parasemionotids, no complete account of the snout has yet been published (Stensiö 1932, fig. 89; Piveteau 1935, figs 40, 47; 1941, fig. 2; Lehman 1952, figs 106–7, 116, 124; Lehman, Chateau, Laurain & Nauche 1959, figs 12–15). Figure 137 is based on specimens from East Greenland. The large nasals (Na), meeting in the mid-line through part of their length and notched by the two nostrils (ano, pno), have been illustrated by several authors. The remarkably long rostral process of the antorbital (rpan) is illustrated by Piveteau (1941, pl. 1, fig. 7) in a Madagascar specimen, and is shown in several Greenland specimens. The diminutive rostral (Ro), best shown by MMK 500, has a pair of small lateral processes above the junction with the antorbital, as in caturids (figure 133). The premaxilla (figure 137*b*) has a nasal process (nprpm), lining the nasal pit, which is about as large as in *Dapedium* (figure 134) and *Acentrophorus* (figure 136).

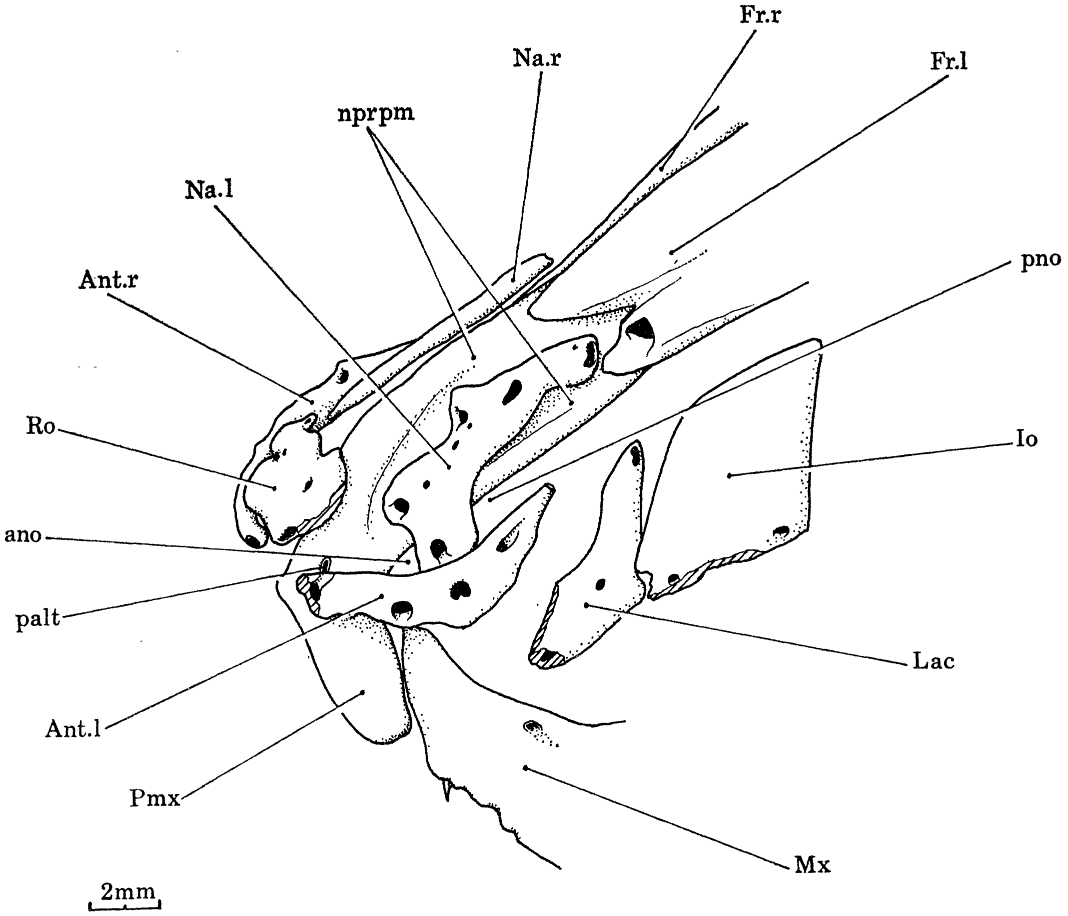
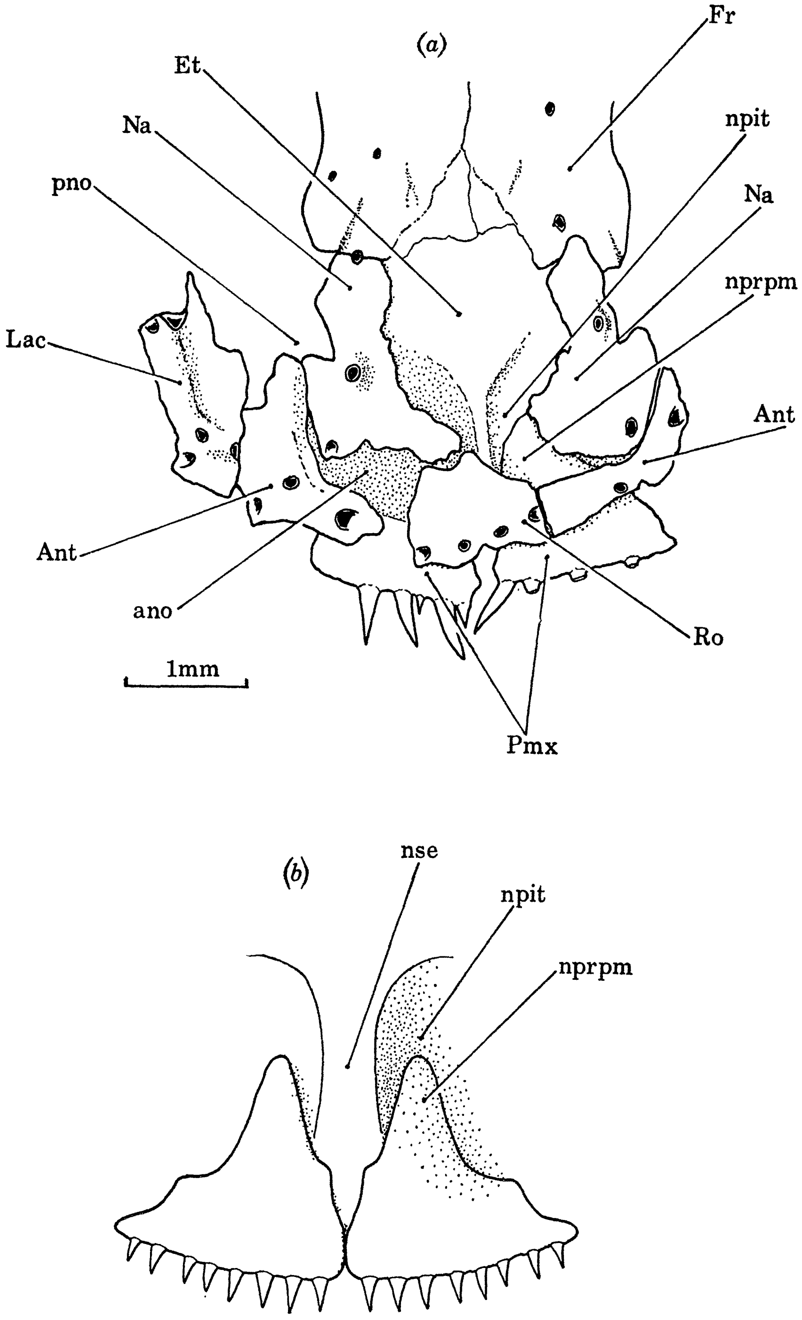


FIGURE 135. *Lepidotes minor* Agassiz. Snout as preserved in P.12211 (Woodward 1919, pl. 26, fig. 4). Broken surfaces cross-hatched. The suffixes l and r after certain abbreviations indicate bones of the left and right side.

In *Perleidus*, the snout is roofed by a pair of nasals separated throughout their length by a median bone carrying the ethmoid commissure, a pair of bones which contain a triradiate portion of the infraorbital sensory canal and pass antero-ventral to the median bone, and a pair of premaxillae (Stensiö 1921, figs 80, 81; 1932, fig. 68; Piveteau 1935, figs 28, 30; Lehman

1952, figs 85, 86; personal observations). Other perleidids show the same pattern (Schaeffer 1955, figs 7, 8). The median bone has been referred to as the postrostral or the rostralo-postrostral (Stensiö), while the bones carrying the triradiate sensory canal have been called rostrals, but the pattern of these bones and their relation to the sensory canals and nostrils seem entirely consonant with the pattern in holosteans, and the median bone should be called the rostral, the paired bones antorbitals. Extension of the rostral processes of the antorbitals below the



IGURE 136. *Acentrophorus varians* (Kirkby). (*a*) Interpretation of snout as preserved in Hancock Museum 9.2526. (*b*) Restoration of premaxillae and underlying part of ethmoid ossification in antero-dorsal view, based on P.37742 and Hancock Museum 9.2524, (magn. x 15 approx.).

rostral also occurs in parasemionotids, caturids and semionotids (figures 137, 133, 135). The premaxillae of an East Greenland *Perleidus* are shown in figure 138. They are small bones, each bearing only two large teeth, and in this individual are fused in the mid-line (evidently in late ontogeny). Dorsally, each bone bears a nasal process (nprpm), lining part of the nasal pit. This is the most primitive actinopterygian in which such processes are known, and here they are in their most rudimentary form.

In the groups just discussed (living holosteans, caturids, semionotids, parasemionotids, perleidids) the pattern of the roofing bones of the snout seems to be uniform, the main

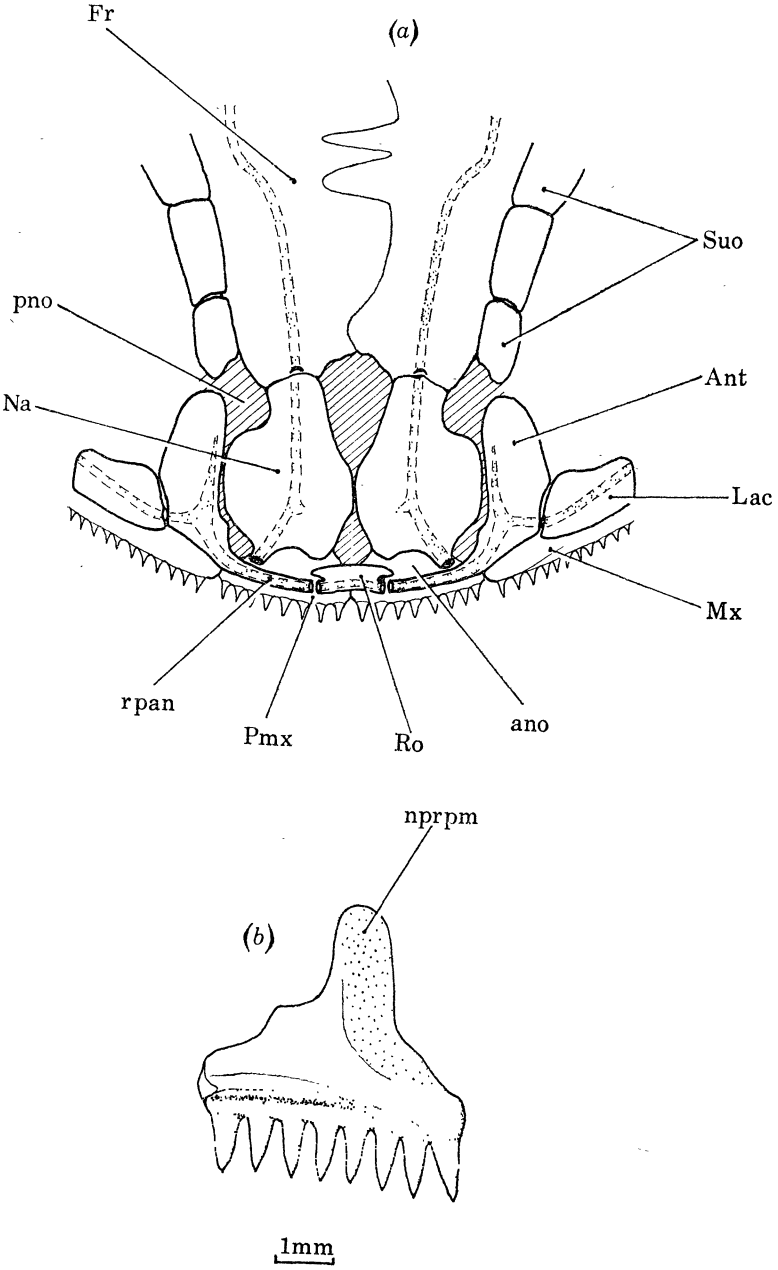


Figure 137. Undetermined parasemionotid from East Greenland. (*a*) Restoration of dermal bones of snout in antero-dorsal view, based on MMK 486, 487, 500 and 501 (magn. × 4 approx.). (*b*) Right premaxilla in medial (internal) view, based on MMK 494.

variations being in the size of the rostral (large in perleidids, diminutive in parasemionotids and living holosteans, intermediate in some semionotids), in the development of unossified lacunae (absent in perleidids and *Dapedium*, large in *Lepidotes*, intermediate in others), and in the development of the nasal process of the premaxilla (diminutive in *Perleidus*, large in *Lepisosteus*, *Lepidotes* and *Semionotus*, intermediate in others). The long rostral process of the antorbital, overlying the premaxilla and meeting the anterior or antero-ventral face of the rostral, which is characteristic of parasemionotids (figure 137), caturids (figure 133) and semionotids (figures 135, 136), is strikingly similar to the form of the 'rostro-antorbitals' of *Pteronisculus*, the most thoroughly investigated palaeoniscoid (Nielsen 1942, fig. 32). In *Pteronisculus* and *Boreosomus* (Nielsen 1942) the rostral processes of the 'rostro-antorbitals' pass medial to the lowermost part of the large postrostral, and the ethmoid commissure does not enter the latter bone. In *Ptycholepis*, which appears to be related to *Boreosomus* (Aldinger 1937; Brough 1939; Wenz 1968) the snout is very similar to that of *Boreosomus*, but the 'postrostral' is penetrated by the ethmoid commissure. Gardiner (personal communication) finds that in some Devonian palaeoniscoids from Western Australia the large 'postrostral' also contains a portion of the ethmoid commissure. It seems clear that the 'postrostral' of palaeoniscoids and the rostral of perleidids, holosteans and pholidophorids is homologous.

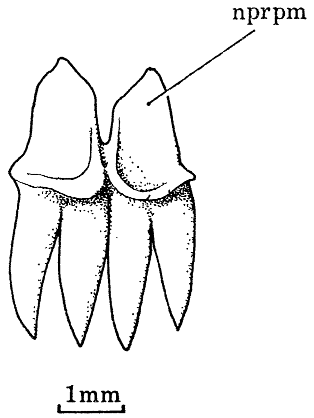


FIGURE 138. *Perleidus* cf. *stoschiensis* Stensiö. Premaxillae of MMK 496 in internal (posterior) view.

If the pattern of the bones roofing the ethmoid region in perleidids, parasemionotids, semionotids, caturids, some palaeoniscoids and living holosteans is compared with the primitive pholidophorid pattern described at the beginning of this section, the following conclusions can be drawn:

(1) The rostral of pholidophorids has a rostro-caudal extent which is only equalled in *Dapedium*, perleidids, *Ptycholepis*, and in the palaeoniscoid 'postrostral'. This is assumed to be primitive.

(2) The rostral of pholidophorids is broader than in any of the groups discussed so far, and contains a greater length of the rostral commissure, extending lateral to the anterior nostril. This might be due only to enlargement of the rostrum in pholidophorids, and consequent topographic distortion of the relationships between the roofing bones, or to incorporation in the rostral of a component which is represented in the rostral process of the antorbital of other groups: in the absence of an acceptable hypothesis on the primitive composition of the

actinopterygian snout, I do not believe it is possible to choose between these alternatives, but in either case the pholidophorid condition would be relatively advanced.

(3) The lateral dermethmoids of pholidophorids line the nasal pit, are often pierced or notched by the terminal branch of the palatine nerve, underlie the rostral, may meet the frontal posteriorly, and primitively bear teeth. They are therefore the topographic homologues of the premaxillae and their nasal processes in parasemionotids, semionotids, caturids and amiids, lacking only the penetration by the olfactory nerve which occurs in some semionotids and caturids (*Semionotus*, *Lepidotes*, '*Eurycormus*') and in amiids. The resemblance between the lateral dermethmoids of pholidophoroids (figures 121, 124, 125, 126) and the nasal processes of the premaxillae of parasemionotids (figure 137), *Acentrophorus* (figure 136) and *Dapedium* (figure 134) is very striking. The lateral dermethmoids of pholidophoroids differ from the premaxillae of the forms mentioned above only in failing to contact the maxilla laterally; in pholidophoroids a plate-like premaxilla is interposed between the margin of the toothed portion of the lateral dermethmoid and the maxilla (Griffith & Patterson 1963, figs 6, 7). Thus the pholidophorid premaxilla and lateral dermethmoid are together the exact topographic homologues of the premaxilla and its nasal process in perleidids, parasemionotids, semionotids, caturids, and amiids. In the second paper in this series it will be shown that fragmentation of the medial part of the premaxilla occurs in various pholidophorids (cf. Patterson 1973, fig. 4), and I therefore regard the pholidophorid premaxilla as the phylogenetic homologue of the lateral part of the holostean premaxilla, and the pholidophorid lateral dermethmoid as the phylogenetic homologue of the nasal process and medial toothed portion of the holostean premaxilla, the two parts having separated in pholidophorids as an adaptation to increased mobility of the upper jaw.

The only 'holostean' group which does not conform to this pattern is the Pachycormidae. In *Pachycormus* (Wenz 1968; figure 106) the snout is capped by a large median bone (Rode, figure 106) which bears teeth, contains the ethmoid commissure, meets the frontals posteriorly, separates the nasals, borders the anterior nostril and meets the antorbital and premaxilla antero-ventrally. Wenz did not describe a premaxilla, but the bone is present in two of the specimens of *Pachycormus* that she illustrates (pl. 26, fig. A and pl. 25, fig. A, displaced in the latter) and is illustrated in *Hypsocormus* by Woodward (1895, pl. 11, figs 3, 5; see also Lehman 1949, pls 5, 6). The rostrum of other pachycormids seems to have the same composition. Wenz calls the median bone in the pachycormid snout the postrostro-rostro-premaxillary, finding the posterior extension of the bone to suggest a postrostral component, the ethmoid commissure a rostral element, and teeth a premaxillary component. An isolated example of this bone is shown in internal (posterior) view in figure 139. The tooth-bearing part of the bone, below the level of the rostral commissure, has a curious double structure, with a pair of internal laminae (ldep) which are separated from the outer shell of the bone by a deep crevice. Anteriorly, there is a pair of rostral depressions (npit) at the base of these laminae, and a pair of small, ear-like processes (npro) project back below the depressions. I assume that these depressions are the anteriormost parts of the nasal pits, and the ear-like processes therefore have the same relations to the pit as the nasal processes of holostean premaxillae and the posterior part of the lateral dermethmoid of pholidophorids. This, and the paired internal laminae of the lower part of the bone suggest that it is indeed compound, a large rostral having grown downwards from its centre of ossification (the midpoint of the ethmoid commissure), overgrowing and eventually fusing with a pair of toothed bones. Since there is a pair of mobile premaxillae articulating with the lateral margins of these toothed bones, they are homologous not with the holostean premaxilla, but with the toothed lateral dermethmoid of pholidophorids, which has just these relationships, and the bone in *Pachycormus* may be called a rostro-dermethmoid.

In living and post-leptolepid teleosts the ethmoid region is roofed by a single median dermal bone, variously named rostral, dermethmoid or mesethmoid, or by a pair of bones, the proethmoids. An unpaired bone occurs in all those forms in which the ethmoid commissure remains bone-enclosed. In *Megalops* (figure 140) this bone has a pair of ventro-lateral processes (plp) which recall the postero-lateral processes of the leptolepid lateral dermethmoid (figures 123, 127–131), and have the same morphological relationships. These processes may arise independently in ontogeny (Weitzman 1967*b*, p. 526). I therefore regard these processes as phylogenetic homologues of the lateral dermethmoids, and consider the 'rostral' of *Megalops* to be a rostro-dermethmoid, as in leptolepids. There is a similar rostro-dermethmoid in the Jurassic elopiform *Anaethalion* (Nybelin 1967*b*, pl. 8, figs 1, 2) and the Cretaceous salmoniform *Gaudryella* (Patterson 1970*b*, fig. 2). In other living teleosts the lateral processes of the rostral are absent, but I consider that this is secondary and that the bone is phylogenetically a rostro-dermethmoid: in most teleosts it fuses with the supraethmoid (p. 514).

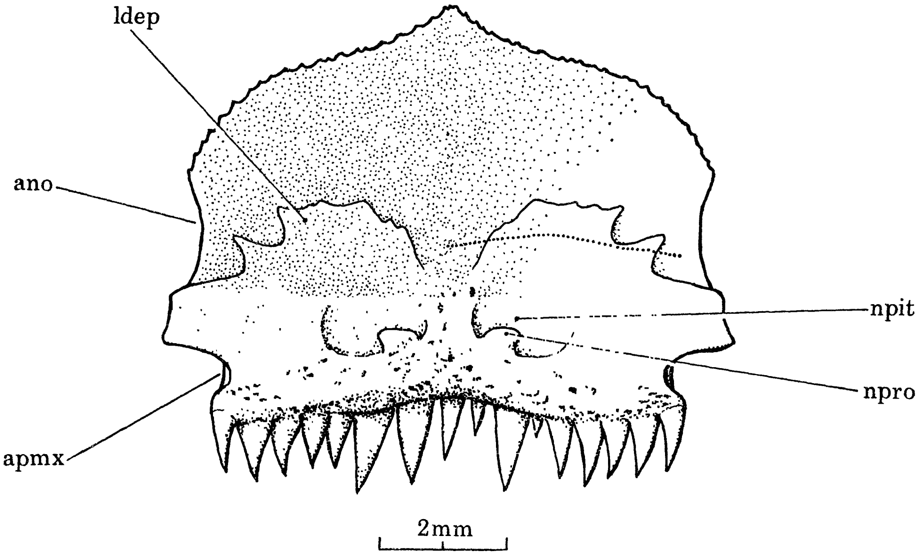


FIGURE 139. *Pachycormus curtus* Agassiz. Restoration of isolated rostro-dermethmoid in internal (posterior) view, based mainly on 32425 (see also figure 106). The dotted line on the right side marks the course of the ethmoid commissural sensory canal.

Paired proethmoids are found in esocoids and in some osmeroids and stomiatoids. In a previous discussion of the teleost ethmoid region (Patterson 1970*b*) I concluded that these paired bones might represent a relatively primitive condition, reflecting the ontogenetic influence of the paired neuromasts of the ethmoid commissure. I now think that these bones are more probably a relatively advanced feature, following reduction in the inductive influence of the ethmoid neuromasts, since proethmoids only occur in teleosts in which the ethmoid commissure is reduced to a pit-line. The proethmoids may be a secondary reappearance of the lateral dermethmoids, but I am unwilling to give the name proethmoid to those bones in pholidophorids and leptolepids since it is likely that teleostean proethmoids also include a rostral component (as indicated by the ontogenetic association between the ethmoid pit-line and the proethmoids in *Esox* (Pehrson 1944), and by the identical relations of the proethmoids of some osmerids and the median rostro-dermethmoid of others).

In summary, the foregoing analysis of the pattern of the bones roofing the ethmoid region in fossil actinopterygians leads to the hypothesis that the rostral of holosteans and teleosts is the homologue of the 'postrostral' of palaeoniscoids. This suggests the further hypothesis that the primitive actinopterygian snout was roofed by a large median rostral (= postrostral), which separated the nasals, and by paired premaxillary and antorbital components which met beneath the rostral, bore teeth, and contained the triradiate foremost part of the infraorbital canal and the greater part of the ethmoid commissure. The premaxillary and antorbital components may have been fused primitively, as Gardiner (1963) suggested, but in *Pteronisculus* and perleidids they are separate, as they are in holosteans and teleosts. The rostral may have subsequently 'captured' the middle part of the ethmoid commissure: this portion is short in parasemionotids, caturids, semionotids and living holosteans, long in pachycormids and pholidophoroids. In the former groups the antorbital has a long rostral process overlying the premaxilla, as it does in *Pteronisculus* and perleidids; in pachycormids and pholidophoroids this process is small.

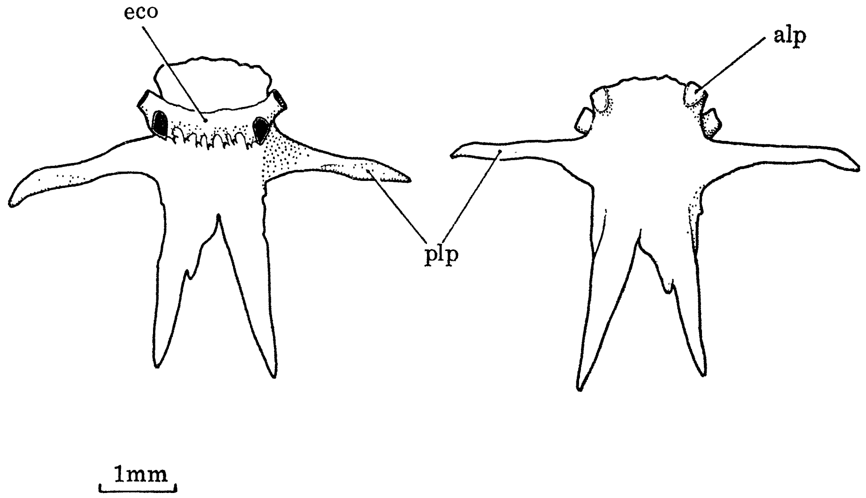


FIGURE 140. *Megalops cyprinoides* (Broussonet). Rostro-dermethmoid of an individual 90 mm in standard length in dorsal (left) and ventral view (from Patterson 1970*b*, fig. 35).

During actinopterygian evolution the premaxillae developed nasal processes in the floor of the nasal pit, presumably for mechanical reasons. These processes are found in their most rudimentary form in *Perleidus*. In some semionotids and caturids and in living holosteans they increased in length so that they came to be penetrated by the olfactory nerve. In pachycormids and pholidophorids the lateral portion of the premaxilla separated from the medial portion, bearing the nasal process, so producing the (mobile) premaxilla and (fixed) lateral dermethmoid. In pachycormids the lateral dermethmoid fused with the large rostral. In leptolepids the lateral dermethmoids became much modified with the development of a complex rostrum and a mobile upper jaw, and later fused with the reduced rostral. In most teleosts the compound rostro-dermethmoid fuses with the endoskeletal supraethmoid (point 4 below).

3. *The vomer.* The probability that the vomer of most teleosts is a compound bone, incorporating the endoskeletal ventral ethmoid of more primitive forms, has been mentioned above (p. 501), and is further discussed on p. 514.

There is a median vomer in pholidophoroids and leptolepids, as there is in all teleosts (except *Hiodon* and *Osmerus*: see below). The only other actinopterygians in which a median vomer occurs are the semionotids *Lepidotes* (Woodward 1916; Holmgren & Stensiö 1936) and *Dapedium*, the pycnodonts and *Bobasatrania* (Nielsen 1952): in all these forms the median vomer has apparently developed in conjunction with a crushing dentition, whereas in pholidophoroids and teleosts the median bone is probably a consequence of increased mobility of the jaws and palate.

There is a paired vomer in two living teleosts, *Hiodon* (paired in 3 *H. alosoides*, unpaired in one *H. tergisus* examined) and *Osmerus*. In *Osmerus* the paired vomer is obviously associated with the development of a pair of large vomerine tusks, and may well be secondary. In *Hiodon* the vomer is diminutive and toothless, but the paired condition might be primitive.

There is a paired vomer in *Amia*, *Lepisosteus*, pachycormids (there are small vomers in *Pachycormus*, Lehman 1949, fig. 4; larger bones in *Hypsocormus*, P.10906), caturids (Brough 1939, p. 81; Gardiner 1960, fig. 36), parasemionotids (figures 30, 41), saurichthyids (Stensiö 1925) and possibly also in *Boreosomus* (Nielsen 1942, p. 322). The so-called paired vomer of *Pteronisculus* (Nielsen 1942, fig. 34) and *Australosomus* (Nielsen 1949, fig. 26) appears to be merely a tooth-plate between the endopterygoid and parasphenoid. There is therefore no vomer in *Polypterus* (Allis 1922), living chondrosteans, *Birgeria*, *Australosomus* or *Pteronisculus*, but a paired vomer occurs in rhipidistians, coelacanths and dipnoans. This raises the question of whether vomers are secondarily absent in *Polypterus*, living chondrosteans and palaeoniscoids, or whether that condition is primary and the vomers of actinopterygians are not phylogenetic homologues of those of crossopterygians and dipnoans.

Jarvik (1954) suggested that the vomer is a premandibular arch structure, serially homologous with the innermost dental plates of upper parts of the mandibular, hyoid and gill-arches, and that the ventral part of the ethmoid region, against which the vomer rests, represents the infrapharyngopremandibular, incorporated into the braincase. In support of this, he cited Holmgren's (1943) investigation of the embryology of the trabeculae and palatoquadrate in *Acipenser*, *Amia*, *Lepisosteus* and teleosts (see also Bertmar 1959; Bjerring 1972). In these fishes the anterior ends of the palatoquadrate and trabeculae are joined by a blastema, the intermediating body. In *Acipenser* the intermediating body gives rise to the ethmo-palatine ligament and the palatoquadrate commissure develops below the ethmoid region. In *Amia* and teleosts the intermediating body chondrifies separately, contributes to the lamella below the trabeculae which forms the palatoquadrate commissure, and eventually fuses into the ethmoid plate. The vomer develops beneath the palatoquadrate commissure. While it does not seem necessary to follow Jarvik, Bertmar and Bjerring in assigning the vomer to a premandibular arch (cf. p. 534 below and Miles 1971, p. 3), it is true that the vomer always lies in sequence with the dermopalatines, and that in actinopterygians where there is a vomer (holosteans, teleosts) this bone develops in relation to a portion of the ethmoid endoskeleton which can be regarded as derived (in ontogeny) from the palatoquadrate, while in forms where there is no vomer (*Acipenser*) there is no such contribution to the ethmoid region. Perhaps all that can be said at present is that the shark-like palatoquadrate commissure of living chondrosteans is not necessarily secondary (as it is usually assumed to be), and that the phylogenetic homology implied by use of the name vomer in actinopterygians, crossopterygians and dipnoans is not yet established: possibly the vomer developed independently in these groups with incorporation of the foremost portion of the palatoquadrate into the neurocranium.

4. *Fusions between the endoskeleton and exoskeleton.* In primitive actinopterygians such as the

palaeoniscoids, where growth was apparently terminated by closure of the sutures in the braincase, it is likely that the endoskeleton and exoskeleton of the braincase fused to some extent in full-grown individuals: this probably also occurred in pholidophorids. Fusion between the endo- and exoskeleton of the ethmoid region early in ontogeny, the process under discussion here, occurs only in leptolepids and more advanced teleosts. It may involve both the vomer and the roofing bones.

Fusion between the roofing bones and the ethmoid endoskeleton is restricted to forms in which the rostral and lateral dermethmoids have already fused into a compound rostro-dermethmoid, except for the Sinemurian *Leptolepis*, where the mesethmoid and lateral dermethmoids fuse at the tip of the rostrum, presumably late in ontogeny. In other leptolepids there is a rostro-dermethmoid, and this fuses with the supra- or mesethmoid wherever the endoskeleton is ossified (*L. coryphaenoides*, *L. dubia*, Wealden species). A similar fusion occurred in the Jurassic ichthyodectid *Allothrissops* (Patterson 1967, fig. 2) and in Cretaceous ichthyodectids (Bardack 1965). Amongst teleost groups with living representatives, the rostro-dermethmoid only remains individualized in primitive forms. In clupeomorphs, the rostro-dermethmoid and supraethmoid are apparently always fused, a condition which had already appeared in the Cretaceous *Diplomystus* (Patterson 1967, fig. 7). In osteoglossomorphs, conditions are still imperfectly known. In *Heterotis* the first ossification in ontogeny is dermal (Daget & d'Aubenton 1957, p. 898), but in the adult this has fused with an endoskeletal ossification. Similar fusions appear to take place in *Hiodon*, notopterids and mormyrids. According to Ridewood (1905) there is only a dermal ossification in *Scleropages* and only an endoskeletal one in *Arapaima*. In elopomorphs, the rostro-dermethmoid remains individualized in elopoids (including the Jurassic *Anaethalion* and the Cretaceous *Notelops*) since the supraethmoid does not ossify. In albuloids, eels, notacanths and halosaurs the rostro-dermethmoid and supraethmoid appear to be fused. In euteleosteans the supraethmoid and rostro-dermethmoid (median or paired) only remain distinct in forms in which the endoskeleton is very weakly ossified (coregonines, Berg 1955, fig. 192; Nybelin 1967*a*, fig. 4: esocoids, osmerids, some stomiatoids, Weitzman 1967*b*). The only exception to this is the Cretaceous salmoniform *Gaudryella* (Patterson 1970*b*), where the well ossified mesethmoid is separate from a rostro-dermethmoid of primitive form. In higher euteleosteans (Neoteleostei of Rosen & Patterson 1969) the rostro-dermethmoid and supraethmoid are apparently fused into a compound mesethmoid *ab initio*: this may be a consequence of the complex upper jaw mechanism of these forms.

Fusion between the vomer and ventral ethmoid of teleosts has been mentioned above (p. 501). It occurs in late ontogeny in *Leptolepis coryphaenoides* and *L. dubia* amongst leptolepids, and in *Megalops* and the Cretaceous *Notelops* (Dunkle 1940, p. 177) among elopomorphs. Examination of adult skulls of albuloids and eels suggests that the vomer also incorporates an endoskeletal component in these groups. In clupeomorphs, the vomer appears to include an endoskeletal ossification in clupeoids (figure 132), but not in *Denticeps* (Greenwood 1968), where the ventral surface of the ethmoid cartilage does not ossify. Among osteoglossomorphs the diminutive vomer of *Hiodon* (paired) and mormyrids (Taverne 1972) is presumably purely dermal. In *Heterotis* the vomer originates perichondrally (Daget & d'Aubenton 1957, p. 898) and therefore probably incorporates the ventral ethmoid, and this may be true of other osteoglossoids. In euteleosteans an independent ventral ethmoid occurs in osmerids, galaxioids and the stomiatoid *Polymetme*, so that the vomer must be entirely dermal in these. In *Argentina* and the Cretaceous salmoniforms *Gaudryella* and *Humbertia* the ventral surface of the mesethmoid is perichondrally ossified (Patterson 1970*b*, figs 2, 16, 35), so that here too there is no fusion with the vomer: this may be true of some other primitive euteleosteans. In *Salmo*, *Cyprinus* and in those higher euteleosteans whose embryology has been investigated in detail the vomer assumes perichondral relations with the underside of the ethmoid cartilage or invades that cartilage in early ontogeny. This indication that the vomer incorporates the ventral ethmoid is corroborated by the relations of the bone in adults (Allis 1909, p. 17). It is probable that the vomer of most, if not all, neoteleosts is a compound 'vomero-ventral ethmoid'.

In summary, the fusions between the rostro-dermethmoid, vomer and ethmoid endoskeleton which occur in late ontogeny in some leptolepids are characteristic of early ontogeny in the majority of living teleosts and are not known to occur in other fishes. The mesethmoid of most higher teleosts is phylogenetically a rostro-dermethmo-supraethmoid, and the vomer is a vomero-ventral ethmoid. Since the limits of these components can rarely be discerned, the use of these cumbersome terms would serve little purpose, and I do not advocate changing the usual terminology.

5. *The anterior myodome.* The anterior myodome of pholidophorids and leptolepids is a median perichondrally lined canal which housed the olfactory nerves and both pairs of oblique eye muscles (except in the Callovian *Leptolepis*, where the inferior oblique muscles originated at the entrance to the canal). The eye muscles extended into the nasal septum between the olfactory organs. An anterior myodome of this type is found only in teleosts.

In living chondrosteans and in *Lepisosteus* there is no anterior myodome; the oblique muscles originate separately in the chondrosteans and together in *Lepisosteus*. In *Polypterus* the superficial oblique muscle originates well above the inferior and penetrates into the canal containing the profundus and superficial ophthalmic nerves and the ophthalmic vessels. In *Amia* both oblique muscles pass through the orbitonasal canal, together with a vein, enter the (paired) canal for the olfactory nerve, and originate on the floor of that canal (Allis 1897, fig. 25). *Sinamia* (Stensiö 1935) seems to show the same type of anterior myodome.

In teleosts the anterior myodome is variable and insufficiently studied. In many teleosts (listed by Norman 1926, p. 407) there is no anterior myodome. This is generally assumed to be due to secondary loss, since the anterior myodome is not developed in forms in which the posterior myodome is reduced, the latter undoubtedly a secondary condition. The presence of a well developed anterior myodome in pholidophorids and leptolepids supports this hypothesis. In *Salmo* (Norman 1926, fig. 41; de Beer 1927; Goodrich 1930, figs 285, 287) both oblique muscles enter the foramen olfactorium evehens, together with the orbitonasal artery, and pass forwards in a long canal in the nasal septum to originate in front of the olfactory organ in a median pocket. Because a canal for the orbitonasal vessels occurs in addition to a median anterior myodome in pholidophorids, it is unlikely that de Beer was right in his hypothesis (1927, p. 306) that the teleostean anterior myodome arose in phylogeny in the same way as it does in the ontogeny of *Salmo*, by penetration of the oblique muscles into the vascular canal. In *Salmo* the anterior part of the anterior myodome is partially divided by a median cartilaginous septum, but in *Galaxias* (Norman 1926, fig. 41) the canal is median, as it appears to be in other forms which have, like *Galaxias* and pholidophorids, an anterior myodome bone (osmerids; some stomiatoids, argentinoids and myctophiforms; Weitzman 1967*b*). According to Weitzman (1967*b*) the anterior myodome of osmerids and stomiatoids only contains the superior oblique muscles: this is also true of the Callovian *Leptolepis*, *Clupea* (Norman 1926) and the characid *Nannocharax* (Daget 1964, p. 209). In some teleosts the anterior myodome contains both oblique muscles but is paired throughout, as in *Cyclopterus* (Norman 1926, fig. 42); in others there are separate, upper and lower anterior myodomes, each containing one pair of oblique muscles, as in *Alepocephalus* (Gosline 1969, p. 197).

Among fossil actinopterygians, the palaeoniscoids (Kansas forms, *Kentuckia*, *Pteronisculus*, *Boreosomus*), *Saurichthys* and parasemionotids have two pairs of shallow anterior myodomes, dorsal (superior oblique muscle) and ventral (inferior oblique muscle) each of which may communicate with its fellow by fenestration of the interorbital septum (Stensiö 1925; Nielsen 1942; Rayner 1951; Lehman 1952; Beltan 1968). In these forms the anterior myodome has no connexion with the olfactory nerve canal, except in *Boreosomus*, where the dorsal anterior myodome was traversed by the olfactory nerve. In *Australosomus* there is a single, paired anterior myodome, housing both oblique muscles, which had no connexion with the olfactory nerve (Nielsen 1949; Lehman 1952; Beltan 1968). In *Dapedium* (P.11177; figure 112), as in palaeoniscoids, there are shallow, separate upper and lower anterior myodomes, the upper one, which lies dorsal to the olfactory nerve, confluent with its fellow through an interorbital fenestra. In caturids (*Caturus chirotes*; *Heterolepidotus*, figure 102; '*Aspidorhynchus*') there is a shallow, paired ventral anterior myodome, as in *Dapedium* and palaeoniscoids, and the olfactory nerves traversed the antero-dorsal part of the orbit through an interorbital fenestra: the superficial oblique muscles may have originated on the anterior margin of this fenestra. In the caturid *Macrepistius*, Schaeffer (1971) interprets the anterior myodome as being 'essentially a duplication of the *Amia* pattern', but his illustration (fig. 6) suggests that there were shallow upper and lower myodomes, as in other caturids. In these caturids the orbitonasal vascular canal lies dorso-lateral to the ventral anterior myodome. In *Pachycormus* (32434; figure 106) the vascular canal is similarly placed, but there is no well defined ventral anterior myodome, and it is

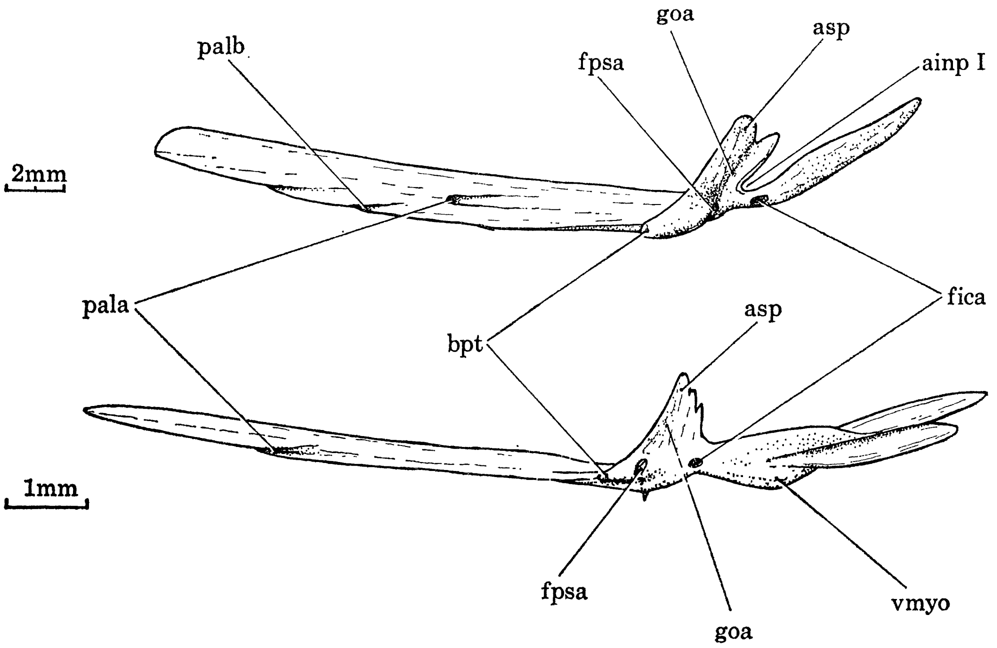


Figure 141. Parasphenoid in left lateral view of *Pholidophorus germanicus* Quenstedt (above, from P.3704) and Callovian *Leptolepis* sp. (below, from P.51736).

possible that both pairs of oblique muscles entered the foramen olfactorium evehens, as in pholidophorids and teleosts.

In summary, while absence of an anterior myodome in teleosts is probably secondary, there are as yet no anatomical criteria by which one may discriminate between the primitive and secondary absence of an anterior myodome. Separate, paired dorsal and ventral anterior myodomes occur in all palaeoniscoids, in parasemionotids, *Dapedium* and caturids, and this condition may well be primitive: if so, the absence of an anterior myodome in living chondrosteans and *Lepisosteus* would be secondary, associated with reduction in size of the eyeball. In *Lepisosteus* the superior and inferior oblique muscles originate together, suggesting that the absence of the anterior myodome is secondary, but in living chondrosteans, where the muscles originate separately, there is no means of testing the hypothesis that the condition is secondary. Whatever the primitive actinopterygian condition, there can be no doubt that the median anterior myodome, terminating in an anterior myodome bone, of pholidophorids and various euteleosteans is a unique specialization.

8. PARASPHENOID

Well preserved, complete parasphenoids are available in *Pholidophorus germanicus*, *P. macrocephalus*, the Callovian *Leptolepis* and *L. dubia*. In *P. bechei*, the Callovian *Pholidophorus*, the Sinemurian *Leptolepis* and *L. coryphaenoides* less complete parasphenoids are available, while in *Pholidophoroides limbata* and *Pholidophorus minor* the parasphenoid is unknown. The parasphenoids of *P. germanicus* and the Callovian *Leptolepis* will be described in detail, and the other species compared with them.

(*a*) Pholidophorus germanicus

The parasphenoid is shown in lateral view in figure 141 and in dorsal and ventral view in figure 142. The anterior part of the bone, below the ethmoid region, is slender and has the form of an inverted V in section. It fits over the dorsal surface of the posterior process of the vomer, as in teleosts. In the anterior part of the orbit the parasphenoid broadens, its breadth increasing posteriorly to reach a maximum at the basipterygoid process. On the dorsal surface of this orbital part of the bone there is a median crest on which the membranous interorbital septum inserted. The palatine nerves and the vessels accompanying them lay on either side of this crest, and about half way between the basipterygoid process and the anterior end of the bone the palatine nerve divided into medial and lateral branches, the lateral branch passing out to the palate through a notch (palb) in the margin of the bone, the medial branch passing through a paired canal (pala), emerging on the underside of the bone, and running forward to the snout in the apex of the groove on this surface.

The basipterygoid process (bpt) is extremely large, and was clearly entirely dermal, with no bony or cartilaginous contribution from the endocranium. The root of the basipterygoid process is perforated by a large, dorso-medially directed foramen (fpsa) for the efferent pseudobranchial artery. Between the lower openings of these foramina there is a U-shaped patch of small, pointed teeth (figure 142*a*), with the lower opening of the narrow bucco-hypophysial canal (bhc) lying between the arms of the U.

Behind the basipterygoid process the posterior part of the parasphenoid is bent upwards through 25°. This posterior part of the bone met the cartilage covering the ventral edges of the prootics, and ended below the anterior part of the basioccipital, forming the floor of the

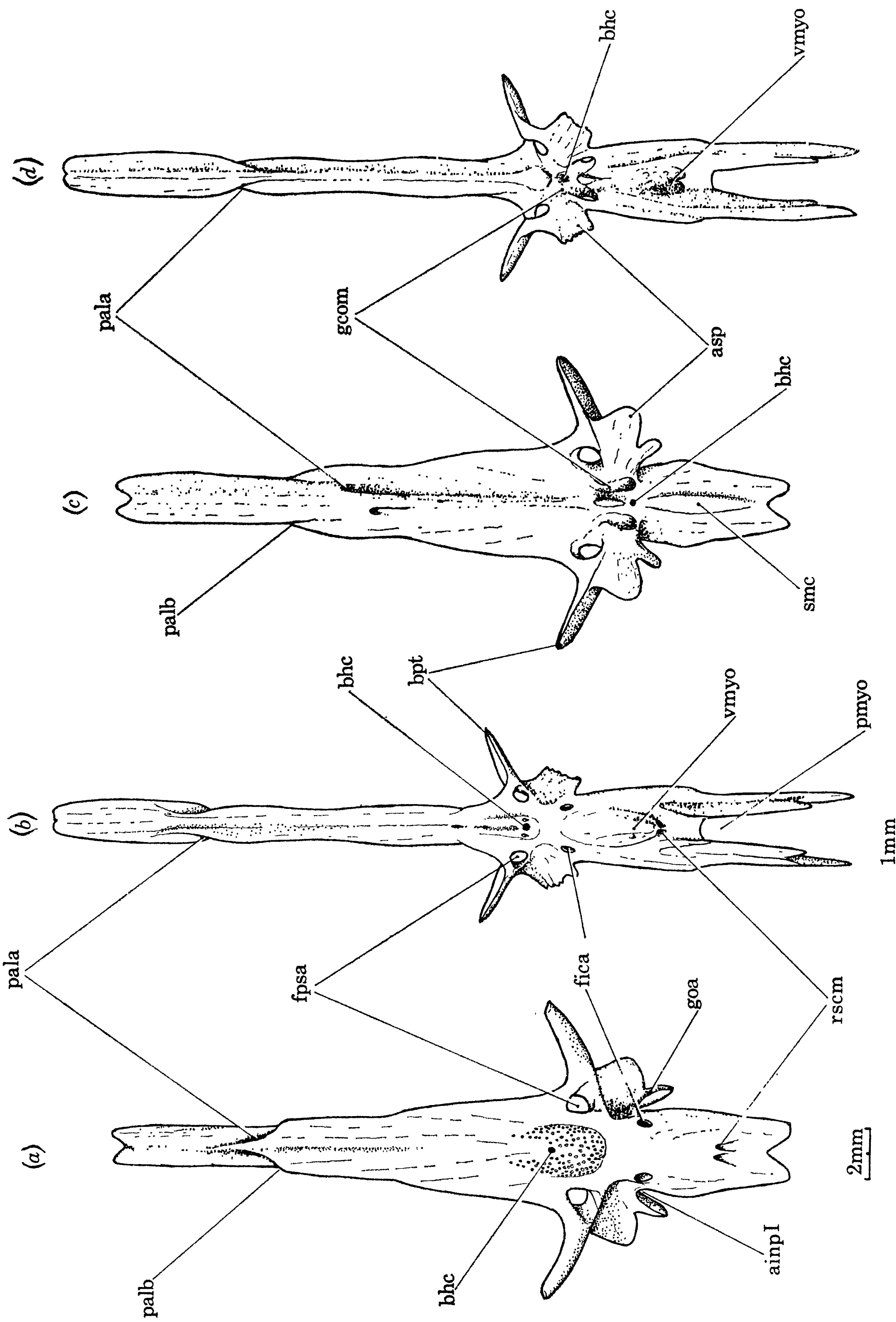


FIGURE 142. Parasphenoid of *Pholidophorus germanicus* Quenstedt (*a*, *c*, from P.3704) and Callovian *Leptolepis* sp. (*b*, *d*, from P.51736) in ventral (*a*, *b*) and dorsal (*c*, *d*) views.

myodome. A broad, low median crest (smc) on the upper surface of this part of the bone marks the area not covered by cartilage. On the underside of the posterior part of the parasphenoid there is a pair of small, antero-dorsally directed pits (rscm) which seem to mark the attachment of some paired muscle or ligament (see p. 535). The ascending process of the parasphenoid (asp), which was applied to the outer surface of the prootic, is short rostro-caudally and directed postero-dorso-laterally. Anteriorly, the ascending process is continuous with the upper margin of the basipterygoid process. In lateral view, the ascending process is separated from the posterior part of the bone by a deep notch or incisure (ainp I). Comparison with *P. bechei* (figures 61, 62) shows that the first infrapharyngobranchial articulated with a cartilaginous area of the endocranium in the apex of this notch. The ascending process consists of two portions separated by a notch dorsally: a broad anterior portion whose external surface faces postero-laterally, and a slender posterior part which faces laterally. There is thus a groove (goa) on the external surface of the process: this groove probably housed the orbital artery, not the spiracular diverticulum.

The internal carotid arteries passed through a pair of antero-dorsally directed canals (fica) entering the parasphenoid just behind the base of the ascending processes. The arteries emerged between the ascending processes, and a pair of curved grooves (gcom) marks the course of the communicating branches between the carotids and the efferent pseudobranchial arteries. There is no sign of a transverse groove linking the efferent pseudobranchial foramina and it is unlikely that there was any anastomosis between these arteries.

Between the arterial foramina on the upper surface of the parasphenoid there is a vertical median process which fitted against the posterior face of the foot of the basisphenoid pedicel. Behind this process and immediately between the internal carotid foramina is the upper opening of the bucco-hypophysial canal (bhc). This narrow canal passed antero-ventrally through the bone and opened in the middle of the tooth patch, as described above.

(*b*) *Callovian* Leptolepis *sp.*

The parasphenoid of this species is shown in lateral view in figure 141 and in dorsal and ventral view in figure 142. In comparison with the parasphenoid of *P. germanicus* the bone is much more slender and lightly built, and also more extensive posteriorly. In both species the centre of ossification lies approximately between the basipterygoid processes. In *P. germanicus* the ratio between the length of the parts posterior and anterior to this point is about 1:2.3; in the leptolepid this ratio is about 1:1.4. The anterior, ethmoid portion of the parasphenoid is similar to the corresponding portion in *P. germanicus* but less sharply angled in section. The orbital portion of the bone is much more slender than in *P. germanicus* but has a similar median crest on its dorsal surface. The medial branch of the palatine nerve did not reach the ventral surface of the bone through a canal as it did in *P. germanicus*, but through a notch (pala) in the margin, like the lateral branch of the nerve in *P. germanicus*. The basipterygoid processes are shorter and more slender than in *P. germanicus* but are still relatively long. The efferent pseudobranchial arteries passed through a pair of large antero-dorsally directed foramina (fpsa) in the root of the basipterygoid process, as in *P. germanicus*. Between the efferent pseudobranchial foramina there is a narrow raised area on the underside of the bone. In the figured specimen (figure 142*b*) this bears only two minute teeth, with the opening of the bucco-hypophysial canal (bhc) between them. Amongst nine other specimens, the distribution of teeth is as follows: no teeth, 3 specimens; 1 tooth, 1 specimen; 2 teeth, 2 specimens; 3 teeth, 1 specimen; 9 teeth, 1 specimen; 12 teeth, 1 specimen. In the specimens with 9 and 12 teeth the teeth are clustered around the lower opening of the bucco-hypophysial canal.

The posterior part of the parasphenoid is bent upwards through about 20°, much as in *P. germanicus*, but this part of the bone is much longer than in the latter, with a pair of processes extending back to the level of the cup for the aortic ligament on the basioccipital (figure 47*d*), and it is also much more complex. On the dorsal surface of this posterior part of the bone there is a pair of lateral grooves which housed the ventral edges of the prootics and basioccipital. The floor of the myodome, between these grooves, is formed by the parasphenoid. This floor is only complete beneath the anterior, prootic part of the myodome. Posteriorly, beneath the basioccipital, the myodome opened to the exterior between the posterior processes of the parasphenoid, as it does in many primitive teleosts (Ridewood 1904*a*, p. 60). The floor of the prootic portion of the myodome (vmyo) is strongly concave in both the longitudinal and transverse planes, and bulges out on the ventral surface of the bone. This concavity ends posteriorly in a small, median process, directed anteriorly, which probably marks the insertion of the hind end of the horizontal myodomic membrane, separating the myodome into a dorsal compartment, housing the external rectus muscles, and a ventral compartment, housing the internal rectus muscles. The latter muscles may have originated on the underside of the horizontal membrane, as they do in some living teleosts (Allis 1919), or on the parasphenoid. On the underside of the bone at the posterior end of the swelling in the floor of the myodome there are one, two or more pits (rscm) or small perforations which I take to be the homologues of the pair of pits in this region in *P. germanicus*. Behind these pits there is a pair of longitudinal crests on the underside of the bone.

The ascending process of the parasphenoid (asp) is aligned more vertically than in *P. germanicus* and is not separated from the posterior part of the bone by a deep incisure. The first infrapharyngobranchial, which articulated with endocranium in that incisure in *P. germanicus*, probably articulated with the parasphenoid at the foot of the ascending process in the leptolepid, as it does in living teleosts (p. 398). The ascending process is about as high as in *P. germanicus*, and bears a groove for the orbital artery (goa), although the groove is less clearly marked than in the pholidophorid. The internal carotid foramina (fica) and grooves for the communicating branch to the efferent pseudobranchials (gcom) are arranged as in *P. germanicus*. As in the latter, the bone provides no evidence of a transverse anastomosis between the efferent pseudobranchials. The upper opening of the bucco-hypophysial canal (bhc) lies further forwards than in *P. germanicus*, midway between the efferent pseudobranchial and carotid foramina, and only just behind the lower opening of the canal. The process fitting against the back of the foot of the basisphenoid pedicel is less obvious than in *P. germanicus* and lies directly between the efferent pseudobranchial foramina.

(*c*) Pholidophorus bechei

In this species only the orbital and posterior parts of the parasphenoid are well known. This portion of the bone (Psp) is shown in lateral and ventral view in figures 56, 61 and 62, and in sagittal section in figure 65. The orbital part of the bone differs from both *P. germanicus* and the Callovian species in being covered dorsally by endochondral bone. It is intermediate between these two species in breadth. The undersurface of this part of the bone is sparsely covered with minute teeth. The posterior teeth are borne in groups on raised areas or pedicels, suggesting that the region between the basipterygoid processes, which is toothed in *P. germanicus* and the

Callovian *Leptolepis*, is toothless in *P. bechei* because it was not in contact with the mucous membrane lining the roof of the mouth. The basipterygoid process (bpt) is smaller than in *P. germanicus* and the Callovian *Leptolepis*, but the distance between the tips of the paired processes is about the same as in the leptolepid because the body of the bone is broader in *P. bechei*. On the dorsal surface of the process there is a groove (figure 64) which appears to have contained cartilage (p. 332). This rudiment of an endoskeletal basipterygoid process did not extend to the tip of the dermal process and did not contribute to the articulation with the palate. The foramina of the efferent pseudobranchial arteries (fpsa) are arranged as in *P. germanicus* and the Callovian *Leptolepis*. The bucco-hypophysial canal (bhc, figures 60, 62) opens on a raised area between the efferent pseudobranchial foramina, as in the Callovian *Leptolepis*.

Because no complete parasphenoid is available in *P. bechei* it is not possible to calculate the ratio between the lengths of the anterior and posterior portions of the bone, but it is evident that this ratio would be close to that in *P. germanicus*, for as in the latter the posterior part of the parasphenoid covers less than half of the ventral surface of the basioccipital (figures 56, 65). In contrast to *P. germanicus* and the Callovian *Leptolepis*, the greater part of the upper surface of this posterior portion of the parasphenoid is covered by endochondral bone, and the parasphenoid only lines a narrow fenestra in the floor of the myodome (figure 65). The underside of the posterior part of the parasphenoid (figure 62) has a rather complex relief. Immediately behind the raised area carrying the lower opening of the bucco-hypophysial canal there is a marked transverse furrow with a median hump behind it. This transverse groove is close to the internal carotid foramina (fica), but appears to be associated not with them but with a groove which passes up the ascending process in front of the groove for the orbital artery (goa), which originates directly above the carotid foramen. This groove (spig) is the lower part of the spiracular groove, and the median furrow on the parasphenoid must mark a median connexion between the spiracular diverticula. This transverse furrow is bounded posteriorly by a median eminence or hump which lies directly between the internal carotid foramina. Behind this hump there is a deep median depression on the parasphenoid, containing a pair of anterodorsally directed pits (rscm, figures 62, 65), obviously comparable with the similar pits in *P. germanicus*. A median groove, limited laterally by a pair of crests, extends from these pits to the posterior end of the parasphenoid. The surface of this groove is ridged and pitted, suggesting that muscles or ligaments originated throughout the area.

The ascending process of the parasphenoid of *P. bechei* is separated from the posterior part of the bone by a deep incisure containing the articulation of the first infrapharyngobranchial (ainp I, figures 61, 62), as in *P. germanicus*. The ascending process carries two grooves, the spiracular groove (spig) and the lower part of the groove for the orbital artery (goa). The internal carotid arteries passed through a pair of almost vertical foramina (fica) beneath the articulation of the first infrapharyngobranchial. After passing through the parasphenoid, the carotid and efferent pseudobranchial arteries and the bucco-hypophysial duct entered canals in the endochondral bone of the foot of the basisphenoid pillar, and their course is described with the orbitotemporal region of the braincase (p. 332).

(*d*) *Callovian* Pholidophorus *sp.*

Only the posterior part of the parasphenoid is known in this species, from just in front of the basipterygoid processes to the rear end of the bone. In front of the basipterygoid processes the bone is embedded in a mass of pyrite and its underside is not visible, so that the extent of the toothed area (if present) is unknown. The posterior part of the bone resembles that region in *P. germanicus* in every way.

(*e*) Pholidophorus macrocephalus

The parasphenoid of this species is shown in ventral view in figure 84. In general, the bone resembles that of *P. germanicus* quite closely. The posterior part of the bone is a little more extensive than in *P. germanicus*, and the ratio between the length of the portions posterior and anterior to the centre of ossification is about 1:2.0, compared with 1:2.3 in *P. germanicus* and 1:1.4 in the Callovian leptolepid. As in *P. germanicus*, the medial branches of the palatine nerves passed through a pair of canals in the bone, emerging on its underside (pala) at the front of the orbit. There is no obvious notch in the margin of the bone for the lateral branch of the palatine nerve. In contrast to *P. germanicus* and *P. bechei* the parasphenoid of *P. macrocephalus* is toothless. The basipterygoid processes (bpt) are even more massive than in *P. germanicus*: in the latter species the ratio between the distance from tip to tip of the basipterygoid processes and the total length of the parasphenoid is about 1:2.3; in *P. macrocephalus* this ratio is about 1:2.1. The efferent pseudobranchial foramina in the roots of the basipterygoid processes are almost transversely directed, so that they are not visible in ventral view as they are in *P. germanicus* and *P. bechei*. The narrow bucco-hypophysial canal (bhc) opens between the basipterygoid processes. The posterior part of the parasphenoid extends further back than in *P. germanicus* and *P. bechei*, reaching the level of the housing of the aortic ligament (haol), as in the Callovian *Leptolepis*. The underside of the posterior part of the bone is flat except for a group of well marked pits (rscm), as in *P. germanicus*, and lacks the complex relief found in *P. bechei* and the Callovian *Leptolepis*. The ascending process of the parasphenoid is separated from the posterior part of the bone by a deep incisure containing the articulation of the first infrapharyngobranchial (ainp I), as in other pholidophorids. The outer face of the ascending process contains a groove for the orbital artery (goa), as in *P. germanicus*. The internal carotid foramina (fica) are positioned as in *P. germanicus* but are directed more horizontally than in the latter.

(*f*) *Sinemurian* Leptolepis *sp.*

No complete parasphenoid of this species is available, but the middle part of the bone is preserved in P.51685 and P.51687. These specimens form the basis of the restorations in dorsal, ventral and lateral view in figure 143. As in the braincase, the parasphenoid of the Sinemurian *Leptolepis* is intermediate between the condition in pholidophorids and in more advanced leptolepids in several features. The underside of the bone is visible only in P.51687. Here the preserved portion is very sparsely toothed, with about ten minute teeth arranged in a single row on either side of a median groove which ends posteriorly in a deep blind pit (figure 143*b*). The bucco-hypophysial canal opens through a small pore (bhc) behind this pit. The basipterygoid processes (bpt) are about the same size as in *P. germanicus* and the Callovian *Leptolepis* and the efferent pseudobranchial foramina (fpsa) are arranged as in those species. Behind the lower opening of the bucco-hypophysial canal there is a small median eminence which resembles the similar eminence in *P. bechei* (figure 62) behind the transverse spiracular furrow; such a furrow is hardly recognizable in the Sinemurian *Leptolepis*. The undersurface of the posterior part of the bone resembles that of *P. bechei* and the Callovian *Leptolepis* in having a pair of ventrolaterally directed crests with an area of muscle insertion (rscm) between them. As in the Callovian *Leptolepis*, this area is confined between these crests and does not extend forwards to the level of the median eminence on this surface as it does in *P. bechei*. On the upper surface of this posterior part of the parasphenoid there is a broad median crest (smc) which forms the floor of the myodome and separates a pair of grooves which received the lower edges of the prootics, as in *P. germanicus*. This Sinemurian *Leptolepis* therefore differs from the Callovian species in lacking a deep hollow in the floor of the otic portion of the myodome. The ascending process of the parasphenoid (asp) is separated from the posterior portion of the bone by a deep incisure (ainp I) containing the articulation of the first infrapharyngobranchial, as in pholidophorids. The outer face of the ascending process contains only one vertical groove (goa), as in *P. germanicus* and the Callovian *Leptolepis*, which is assumed to have contained the orbital artery. The internal carotid foramina (fica) lie antero-ventral to the articulation of the infrapharyngobranchial and close behind the efferent pseudobranchial foramina, as in *P. bechei*, further forwards than in *P. germanicus* or the Callovian leptolepid. On the upper surface of the bone, the internal carotid and efferent pseudobranchial foramina are linked by paired grooves (gcom), as in the other

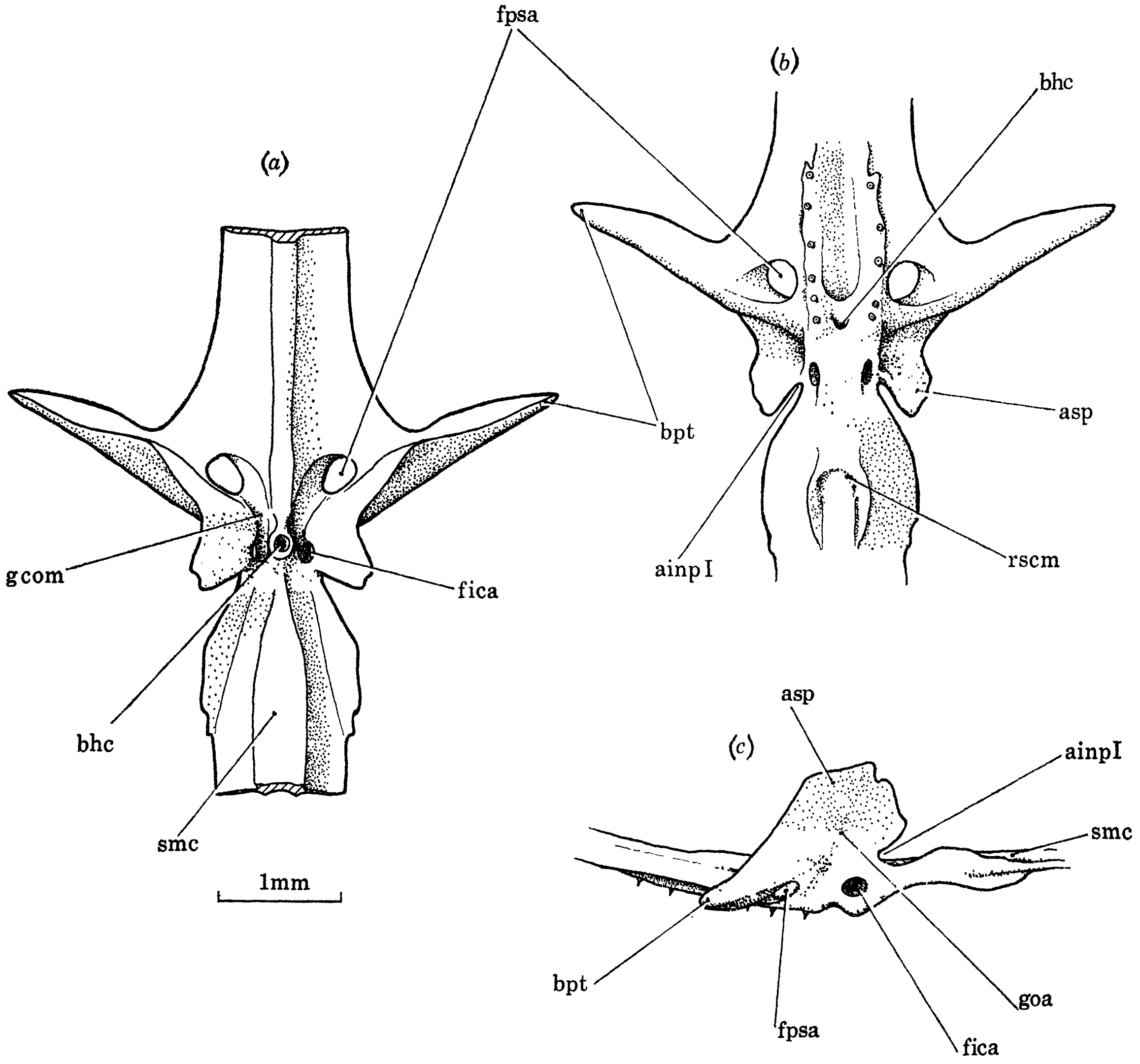


FIGURE 143. Sinemurian *Leptolepis* sp. Central part of parasphenoid (the only part known) in dorsal (*a*), ventral (*b*) and left lateral (*c*) views. Based on P.51685 and (principally) P.51687.

forms. Between the upper openings of the internal carotid foramina there is a median vertical process which fitted behind the basisphenoid pedicel, as in *P. germanicus* and the Callovian leptolepid, but in the Sinemurian species this process contains the upper opening of the buccohypophysial canal (bhc).

(*g*) Leptolepis coryphaenoides

Rayner (1937) and Wenz (1968) have illustrated complete parasphenoids of this species: the posterior part of the bone is shown in figure 144. Measurements of Wenz and Rayner's drawings give ratios between the length of the portions posterior and anterior to the centre of ossification of 1:1.8–2.2, and of the width of the basipterygoid processes to the total length of the bone of 1:3.3–4.2. The first of these ratios is closer to that in *P. germanicus* (1:2.3) and *P. macrocephalus* (1:2.0) than to that in the Callovian *Leptolepis* (1:1.4); the second is closer to that in the Callovian leptolepid (1:3.8) than to that in the two pholidophorids (1:2.1–2.3).

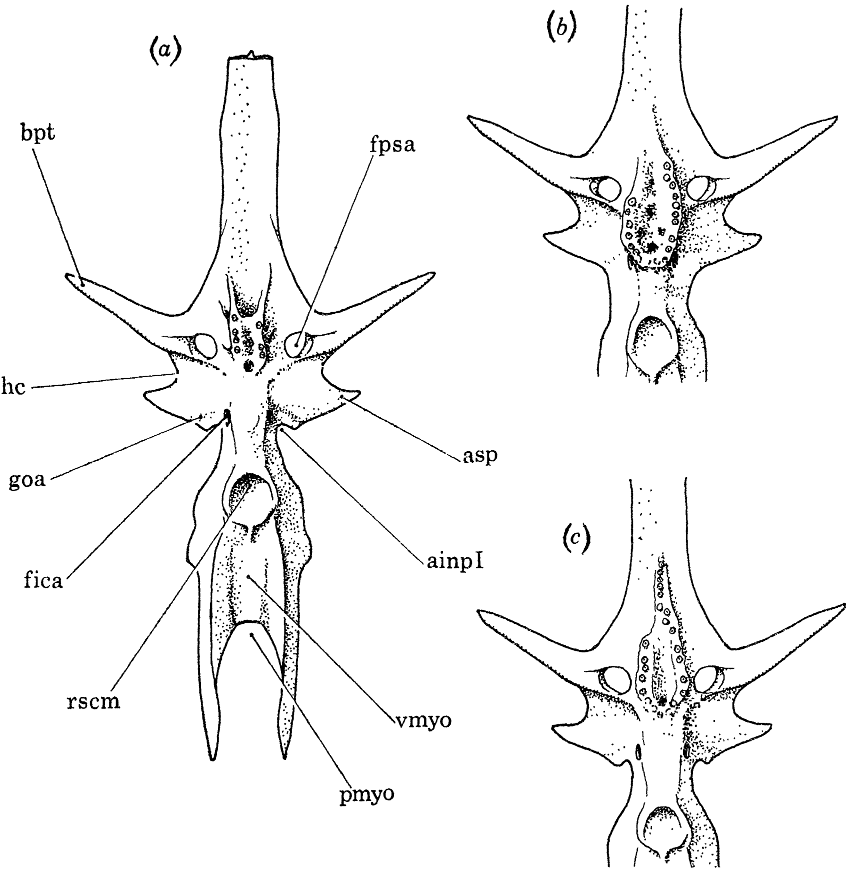


FIGURE 144. *Leptolepis coryphaenoides* (Bronn). Restorations of posterior part of parasphenoid in ventral view to illustrate variations. (*a*) Composite restoration based on P.7038*c* (posterior part), P.51702*a* (middle part) and P.51712 (anterior part and tooth patch). (*b*) Type represented by P.51702*b*, with posteriorly placed tooth patch and no notch for the articulation of the first infrapharyngobranchial. (*c*) Type represented by P.51702*a*, with elongate tooth patch. (All × 15 approx.)

The medial branch of the palatine nerve passed through a notch in the margin of the bone, as in the Callovian leptolepid, not through a canal as in pholidophorids. Rayner and Wenz both found the parasphenoid to be toothless, but in all the parasphenoids of this species from the Byfield bone-bed (figure 144) there is a sizable tooth patch surrounding the 'short wide trough'

(Rayner) on this surface, and a similar tooth patch is visible in some of the mechanically prepared specimens from Dumbleton used by Rayner. The 'trough' on this surface is clearly homologous with the blind-ending groove in the same position in the Sinemurian species (figure 143). Some variations in the form of this tooth patch are illustrated in figure 144. The teeth surround the opening of the bucco-hypophysial canal (bhc). In some specimens the 'trough' is not recognizable. This trough seems to be only due to the fact that the teeth are raised above the surface of the parasphenoid (as they are in *P. bechei* and the Sinemurian leptolepid), implying that this part of the bone was not in close contact with the mucous membrane lining the posterior part of the roof of the mouth. The posterior end of the tooth patch is raised on an eminence which recalls the eminence beneath the carotid foramen in *P. bechei* (figure 62) and the Sinemurian species (figure 143). On the underside of the posterior part of the bone there is a median pocket (rscm), limited laterally by a pair of crests, which resembles the similar area for muscle insertion in the Sinemurian species. On the upper surface of the posterior part of the bone there is a pair of lateral grooves which contained the lower margins of the prootics, as in other forms. The area between these grooves, which forms the floor of the myodome (vmyo), is broader than in pholidophorids and the Sinemurian *Leptolepis* and is slightly concave, but is not deeply hollowed out as it is in the Callovian *Leptolepis* (figures 141, 142). Wenz's figures of the parasphenoid and mechanically prepared braincases indicate that the myodome opened posteriorly between the posterior processes of the parasphenoid, but since there is an aortic canal immediately behind this opening in some specimens, it is unlikely that the external rectus muscles extended far into the opening. In intact, mechanically prepared braincases (P.7038*a*, *c*) the ascending process (asp) is separated from the posterior part of the bone by a deep incisure (ainp I), and the first infrapharyngobranchial still articulated with the endocranium, as in pholidophorids and the Sinemurian *Leptolepis*. But in at least one of the isolated parasphenoids (figure 144*b*) the incisure is represented by a shallow notch and the pharyngobranchial must have articulated with the parasphenoid, as in the Callovian species and living teleosts: *L. coryphaenoides* was evidently variable in this feature, as in many others.

(*h*) Leptolepis dubia

The parasphenoid of this species is shown in ventral view in figure 92. That illustration is based on the large, intact braincases, but two small examples of the bone are also visible amongst the stomach contents of P.12070, *P. macrocephalus*. In general the bone is very similar to the parasphenoid of the Callovian *Leptolepis*. The ratios between the length posterior and anterior to the centre of ossification, and between the width of the basipterygoid processes and the total length, are 1:1.7 and 1:4.1 in a small specimen, compared with 1:1.4 and 1:3.8 in the Callovian species. As in the latter, the first infrapharyngobranchial articulated with the parasphenoid, not with the endocranium, the floor of the otic portion of the myodome is deeply concave and bulges out on the underside of the bone (vmyo), and the myodome opened widely posteriorly (pmyo) between the long posterior processes of the bone. The bone is toothless, like about 30 % of the sample of the Callovian species. The bucco-hypophysial canal (bhc) is open, but is extremely narrow.

(*j*) *Parasphenoid: summary and discussion*

(i) *Summary of conditions in pholidophorids and leptolepids*

(1) The parasphenoid is slender in leptolepids and rather broad in pholidophorids except for *P. bechei*, in which the breadth of the bone is intermediate between the two. In *P. bechei* and *P. germanicus* the posterior portion of the bone, behind the centre of ossification (at the level of the basipterygoid process), forms less than one-third of the total length of the bone, and the parasphenoid ends posteriorly beneath the anterior half of the basioccipital. In *P. macrocephalus* and most leptolepids the parasphenoid extends almost to the posterior end of the basioccipital and the posterior portion forms more than one-third of the total length of the bone. The anterior end of the parasphenoid overlies the median vomer in all pholidophorids and leptolepids.

(2) In *P. bechei* the dorsal surface of the orbital portion of the parasphenoid is covered by endoskeletal bone. In other pholidophorids and in leptolepids a membranous interorbital septum attached to this part of the parasphenoid.

(3) The basipterygoid processes are very long in all pholidophorids and leptolepids: the distance from tip to tip of these processes is equal to about a third of the total length of the bone in *P. germanicus* and *P. macrocephalus*, and to about 20 % of the total length in leptolepids. In *P. bechei* there was a rudiment of an endoskeletal basipterygoid process in the groove on the antero-dorsal surface of the dermal process but this rudiment did not reach the end of the dermal process or contribute to the articulation with the palate. In the other forms the endoskeletal process was probably completely reduced, although the groove on the dermal process persists.

(4) The parasphenoid is toothed in all pholidophorids except *P. macrocephalus*, and in all leptolepids except *L. dubia* and about one-third of the sample of the Callovian species. The teeth surround the lower opening of the bucco-hypophysial canal in all forms except *P. bechei*, where they lie further forwards and the region of the bucco-hypophysial canal was probably not in contact with the mucous membrane of the roof of the mouth.

(5) There is a patent bucco-hypophysial canal through the parasphenoid in all pholidophorids and leptolepids.

(6) The anterior branch of the palatine nerve passed through a canal in the orbital portion of the parasphenoid in pholidophorids, and through a notch in the margin of the bone in leptolepids.

(7) In all pholidophorids and leptolepids the root of the basipterygoid process is penetrated by a canal for the efferent pseudobranchial artery, and the base of the ascending process or the body of the bone at that level is penetrated by a canal for the internal carotid artery. In *P. bechei* both pairs of canals are almost vertical and originate close to the mid-line. In other forms both pairs of canals are more horizontally directed and the internal carotid canal is in the base of the ascending process. On the upper surface of the parasphenoid there are always paired grooves marking the course of a connecting branch between the efferent pseudobranchial and carotid arteries of each side. There is no evidence of a transverse anastomosis between the efferent pseudobranchial arteries.

(8) In *P. bechei* the ascending process of the parasphenoid carries two vertical grooves, an anterior one for the lower part of the spiracular diverticulum and a posterior one for the orbital artery. The paired spiracular grooves are joined by a transverse furrow on the underside of the

bone. In other pholidophorids and in leptolepids there is only a single groove, for the orbital artery, on the ascending process. The transverse furrow linking the spiracular grooves is just recognizable in the Sinemurian *Leptolepis*, but is not visible in the other forms.

(9) In pholidophorids the ascending process of the parasphenoid is separated from the posterior portion of the bone by a deep incisure which contained the articulation between the first infrapharyngobranchial and the endocranium. In the Sinemurian *Leptolepis* and in some individuals of *L. coryphaenoides* this incisure persists, but in other leptolepids it is lost and the infrapharyngobranchial articulated with the parasphenoid.

(10) In *P. bechei* the underside of the posterior portion of the parasphenoid contains a median groove which terminates anteriorly in a pair of antero-dorsally directed pits, close behind the internal carotid foramina. In other pholidophorids the underside of this part of the parasphenoid is flat, but there is a similar pair of pits placed further back than in *P. bechei.* In leptolepids there is a groove on the underside of the posterior part of the parasphenoid, as in *P. bechei*, but it terminates, sometimes in a pair or group of pits or perforations, at the same level as the pits in *P. germanicus* and other pholidophorids.

(11) In *P. bechei* the parasphenoid only forms the floor of a small portion of the myodome, in a narrow median fenestra beneath the prootics and the foremost part of the basioccipital. In other pholidophorids and in the Sinemurian *Leptolepis* the upper surface of the posterior part of the parasphenoid bears a broad median crest which forms the floor of the myodome beneath the prootics and the anterior part of the basioccipital. In *L. coryphaenoides* the floor of the otic part of the myodome is slightly concave and the myodome opened posteriorly, beneath the basioccipital, between the posterior processes of the parasphenoid. In the Callovian *Leptolepis* and *L. dubia* the myodome also opened posteriorly, and the floor of the otic part of the myodome is deeply concave, so that it bulges out on the underside of the parasphenoid.

(12) In all pholidophorids and leptolepids there is a small median process on the upper surface of the parasphenoid, between the internal carotid foramina, which fitted against the posterior face of the basisphenoid pedicel. In the Sinemurian *Leptolepis* this process contains the upper part of the bucco-hypophysial canal.

(ii) *Comparison with other groups*

1. *Proportions of the parasphenoid.* In all actinopterygians the centre of ossification of the parasphenoid is beneath the hypophysis, and where a patent bucco-hypophysial duct persists it passes through the centre of ossification, although the position of the lower opening of the canal does not always coincide with the centre of ossification of the bone since the canal may pass through it almost horizontally, opening well in front of its point of entry. In some Devonian palaeoniscoids (Gardiner 1970, 1973; Miles 1971, fig. 5. 6) the parasphenoid ends posteriorly at the fissura oticalis ventralis, which lies directly behind the hypophysial fossa. This type of parasphenoid, with a very short portion posterior to the centre of ossification, is evidently primitive for actinopterygians since it agrees with the parasphenoid of Devonian rhipidistians and coelacanths (Jarvik 1954, 1972), and since it appears to terminate at the junction between the trabeculae and parachordals. In other palaeoniscoids and in higher actinopterygians the parasphenoid has a greater posterior extent. In post-Devonian palaeoniscoids the parasphenoid ends at the fissura oticalis ventralis, but that fissure lies further back than in the Devonian forms (*Pteronisculus*, Nielsen 1942, Lehman 1952; *Kentuckia*, Rayner 1951; Kansas forms, Watson 1925, Eaton 1939, Rayner 1951; *Paramblypterus*, Heyler 1969; '*Ambodipia*',

Beltan 1968; *Boreosomus*, Nielsen 1942, Lehman 1952; Schaeffer 1967, fig. 4). This is also true of the pholidopleurid *Australosomus* (Nielsen 1949). In all other actinopterygians the parasphenoid extends across the fissure, beneath the basioccipital. In *Perleidus* (figure 116) it ends in front of the glossopharyngeal foramen. In parasemionotids (Stensiö 1932, fig. 87; Beltan 1968, figs 24, 26; figure 98) and in *Pachycormus* (figure 106) it extends to the level of the vagus foramen, ending on either side of the housing of the aortic ligament. In *Birgeria* (Nielsen 1949), *Saurichthys* (Stensiö 1925), *Bobasatrania* (Nielsen 1952), *Errolichthys* (Lehman 1952), living chondrosteans (and *Polypterus*), semionotids (figures 109, 112), caturids (figures 99, 103), and in living holosteans and teleosts (except trachichthyids and *Denticeps*; Starks 1904; Patterson 1964; Greenwood 1968) the parasphenoid reaches the posterior end of the basioccipital, ending beneath the occipital condyle. In *P. bechei* and *P. germanicus* the parasphenoid ends beneath the anterior half of the basioccipital, midway between the glossopharyngeal and vagus foramina, and is therefore less extensive than in other actinopterygians except palaeoniscoids and *Perleidus*. In *P. macrocephalus*, *L. coryphaenoides* and the Callovian *Leptolepis* the bone ends at the level of the housing of the aortic ligament, as in parasemionotids and *Pachycormus*. In *L. dubia* the bone reaches the posterior end of the basioccipital, as in living teleosts and the majority of actinopterygians.

The progressive increase in length of the posterior portion of the parasphenoid, evident in such morphological series as: Devonian palaeoniscoid – *Pteronisculus* – *Perleidus* – *Pholidophorus bechei* – *Leptolepis coryphaenoides* – *Elops*, does not support Jarvik's (1954; 1972, p. 256) hypothesis that the posterior part of the parasphenoid of advanced actinopterygians has been formed by the incorporation of homologues of the subotic, paraotic and suboccipital tooth-plates of *Eusthenopteron* (on paraotic plates in *Polyodon* see Nelson 1969*b*, p. 522). As will be shown below (point 6) the parasphenoid of Devonian palaeoniscoids is the exact topographic homologue of the rhipidistian parasphenoid, and Jarvik's (1954, fig. 35) assertion that the palaeoniscoid parasphenoid incorporates the paraotic and subotic tooth-plates cannot be justified. Increase in length of the posterior portion of the actinopterygian parasphenoid can be accounted for by two processes, posterior migration of the fissura oticalis ventralis as a consequence of enlargement of the myodome (p. 541), and growth across the fissure. This posterior portion of the parasphenoid is never toothed, as it should be if Jarvik's hypothesis were correct.

In palaeoniscoids the parasphenoid is relatively broad, and this condition, assumed to be primitive, persists in other actinopterygians except *Pachycormus*, semionotids, *Macrepistius*, *Lepisosteus* and most teleosts. In *Pachycormus* the parasphenoid (Lehman 1949, fig. 4) is about as broad as in *P. germanicus* and *P. macrocephalus*. The narrower parasphenoid of *P. bechei* is a specialization relating it to leptolepids and teleosts.

2. *Basipterygoid process.* Rayner (1951, p. 81) recognized four conditions of the basipterygoid process: (i) where it is almost entirely endoskeletal, with little or no support from the parasphenoid, as in *Kentuckia* and Kansas palaeoniscids A and C; (ii) where the endoskeletal and dermal components are about equal, as in *Pteronisculus*, Kansas palaeoniscid B and parasemionotids; (iii) where the process is composed of the parasphenoid alone, as in *Leptolepis*; (iv) where the process is lost. This last condition is found in the majority of actinopterygians, including *Birgeria*, *Saurichthys*, *Errolichthys*, *Australosomus*, amiids, some caturids (*Caturus furcatus*, '*Aspidorhynchus*', *Macrepistius*), pachycormids, and almost all teleosts. Palaeoniscoids have basipterygoid processes of the first or second type, while in *Acipenser* it is of the first type. In *Lepisosteus* and *Dapedium* (figures 112, 113) the process is large and is transitional between the first and second types. *Perleidus* seems to have a similar, mainly endoskeletal process (Stensiö 1932,

fig. 59; figures 115, 116). In those caturids which still retain a basipterygoid process (Rayner's Toarcian *Caturus*, *C. chirotes*, *Heterolepidotus*) the process is very small, almost vestigial, and may be mainly endoskeletal (figures 93, 103) or mainly dermal (Rayner 1948, fig. 7). In *P. bechei* the basipterygoid process is transitional between Rayner's third and fourth types, with a rudiment of an endoskeletal process. The same type of process probably occurred in *Lepidotes* (Rayner 1948, fig. 13; figures 108, 109), where the groove on the upper surface of the massive dermal process may have contained cartilage which ossified in large individuals. A basipterygoid process of Rayner's third type, entirely dermal as in leptolepids and most pholidophorids, is otherwise known only in teleosts (and *Polypterus*). A massive process, of the same form as those of pholidophorids and leptolepids, occurs in osteoglossoids amongst living teleosts, and in the Mesozoic ichthyodectids (Bardack 1965; Patterson 1967, fig. 2) and the Cretaceous clupeomorph *Diplomystus* (Patterson 1967, fig. 7). There is a shorter basipterygoid process on the parasphenoid of the Cretaceous salmoniform *Humbertia* (Patterson 1970*b*, fig. 17) and some mormyroids (Taverne 1968, 1972), and the living alepocephaloid *Searsia* is said to have a rudimentary process (Gosline 1969, p. 196). All other teleosts have lost the basipterygoid process (T. M. Cavender, private communication, has pointed out that the basipterygoid process described in the Mesozoic hiodontid *Lycoptera* by Gaudant (1968) and Greenwood (1970*b*) is due to misinterpretation of an articulated post-temporal and supracleithrum).

In summary, the massive, dermal basipterygoid process of pholidophorids and leptolepids is of a type otherwise only known in teleosts and possibly in *Lepidotes*. In retaining a well developed basipterygoid process with a rudimentary endoskeletal component (in *P. bechei*) pholidophorids are more primitive than other actinopterygians in which this region is known except palaeoniscoids, sturgeons, *Perleidus*, parasemionotids, some caturids, *Dapedium* and *Lepisosteus*.

3. *Parasphenoid teeth.* Primitively, the oral surface of the actinopterygian parasphenoid was probably toothed throughout from the level of the ascending process forwards, as it is in palaeoniscoids, *Errolichthys* (Lehman 1952, fig. 79), *Perleidus* (figure 116), parasemionotids (figure 98), caturids (except *Macrepistius*), *Ichthyokentema* (figure 151), *Catervariolus* (Saint-Seine 1955, fig. 42) and a few teleosts (albulids *sensu* Estes 1969, plethodids, *Hiodon*, *Arapaima*, *Pristolepis*). In *Saurichthys*, *Lepisosteus*, pachycormids (Lehman 1949), amiids and elopoids there is a tooth patch on the posterior part of the parasphenoid, similar to that in *P. germanicus*. A very small parasphenoid tooth patch, lying between the ascending or basipterygoid processes, as in leptolepids, is also found in *Lepidotes* (figure 109) and a few teleosts, including the Jurassic ichthyodectid *Allothrissops* (Patterson 1967, fig. 2), several living osteoglossoids and mormyroids (Ridewood 1904*c*, 1905), the Cretaceous clupeomorph *Diplomystus* (Patterson 1967, fig. 7), the anabantoids (Liem 1963), *Nandus* (Liem 1970), *Badis* (Barlow, Liem & Wickler 1968) and *Polymixia*.† All other teleosts have lost the parasphenoid teeth, as have living chondrosteans, *Birgeria*, *Australosomus*, *Bobasatrania*, *Dapedium*, pycnodonts and *Macrepistius*.

† Among a sample of six *Polymixia lowei* Günther taken in a single haul off Haiti, there is a small patch of parasphenoid teeth in three individuals and in the other three the bone is toothless; a small parasphenoid tooth patch has also been observed in one out of four specimens of *P. nobilis* Lowe. No such teeth were found in three specimens of *P. japonica* Günther. The parasphenoid teeth of anabantoids and nandids have been thought to be secondary (Gosline 1968, p. 10) since no lower euteleostean is known to retain parasphenoid teeth. The discovery of such teeth in *Polymixia*, probably the most primitive living acanthopterygian, makes it more likely that the condition in anabantoids and nandids is primary, although the sporadic occurrence of the teeth in *Polymixia* (as in the Callovian *Leptolepis*) suggests that the parasphenoid teeth of the ancestor of anabantoids and nandids may have been potential rather than actual (cf. Liem 1970, p. 147).

In *Pholidophorus bechei* the parasphenoid tooth patch does not extend back to the bucco-hypophysial canal, and the teeth at the rear of the patch are borne on raised pedicels. This implies that the region of the bucco-hypophysial canal, which is toothed in other pholidophorids and primitive actinopterygians, was not in contact with the mucous membrane lining the roof of the mouth. The slender parasphenoid of *P. bechei* is probably derived relative to the broad bone of other pholidophorids (point 1 above), and the condition of the tooth patch is also probably derived But it is possible that the posterior part of the tooth patch in *P. bechei* was represented by small tooth-plates lying free in the mucous membrane, like those surrounding the parasphenoid teeth of *Elops* (Nybelin 1968) and rhipidistians (Jarvik 1972). In leptolepids (Sinemurian species, *L. coryphaenoides*, Callovian species) the parasphenoid teeth are also borne on a raised area, surrounding a 'trough' in the Sinemurian species and some specimens of *L. coryphaenoides*. In these fishes there may also have been free tooth-plates in the surrounding mucous membrane. Among those teleosts in which the oral surface of the parasphenoid is toothed throughout, only *Arapaima* has small teeth like those of pholidophorids and other primitive actinopterygians. Other such teleosts (albulids, phyllodontids, plethodids, hiodontids, *Pristolepis*) have the parasphenoid teeth enlarged or specialized in some other way which could account for extension of a smaller ancestral tooth patch of pholidophorid type. *Arapaima* can be interpreted as exhibiting a more primitive condition than any known pholidophorid.

4. *Bucco-hypophysial canal.* The parasphenoid contains a patent bucco-hypophysial canal in all pholidophorids and leptolepids. This is undoubtedly a primitive feature. Among living fishes, such a canal is known only in *Latimeria*, *Polypterus*, *Calamoichthys* and *Elops* (Olsson 1958), while in the clupeoids *Hilsa*, *Gadusia* and *Engraulis* there may be a small foramen in the parasphenoid although the canal itself is interrupted (Misra & Sathyanesan 1959). In fossil actinopterygians the canal in the parasphenoid has only been recorded in saurichthyids (Stensiö 1925; Gardiner 1960), parasemionotids (Stensiö 1932; figure 98), the teleost *Humbertia* (Patterson 1970*b*), and possibly in *Kentuckia* and Kansas palaeoniscid C (Rayner 1951), but it is probably much more widely distributed since it occurs in *Perleidus* (figure 116), *Dapedium* (P.11189), *Lepidotes* (figure 109), *Heterolepidotus* (figure 103), *Caturus chirotes* (GSM 97417) and *C. furcatus* (P.904*a*). It appears to be absent in *Pachycormus*.

5. *Internal carotid and efferent pseudobranchial arteries.* The relation of these arteries to the parasphenoid is constant in pholidophorids and leptolepids, the efferent pseudobranchial passing through the root of the basipterygoid process and the internal carotid through the base of the ascending process or the body of the bone medial to this, beneath the articulation of the first infrapharyngobranchial. In *P. bechei* both arterial canals are almost vertical, and originate close to the mid-line. This disposition of the carotid canals may be primitive, but the efferent pseudobranchial canals are probably specialized relative to the more horizontal canals in other pholidophorids (see below).

Primitively in actinopterygians it appears that neither the internal carotids nor the efferent pseudobranchials passed through the parasphenoid. In *Pteroniscutus*, the best known palaeoniscoid, the foramina of the internal carotid and efferent pseudobranchial arteries on the underside of the endocranium (Nielsen 1942, fig. 6; Bjerring 1971, fig. 6) are arranged in the same way (relative to the basipterygoid processes and 'fenestra ventralis myodomus', the homologue of the bucco-hypophysial canal: see p. 541) as they are in pholidophorids. The efferent pseudobranchial artery notched the parasphenoid, and Nielsen (1942, p. 105) describes a longitudinal canal in the posterior part of the parasphenoid which transmitted the internal carotid. He was unable to trace the latter canal throughout its length in *P. magna*, and in the serially ground specimen of *P. stensioei* the horizontal plane of the sections would make it very difficult to distinguish a longitudinal canal in the parasphenoid from a groove on its upper surface. In the Devonian palaeoniscoids from Australia (Gardiner 1970, 1973; Miles 1971, fig. 5. 6) the internal carotids passed into the endocranial bone through a notch in the posterior margin of the parasphenoid, and it is likely that they pursued the same course in *Pteronisculus*. In some of the Devonian palaeoniscoids there is a pair of deep, blind pits in the posterior margin of the parasphenoid, immediately medial to the endoskeletal carotid foramina (B. G. Gardiner, private communication); similar pits are prominent in several other primitive actinopterygians (point 7 below) and the canals which Nielsen found in the parasphenoid of *Pteronisculus* could well be such blind pits. In other palaeoniscoid braincases (*Kentuckia* and the Kansas forms) the margins of the posterior part of the parasphenoid are indistinct so that the exact relations of the carotids to the bone have not been elucidated, but in *Boreosomus* Nielsen (1942) and Lehman (1952) both found that the internal carotid passed through a foramen in the base of the ascending process, as in pholidophorids and leptolepids. In living chondrosteans, and in *Birgeria* and *Australosomus* neither the efferent pseudobranchial nor carotid artery passed through the parasphenoid.

In *Perleidus*, Stensiö and Lehman (1954) failed to find any vascular foramen in the parasphenoid. In the specimen of *Perleidus* illustrated here (figures 115, 116) there appears to be a foramen in the parasphenoid medial to the base of the ascending process, but this is asymmetrical (in size) on the two sides of the specimen and is more likely to be a deep, blind pit: a similar pit is visible in P.19590, a *Perleidus* from Madagascar. In *Perleidus* the efferent pseudobranchial and carotid arteries appear to have passed into the endocranium above the parasphenoid, as in palaeoniscoids.

In parasemionotids, Stensiö (1932) found a foramen (interpreted as for the common carotids) in the antero-ventral part of the ascending process of *Ospia*. In both *Ospia* and *Broughia* he found a notch for the efferent pseudobranchial artery in front of the basipterygoid process, and in *Broughia* he found that the carotids entered the endocranium through a notch behind the ascending process. In subsequent studies of parasemionotids (Lehman 1952; Beltan 1968) no foramina were found in the parasphenoid, only notches for the efferent pseudobranchial and carotid arteries, as in Stensiö's restoration of *Broughia* and the specimen illustrated here (figures 97, 98). In Stensiö's restoration of the parasphenoid of *Ospia*, including a carotid foramen, the outline of the ascending process is very different from the slender strut in *Broughia* and other parasemionotids (Beltan 1968, figs 24, 26; figures 97, 98), and one can only suppose that the foramen restored in *Ospia* is a misinterpretation, due to imperfect preservation of the specimen.

In saurichthyids (Stensiö 1925; Gardiner 1960, fig. 21) there is a large, paired foramen in the underside of the parasphenoid, beneath the posterior margin of the ascending process. Stensiö and Gardiner assign the external carotid (= orbital artery) to this foramen, but it may have transmitted the common carotid, the efferent pseudobranchial passing through the foramen in the endocranial bone, lateral to the parasphenoid and in front of the bucco-hypophysial canal, which Stensiö interpreted as the internal carotid.

In *Lepisosteus* and *Amia* the efferent pseudobranchial and internal carotid arteries pass through notches in the parasphenoid, the internal carotid behind the base of the ascending process, the efferent pseudobranchial in the anterior margin of the ascending process in *Amia* and the base of the anterior face of the basipterygoid process in *Lepisosteus*. In caturids, the vessels passed through similar notches in the parasphenoid in *Caturus groenlandicus* (Aldinger 1932), *C. chirotes* (GSM 97417; the 'efferent pseudobranchial foramina' in Gardiner's drawing of this specimen, 1960, fig. 36, are blind pits), *C. furcatus* (P.904*a*), *Heterolepidotus* (figures 102, 103), and '*Aspidorhynchus*' (figure 99; the internal carotid foramen in Rayner's restoration, 1948, fig. 20, is shown to be a blind pit by further preparation). In *Macrepistius* Schaeffer (1971) describes an internal carotid foramen in the ascending process, but in his detailed drawing of this region (fig. 5) the suture bounding the parasphenoid is not shown and it is possible that the foramen lay in a notch in the margin of the ascending process.

Among semionotids, the arteries passed through notches in the parasphenoid, positioned as in *Lepisosteus*, in *Lepidotes* (figures 108, 109), but in *Dapedium* (figure 112) both arteries passed through foramina in the parasphenoid. These foramina lie close to the mid-line and lead into almost vertical canals, producing an arrangement which is virtually identical with that in *Pholidophorus bechei*.

In *Pachycormus* (Rayner 1948, fig. 18; figure 106) the efferent pseudobranchial artery notched the parasphenoid but the internal carotid passed through a foramen in the base of the ascending process, as in pholidophorids and leptolepids.

In teleosts the internal carotid passes through a foramen in the ascending process of the parasphenoid in the great majority of forms, and where this foramen is absent or only notches the margin of the ascending process, as in *Brycon* (Weitzman 1962) and some other characids (Roberts 1969), *Scomber* and some scorpaenoids (Allis 1903, 1909), the condition can be regarded as due to secondary reduction of the process. A foramen for the efferent pseudobranchial artery is less frequent in teleosts, but it is always present (in the same position as in pholidophorids and leptolepids) where a well developed basipterygoid process persists (ichthyodectids, osteoglossoids, *Humbertia*), and occurs sporadically amongst teleosts in which the basipterygoid process is lost (*Pterothrissus*, *Salmo*, *Stenodus*, *Coregonus*, *Argentina*, the Cretaceous ctenothrissoids and polymixiids, for example). In *Hiodon* the carotid and efferent pseudobranchial arteries pass together through a single foramen in the parasphenoid (Allis 1919, p. 224; Greenwood 1970, fig. 5): this is probably also the case in mormyroids, where there is a single foramen and sometimes a rudimentary basipterygoid process (Taverne 1968, 1972), and may be true of other teleosts, for few have been investigated in sufficient detail. In general, it is reasonable to interpret absence of an efferent pseudobranchial foramen in the parasphenoid of teleosts as a secondary condition, following loss of the basipterygoid process, reduction in breadth of the parasphenoid, or coalescence of the foramen with that of the internal carotid.

In pholidophorids, where the basisphenoid pedicel is extensive rostro-caudally, it is clear that there was no transverse anastomosis between the efferent pseudobranchial arteries. Such an anastomosis could have existed in leptolepids, where the pedicel is shorter. A transverse anastomosis between the efferent pseudobranchial arteries appears to be a specialization, found only in teleosts among living fishes (Goodrich 1930, p. 518; Bertin 1958, p. 1419; Bertmar 1962, p. 280), although it is not developed in *Hepsetus*. In the ontogeny of *Heterotis* the efferent pseudobranchial artery joins the internal carotid (as it does in pholidophorids and other primitive actinopterygians) up to 12.5 mm, but in a 33 mm specimen this connexion has disappeared and been replaced by the efferent pseudobranchial anastomosis (Daget & d'Aubenton 1957, p. 903); the same sequence is followed in *Salmo* (Holmgren 1943, p. 26). An anastomosis between the efferent pseudobranchials has been indicated in Kansas palaeoniscid A by Watson (1925) and Rayner (1951), but no such anastomosis could have occurred in other primitive actinopterygians in which the basisphenoid region is known in detail.

In summary, the presence in the parasphenoid of pholidophorids and leptolepids of foramina for the internal carotid and efferent pseudobranchial arteries is a specialization otherwise found only in primitive teleosts and in *Dapedium*; a carotid foramen in the parasphenoid occurs in *Pachycormus*, *Saurichthys* and *Boreosomus*. The transverse anastomosis between the efferent pseudobranchial arteries which occurs in most teleosts was not developed in pholidophorids.

6. *Ascending process and spiracular groove.* Primitively in actinopterygians the ascending process of the parasphenoid was very short and did not extend across the fissura oticalis ventralis on to the lateral commissure: this is the condition in some Devonian palaeoniscoids from Australia (Gardiner 1970, 1973; Miles 1971, fig. 5.6). In Devonian rhipidistians and coelacanths the ascending process (anterior ascending process of Jarvik 1954) has the same relations. Jarvik (1954, p. 51) considered the ascending process in rhipidistians and coelacanths to be the homologue of the 'anterior ascending process' (basipterygoid process) of the parasphenoid in *Pteronisculus*, but as pointed out by Rayner (1951, p. 81), the dermal basipterygoid process is only represented by a slight enlargement of the anterior margin of the ascending process in some primitive actinopterygians (*Kentuckia*, Kansas palaeoniscids A and C), while in some porolepids a dermal basipterygoid process is developed from the anterior border of the ascending process (Jarvik 1972, p. 86), in exactly the same position as in *Pteronisculus*.

In more advanced palaeoniscoids such as *Kentuckia* (Rayner 1951), *Pteronisculus* and *Boreosomus* (Nielsen 1942) the ascending process extends on to the lateral commissure and its tip approaches or enters the lower opening of the spiracular canal. The ascending process has the same form in *Perleidus* (figures 115, 116), parasemionotids (figures 97, 98), *Dapedium* (figure 112), *Lepidotes* (figures 108, 109), caturids (figures 99, 102, 103) and *Pachycormus* (figure 106). In all these forms the ascending process is a slender strut, grooved by the spiracular diverticulum, and it seems, as Jarvik (1954, p. 59) says, to have developed solely in relation to that diverticulum, forming the medial wall of the spiracular groove. This is indicated by the presence of teeth in the groove in some specimens of *Pteronisculus* (Lehman 1952, fig. 20): a few small teeth are also present in the groove in the illustrated specimen of *Perleidus* (figures 115, 116).

The ascending process of the parasphenoid is therefore developed primarily in relation to the spiracular diverticulum. In palaeoniscoids, *Perleidus*, parasemionotids, caturids, most pholidophorids and *Amia* the toothed area of the parasphenoid between the ascending processes is rather broad, and the spiracular groove dies out at the base of the ascending process, turning forwards there towards the centre of ossification of the bone in the more primitive forms (*Pteronisculus*, Lehman 1952, fig. 20; *Perleidus*, figure 116). In *Australosomus*, where the parasphenoid is toothless, the groove extends almost to the centre of ossification in some specimens (Lehman 1952, fig. 100). In *Pholidophorus bechei* the parasphenoid teeth do not extend back as far as the ascending processes, the parasphenoid is narrow between those processes and the spiracular grooves are linked by a transverse groove on the underside of the bone (figure 62), immediately behind the lower opening of the bucco-hypophysial canal and immediately in front of the internal carotid foramina. Such a groove is just recognizable in the Sinemurian *Leptolepis* (figure 143) but is not found in other actinopterygians with a narrow parasphenoid, such as *Dapedium*. This transverse groove, linking the spiracular grooves, has the same relations as the groove on the parasphenoid of the porolepiforms *Holoptychius* (Jarvik 1954, fig. 19B; 1972, pl. 25, fig. 2), *Glyptolepis* (Jarvik 1954, figs 19, 20; 1972, figs 31, 92A) and

Porolepis (Jarvik 1972, pl. 9). In *Glyptolepis* this groove may contain teeth, like the spiracular groove of *Pteronisculus*. The groove in porolepiforms, identified by Jarvik (1954, 1972) and Bjerring (1971) as the impression of a prespiracular gill-slit, passes antero-ventrally down the ascending process of the parasphenoid (shown above to be homologous with the ascending process of primitive actinopterygians), close behind the basipterygoid process, and on the underside of the bone is directed towards the lower opening of the bucco-hypophysial canal, meeting its fellow at or immediately behind (Jarvik 1972, fig. 31) that opening. In *P. bechei* the transverse spiracular groove lies close in front of the internal carotid foramina in the parasphenoid, and in other primitive actinopterygians the internal carotids enter the braincase behind the spiracular groove, where this is recognizable (point 5 above). In porolepiforms the internal carotids entered the braincase in front of the 'prespiracular' groove (Jarvik 1972, fig. 92) as in *Polyodon* (Danforth 1912, fig. 15) and *Acipenser* (Splechtna 1973), but in all three well known porolepiform genera there is a vascular foramen in the parasphenoid behind the groove, in the same position as the internal carotid foramen of *P. bechei* (*Glyptolepis*, Jarvik 1972, fig. 31; *Holoptychius*, Jarvik 1972, pl. 25, fig. 2, c.a.cib; *Porolepis*, Bjerring 1967, fig. 17, c.v). Jarvik (1972, p. 209) interprets this foramen as having transmitted a medial branch of the internal carotid. The 'prespiracular' groove on the parasphenoid of porolepiforms (and osteolepiforms, Jarvik 1954) has precisely the same morphological relations as the spiracular groove of *P. bechei* (to the ascending process, basipterygoid process, bucco-hypophysial canal and the vascular foramen in the parasphenoid). In view of this, I am unable to follow Jarvik (1954, p. 59) in his assertion that these grooves are only serial homologues, and conclude that the 'prespiracular' groove of porolepiforms (and *Eusthenopteron*) is a spiracular groove (cf. Miles 1971, p. 3).

In primitive actinopterygians, where the base of the ascending process of the parasphenoid is confined between the basipterygoid process and the incisure containing the internal carotid foramen and the endoskeletal articulation of the first infrapharyngobranchial, the ascending process is slender and limited to the spiracular groove. In more advanced forms where the basipterygoid process is lost, and the internal carotid foramen and/or the pharyngobranchial articulation move on to the parasphenoid, the ascending process may increase in length and cover a major part of the wall of the otic and orbitotemporal regions, as in *Saurichthys*, *Birgeria* and living chondrosteans. In *Amia* the lower part of the pterosphenoid pedicle is formed by an outgrowth of the anterior part of the ascending process (as in '*Aspidorhynchus*', figure 101, pasp), while in *Lepisosteus* the process is considerably reduced. In *P. bechei* (figures 61, 62), where the internal carotid foramen is enclosed in the parasphenoid, the ascending process carries two grooves, the spiracular groove in front and the lower part of the groove for the orbital artery behind. In other pholidophorids and leptolepids, with reduction in the spiracular diverticulum or in the intimacy with which the diverticulum is associated with the parasphenoid, the ascending process only carries the groove for the orbital artery. In teleosts, the process carries the groove for the orbital artery in some primitive forms, but in most teleosts this groove is no longer recognizable and the ascending process serves as the area of origin of a major portion of the adductor arcus palatini muscle. In most teleosts the ascending process is reduced in height in comparison with more primitive actinopterygians, but in others it is enlarged so that it develops contacts with the frontals, as in *Gasterosteus*, some eels, *Lophius*, etc.

In summary, the ascending process developed in the wall of the spiracular diverticulum within the actinopterygians. The actinopterygian ascending process has precisely the same relations as the ascending process in rhipidistians, and the 'prespiracular' groove in rhipidistians must be a spiracular groove. With reduction in the spiracular diverticulum, the ascending process may take on other functions or be reduced.

7. *Subcephalic muscles.* A paired subcephalic (or basicranial) muscle, extending beneath the intracranial joint from the otico-occipital to the parasphenoid, is found in *Latimeria* among living vertebrates, and is inferred to have been present in fossil coelacanths and in rhipidistians (Bjerring 1967). More recently it has been suggested that such muscles may also occur in actinopterygians. Nelson (1970*b*) pointed out that in *Polypterus* the body musculature extends forwards beneath the braincase as far as the ascending process of the parasphenoid, where it inserts, and proposed that this muscle is homologous with the subcephalic muscle of coelacanths and rhipidistians, but represents a more primitive condition. Bjerring (1971) has restored a subcephalic muscle of crossopterygian type in the palaeoniscoid *Pteronisculus*.

The grounds on which Bjerring (1967) restored subcephalic muscles in fossil coelacanths and in rhipidistians were the presence of the intracranial joint, and of areas which could have housed the origin and insertion of the muscles on the otico-occipital and parasphenoid or ethmosphenoid. The area of insertion of the muscle, on the parasphenoid, is represented in *Eusthenopteron* by a pair of pits, lying close to the mid-line, extended postero-dorsally by a shallow groove (Bjerring 1967, pl. 2A, text-figs 8A, C, 10A). These pits lie immediately posterior to the tooth patch on the parasphenoid, just behind the lower opening of the bucco-hypophysial canal, and medial to the spiracular ('prespiracular', see above) groove. In *Eusthenodon* there is a similar pair of pits (Bjerring 1967, pl. 2C). In *Megalichthys* and *Ectosteorachis* there is a pair of pits in the same position, interpreted by Romer (1937) as internal carotid foramina, but by Bjerring, following Jarvik (1966, p. 91), as blind pits housing the muscle insertion. In the porolepiform *Glyptolepis* Bjerring (1967, p. 244) restored the subcephalic muscle as inserting in a depression on the ethmosphenoid behind the basipterygoid process and above the ascending process of the parasphenoid. Jarvik (1972, p. 58, figs 21, 31, 39) accepts this and also illustrates such a depression in *Porolepis* (fig. 20A), but points out (p. 86) that in 'specimens of various species' of porolepiforms (including species of both *Porolepis* and *Glyptolepis*) the postero-medial margin of the spiracular ('prespiracular') groove on the parasphenoid may form a projecting edge at a lower level than the more posterior part of the parasphenoid, and he suggested 'that at least some fibres or tendons of the subcranial muscle' inserted in the crevice above this edge.

In the palaeoniscoid *Pteronisculus*, Bjerring (1971, p. 203, fig. 6) restored a subcephalic ('basiotic') muscle because of the presence of a median depression, interpreted as the area of origin of the muscle, on the underside of the basioccipital, between the grooves for the lateral dorsal aortae and immediately behind the fissura oticalis ventralis. Bjerring did not discuss the area of insertion of this muscle in *Pteronisculus*, but in his restoration it is shown inserting on the posterior edge of the parasphenoid over a considerable part of the area between the internal carotids. By analogy with coelacanths and osteolepiform rhipidistians, if a subcephalic muscle were present in primitive actinopterygians it would be expected to insert in a pair of pits in the parasphenoid immediately behind the tooth patch (or bucco-hypophysial opening, where the tooth patch is less extensive), medial to the internal carotid foramen and postero-medial to the lower part of the spiracular groove. There is a pair of pits (rscm) in this position in several relatively primitive actinopterygians, including *Pholidophorus bechei* (figure 62), *Ichthyokentema* (figure 150), *Heterolepidotus* (figure 103), *Caturus chirotes* (Gardiner 1960, fig. 36, interpreted as foramina of the efferent pseudobranchial arteries), *Lepidotes latifrons* (P.9998), and probably *Macrepistius* (Schaeffer 1971, fig. 7A). In other pholidophorids and in leptolepids the pits are placed further back on the parasphenoid, below the posterior half of the prootic, and this is also their position in *Pachycormus* (32443) and *Lepidotes toombsi* (figure 109). In some living teleosts there is a similar pair of pits on the underside of the parasphenoid, at the anterior end of a conspicuous median groove, as in *Osteoglossum*, *Scleropages* and various characins (see, for example, Roberts 1969, fig. 20). In osteoglossids this groove houses the heads of the second and third infrapharyngobranchials, which are approximated in the mid-line, an advanced condition (Nelson 1968*a*, p. 267). No such interpretation can be placed on the pits in the parasphenoid of the fossil forms named above, since in all there is a well marked endoskeletal articulation for the first infrapharyngobranchial behind the ascending process of the parasphenoid. If the presence of similar pits, in an identical position, on the parasphenoid of rhipidistians like *Eusthenopteron*, *Eusthenodon*, *Megalichthys* and *Ectosteorachis* is evidence of the insertion of subcephalic muscles, the same interpretation may be placed on the pits in actinopterygians.

In some primitive actinopterygians like *Perleidus* (figures 115, 116) and parasemionotids (figures 97, 98), instead of a pair of pits behind the parasphenoid tooth patch there is an irregular recess (rscm) running the whole width of the posterior margin of the tooth patch and containing a series of anteriorly directed pits. In the figured specimen of *Perleidus* (from Greenland) and in P.19590 (from Madagascar) the most lateral pit on each side, lying immediately next to the notch for the internal carotid, is especially large, and may be the homologue of the paired pits in pholidophorids, caturids, etc. In the figured parasemionotid there are no particularly large pits. The conditions just described in *Perleidus* and parasemionotids invite comparison with the elongate crevice behind the spiracular groove (toothed in some specimens) on the underside of the parasphenoid of *Porolepis* and *Glyptolepis* (Jarvik 1972, p. 86; see above). Jarvik supposes that a portion of the subcephalic muscle inserted in this crevice. There may be a similar recess at the back of the parasphenoid in the palaeoniscoid *Boreosomus* (Nielsen 1942, fig. 62; Lehman 1952, fig. 47). In *Pteroniscul*us, it is suggested above (p. 531) that the canals in the posterior edge of the parasphenoid which Nielsen (1942) identified as carotid foramina may be pits which would have served for the insertion of subcephalic muscles (cf. Jarvik's reinterpretation of the supposed carotid canals in *Ectosteorachis*), and in some Devonian palaeoniscoids from Australia there is a pair of pits immediately medial to the carotid notches in the posterior margin of the parasphenoid (B. G. Gardiner, private communication). It is therefore likely that a paired subcephalic muscle, inserting on the parasphenoid, was widely distributed in primitive actinopterygians, since areas of muscle insertion are identifiable by the same topographic and morphological criteria as are used to recognize the insertion of the muscle in fossil crossopterygians.

As to the area of origin of subcephalic muscles in fossil actinopterygians, one available interpretation is that, as in rhipidistians and coelacanths, the muscle spanned the fissura oticalis ventralis and originated on the underside of the occipital ossification: this is the form of the muscle restored in *Pteroniscul*us by Bjerring (1971). A second possible interpretation is that, as in *Polypterus*, the subcephalic muscle was merely the foremost trunk myomere (or myomeres), extending forwards beneath the cranium and across the fissura oticalis ventralis: Nelson (1970*b*) puts this forward as the primitive gnathostome condition, the separate subcephalic muscle and intracranial joint of rhipidistians and coelacanths representing a relatively derived condition. Discrimination between these two rival hypotheses does not depend primarily upon whether or not a subcephalic muscle of rhipidistian type can be restored in palaeoniscoids, although this is worth discussing, but on whether an intracranial joint, which might be expected to be furnished with a separate subcephalic muscle, is a primitive gnathostome feature, as Bjerring (1971) and Jarvik (1972) say it is.

The thesis that the intracranial joint is a primitive feature, representing a relic of the original metamerism of the vertebrate head, was first suggested by Jarvik (1960, p. 39). It has since been developed by Jarvik and Bjerring to the point where in the braincase of *Eusthenopteron* the intracranial joint is interpreted as the foremost of five intrametameric joints, traces of four of which are found in the otico-occipital ossification (Bjerring 1971; Jarvik 1972, fig. 99). I do not propose to review the evidence upon which these interpretations are based, but only the consequences of the conclusion to which they lead, that porolepiforms and osteolepiforms 'include the most primitive vertebrates known so far' (Jarvik 1972, p. 294). Because of shared specializations in the lower jaw, dermal bones of the skull, sensory lines and dentition, Jarvik (1972, p. 273) finds that 'undoubtedly, porolepiforms and osteolepiforms are closer related to each other than to any other contemporaneous group of fishes'. That is, porolepiforms and osteolepiforms are sister-groups, and since Jarvik concludes that they include the most primitive vertebrates known, they are the plesiomorph sister-group of all other gnathostomes. Regardless of how the other major gnathostome groups are interrelated, this would mean that coelacanths, lungfishes and actinopterygians are more closely related to elasmobranchiomorphs than to rhipidistians, and the hypothesis that rhipidistians include the most primitive known gnathostomes is therefore to be rejected. The hypothesis that the intracranial joint of rhipidistians and coelacanths is a primitive feature leads to the conclusion that actinopterygians are more closely related to acanthodians than to rhipidistians and coelacanths, since in actinopterygians and acanthodians there is no intracranial joint and the braincase is very similar, as Nielsen (1949) and Miles (1965) have emphasized. Miles (1965) points out that such a conclusion is opposed by the presence in all 'bony fishes' of homologous bones in the palate, jaws and shoulder girdle, and Schaeffer (1968) adds the presence of homologous bones in the opercular series and the presence of three ossifications in the ventral part of the hyoid arch. For these reasons, the hypothesis that the intracranial joint is primitive is rejected. It is possible that Jarvik and Bjerring do not consider the whole intracranial joint to be primitive, since Jarvik (1968, p. 226) writes that the supracerebral part of the joint 'certainly appears to be a secondary formation having arisen independently in the three groups [porolepiforms, osteolepiforms, coelacanths] as a consequence of the persistence of the intrasegmental joint in the axial part'. With this hypothesis, that the infracerebral part of the intracranial joint is primitive, we are on firmer ground, for a fissure through the lower part of the ossified braincase, at the level of the tip of the notochord and close behind the hypophysis and basipterygoid process, is found in rhipidistians, coelacanths, Devonian palaeoniscoids and acanthodians, and corresponds to the division between the trabecular and parachordal portions of the base of the cranium in all vertebrates. But to refer to this fissure as a 'joint', with the implication of some mobility which might appropriately be controlled by a subcephalic muscle, is hardly justified. In primitive actinopterygians (Miles 1971, fig. 5.6) there was certainly no possibility of movement at this fissure, and this was probably true of acanthodians (Miles 1971, fig. 4.7), in which the fissure seems to have been cartilage-filled, as in actinopterygians. Nelson's comment (1970*b*, p. 470) that 'this "joint" might never have been more flexible than a typical intervertebral articulation' is perhaps overstating the flexibility of the fissure in the ancestral teleostome. Under these conditions, it is unlikely that a highly developed subcephalic muscle of the type found in *Latimeria* would have been present in the earliest teleostomes, and I accept Nelson's hypothesis that the primitive subcephalic muscle was simply the foremost trunk myomere, and was continuous posteriorly with the trunk musculature.

In Bjerring's restoration of subcephalic muscles in *Pteronisculus*, the muscles originate on the underside of the basioccipital, in the triangular area circumscribed by the grooves for the lateral dorsal aortae and by the fissura oticalis ventralis. The only other known actinopterygians in which there is such an area are *Kentuckia* (Rayner 1951, fig. 4) and the Devonian palaeoniscoids from Australia (Gardiner 1973, fig. 3). In the Kansas palaeoniscids (Watson 1925, figs 14, 15; Eaton 1939, fig. 1) and in *Boreosomus* (Nielsen 1942, fig. 63) the carotids emerged from the aortic canal close to the mid-line and close behind the fissura oticalis ventralis, while in *Australosomus* (Nielsen 1949) there is only a narrow longitudinal ridge between the grooves for the aortae. In all other known actinopterygians the parasphenoid extends back across the ventral otic fissure, covering this area (e.g. *Perleidus*, figure 116). The presence of a triangular area between the lateral dorsal aortae in *Pteronisculus*, *Kentuckia* and Devonian palaeoniscoids suggests that such an area may well be a primitive feature in actinopterygians, and it could have served for muscle attachment. But it does not follow that the muscles attaching there were directed forwards and spanned the fissura oticalis ventralis: they could as well have been anterior trunk muscles, serially homologous with those attaching to the back of the parasphenoid and continuous posteriorly with the body musculature, as in *Polypterus* and the primitive gnathostome condition postulated by Nelson. In this case, it would be immaterial if the area became covered by the parasphenoid, for the muscles could as well insert on the underside of the bone or on the underside of the aortic canal in forms like *Boreosomus* and the Kansas palaeoniscids.

These considerations lead me to accept Nelson's thesis that subcephalic muscles of the type found in *Polypterus* were primitively present in actinopterygians, inserting on the posterior part of the parasphenoid and the underside of the occipital ossifications. Alternative forms of the insertion area on the parasphenoid are the paired pits found in pholidophorids, caturids and *Lepidotes*, implying a narrow insertion by means of a pair of ligaments, and the broad shelf in *Perleidus* and parasemionotids, implying a broad insertion. These two conditions respectively resemble those found in osteolepiforms and porolepiforms: this distribution suggests that the broad insertion may be more primitive (as in *Polypterus*). In relatively advanced actinopterygians, the parasphenoid extended back beneath the occipital ossifications and replaced the primitive endoskeletal surface of insertion of the posterior subcephalic myomeres.

Subcephalic muscles are lost in all living actinopterygians, except possibly in *Alepocephalus*, where epaxial musculature extends forwards on to the prootic, on either side of the parasphenoid (Gosline 1969). In *Chauliodus* muscles extend forwards to the vomer (Tchernavin 1953), but this is presumably secondary. Gosline (1969) reviews the insertion of the epaxial musculature beneath the braincase in other teleost groups and in *Amia*, and points out that an otophysic connexion and subcephalic musculature are unlikely to occur together. In teleosts, the primary cause of the retreat of the subcephalic musculature may have been the development of a posterior opening of the myodome, for in leptolepids the inferred insertion of the foremost muscle lies immediately behind the swelling on the parasphenoid marking the end of the ventral chamber of the myodome (p. 520). In many teleosts the gill-arches have become secondarily approximated in the dorsal mid-line (e.g. some osteoglossomorphs, Nelson 1968*a*; clupeoids, Nelson 1970*a*), and this would be expected to displace subcephalic muscles, while in other groups (some eels, neoteleosts, etc.) the retractor arcuum branchialium muscles would displace the subcephalic muscles. Retractor muscles are also developed in living holosteans (Edgeworth 1935), and this would account for the absence of subcephalic muscles in those fishes. In living chondrosteans the muscles may have been displaced only by the extreme elongation of the parasphenoid, with incorporation of numerous vertebrae in the braincase.

9. MYODOME: SUMMARY AND DISCUSSION

Discussion of the posterior myodome has been deferred until after the section on the parasphenoid because in leptolepids, as in teleosts, this dermal bone lines a major part of the myodome.

(*a*) *Summary of conditions in pholidophorids and leptolepids*

(1) In all pholidophorids and leptolepids the posterior myodome is very large, and has otic and occipital portions. The *occipital portion of the myodome* (figures 45, 47, 51, 53, 65, 73, 89, 90, 92) is enclosed in the basioccipital in pholidophorids, the only interruption in the endoskeletal wall of the cavity being a median notch, covered by the parasphenoid beneath, in the anterior margin of the floor. In the Sinemurian *Leptolepis* this notch is a little larger, but the floor is still mainly ossified endoskeletally. In some specimens of *L. coryphaenoides* a small posterior part of the floor is endoskeletal, but in other specimens and in the Callovian *Leptolepis* and *L. dubia* the occipital division of the myodome has no endoskeletal floor, and in these forms the myodome opens posteriorly, between the posterior processes of the parasphenoid.

(2) In *P. bechei* the occipital division of the myodome occupies about one-third of the length of the basioccipital, while in the Callovian *Leptolepis* it occupies about two-thirds of that length and in *L. dubia* almost three-quarters. Intermediate conditions between these extremes are found in other pholidophorids and in early leptolepids.

(3) The *otic portion of the myodome* in pholidophorids and leptolepids (figures 63, 64, 65, 68, 72, 73, 76, 83, 85, 89, 90, 142, 143) is roofed by the prootic bridge. This is perforated by paired canals for the abducens nerves and notched anteriorly by the median pituitary fossa in the usual way. The palatine foramen or fenestra opens into the upper antero-lateral corner of the myodome, and the palatine nerve ran through the myodome to reach the palatine canal in its floor.

(4) The side walls of the otic portion of the myodome are formed entirely by the prootics in *P. bechei*, and this was probably also the case in other fully ossified pholidophorids. In leptolepids the antero-ventral corner of the prootic ossifies in membrane bone and is reduced in comparison with pholidophorids, so that the ascending process of the parasphenoid comes to line this corner of the myodome.

(5) The floor of the otic portion of the myodome is mainly endoskeletal in *P. bechei*, with an ossified extension of the foot of the basisphenoid pedicel containing the bucco-hypophysial canal in the foremost part of the floor, and a flange from the foot of the prootic bordering an elongate median fenestra, which is floored by the parasphenoid. The crest on the upper surface of the parasphenoid which fills this fenestra is broader in the Sinemurian *Leptolepis* (figure 143) than in pholidophorids (figure 142), indicating a reduction of the endoskeletal floor, while in *L. coryphaenoides* this part of the parasphenoid is broader and concave, and in the Callovian *Leptolepis* and *L. dubia* it is deeply excavated. The endoskeletal portion of the floor containing

the bucco-hypophysial canal appears to be absent in all pholidophorids except *P. bechei*, and is certainly lost in leptolepids.

(6) The orbital opening of the myodome is paired in pholidophorids and leptolepids, being divided by the basisphenoid pedicel. This pedicel is quite broad in *P. bechei*, containing paired vertical canals for the internal carotids and having a transverse 'bolster' at its foot which encloses canals for the internal carotid artery and palatine nerve (parabasal canal) and for the efferent pseudobranchial artery. These canals in the foot of the basisphenoid persist in the Callovian *Pholidophorus*, fail to ossify in *P. germanicus*, and in *P. macrocephalus* (figure 85) the parabasal canal becomes confluent with the ascending canal in the pedicel, so that there is a second paired opening into the myodome in this species, bordered by a strut of the basisphenoid. In leptolepids the basisphenoid pedicel is laminar and hardly obstructs the entrance to the myodome.

(7) Depressions on the upper surface of the prootic bridge in pholidophorids and primitive leptolepids indicate that the hypophysis and saccus vasculosus lay on the floor of the cranial cavity, not in the myodome (p. 390).

(*b*) *Comparison with other groups*

A posterior myodome occurs only in actinopterygians. Among living fishes, it is found only in *Amia* and in teleosts. Extensive discussions of the composition and mode of origin of the myodome have been written by many workers, especially Allis (1919, 1928), Stensiö (1925), de Beer (1926*a*) and Holmgren (1943). The basis of these accounts is primarily the embryology of living fishes. In brief, it is supposed that the dorsal compartment of the teleostean myodome (which is equivalent to the entire myodome of *Amia*) arose by the external rectus muscles shifting their origin into the foramina of the pituitary vein, so entering the pituitary space and displacing the hypophysis and saccus vasculosus upwards, while the ventral compartment of the teleostean myodome arose by the internal rectus muscles shifting their origin into the parabasal canals (containing the internal carotids and palatine nerves). In teleosts both compartments of the myodome have no endoskeletal floor, the rectus muscles having extended through the hypophysial fenestra on to the underside of the parachordal plate.

Among fossil actinopterygians, a myodome has been found in all forms investigated except for some Devonian palaeoniscoids (Gardiner 1970, 1973). These Devonian forms show extremely primitive features in the base of the otic and orbitotemporal regions, and there can be no doubt that absence of the myodome is primary. This shows that the myodome developed within the Actinopterygii, and offers a simple explanation for the absence of a myodome in living chondrosteans and *Lepisosteus*, a condition which has often been held to be secondary.

In the palaeoniscoid *Kentuckia* (Rayner 1951) and in *Birgeria mougeoti* (Stensiö 1921) there is a small posterior myodome, but it is paired, the septum between the two cavities being perforated by an opening which must have transmitted the pituitary vein into the median pituitary cavity. In other palaeoniscoids (Watson 1925; Nielsen 1942; Rayner 1951; Beltan 1968) the myodome is larger and is unpaired posteriorly. The communication between the originally paired chambers presumably involves the foramen of the pituitary vein, since no such foramen is found in any fish with a partially unpaired myodome. But in *Kentuckia* and *Birgeria* the foramen lies well forwards in the medial wall of the paired myodome, and the deduction made by Allis and others from the embryology of living fishes, that the myodome originally developed by the external rectus muscles entering the foramen of the pituitary vein, is not necessarily true (cf. Daget 1950, p. 54).

In *Pteronisculus* (Nielsen 1942, figs 9, 14) there is a deep recess in the hind wall of the pituitary fossa, excavated in the front margin of the prootic bridge, above the myodome. A similar recess is recognizable in parasemionotids, '*Aspidorhynchus*' and *Lepidotes*, while in pholidophorids it is represented by a depression on the upper surface of the prootic bridge. This recess housed the saccus vasculosus, and is the homologue of the cavum sacci vasculosi in *Lepisosteus*, sturgeons and *Polypterus* (p. 390). Allis's (1919) deduction that the cavum sacci vasculosi is the phylogenetic homologue of the myodome of *Amia* and of the dorsal compartment of the teleostean myodome is therefore inexact, for a cavum sacci vasculosi co-exists with a well developed myodome in *Pteronisculus*, parasemionotids, '*Aspidorhynchus*' and *Lepidotes.*

In all palaeoniscoids and in *Birgeria*, *Saurichthys* (Stensiö 1925), *Australosomus* (Nielsen 1949) and *Perleidus* (Stensiö 1932) the myodome is entirely lined by endoskeletal bone, except for a small contribution from the ascending process of the parasphenoid in the antero-lateral margin in some forms, and a median 'fenestra ventralis myodomus', lined by the parasphenoid, in the floor in *Pteronisculus.* This fenestra in *Pteronisculus* lies directly below the pituitary fossa and above the ossification centre of the parasphenoid, and is clearly the homologue of the bucco-hypophysial canal of *Kentuckia*, *Perleidus*, pholidophorids, etc., not of the true fenestra ventralis myodomus (see below). The myodome is therefore intramural in all these primitive actinopterygians. In all these forms the myodome lies in front of the fissura oticalis ventralis, and is always separated from that fissure by a thin transverse wall (Nielsen 1942, fig. 9; 1949, fig. 7; Rayner 1951, fig. 10). The position of the fissura oticalis varies considerably in primitive actinopterygians. In Devonian palaeoniscoids it lies directly behind the hypophysis and runs into the rear of the orbit, while in *Australosomus* and *Pteronisculus stensioei* it has become confluent with the vestibular fontanelles (p. 416). These variations are exactly correlated with the development of the myodome: where there is no myodome the fissure is far forwards, and the hind margin of the myodome is separated from the fissure only by a thin partition. Since there are no other major differences in the base of the otic and orbitotemporal regions in these forms, it is evident that the development of the myodome is responsible for posterior migration of the fissure.

In *Amia*, the myodome houses the external rectus muscles only, the remaining rectus muscles taking origin on the lateral part of the sphenoid 'bolster', below the paired orbital openings of the myodome. The myodome is confined within the prootics, and ends just in front of the cartilage separating the prootic and basioccipital (Allis 1897, fig. 11); this cartilage is the homologue of the fissura oticalis ventralis (p. 416). The myodome is lined by endoskeletal bone or cartilage throughout, except for a small contribution from the ascending process of the parasphenoid antero-laterally and an elongate median fenestra in the floor (Allis 1897, fig. 10), which is filled by a crest on the parasphenoid. There is a similar fenestra in the floor of the myodome of some caturids (*Caturus chirotes*, *Heterolepidotus*), but not in others (Aldinger 1932, p. 19; Rayner 1948, p. 298). There may be a small fenestra in some parasemionotids (Stensiö 1932, fig. 76). In *Lepidotes* the lower parts of the prootics are incompletely ossified in the available specimens, so that no fenestra is preserved, but there is a crest on the dorsal surface of the parasphenoid (Rayner 1948, fig. 13B) suggesting that a fenestra was present. In *Dapedium* there is no such crest, and the myodome appears to have been floored throughout by the basisphenoid (P.11177). This fenestra in the floor of the myodome only appears in relatively advanced actinopterygians and is undoubtedly a new formation, caused by enlargement of the myodome, endoskeletal regression, or both. This fenestra may be called the fenestra ventralis myodomus, although Allis (1919, p. 228) originally gave this name to the much larger, and not strictly comparable, opening in the floor of the teleostean myodome. The latter is not exactly homologous with the small fenestra in more primitive actinopterygians because it also includes a sub-pituitary portion and the point of entry of the carotid arteries, and must represent the entire hypophysial fenestra of embryos (see, for example, de Beer 1926*a*, fig. 43). The small fenestra of more primitive actinopterygians must represent a persisting part of the embryonic hypophysial fenestra, but in parasemionotids, caturids and pholidophorids the true hypophysial fenestra is represented in the adult by the bucco-hypophysial canal, and the fenestra ventralis myodomus is no more homologous with that than are the internal carotid foramina, which also originate in ontogeny as a part of the hypophysial fenestra.

In the fossil groups just mentioned (caturids, parasemionotids, semionotids) the myodome has the same extent as in *Amia* and the basisphenoid 'bolster', containing the parabasal canals and canals for the efferent pseudobranchial arteries, is developed in just the same way as in *Amia*. It must therefore be assumed that in these fossil groups the rectus muscles originated in the same place as in *Amia*, the external rectus in the myodome and the internal, superior and inferior recti on the antero-lateral part of the 'bolster'. The 'bolster' has the same form in *Pholidophorus bechei*, and the same inference on the point of origin of the rectus muscles must be drawn. The major difference between the myodome of *P. bechei* and that of *Amia* or a caturid is that in *P. bechei* the myodome has extended across the fissura oticalis ventralis (the prootic/basioccipital suture) into the basioccipital. This is a unique specialization relating pholidophorids to teleosts, for in all other actinopterygians, including the pholidophoroid *Ichthyokentema* (Griffith & Patterson 1963), the myodome is confined to the prootic region, in front of the fissura oticalis ventralis. Extension of the myodome into the basioccipital has been described in the semionotids *Dapedium* (Woodward 1893, p. 564; Frost 1913, p. 221) and *Lepidotes* (Woodward 1893, p. 560; 1916, p. 39; Rayner 1948, p. 307; Gardiner 1960, p. 310), and in the caturid '*Aspidorhynchus*' (Rayner 1948, p. 317), but re-examination of the specimens concerned shows that in all the myodome is confined within the prootics, the supposed occipital part of the myodome being the aortic canal in *Dapedium* and the aortic groove (Woodward, Gardiner) or saccular recesses (Rayner) in *Lepidotes*.

In *P. bechei* the occipital portion of the myodome is intramural, its walls being entirely endoskeletal except for a notch in the anterior margin of the floor, the posterior part of the narrow fenestra ventralis myodomus. In pholidophorids, the basisphenoid 'bolster' regresses, failing to ossify, or, as in *P. macrocephalus*, producing a second, ventro-medial opening into the myodome by the confluence of the anterior opening of the parabasal canal with the ascending canal for the internal carotid. In Kansas palaeoniscid A and *Perleidus*, where there is a similar ventro-medial opening into the myodome (Stensiö 1932), the course of the canals in the foot of the basisphenoid is not yet sufficiently well known to say whether this opening has the same relationships as in *P. macrocephalus*. A membrane closing the opening in *P. macrocephalus* and giving origin to the internal rectus muscle would have the necessary relations to be the precursor of the horizontal myodomic membrane of teleosts. Whether any rectus muscle passed through the opening in *P. macrocephalus* is unknown, since the upper surface of the parasphenoid is not visible in this species, but in other pholidophorids and in the Sinemurian *Leptolepis* there is no indication of the attachment of a horizontal myodomic membrane or any eye muscle to the parasphenoid. In the Callovian *Leptolepis* and in *L. dubia*, however, there is such evidence, in the form of a deep hollow in the parasphenoid beneath the otic portion of the myodome, ending posteriorly in a process which could have given insertion to the hind end of the horizontal myodomic membrane (figure 142*d*). The ventral compartment of the myodome produces a broadly similar impression on the upper surface of the parasphenoid in *Elops*, *Hiodon*, *Clupea*, *Salmo*, etc. The appearance of a ventral compartment of the myodome in leptolepids seems to coincide with the development of a posterior opening of the myodome, beneath the basioccipital. A prerequisite for the development of such an opening is loss of the endoskeletal floor of the occipital portion of the myodome. This took place in leptolepids, and was accompanied by increase in length of the occipital portion and by posterior migration of the housing of the aortic ligament (p. 316), which marks the point at which the dorsal aorta forked. This shows that Allis (1919) was wrong in supposing that the hindmost part of the myodome in such teleosts as *Hidon* (and leptolepids), which takes the form of an open groove on the underside of the basioccipital, is homologous with the aortic groove or canal. Although these two structures are similar in appearance and topographic relations, pholidophorids and leptolepids show that the aortic groove was reduced as a consequence of loss of the endoskeletal floor of the occipital part of the myodome, and the posterior opening of the myodome is a new formation.

In summary, palaeontological evidence indicates that the history of the actinopterygian myodome was as follows. In the earliest actinopterygians there was no myodome (e.g. some Devonian palaeoniscoids). The myodome first appeared as a paired depression housing the external rectus muscle and lying lateral to the pituitary vein foramen and ventral to the abducens foramen (e.g. *Kentuckia*). Increasing in size, the paired myodomes met posteriorly in a median cavity which was confluent anteriorly with the pituitary space and incorporated the pituitary vein foramina. The hypophysis and saccus vasculosus remained dorsal to the myodome, and only the bucco-hypophysial stem passed through it. In consequence of this enlargement of the myodome the fissura oticalis ventralis (prootic/basioccipital suture) migrated posteriorly until it became confluent with the vestibular fontanelles (e.g. *Pteronisculus stensioei*). Up to this stage, the myodome was entirely intramural and lined by endoskeletal bone. As a consequence of further enlargement of the myodome, and perhaps also of skeletal regression, a median fenestra, occluded by the parasphenoid, appeared in the floor of the myodome, behind the bucco-hypophysial canal (e.g. *Amia*, some caturids). In the line leading to teleosts, the myodome broke through the fissura oticalis ventralis and extended into the basioccipital, as an intramural cavity with a continuation of the fenestra ventralis myodomus in its floor (e.g. *Pholidophorus bechei*). With further enlargement of the myodome and endoskeletal regression, the cavity extended further into the basioccipital, causing reduction in the notochordal canal, the fenestra ventralis myodomus became enlarged, and the basisphenoid 'bolster', which had previously given origin to three of the rectus muscles, became reduced so that in some forms there was a second, ventro-medial opening into the myodome (e.g. *Pholidophorus macrocephalus*). The basisphenoid 'bolster' finally disappeared, persisting only as membrane, and while the superior and inferior rectus muscles continued to take origin on the edge of this membrane, the internal rectus extended back beneath it and above the parasphenoid into the fenestra ventralis myodomus, taking origin on the underside of the membrane or on the parasphenoid, so forming the ventral compartment of the teleostean myodome. At or about this time, continuing reduction of the floor of the occipital part of the myodome resulted in it opening beneath the braincase, between the posterior processes of the parasphenoid (e.g. Callovian

Leptolepis, *Hiodon*, *Elops*, *Salmo*, *Clupea*). Since there is a ventral compartment of the myodome in primitive members of all extant teleostean cohorts, as well as in advanced leptolepids, it is economical to explain the absence of this chamber in some teleosts (*Heterotis*, *Hepsetus*, *Merlangus*) as due to secondary loss, like the complete reduction of the myodome in siluroids, mormyroids, *Anguilla* and *Gadus*.

10. Dermal roofing bones; the frontals, parietals and dermopterotics

The roofing bones are included here, although they are not part of the primordial neurocranium, since in teleosts they become very intimately associated with the endoskeletal braincase and line a major part of the cranial cavity. The dermopterotic, in particular, is fused with the endoskeletal pterotic in all living teleosts and in leptolepids.

(*a*) *Conditions in pholidophorids and leptolepids*

The roofing bones will not be described in any detail, since adequate accounts of them have already been given in several pholidophorids (especially Rayner 1948, *Pholidophorus bechei*; Saint-Seine 1949, *P. similis* Woodward and *P. segusianus* Saint-Seine; Nybelin 1966, various species of the genera *Pholidophorus*, *Pholidolepis*, *Pholidophoroides* and *Pholidophoropsis*) and leptolepids (especially Rayner 1937, Nybelin 1962 and Wenz 1968, all on *Leptolepis coryphaenoides*; Saint-Seine 1949, *L.* '*sprattiformis*'; Patterson 1967, *L. dubia*; Cavender 1970, *L. talbragarensis* Woodward; Waldman 1971, *L. koonwarri* Waldman). In this paper, the external surface of the roofing bones is illustrated in *Pholidophoroides limbata* (figure 82), *Pholidophorus bechei* (figures 56, 60), *P. minor* (figure 83), *P. macrocephalus* (figures 125, 145) and the Callovian *Leptolepis* (figures 74, 147), while figures 146 and 148 show the internal surface of the bones in *P. germanicus* and the Callovian *Leptolepis*. These illustrations will serve as the basis for a brief comparative account.

In general, the roofing bones of pholidophorids are thick, with plane outer surfaces ornamented with ganoin-covered ridges or tubercles (except in *P. minor*, where the ganoin forms a smooth sheet, also tending to cover the sutures between the bones). The sensory canal tubes are concealed within the thickness of the bone, and are only traceable by the pores opening to the surface. In leptolepids the bones are thin, with raised tubes marking the course of the sensory canals, and if ornamented bear only weak ridges without enamel (ganoin has been reported on the dermal bones and scales of various leptolepids by many authors, including Rayner (1937), Saint-Seine (1949) and Wenz (1968), but Schultze's (1966) histological investigation of leptolepid scales show that it is absent there, and this also seems to be true of the dermal bones). Intermediates between the typical leptolepid and pholidophorid conditions are found in *Pholidolepis* and *Pholidophoropsis*, where the ganoin covering of the skull bones is greatly reduced or absent (as it is in small specimens of *P. bechei*), and the supraorbital canal may run in a raised tube (as it does in *P. latiusculus* Agassiz) (Nybelin 1966). In the Sinemurian *Leptolepis* the roofing bones are rather thick and may bear traces of ganoin, but this species will not be dealt with here since the skull roof is described in detail in Professor Nybelin's forthcoming account.

The *frontal* (Fr) of pholidophorids (figures 56, 60, 82, 83, 145) is approximately triangular, with a more or less well-marked antero-lateral excavation housing the nasal. The supraorbital sensory canal penetrated the bone from this excavation to the posterior edge, with a characteristic sigmoid curve above the posterior part of the orbit, and gave off numerous short branches ending in pores (about 12 branches in *P. limbata* and *P. bechei*, 13 in *P. macrocephalus* and *Pholidophoroides crenulata*, 15 in *P. segusianus*, 20 in *P. similis*, 25 in *P. germanicus*). Posteriorly the frontal overlaps the parietal and dermopterotic, and the median suture between the frontals is sinuous posteriorly. At the point where the supraorbital sensory canal leaves the frontal to pass into the nasal, the frontal bears a tongue-like process (alfr, figures 121, 124, 125,

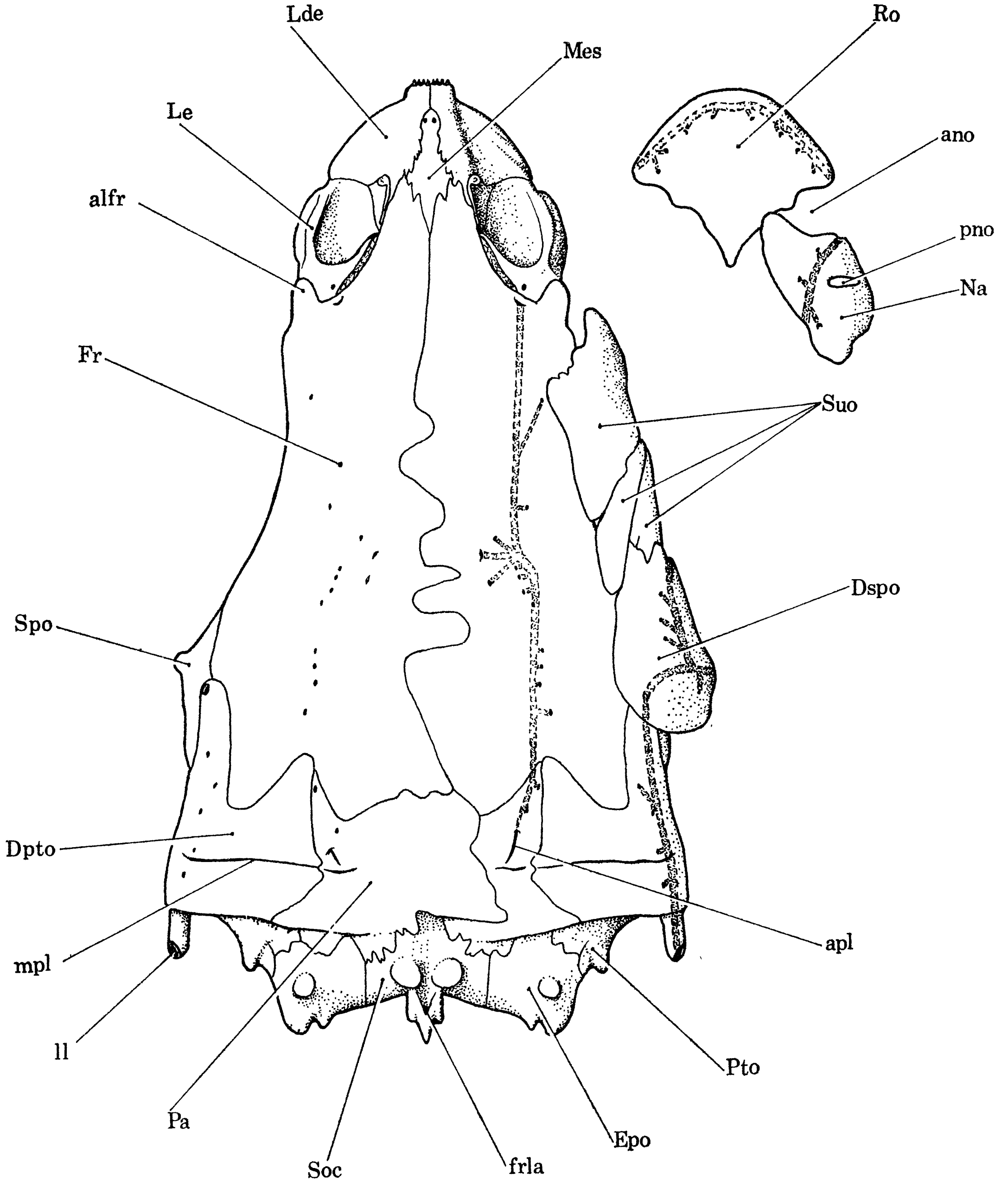


FIGURE 145. *Pholidophorus macrocephalus* Agassiz. Skull roof in dorsal view (magn. × 2.5 approx.). The rostral and right nasal are displaced to the right; the course of the sensory canals is indicated on the right side. Based on P.1066, P.12070 and P.52518. Ornament of dermal bones not shown. For details of the ethmoid region see figure 125.

145, 146) which is applied to the upper surface of the lateral ethmoid. On the underside of the frontal, which is only known throughout its length in *P. germanicus* (figure 146), there is a pronounced descending lamina (dlfr) which follows the course of the sensory canal. Above the orbit this lamina fits against the outer wall of the supraorbital fossa on the dorsal surface of the orbitosphenoid and pterosphenoid (figures 69, 80). At the centre of ossification of the frontal the lamina is interrupted, and behind this point it fits against the medial wall of the fossa bridgei in the pterosphenoid and pterotic (figures 69, 75).

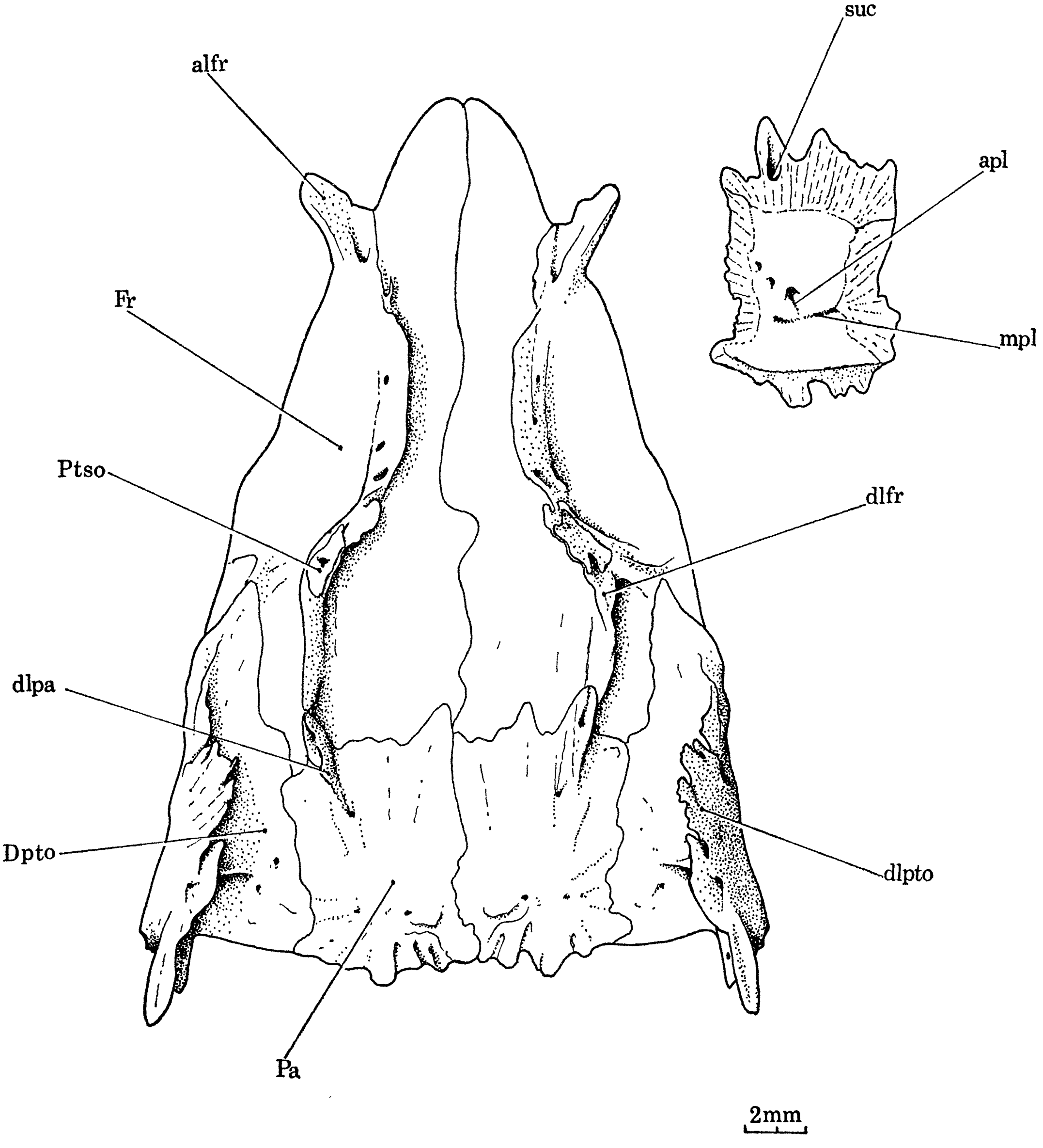


FIGURE 146. *Pholidophorus germanicus* Quenstedt. Dermal roofing bones of braincase in ventral (internal) view, and (top right) left parietal in dorsal view. From P.3704.

In leptolepids the frontal (figure 147; Wenz 1968, figs 82, 83, 86; Patterson 1967, fig. 4) is narrower than in pholidophorids, and has a narrow, strip-like anterior portion which separates the nasals and ends over (Sinemurian *Leptolepis*, *L. coryphaenoides*, figure 128) or under (Callovian species, *L. dubia*, figure 130) the rostro-dermethmoid. The supraorbital sensory canal ran in a raised tube which has the usual sigmoid curve over the posterior part of the orbit, and passes back to the junction with the parietal, without joining the infraorbital canal, as in pholidophorids. The posterior part of the tube is slender in *L. dubia* (Patterson 1967), and according to Saint-Seine (1949) it is entirely reduced in *L.* '*sprattiformis*'. The canal has fewer pores than in pholidophorids. In *L. talbragarensis* Cavender (1970) found only three or four pores, while Rayner (1937) and Nybelin (1962) illustrate a range of 6–8 in *L. coryphaenoides*. *L. dubia* has about ten pores and the Callovian species (figure 147) about twelve. In leptolepids there is no trace of the tongue-like antero-lateral process which fits over the lateral ethmoid in pholidophorids. On the underside of the frontal, which is only known throughout its length in the Callovian species (figure 148) and *L. coryphaenoides*, the descending lamina (dlfr) is restricted to the middle part of the bone, and does not follow the course of the sensory canal as it does in pholidophorids. The lamina lies beneath the sensory canal at the centre of ossification of the frontal, but it passes medial to the canal anteriorly and diverges from it posteriorly,

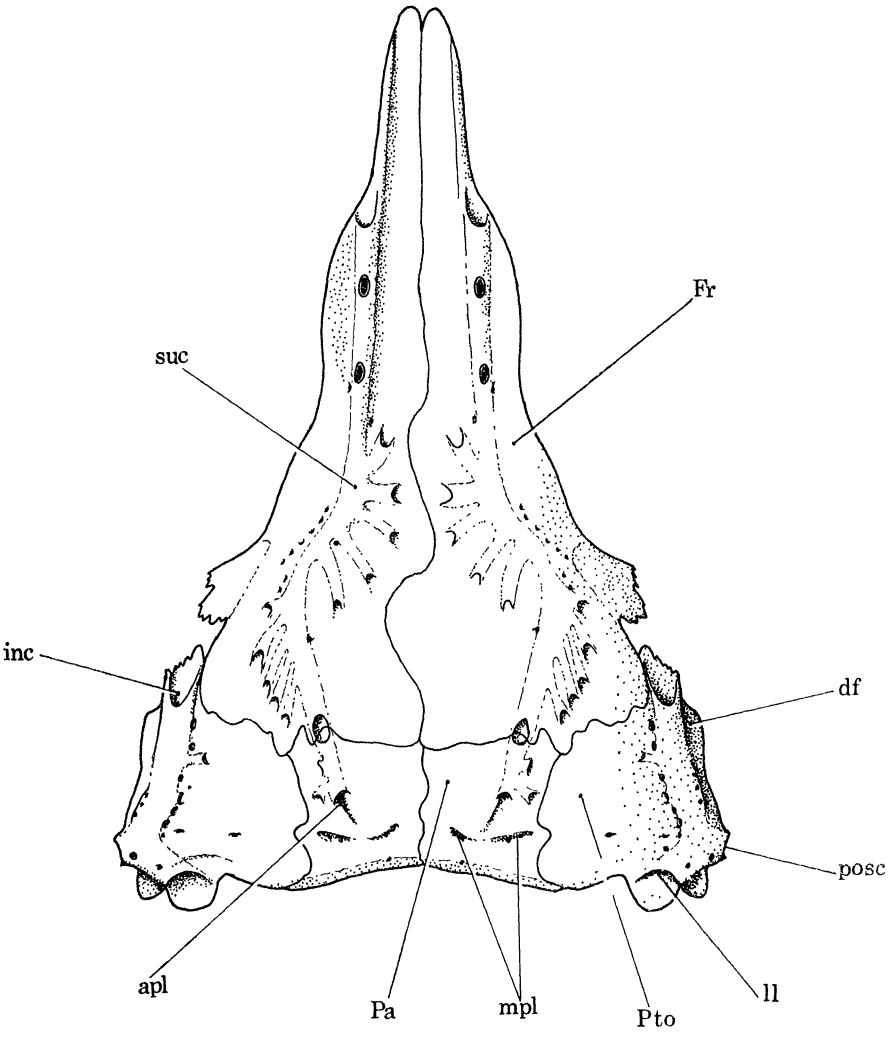


Figure 147. Callovian *Leptolepis* sp. Dermal roofing bones of the braincase in dorsal view, restored on the basis of isolated frontals (P.51740, P.51755), parietals (P.51739, P.51741) and dermopterotic (P.51727). (Magn. × 7 approx.)

passing out to the postorbital process, where it ends in a splint-like ventro-lateral process which sutures with the sphenotic. Behind the descending lamina there is a curved ridge which probably marks the position of the hind margin of the cartilaginous epiphyseal bar. There is no descending lamina beneath the posterior part of the frontal, only a weak ridge (lptf) or pocket marking the outline of the post-temporal fossa.

The *dermopterotic* of pholidophorids (Dpto, figures 56, 60, 82, 83, 145, 146) varies considerably in shape, but the exposed surface is usually more or less L-shaped, the stem of the L carrying the temporal sensory canal and forming the lateral margin of the skull roof, and the foot of the L carrying the middle pit-line and overlapping the parietal medially. The L-shape of the exposed surface of the dermopterotic is probably mainly due to the frontal overlapping the antero-medial corner of the bone, for in *P. minor* (figure 83), where the bones meet almost edge-to-edge, the dermopterotic is nearly rectangular, and in *P. germanicus*, where the inner surface of the bone is known (figure 146), it is an elongate triangle. The lateral line from the supratemporal entered a tubular process (ll) which projects back, beneath the supratemporal, from the postero-lateral corner of the dermopterotic. This process is long in *P. macrocephalus* and *P. germanicus* (figures 145, 146), very short in *P. minor* and *Pholidophoroides limbata* (figures 82, 83), and intermediate in *P. bechei* (figure 60). The process is directed postero-medially in *P. bechei* (cf. leptolepids, below), and posteriorly in other species. The canal anastomosed with the preopercular canal through a large, ventro-laterally directed pore (posc) at the postero-lateral corner of the dermopterotic, and the sensory canal then passed forwards to the dermosphenotic. There are about five pores along the canal in *P. limbata* and *P. macrocephalus*, four in *P. crenulata*, two or three in *P. bechei* and only two in *P. minor*. The dermopterotic part of the middle pit-line groove (mpl) is deeply incised laterally, with several small foramina in its floor, but weaker medially. On the underside of the dermopterotic there is a pronounced descending lamina beneath the sensory canal (dlpto, figures 59, 60, 69, 82, 84, 146). The lamina fits against the lateral wall of the post-temporal fossa posteriorly and the fossa bridgei anteriorly, where it ends in a process which approaches or enters the upper opening of the spiracular canal. Beneath the deeply incised lateral part of the middle pit-line groove there is a short transverse descending lamina which fits against the partition between the fossa bridgei and post-temporal fossa where these are separate (*P. limbata*, figure 82; *P. bechei*, figure 60; *P. germanicus*, figure 146), and forms the upper boundary of the fenestra between these chambers in the Callovian species (figure 70). In *P. macrocephalus* this transverse descending lamina is lost.

In leptolepids, the dermopterotic (figures 74, 147) is always fused to the pterotic, and the dermal portion of this compound bone has been described with the endoskeletal portion in §5. The exposed portion of the bone is L-shaped, as in pholidophorids (Rayner 1937, fig. 2; Wenz 1968, figs 82, 84, 86; Patterson 1967, fig. 4), and although the antero-medial corner of the bone is embayed (figure 74), the shape of the exposed surface is mainly due to overlap by the frontal, as in pholidophorids. The lateral line from the supratemporal entered the posterior face of the bone (ll), and at first passed almost transversely to reach the anastomosis with the preopercular canal (posc) at the postero-lateral corner of the bone, then passing straight forwards to the dermosphenotic. There is no descending lamina beneath the posterior, transverse part of the canal, but the descending lamina beneath the longitudinal portion, which fuses with the pterotic in the lateral wall of the post-temporal fossa, extends posteriorly as a splint, partially fused into the autopterotic, which appears to be the homologue of the posterior process in pholidophorids. In *L. coryphaenoides*, Wenz (1968) records four or five branches from the sensory canal in the pterotic, but Nybelin (1962) illustrates only one, which is the topographic homologue of the single large pore in *Pholidophorus bechei* (figures 60, 61). In *L. talbragarensis* there are about three pores (Cavender 1970), in the Callovian species 4–7, and in *L. dubia* 5–7. Lateral to the anterior part of the sensory canal there is a depressed area which forms the upper part of the dilatator fossa (df). This area is not developed in pholidophorids, indicating that the fossa is enlarged in leptolepids. In *L. coryphaenoides* the middle pit-line groove extends on to the pterotic in some specimens but not in others. In *L. dubia* and the Callovian species the pterotic portion of the middle pit-line is only recognizable by an alignment of two or three minute foramina (figure 147).

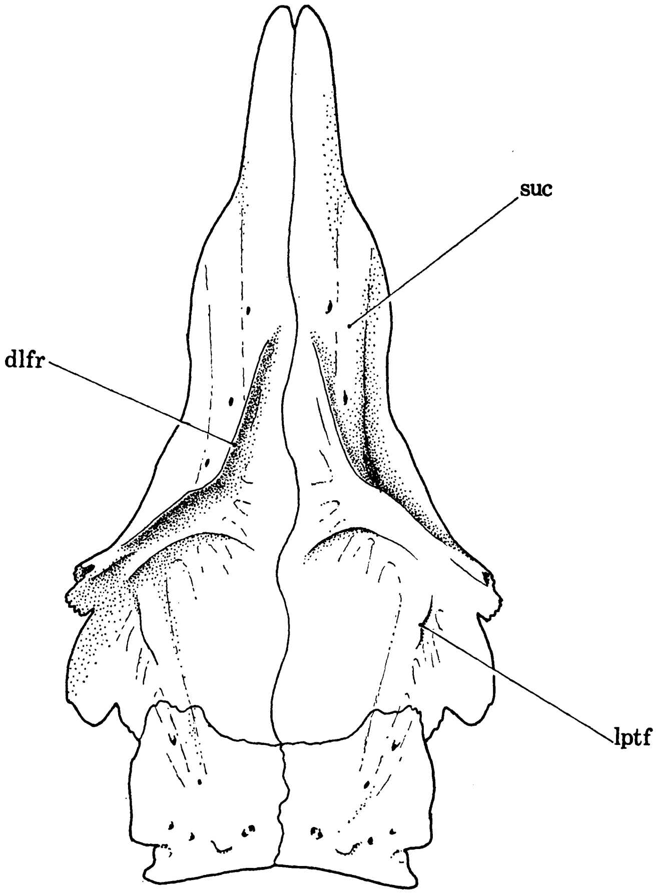


FIGURE 148. Callovian *Leptolepis* sp. Frontals and parietals in ventral (internal) view, restored on the basis of isolated frontals (P.51740, P.51755) and parietals (P.51739, P.51741). (Magn. × 7 approx.)

The *parietal* of pholidophorids (Pa, figures 57, 60, 82, 83, 145, 146) varies in shape but is approximately square. The bone is overlapped by the frontal anteriorly and the dermopterotic laterally, and the median suture between the parietals is very asymmetrical and variable in form. A depressed, unornamented zone at the posterior edge of the bone is overlapped by the supratemporal. The parietal contains the posterior part of the supraorbital sensory canal, sometimes with two pores given off within the bone, but Rayner (1948) records specimens of *P. bechei* in which the enclosed portion of the canal ends in the frontal. The anterior pit-line groove (apl) extends from the termination of the enclosed portion of the canal towards the radiation centre of the bone, which is crossed by the middle pit-line groove (mpl). Wenz (1968) has identified the medial portion of this groove in *L. coryphaenoides* as the posterior pit-line, without giving reasons. The groove is sometimes interrupted at the ossification centre of the parietal in pholidophorids and leptolepids (e.g. figures 57*b*, *c*, 82; Wenz 1968, figs 85, 86B), but the two parts are always aligned. Decisive identification of the middle and posterior pit-lines depends upon innervation, not alignment, for in *Lepisosteus* (Norris 1925, fig. 15) the middle pit-line (innervated by the supratemporal branch of the glossopharyngeal) and the posterior pit-line (innervated by the supratemporal branch of the vagus) occupy the lateral and medial portions of a single pit-line groove, resembling the groove in pholidophorids and leptolepids. Direct evidence on innervation will presumably never be available in pholidophorids and leptolepids, and the problem cannot be resolved by comparison with living teleosts, for there the evidence is conflicting. In *Esox*, where there is a pit-line groove on the parietal in adults, Pehrson (1944, figs 5, 6, 8) found that the parietal originates beneath the centre of a transverse alignment of pit organs innervated by the glossopharyngeal, and therefore a middle pit-line. In *Salmo*, Devillers (1947) found the similar alignment of pit organs to be innervated by the vagus, implying that it is the posterior pit-line, but the supratemporal branch of the vagus in *Salmo* is presumably mixed, receiving fibres from the glossopharyngeal intracranially, as it does in *Menidia* (Herrick 1899), and the most sophisticated techniques would be necessary to decipher the real innervation of the pit organs. In cyprinoids (Manigk 1933; Lekander 1949) there are groups of free neuromasts over the lateral part of the parietal and the pterotic which are innervated by the glossopharyngeal, and a group of neuromasts over the medial part of the parietal, innervated by the vagus. Manigk identified these as the middle and posterior pit-lines, in accordance with their innervation. Lekander questioned both these identifications, the first because in *Gobius* the lateral groups of neuromasts are accompanied medially by a well developed pit-line, similarly innervated, the second because the 'posterior pit-line' lies close in front of the supratemporal commissure (which overlies the parietal in cyprinoids). In my opinion, neither of Lekander's arguments is decisive.

Since there is as yet no satisfactory means of deciding whether pholidophorids and leptolepids has a posterior pit-line, the simplest solution is to accept Nelson's (1972*b*, p. 6) conclusion, from an analysis of the pattern of sensory canals and pit-lines in a wide variety of primitive teleosts, that the teleosts primitively had only anterior and middle pit-lines on the skull roof. I will therefore continue to refer to the pit-line groove on the parietal of pholidophorids and leptolepids as the middle pit-line. In *Pholidophorus minor*, however, there may be a very small posterior pit-line, visible on the right side of P.1072 (? ppl, figure 83), and on both sides of P.3597, the holotype.

On the underside of the pholidophorid parietal, well known only in *P. germanicus* (figure 146) and the Callovian species, the descending lamina beneath the sensory canal in the frontal is continued back by a short descending lamina beneath the bone-enclosed portion of the canal in the parietal (dlpa), fitting against the medial wall of the fossa bridgei. In the Callovian species there is also a collar-stud-like process passing down from the ossification centre of the parietal.

In leptolepids, the parietal of *L. coryphaenoides* has been fully described by Wenz (1968). In the Callovian species (figures 147, 148) there is little variation among the nine available parietals, all having a long bone-enclosed portion of the supraorbital sensory canal, giving off two major branches, so that the anterior pit-line groove (apl) is very short. The middle pit-line groove (mpl) is curved and less deeply incised than in *L. coryphaenoides*. In *L. dubia* the parietal is similar, but in large individuals the pit-lines are deeply incised. The underside of the parietal is smooth in leptolepids, lacking the descending lamina found in pholidophorids.

(*b*) *Comparison with other groups*

The dermal roofing bones of leptolepids seem to be very similar to those that would be expected in a teleostean morphotype. While of typical generalized teleostean form, they retain a few primitive characters which are found in mosaic distribution among teleosts. These primitive characters include the absence of a postorbital connexion between the supra- and infraorbital sensory canals, also lacking in *Hiodon*, *Chanos*, *Phractolaemus*, some characoids and many cyprinoids (Gosline 1965; Nelson 1972*b*); a bone-enclosed portion of the supraorbital canal in the parietal, also found in some individuals of *Elops* and in many cyprinoids (Lekander 1949); and a transverse pit-line groove on the parietal, also found in *Esox* (Allis 1905) and the Cretaceous clupeoid *Spratticeps* (Patterson 1970*a*). In the dermal roofing bones, leptolepids show particular resemblances to the teleosts in the form of the descending lamina on the frontal, fusion between the autopterotic and dermopterotic (said not to occur in alepocephaloids by Gosline (1969), but judging from the illustrations of alepocephaloid skull roofs given by Greenwood & Rosen (1971, figs 23, 24) this is a secondary condition, due to reduction in ossification), and the transverse alignment of the sensory canal in the posterior part of the dermopterotic.

The dermal roofing bones of pholidophorids are more primitive than those of leptolepids in being thicker and ganoin-covered; in the triangular form of the frontal; in having the descending laminae confined to the course of the sensory canals, with the lamina beneath the frontal ending anteriorly in a tongue-like process over the lateral ethmoid, a descending lamina beneath the parietal, and the lamina on the dermopterotic sending a process towards the spiracular canal and including a transverse lamina beneath the lateral part of the middle pit-line groove; in having the dermopterotic separate from the autopterotic; and in the longitudinal course of the sensory canal in the posterior part of the dermopterotic, with a posterior process which received the sensory canal from the supratemporal.

I do not propose to compare the pattern of the roofing bones in pholidophorids with that in other actinopterygian groups, for the pattern was already well known and has been discussed by Schaeffer & Dunkle (1950), Saint-Seine (1949), Gardiner (1960) and Wenz (1968), among others. It is worth noting that no examples of supernumary bones have been observed in the pholidophorid skull roof: such bones occur frequently in other primitive actinopterygian groups (see especially Lehman 1952).

Descending laminae beneath the sensory canals in the roofing bones have been recorded in various primitive actinopterygians (Nielsen 1942, p. 120). In chondrosteans a lamina is only found beneath the canal in the dermopterotic, and this is absent in some forms (*Boreosomus*, *Australosomus*). In *Pteroniscus* and *Saurichthys* the anterior part of the dermopterotic lamina passes down into the upper opening of the spiracular canal, as in pholidophorids; this is also true of *Perleidus* (MMK 495) and probably of many other primitive forms. There is a descending lamina on the dermopterotic in *Amia* and *Lepisosteus*, and in all the fossil holosteans where I have been able to observe this region. A descending lamina on the frontal is less common. There is none in *Amia*, and in *Lepisosteus* it is only developed anteriorly. In *Lepidotes* a lamina is developed anterior to the ossification centre of the frontal, and there is a lamina in the roof of the orbit (the only part of the underside of the frontal visible) in *Dapedium* and *Heterolepidotus*.

There is no frontal descending lamina in *Perleidus* (MMK 495) or a Greenland parasemionotid (MMK 491). I have not observed a descending lamina on the parietal, like that in *P. germanicus* and the Callovian *Pholidophorus*, or a transverse lamina beneath the middle pit-line on the dermopterotic, in any other fish.

The tongue-like process from the frontal which covers the upper surface of the lateral ethmoid in pholidophorids may be an extension of the descending lamina. There is no such process in *Amia*, *Lepisosteus* or *Lepidotes*, but it is present in *Dapedium* and may occur in parasemionotids and caturids. The process is not recorded in more primitive actinopterygians.

The posterior process of the dermopterotic in pholidophorids which received the lateral line from the supratemporal is only large in relatively advanced species, being very short in *Pholidophoroides limbata* and *Pholidophorus minor*. There is a similar short process behind the dermopterotic in *Amia*, *Lepisosteus*, caturids, *Dapedium*, parasemionotids and *Perleidus*, and such a process is probably widely distributed in primitive actinopterygians. In *Pachycormus* and *Lepidotes* there is a long process, as in advanced pholidophorids.

11. COMPARISON OF THE PHOLIDOPHORID AND LEPTOLEPID BRAINCASE WITH THAT OF ICHTHYOKENTEMA

Ichthyokentema purbeckensis (Davies), from the Purbeck of Dorset and Wiltshire, is the only other pholidophorid-like fish in which the braincase is known. So far in this paper, *Ichthyokentema* has only been considered in connexion with the ethmoid region (p. 486). Griffith & Patterson (1963), who described the skeleton of *I. purbeckensis*, found that it was in many ways more primitive than *Pholidophorus*, and made a new family Ichthyokentemidae to include it. At that time, the pholidophorid braincase was poorly known, and in the light of the new information in this paper it is necessary to reconsider the braincase of *Ichthyokentema*, since according to our 1963 account it appears to be more advanced and teleost-like than the pholidophorids as described here.

Re-examination of the materal of *I. purbeckensis* shows that our 1963 account of the braincase was inadequate in some ways and inaccurate in others, these inaccuracies stemming partly from lack of experience and partly from deficiencies in the material as compared with the pholidophorid material described here: for example, I am unable to be certain whether *Ichthyokentema* had a lateral cranial canal or a spiracular canal since the specimens are not sufficiently well preserved. Our 1963 account requires modifying in two ways: first, regarding structures which were wrongly described, and secondly, structures which were not described or whose significance was not recognized.

The first category, wrongly described structures, mainly concerns the sutures in the otic region. It was said that 'sutures between the cartilage bones are often indistinguishable on the external surface of the neurocranium, but they can usually be recognized on the internal surface of the bones' (Griffith & Patterson 1963, p. 8). Sutures recognizable externally include those between the epioccipital and supraoccipital, between the exoccipital and the epi- and supraoccipital, around the posterior part of the intercalar, and between the pterosphenoid and the orbitosphenoid, sphenotic and prootic. A few more sutures are visible on the internal surface of the braincase in broken specimens (especially that shown in Griffith & Patterson 1963, pl. 3, fig. 8), including parts of the basioccipital/exoccipital suture, the basioccipital/prootic suture in the roof of the myodome, and a junction between the prootic and a bone behind it in the floor of the post-temporal fossa and the wall of the saccular recess. The position of the other sutures in our 1963 figures, especially those around the pterotic and the antero-lateral part of the exoccipital, seems to have been influenced by the expectation that the ossification pattern would agree with that known in leptolepids and teleosts, and inferred by Rayner (1948) to occur in pholidophorids.

It is clear that the upper part of the cranial fissure was closed in *Ichthyokentema*, the supra- and epioccipital having extended forwards into the otic region so that the upper part of the posterior semicircular canal was enclosed in the epioccipital (Griffith & Patterson 1963, pl. 3, fig. 8, p.s.c; figure 149, psc.), as in leptolepids and teleosts. But this did not have the same consequence as in leptolepids and teleosts, shifting of the ossification centre of the pterotic to a position above the hyomandibular facet, since the facet in *Ichthyokentema* (fhm, figure 150) is a deep fissure, cartilage-filled in life, which clearly marks the junction of two or more bones and does not lie in the centre of the pterotic, as does the teleostean and leptolepid hyomandibular facet (figures 74, 89, 92). The facet in *Ichthyokentema* agrees with those of pholidophorids, *Amia*, caturids, parasemionotids, etc. (figures 68, 83, 84, 103, 109), and as in those forms its outer border must be formed by the sphenotic, the posterior boundary of that bone being wrongly shown in the 1963 paper (figs 2, 3). The ossification centre of the pterotic of *Ichthyokentema* has presumably shifted from the primitive position, in the dorso-lateral shoulder of the otic capsule,

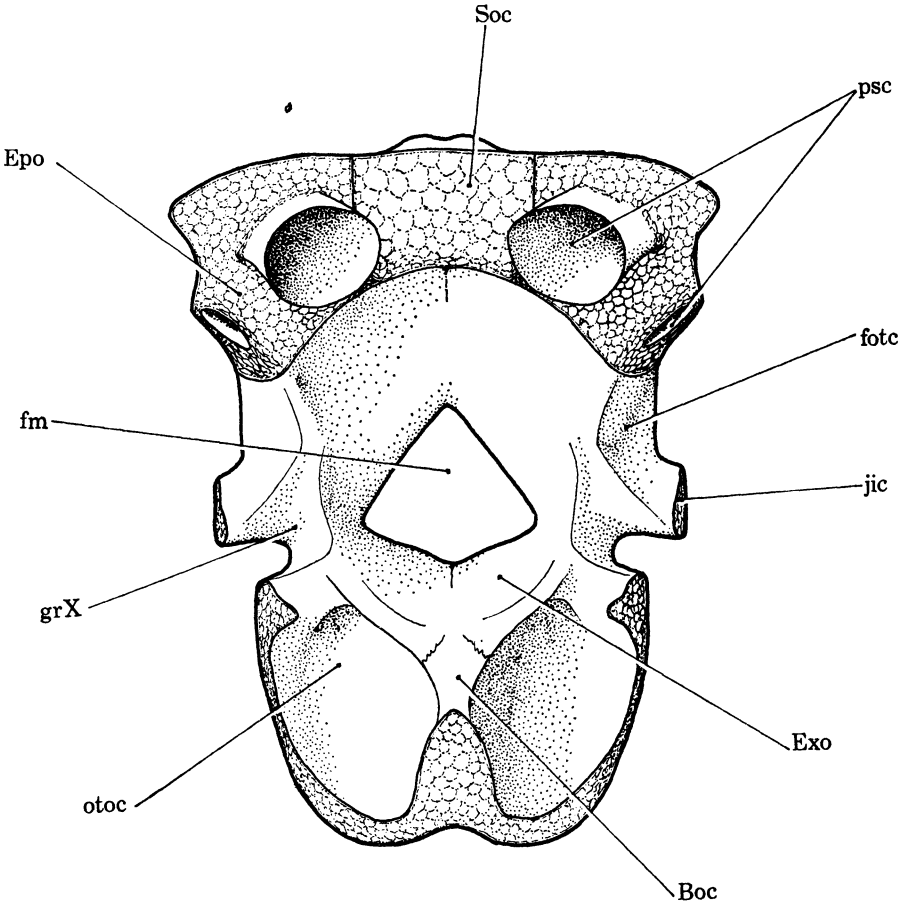


FIGURE 149. *Ichthyokentema purbeckensis* (Davies). Restoration of occipital ossifications in anterior view, based mainly on P.45039 and P.44934. (Magn. × 15 approx.)

and may lie in the floor of the post-temporal fossa, not having moved so far laterally as in leptolepids and teleosts, perhaps because there is no deep subtemporal fossa.

Regarding the supravagal portion of the cranial fissure in *Ichthyokentema*, amongst the material there are three isolated occiputs, interpreted in 1963 as being merely broken away from the remainder of the braincase. Figure 149 is based on the most complete of these specimens, with additions from others: all three show the same notch (gr X) for the vagus nerve, with a vertical, perichondrally lined surface (fotc) above it. Comparison with pholidophorids and primitive leptolepids (figures 45, 51) shows that this surface represents the supravagal portion of the cranial fissure, and that *Ichthyokentema* agrees with the Sinemurian *Leptolepis* in the development of the fissure: it is open and perichondrally lined from the lower margin of the epioccipital down to the vagus canal. This region is crushed in all the intact braincases of *Ichthyokentema*, but the perichondrally lined anterior face of the fissure is visible in P.45032, an isolated fragment of the otic region, and the line of the fissure is visible in P.45035, an incomplete occiput and otic region. The vertical surface dorso-lateral to the vagus notch (jic, figure 149) obviously met the intercalar, and as in pholidophorids and the Sinemurian *Leptolepis* that bone must have had an endochondral component beneath the small membrane bone outgrowths on its posterior surface. I think it unlikely that the anterior face of the intercalar was perichondrally lined, as it is in pholidophorids and the Sinemurian *Leptolepis*, since the anterior margin of the bone can only be inferred from a change of texture in the intact braincases, implying fusion with the otic ossifications.

Beneath the vagus notch, the upper part of the anterior margin of the exoccipital appears to be intact in the specimen shown in figure 149 and is without perichondral lining, implying that the subvagal part of the fissure was closed, but that the exoccipital had not extended forwards beyond the line of the fissure, as in *Pholidophorus germanicus* and *P. macrocephalus*.

The occipital ossifications of *Ichthyokentema* are therefore more primitive in structure than was previously supposed, and comparison with pholidophorids and the Sinemurian *Leptolepis*, in which the supravagal portion of the cranial fissure and an endochondral intercalar are retained, shows that the exoccipital could not have extended forwards in the way shown in our 1963 restorations (as stated, the exoccipital/pterotic suture could not be seen: Griffith & Patterson 1963, p. 13), where it includes the glossopharyngeal foramen. The area in front of the vagus canal, shown as part of the exoccipital in the 1963 restorations, must therefore be some other bone. It might be the lower part of a large pterotic, as in the Callovian *Pholidophorus* (figure 71), or an opisthotic, as in *P. bechei*, *P. germanicus* (figures 45, 46) and other primitive actinopterygians. The material is too imperfect for certainty, but there are indications in P.45032 that both bones (pterotic, opisthotic) were present. Figures 150 and 151 show the ossification pattern of *I. purbeckensis* as I now interpret it, drawn within the outlines of the 1963 restorations.

The other major correction to the 1963 account of *Ichthyokentema* concerns the extent of the basisphenoid. In well ossified specimens it is clear that the upper surface of the parasphenoid beneath the orbit is coated with substitution bone which roofs the palatine canals, forms a median crest, and rises anteriorly into a process (shown in 1963 in fig. 2) which was joined to the lateral ethmoids by cartilage. The short parabasal canals, containing the internal carotids and the palatine nerves, are also roofed by substitution bone, not by the parasphenoid as they were said to be in 1963, and this part of the basisphenoid (the sphenoid 'bolster') extends out to the tip of the upper surface of the dermal basipterygoid process and back into the floor of the

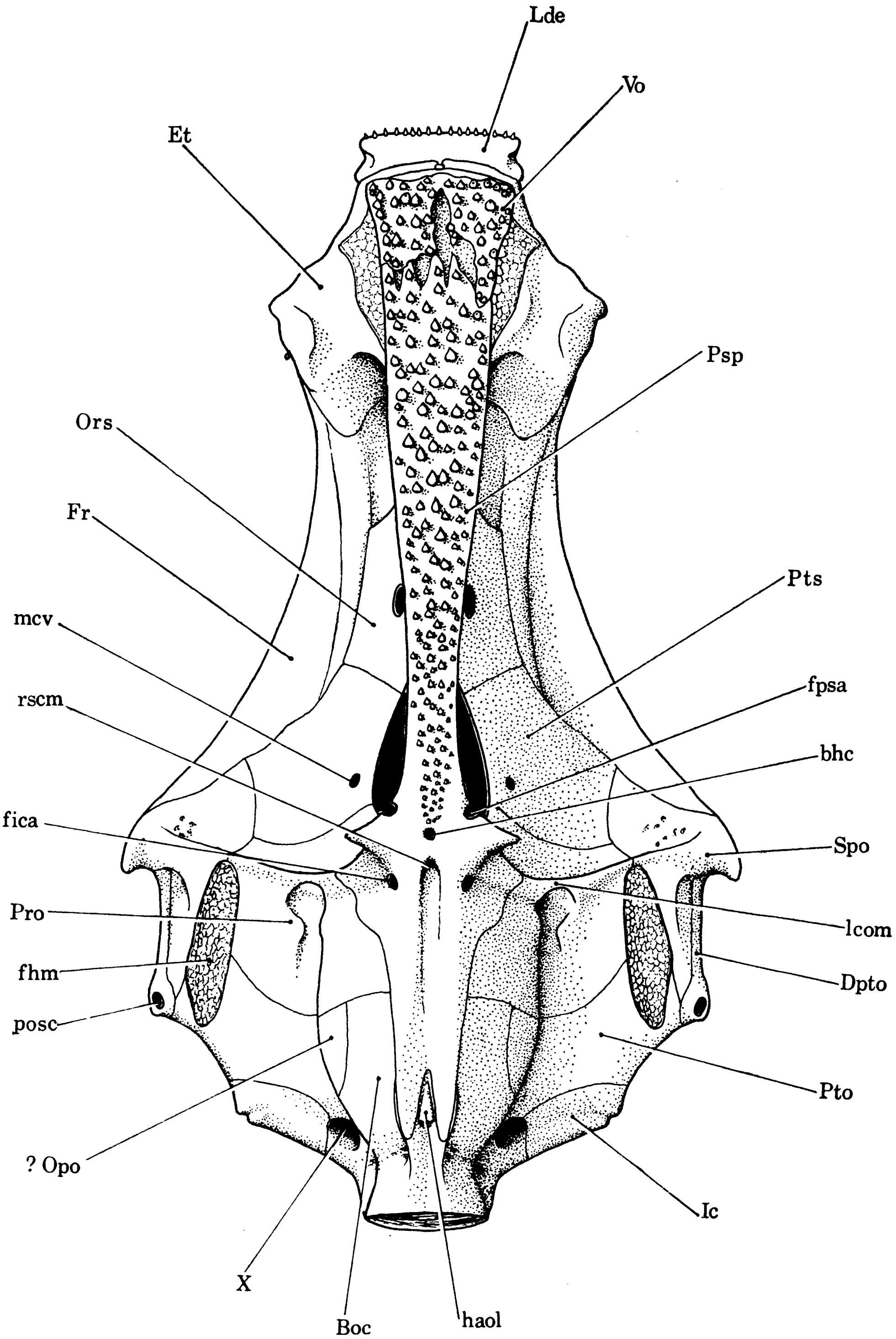


FIGURE 150. *Ichthyokentema purbeckensis* (Davies). Restoration of braincase in ventral view, modified from Griffith & Patterson (1963, fig. 3). (Magn. × 10 approx.)

myodome, enclosing the upper part of the bucco-hypophysial canal. It is not possible to say whether the endoskeletal floor of the myodome was complete, or whether it contained a fenestra ventralis myodomus lined by the parasphenoid, as in pholidophorids, but isolated parasphenoids lack the crest on the upper surface of the parasphenoid which occurs in pholidophorids and leptolepids (figures 142, 143) where there is such a fenestra.

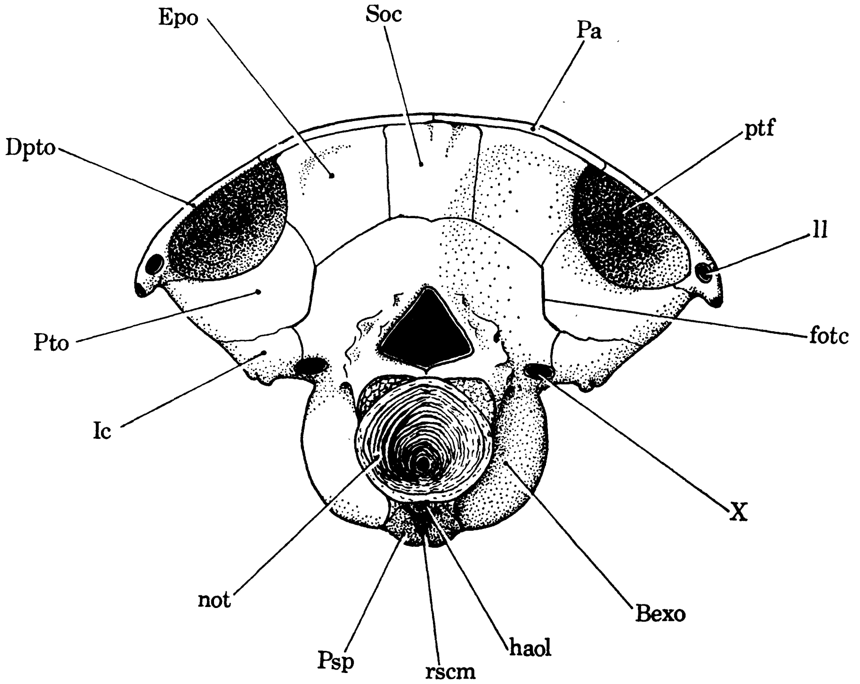


FIGURE 151. *Ichthyokentema purbeckensis* (Davies). Restoration of braincase in posterior view, modified from Griffith & Patterson (1963, fig. 4). (Magn. × 10 approx.)

Structures which were not described or whose significance was not recognized in 1963 include a small cup-like housing for the aortic ligament beneath the basioccipital (haol, figure 150); paired canals through the parasphenoid beneath the orbit for the anterior branches of the palatine nerves; a tongue-like antero-lateral process of the frontal which overlies the lateral ethmoid; the descending lamina of the frontal, which is of leptolepid or teleostean type, passing out to the postorbital process postero-laterally (cf. p. 547); the fact that the anterior semicircular canal was bone-enclosed throughout its course; a deep, median groove on the underside of the posterior part of the parasphenoid, ending in a pit (rscm, figure 150) close behind the opening of the bucco-hypophysial canal and resembling the housing of the subcephalic muscles in pholidophorids and other primitive actinopterygians (cf. p. 535); and a cone of dense tissue lining the deep notochordal pit (not, figure 151). I have made thin sections of centra of *Ichthyokentema*, which are composed of tissue resembling that lining the notochordal pit, and I am uncertain whether the tissue is notochordal, as in pholidophorids, or osteoid, as in leptolepids: the fact that the centra are perfect cylinders, not constricting the notochord in any way (Griffith & Patterson 1963, fig. 12), and their fibrous texture and colour in the complete fishes suggest that the centra and the tissue lining the notochordal pit are notochordal, as in pholidophorids.

With the above amendments to our 1963 account, the braincase of *Ichthyokentema* can now be compared with those of pholidophorids and leptolepids. In 1963, we found that the braincase of *I. purbeckensis* differed from that of *Pholidophorus bechei*, then incompletely known, in having no aortic groove or canal beneath the basioccipital and a stouter basisphenoid pedicel. The first of these differences remains, and *Ichthyokentema* also lacks the foramina for the occipital arteries which are found in the basioccipital of all pholidophorids: in both these features it is more advanced than the pholidophorids. But in *Ichthyokentema* the housing of the aortic ligament (haol, figure 150) lies well in front of the occipital condyle, as in pholidophorids, the pit interpreted as for the insertion of the subcephalic muscles (rscm, figure 150) lies close behind the bucco-hypophysial canal, in the same position as in *P. bechei* alone amongst pholidophorids, and the myodome does not extend into the basioccipital. These primitive features show that the cause of the loss of the aortic canal and occipital artery foramina in *Ichthyokentema* was not the same as in leptolepids, where it is associated with the development of a posterior opening of the myodome (p. 543).

The basisphenoid of *Ichthyokentema* is now known to be more extensive than that of any pholidophorid. *P. bechei* is closest to *Ichthyokentema*, retaining a thin layer of substitution bone over the orbital part of the parasphenoid, and rudiments of the endoskeletal basipterygoid process and myodome floor.

The comparison between *Ichthyokentema* and pholidophorids could now be considerably extended, with increased knowledge of the latter, but this does not seem necessary. In the summary below (p. 562) it is shown that the pholidophorids are linked with leptolepids and teleosts by seven specializations in the braincase: extension of the myodome into the basioccipital; the form of the intercalar, with a strut across the large subtemporal fossa; the median anterior myodome terminating in an anterior myodome bone; the presence of a median mesethmoid; the median vomer; the presence of paired lateral dermethmoids in addition to premaxillae; and the very large dermal basipterygoid process, its base pierced by a canal for the efferent pseudobranchial artery. In *Ichthyokentema* the condition of the anterior myodome is unknown, but of the six remaining features only two are definitely present, the median vomer and the lateral dermethmoids (figure 126). A mesethmoid may have been distinct in early ontogeny, and an efferent pseudobranchial foramen is incipient, being enclosed in the base of the short basipterygoid process in some individuals (Griffith & Patterson 1963, p. 13). The intercalar of *Ichthyokentema* probably resembled those of parasemionotids (figure 96) or *Pachycormus* (figure 106), but lacked a perichondral covering anteriorly. The small myodome of *Ichthyokentema* is particularly significant, since the long notochordal canal shows that restriction of the myodome to the prootics is primary, not due to secondary reduction as it is in some teleosts. These indications that *Ichthyokentema* is less closely related to the teleosts than are the pholidophorids are corroborated by the extensive basisphenoid, bone-enclosed anterior semicircular canal, thick endochondral bone of the braincase, toothed lateral dermethmoids, broad, extensively toothed parasphenoid and vomer, etc. All these facts are consonant with Griffith & Patterson's conclusion that *Ichthyokentema* is more primitive than the pholidophorids.

Characters in which *Ichthyokentema* is more advanced than primitive pholidophorids include partial closure of the cranial fissure, involving extension of the supra- and epioccipital into the otic region and a shift in the ossification centre of the pterotic, loss of the aortic groove and occipital artery foramina, confluence of the post-temporal fossa and fossa bridgei, enlargement of the optic fenestra so that it included the oculomotor nerve, the relatively long posterior part of the parasphenoid, and the teleostean type of descending lamina on the frontal. Only one of these specializations is unique to the teleostean lineage, the shift in the ossification centre of the pterotic, and in *Ichthyokentema* this has not taken place in the same way as in teleosts. On the evidence of the braincase, I conclude that *Ichthyokentema* is more closely related to the pholidophorids and teleosts than any other form discussed here, but that it diverged from a pre-pholidophorid ancestor.

12. GENERAL SUMMARY

(*a*) *Trends in the pholidophorid and leptolepid braincase*

In this paper the braincase has been partially or completely described in six pholidophorids (*Pholidophoroides limbata*, *Pholidophorus bechei*, *P. germanicus*, *P. minor*, a Callovian *Pholidophorus* and *P. macrocephalus*) and four leptolepids (a Sinemurian *Leptolepis* sp., *L. coryphaenoides*, a Callovian *Leptolepis* and *L. dubia*). The structure of the various regions of the braincase in these forms is summarized in §§4(*k*)(i), 5(*k*)(i), 6(*a*), 7(*m*)(i), 8(*j*)(i), 9(*a*) and 10(*a*), and this information will only be further abstracted here in the form of a list of trends. It would be premature to propose a phylogenetic scheme for these species solely on evidence from the braincase. Among the ten species, *P. limbata* and *P. minor*, though incompletely known, may be the most primitive (uninterrupted cranial fissure in both; probable absence of a strut across the subtemporal fossa in *P. minor*). *P. germanicus*, the Callovian *Pholidophorus* and *P. macrocephalus* may form a related group, characterized by large size, a hypertrophied subtemporal fossa, closure of the supraoccipital and subvagal portions of the cranial fissure, and a broad, almost flat skull roof. *P. bechei* is more primitive than the three large pholidophorids in many ways, and it agrees with the leptolepids (especially the Sinemurian species) in several features, including the moderate subtemporal fossa, slender parasphenoid, convex skull roof, form of the known parts of the mesethmoid, presence of paired fenestrae in the roof of the myodome, and so on. The four leptolepids form a stratigraphic series, and according to available facts about the braincase this could correspond to a phylogenetic series, at the base of which *P. bechei* could stand.

Because the Sinemurian *Leptolepis* is in many ways intermediate between pholidophorids and other leptolepids, it is difficult to speak of differences between the two groups (but see the end of this subsection) and more convenient to list those trends which are evident in a morphological series such as: *P. limbata*, *P. bechei*, *P. germanicus*, Sinemurian *Leptolepis*, *L. coryphaenoides*, Callovian *Leptolepis*. It is, of course, not implied that this is a phylogenetic series. In such a series, the following trends are found:

(1) Decrease in the thickness and extent of the cartilage-bone parts of the braincase, and reduction in the size of the medullary spaces within this bone. Primitive pholidophorids are similar to palaeoniscoids in the structure of the endochondral bone, while advanced leptolepids are teleost-like. Reduction in the extent of the endochondrally ossified parts of the braincase involves especially the basisphenoid in the floor of the orbit and myodome, and increase in the size of the anterior dorsal fontanelle, with loss of the bony lining of the anterior semicircular canal and utricular recess and the supracerebral part of the orbitosphenoid.

(2) Replacement of cartilage-bone by membrane bone, and the development of membrane bone outgrowths from the cartilage bones. The first of these trends is evident in the orbitosphenoid and pterosphenoid, in the basisphenoid pedicel, in the medial wall of the trigeminofacial chamber and the antero-ventral part of the prootic, in the anterior part of the supraoccipital and the lower part of the basioccipital. Membrane bone outgrowths from the cartilage bones develop on the lateral surface of the prootic, forming the outer wall of the jugular canal

and the prootic part of the strut across the subtemporal fossa, from the intercalar, on the dorsal surface of the sphenotic, pterotic, epioccipital and supraoccipital where these contact the roofing bones, and on the orbital surface of the prootic and pterosphenoid, forming the pterosphenoid pedicle.

(3) Retention of sutures between the cartilage-bones in the adult braincase. This is one of the few trends with an obvious functional explanation – continued growth – and is characteristic of the large pholidophorids as well as the more advanced leptolepids. Primitive leptolepids still fused all the bones in the braincase, terminating growth.

(4) Closure of the cranial fissure, stepwise from above and below, with attendant changes in the ossification pattern. From above, the supraoccipital and then the epioccipital extended forwards into the otic region, the epioccipital displacing the pterotic so that the latter came to ossify from a centre above the hyomandibular facet and external semicircular canal. From below, the subvagal and then the supravagal portions of the exoccipital extended into the otic region, the first involving loss of the opisthotic, the second loss of the endochondral portion of the intercalar.

(5) Fusion between endoskeletal bones and dermal bones early in ontogeny. This involves the pterotic and dermopterotic in leptolepids (consequent upon the shift in the ossification centre of the pterotic, so that it lies directly beneath the ossification centre of the dermal bone), and the mesethmoid and the lateral dermethmoids or rostro-dermethmoid of some leptolepids.

(6) Reduction in the depth of the notochord pit in the basioccipital. This is exactly correlated with increase in length of the occipital portion of the myodome.

(7) Replacement of notochordal calcification by dense osteoid tissue in the notochordal pit. Osteoid tissue is found only in leptolepids, but some notochordal tissue persists in some leptolepids.

(8) Reduction in the aortic canal or groove beneath the basioccipital, with loss of the foramina of the occipital arteries and posterior migration of the housing of the aortic ligament. This trend is closely correlated with loss of the floor of the occipital portion of the myodome.

(9) Increase in relative size of the sphenotic, at the expense of the upper part of the prootic and pterosphenoid, so that the sphenotic comes to house the foremost part of the anterior semicircular canal and form the anterior part of the hyomandibular facet, while the pterosphenoid ceases to contribute to the roof of the neurocranium, and the prootic ceases to line a part of the post-temporal fossa.

(10) Increase in size of the post-temporal fossa, followed by fenestration and eventual loss of the partition separating it from the fossa bridgei, so that the latter becomes a functional part of the post-temporal fossa, receiving trunk musculature.

(11) Increase in size of the dilatator fossa, which extends on to the dermopterotic in leptolepids and becomes separated from the area of origin of the levator arcus palatini muscles.

(12) Development of a secondary, membrane bone wall over the grooves for the jugular vein and orbital artery on the lateral surface of the prootic in leptolepids, with the formation of separate foramina for the jugular vein, orbital artery and hyomandibular nerve, and the eventual formation of the prootic part of the strut across the subtemporal fossa by the wall of the jugular canal.

(13) Decrease in the size of the palatine fenestra in the roof of the myodome, producing a palatine foramen. This change seems to be due to retreat of the geniculate ganglion from the trigeminofacial chamber into the facial canal.

(14) Shifting of the exit of the profundus nerve from close to the trigeminal nerve to close to the oculomotor nerve.

(15) Migration of the oculomotor foramen from the prootic/pterosphenoid suture into the prootic.

(16) Reduction and eventual loss of the spiracular canal, with initial reduction of the spiracular groove on the parasphenoid and prootic, and reduction in size of the spiracular canal relative to the otic nerve canal which joins it, until in advanced leptolepids the spiracular canal is replaced by the otic nerve canal, now opening into the dilatator fossa rather than into the fossa bridgei, its primitive position.

(17) Disappearance of the articular area for the first suprapharyngobranchial on the prootic.

(18) Migration of the articulation of the first infrapharyngobranchial from the anteroventral corner of the prootic on to the ascending process of the parasphenoid.

(19) Loss of the ossified medial wall of the lateral cranial canal, followed by reduction and loss of the diverticulum in the epioccipital which represents the remains of the canal.

(20) Loss of the basal sclerotic bone, which is found in pholidophorids but not in leptolepids.

(21) Change in the ossification pattern of the sclerotic ring from four segments to two segments.

(22) Reduction in the breadth of the rostral and the enclosed portion of the ethmoid commissural sensory canal; reduction of the ethmoid commissure to a pit-line.

(23) Change in form of the lateral dermethmoid from a toothed, plate-like bone to a complex, toothless bone which has two pairs of lateral processes and forms a prominent rostrum; change in form of the foremost part of the mesethmoid, with the development of a vertically keeled rostrum.

(24) Fusion between the rostral and the lateral dermethmoids at successively earlier ontogenetic stages in leptolepids.

(25) Fusion between the mesethmoid and the lateral dermethmoids or rostro-dermethmoid at successively earlier ontogenetic stages in leptolepids.

(26) Change in form of the vomerine tooth patch from transverse (pholidophorids) to longitudinal (leptolepids); loss of vomerine teeth.

(27) Fusion between the vomer and the ventral ethmoid in some leptolepids.

(28) Reduction in the breadth of the parasphenoid; reduction and eventual loss of parasphenoid teeth.

(29) Increase in the relative length of the posterior portion of the parasphenoid.

(30) Loss of the endoskeletal floor of the myodome, eventually producing a posterior opening into the myodome, beneath the basioccipital and between the posterior processes of the parasphenoid.

(31) Loss of the endoskeletal walls of the parabasal canals or increase in size of the orbital openings of those canals, so that they may become confluent with the ascending canals for the carotid arteries in the basisphenoid, followed by the development of a ventral compartment to the myodome, containing the internal rectus muscles and recognizable externally as a bulge beneath the otic portion of the parasphenoid.

(32) Posterior migration of the point of origin of the subcephalic muscles on the parasphenoid.

(33) Loss of ganoin from and thinning of the dermal roofing bones.

(34) Reduction in the anterior and posterior parts of the descending lamina beneath the supraorbital sensory canal, with the development of a lamina beneath the frontal passing out to the postorbital process.

(35) The development of an angle in the temporal sensory canal in the dermopterotic, so that its posterior part becomes almost transversely directed.

(36) Reduction in the number of branches given off by the sensory canals in the skull roof; reduction in the middle pit-line groove.

In a few of the listed trends one can contrast a primitive condition characteristic of all pholidophorids with an advanced condition characteristic of all leptolepids. Such trends include the replacement of notochordal calcification in the notochordal pit by osteoid tissue (correlated with a change in centrum formation, and more appropriately considered with the axial skeleton in the third paper in this series); the development of a membrane bone cover over a part of the jugular groove, separating a foramen for the hyomandibular nerve from that of the jugular vein; and the development of a rostrum, with a narrow rostral and complex lateral dermethmoids. These characters could be used to define the lower boundary of a leptolepid grade. Other trends which might fall in this category include the shift in the ossification centre of the pterotic and fusion between this bone and the dermopterotic; loss of the basal sclerotic bone; the form of the vomerine tooth patch; the development of the posterior opening of the myodome; and the form of the descending lamina on the frontal, but in each case the structure is not yet known in the Sinemurian *Leptolepis*, which is intermediate between pholidophorids and other leptolepids in so many trends.

(*b*) *Comparison with teleosts*

The preceding section contains a list of 36 trends in which the braincases of some or all leptolepids are more advanced than those of pholidophorids. Some of these trends involve major structural changes, others only minor adjustments. Almost without exception, the leptolepid condition in each of these trends is the one found in generalized living teleosts, and the leptolepids exhibit at least 16 features of the braincase which are unique specializations shared by them and teleosts alone. These features include the thickness and extent of cartilage bone; the extent to which membrane bone replaces and extends from cartilage bone; the form of the pterotic and fusion between this bone and the dermopterotic; the form of the sphenotic; separation of the dilatator fossa from the area of origin of the levator arcus palatini by a crest; the development of a membrane bone cover over the jugular groove; the form of the prootic/intercalar strut across the subtemporal fossa; loss of the spiracular canal; the form of the lateral dermethmoids and mesethmoid, fusion of the lateral dermethmoid with the rostral and with the supraethmoid; fusion between the vomer and ventral ethmoid; development of a ventral compartment and a posterior opening of the myodome; and the course of the temporal sensory canal in the dermopterotic. This is a most convincing demonstration of the relevance of the leptolepids to the origin and deployment of the existing teleostean cohorts.

Nevertheless, there are a few features found in the braincase of one or another primitive living (or fossil) teleost which recall the condition in pholidophorids rather than leptolepids. Such features include the hypertrophied subtemporal fossa of elopoids, osteoglossids and ichthyodectids; contributions to the floor of the post-temporal fossa from the prootic in elopoids, some characins and *Chanos*, from the pterosphenoid in *Elops* and *Notelops*, and from the pterosphenoid and orbitosphenoid in *Megalops*; junction of the pterosphenoid and prootic medial to the sphenotic in *Elops*, *Megalops* and *Albula*, excluding the sphenotic from the cavity housing the anterior semicircular canal; the presence of a transient opisthotic in the ontogeny of *Heterotis*; the possibility that the otophysic connexion of clupeomorphs and mormyroids arose while the subvagal portion of the cranial fissure was still open; the presence of a basal sclerotic bone in ichthyodectids; the paired vomer of *Hiodon* (as in holosteans, but not pholidophorids); the extensive patch of unspecialized teeth on the parasphenoid of *Arapaima*; and the short posterior portion of the parasphenoid in *Denticeps* and trachichthyids. So far as I know, this list includes all those features of the teleostean braincase which might be interpreted as resembling some pholidophorid rather than leptolepids such as *L. coryphaenoides* and the Sinemurian species.

Some might conclude from this list of primitive features that such groups as the elopoids and osteoglossomorphs, which figure in it most frequently, are more closely related to pholidophorids than to leptolepids. I believe that such hypotheses are easily refuted, for they imply that the group concerned has independently evolved all those specializations in which leptolepids differ from pholidophorids and agree with all groups of primitive teleosts. At least sixteen such specializations are listed above, all unique to leptolepids and teleosts, and other specializations, not unique, include the closure of the epioccipital and supravagal portions of the cranial fissure, with change in form of the epioccipital and loss of the endochondral intercalar; the development of perichordally ossified centra; withdrawal of the geniculate ganglion into the cranial cavity; enclosure of the oculomotor foramen in the prootic; loss of the endoskeletal articulation of the first infrapharyngobranchial; loss of the lateral cranial canal; and change in the form of the descending lamina of the frontal. It is clearly unparsimonious to assume independent acquisition of so many specializations, and it must be accepted that on the evidence of the braincase the living teleosts form a monophyletic group whose origins lie within the leptolepid grade, not the pholidophorid.

Although the pholidophorids are more primitive than leptolepids and teleosts in so many ways, all pholidophorids are related to the teleosts by several unique specializations of the braincase, in addition to those features of the skull and postcranial skeleton which indicate such relationships. These teleostean specializations of the pholidophorid braincase are:

(1) Extension of the myodome into the basioccipital (condition unknown in *Pholidophoroides limbata*; present in all other pholidophorids).

(2) The intercalar is of characteristic form, lacking the antero-ventral outgrowth over the lateral wall of the saccular chamber which is found in caturids and amiids and having an anterior outgrowth which meets a process from the prootic, forming a bridge across the subtemporal fossa (condition unknown in *P. limbata*; intercalar unknown in *P. minor*, but there is no process on the prootic, suggesting that the strut may have been absent).

(3) There is a median anterior myodome, terminating in a conical anterior myodome bone (condition unknown in *P. limbata*, *P. minor*, *P. bechei* and the Callovian species).

(4) There is a median mesethmoid (originating from dorsal supraethmoid and ventral ethmoid centres in *P. macrocephalus* and probably also in *P. bechei*) which remains separated from the lateral ethmoids by a suture (condition unknown in *P. minor* and the Callovian species).

(5) There is a median vomer (condition unknown in *P. limbata*, *P. minor*, *P. bechei* and the Callovian species).

(6) There are paired lateral dermethmoids, lining the anterior part of the nasal pit and projecting beyond the rostral in a rudimentary rostrum which separates the premaxillae (condition unknown in *P. minor* and the Callovian species).

(7) There is a very large dermal basipterygoid process on the parasphenoid, its base pierced by a canal for the efferent pseudobranchial artery (condition unknown in *P. limbata* and *P. minor*).

(*c*) *Comparison with other groups*

In the preceding section it is shown that pholidophorids are related to leptolepids and teleosts by several unique specializations of the braincase, in addition to those features of the rest of the skeleton which are already known to indicate such relations. The pholidophorids, leptolepids and teleosts therefore form a monophyletic group, and it is only necessary to compare the braincase of primitive pholidophorids with those of other groups.

Among the specializations of the braincase relating primitive pholidophorids to teleosts, three are known elsewhere. *Ichthyokentema* has a median vomer and lateral dermethmoids (and also an incipient efferent pseudobranchial foramen in the parasphenoid). These features, and others in the rest of the skeleton, show that *Ichthyokentema* is more closely related to the pholidophorid-teleost assemblage than any other fish in which the braincase is known. *Pachycormus* has lateral dermethmoids of a peculiar type, fused with the rostral, as in leptolepids, and may be related to teleosts because of this. A median vomer occurs in some semionotids, in pycnodonts and in *Bobasatrania*, but in these forms it is developed in conjunction with a crushing dentition. There is an efferent pseudobranchial foramen in the parasphenoid of *Dapedium*.

Disregarding these teleostean specializations, the pholidophorid braincase shows a number of other specializations which appear to be characteristic of the holostean grade. These include:

(1) The cup-like housing of the aortic ligament, also found in *Ichthyokentema*, some caturids, parasemionotids, *Dapedium* and *Pachycormus*. In more primitive forms the ligament inserted on the median septum at the bifurcation of the aortic canal.

(2) The development of a small post-temporal fossa, as in parasemionotids. In *Perleidus* there is a rudimentary fossa; in *Amia* and caturids the fossa has the same relations but is larger; in *Ichthyokentema*, *Pachycormus* and *Dapedium* it is confluent with the fossa bridgei.

(3) The development of a well marked subtemporal fossa (within the arch of the external semicircular canal), housing the adductor muscle of the operculum and distinct from the area of origin of the adductor hyomandibulae muscle. This is also found in caturids, semionotids, *Pachycormus* and parasemionotids; in more primitive forms the dorsal hyoid constrictor muscle is not yet differentiated into these two portions.

(4) The development of a dilatator fossa, distinct from the area of origin of the levator arcus palatini muscle. This is also found in living holosteans, caturids, semionotids and *Pachycormus*; in parasemionotids and *Perleidus* there is an undifferentiated area giving origin to both muscles.

(5) The hyomandibular facet is almost horizontal, as in living holosteans, caturids, semionotids, *Pachycormus* and parasemionotids. In *Perleidus*, *Australosomus*, palaeoniscoids and living chondrosteans the facet is strongly inclined antero-ventrally.

(6) Reduction of the lateral commissure to a slender bar or strut, with a common opening for the jugular vein, hyomandibular nerve and orbital artery behind it. This is also found in *Lepisosteus*, caturids, semionotids, *Pachycormus*, *Ichthyokentema* and parasemionotids; *Amia* has a separate foramen for the orbital artery, while more primitive forms have a massive lateral commissure, usually with three separate posterior openings.

(7) The facial canal opens into the jugular canal, beneath or behind the lateral commissure, not into the orbit, and the trigeminofacial chamber has a prepalatine floor. This is also found in caturids, semionotids and *Pachycormus*.

(8) The development of a lateral cranial canal, separate from the fossa bridgei and with anterior and posterior openings into the cranial cavity. A lateral cranial canal of this type is found in caturids and *Dapedium*, and possibly in parasemionotids. *Lepisosteus* and *Lepidotes* have the canal represented only by a diverticulum of the cranial cavity, as in some leptolepids. More primitive forms have only an anterior opening (*Perleidus*) or a posterior opening (palaeoniscoids), and the canal is more or less confluent with the fossa bridgei.

(9) A basal sclerotic bone, found in *Lepidotes* and *Caturus* as well as in pholidophorids, is probably more widely distributed and must be a relic of an original complete bony cup around the eyeball.

(10) The opisthotic is much reduced. This bone is lost in living holosteans and in *Lepidotes*, is moderately large in parasemionotids, caturids and *Pachycormus*, and was primitively larger, as in *Perleidus*.

(11) There is a moderately well developed endoskeletal rostrum, in front of the postnasal wall, with a low nasal septum, as in *Amia*, caturids, semionotids, parasemionotids and *Australosomus*. In palaeoniscoids there is little or no endoskeleton developed in front of the postnasal wall. In living chondrosteans and saurichthyids the rostrum is hypertrophied.

(12) The rostral bone is reduced from the large cup-like bone ('postrostral') found in palaeoniscoids and *Perleidus*. The bone is similarly reduced in *Pachycormus* and *Dapedium*, while in living holosteans, caturids, *Lepidotes* and parasemionotids it is reduced to a tube around the ethmoid commissural sensory canal.

(13) The nasal process of the premaxilla (assuming that the lateral dermethmoid of pholidophorids, *Ichthyokentema* and *Pachycormus* is homologous with that process) is developed in pholidophorids as in parasemionotids, *Dapedium*, *Acentrophorus* and some caturids. In living holosteans, *Lepidotes*, *Semionotus* and some caturids the process is longer, while in *Perleidus* it is rudimentary.

(14) Differentiation of the vomer, as in living holosteans, caturids, pachycormids, semionotids, parasemionotids, saurichthyids, etc.

(15) Extension of the parasphenoid across the fissura oticalis ventralis, as in *Perleidus*: the parasphenoid is more extensive posteriorly than in primitive pholidophorids in all other 'holosteans', and is only shorter in palaeoniscoids and *Australosomus*.

(16) Development of a large dermal basipterygoid process, as in semionotids and *Lepisosteus*. The process is smaller in parasemionotids and some caturids, and is lost in *Amia*, some caturids and *Pachycormus*.

(17) Development of a large myodome, with a fenestra ventralis myodomus (behind the hypophysis) in its floor, as in *Amia*, some caturids, *Lepidotes*, and possibly some parasemionotids. In more primitive forms with a myodome, the endoskeletal floor of the chamber is complete.

(18) Enclosure of an internal carotid foramen within the ascending process of the parasphenoid, as in *Dapedium*, *Pachycormus* and *Boreosomus*.

In addition to the above characters, which are more or less widely distributed among holostean level actinopterygians, the pholidophorid braincase exhibits two specializations of more restricted or less coherent distribution:

(1) Occlusion of the notochordal canal in the basioccipital by a cone of thick notochordal

calcification. A thinner lining of this tissue is found in *Australosomus* (and probably in all pholidopleurids) and perhaps in some caturids (*Caturus chirotes*). The same tissue may occur in other forms in which chordacentra develop (pachycormids, caturids, the semionotid *Tetragonolepis*), but has not been observed.

(2) A junction between the otic nerve canal and the spiracular canal. This also occurs in *Boreosomus*, *Australosomus*, *Lepidotes* and probably in *Pachycormus*.

Finally, the pholidophorid braincase retains a series of primitive actinopterygian characters, typical of palaeoniscoids. These include:

(1) The proportions and relief of the braincase, with a short occipital region, comprising 10 % or less of the total length, the maximum breadth and depth about equal, and strong superficial relief, so that the course of the semicircular canals is visible externally and the external canal runs in a prominent horizontal ledge (cf. Nielsen's 'central palaeonisciform type'; 1949, p. 67). In shape, the pholidophorid braincase most closely resembles that of *Australosomus*.

(2) In the adult braincase all sutures are eliminated, and growth was terminated by fusion of the endoskeletal ossifications. This condition occurs in palaeoniscoids, *Australosomus*, *Perleidus*, parasemionotids, *Dapedium* and some caturids.

(3) The presence of an uninterrupted, perichondrally lined fissura otico-occipitalis. This is otherwise known only in palaeoniscoids and *Australosomus*. All other actinopterygians, including relatively primitive forms like *Perleidus*, have the fissure closed to some extent.

(4) The presence of an endoskeletal aortic canal. This is otherwise known only in palaeoniscoids, *Australosomus*, *Perleidus*, some parasemionotids and *Dapedium* (and also in *Polypterus*).

(5) There is only a single occipital nerve foramen, as in palaeoniscoids, *Australosomus*, *Perleidus* and some parasemionotids and caturids. In some *Perleidus*, parasemionotids and caturids a second occipital nerve becomes enclosed in the exoccipital during growth. In other groups one or more neural arches are incorporated in the exoccipital, together with their segmental nerves.

(6) There is a pair of foramina for the occipital arteries beneath the basioccipital. These are also found in palaeoniscoids, *Australosomus*, *Perleidus*, parasemionotids, semionotids, caturids and living holosteans.

(7) There is an endoskeletal articulation for the first suprapharyngobranchial, antero-dorsal to the vestibular fontanelle. The suprapharyngobranchial articulated with the braincase just behind the fontanelle in palaeoniscoids and *Australosomus*, in the same position as in living chondrosteans. In caturids and *Pachycormus* the articulation was placed as in primitive pholidophorids, and in *Perleidus* and parasemionotids the articulation was probably contained in the vestibular fontanelle.

(8) There is an endoskeletal articulation for the first infrapharyngobranchial, in an incisure between the ascending process of the parasphenoid and the posterior part of that bone. There is a similar articulation in palaeoniscoids, *Australosomus*, *Polyodon*, *Perleidus*, parasemionotids, semionotids, *Pachycormus* and caturids (except *Macrepistius*).

(9) The gasserian and geniculate ganglia were extracranial, as in palaeoniscoids, *Australosomus*, *Perleidus*, parasemionotids, semionotids and caturids.

(10) The trigeminal and facial canals originate in the cranial cavity, in front of the utricular recess, as in palaeoniscoids and *Australosomus*. In this feature pholidophorids are more primitive than *Perleidus*, parasemionotids and fossil and living holosteans, in which one or both canals originate in the utricular recess.

(11) There is a canal for the middle cerebral vein in the pterosphenoid, postero-dorsal to the trochlear canal, as in *Pteronisculus*, *Saurichthys*, *Perleidus*, parasemionotids, fossil holosteans and *Lepisosteus*.

(12) There is a canal for the anterior cerebral vein, as in *Pteronisculus*, *Australosomus*, *Acipenser*, parasemionotids, semionotids, some caturids, *Pachycormus* and *Amia*.

(13) The sclerotic ossifies in four sections, as in palaeoniscoids, *Chondrosteus*, *Bobasatrania* and *Dorypterus*. In *Australosomus*, living chondrosteans, pycnodonts, semionotids, caturids, pachycormids and living holosteans the sclerotic ossifies in two sections or fails to ossify. In perleidids and parasemionotids the sclerotic is still unknown. The three layers of the pholidophorid sclerotic – dermal and inner and outer perichondral – are also undoubtedly primitive, but comparative information is lacking for most fossil actinopterygians.

(14) There is a patent bucco-hypophysial canal in the parasphenoid, as in some palaeoniscoids, *Saurichthys*, *Perleidus*, parasemionotids, semionotids and some caturids.

(15) The pits in the parasphenoid interpreted as having housed the subcephalic muscles lie close behind the lower opening of the bucco-hypophysial canal. This condition is also found amongst actinopterygians in palaeoniscoids, *Perleidus*, parasemionotids, some caturids, *Ichthyokentema* and *Lepidotes*.

Abstracting these two lists, of 'holostean' and primitive actinopterygian features of the pholidophorid braincase, the first list suggests that pholidophorids, pachycormids, caturids, semionotids, parasemionotids and living holosteans form a monophyletic group, characterized by specializations of the hyomandibular facet (5), lateral commissure (6), rostral (12) and premaxilla (13). In the second list, characters 1, 3, 10 and 13 show that the pholidophorid braincase is in some ways more primitive than that of any holostean, or of *Perleidus* and *Australosomus*, and can only be derived from a palaeoniscoid type.

(*d*) *Anatomical conclusions*

(1) *Ossification patterns.* The fully ossified, sutureless braincase of primitive actinopterygians (palaeoniscoids, *Australosomus*, *Perleidus*, parasemionotids, pholidophorids, *Dapedium*, some caturids) is a feature of late ontogeny, terminating growth. In pholidophorids, *Perleidus*, parasemionotids and caturids this type of braincase results from the fusion of numerous endochondral ossifications. Common to all are the basioccipital, basisphenoid, orbitosphenoid (three bones which are median in the adult but may originate from paired centres), exoccipitals, intercalars (primitively endochondral bones), epioccipitals (a term introduced to replace 'epiotic' in most actinopterygians), pterotics, opisthotics, prootics, sphenotics, pterosphenoids (not certainly distinct in *Perleidus*) and lateral ethmoids. In addition, a supraoccipital is present in pholidophorids (and possibly in *Perleidus*) and there is a median supraotic in one caturid ('*Aspidorhynchus*', supraotic also present in *Lepidotes minor*).

A review of the ossification pattern of the actinopterygian neurocranium, especially the fact that teleosts, previously thought to have more bones in the braincase than any other fishes, lack the opisthotic and endochondral intercalar present in pholidophorids, and similarities between the braincase of palaeoniscoids, *Perleidus*, parasemionotids and pholidophorids, lead to the conclusion that a general hypothesis of loss of neurocranial ossification centres is preferable to one of increase or fragmentation in actinopterygian evolution (phylogenetic fusion appears to be without meaning in the neurocranium). The primitive actinopterygian neurocranium is assumed to have contained all those ossifications which are common to *Perleidus*, parasemionotids and pholidophorids, and in addition one or more zygals, found in some palaeoniscoids but lost in more advanced forms. At present, it is not possible to say whether a supraoccipital was primitively present, or whether the ptero- and orbitosphenoid were primitively separate. The opisthotic was primitively very large, the prootic and pterotic small.

From this primitive pattern, the pattern found in other actinopterygians can be derived by changes in the relative size of the bones and/or loss of bones, the causes of the latter being closure of the cranial fissure and regression in ossification or chondrification. New bones only appear under special conditions, such as the development of a rostrum (paired pre-ethmoids of *Amia* and pachycormids; median supraethmoid, ventral ethmoid and anterior myodome bones of pholidophorids and teleosts) and ossification of the taenia tecti medialis (supraotic). Fragmentation only occurs in conditions of extreme reduction in ossification (numerous ethmoid bones of some teleosts, double opisthotic of *Polyodon*, for example).

On this hypothesis, *Lepidotes* has lost the opisthotic, intercalar and epioccipital, *Lepisosteus* has lost these bones and the basisphenoid and lateral ethmoids, *Pachycormus* has lost the epioccipital, *Amia* has lost the pterotic, opisthotic and endochondral intercalar, and so on. The braincase of *Polypterus* can be interpreted on this hypothesis.

(2) *Cranial fissure.* The cranial fissure consists of two portions, differing in origin and fate, the fissura oticalis ventralis and the fissura otico-occipitalis. The fissura oticalis ventralis was always cartilage-filled, and primitively it lay close behind the hypophysis, at the junction of ossification in the parachordals and trabeculae. The fissure migrated posteriorly as a result of the development of the myodome, and has become confluent with the fissura otico-occipitalis except in most palaeoniscoids. Even when the two parts of the fissure become confluent, the cranial fissure is not a kinetic joint in actinopterygians. The fissura oticalis ventralis persists as the prootic/basioccipital suture in teleosts.

The fissura otico-occipitalis represents the persisting metotic fissure of the embryo. In palaeoniscoids, *Australosomus* and primitive pholidophorids it is perichondrally lined throughout, except for the vestibular fontanelle (anterior basicapsular fenestra of embryos) at its foot, which may be cartilage-filled. Pholidophorids and leptolepids provide a complete morphological sequence illustrating closure of the fissure in phylogeny, corresponding to successive stages of closure in their ontogeny by fusion of the otic capsule and occipital arch in cartilage. Closure proceeded stepwise from above and below, the two processes not being synchronized. From above, the section opposite the supraoccipital closed first, followed by the section opposite the epioccipital. From below, the section beneath the vagus canal closed first, followed by the section above the canal. Having closed in cartilage, the fissure may remain as a suture between two bones, or may be obliterated by extension of a bone across the line of the fissure. In pholidophorids and leptolepids, the latter was the dominant process, the supraoccipital, epioccipital and exoccipital extending forwards into the otic region. Consequences of this were the loss of the opisthotic and endochondral intercalar, and a shift in the ossification centre of the pterotic from the postero-dorsal shoulder of the otic capsule to a position above the external semicircular canal and hyomandibular facet, its position in teleosts. Parts of the fissura otico-occipitalis persist as a suture in some pholidophorids.

In *Perleidus*, parasemionotids, *Ichthyokentema* and *Pachycormus*, parts of the fissura otico-occipitalis survive in the primitive, perichondrally lined form. In *Ichthyokentema* the supra- and epioccipital parts of the fissure are obliterated by extension of these bones into the otic region, as in leptolepids. In *Perleidus*, parasemionotids and *Pachycormus* those parts of the fissure which are not perichondrally lined were closed in cartilage but persisted (or are inferred to have occurred in late ontogeny) as a suture, without extension of otic or occipital bones across the line of the fissure. The same is true of some groups in which the fissure is completely closed (caturids, and probably *Dapedium*). In *Lepidotes*, *Lepisosteus* and amiids the exoccipital has extended forwards into the otic region, as in leptolepids and teleosts, and this must be responsible for the absence of an endochondral intercalar and an opisthotic in these forms. In *Amia*, it is probable that the epioccipital ('epiotic') has extended forwards into the otic region, and the pterotic has been lost, while in *Lepidotes* and *Lepisosteus* it is probable that the pterotic ('epiotic') has extended back into the occipital region, and the epioccipital has been lost.

(3) In primitive actinopterygian braincases like those of palaeoniscoids, *Perleidus*, parasemionotids and pholidophorids, where sutures are obliterated and all cartilage is replaced by bone in full-grown individuals, the presence or absence of a fissura oticalis ventralis, a vestibular fontanelle and a complete aortic canal, and variations in the size of the anterior dorsal fontanelle are all ontogenetic features, without phylogenetic or taxonomic significance.

(4) There is no 'half-centrum' fused to the occipital condyle of primitive teleosts: the cone of osteoid tissue which fills the notochord pit in the basioccipital of these fishes has been mistaken for a 'half-centrum'.

(5) The teleostean post-temporal fossa incorporates the fossa bridgei of pholidophorids and more primitive actinopterygians, the partition between the two cavities having broken down at the pholidophorid level. The post-temporal fossa of *Dapedium*, *Ichthyokentema* and *Pachycormus* is also confluent with the fossa bridgei. The pre-epiotic pocket in the medial wall of the post-temporal fossa of elopiforms, *Chanos* and osteoglossids, and the pre-epiotic fossa of clupeoids and characoids is homologous with the shallow, postero-medial portion of the fossa bridgei of pholidophorids and primitive leptolepids.

(6) The pons moultoni of teleosts, a loop of bone on the inner face of the sphenotic which surrounds the anterior semicircular canal, is a derived feature, found only in acanthopterygians.

(7) The lateral wall of the jugular canal of teleosts is formed by membrane bone and is a new formation, developed at the leptolepid level by the addition of membrane bone outgrowths to a narrow lateral commissure of pholidophorid type.

(8) A pterosphenoid pedicle of some sort may be a primitive actinopterygian feature. It occurs in some palaeoniscoids, some pholidophorids, some teleosts, some caturids and *Amia*. In some palaeoniscoids and in caturids there is a pocket above the external opening of the trigeminal canal which encloses the superficial ophthalmic nerves: the outer wall of this pocket is homologous with the pterosphenoid pedicle.

(9) The actinopterygian cranial cavity is primitively drained by three veins, the anterior, middle and posterior cerebral veins. All three veins persist in the adult in few actinopterygians; the anterior and/or middle veins may fail to develop, atrophy or be replaced by secondary veins. The foramen of the middle cerebral vein lies close behind the trochlear foramen in pholidophorids, leptolepids and many fossil actinopterygians.

(10) The lateral cranial canal and fossa bridgei seem to have been fat-filled spaces, without obvious function, but there is evidence that the tissue in the lateral cranial canal was richly vascularized.

(11) The eyeball of actinopterygians was primitively surrounded by a double-walled cup of perichondral bone ossifying from five centres, one basal and four peripheral. Each of the four peripheral endoskeletal ossifications was associated with a dermal sclerotic bone.

(12) The postrostral of palaeoniscoids is homologous with the rostral of holosteans and teleosts, and should be so named.

(13) In *Perleidus* and holosteans the premaxillae developed nasal ('ascending') processes, lining the anterior part of the nasal pit and presumably giving rigidity to the snout. In pachycormids, *Ichthyokentema* and pholidophorids the lateral part of the premaxilla apparently became separated from the medial part, bearing the nasal process, as an adaptation to mobility of the upper jaw. In leptolepids, this separate medial portion, the lateral dermethmoid, lost its dentition and came to form a complex rostrum, associated with a highly kinetic upper jaw. In most leptolepids and in teleosts and *Pachycormus* the rostral fuses with the lateral dermethmoid, producing a rostro-dermethmoid, and in some leptolepids and most teleosts this compound dermal bone fuses with the endoskeletal supraethmoid. The mesethmoid of most teleosts is phylogenetically a rostro-dermethmo-supraethmoid.

(14) Vomers may not have been present in the most primitive actinopterygians, and the actinopterygian vomer is not necessarily the phylogenetic homologue of the vomer of dipnoans and crossopterygians.

(15) The vomer of most teleosts incorporates the endoskeletal ventral ethmoid.

(16) The parasphenoid of primitive actinopterygians is the exact topographic homologue of the rhipidistian parasphenoid, and there is no evidence of a prespiracular gill-slit in the latter group.

(17) In actinopterygians the development of a long ascending process on the parasphenoid and increase in length of the posterior part of the parasphenoid were due only to differential growth, not to the incorporation of separate bones or tooth-plates.

(18) In actinopterygians the internal carotid and efferent pseudobranchial arteries primitively passed into the neurocranium through notches in the margin of the parasphenoid, not through foramina or canals in that bone.

(19) Parasphenoid teeth are present in some individuals of *Polymixia*, and this makes it probable that the parasphenoid dentition of acanthopterygians like *Pristolepis*, nandids and anabantoids is primary, not secondarily redeveloped.

(20) In primitive actinopterygians there is a pair of pits or a transverse crevice in the parasphenoid immediately behind the lower opening of the bucco-hypophysial canal which correspond in form and position to the insertion of the subcephalic muscle in porolepiform and osteolepiform rhipidistians and coelacanths. It is therefore likely that subcephalic muscles were primitively present in actinopterygians, but that they took the same form as in *Polypterus*, and were anterior extensions of the trunk musculature. The separate subcephalic muscle and intracranial joint of crossopterygians are interpreted as specializations.

(21) The posterior myodome arose within the Actinopterygii. It was originally paired. Increase in size of these paired spaces resulted in their confluence, behind and with the pituitary space. The fissura oticalis ventralis migrated posteriorly because of increase in size of the myodome, not because of a change in segmental position. The development of a fenestra ventralis myodomus, behind the bucco-hypophysial canal, is a specialization. The myodome only extends across the fissura oticalis ventralis, into the basioccipital, in pholidophorids and teleosts, and a ventral compartment of the myodome only develops in leptolepids and teleosts.

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Explanation of abbreviations used in figures

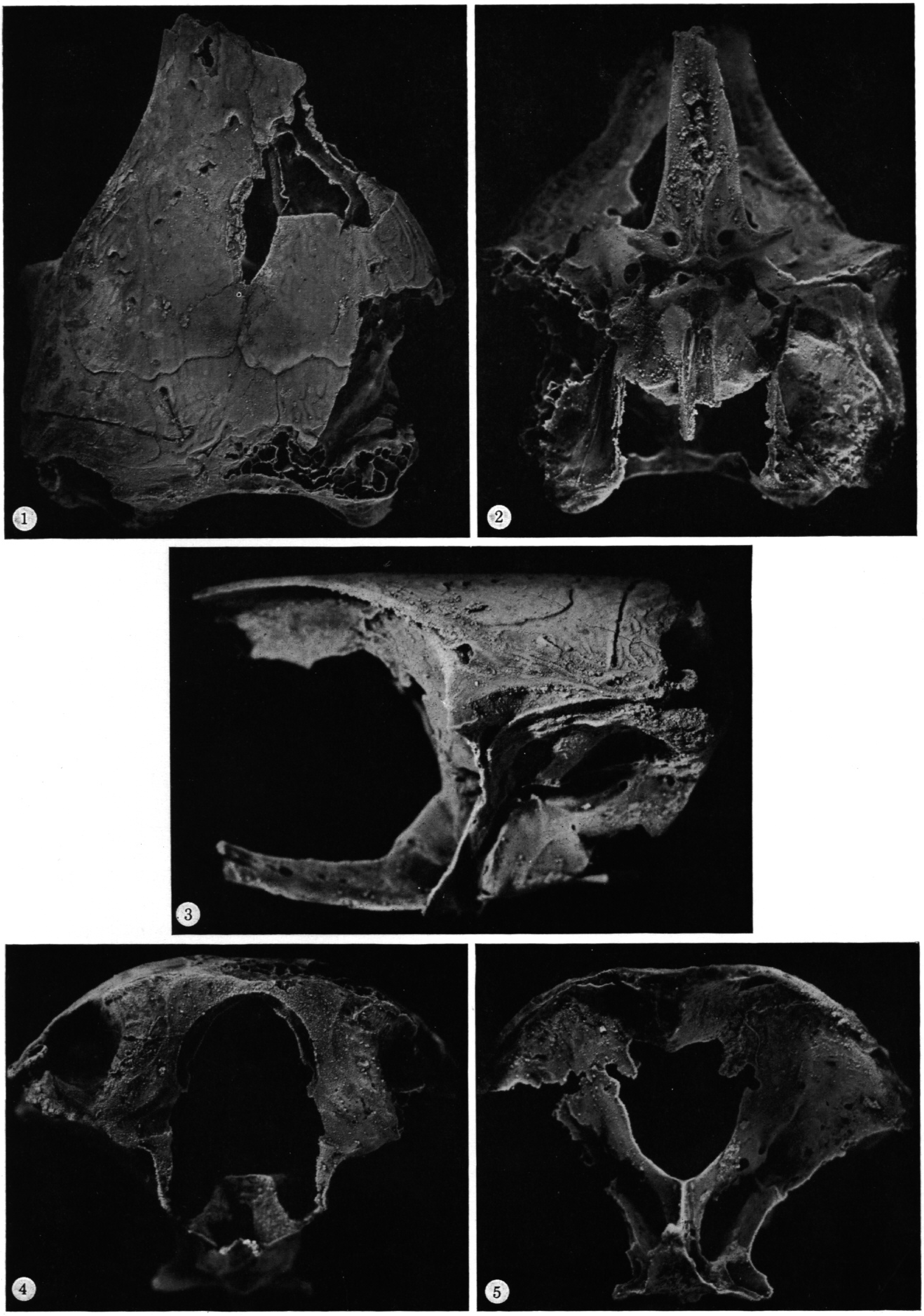
acic	area of exoccipital or pterotic covered by intercalar
acom	commissural vessel connecting internal carotid and efferent pseudobranchial arteries
acv	foramen of anterior cerebral vein
adf	anterior dorsal fontanelle
adhm	area of origin of adductor hyomandibulae muscle
aeff	foramen of efferent branchial artery
ainp I	articular facet for first infrapharyngobranchial
airm	area of origin of anterior and inferior rectus muscles
alcc	anterior opening of lateral cranial canal
alfr	antero-lateral tongue-like process of frontal
alp	antero-lateral process of lateral dermethmoid or rostro-dermethmoid
alpm	antero-lateral process of endoskeletal mesethmoid
Amb	anterior myodome bone
ampa, ampe, ampp	anterior, external and posterior ampullary chambers
amx	articular surface for maxilla and premaxilla
amyo	anterior myodome
amyv	ventral anterior myodome
ano	anterior nasal opening (external nostril)
Ant	antorbital bone
aol	area of origin of aortic ligament
apal	articular facet for palatine
apmx	articular surface on lateral dermethmoid for premaxilla
arfr	area of lateral ethmoid or mesethmoid articulating with frontal
arvo	area covered by vomer
asc	cavity occupied by, or ridge over, anterior semicircular canal
asp	ascending process of parasphenoid
asup I	articular facet for first suprapharyngobranchial
atlig	projections on exoccipital for attachment of intermuscular septa
Bexo	basi-exoccipital bone
bhc	bucco-hypophysial canal
Boc	basioccipital bone
bpt	basipterygoid process
Bsp	basisphenoid bone
cao	aortic canal
coa	canal for orbital artery
csim	cavum sinus imparis
cson	canal for superficial ophthalmic nerves
cvlcc	crest covering canal for vein from lateral cranial canal
df	dilatator fossa
dlfr	descending lamina of frontal
dlpa	descending lamina of parietal
dlpto	descending lamina of dermopterotic
Dpto	dermopterotic bone
Dspo	dermosphenotic bone
eco	ethmoid commissural sensory canal
Epi	'epiotic' bone
epl	ethmoid pit-line
Epo	epioccipital bone
epsa	efferent pseudobranchial artery
esc	cavity occupied by, or ridge over, external semicircular canal
Et	ethmoid bone

Exo	exoccipital bone
exocc	exoccipital condyle
fagl	foramen for branch of glossopharyngeal nerve entering jugular canal
fapcv	foramen for anterior tributary of posterior cerebral vein in front wall of vagus groove
fb	fossa bridgei
fbam, fbl, fbp	antero-medial, lateral and postero-medial portions of fossa bridgei
fdoc	foramen in inner wall of foramen magnum, in front of occipital nerve foramen
ferm	fenestra in roof of myodome
fet	pit or fenestra in ethmoid region, significance unknown
fhm	hyomandibular facet
fhmv	foramen of hyomandibular vein
fhm VII	foramen of hyomandibular trunk of facial nerve
fic	facet for anterior process of intercalar on prootic
fica	foramen of internal carotid artery
fica$_2$	ascending foramen of internal carotid artery in basisphenoid pedicel
flcc	fenestra between subtemporal fossa and lateral cranial canal
flcom	fenestra in lateral commissure
fm	foramen magnum
foa	foramen of orbital artery
foca	foramen of occipital artery
focn	foramen or notch for occipital nerve
fopa	foramen or notch for optic artery
fotc	fissura otico-occipitalis
fotn	foramen of otic nerve
fotn$_1$, fotn$_2$	foramen of branch of otic nerve
fotv	fissura oticalis ventralis
fpal	entry foramen of palatine nerve into parabasal canal or palatine canal
fpsa	foramen of efferent pseudobranchial artery
fpt	facet for ligament to post-temporal
Fr	frontal bone
frd	foramen for ascending branch of superficial ophthalmic nerves
fri	facet for cranial rib on basioccipital
frla	foramen of ramus lateralis accessorius (recurrent branch of facial nerve)
fson	foramen of superficial ophthalmic nerves
fst IX	foramen of supratemporal branch of glossopharyngeal nerve
fst X	foramen of supratemporal branch of vagus nerve
ftpcv	foramen for posterior tributary of posterior cerebral vein in hind wall of vagus groove
fva	vascular foramen
fve	vascular foramen in ethmoid region
fvii	venous foramen
fvoc	foramen for tributary of posterior cerebral vein in exoccipital
fvptf	foramen in intercalar transmitting vessels into post-temporal fossa
gcom	groove on parasphenoid for connecting vessel between internal carotid and efferent pseudobranchial arteries
gic	groove for internal carotid artery

gmx	groove for maxillary nerve
goa	groove for orbital artery
gpal	groove for palatine nerve
grao	groove for dorsal aorta
groca	groove for occipital artery
grpcv	groove for posterior cerebral vein
grst IX	groove for supratemporal branch of glossopharyngeal nerve
gr X	groove for vagus nerve
gson	groove for superficial ophthalmic nerves
gvlcc	groove for vein from lateral cranial canal
haol	housing of aortic ligament
hlms	recess in lateral ethmoid housing levator maxillaris superioris muscle
hsnl	housing of longitudinal ligament
Ic	intercalar bone
ica	internal carotid artery
inc	tube or foramen for infraorbital sensory canal
Io	infraorbital bone
iom	area of origin of inferior oblique muscle
jc	jugular canal
jexo	area of intercalar joining exoccipital
jg	jugular groove
jic	area of exoccipital joining intercalar
Lac	lachrymal bone
lamb	laminar bone lining notochordal pit
lapf	area of origin of levator arcus palatini muscle
lcc	lateral cranial canal
lcom	lateral commissure
Lde	lateral dermethmoid bone
ldep	process of 'rostral' of *Pachycormus* representing lateral dermethmoid
Le	lateral ethmoid bone
ll	foramen through which lateral line enters dermopterotic
lmt	impression of 'metencephalic lobe'
lptf	lamina beneath frontal in medial wall of post-temporal fossa
mbr	membranous 'brush' on epiotic
mcv	foramen of middle cerebral vein
Mes	mesethmoid ossification
Mx	maxillary bone
myo	posterior myodome
myocc	occipital portion of myodome
myom	ventro-medial opening of posterior myodome
myot	otic portion of myodome
Na	nasal bone
nbr X	notch for auricular branch of vagus nerve
nbu	notch for buccal nerve
nhm VII	notch for hyomandibular trunk of facial nerve
nica	notch for internal carotid artery
njv	notch for jugular vein
not	notochordal calcification in notochordal pit
notn	notch for branch of otic nerve
npal	notch for branch of palatine nerve
npit	nasal pit
npro	nasal process of 'rostral' of *Pachycormus*
nprpm	nasal ('ascending') process of premaxilla
npsp	notch housing tip of ascending process of parasphenoid
nse	nasal septum
nspi	notch for spiracular canal
nson	notch for superficial ophthalmic nerves

occ	occipital condyle
onc	canal for orbitonasal vessels
onv	canal for optic nerve and vessels
opa	ophthalmic artery
Opo	opisthotic bone
Ors	orbitosphenoid bone
otoc	occipital portion of otolith chamber
Pa	parietal bone
pal	palatine nerve
pala	notch or canal for anterior branch of palatine nerve
palb	notch or canal for branch of palatine nerve
palf	palatine foramen or fenestra in roof of myodome
palp	notch or foramen for posterior branch of palatine nerve
palt	notch or foramen for terminal branch of palatine nerve
parc	opening of parabasal canal
pasp	parasphenoid portion of pterosphenoid pedicle
pitf	pituitary fossa
plcc	posterior opening of lateral cranial canal
plecp	pit housing origin of ligament to ectopterygoid
plig	pit housing origin of ethmo-palatine ligament
plp	postero-lateral process of lateral dermethmoid
Pmx	premaxillary bone
pno	posterior nasal opening (external nostril)
pnw	prenasal wall
posc	foramen transmitting anastomosis between preopercular and temporal sensory canals
prlm	process on prootic giving origin to branchial levator muscles
Pro	prootic bone
prob	prootic bridge
prof	notch, foramen or canal for profundus nerve
pron	notch for profundus nerve on mesethmoid
psc	cavity occupied by, or ridge over, posterior semicircular canal
Psp	parasphenoid bone
psv	recess or depression in prootic housing saccus vasculosus
ptf	post-temporal fossa
Pto	pterotic bone
Pts	pterosphenoid bone
Ptsl	separate ossification beneath descending lamina of dermopterotic in *Pholidophorus macrocephalus*
Ptsn	separate portion of pterotic attached to exoccipital in *P. germanicus*
Ptso	separate ossification beneath descending lamina of frontal in *P. germanicus*
ptsp	pterosphenoid pedicle
rbu	buccal nerve
rdic	recess housing diencephalon
rdo	dorsal (ascending) branches of superficial ophthalmic nerves
rla	ramus lateralis accessorius (recurrent branch of facial nerve)
rmd, rmx	maxillary and mandibular rami of trigeminal nerve
Ro	rostral bone
rolf	recess housing olfactory lobes
ropl	recess housing optic lobe
rot	otic nerve
rpan	rostral process of antorbital bone
rscm	recess on parasphenoid housing origin of subcephalic muscles

rsoc	recess on roof of otic region housing membranous extension of supraoccipital bone
rtel	recess housing telencephalon
sacr	saccular recess
sef	subepiotic fossa
smc	crest on upper surface of parasphenoid forming floor of myodome
Smx	supramaxillary bone
Soc	supraoccipital bone
sof	supraorbital fossa
son	superficial ophthalmic nerves
Sot	supraotic bone
spic	spiracular canal
spig	spiracular groove
spld	spur-like process of lateral dermethmoid in prenasal wall
Spo	sphenotic bone
ssu	sinus superior (crus commune) or bone supporting it
stf	subtemporal fossa
str	prootic or intercalar portion of strut across subtemporal fossa
sts	spur projecting into cranial cavity at front margin of optic fenestra
suc	tube or foramen for supraorbital sensory canal
Sue	supraethmoid bone
Suo	supraorbital bone
sup	supraotic pocket in 'epiotic' bone
svfotc	sub-vagal portion of fissura otico-occipitalis
tsp	depression on descending lamina of dermopterotic housing tip of spiracular tube
utr	utricular recess
Ve	ventral ethmoid bone
vfon	vestibular fontanelle
vmyo	depression in parasphenoid marking floor of ventral compartment of myodome
Vo	vomer
vped	rudiment of prootic portion of pterosphenoid pedicle
I	foramen of olfactory tracts
II	optic fenestra
III	notch, foramen or canal of oculomotor nerve
IV	notch or foramen of trochlear nerve
V	foramen of trigeminal nerve
VI	foramen of abducens nerve
VII	foramen of facial nerve
IX	foramen of glossopharyngeal nerve
X	foramen of vagus nerve



Figures 1–5. *Pholidophorus bechei* Agassiz. Isolated, incomplete braincase, P.51682, in dorsal (figure 1), ventral (figure 2), left lateral (figure 3), posterior (figure 4) and anterior views (magn. × 7 approx.). Specimen whitened with ammonium chloride.

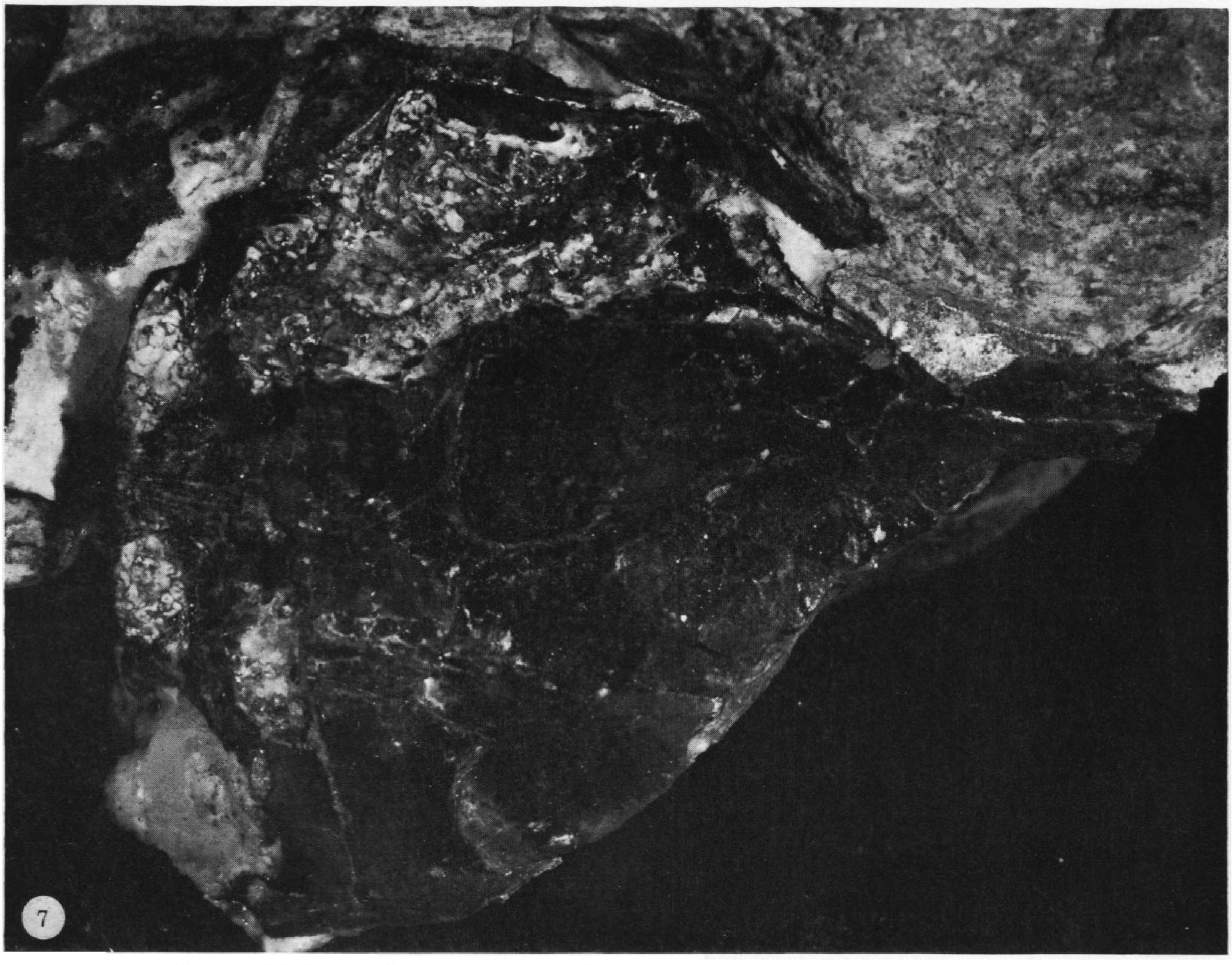
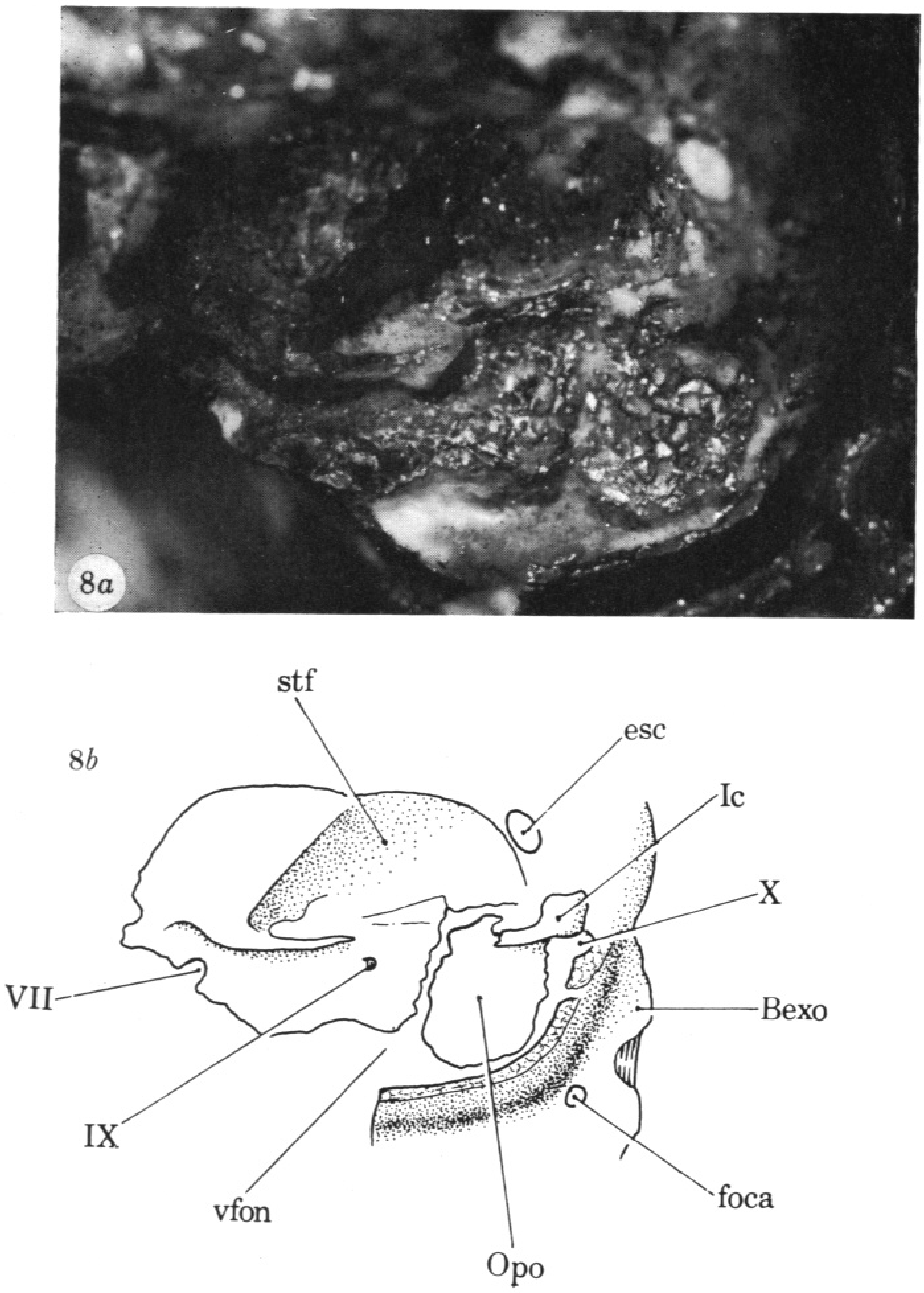


FIGURE 6. *Pholidophoroides limbata* (Agassiz). Skull roof of P.40588, mechanically prepared to show the fossa bridgei of the right side (magn. × 4). See also figures 22, 23.

FIGURE 7. *Pholidophorus bechei* Agassiz. Skull roof of 19010, mechanically prepared to show the fossa bridgei of the left side (magn. × 7.5). See also figure 9.



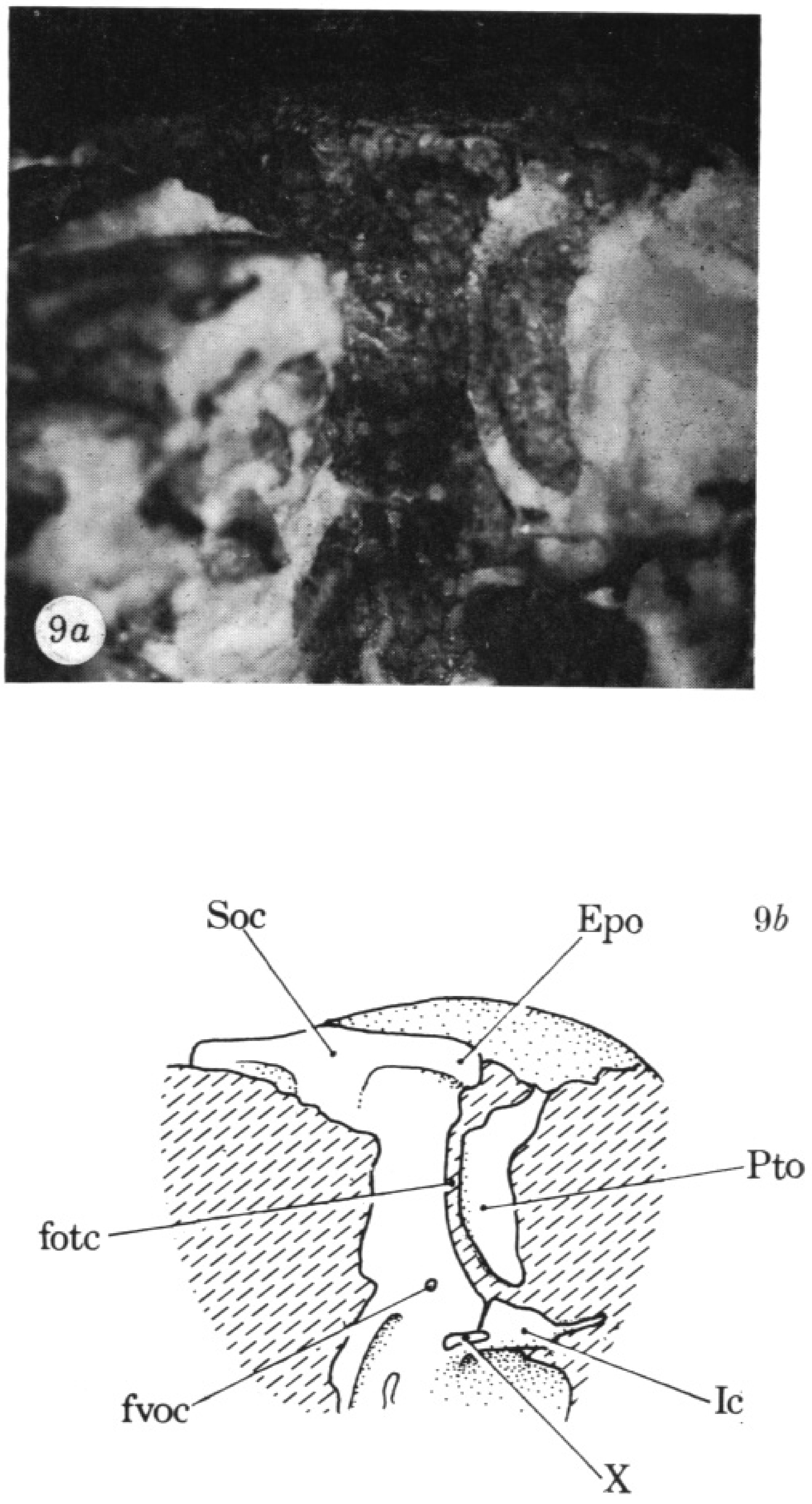


FIGURE 8(*a*, *b*). *Pholidophorus bechei* Agassiz. Postero-ventral part of imperfect neurocranium, SM J4851, in left lateral view to show the opisthotic. (Photograph, magn. × 10; key diagram, magn. × 7 approx.)

FIGURE 9(*a*, *b*). *Pholidophorus bechei* Agassiz. Right side of braincase of 19010 (figure 7) in oblique posterior view to show the dorso-lateral part of the cranial fissure. (Photograph, magn. × 8; key diagram, magn. × 5 approx.)

FIGURE 10. Callovian *Pholidophorus* sp. Isolated, incomplete braincase, 32579, in left lateral view (magn. × 4). Specimen lit from below to illuminate the subtemporal fossa. See also figures 11–14.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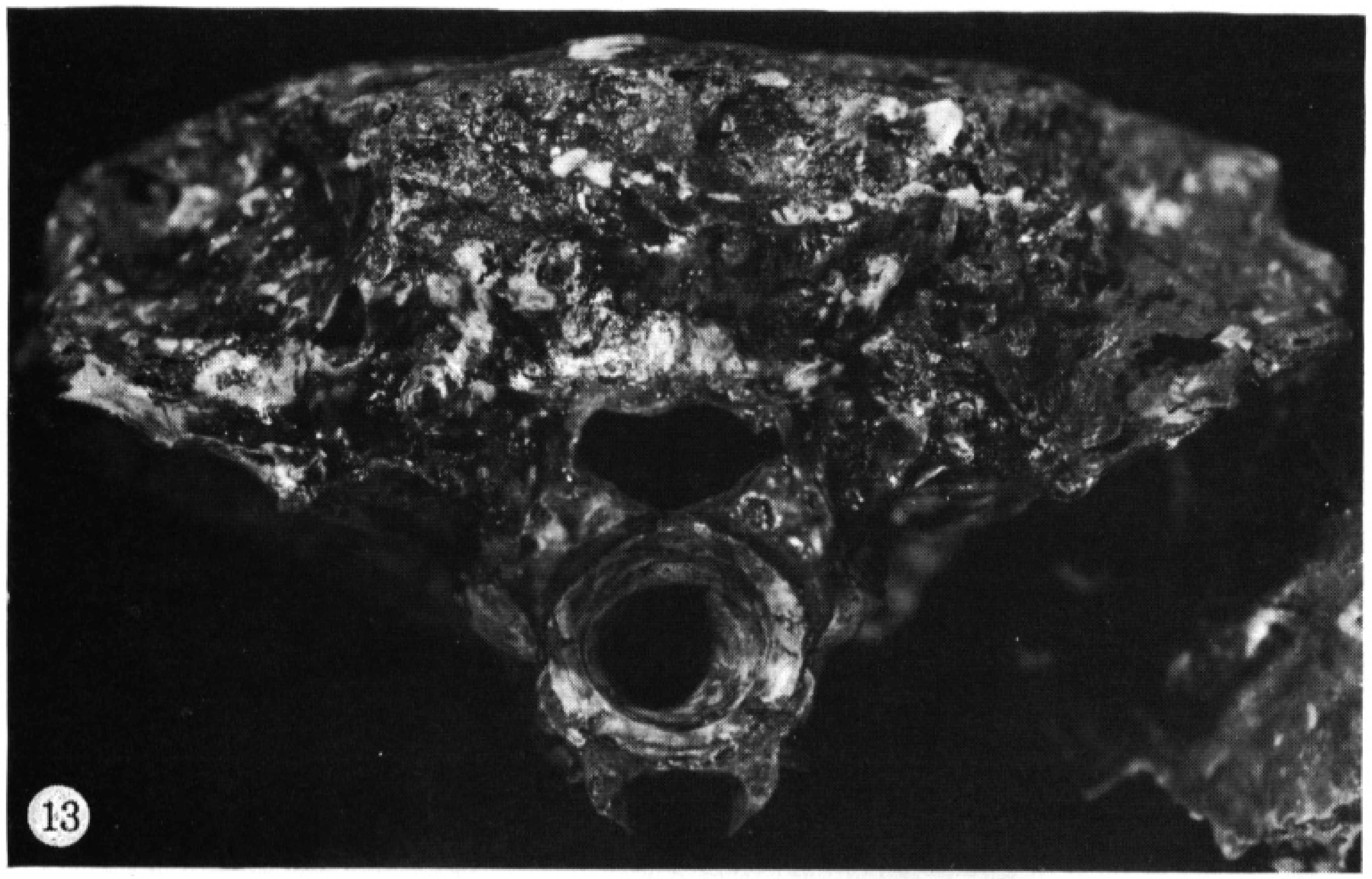
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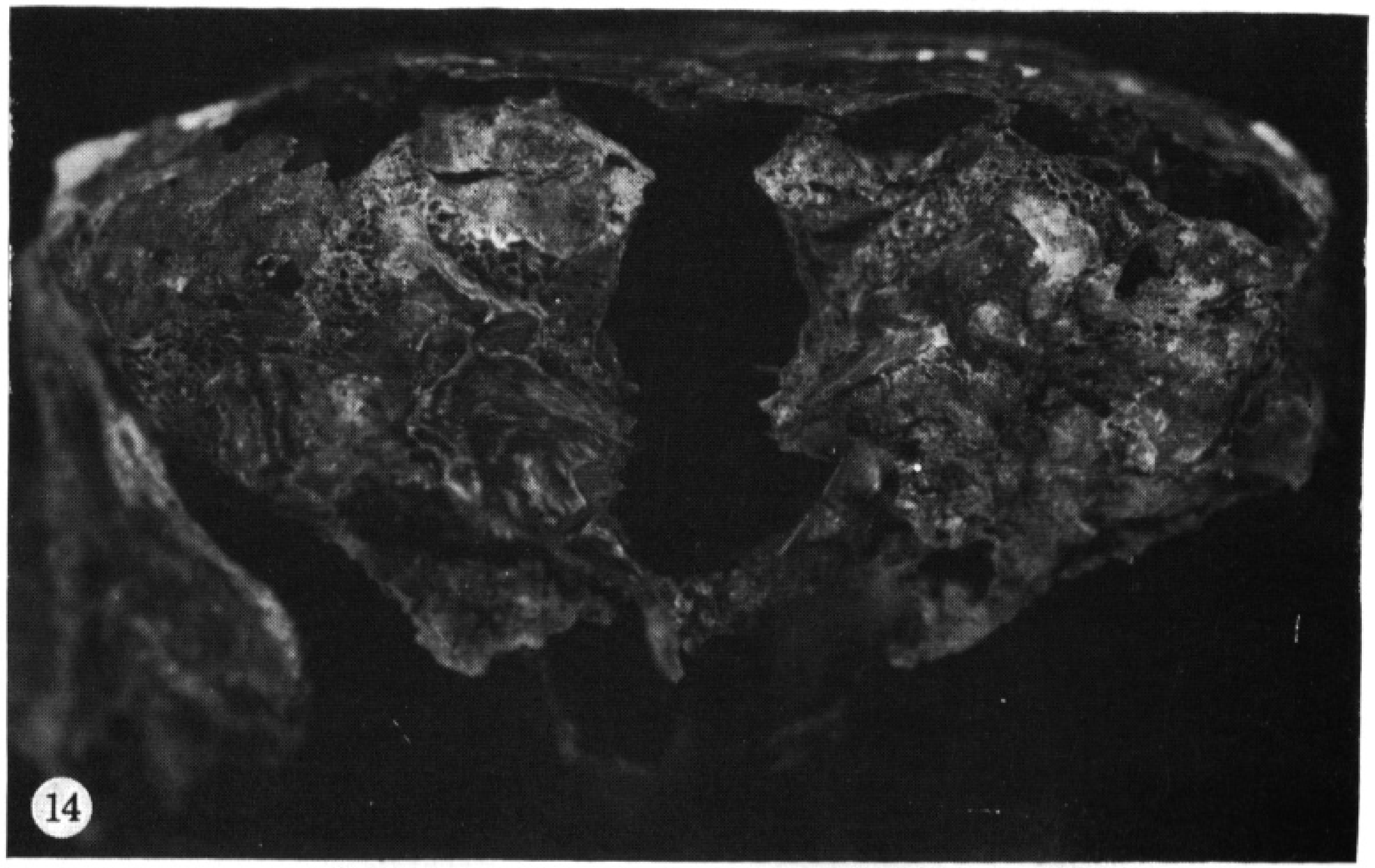
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FIGURES 11–14. Callovian *Pholidophorus* sp. Isolated, incomplete braincase, **32579**, in dorsal (figure **11**), ventral (figure **12**), posterior (figure **13**) and anterior (figure **14**) views (magn. × **3** approx.). See also figure **10**.

FIGURE 15. *Pholidophorus germanicus* Quenstedt. Head and anterior part of trunk, P.3704, seen from the left side after removal of most of the bones of the left cheek and palate, exposing the braincase in ventro-lateral view (magn. × 3 approx). The left lachrymal is at the edge of the photograph, and the basal sclerotic bone is conspicuous in the orbit behind it.

FIGURE 16. *Pholidophorus macrocephalus* Agassiz. Partially disarticulated head, P.3582, seen from the right side (magn. × 2¼). The braincase is exposed in ventro-lateral view, with the displaced right hyomandibular covering much of the orbit. The gill-arch skeleton of the left side is exposed in medial view below the braincase.

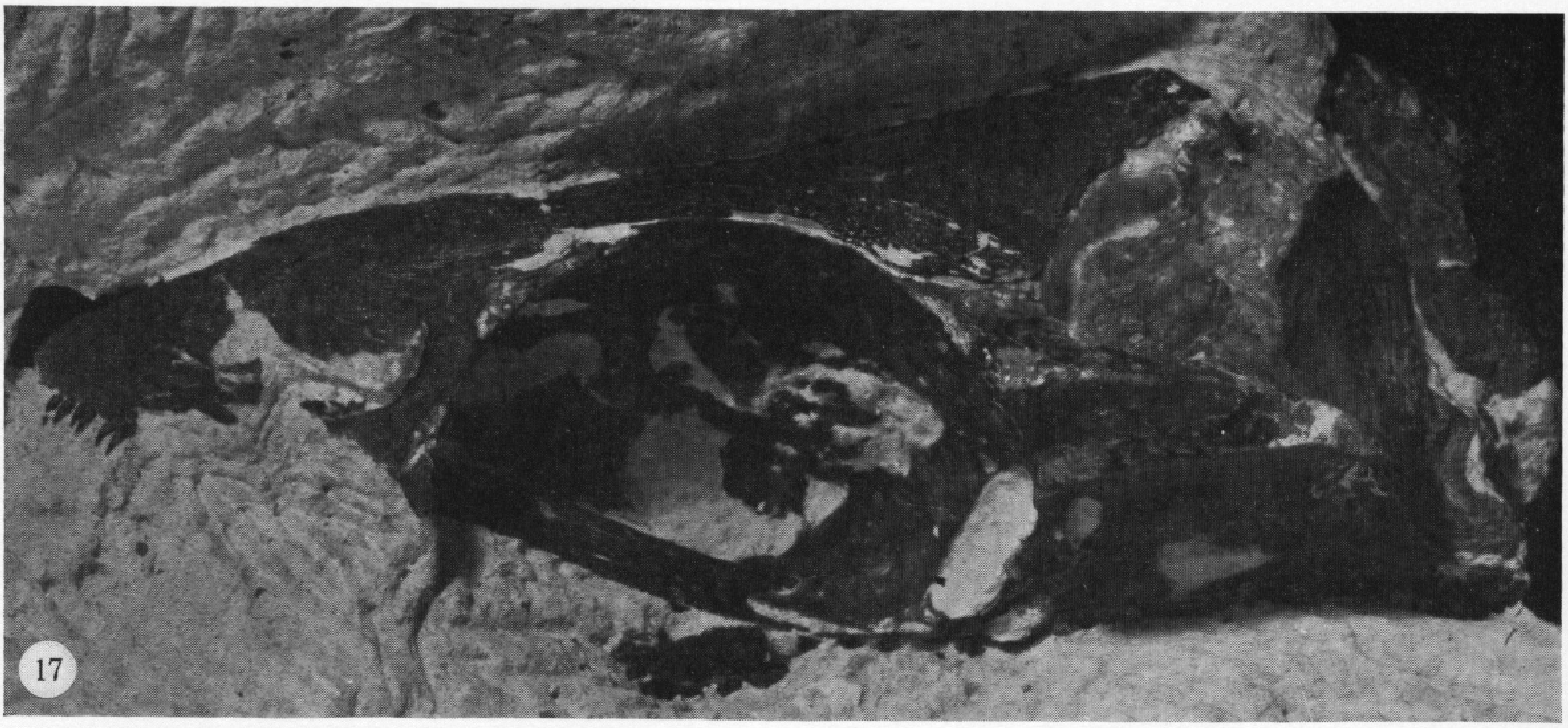
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FIGURE 17. *Pachycormus curtus* Agassiz. Mechanically prepared braincase, 32434, in left lateral view (magn. × 3). See also figure 29.

FIGURES 18, 19. *Pholidophorus macrocephalus* Agassiz. Two isolated braincases in ventral view, P.12070 (figure 18) and P.52518 (figure 19), both magnified × 2 approx.

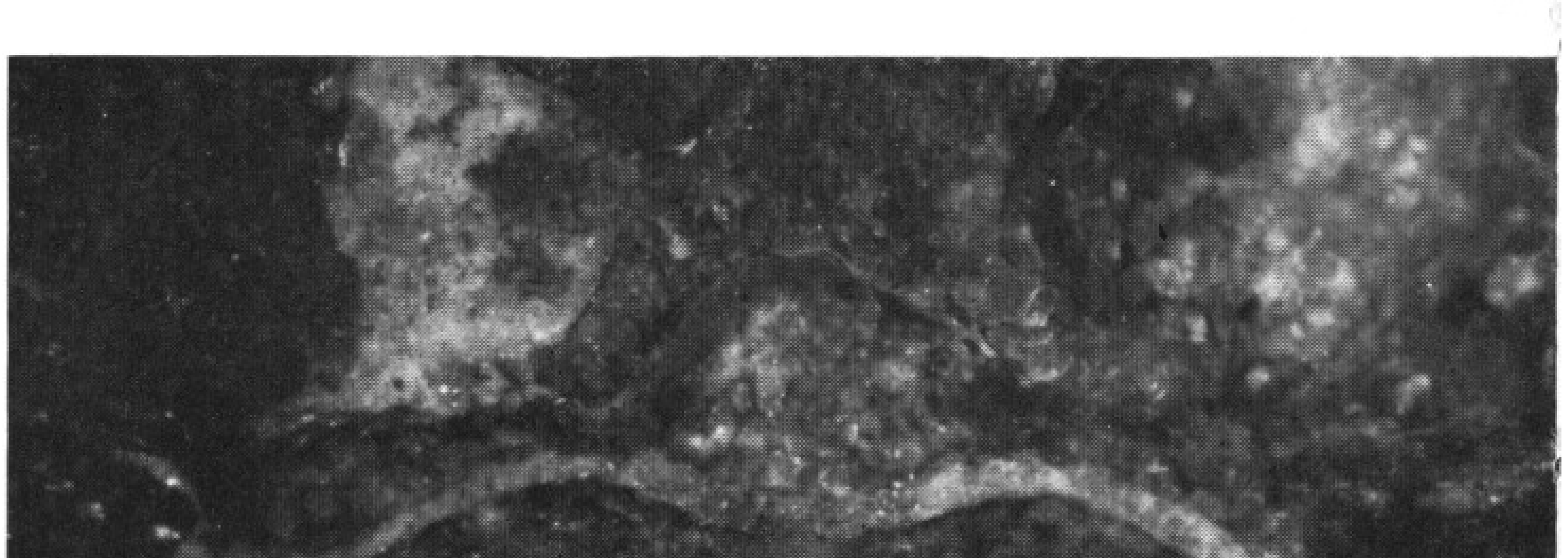
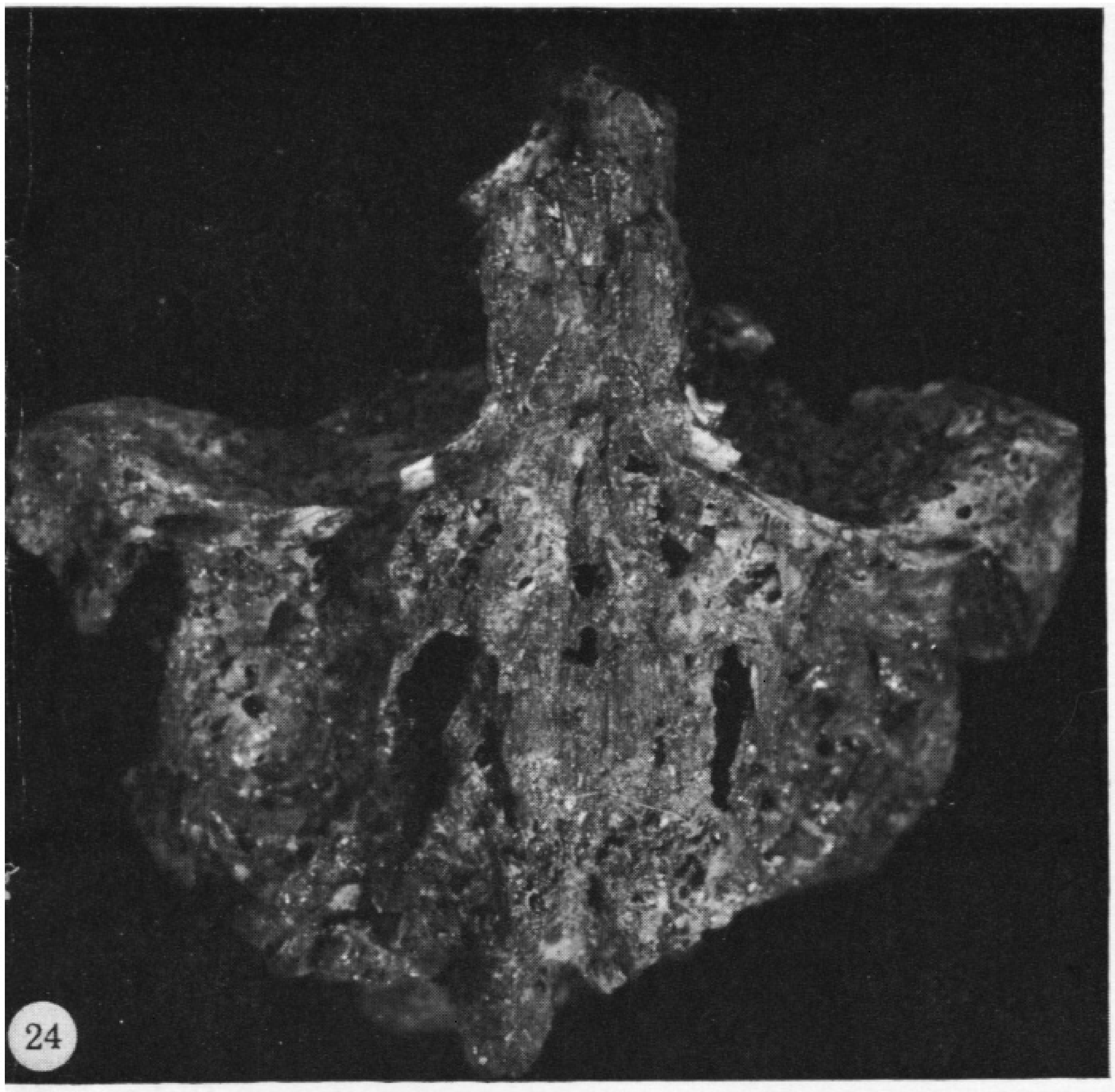
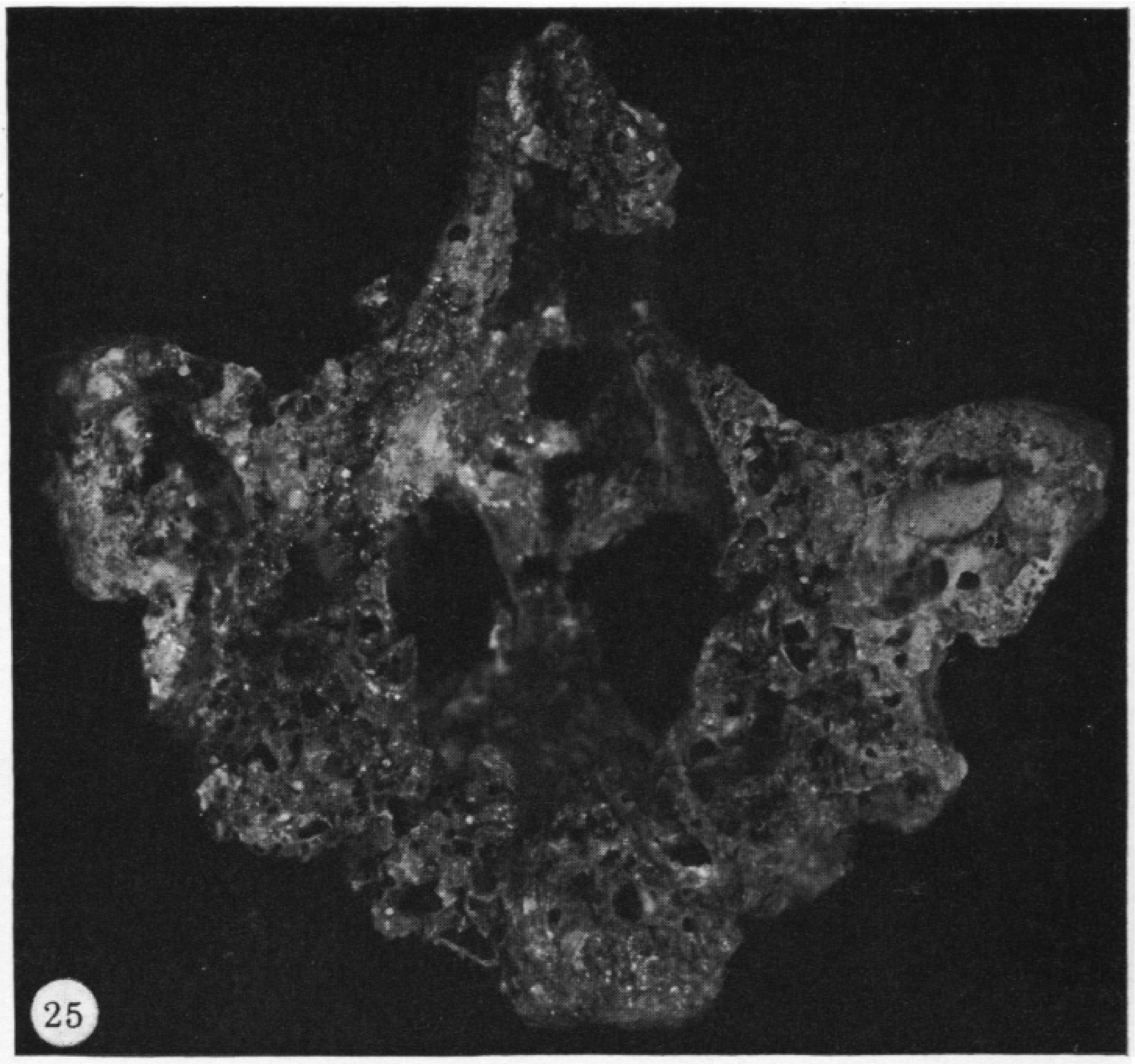


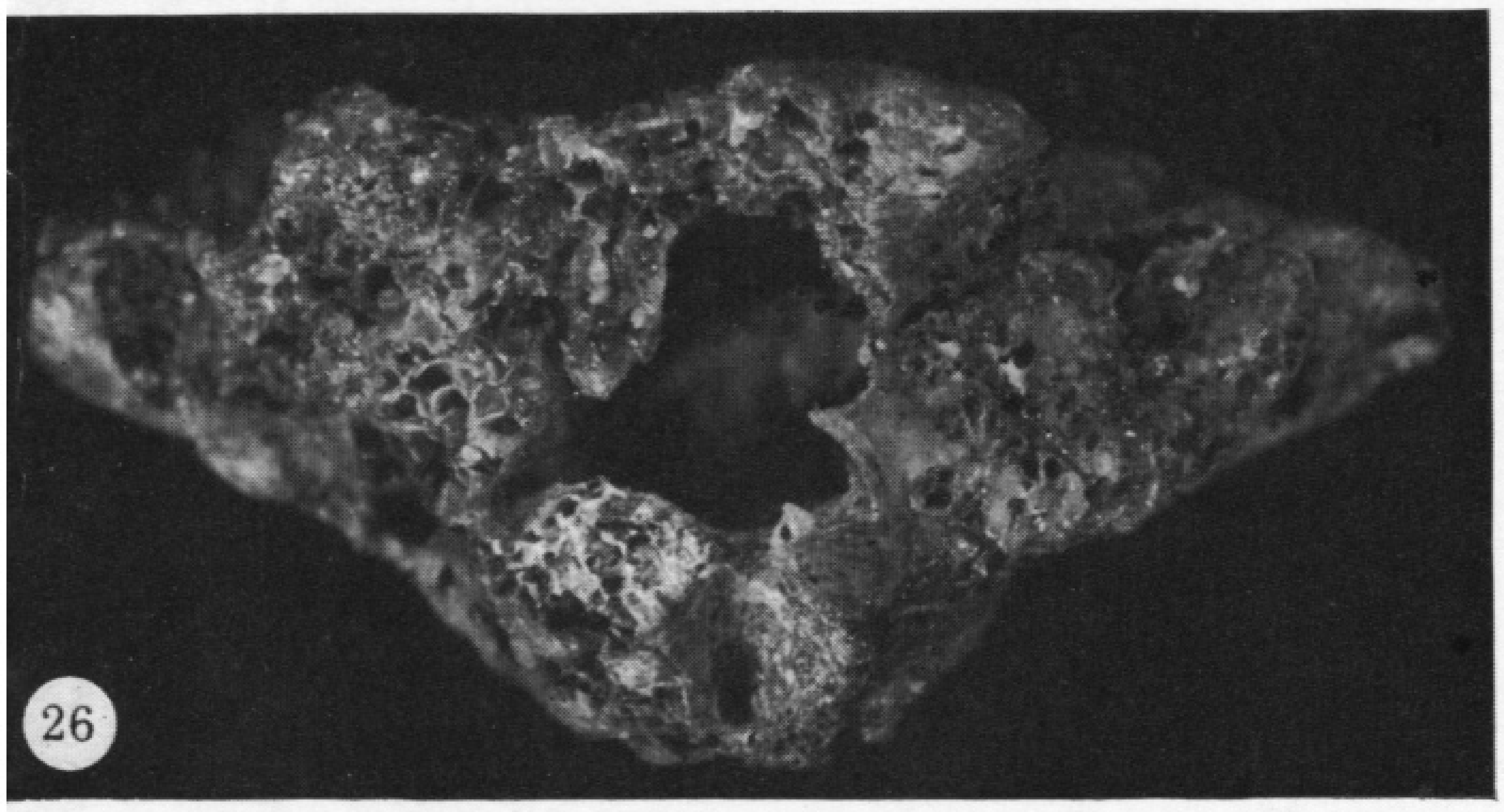
FIGURE 20. *Pholidophorus* cf. *macrocephalus* Agassiz. Braincase of P.1085 in left lateral view (magn. × 4 approx.).

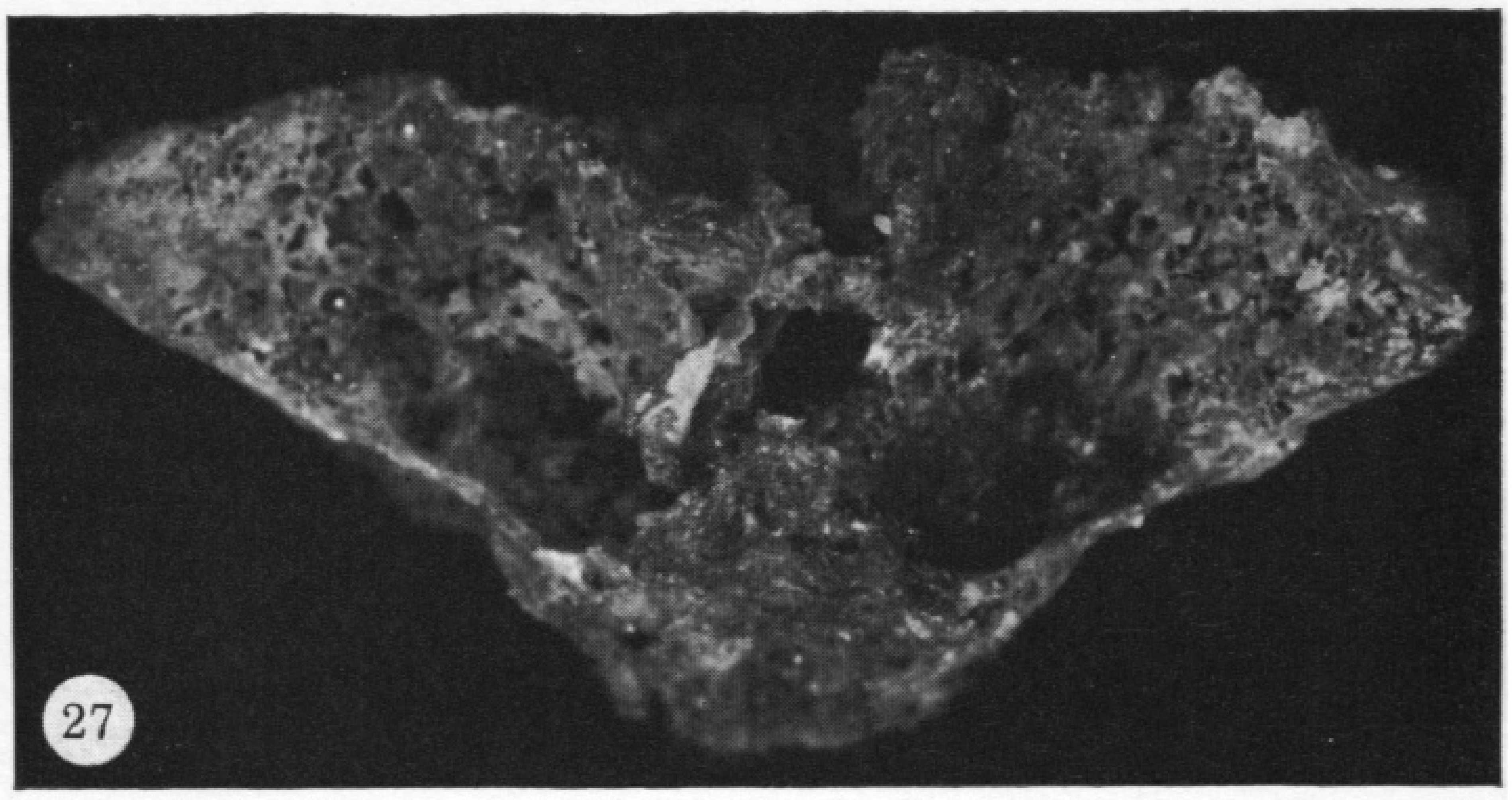
FIGURE 21. *Leptolepis dubia* (Blainville). Isolated braincase, P.919, in ventral view (magn. × 4.5). Most of the parasphenoid is missing.

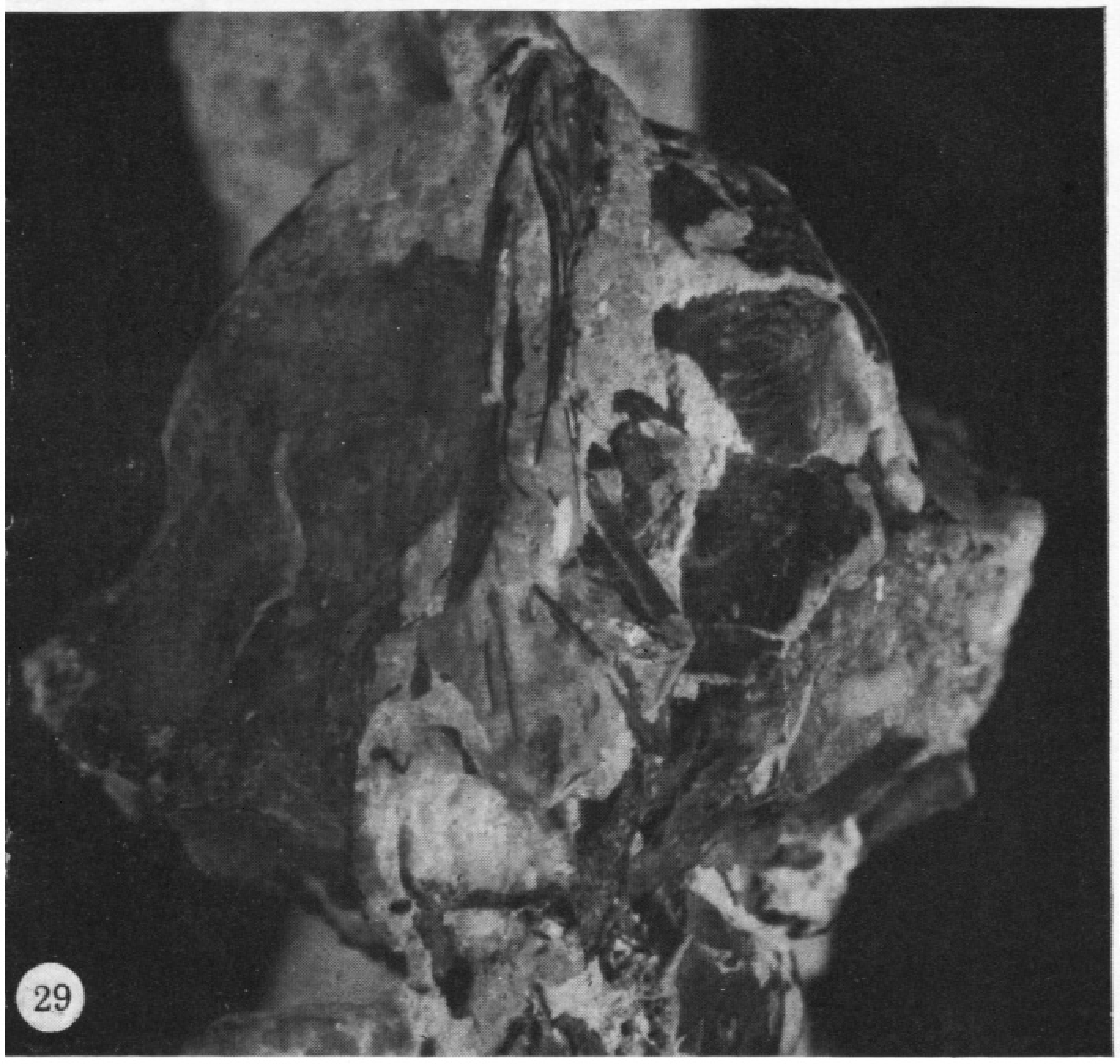
FIGURES 22, 23. *Pholidophoroides limbata* (Agassiz). Dorsal view of ethmoid region (figure 22) and occiput (figure 23, to show the uninterrupted dorsal portion of the cranial fissure) of P.40588, the skull shown in figure 6. (Both magnified × 8.5.)

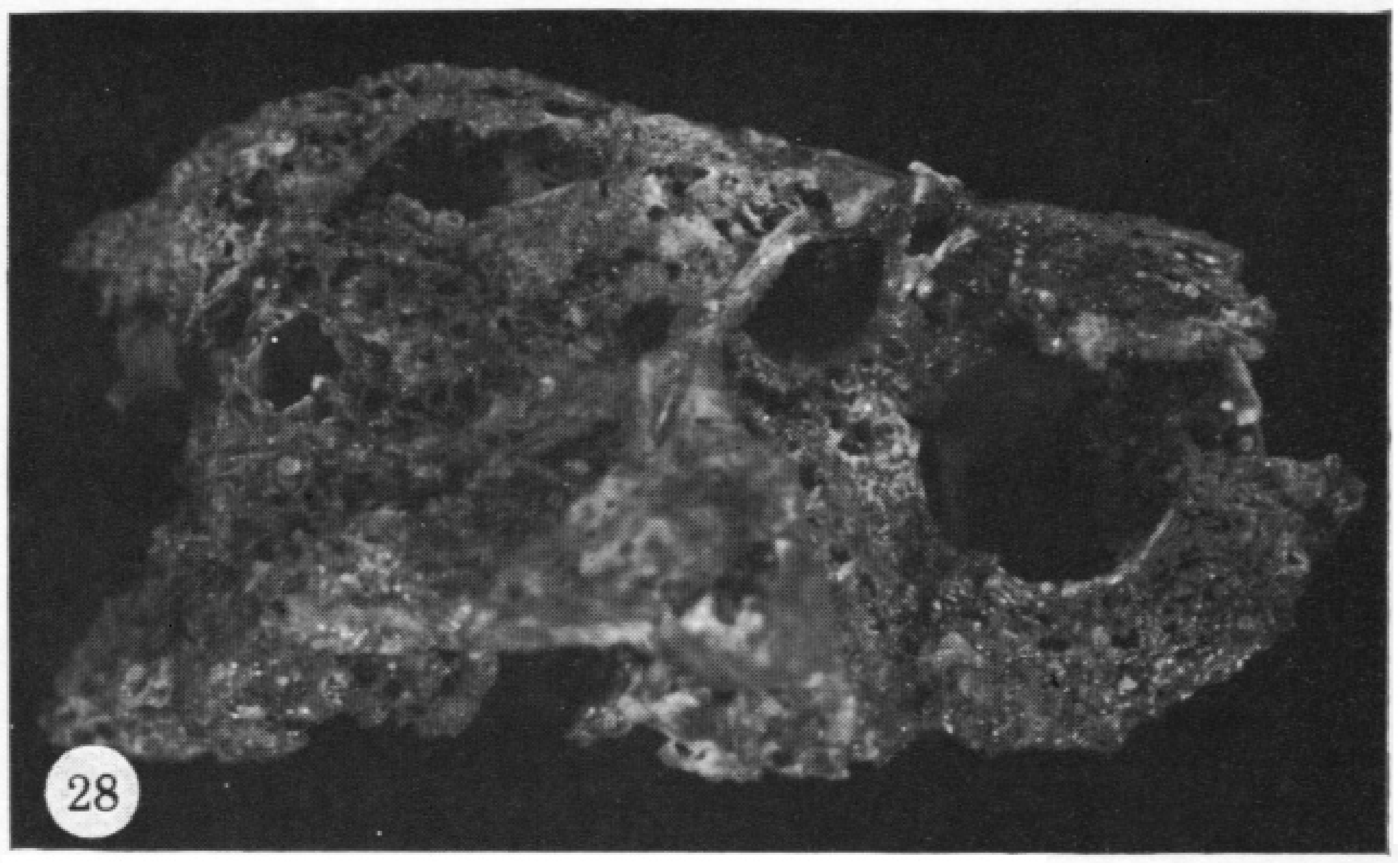












FIGURES 24–28. Undetermined parasemionotid. Isolated, incomplete braincase, MMK 492, in ventral (figure 24), dorsal (figure 25), posterior (figure 26), anterior (figure 27) and right lateral (figure 28) views, all magnified × 4 approx.

FIGURE 29. *Pachycormus curtus* Agassiz. Mechanically prepared braincase, 32434, in posterior view (magn. × 4 approx.). See also figure 17.

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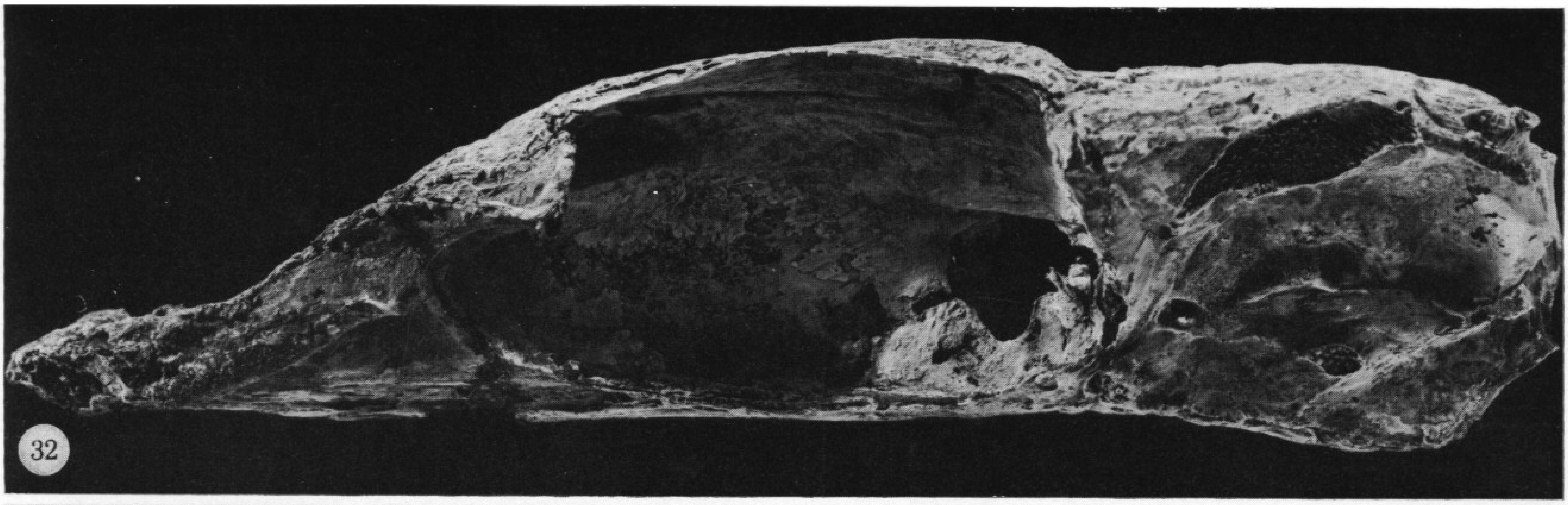
FIGURE 30. Undetermined parasemionotid. Part of disarticulated head, MMK 491A, showing the braincase in ventral view (magn. × 5 approx.). See also stereo-pair, figure 41, plate 20.

FIGURE 31. *Caturus furcatus* Agassiz. Part of disarticulated head, P.904*a*, showing the braincase in ventral view (magn. × 3 approx.)



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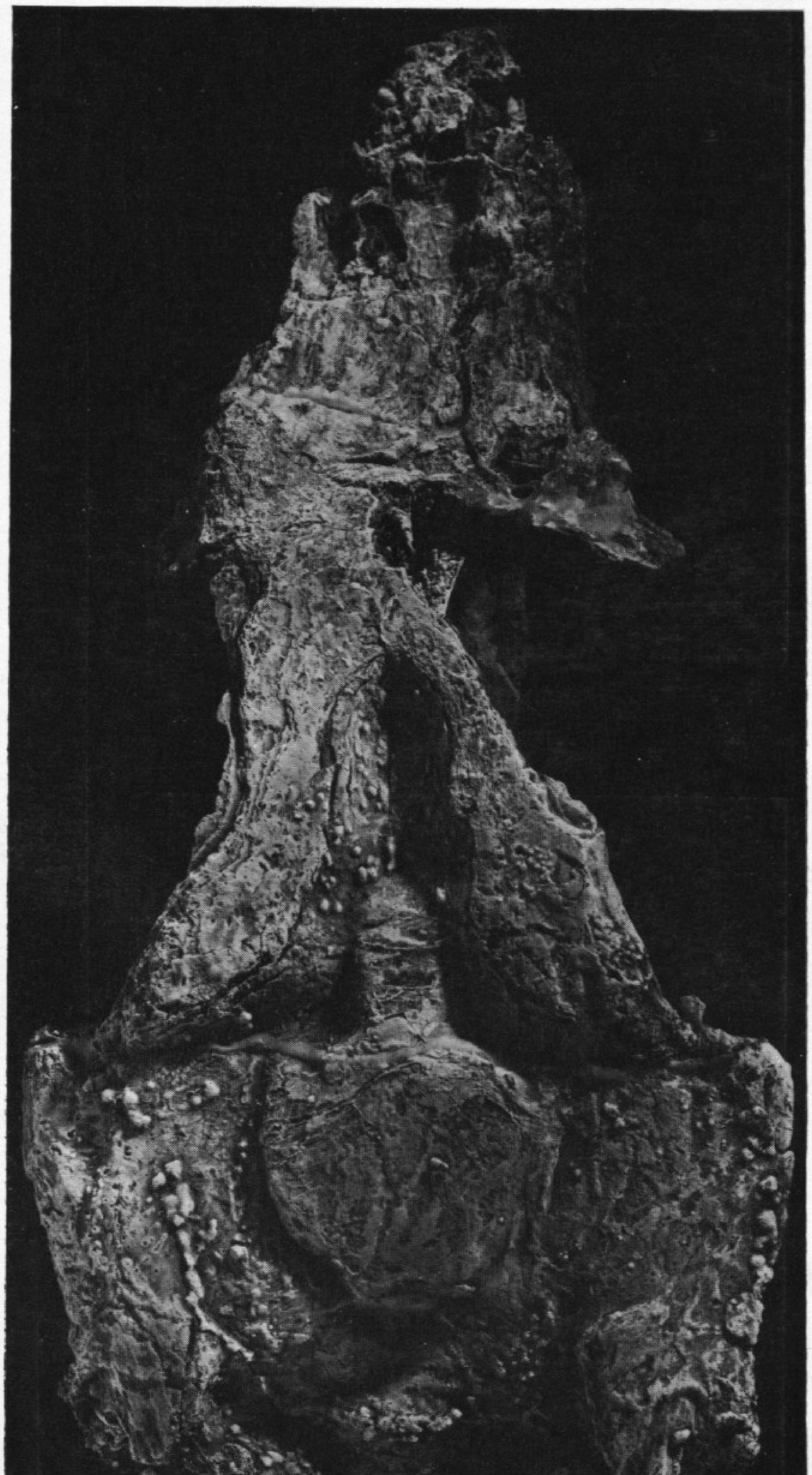

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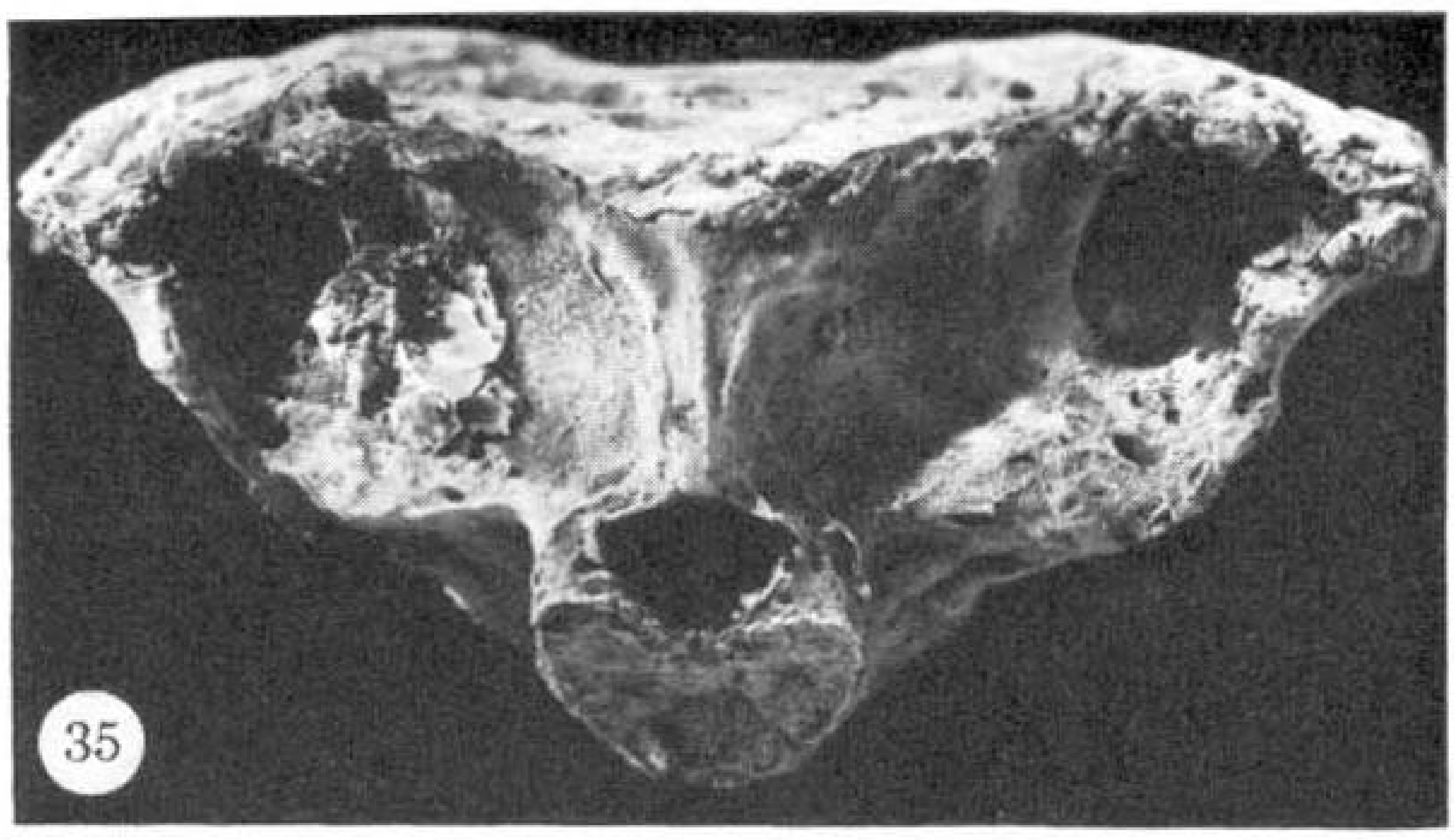
FIGURES 32–34. *Heterolepidotus* sp. Isolated braincase, P.13260, in left lateral (figure 32), ventral (figure 33) and dorsal (figure 34) views (magn. × 1.5 approx.). Specimen whitened with ammonium chloride. See also figure 35, plate 19.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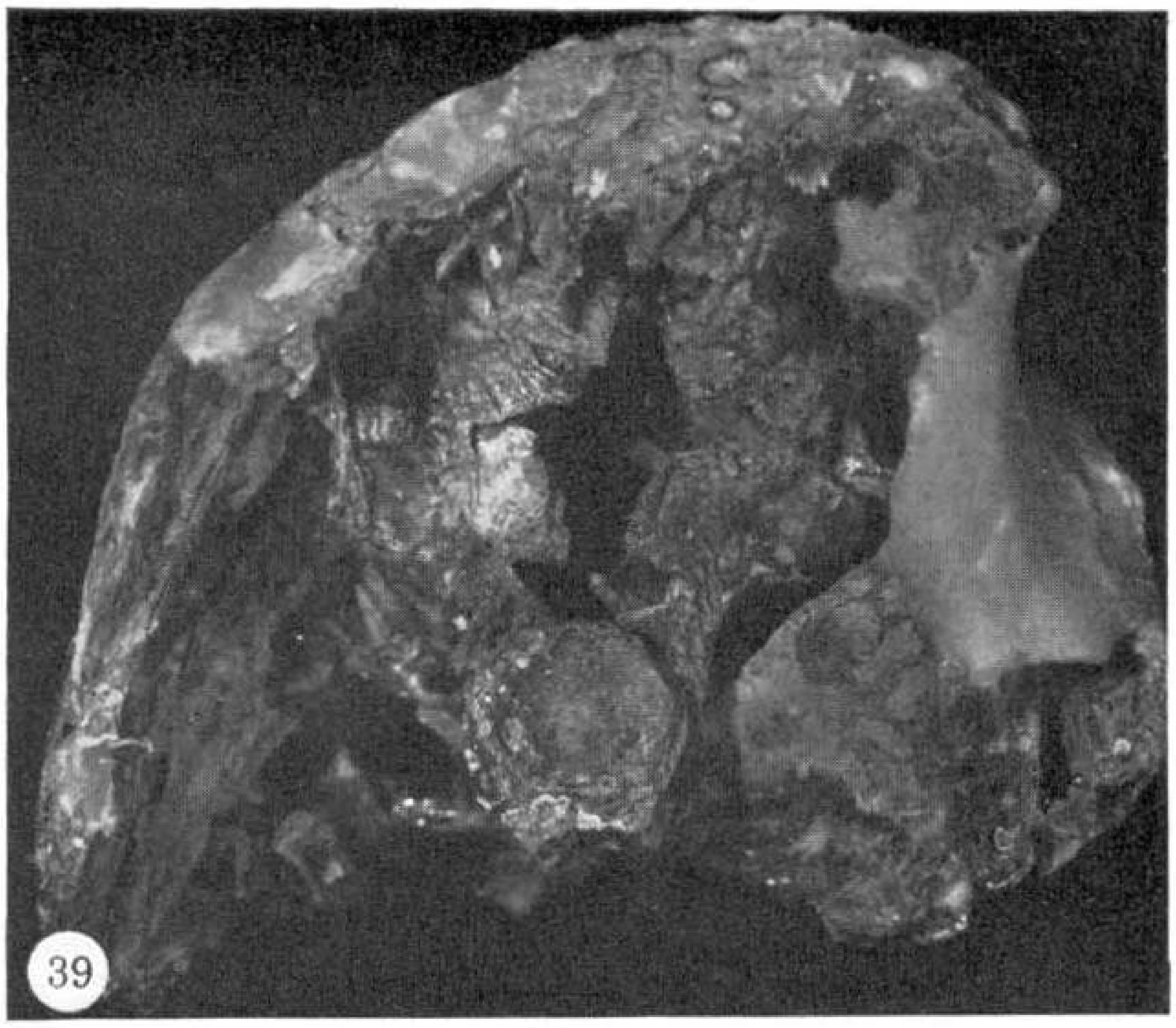
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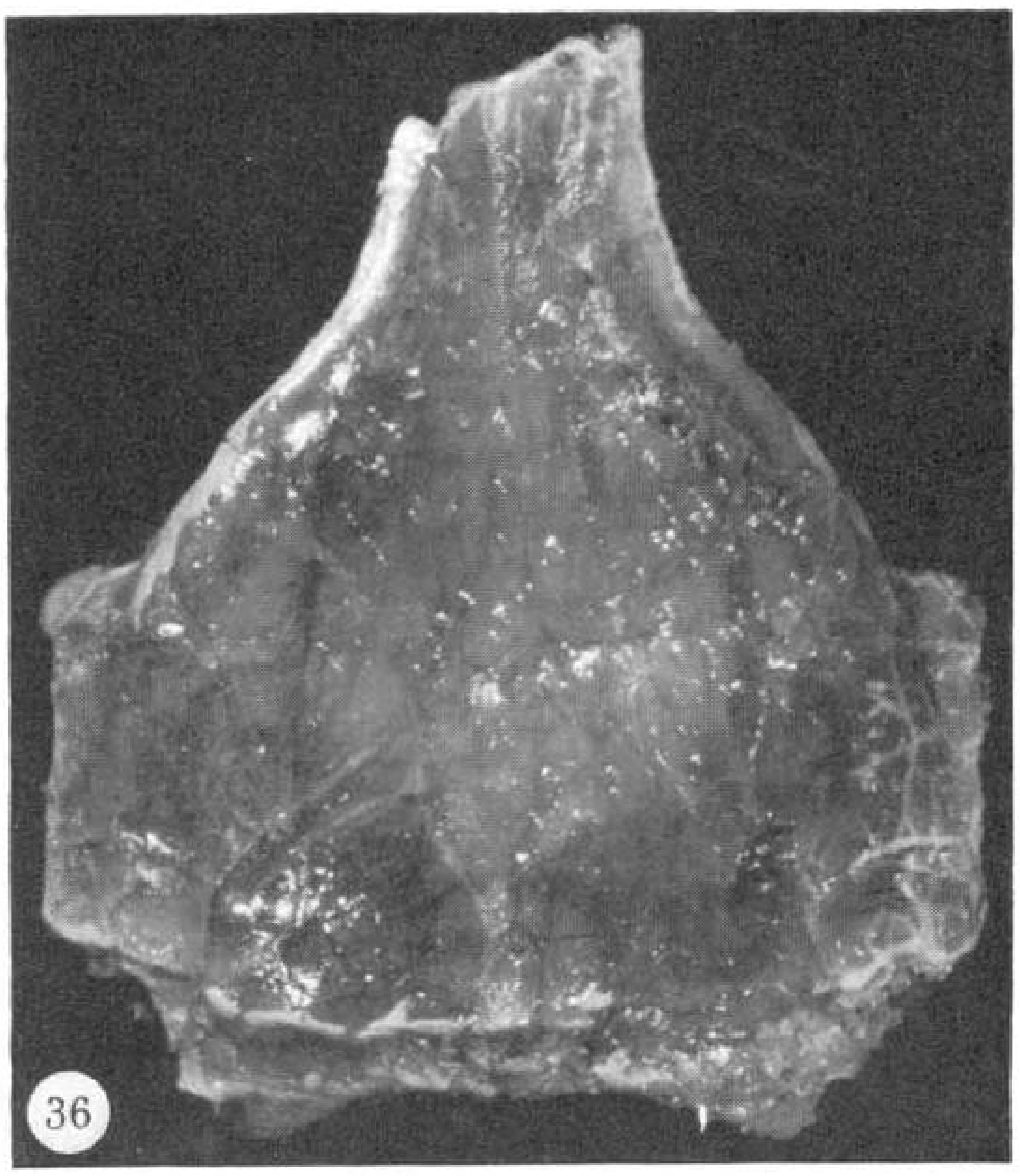
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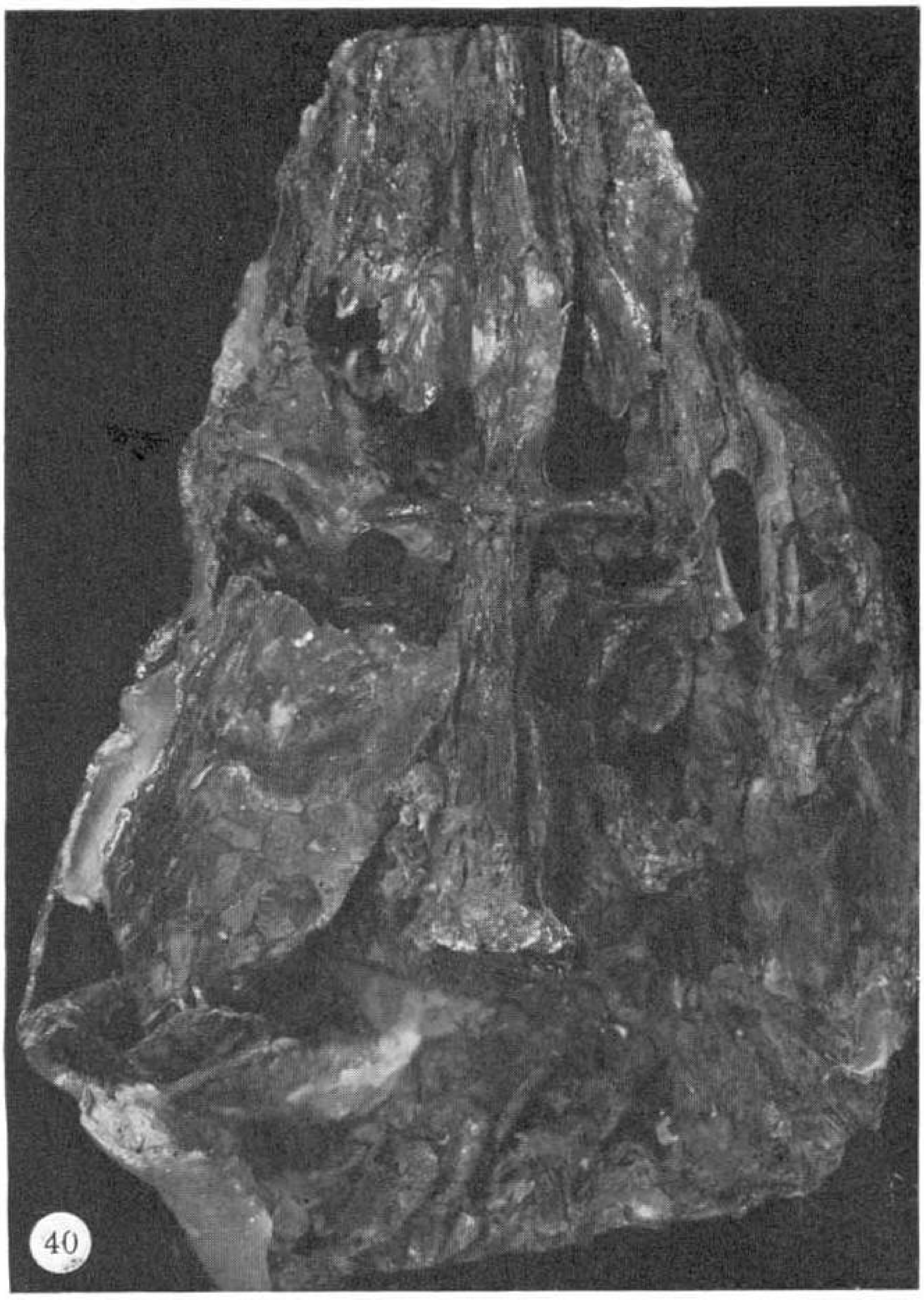
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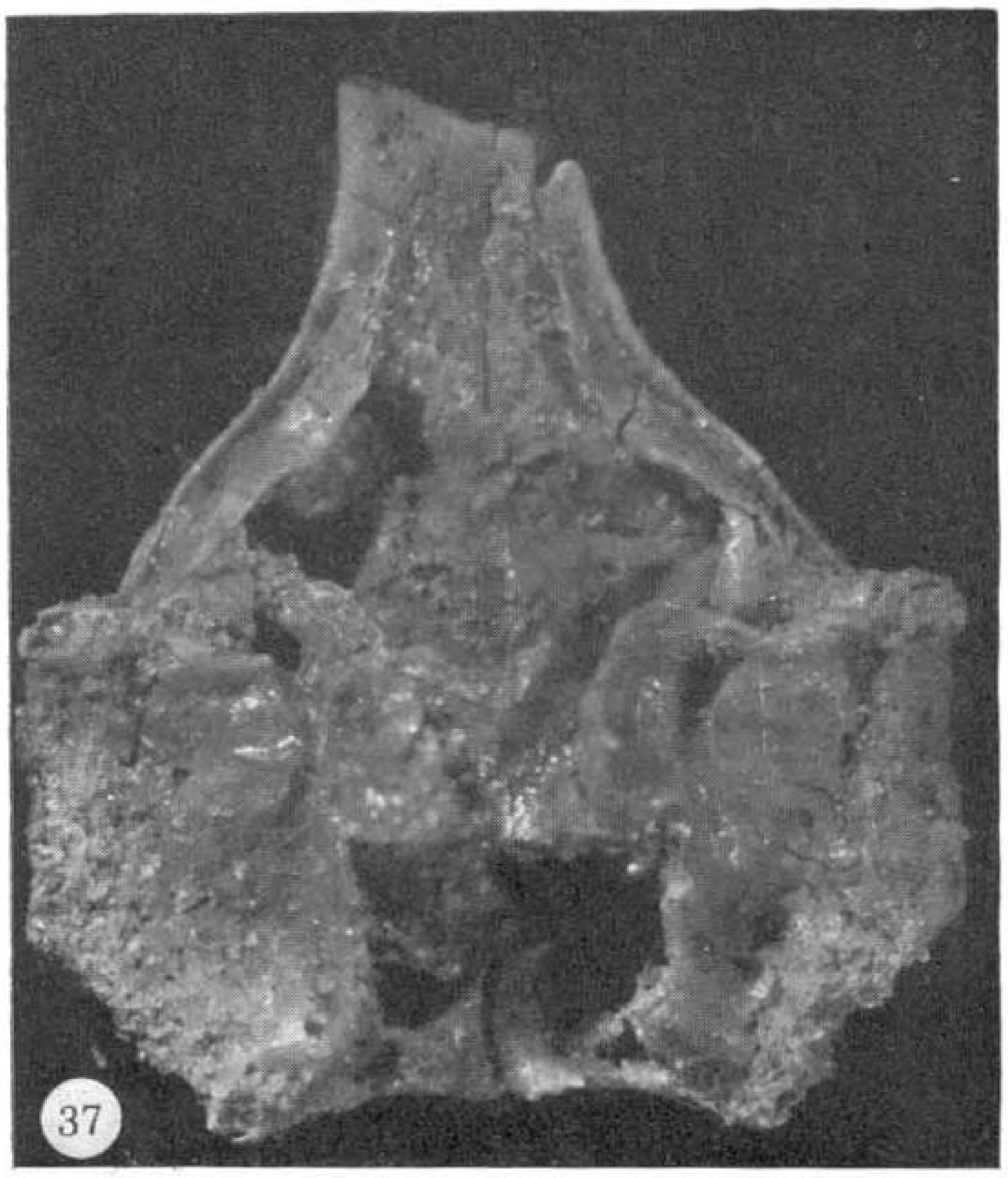
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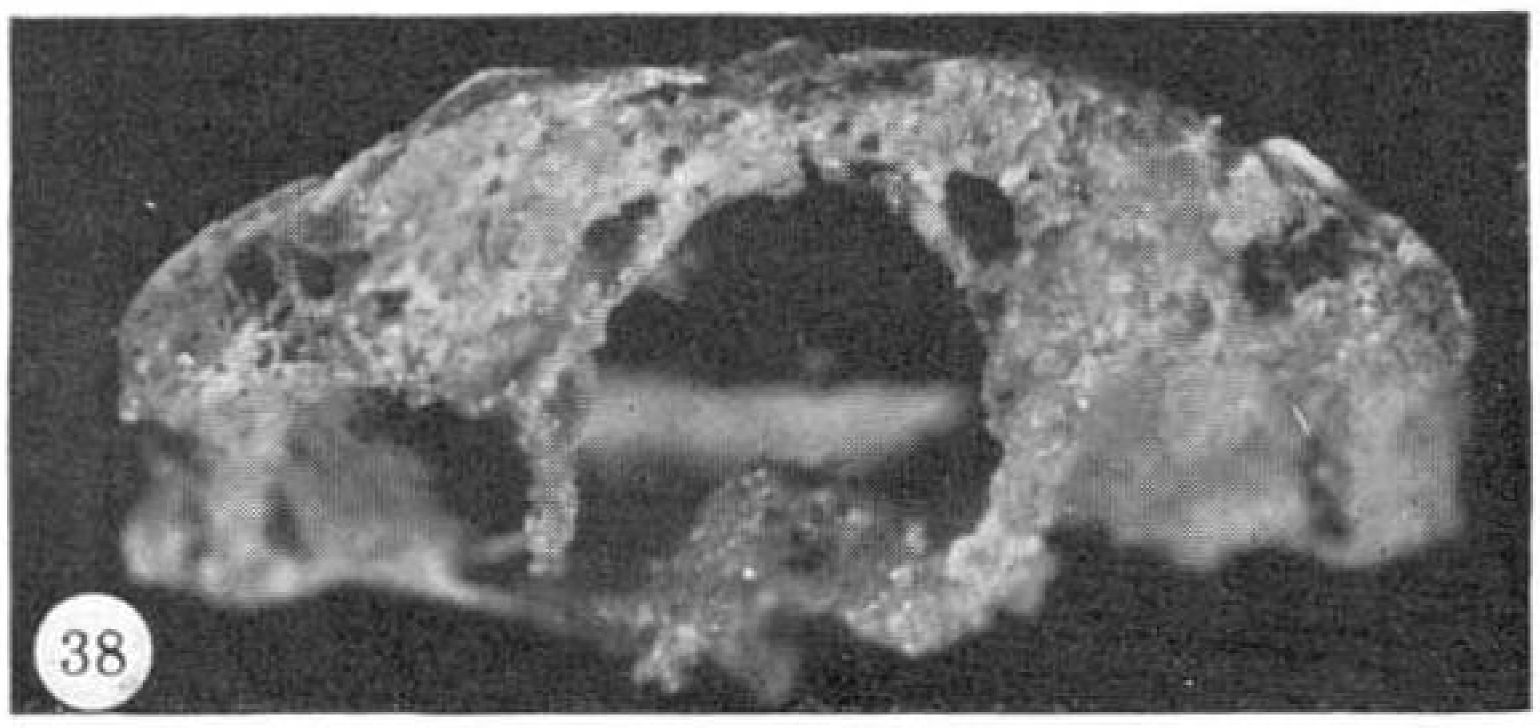
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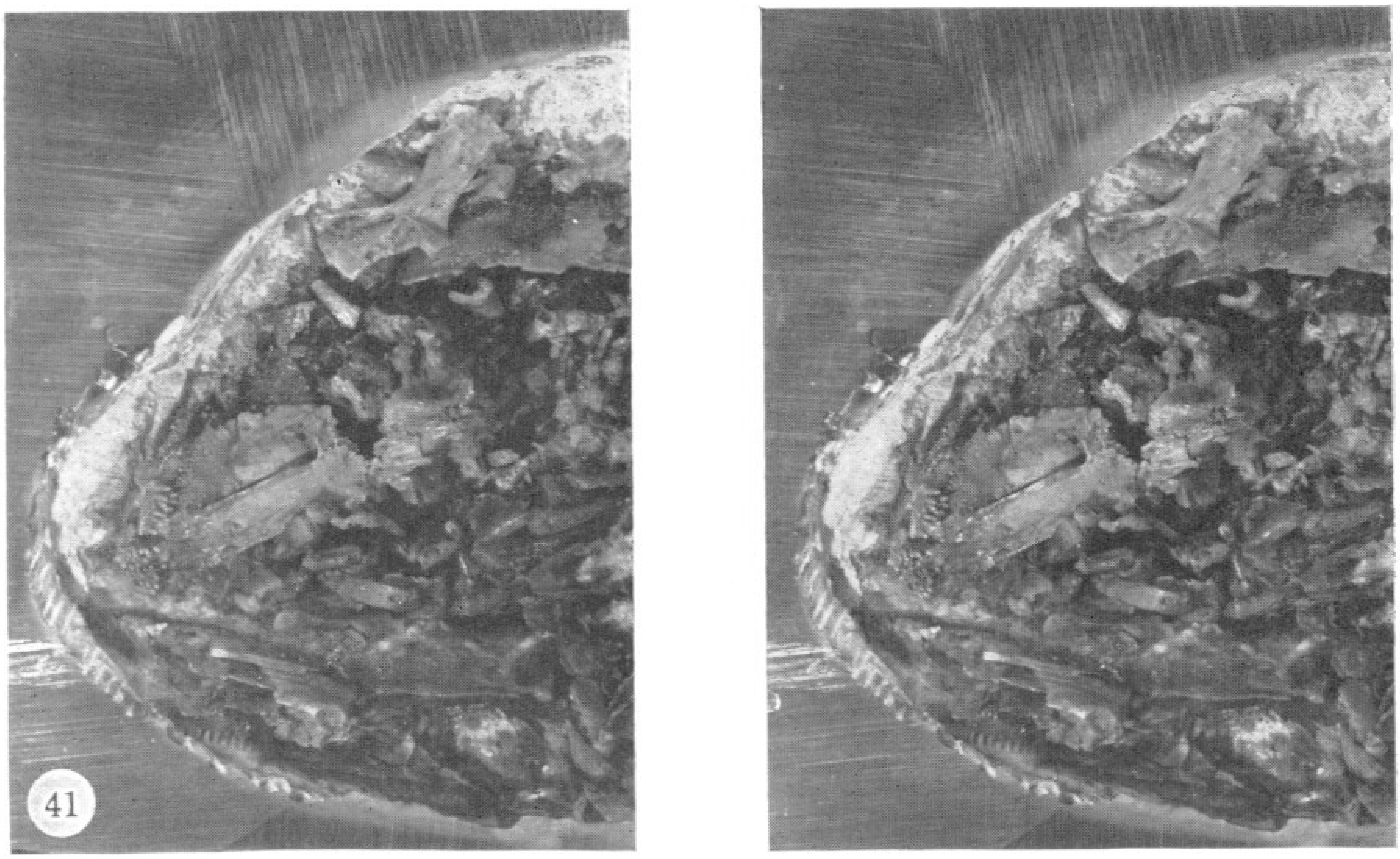
FIGURE 35. *Heterolepidotus* sp. Isolated braincase, P.13260, in posterior view (magn. × 1.5 approx.). See also figures 32–34.

FIGURES 36–38. *Pholidophorus minor* Agassiz. Isolated, incomplete braincase in dorsal (figure 36), ventral (figure 37) and posterior (figure 38) views (magn. × 10 approx.).

FIGURES 39, 40. *Lepidotes toombsi* Jain & Robinson. Imperfect skull, P.34511, showing the braincase in posterior (figure 39) and ventral (figure 40) views (magn. × 1 approx.). See also stereo-pairs, figures 42, 43.



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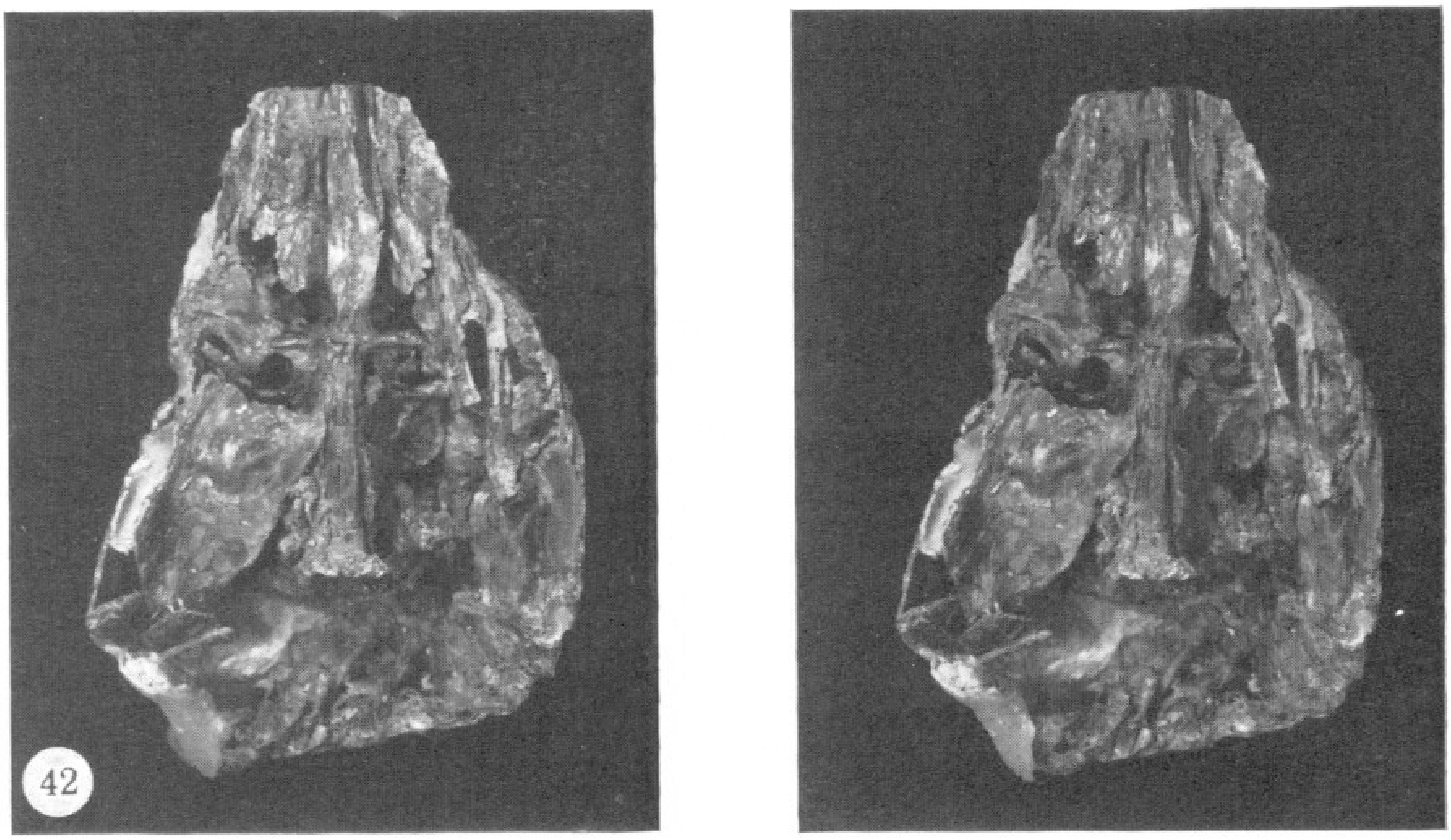

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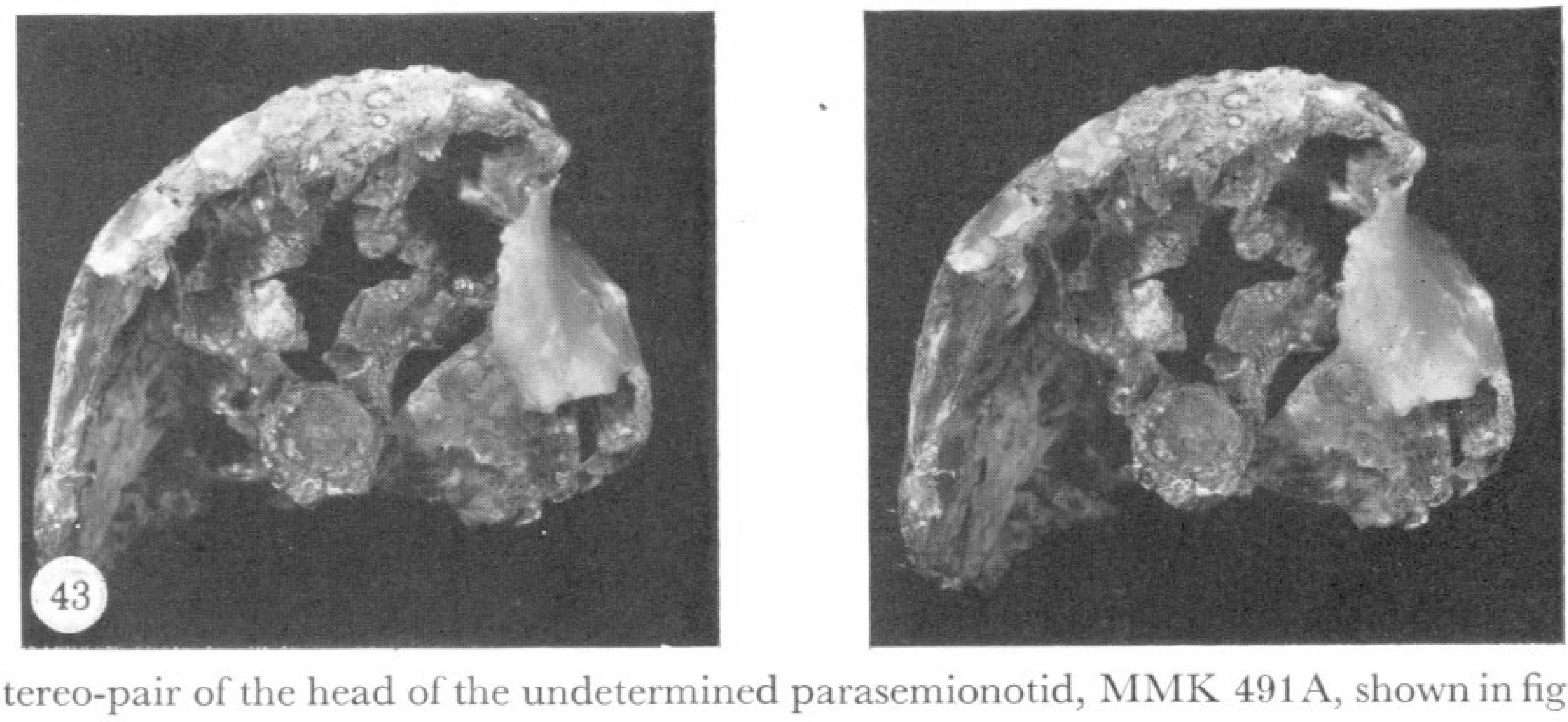

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FIGURE 41. Stereo-pair of the head of the undetermined parasemionotid, MMK 491A, shown in figure 30 (magn. × 0.9).

FIGURES 42, 43. Stereo-pairs of the skull of *Lepidotes toombsi*, P.34511, shown in figures 39 and 40 in ventral (figure 42, magn. × 0.4) and posterior (figure 43, magn. × 0.5) views.