Phil. Trans. R. Soc. Lond. B **318**, 1–107 (1987) [1]
Printed in Great Britain

PHOLIDERPETON SCUTIGERUM HUXLEY, AN AMPHIBIAN FROM THE YORKSHIRE COAL MEASURES

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(*Communicated by H. B. Whittington, F.R.S. – Received* 19 *March* 1986)

[Pullouts 1–4]

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Vol. 318. B 1188 [Published 15 December 1987

Pholiderpeton scutigerum is an eogyrinid amphibian from the Coal Measures of Yorkshire (Westphalian A). The holotype has been prepared by airbrasive and dental-mallet techniques to reveal the most completely preserved of British embolomeres.

The skull and braincase morphology of *Pholiderpeton* is closely similar to that of *Eogyrinus* but has provided new information about many of the skull roofing bones and palate, in particular the pterygoid–epipterygoid complex. The braincase has augmented information gained from other embolomere specimens and a new reconstruction has been attempted. A supraoccipital was not present but the otic capsule was roofed dorsally by the opisthotics, as in loxommatids. Study of jaw function in *Pholiderpeton* suggests that it did not conform to a pure 'kinetic inertial' system but that it was essentially unspecialized. The so-called 'kinetic line' at the junction of the eogyrinid skull table and cheek was not mobile but was probably a butt joint to resist vertical compression generated during jaw closure.

Present on the specimen, and previously undescribed in eogyrinids, were elements of the cervical region, including the atlas neural arch and pleurocentrum, the axis neural arch and rib as well as the pectoral girdle and forelimb, allowing reconstruction of these regions to be made. The eogyrinids resemble *Archeria* in the structure of pectoral limb and girdle. Forelimb function in *Pholiderpeton* was more flexible than that proposed for the related *Proterogyrinus*. The evidence suggests that the eogyrinids, like the archeriids, were long-bodied with a presacral count of 40. The cervical region of embolomeres shows some similarities with that of *Proterogyrinus* but with a more fully ossified atlas pleurocentrum. The atlas vertebra is also compared with that of *Archeria*, previously undescribed.

A study of the skull table in the genus *Archeria* is included to assist in taxonomic studies of eogyrinids. A number of consistent characters were found to exist in this region within one species of embolomere. The genus *Pholiderpeton* Huxley (1869) is shown to be synonymous with *Eogyrinus* Watson (1926) and therefore takes nomenclatural priority, but it may be distinguished from the related *Palaeoherpeton* on a number of characters. The isolated skull table pertaining to *Pteroplax* is not that of an eogyrinid, and is removed from the family. It shows resemblances to *Archeria* and *Proterogyrinus*. The North American eogyrinids are retained within the family Eogyrinidae. The family Eogyrinidae is most closely related to the monogeneric family Anthracosauridae, and together these two form the sister-group of the Archeriidae. The Proterogyrinidae is the sister-group of all three, and together these families form the group Embolomeri. A cladogram to express these relationships is presented.

INTRODUCTION

Pholiderpeton scutigerum, an anthracosaur amphibian, represents the oldest and most complete embolomere to come from the British Coal Measures, but until now has never been fully described. It was found in the roof of the Black Coal Bed at Toftshaw, near Bradford, Yorkshire (lower Communis zone, Westphalian A), the holotype being first described and named by T. H. Huxley (1869).

Little detailed information was available from the specimen at the time of its discovery because of its disarticulation and because the visible surface (the obverse) was almost completely covered with scutes. Hence Miall's (1870) and Huxley's (1869) accounts are contradictory and contain misinterpretations. Some fifty years later, Watson (1926, 1929) redescribed the specimen, figuring a bone which he interpreted as the 'post-temporal' (now recognized as a cleithrum (Romer 1947, 1957, 1963)). Watson was prevented from making a detailed study by the specimen's condition, so a second attributed specimen from Airdrie formed the basis of the skull description. The latter was about thirty percent larger and from a higher horizon (Panchen & Walker 1961).

At the time when Watson saw the holotype, and as it was received by the author, it was embedded in a plaster mount with some of the pieces wrongly orientated with respect to each other. On preparation it became apparent that much more of the animal was preserved than had been suspected. The skull, although disarticulated, is almost complete and includes a well-preserved braincase and stapes (Clack 1983). The right shoulder girdle and forelimb, except for the manus, are present, as are parts of the left. The interclavicle is almost complete. In the cervical region the atlas and axis arches are present with the axis pleurocentrum and some cervical ribs, but the rest of the vertebral column is disrupted. There is no indication of pelvic girdle, hindlimbs or tail.

Watson's work on embolomeres, which he considered to be the most primitive amphibians, laid the foundations for study of the group. They were characterized by having diplospondylous vertebrae in which the two elements, intercentrum and pleurocentrum, were complete and subequal biconcave discs. He believed that all early Carboniferous amphibia were embolomerous, including the loxommatids, now considered to be rhachitomous. He described '*Palaeogyrinus*' (= *Palaeoherpeton* (Panchen 1970)) for the first time and clarified the relationships of the other members of the group, revealing previous confusion of names and species. Thus he erected the name *Eogyrinus attheyi* (1926) for a particularly fine embolomere skull and associated partial skeleton from the Low Main Seam of Newsham, Northumberland and separated it from two other embolomere genera, *Pteroplax* and *Anthracosaurus*. For the latter three genera he established the family Eogyrinidae, but placed '*Palaeogyrinus*' in a family of its own.

The genera and families of embolomeres were reassessed by Romer (1947) who recognized four families: the Anthracosauridae, Palaeogyrinidae, Cricotidae and Pholidogasteridae. In 1958, Romer attributed an incomplete lower jaw, with great uncertainty, to the genus *Pholiderpeton*, and in 1963 a second jaw fragment was added. Both of these derived from the Point Edward Formation, Nova Scotia; both, however, lack diagnostic elements, such as the surangular crest, and the mesial surface of the jaw. In 1947 and 1966 Romer treated *Eogyrinus* as a synonym of *Pteroplax*.

Panchen (1964, 1970, 1972, 1975, 1977, 1981) has redescribed many embolomere genera and revised their taxonomy in a series of papers. In 1964 *Eogyrinus* was again separated from *Pteroplax*, following Watson, but Panchen was uncertain that '*Palaeogyrinus*' was separate from *Eogyrinus*. In 1970 he placed *Palaeoherpeton*, *Pteroplax*, *Eogyrinus*, and *Pholiderpeton* together in the family Eogyrinidae; *Anthracosaurus* was again removed to a separate family. He noted that each of the four eogyrinid genera above fell at a separate point on an allometric graph and that each derived from a different horizon. Thus the generic distinctions were maintained. A complete and detailed description of *Eogyrinus* followed in 1972, and subsequently papers on *Eoherpeton* (1975) and *Anthracosaurus* (1977, 1981) completed the series and consolidated the taxonomy. *Eoherpeton* was the name Panchen gave to the anthracosaur skull which both Watson and Romer had previously attributed to the genus *Pholidogaster*. In the same paper he showed *Pholidogaster* to be an early temnospondyl with rhachitomous vertebrae and in no way related to anthracosaurs.

As a result of preparation, the holotype of *Pholiderpeton scutigerum* has provided a wealth of new information about the anatomy of embolomeres, helping to solve some of the problems met by previous authors and allowing a reassessment of eogyrinid functional anatomy and relationships.

Several embolomere specimens consist of isolated skull tables, which have until now proved difficult to classify. To assist with this, a series of undescribed skull tables of the Permian embolomere *Archeria crassidisca* from the U.S.A. was studied. Combined with information from *Pholiderpeton*, this has permitted further clarification of embolomere taxonomy.

Here the terms 'Anthracosauria' and 'anthracosaur' are used in the sense of Panchen (1970, 1975) to include only *Eoherpeton* and the families Gephyrostegidae, Proterogyrinidae, Anthracosauridae, Eogyrinidae and Archeriidae. The relationships of this group to the Seymouriamorpha, which Romer included in the Anthracosauria, have yet to be demonstrated unequivocally, and are the subject of current discussion (Holmes 1984; Panchen 1985; Smithson 1985, 1986).

Materials and methods

The holotype of *Pholiderpeton scutigerum* is preserved in about 25 slabs of shale or fossil wood containing the anterior half of the disarticulated skeleton. On removal of the blocks from the plaster, it became obvious that, when correctly aligned, the slabs form three units, two of considerable length (braincase block, figure 39, pullout 1; main skull block, figures 40 and 41, pullouts 2 and 3) and one much smaller one (figure 39). The three cannot be matched to form one continuous specimen but the spatial relation of the three units in the original stratum could be inferred by reference to two straight slickensided faults, about 1 cm in depth, running in the matrix on the reverse of the specimen. Because they were not quite parallel to each other, they allowed determination of the order of the blocks, and indicated that the smallest unit lay between the larger ones. Most of this matrix has now been removed.

The slabs were reinforced, where necessary, with a dilute solution of Perspex in ethyl acetate, major breaks being mended with Glyptal (a proprietary resin soluble in butanone). The thin film of matrix on the obverse of the specimen was removed by airbrasive with sodium bicarbonate, and the reverse was prepared by using a dental mallet and airbrasive.

Where possible, some of the scutes overlying the obverse of the specimen were carefully removed, although as they often disintegrated it was not possible to preserve them all. A pictorial record was made of the original distribution (figures 39 and 41). In addition to scutes, bones overlie and obscure each other, rendering some important information inaccessible. The preservation of that material which is accessible is exceptionally good and the finest surface detail is visible.

In addition to the main blocks, the Keighley Museum houses several small isolated fragments from the same locality, including centra, neural arches, ribs, scutes, lower jaw fragments and the stem of a clavicle. Some of these, notably the latter two, originally belonged to the main blocks and have been fitted on. Others, preserved in identical lepidodendroid matrix, I was unable to fit onto the main specimen, but they may well have been collected along with it.

One lower jaw fragment had one edge cleanly cut and polished. A matching piece was located in the British Museum (Natural History), as were several other fragments which pertained to the holotype specimen. This museum houses other fragments from Low Moor, a locality very close to Toftshaw.

The Museum of Comparative Zoology, Harvard University (MCZ), houses a collection of material catalogued originally as *Pholiderpeton* MCZ 2550, and recorded as being from Low Moor. On examination it was found to include loxommatid lower jaw fragments, a lungfish rib, the suspensorial region of an anthracosaur, and vertebrae, ribs and scutes of an embolomere. One of these pieces was found to be part of the holotype specimen and so came not from Low Moor but from Toftshaw. It is not possible therefore to be certain which of the whole collection was from Low Moor and which from Toftshaw, but the anthracosaur suspensorium is almost certainly from the Better Bed Coal from Low Moor. These items were purchased during the nineteeth century from one of a group of well-known local naturalists who would all have had access to the Bradford material. Enquiries to other museums as to whether other pieces of the holotype of *Pholiderpeton* found their way elsewhere have proved negative.

Drawings were made from photographs or by means of a camera lucida attachment to a Wild M5-72049 binocular microscope.

The following abbreviations, taken from the unique accession or catalogue numbering system in most cases, are used to indicate the institution from which each specimen derives.

AMNH, American Museum of Natural History, New York.
R, British Museum of Natural History, London.
NS, Cliffe Castle Museum, Keighley, W. Yorkshire.
G, Hancock Museum, Newcastle upon Tyne.
MB, Museum für Natürkunde, Humboldt Universität, Berlin.
GS, British Geological Survey, Keyworth, Nottinghamshire.
L, Manchester Museum, Manchester University.
MCZ, Museum of Comparative Zoology, Harvard University.
NMP, National Museum, Prague.

RSM, Royal Museum of Scotland, Edinburgh.
T, University Museum of Zoology, Cambridge.
YPM, Yale Peabody Museum, Yale University.
All scale bars used in the figures represent 10 mm unless otherwise indicated.

CRANIAL ANATOMY OF *PHOLIDERPETON SCUTIGERUM*

Dermal skull roof

All but a few skull bones are present in the holotype. Both palatines, one postorbital, the right squamosal and right quadrate are missing (*contra* Clack 1983). Most of the skull bones are disarticulated, except for the skull table and snout roofing bones, which have remained in contact with each other and with the braincase (figure 38, p. 98). The preservation has allowed the internal (visceral) surface and many of the sutural surfaces to be described for the first time. Skull reconstructions are presented below (figures 17–19, pp. 43–45). The relations of the bones to one another in the intact skull are those seen in all eogyrinids (Panchen 1964, 1970, 1972) and will not be described in detail. Detailed specimen drawings are also provided (figures 38–41).

The premaxillae lie adjacent to one another (figure 41) but one has been rotated through 180° with respect to the other. The right element shows the overlap for the suture with the nasal and the emargination for the right naris. There are four teeth but no lateral-line grooves present. Three of the teeth from the left element are visible on the internal surface. A complex fragment overlying the left premaxilla probably represents part of a shelf-like attachment for the vomer. This shows part of the midline suture and the ventral surface, which is smooth except for a nutrient foramen. The junction with the maxilla cannot be seen in either element. In the right element, the outer surface shows a rounded margin below the naris. It remains uncertain whether the premaxilla sutured to the maxilla in palatal view, or what contribution it made to the choanal margin.

Neither maxilla is completely visible (figure 41). The posteriormost teeth of the right have now been exposed by removal of scutes and the length of the tooth-row has thus been determined. Ornament on premaxillae and maxillae is represented as faithfully as possible in the figures. The maxillae taper from a widest point of 25 mm, lying 50 mm back in the left element, to about 10 mm anteriorly and 7–8 mm posteriorly. The right element tapers less strongly. The widest point lies behind the moderate 'canine peak' seen in *Pholiderpeton*, but in the maxilla of the Airdrie specimen and G 40.28, an isolated maxilla from Newsham (Barkas 1873, type of '*Leptognathus*'), the widest point coincides with the canine peak. The anterior tips of the holotype maxillae differ from each other, presumably as a result of differential preservation. The right maxilla has a rounded anterior margin in external view, as have those of G 40.28, the Airdrie specimen and the lectotype of *Eogyrinus attheyi*, and probably represents the natural condition.

The internal surface of the left maxilla has been exposed at the anterior end, as have parts of the internal surface of the right. Supplemented by information from G 40.28, much of this surface can be described. A broad sutural surface for contact with the lachrymal dorsally runs over the expanded end, narrowing posteriorly. A shelf *ca.* 8–9 mm wide runs down the length of the bone internally. The smooth dorsal surface slopes down towards the midline; the ventral surface is striated for suture with the palatal bones. Anteriorly, level with the large teeth of the 'canine peak', the shelf provides the lateral margin of the internal naris. Posterior to the naris, the shelf is drawn out into a buttress bearing facets for contact with the palatine. Anterior to the naris, the shelf terminates in a surface for contact with the premaxilla. In *Palaeoherpeton* the lateral margin of the naris is similar in structure, although again the type of contact with the premaxilla is uncertain.

Both lachrymals are represented (figures 38 and 41), the right still in its natural relation to the nasal and the prefrontal. Its anterior part is well preserved in internal view, some of its posterior part being missing and some preserved in MCZ 6976 (ex MCZ 2550). A little of its external surface has been prepared out to reveal the lateral-line canal. The left element is preserved in contact with the left jugal, close to other bones of the cheeks and jaws. Whereas the left jugal is preserved in external view on the obverse of the specimen, the left lachrymal has been turned under to be exposed, like the right, primarily in internal view. A little of its external surface is visible between the right epipterygoid and left squamosal on the reverse of the specimen (figure 40).

The lachrymal is an elongate triangle produced into a narrow tapering process anteriorly, which apparently reached the naris. However, the extent of its exposure in external view is uncertain. At the anterior tip it could have been sheathed externally by the nasal making contact with the maxilla as shown in the reconstruction (figure 17). In *Eogyrinus* (Panchen 1972) the nasal and maxilla exclude the lachrymal from the naris in external view, but in *Anthracosaurus* (Panchen 1977) the lachrymal makes a small contribution to the narial margin. The lachrymal is not visible in internal view in any specimen of *Eogyrinus*, where it may have reached the naris internally. *Pholiderpeton* may show a condition intermediate between *Eogyrinus* and *Anthracosaurus*.

Five prominent buttresses mark the anterior part of each lachrymal internally, coalescing ventrally (figures 19*a*, 38 and 41). The most highly developed continue dorsally onto the nasals, but apparently not onto the maxillae. They occur above and posterior to the canine peak. The sutural surface of the lachrymal is bowed to fit over the expanded maxilla. The surface is broad, flat and pitted, rather than being an interdigitated overlapping suture. It is consistent with a butt-joint, designed to resist vertical stress. The buttressed lachrymal must also have strengthened this part of the snout, which would have been subject to compressional forces during biting.

The right lachrymal provides a cross section of the bone. A foramen about 2 mm in diameter could represent the lachrymal duct, although it seems a little small. The lachrymal duct can be seen in cross section in *Anthracosaurus* (Panchen 1977*a*).

The nasals, in internal view (figure 38), are preserved in their natural relation to one another and to the frontals. Each is roughly rectangular, except that the posterior margin is strongly concave on either side of the midline. The anterior end is slightly expanded. The internal (ventral) surface is marked by prominent ridges, grooves, foramina and sculpturing (figure 38). The grooves probably mark the course of blood vessels, and are interrupted by foramina. A roughened sculptured region runs down the midline where the cartilaginous nasal capsule probably attached. Curved ridges probably mark the mesial extent of the nasal capsule, corresponding to similar ridges in *Eryops* (Sawin 1941).

The anterior margin of the nasals formed the dorsal boundary of the external naris laterally, the premaxilla fitting under it mesially. The nares were apparently 'flared' as in *Eogyrinus* (Panchen 1972). Anteriorly, the lateral edges form a deeply interdigitated sutural surface broad enough to have covered the anterior tip of the lachrymal externally, to exclude it from the naris in lateral view. More posteriorly the nasals narrow, and would presumably have left the lachrymals exposed thereafter.

The prefrontals (figure 38) are large and roughly triangular, and, as in other embolomeres, exclude the lachrymal from the orbit. They are characterized internally by a strongly developed ridge running from the anterodorsal margin of the orbit, across the bone, to a point roughly midway along the opposite margin. A similar ridge is found in *Palaeoherpeton*, where it forms the mesial edge of the thickened rim of the orbit (Panchen 1964). Although it may have buttressed part of the cartilaginous anterior extension of the braincase, as Panchen suggested, it seems unlikely to indicate the posterior limit of the nasal capsule as Beaumont (1977) suggested for loxommatids. Rather, the capsules were probably narrow and rather short, although their area might have been increased by the lachrymal buttressing.

The frontals are also in natural association with surrounding bones. The anterior suture with the frontals is obscured by the processus cultriformis and the posterior suture with the parietals is overlain by the sphenethmoid. Ridges and grooves on the nasals continue onto the frontals but are less prominent. Mesial to the suture with the postfrontal, the suture with the sphenethmoid is rugose, corresponding to the roughened surface seen in *Palaeoherpeton*. The braincase was obviously tightly applied to the skull roof here.

The jugals lie exposed in external view on the obverse of the specimen, at 180° to one another. The left has its posterior margin missing, but this is adequately preserved on the right (figure 41). Ornament consists of an irregular mesh, except near the suture with the quadratojugal, where radiating grooves converge towards a point below the orbit. The infraorbital sulcus is well defined, particularly anteriorly, and another groove runs from the posterior margin close to and parallel with the ventral margin but does not join the infraorbital sulcus. Overlap areas show that squamosal and lachrymal lapped over the jugal but that this itself lapped over quadratojugal and postorbital. It has a butt-joint with the maxilla. The flattened surface formed the processus alaris just behind the orbit.

The jugal did not contribute to the jaw margin as Panchen (1964, 1972) suggested for *Eogyrinus* and *Palaeoherpeton*. In the lectotype of *Eogyrinus* the quadratojugal–jugal suture, which can be seen in internal view on the left, shows that the jugal was excluded from the jaw margin. However, in *Palaeoherpeton* the jugal does have a marginal component. This represents a difference between *Palaeoherpeton* and the two larger genera, and also *Eobaphetes*.

Part of an exposed postorbital shows the lateral-line canal. The left squamosal is complemented by that in MCZ 6977 (figure 1*a*) (Clack 1983). In the latter specimen, the squamosal, quadrate and quadratojugal are preserved with their sutures almost intact. The ornament is similar to that on the jugal in being shallow and irregular. It is finest just below the dorsal margin.

The squamosal is an important bone in the architecture of the skull; this importance is reflected in the complex structure of its dorsal and posterior margins where it meets the skull table and palatoquadrate ossifications. The dorsal border is unfortunately incomplete in the type specimen but is well preserved in MCZ 6977. The articular facet for junction with the skull table resembles those described by Panchen for *Palaeoherpeton* and the Swanwick *Pholiderpeton*, being concave, pitted and roughened with a rounded posterior margin. As in *Palaeoherpeton* it is set at an angle of about 30° to the rest of the bone, but was probably nearer 45° in life. In MCZ 6977 the facet extends along the whole dorsal margin of the squamosal,

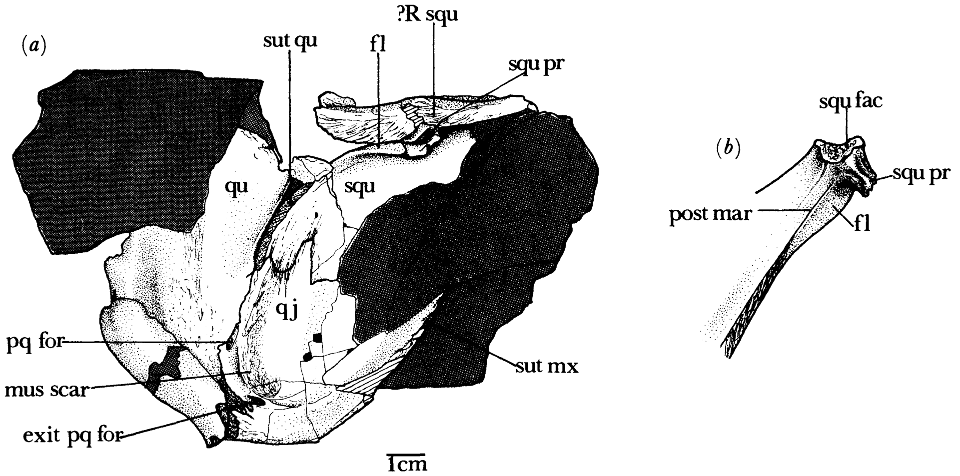


FIGURE 1. (*a*) *Pholiderpeton scutigerum* MCZ 6977, squamosal, quadratojugal and quadrate, internal view; (*b*) *Pholiderpeton scutigerum*, reconstruction of posterior view of squamosal.

with a notch for a process of the postorbital. The postorbital must also have contributed in part to the articular facet.

On both specimens the underside of the squamosal reveals new and important detail. The articular facet is borne on a complex boss, quite distinct from the rest of the plate-like bone. Projecting from the underside of the boss is a stout process (the 'squamosal process') which terminates in an irregular grooved and ridged facet. Unfortunately, in the holotype, the more anterior parts are broken, and obscured in MCZ 6977, but where complete the surface appears covered in finished bone. The process is set at an angle of nearly 90° to the main squamosal plate, although, like the angle of the articular facet, it has probably been exaggerated by *post mortem* compression. The boss bears a complicated relation to the posterior margin of the squamosal, best conveyed by an illustration (figure 1*b*).

The squamosal process probably provided surface for a ligamentous attachment to the pterygoid. Lower down along the posterior margin, MCZ 6977 exhibits the diagonal grooves of a sutural surface for attachment of the quadrate. Further ventrally the quadrate is still in articulation. The whole posterior edge of the squamosal is gently convex in both specimens, except for about 6 mm below the squamosal facet.

The region is also preserved in the holotype of *Palaeoherpeton decorum* but it is not so well preserved, nor is the quadrate present. This has led to differences in interpretation between the above and Panchen's account of *Palaeoherpeton*. First, Panchen described the posterior edge of the squamosal as probably turned inwards, perpendicular to the lateral surface. However, specimen MCZ 6977, with the squamosal in clear relation to the quadrate, shows that this was not the case in *Pholiderpeton*, where the quadrate–squamosal suture ran exactly down the posterior edge of the suspensorial region. Secondly, Panchen restored the posterior edge of the squamosal as being emarginated dorsally to form the ventral and anterior margins of the otic notch. The squamosal in the holotype of *Palaeoherpeton* is broken over the right tabular horn of the specimen and the edge does indeed resemble his restoration. However, there is no such emargination in the squamosal of *Pholiderpeton*. Unless *Palaeoherpeton* is considerably different from *Pholiderpeton* it seems more likely that distortion as the result of the break has caused the discrepancy. The implications of this with regard to the shape of the 'otic notch' have been discussed elsewhere (Clack 1983). A distinct muscle scar (figure 1*a*) passed down the posterointernal margin of the squamosal onto the quadratojugal, seen in MCZ 6977.

A small but taxonomically significant difference between *Pholiderpeton* and *Palaeoherpeton* lies in the course of the lateral-line canals. Two clear sulci run over the squamosal in *Palaeoherpeton*, forming a y-shape, with the longer arm curving dorsally across the bone to continue on the jugal. Its lower arm continues onto the quadratojugal. In *Pholiderpeton* no significant lateral lines appear on the squamosal, but a short length runs parallel to the ventral margins of quadratojugal and jugal, as in *Eogyrinus* (figure 35).

The left quadratojugal is almost complete in the holotype of *Pholiderpeton*. The missing anterior and anteroventral parts are represented in a portion of the right quadratojugal, preserved overlying part of the left jaw ramus (specimen NS 62-78/15). The left quadratojugal is also preserved in MCZ 6977, where it has remained sutured to the quadrate and squamosal, although it has been broken and partly pushed under the squamosal. A good internal view is available and the ventral border is complete (figures 1*a* and 40). Anteriorly, where it joins the jugal, the ornament is deeply grooved and matches that on the posterior part of the jugal. It is also quite well defined along the ventral border, but further dorsally it becomes shallow, resembling that on the squamosal. At its posterior corner, the ornament disappears altogether to leave smooth bone.

Irregular pits and roughening along the posterior border provide the sutural attachment for the quadrate. The bone is considerably thickened here, producing a distinct hollowing out of the internal surface. A break runs across this thickened region and it seems probable that the whole bone was strongly curved inwards, the break occurring at the apex of the curve. In *Palaeoherpeton* a break occurs in a similar position, which Panchen (1964) interpreted as the suture with the quadrate.

Re-examination of *Palaeoherpeton* reveals the same basic structure in each. Above the suture with the quadrate the margin forms the ventral border of a foramen, whose upper border would be formed by the squamosal. This is also seen in *Palaeoherpeton* and is the paraquadrate foramen, present in many early tetrapods. It is confluent with another foramen anterior to the thickened border of the quadratojugal and 11 mm above the ventral border on the internal surface. They are linked by a tunnel running through the thickened part of the bone, revealed by a break in MCZ 6977. The anterior part of the ventral border forms a notch and sutural edge for attachment of the maxilla.

The holotype of *Pholiderpeton scutigerum* is preserved with an almost complete skull table, lacking only the right tabular horn (figure 38). The braincase has remained *in situ*, and a pleurocentrum obscures parts of the left tabular and supratemporal. The internal surface has been prepared as far as possible, but the external surface is largely covered by scutes. These have been removed in places.

Skull tables are known from several embolomeres and that of *Pholiderpeton* bears a general similarity to those described, and can be compared with them: *Eogyrinus* (Panchen 1972), specimens G 13.71 (lectotype of *E. attheyi*), isolated specimens R 8426 and G 13.78, both attributed to *Eogyrinus* by Watson (1926) and Panchen (1972); *Palaeoherpeton* (Panchen 1964), specimens G 15.71 (holotype of *P. decorum*) and A1, attributed by Panchen (1964); *Pholiderpeton* (Panchen 1964, 1970) specimen A2, attributed by Panchen (1970); *Pteroplax* (Atthey 1877; Boyd 1978), specimen G 15.72 (holotype); *Eobaphetes* (Panchen 1977); *Anthracosaurus*

(Panchen 1977); and *Proterogyrinus* (Holmes 1984). A skull table of *Archeria* (MCZ 2121), not described before, is available to me and is included in the analysis.

The ornament revealed in *Pholiderpeton* conforms to that found in *Eogyrinus*, *Palaeoherpeton* and A2 in pattern and distribution: well-defined pits on intertemporal, supratemporal and tabular; elongated pits and ridges on postparietal; diffuse and shallow pits on parietal. The ornament on *Eobaphetes* is similarly distributed but finer. In *Pteroplax*, the ornament on the parietal is rather different from that in the above, consisting largely of attenuated pits radiating from the region of the parietal foramen. This is also the case in *Proterogyrinus* (Holmes 1984). Ornament on the skull table of *Archeria* is most like that of *Pteroplax*. The ornament of G 13.78 is much less well defined than in the *Eogyrinus* lectotype, to which genus it has been attributed, and is usually described as 'eroded'. There is no evidence as to the presence or absence of lateral-line canal grooves on the skull table on the holotype of *P. scutigerum*.

Good internal and occipital views are available from the holotype of *P. scutigerum*. Internal views of skull tables are available for *Palaeoherpeton* (holotype), *Eogyrinus* (R 8426 (figure 2*a*),

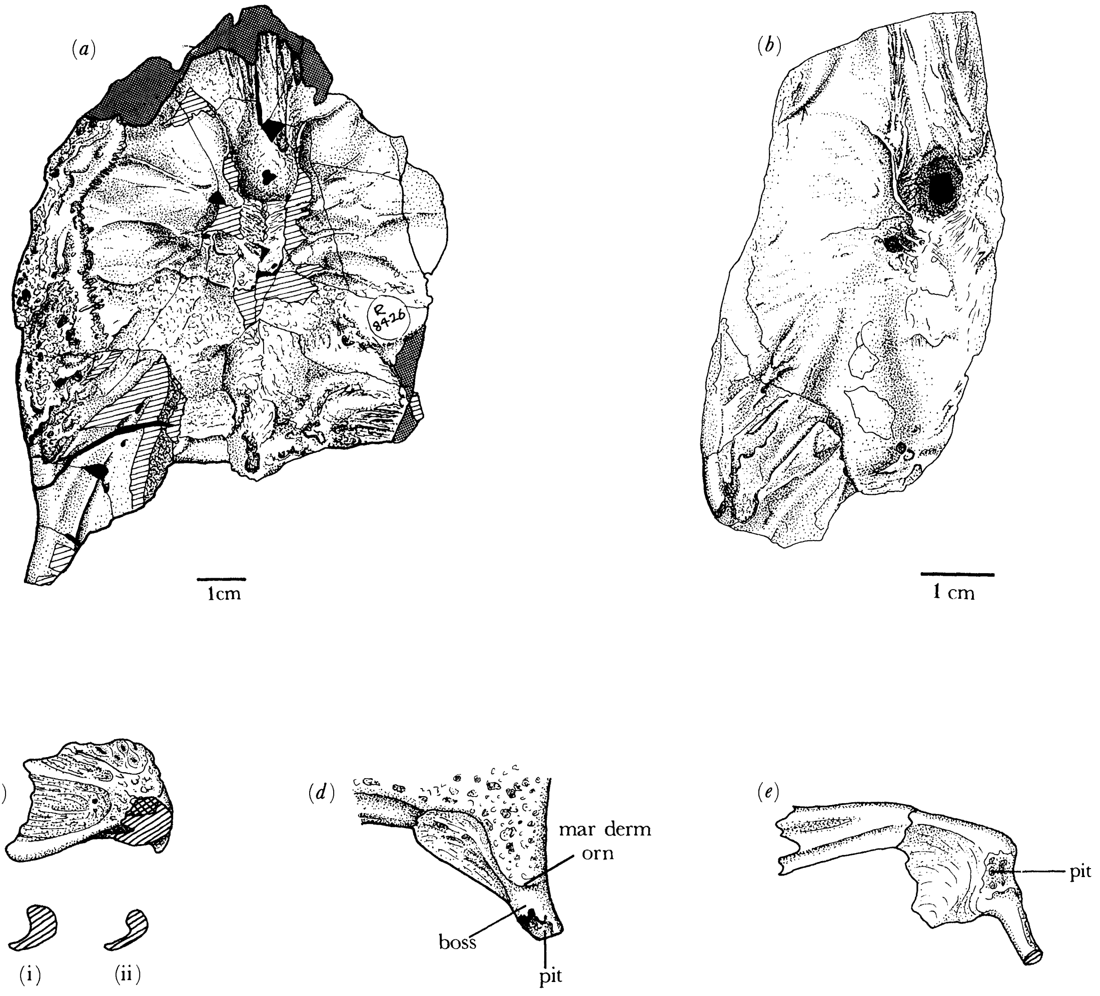


FIGURE 2. Embolomere skull tables and tabulars: (*a*) R 8426, ventral view of skull table; (*b*) *Pteroplax cornuta* holotype, internal view of skull table; (*c*) *Pholiderpeton scutigerum* holotype, posterior view of right tabular; below, (i, ii), successive sections through tabular horn; (*d*) R 8426, dorsal view of tabular; (*e*) *Archeria crassidisca* MCZ 2063, posterior view of tabular.

G 13.78) and *Archeria* (MCZ 2121). Holmes has figured specimens of *Proterogyrinus*, and *Pteroplax* has been prepared further by the author to reveal most of one half of the internal view and can be described for the first time (figure 2*b*).

The postfrontal, forming the dorsal margin of the orbits, is greatly thickened with a smooth ventral surface, as in other embolomeres. As in both *Palaeoherpeton* and *Archeria*, its suture with the frontal runs in a deep groove which could have carried a minor blood-vessel. At the posterior end the lateral margin of the postfrontal has a sutural surface for contact with the postorbital. The intertemporal was thereby excluded from the orbit as it was in *Palaeoherpeton*, *Archeria* and G 13.78. The area is not preserved in R 8426.

In the lectotype of *Eogyrinus*, the intertemporal is described (Panchen 1972) as having a point contact with the orbital border, although this could have been a variable feature. It is barely excluded in *Proterogyrinus* and may have contributed a small part of the orbit margin in *Pteroplax* (Boyd 1978). The lateral margin of the intertemporal of *Pholiderpeton* bears a groove which fades out anteriorly. Pits and nutrient foramina are also present along the margin, similar to those seen in *Palaeoherpeton*, R 8426, G 13.78, and *Archeria*. This area has not been exposed in *Pteroplax*. The groove and pitting are continued along the lateral edge of the supratemporal in *Pholiderpeton*, *Palaeoherpeton* and R 8426. It is less marked in *Archeria*, and in G 13.78 the edge of the supratemporal is almost smooth, with only a slight incurling of the margin. This is also true of what can be seen in *Pteroplax* and seems to be the case in *Proterogyrinus* (Holmes 1984). Posteriorly on the supratemporal of *Pholiderpeton* the groove fades out and is replaced by a deeply pitted and roughened surface. In R 8426 a similar surface is found just mesial to the margin, the margin itself being essentially smooth. In *Pholiderpeton* the roughened margin is separated from the parietal suture by a smooth area of bone, forming a wide, shallow groove, seen also in *Palaeoherpeton* and *Archeria*, though not in R 8426. In both G 13.78 and *Pteroplax*, the internal surface of the supratemporal is more or less smooth throughout. This area is significant in that it has been perceived (see, for example, Watson 1926) as part of a kinetic junction between skull table and cheek, and its counterpart as the dorsal squamosal facet. It has usually been accepted as a remnant of the kinetic line in this position in rhipidistians, and therefore a primitive feature in tetrapods. It will be discussed further below.

Areas of attachment for the braincase can be seen on the parietals in *Palaeoherpeton* and R 8426 as roughened surface, and they match what can be inferred of the dorsal surface of the braincase from the holotype of *Pholiderpeton*. In both the above, this includes laterally orientated extensions corresponding to the prootic buttresses.

The posteromesial portion of the parietal is greatly thickened in all skull tables in which it can be seen, and is assumed to have been so in *Pholiderpeton*. The parietal typically bears an oval excavation for the parietal foramen, bounded by steeply rising ridges. The feature as preserved in *Palaeoherpeton* resembles a section through a goblet. The ridges were presumably contiguous with the braincase in life and the very thin walls inferred for the braincase in this region are found in *Pholiderpeton*. On either side of the 'stem' of the goblet is a depression (in *Palaeoherpeton*), or a facet (in R 8426), or a deep pit (in *Archeria* and *Pteroplax*), which presumably received the columella cranii. The deep pit in *Archeria* runs into the body of the bone (for example, in MCZ 2063, 2051, 2053, 2072). The braincase continued forward from the parietal along parallel ridges, seen in all available skull tables.

In *Pholiderpeton* and other embolomeres, the remaining surface of the parietal is covered by smooth bone. In *Pholiderpeton*, *Palaeoherpeton* and R 8426 it is characterized by radiating ridges and grooves, giving the bone a fluted appearance. These can also be seen in the lectotype of *Eogyrinus*, and could have served as strengthening struts. In G 13.78, the ridges are poorly developed and are hardly distinguishable at all in *Pteroplax*, *Archeria* or *Proterogyrinus*.

In *Pholiderpeton*, the sutures of the parietals with surrounding bones have been somewhat dislocated by compression, but anteriorly that with the frontal is smooth. Buttresses of the sphenethmoid almost reach the edge of the parietal bone here, and on the left appear coossified with it. The parietal runs beneath the surrounding bones of the skull table; its boundary sutures on the dorsal surface would therefore have been more mesially placed.

The postparietal is exposed in occipital and dorsal views in *Pholiderpeton*. As in other embolomeres, the transition between dorsal and occipital faces of the bone is marked by a ridge. It is less strongly developed than that in *Pteroplax*, where it is produced into a keel, but it is better developed than in *Palaeoherpeton*. It is closest to R 8426. A groove runs along the occipital face of the postparietal just below the ridge, and it continues onto the tabular as seen in both *Pteroplax* and *Palaeoherpeton*. The postparietals are produced posteriorly into the 'widow's peak' so characteristic of embolomere skull tables. In *Palaeoherpeton*, on either side of the 'widow's peak' on the occipital surface, a pair of grooves curve mesially onto the ventral surface and subsequently curve laterally once more. They define and enclose a pair of oval facets standing proud of the rest of the bone surface. Nothing similar is evident on other skull tables, although deep pits are found in an equivalent position to the facets in *Pteroplax* and *Archeria*. The facets in *Palaeoherpeton* presumably received parts of the opisthotic, and a blood vessel probably ran along the groove.

The tabular is a most complex bone and forms the 'cornerstone' of the embolomere skull table (Panchen 1972) (figure 38). It is very similar to that in *Palaeoherpeton* and R 8426, with a smooth lateral margin, thickened with respect to the rest of the skull-table margin. It is produced posteriorly into the tabular horn, which is essentially an outgrowth from the ventral surface. The lateral margin of the horn is smooth until about 8 mm anterior to its tip, where it becomes longitudinally furrowed. The ventral surface of the blade in *Pholiderpeton* lies at a shallow angle to the horizontal in the transverse plane, but it is likely to have been distorted by compression. Originally it was probably nearer to 40°, approaching the conditions in *Palaeoherpeton* and *Pteroplax*. In the longitudinal plane it lay almost exactly horizontally. The horn lies at a similar angle to the skull table in dorsal view as does the left horn of *Pteroplax*, Panchen's restoration of *Palaeoherpeton* and that suggested by the horn base of R 8426.

Posteriorly the tabular bears the deep triangular buttress bearing a facet for the opisthotic as in other embolomeres. It shows no evidence of a finger-like process which might have interlocked with the digitiform process of the opisthotic. I am unable to find such a structure in the type of *Palaeoherpeton*, R 8426, or G 13.78. The buttress has been compressed into the same plane as the rest of the skull table, but probably would have dropped well below it in life. The posterior face is excavated into two hemielliptical depressions, one above the other, the dorsal one rather narrow and continuous with the groove on the postparietal (figure 2*c*). The surface bears irregular sculpturing but not typical dermal ornament, which is confined to the dorsal surface. A boss arises where the posterior face meets the lateral margin in R 8426 (figure 2*d*), *Pteroplax*, *Palaeoherpeton*, G 13.78 and *Proterogyrinus* (Holmes 1984). In *Pteroplax* it is extremely well developed; in *Palaeoherpeton* it is less so. It is the equivalent of this boss which forms the upper ramus of the bifurcate horn of *Anthracosaurus russelli* (Panchen 1977) and probably *Eobaphetes* (Panchen 1977). In G 13.78 the tabular boss is broken off but the boss can be seen in *Archeria*, e.g. MCZ 2063 (figure 2*e*). Beneath the boss in R 8426, *Pteroplax* and MCZ 2063 (figure 2*d*, *e*) lies a deep pit with a rugose surface suggestive of a ligamentous attachment. The area is not preserved in *Pholiderpeton*.

In *Pholiderpeton*, a second, anterior facet for the opisthotic is borne on a ridge curving posterolaterally to merge into the ventral surface as in *Palaeoherpeton*. It separates deep grooves anterolateral and posteromesial to it. The anterior groove runs back to coalesce with the ridge as it joins the ventral surface. At this point in *Pholiderpeton* there is a small depression bounded laterally by a prominent rugose knob of bone (figure 38). There is a pit at this point in both R 8426 and *Pteroplax*. The anterior of the two grooves is unlikely to mark the course of the stapes as Panchen (1964) suggested for *Palaeoherpeton*. The stapes of both animals are now known (Clack 1983) and the ossified portion at least cannot have reached to the skull table. If a cartilaginous extension existed, it could have contacted the tabular further laterally. The knob or pit could represent the site of its attachment.

The posterior groove was interpreted by Panchen (1964) as marking the course of the vena capitis lateralis, which then passed into the braincase. However, as pointed out by Holmes (1984) this vessel would then take a unique course. It normally runs dorsal to the stapes and alongside the otic capsule, ventrolateral to the paroccipital process. It continues forward as the vena capitis medialis in *Sphenodon* (O'Donoghue 1921) and does not normally enter the braincase in the otic region in tetrapods. In *Eusthenopteron* this vein (Jarvik 1954) apparently pierced the braincase ventrally on the expanded paroccipital process. On the other hand, in *Sphenodon*, the vena capitis dorsalis enters the braincase between the parietal and prootic or supraoccipital, or through a foramen in the parietal. The groove could be interpreted as carrying the vena capitis dorsalis (but see braincase description below).

The double tabular facet for the opisthotic with associated grooves is found in a very well-developed form in *Pholiderpeton*, *Palaeoherpeton*, and also *Proterogyrinus* (Holmes 1984). The deep grooves however are less well-developed in *Pteroplax* and not at all in G 13.78, although double facets are evident in both. In *Archeria*, the second anterior facet and ridge are barely present.

Palate

All the preserved palatal bones have been disarticulated. The right ectopterygoid has been exposed in dorsal view by removal of the covering layer of scutes, and in ventral view by removal of matrix. The ventral surface closely resembles that of *Eogyrinus* and the specimen A2 from Swanwick attributed to *Pholiderpeton* by Panchen (1970). It is covered with deep and irregular pits and grooves and each bears a tusk replacement pit. The lateral margin of the left element has been exposed to show the sutural surface for contact with the maxilla. Varying between 3 and 5 mm thick, the sutural surface bears deep longitudinal grooves which presumably formed a 'tongue and groove' joint with the maxilla. By contrast the mesial margin forms a thin shelf projecting from the dorsal surface. It is about 4 mm wide and tapers in cross section to a fraction of a millimetre thick. The lateral margin of the pterygoid must have lain beneath this shelf in an overlapping suture, butting against a step on the ectopterygoid. The suture of the ectopterygoid with the pterygoid at this point shows no strong interdigitations but is a plain surface, as in loxommatids (Beaumont 1977). The ectopterygoid also overlaps the pterygoid in both *Anthracosaurus* and *Eobaphetes* (Panchen 1977), but the reverse situation is described in *Eogyrinus* (Panchen 1972). In dorsal view (figure 3) the

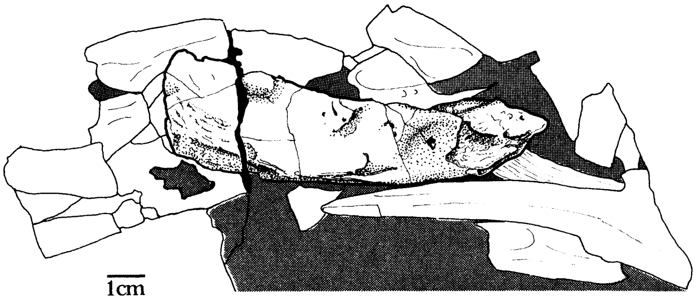


FIGURE 3. *Pholiderpeton scutigerum* holotype, dorsal view of right ectopterygoid.

ectopterygoid is a narrow wedge in shape, with the lateral margin very slightly convex and the mesial very slightly concave. The surface is almost completely smooth, except for an irregular, pitted depression anteriorly, presumably where the palatine overlapped, and a narrow triangular area posterolaterally where the processus alaris from the jugal probably overlay it.

The most completely exposed vomer is probably the left, exposed in ventral view. Its heavily sculpted surface resembles that described in *Eogyrinus* by Panchen (1972) (figure 40). The straight mesial margin is grooved longitudinally. The anterior half is longitudinally grooved and ridged, but more posteriorly a single deep groove enters a pocket in the mesial surface anteriorly. Its internal surface is longitudinally striated and must have housed the anterolateral margin of the pterygoid. Laterally a curved strap-shaped area of very finely sculpted bone marks the mesial margin of the internal naris. It was presumably covered with mucous membrane in life.

There is no evidence for the presence of Jacobson's organ, which Watson claimed as present in the vomer of the Airdrie specimen of *Pholiderpeton* (1929), nor of a vertical internasal septum as seen in section in *Anthracosaurus* (Panchen 1977). The vomers of *Pholiderpeton* are narrow and toothless, and thus typical of those of anthracosaurs.

The left quadrate of *Pholiderpeton* is preserved in part on the holotype specimen (figures 40 and 41), but is far better and more completely represented in MCZ 6977 (figure 1*b*), and a comprehensive picture of the bone is available for the first time. In the holotype the left quadrate is exposed partially in internal (anterior) view. In MCZ 6977 the left quadrate has only the dorsolateral corner obscured by matrix. It consists of a large thin rectangular plate, the articular surface occupying the thickened lower border. This continues laterally on a process which sutures with the posteroventral margin of the quadratojugal, although the latter does not contribute to the articular surface. The arrangement is similar to that in *Eogyrinus* (Panchen 1972) and loxommatids (Beaumont 1977), although Beaumont describes the adjoining quadrate and quadratojugal surfaces as articulating rather than sutural. In MCZ 6977, where this junction has opened up, the surfaces are clearly sutural. In *Proterogyrinus*, however, Holmes describes the quadratojugal–quadrate suture as poorly consolidated, because the two bones have frequently separated during preservation. The articular surface has been fractured in MCZ 6977, and probably somewhat flattened. A silicone rubber cast, cut and restuck, gave the corrected shape. It has a complex 'toroidal' shape, as in *Eogyrinus*: a gentle sigmoid curve in posterior view and strongly convex in cross section, except mesially where it flattens somewhat. The margins are sharply defined as in *Eogyrinus*.

A small process is present above the dorsalmost part of the condyle similar to that in

Proterogyrinus which Holmes (1984) plausibly suggests bore a ligament to the lower jaw (figure 19*b*). Mesially the margin is carried on a projecting lip, above which runs a groove interpreted as possibly carrying a hyoid ligament (Clack 1983). The margin of the articular surface is continued on the internal surface as a smooth convex line. The helical structure of the articulation was possibly associated with some degree of lateromesial movement of the jaws during opening and closing. A complex sequence of movements of this kind was described by Panchen (1972) for *Eogyrinus*, but only carefully constructed models, beyond the scope of this study, could confirm such a phenomenon in *Pholiderpeton*.

The form of the condyle contrasts strongly with that of the loxommatids (J.A.C., personal observations; Beaumont 1977) in that, in *Pholiderpeton*, the curvature in posterior view is convex at the midpoint of the condyle, flattening laterally and mesially to become somewhat concave. In the loxommatids *Megalocephalus* and *Baphetes*, the curvature is concave at the midpoint of the condyle but becomes strongly convex laterally and mesially. The functional significance of this reversal is not clear, although it may be associated with the mode of cranial kinesis in loxommatids (Beaumont 1977) and the jaw action in eogyrinids as described by Panchen. Holmes figures the profile of the quadrate condyle of *Proterogyrinus* as similar to that of loxommatids. The quadrates of other anthracosaurs are not sufficiently well known for comparison; that in the early temnospondyl *Greererpeton* (Smithson 1982) presents a further contrast in form, being almost entirely concave in posterior view.

In the holotype the lower parts of the sutural surface for the squamosal can be seen. It consists of a complex system of longitudinal ridges and grooves. One very broad groove appears continuous along the length of the sutural surface. The dorsal margin of the quadrate, seen in MCZ 6977, is essentially smooth. The mesial margin is roughly straight and the bone thin until about 25 mm above the condyle in MCZ 6977, where it becomes thickened and bears rugosities, one of these being borne on a sharp crest about 14 mm above the condyle (figure 1*a*). The margin then turns smoothly inwards to form a notch above the condyle. The internal surface of the quadrate plate is smooth except for an area of striations running longitudinally down the centre, presumably representing the area of origin of part of the external adductor musculature.

A conspicuous feature of the external surface is a rectangular rugose area about 15 mm above the condyle and about 14–15 mm square. A similar area was noted by Panchen on G 15.88, (this specimen, described by Panchen (1972) as an isolated condyle, was found to be part of the lectotype of *Eogyrinus*), on an embolomere quadrate from Swanwick (uncatalogued, Coope Colln) and quadrates of *Archeria* MCZ 6732, 6733. In G 15.88 Panchen notes that 'these interdigitations...stand above the bone in front of them, yet in ventral view the transition across the suture is smooth, suggesting that the bone in front of the quadrate is the epipterygoid and that at that point the pterygoid is missing'. It is clear that such interdigitations do not mark the dorsal limit of the quadrate but that internally it continues as a smooth and extensive plate. The interdigitations mark a considerable overlap area for the pterygoid, the quadrate ramus of which bears a matching set of interdigitations.

A groove about 7 mm wide runs over the posterior face from the dorsal margin parallel to the lateral margin and 6 mm distant from it (figure 41). A similar though shallower groove on MCZ 6977 is marked by longitudinal striations. The groove is interpreted (Clack 1983) as similar to the 'stapedial groove' noted by Beaumont (1977) in loxommatids, and a pair of pits on the quadrate of *Anthracosaurus*. They possibly mark the course of an extension of the stapes in cartilage or ligament (Panchen 1977).

The embolomere quadrate is remarkably extensive dorsally. This was suspected by Romer (1963) after examination of *Neopteroplax* and is also found in both *Anthracosaurus* (Panchen 1977) and *Proterogyrinus* (Holmes 1984). As reconstructed in *Pholiderpeton*, the quadrate plate reaches well up the posterior margin of the cheek. The squamosal ceases to show a sutural surface for it at about 22 mm below the squamosal facet in MCZ 6977. The quadrate is thus not only extremely well developed but is very firmly attached to the cheek. It shows a considerable advance over the condition in rhipidistian fishes, in which there is no direct connection between the palatoquadrate and the posterior margin of the cheek. Dorsally, however, the cheek in *Pholiderpeton* loses its connection with the pterygoid–epipterygoid complex, in what appears to be a remnant of the fish condition (see below), although this is not indicated in *Proterogyrinus* in Holmes's description. There was clearly no kinesis of the kind described by Beaumont (1977) for loxommatids, between the quadrate and the quadratojugal and squamosal.

Both left and right pterygoid–epipterygoid complexes are preserved on the reverse of the holotype of *Pholiderpeton*, flattened into a single plane, and each exposed primarily in dorsal–lateral (internal) view (figures 4*a*, *b* and 40). Part of the left epipterygoid is missing; part of its columella cranii has been displaced and lies close by. The information from each element is complementary and gives an almost complete picture of this important unit. By contrast little information is available from the ventral–mesial (external) surface of either element, except for parts of the quadrate rami and occasional patches of denticles visible on the obverse. A low ridge can be seen in cross section to run longitudinally on the ventral surface

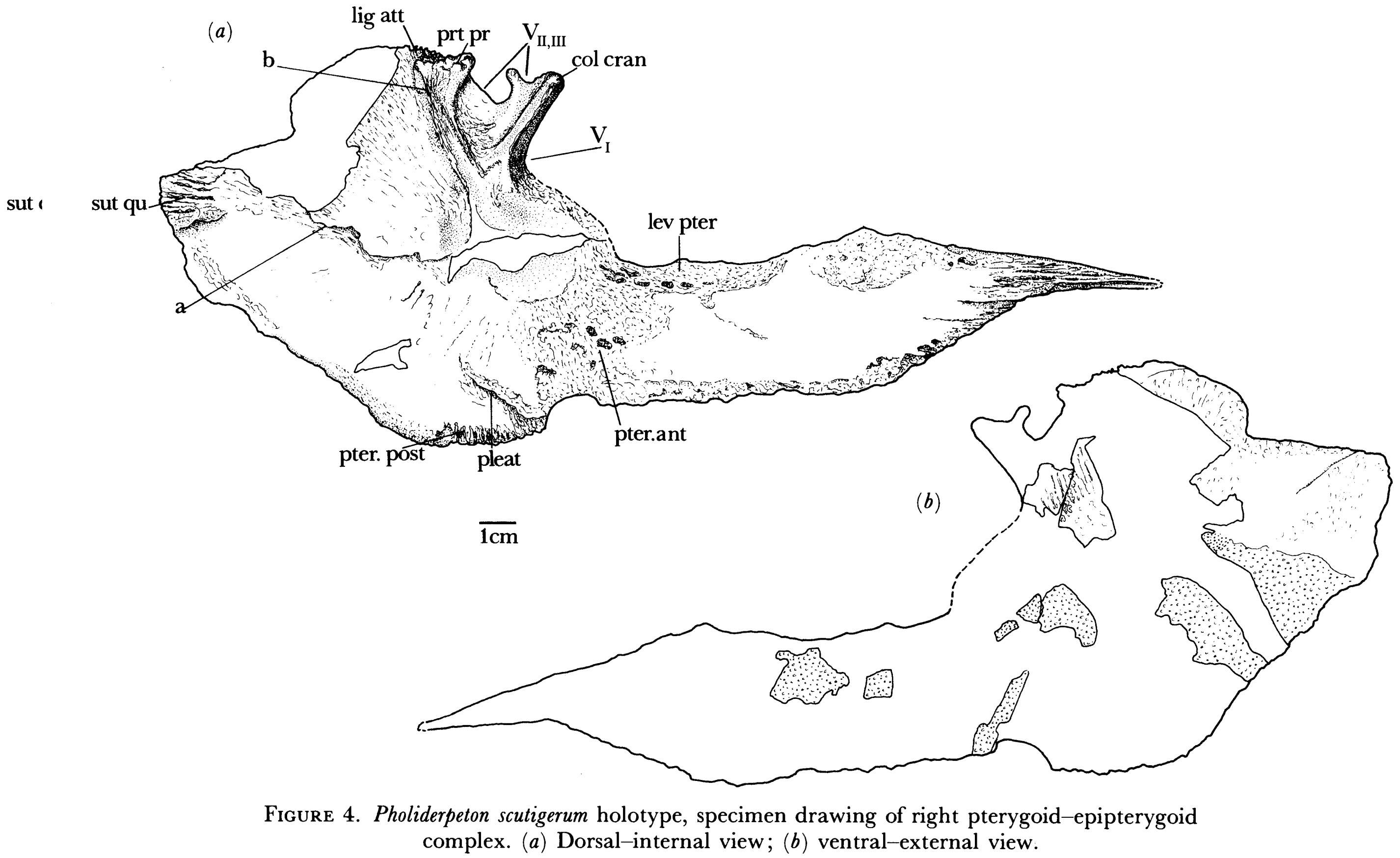


FIGURE 4. *Pholiderpeton scutigerum* holotype, specimen drawing of right pterygoid–epipterygoid complex. (*a*) Dorsal–internal view; (*b*) ventral–external view.

at the extreme anterior end of the pterygoid, resembling that in *Eogyrinus*. The mesial margin bears a narrow undenticulated band.

The dorsal surface of the anterior portion of the pterygoid is strongly grooved and ridged and is produced into a long tapering point. The lateral edge is thickened and bears longitudinal grooves and ridges suturing with the vomer. It broadens significantly from a point about 35 mm back from the tip. The lateral margin shows sculpturing for a strongly interdigitating suture with the palatine, but thereafter is more or less smooth, for the overlapping suture with the ectopterygoid.

The mesial margin bears only shallow grooving at the anterior tip, suggesting that the junction with its fellow was made only by soft tissue. In MCZ 2054, an isolated pterygoid of *Archeria*, this margin is apparently sutural. The margin runs straight along the midline initially then curves laterally to form short narrow interpterygoid vacuities.

There is a shallowly depressed area bearing minimal sculpturing bordering the interpterygoid vacuities, but the ornament appears insufficiently defined to be an area of muscle attachments, although absence or poor development of surface marking may not always correlate with absence or poor development of muscle. This area, however, could correspond to the position of connective tissue surrounding the unossified region of the sphenethmoid. Alternatively it could represent the area of origin of one of the eye muscles, perhaps the inferior oblique. More posteriorly along the margins of the interpterygoid vacuities is an area of striated bone, slightly depressed, which is also marked by deep and elongated pits. It probably represents the area of insertion of the levator pterygoideus muscle (l. palatoquadrati, l. arcus palatini), which originated on the sphenethmoid. Such a muscle is found in *Sphenodon* and *Lacerta* (Edgeworth 1935), in which the basal articulation is unsutured, but is absent in those animals in which it has fused. It is absent in living amphibia, for example. The levator arcus palatini is strongly developed in fish such as *Amia* (Adams 1919) and was possibly present in rhipidistians and served to raise the palate with respect to the braincase (figure 4, lev. pter.). This muscle scar is continuous laterally with another, which is most likely to be the area of origin for part of the pterygoideus muscle. At this point, the lateral margin of the bone is embayed strongly and the margin bears little ornament except for small pits posteriorly. Further posteriorly still the margin flares outwards to produce the deep quadrate ramus. The margin is very strongly rugose for *ca.* 24–25 mm, and this corresponds in position to the sculptured area which Panchen described on the ventral surface of the quadrate ramus of *Eogyrinus*. The rugosity terminates in a shallow unornamented notch on the right element.

A rather curious feature in this region is a curved, ornamented 'pleat' in the bone (figure 4, pleat). It runs from a point on the margin just posterior to the embayment and curves dorsally, diminishing in prominence. The anterior edge of the pleat overlies the posterior, reminiscent of a suture. It is clearly not an artefact of preservation, being found in a similar position on each element, but a suture at this point would be unexpected. The only possibility would be the overlap suture of an enormously expanded epipterygoid onto the quadrate ramus of the pterygoid, although more likely interpretations of the position of this suture are given below. The pleat does not appear to continue towards known regions of the epipterygoid. A posterior slip of the pterygoideus muscle probably originated from the rugose margin of the quadrate ramus and a more likely explanation for the pleat is that it too was associated with the origin of this muscle (figure 4, pter. post.). Ornament continues along this margin as faint striations and minute pits for a further 30 mm before vanishing, and further ornament occurs more posteriorly still, just within the bone margin, taking the form of shallow puckering.

At the posterior-most tip of the pterygoid an area of about 15 mm square bears strong ridges and grooves (figure 4, sut qu), also seen in MCZ 6977. The pterygoid was attached to the quadrate here in an overlapping joint. The surface of the quadrate ramus lining the subtemporal fossae is marked with shallow radiating grooves, which probably carried nutrient vessels and nerves in a connective tissue membrane over the surface of the bone, perhaps contributing to the supply of the adductor musculature.

The quadrate ramus of the unit is a thin plate of bone which generally resembles that of *Palaeoherpeton*. It is bounded anterodorsally by two thickened buttresses, rising in a V-shape, which are presumed to be part of the epipterygoid. Posterior to the buttresses the dorsal margin is at first thickened and has a pitted and grooved margin suggestive of a ligamentous attachment (figure 4, lig att). It appears separated from the more posterior of the two buttresses by differences in the surface characteristics of the bone and the separation continues ventrally by a groove and changes in the type of ornament. Thereafter the margin thins rapidly; although the edge is slightly damaged, it was clearly of finished bone. The surface of the dorsal part of the quadrate ramus is densely covered with striations radiating away from a central point just posterior to the common base of the two epipterygoid buttresses. At this point the bone is strongly depressed, a feature not noted in *Palaeoherpeton*.

The epipterygoid buttresses in *Pholiderpeton* are generally similar to those of other early amphibia. The ascending process or columella cranii is a stout forwardly directed buttress angled at about 30° to the vertical (figure 4, col cran). The anterior margin is thickened and essentially straight. The tip of the columella cranii bifurcates into a massive rounded knob continuing the line of the buttress and facing anteromesially, and a small, slender, laterally compressed, posteriorly directed process, arising from the thinner flange of bone which constitutes the posterior margin of the columella cranii. Between the two processes is a smooth-surfaced groove which is probably homologous with that in *Palaeoherpeton*, interpreted by Panchen (1964) as bearing one of the branches of the trigeminal nerve. The posteriorly directed process is presumably homologous with that in *Palaeoherpeton* interpreted by Panchen as separating mandibular and maxillary branches of that nerve. The anterior knob is finished in smooth bone as far as it can be seen. The ascending process is usually interpreted (see, for example, Sawin 1941) as extending dorsally to meet the parietal bone slightly posterior to the braincase in the region of the parietal foramen. There are roughened depressions in this position of the skull table of *Palaeoherpeton* and corresponding pits are found on many *Archeria* skull tables (e.g. MCZ 2053, 2121). The tip of the anterior process of the columella cranii is finished in smooth bone, which was apparently not continued in cartilage. Whether it reached the skull table remains uncertain. The ascending process approaches, but does not quite meet, the skull table in *Edops* (Romer & Witter 1942). In other forms, such as loxommatids (Beaumont 1977) and *Greererpeton* (Smithson 1982), the process was almost entirely cartilaginous.

At the base of the columella cranii the palatal ramus of the epipterygoid is broken but the margin probably curved forward smoothly to join the palatal ramus of the pterygoid. At the point where the margin turns forward the groove so formed could have accommodated the ophthalmic branch of the trigeminal nerve (figure 4*a*), which apparently followed a similar course in *Palaeoherpeton* (Panchen 1964).

A second process presumed to be of the epipterygoid arises jointly with the columella cranii from the thickest part of the pterygoid–epipterygoid complex. By comparison with *Palaeoherpeton* this is likely to correspond to a position just above the basal articulation. This process slopes backwards at an angle of 30° to the vertical. It broadens dorsally to form a laterally compressed cone, the concave dorsal surface of which is of unfinished bone (figure 4). No such development is evident in *Palaeoherpeton*. The process is connected to the columella cranii by a thin web of bone with a concave margin. In animals in which the tip of the ascending process is not bifurcate, such as *Edops* (Romer & Witter 1942) and *Capitosaurus* (Sushkin 1927), the maxillary and mandibular branches of the trigeminal are usually both interpreted as passing over the epipterygoid at this point. In *Pholiderpeton* the prootic buttress must have passed through this emargination.

In amphibia such as *Edops* and *Eryops* (Sawin 1941) a process of the epipterygoid abuts the braincase at the crista parotica (figure 5*a*, *b*, prot. pr). In *Edops* this is situated in the prootic region anterodorsal to the fenestra ovalis, although in *Eryops* Sawin described the junction as cartilaginous. Similar relations were found in *Capitosaurus* by Sushkin and his name 'prootic process' for the structure was adopted by Sawin. In the loxommatid *Megalocephalus* (Beaumont 1977) the epipterygoid and braincase articulate in the region of the basisphenoid, where two facets are situated dorsal and slightly posterior to the basipterygoid process and anterior to the fenestra ovalis. Panchen (1972) noted the possibility of an articulation in a similar place in

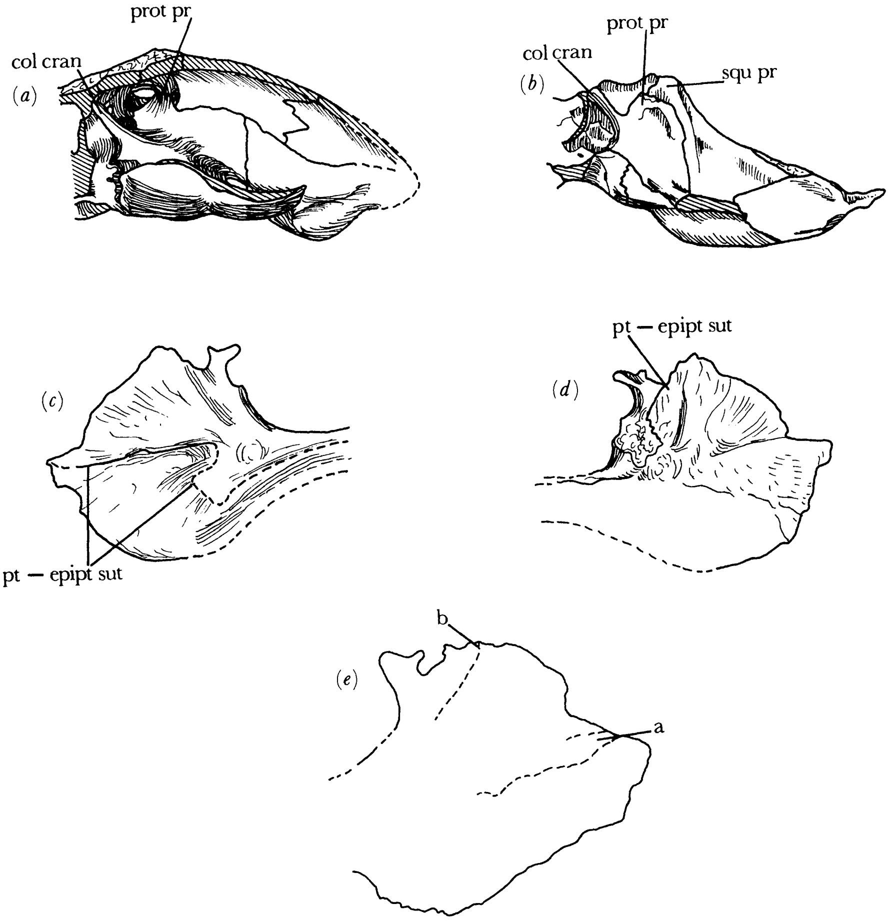


FIGURE 5. Pterygoid–epipterygoid complexes: (*a*) *Edops craigi*, anterior view of suspensorium (from Romer & Witter 1942); (*b*) *Eryops megacephalus*, anterior view of suspensorium (reversed from Sawin 1941); (*c*) *Palaeoherpeton decorum*, lateral face (from Panchen 1964); (*d*) *Palaeoherpeton decorum*, mesial face (from Panchen 1964); (*e*) *Pholiderpeton scutigerum*, from holotype.

Eogyrinus. Whether these articulation points are homologous to the prootic articulation of *Edops* and *Eryops*, as Beaumont suggested, is in some doubt. Their positions are somewhat different. In *Eryops* an additional articulation is described by Sawin between the epipterygoid and the basisphenoid, and the above could be homologous with this. Unfortunately, the mesial face of the epipterygoid of *Pholiderpeton* is not visible, nor is there sufficient evidence from the braincase to establish the existence of a basisphenoid–epipterygoid articulation in addition to the normal basipterygoid junction. The structure of the second epipterygoid buttress in *Pholiderpeton* most closely resembles the 'prootic process' described in *Eryops* and *Capitosaurus*. However, no embolomere braincase seems to display a suitably placed crista parotica to receive it. Dorsally, the sidewalls of the otic capsule, where known, for example in *Palaeoherpeton* and *Eogyrinus*, are all finished in smooth bone. The possible articulation point on the basisphenoid in *Eogyrinus* seems the only point of contact.

There is an alternative interpretation for the contact point of the second epipterygoid buttress, derived from its spatial relations. On the parietal of *Pholiderpeton*, close to its suture with the tabular and supratemporal, a cancellous pad of bone rests on a low mound which forms the lateral end of the most posterior of the radiating ridges described above. It is particularly well seen on the left-hand side, but it is also present on the right. It lies just posterior to the tip of the prootic buttress of the braincase (figure 38, pad). A similar raised area is found on each side of the parietal of *Palaeoherpeton*. Placing a paper model of the pterygoid–epipterygoid unit over the braincase shows that the pads fall exactly under the end of the second epipterygoid buttress. The pad may represent an ossification of part of a cartilaginous junction between the epipterygoid buttress and the skull table. I propose that the second epipterygoid buttress is homologous with the prootic process of the epipterygoid as recognised in *Eryops* and *Capitosaurus*, but that, rather than contacting the prootic itself, it is associated with the skull table in the nearby region. From the preservation it is clear that the prootic buttress of the braincase did not contact the epipterygoid in *Pholiderpeton*. The epipterygoid contacts the skull table at a process of the tabular in *Greererpeton* (Smithson 1982) rather than at a prootic process of the braincase. Association of the epipterygoid and the dermal bones of the skull table in this region is not therefore unprecedented.

'Prootic process' is thus an inappropriate name for this structure in *Pholiderpeton*, and presumably in other embolomeres; an alternative might be 'paratemporal process' (Jarvik 1954). In *Eusthenopteron*, posterior to the notch for the maxillary and mandibular rami of the trigeminal, Jarvik describes a second process which in section (figure 12, p. 28) is shown to approach the dermal skull roof very closely. Although it is not described as contacting it, it is described as having a dorsal end expanded into a horizontal plate with a partly roughened surface. It surely made contact with something, most probably the skull roof in the region of the tabular–supratemporal junction. Mesial to this process runs a groove which Jarvik interprets as contacting the otic shelf of the braincase. Thus contact between the epipterygoid and both the skull table and the otic capsule could well be the primitive condition for tetrapods. Adoption of the name 'paratemporal process' for that seen in embolomeres is therefore appropriate (figure 4*a*, prt pr).

Just posterior to the paratemporal process, the pterygoid–epipterygoid unit has a thickened margin with evidence of a ligamentous attachment (figure 4, lig att). A similar structure in *Eryops* contacts a descending process of the squamosal (figure 5*b*, squ pr). The squamosal process in *Pholiderpeton* probably served similarly, contacting the pterygoid–epipterygoid complex near the paratemporal–skull-table junction. The pterygoid–epipterygoid complex commonly contacts a descending process of the squamosal in early tetrapods, e.g. *Dendrerpeton* (Watson 1956 (as *Platystegos*)), loxommatids (Beaumont 1977), *Seymouria* (White 1939) and *Tersomius* (Carroll 1964), but contact is usually continued further posteriorly, as for example in *Greererpeton* (Smithson 1982). In *Pholiderpeton*, by contrast, both the squamosal and the pterygoid–epipterygoid complex display finished margins at this point, and clearly they did not suture. The reflected posterodorsal margin of the squamosal suggests a distinct though narrow gap (figure 1*a*, fl). More posteriorly the pterygoid–epipterygoid complex overlay the quadrate and no further contact was made with the squamosal. This condition I interpret as primitive. A comparable gap occurs between the ossification of the palatoquadrate complex and the dermal bones of the skull roof in *Eusthenopteron* (Smithson & Thomson 1982), which I regard as homologous. These two units sometimes lose contact, for example in *Dvinosaurus* (Bystrow 1938). However, this animal shows greatly reduced ossification in association with both its aquatic habits and paedomorphic form. Embolomeres show no such reduction of ossification and are thus more likely to be truly primitive in this respect. The paedomorphic condition presumably reflects the primitive condition but it has been achieved secondarily. Early reptiles also retain the primitive condition in this respect.

Turning once more to the quadrate ramus as a whole, a conspicuous crack runs across the unit from the thickest part of the bone, presumed to be the region of the conical recess. It is present in each element. The edges of the crack in this region are 'clean', and the bone retains its original curvature on each side. By use of a silicone rubber cast the crack can be vicariously 'mended' to obtain the natural form of the bone. It was not a simple vertical sheet of bone as described in *Palaeoherpeton*, *Eogyrinus* or in loxommatids, but curved through an angle of about 60°.

In the left element the crack continues along an irregular course towards and just dorsal to the strongly ridged quadrate overlap. Along much of its course, where it runs through thin bone, the surface of the dorsal part of the unit overlies the ventral, and is accompanied by a slight but noticeable change in the direction of the surface ornament between the two component layers. The type of ornament on the ventral component might suggest that the dorsal component was originally more extensive, overlapping the region of the now exposed ornamented area on the surface of the ventral. The feature can be traced on the small exposure of the mesial face of the right element and the area of overlap of the two surfaces can be discovered by superimposing tracings of the two. The structure could indicate that two separate elements of bone were present and overlapping along this line. A simpler explanation might be that a single element has been cracked and the two edges forced over each other. An overlapping crack occurs in an almost identical position in *Palaeoherpeton*, though the overlap is reversed. The occurrence of a similar feature, due solely to preservation, in each of the three separate elements might be regarded as rather more than coincidence. However, it could be explained by the fact that not only is the bone here thin, but also that it is in this region that the pterygoid–epipterygoid unit curves strongly round the suspensorium. It would thus be under a great deal of stress during diagenesis.

Although the pterygoid–epipterygoid complex is well preserved in both *Palaeoherpeton* and *Pholiderpeton*, the interpretation of the region remains problematical. The pterygoid–epipterygoid sutures are very difficult to trace, not only in embolomeres, but also in many other early amphibia such as loxommatids and *Greererpeton*, the bones having become co-ossified in many cases. In addition the complex three-dimensional shape of the unit is usually distorted in one or other of its two major planes either by horizontal or lateral compression. As noted above, important information from the mesial face of the unit in *Pholiderpeton* is unavailable. This, combined with equivocal evidence from what remains, means that the problem cannot yet be resolved. At least two interpretations for the position of the posterior suture are possible based on the above evidence, and require a detailed explanation.

In 1926, Watson first described the pterygoid–epipterygoid complex in *Palaeoherpeton*, defining the epipterygoid as 'a small bone, rigidly fixed to the anterior border of the para-otic part of the pterygoid'. In the type specimen there is an obvious suture in this position on the mesial face of the bone. In 1964, Panchen agreed with this interpretation and it is accepted here. Watson, however, did not describe the lateral face of the same region. Panchen did so, interpreting the exposure of the epipterygoid here as 'a sheet of bone covering the whole of the upper half of the quadrate ramus of the pterygoid and continuous with the columella cranii' (figure 5*c*, *d*). He judged the lower border of the quadrate ramus of the epipterygoid to run from the level of the basis cranii to the quadrate condyle. Such an interpretation requires the upper part of the quadrate ramus to have a duplex structure. Extensive ossification of the palatoquadrate cartilage would be a primitive feature; a similar condition was reported in *Edops* (figure 5*a*). In this case the epipterygoid was restricted posteriorly by an extensive quadrate ossification. According to Beaumont (1977) the situation is similar in loxommatids, although having examined her material I believe the quadrate to be more extensive than in her interpretation, being similar to that in MCZ 6977.

There are two possible interpretations of the pterygoid–epipterygoid suture in *Pholiderpeton* and the evidence in favour of each must be assessed. First is the overlapping crack running across the unit (figures 4*a* and 5*e*, a) which, as described, could be indicative of a broad overlapping suture. If this were the case, *Pholiderpeton* would differ markedly in some ways from *Palaeoherpeton* despite superficial similarities. It would mean that there was no dorsal expansion of the palatal ramus of the pterygoid. The bone here is a single layer and must have been entirely formed from the epipterygoid, this bone alone contacting the squamosal posteriorly. The obvious suture between pterygoid and epipterygoid on the mesial face in *Palaeoherpeton* must have been absent in *Pholiderpeton*. Smithson (1982) described a comparable situation in *Greererpeton*. According to him the epipterygoid has an extensive exposure in occipital view and is not covered by the dermal pterygoid as it is for example in *Edops*. It is thus the epipterygoid which makes broad contact with the squamosal. Holmes (1984) interprets *Proterogyrinus* in this way.

The second possibility is along a line just posterior to the paratemporal process (figures 4*a* and 5*e*, b). Here, as noted, there appears to be a groove dorsally, continued further ventrally as a change in the character of the ornament. To add weight to this interpretation, in the left element, in which the epipterygoid buttresses are missing, they have separated off along precisely this line, leaving a surface bearing longitudinal grooves and ridges. In *Eryops* the pterygoid–epipterygoid suture runs in a similar position with the pterygoid contacting the descending flange of the squamosal close to the dorsal facet of the paratemporal (prootic) process (figure 5*b*).

If this second interpretation is correct, the mesial face should display a condition similar to that seen in *Palaeoherpeton*, with an anterior suture in the region of the columella cranii. In this case the epipterygoid would be a very small bone, as Watson suggested, and unusually so for an animal primitive in many other skull characters. It would, for example, have a much smaller quadrate ramus than *Edops*. This interpretation would still imply considerable differences between *Pholiderpeton* and *Palaeoherpeton* as interpreted by Panchen, in the lack of a quadrate ramus of the epipterygoid in the former. Only knowledge of the mesial face of the unit in *Pholiderpeton* could resolve the matter for certain. Failing that, I favour the second interpretation. This is the simpler to reconcile with the assumption that the two closely related embolomeres would differ little in fundamental structure, even though they differ in detail. If both the anterior position of the suture between the epipterygoid and pterygoid in *Palaeoherpeton* and the single-layered structure of the quadrate ramus of the unit in *Pholiderpeton* are accepted, the two can only be reconciled if the second interpretation is also accepted. This means a re-interpretation of the posterior pterygoid–epipterygoid suture in *Palaeoherpeton*.

In Swanwick specimen A2 (*Pholiderpeton*, Panchen 1970), Panchen (1964) described an extensive quadrate ramus of the epipterygoid revealed by removal of the pterygoid. This layer is surely equivalent to the dorsal part of the pterygoid–epipterygoid unit as described in the holotype, the whole unit having been folded under along the line of weakness noted above. Panchen makes no mention of a duplex structure to this layer of bone, but I have subsequently been unable to trace this piece of bone. Without this evidence, it is impossible to ascertain the identity of the sheet of bone; it could equally well be part of the pterygoid.

One further factor influences my interpretation, and that is the condition of the quadrate. In *Pholiderpeton*, the quadrate is known to have an extensive dorsal ramus which overlaps the pterygoid–epipterygoid unit to a considerable degree. The quadrate of *Palaeoherpeton* is unknown, but the quadratojugal is very much like that of *Pholiderpeton* (see above). If the quadrate is also assumed to be similar (I believe this to be a justifiable assumption), the interpretation given by Panchen would mean that over a large area the epipterygoid must have been 'sandwiched' between pterygoid and quadrate, rather than restricted by the latter, as in *Edops*. This situation is not impossible, but I regard it as unlikely.

Lower jaw

The right lower jaw ramus is about two thirds exposed in external view. The internal view (figure 40) has been exposed by preparation, allowing reconstructions of both surfaces to be made (figures 6*a*, *b*). The left ramus is represented by one large fragment consisting of the posterior half of the ramus plus four fragments. One of these has a sawn polished surface which provided cross sections useful to preparation of the reconstruction (figure 7*a*, *b*).

The lower jaw measures about 310 mm from symphysis to posterior margin, measured in the plane of the ramus. Its greatest depth, measured from the apex of the surangular crest to the ventral margin, is about 104 mm, and so it is roughly three quarters of the size of the *Eogyrinus* lectotype lower jaw. The tooth-row in *Pholiderpeton* measures about 190 mm.

The shape, configuration of dermal bones and lateral-line canals conform to those typical for an embolomere and are similar in most respects to those described for *Eogyrinus* and *Eobaphetes* (Panchen 1972, 1977); only points of particular interest will be described further. The ornament is like that of a typical embolomere, and is represented as accurately as possible in the reconstruction.

Pholiderpeton has a very strongly convex surangular crest like that of *Eogyrinus* but unlike those of *Eobaphetes* and many *Archeria* specimens, in which it is flattened, or *Neopteroplax*, in which it is not emphasized at all. Unlike *Eogyrinus*, but like *Eobaphetes* and *Neopteroplax*, the dentary

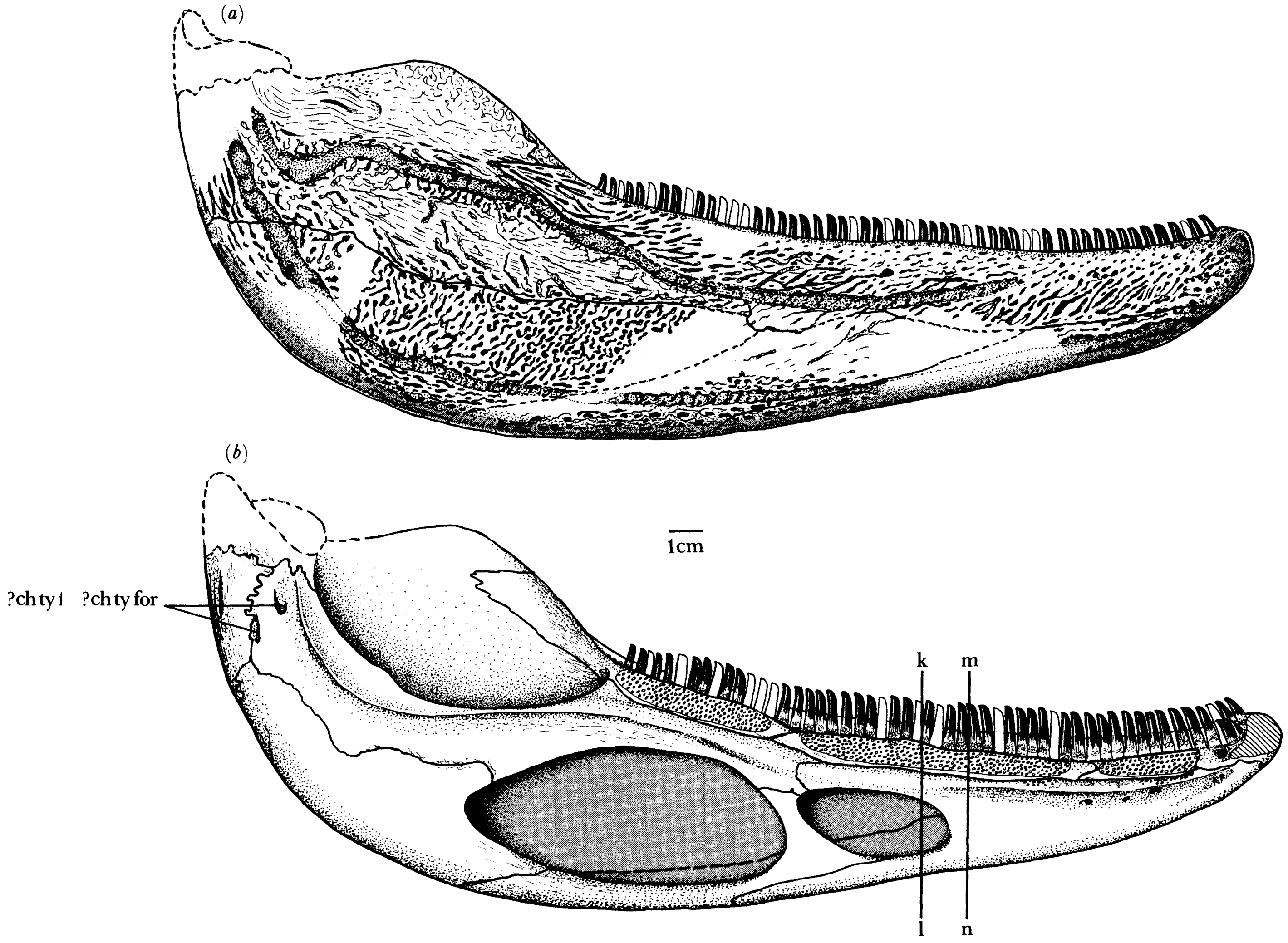


FIGURE 6. *Pholiderpeton scutigerum* holotype, reconstructions of lower jaw: (*a*) lateral view; (*b*) mesial view; k–l, m–n, sections illustrated in figure 7.

margin bearing the teeth is concave. There are two Meckelian fenestrae, the posterior one being roughly four times the area of the anterior. Both are approximately oval, with their long axes parallel to the jaw ramus. In the lectotype of *Eogyrinus* the anterior Meckelian fenestra is proportionately larger than it is in *Pholiderpeton* but the difference is probably not taxonomically significant. The reconstruction of the lower jaw of *Pholiderpeton* presented here differs in several respects from that figured by Panchen (1972) for *Eogyrinus*. However, for the reasons given below these differences are not considered to be of taxonomic significance; they can all be accounted for by differences in preservation of the specimens. The posterior coronoid of *Pholiderpeton* enters substantially into the surangular crest internally and also has a small lateral exposure. Isolated jaw fragments of *Eogyrinus* (for example, G 13.80 and an uncatalogued piece of eogyrinid lower jaw from Swanwick attributed to *Pholiderpeton*) also revealed the same feature. The lectotype of *Eogyrinus* is probably similar, but the area is obscured by rib on the left ramus. On the right the suture has been almost entirely closed up. This condition of the coronoid is seen in *Archeria crassidisca* (personal observation) and is figured in *A. victori* (Stovall 1948) and *Neopteroplax* (Romer 1963). Extension of the posterior coronoid to form a long interdigitating suture with the surangular seems to be the usual and probably primitive condition for tetrapods, exemplified by *Seymouria* (White 1939) and *Eryops* (Sawin 1941).

The exact position of the suture between posterior and middle coronoids is uncertain. However, the boundaries of the anterior coronoid are very clear. Surprisingly, the anterior coronoid extends forward almost to the symphysis. A gap of about 7 mm separates the anterior extent of the denticulated area from two symphysial teeth. *Eogyrinus* is figured (Panchen 1972) with a gap of about 61 mm. Characterized by a deep concavity, previously matrix-filled, the gap may represent an area formerly occupied by part of the anterior coronoid which has fallen out before preservation.

In *Pholiderpeton* the lower borders of the coronoids form a smooth line parallel with the tooth row. The sutures can be confirmed from the jaw sections which show the coronoids to be comma-shaped in section. The tail of the comma fits down between the dentary and either the prearticular or presplenial. These latter bones bear a thickened, rounded ridge which runs parallel to the coronoids and just below them. In places the ridge bears denticles like those on the coronoid; these may account for the differences in interpretation between *Pholiderpeton* and *Eogyrinus* (Panchen 1972). *Proterogyrinus* (Holmes 1984; Smithson 1985, 1986) shows a similar condition to *Pholiderpeton*.

Both lower jaw rami of *Pholiderpeton* show a break running from a point just behind the anterior end of the anterior coronoid to the ventral margin of the anterior Meckelian fenestra. Panchen (1972) restores a suture at this point in the lower jaw of *Eogyrinus*, but I believe that here too it is more correctly interpreted as a break. Its interpretation as a suture produces anomalies in comparison with other specimens. The Airdrie specimen of *Eogyrinus* shows no trace of either a break or a suture at this point. Accepting the configuration of the coronoids given above, but also restoring a suture at this point, would require acceptance of one of two unusual configurations for the bones beneath the coronoids. Either the prearticular must be interpreted as extremely long, forming the upper borders of both fenestrae with the restored prearticular–presplenial 'suture' in reality a break, or an extra bone must be postulated in the lower jaw. Both of these possibilities seem unlikely. Holmes's interpretation of the lower jaw in *Proterogyrinus* has produced just this difficulty and his reconstruction shows, outlined by dotted lines, a bone interposed between prearticular and presplenial. If Panchen is correct in his interpretation of the lower jaw of *Eogyrinus*, however, there would be considerable difference between the two animals, of taxonomic significance. I believe their extreme similarity in other respects makes this unlikely.

The presplenial of *Pholiderpeton* is a substantial bone in internal view and forms the greater part of the border of the anterior Meckelian fenestra. In the reconstruction, the presplenial–postsplenial suture apparently disappears, but in fact continues within the jaw cavity and is visible in external view. This is illustrated by cross sections (figure 7). The postsplenial has exactly those relations described by Panchen for *Eogyrinus*.

The relation between the angular and prearticular of *Pholiderpeton* is different from that given by Panchen for *Eogyrinus*. Panchen shows a rugose area on the angular which he concludes is for the insertion of the depressor mandibulae muscle, and he interprets the angular–prearticular suture as running above it. There is a closely comparable rugose area on both lower jaws of *Pholiderpeton*. The rugosities are however, orientated ventrally and are therefore unlikely as

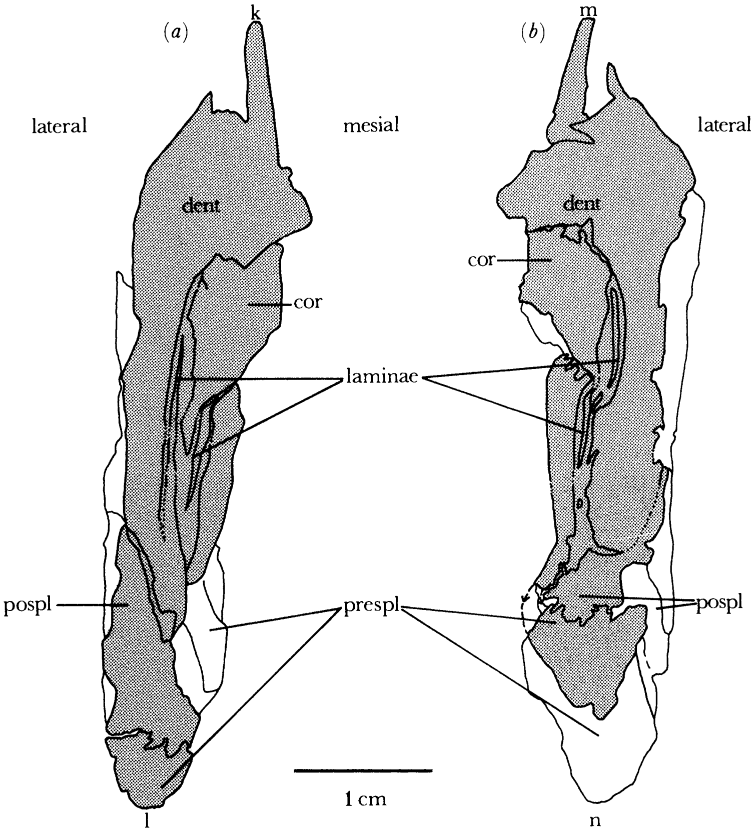


FIGURE 7. *Pholiderpeton scutigerum* holotype, sections of lower jaw. Stipple indicates sectioned bone.

attachment points for a muscle attached to them from above. The rugose area was probably sutural surface, where the angular–prearticular suture has opened up. In G 12.80, for example, this area is well preserved and has no rugosity. The suture curves upwards as Panchen restores it, but the 'rugose area' is absent being enclosed within the intact jaw. This specimen is broken instead on the corresponding external surface because the angular is a thick bone at the jaw angle, whereas the prearticular and surangular are thin. The depressor mandibulae insertion probably lay in the groove running down the posterior margin of the surangular, which terminates in a flattened area on the posterior face of the angular. The 'angle' of the jaw is strengthened to resist vertical forces during jaw closure and would provide a firm area of attachment for jaw-opening musculature.

Two well-defined oblique pits perforate the prearticular, one of which presumably marks the point of entry of the chorda tympani into the lower jaw ramus. Part of the left articular of *Pholiderpeton* is exposed to show its suture with the surangular and prearticular. Isolated specimens attributed to *Eogyrinus* and *Pholiderpeton* (G 13.72, G 13.89, R 2648, R 2649) confirm that the articular is wedge-shaped, fitting firmly between the surangular and prearticular, with minimal surface exposure apart from the glenoid. Differences between this and *Eogyrinus* are probably accounted for by the fact that the lectotype of *Eogyrinus* is apparently the skeleton of a large old animal, in which the sutures have become sealed or difficult to see. In many other primitive tetrapods the articular is likewise minimally exposed in lateral and mesial view, for example *Eoherpeton* (Smithson 1980, 1985), *Proterogyrinus* Holmes 1984) and *Seymouria* (White 1939).

As in *Eogyrinus* the symphysis in *Pholiderpeton* consists of a roughened and pitted surface suggesting an originally cartilaginous lining. One further feature of the lower jaw of *Pholiderpeton* deserves comment. In the sections, thin laminae of bone are visible (figure 7, laminae) whose identity is uncertain. It is possible that one may pertain to the coronoid, but in other cases, interpretation is more difficult. It is possible that they are ossifications of the original Meckel's cartilage, which primitively forms the lower jaw in gnathostomes, but which usually disappears in tetrapods.

Dentition

The right dentary tooth-row is complete, with remains of 41 teeth plus 12 tooth spaces, giving a maximum of 53. The teeth are closely spaced along the dentary and in addition two small symphysial teeth were present, a feature noted before by Romer (1963) in '*A. lancifer*' (= *Leptophractus obsoletus* (Panchen 1977)), but otherwise unknown in eogyrinids. Holmes reports symphysial teeth in *Proterogyrinus* (1984). The majority of teeth measure 12–14 mm from tip to base, 7–8 mm being visible in lateral view. At the symphysial end the row begins with two small teeth, the next two or three successively increasing in size. The row ends with 4 teeth which are much smaller than the rest, the last being only 6–7 mm long.

The tooth shape is similar to that described for *Eogyrinus* (Panchen 1972), bases tapering slightly from about 5 mm, with irregular surface sculpturing for about 4 mm of their length. The oval transverse sections have the major axis orientated buccolingually. From a crown height of about 4 mm, teeth are covered in enamel, marked at first by fine regular longitudinal grooves and nearer to the tip by very fine regular striations (figure 8*a*). The tip of each tooth is smooth. The crowns are barely tapering cylinders with slightly recurved tips, the best preserved bearing a marked anterior crest reminiscent of the chisel-shaped teeth of *Archeria* (Case 1915; Stovall 1948). This is seen on the well-preserved posterior tooth in the right ramus and on the symphysial teeth (figure 8*c*). The keel can also be seen on well-preserved teeth of *Eogyrinus* (figure 8*d*). Keeled teeth are also found in *Proterogyrinus* (Holmes 1984). The chisel-shaped teeth of *Archeria* could easily be derived from those in *Pholiderpeton*, *Eogyrinus* and *Proterogyrinus*.

The dentary teeth of the specimen from Airdrie, attributed to *Eogyrinus* (Panchen 1970), show some marked differences from those described above. No anterior keel is present, the teeth tapering much more noticeably, and the base of the enamel is more fluted than that of *Pholiderpeton* or *Eogyrinus*. There is no fine irregular sculpturing present nearer the tips of the teeth (figure 8*e*).

In *Pholiderpeton*, although neither maxilla is complete, an estimate of the tooth-row is possible. The left maxilla bears remains of 26 teeth, with space exposed for about a further 22; the right bears remains of 28 teeth with spaces for a further 20–22. Four teeth are present in the premaxilla, giving a total of 52–54 for the upper marginal teeth. The premaxillary teeth vary in size, although they appear to be complete. The smallest has 10 mm and the largest 15 mm exposed in external view. They are somewhat crushed, making accurate measurements of width difficult.

There is some regional variation in maxillary tooth size. Most match those of the lower jaw, but at the anterior end of each maxilla enlarged second and third teeth produce a canine peak. These teeth measure 20 mm from tip to base, with 13 mm visible in lateral view, and have a

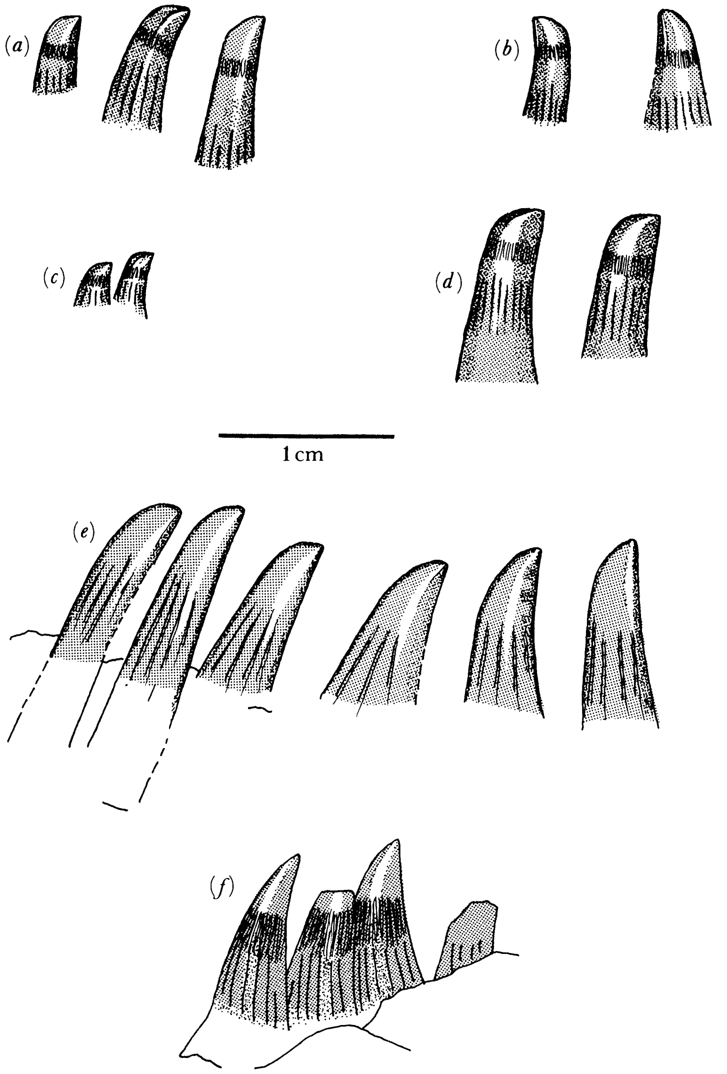


FIGURE 8. Teeth of embolomeres in lateral view. (*a–c*) *Pholiderpeton scutigerum* holotype, (*a*) dentary teeth, (*b*) maxillary teeth, (*c*) symphysial teeth, somewhat foreshortened; (*d*), dentary teeth of *Eogyrinus attheyi*; (*e*) dentary teeth of Airdrie specimen L 11614; (*f*) premaxillary teeth of G 24.40.

maximum width of about 4 mm. Two small teeth are present at the posterior end of the tooth-row corresponding to those in the lower jaw. Maxillary teeth resemble those of the lower jaw in shape (figure 8*b*), with one consistent difference: on the maxilla, each tooth bears a very slight but definite posterior keel.

No studies of replacement pattern have been undertaken on the teeth of *Pholiderpeton*. The preservation is such that it is often impossible to distinguish naturally occurring gaps in the tooth-row from those resulting from *post mortem* damage.

The premaxillary teeth of the specimen G 24.40 (figure 8*f*) attributed to *Pteroplax* by Boyd (1978) are quite different from those of *Pholiderpeton* or *Eogyrinus*. Tapering strongly over their whole length, the tips are sharply pointed with no suggestion of a crest or a keel. This specimen is thus unlikely to pertain to either of the two latter genera, and its attribution to *Pteroplax* is all the more likely.

Palatines are not preserved in the holotype of *Pholiderpeton*, except for one isolated palatal tusk. Each ectopterygoid bears one large tusk and an adjacent replacement pit, plus five smaller teeth. The second of these is the largest, being about 15 mm from tip to base and 5–7 mm in diameter. The first and third teeth are slightly smaller, about 12 mm long, 3 mm in diameter and the final two smallest, 6–7 mm long and 2 mm in diameter. The largest tusk is 29 mm long and 7 mm in diameter (measured at the base of the enamel). The crowns of the left ectopterygoid teeth are well preserved, resembling the marginal teeth in being gently tapering with slightly recurved tips. There is a slight posterior keel but no anterior crest.

Braincase

The braincase of *Pholiderpeton* is preserved in its natural relation to the skull table and snout region (figure 38). Fine surface detail is preserved but dorsoventral crushing has broken the sidewalls, pushed the ventral region of the sphenethmoid to the morphological left side and fractured the basipterygoid processes, pushing them dorsally. Little of the basioccipital is visible, but one exoccipital remains in association although crushed and disarticulated. The opisthotics are adequately preserved in occipital view. Good longitudinal sections are available (figures 9, 10 and 14).

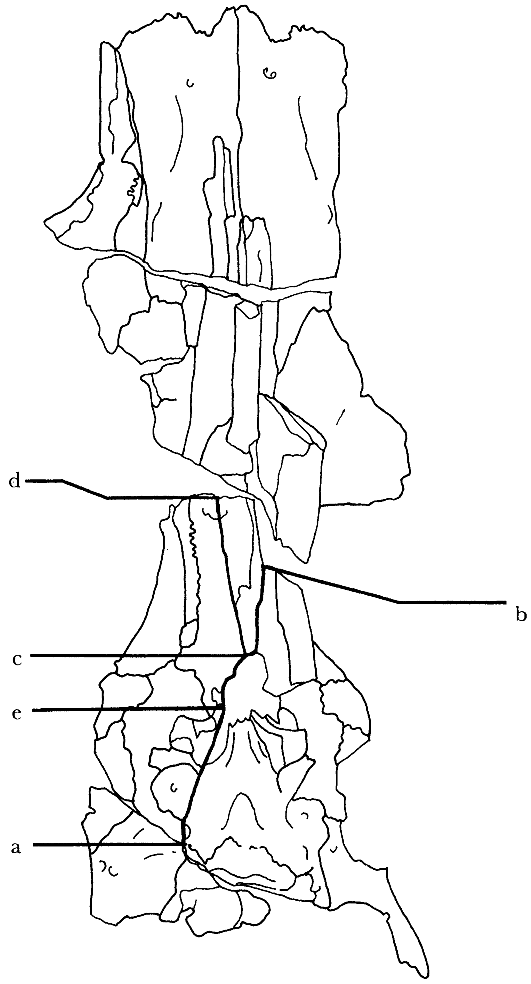


FIGURE 9. *Pholiderpeton scutigerum* holotype, diagram to show courses of sections through braincase in figures 10 (*a*, *b*) and 14 (*a*, *b*).

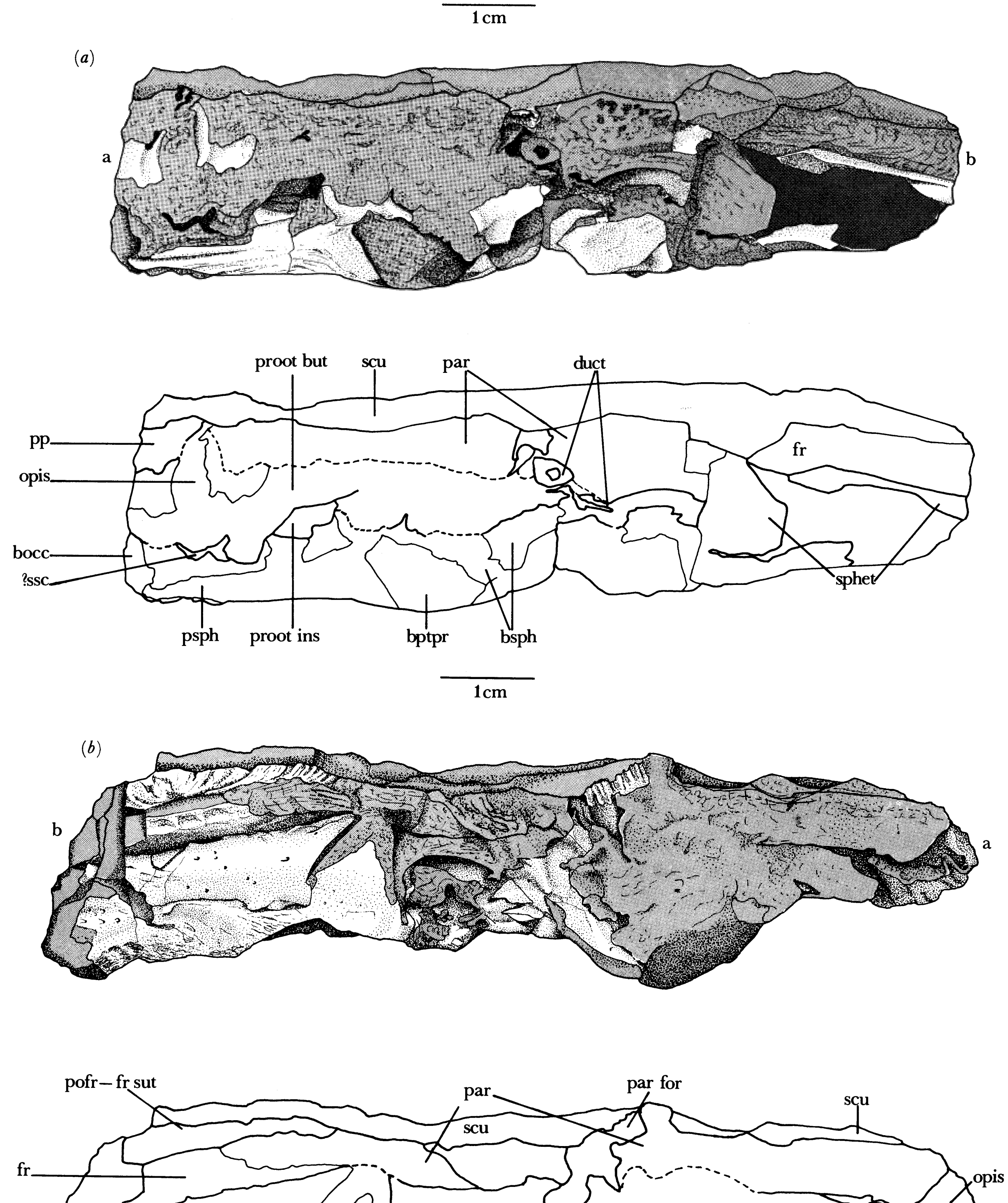


FIGURE 10. *Pholiderpeton scutigerum* holotype, sections through braincases. (*a*) View of morphological left side of section; (*b*) view of morphological right side of section.

A clearer picture of the embolomere braincase results from comprison of this with other specimens. I have drawn on information from the following: *Eogyrinus attheyi* (lectotype G 13.71; the Newarthill specimen RSM 1896/112/23–24; G 13.74); *Pholiderpeton scutigerum* (A2); *Palaeoherpeton decorum* (holotype G 15.71; A1); *Anthracosaurus russelli* (holotype GS 28317), all described by Panchen (1964, 1972, 1977), plus personal observation and also new information on *Archeria crassidisca*, provided by T 612 and MCZ 6785.

In the holotype of *P. scutigerum* the opisthotics appear in occipital view (figures 10 and 11) as two separate unfinished oval ossifications separated by a midline suture, and capped dorsally by the 'widow's peak' formed by the postparietals. A similar condition is reported by Holmes (1984) in *Proterogyrinus*, although there the opisthotics do not meet in the midline. The left exoccipital facet is visible, approximately oval and marked off from the body of the opisthotic by a raised rim. Laterally a groove finished in perichondral bone runs above the exoccipital facet (figure 11). At the lateral corner of each facet lies a digitiform process like that noted by Panchen (1972) in G 13.74. This is covered dorsally, laterally and ventrally by striated perichondral bone continuous with that lining the opisthotic laterally and ventrally. The posteromesial face of the digitiform process is roughly oval and has an unfinished surface suggestive of continuation in cartilage or articulation with another bone. It is not in continuity with the exoccipital facet. The dorsomesial corner of the tabular lies above the digitiform process, but it is evident that finished bone completely covered the process dorsally as in G 13.74. Crushing has apparently brought the process closer to the body of the opisthotic and narrowed the groove between them.

The digitiform process was first noted by Panchen in the Swanwick specimen of *Palaeoherpeton*, where he described it as part of an interlocking mechanism between the tabular and opisthotic.

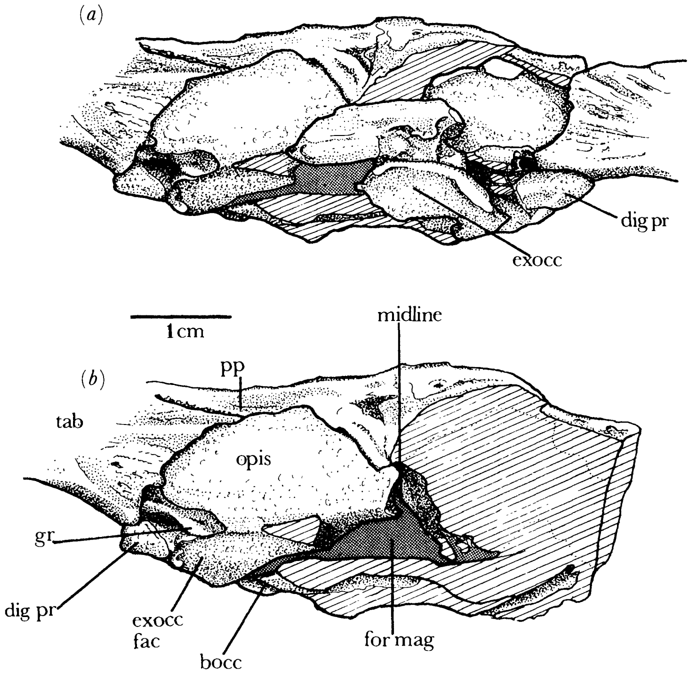


FIGURE 11. *Pholiderpeton scutigerum* holotype, specimen drawing of occipital region: (*a*) with right exoccipital *in situ*; (*b*) with right exoccipital and tabular removed.

The presence of finished bone on the dorsal and lateral surfaces of the process in *Pholiderpeton* and G 13.74 suggests that such a contact is unlikely. Proximity to the tabular in *Pholiderpeton* appears to be an artefact of preservation. The posteroventral corners of the tabulars in both G 13.74 and the holotype of *Palaeoherpeton decorum* are smooth, showing no contact area for another bone. The digitiform process and interlocking mechanism is also described by Panchen in *Anthracosaurus* (1977). Although a digitiform process is certainly present, I suspect that it did not contact the tabular. A channel of matrix separates the two on each side of the specimen and the process lies equally close to the exoccipital. Crushing is more likely to have forced these structures closer together than to have separated them. In the braincase of *Proterogyrinus* (Holmes 1984) a larger, more broadly based process is found in a similar position, which Holmes suggests may have served as an attachment surface for the dorsal process of the stapes. If this were the case, the distal tip of the stapes would have a similar relation to the opisthotics, which the dorsal process bears in *Eusthenopteron*. This would add weight to the interpretation (Clack 1983) of the distal tip as a dorsal process, but would weaken the suggestion that at the same time it was homologous to the 'opercular' process of temnospondyls and diadectids. However it is not possible to be sure from the material of *Pholiderpeton* that this contact was actually made and other interpretations are possible. The facet on the digitiform process may have articulated with the exoccipital in *Pholiderpeton*, paralleling the arrangement in loxommatids where the exoccipital is produced into two buttresses meeting the opisthotic on two separate facets (Beaumont 1977). The digitiform process and its putative contact with the exoccipital may be homologous with the more lateral of the two buttresses in *Megalocephalus*.

The groove above the digitiform process continues anteriorly along the wall of the opisthotic and can be seen in lateral view in both *Pholiderpeton* (holotype) and G 13.74. In *Pholiderpeton* there is a foramen piercing the opisthotic along the course of the groove which may have provided passage for the vena capitis dorsalis.

The section which passes through the right otic capsule shows some finished bone in lateral view (figure 10*a*). The most posterior area lines a groove running dorsoventrally and turns inwards to meet the skull roof. It lines up with the posterior groove on the tabular between the first and second tabular facets and which Holmes (1984) suggests carried the vena capitis dorsalis in *Proterogyrinus*. However, there is no evidence for a foramen into the braincase here in either the holotype of *Pholiderpeton* or in G 13.74.

Broken bone, probably the base of the second tabular facet, lies posterior to a second area of finished bone. This area lines up with the more anterior groove on the tabular, and could correspond to the area termed 'spherical depression' by Panchen (1972) in G 13.74. In *Pholiderpeton*, ventral to this area is a large cavity which is roughly W-shaped in section (figure 10*a*, ssc). Its ventral border is demarcated by the parasphenoid. It is probably a section across the semicircular canal chamber corresponding to pits A and C in the opisthotic of G 13.74 (Panchen 1972, figure 9).

In ventral view (figure 38, proot but) the braincase shows two prominent prootic buttresses diverging from the otic capsules to meet the parietals, and on the left the suture with the parietal is indistinguishable. The lectotype of *Eogyrinus* shows them less clearly, as does *Palaeoherpeton*, both on the type and on the Swanwick specimen A1. In the latter, finished bone sheathes them anteriorly and is confluent with the dorsal lining of the brain cavity. They mark the posterior boundary of the prootic incisure. The anterior vertical semicircular canal ran some way into the buttress, as it does also in *Eoherpeton* (Smithson 1985). This corresponds to pit A in G 13.74 (Panchen 1972). The holotype of *Pholiderpeton* shows a section across the buttress in lateral view (figure 10*a*, proot but) with the prootic incisure visible beneath it.

In ventral view (figure 38, sac cham), irregularly shaped pieces of bone are visible on each side of the specimen, partly covered by pieces of broken periosteal or perichondral bone. The better defined left element is roughly a hemisphere whose centre is somewhat hollowed out. Panchen noted a similar structure on the lectotype of *Eogyrinus*, which he tentatively identified as the stapes. However, the embolomere stapes is now known (Clack 1983). Comparison with G 13.74 resolves the hemisphere's identity, when both are similarly orientated with respect to the exoccipital facet and hence the otic capsule. The hemispherical structure of *Pholiderpeton* exactly matches that identified by Watson (1926) as a 'pseudofenestra' and by Panchen as part of the semicircular canal system in G 13.74. The central foramina are not as well defined in *Pholiderpeton*, but the homology of the structures is clear. They are parts of the prootic and probably housed the saccular chamber of the system. Romer & Witter (1942) figure a structure which is also probably homologous in *Edops* anterodorsal to the fenestra ovalis (see also Romer & Edinger 1942). No such structure is apparent in other specimens, for example the Swanwick skulls A1 (*Palaeoherpeton*) and A2 (*Pholiderpeton*) or in *Proterogyrinus* (Holmes 1984). The preservation of the holotype of *Pholiderpeton* and G 13.74 suggests that during dorsoventral compression the otic capsules have been forced apart. The side-walls of the otic capsules and their junction with the basioccipital were poorly ossified in embolomeres. In G 13.74 the anterodorsal wall of the hemispherical structure is finished and continuous with the anterior wall of the prootic buttress, but the lateral walls are unfinished.

In the lateral view (figure 10*a*), anterior and posterior to the basipterygoid process, two areas of finished bone, originally confluent, are all that remain of the margin of the large foramen occupied by the interorbital vein. The posterior area represents the wall of the processus sellaris (Heaton 1979). A change in direction of the surface ornament below this area could represent the junction between parasphenoid and basisphenoid, which are otherwise fused.

The basipterygoid processes are probably the best preserved in any British embolomere. By use of a silicone rubber cast it was possible to reproduce their original orientation. They are almost identical to those of *Archeria* represented by two specimens to hand: a cast of an isolated braincase illustrated by Williston (1918) (T612) and MCZ 6785 (figure 12), an exquisitely preserved isolated basisphenoid. In all these the processes are preserved in their natural positions. They will be described together with those of *Pholiderpeton*. In both genera, the articular surface is divisible into two planes, one approximately anteroventral, the other anterodorsal, which round gently into one another. In *Pholiderpeton* and in the Williston braincase this junction is slightly concave from mesial to lateral to form slightly saddle-shaped surface. In MCZ 6785 the surface is more bulbous. The anteroventral face is the smaller, being shaped like the lower third of a circle. The anterodorsal face is roughly an equilateral triangle with curved sides. The apex is posterior and the base anterior. Whereas the base is concave in *Pholiderpeton*, the remaining two sides are convex. In anterior view, the junction between the two faces slopes down from the braincase at an angle of about 45°; in lateral view it slopes posteriorly at an angle of 20–25°. The Swanwick specimen A2, the Newarthill *Eogyrinus* and the holotype of *Palaeoherpeton* are all similar, though less well preserved.

The embolomere basipterygoid process may now be compared with that of loxommatids

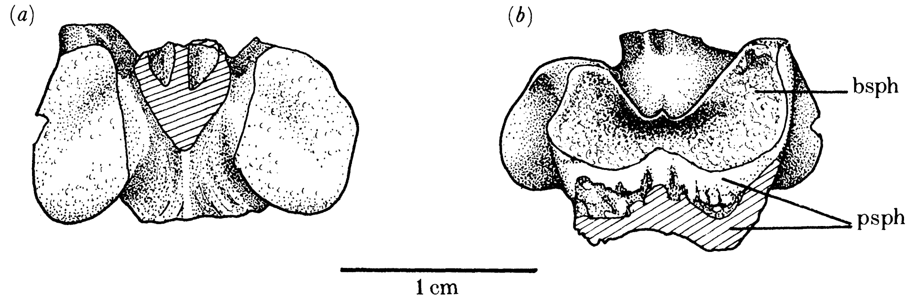


FIGURE 12. *Archeria crassidisca* MCZ 6785, specimen drawings of basisphenoid: (*a*) anterior view; (*b*) posterior view.

(Beaumont 1977). Although both are 'cartilage-finished', subtle differences exist in the shape and orientation of the articular surfaces. The whole articular surface in *Megalocephalus* appears as though rotated by about 45° posteroventrally and somewhat mesially with respect to that in embolomeres. This is not an artefact of preservation as demonstrated by the state of the finished bone surrounding the process. The barely concave anterodorsal surface of the embolomere process is thus represented by a deeply grooved anterior surface in loxommatids. In the latter, the faces are divided by a distinct ridge rather than rounding one into the other. In anterior view the junction of the two faces slopes down at an angle of about 20–30°; in lateral view, the angle is 45°.

Parasphenoid and basisphenoid are indistinguishable around the basipterygoid processes. In 1964, Panchen described the parasphenoid as lining the basipterygoid process in *Palaeoherpeton*, but in 1972 the arguments of Shishkin (1968) persuaded him that this was unlikely. Shishkin's conclusion took account of the relation between the internal carotid, palatine artery and parasphenoid in modern reptiles. Embolomeres, as 'reptiliomorphs', were expected to resemble reptiles in this region where, although the perichondral surfaces of the basisphenoid and parasphenoid are indistinguishably fused, the parasphenoid does not, in ontogeny, line the groove for the internal carotid, nor cover the basipterygoid process. However, in most embolomere specimens there is no evidence for a parasphenoid–basisphenoid suture between the basipterygoid processes. Even in the region of the *Archeria* braincase (MCZ 6785) the two appear totally fused, the groove for the internal carotid running around and above the process anteriorly.

In the Newarthill *Eogyrinus*, parasphenoid and basisphenoid are apparently separated by a suture (Panchen 1964). Between the two carotid grooves is a richly ornamented region bounded laterally by two sharp ridges, also particularly well developed in *Pholiderpeton*. In the Newarthill specimen the ridges have been pushed over onto the groove, appearing like a suture. The condition is incipient in *Pholiderpeton*. Additionally, neither *Pholiderpeton* nor *Archeria* shows a foramen for the internal carotid. A small foramen, probably nutrient, varying in position in different specimens is sometimes present, and a larger one is present in G 13.74. The internal carotid apparently did not penetrate the body of the basisphenoid in all embolomeres, but passed round the process to enter the brain through the large foramen for the interorbital vein. In early reptiles such as *Eocaptorhinus*, there is, as in embolomeres, no distinction between the surfaces of the basisphenoid and parasphenoid in this region (Heaton 1979). The same is true of loxommatids (Beaumont 1977); perhaps this condition is primitive for tetrapods. Although the parasphenoid does not sheath the basipterygoid processes in many modern reptiles, this condition could easily have been derived by reduction from a condition resembling that in embolomeres and other early tetrapods. In *Lacerta*, for example, the parasphenoid partly covers the basipterygoid processes, and the internal carotid and palatine nerve run in a canal between the two (de Beer 1937).

The basipterygoid processes of embolomeres are strikingly similar to those of the early reptile *Eocaptorhinus* (Heaton 1979), whereas both differ from those of other tetrapods in which the processes are known in detail (e.g. loxommatids (Beaumont 1977), *Greererpeton* (Smithson 1982) and *Eryops* (Sawin 1941)). Until more is known of the primitive condition of the basipterygoid process in early tetrapods the significance of this similarity cannot be assessed, but it is potentially interesting and may prove to be a synapomorphy uniting reptiles and anthracosaurs.

Most of the condylar region of the basioccipital is missing in *Pholiderpeton*, the remainder having been pushed inwards dorsally. A small part of the true posterior margin is present, the parasphenoid reaching within 10 mm of it.

The right exoccipital (figure 13) is almost completely exposed but somewhat crushed. Exoccipitals are also present on the holotype of *Palaeoherpeton*, the right one *in situ*. Natural moulds on both slabs together provide a good cast of the left. These can be compared with the exoccipitals present *in situ* in the holotype of *Anthracosaurus russelli* (Panchen 1977). The exoccipital of *Pholiderpeton* consists of a condylar region with a facet, a neck region, an opisthotic facet and a projecting flange. Dorsally and laterally the condylar region thins out so that here the bone is wedge-shaped in section. The condylar facet is roughly hexagonal and is rimmed with finished bone dorsally and laterally. Ventrally and mesially the margin is unfinished and

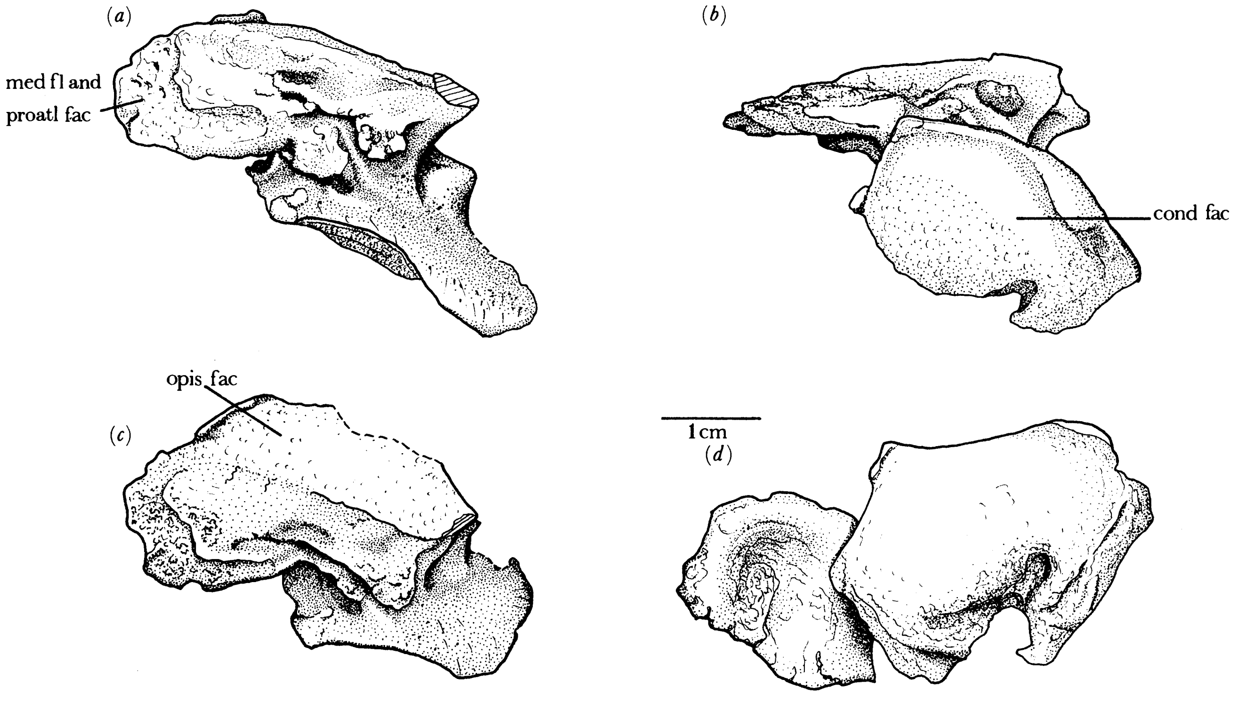


FIGURE 13. *Pholiderpeton scutigerum* holotype, drawings of right exoccipital; (*a–d*) approximately posterodorsal, approximately posterior, approximately dorsal, approximately ventral views, respectively.

there is an emargination of the most ventral part indicating completion in cartilage, possibly the remnant of a notochordal pit. These features are also evident in the cast from the natural mould of *P. decorum*.

The opisthotic facet is an elongated hexagon in both *Pholiderpeton* and *Palaeoherpeton*. A thin flange projects mesially (figure 13*a*, med f). The flange is broken off in *Palaeoherpeton*, but the bone itself is still present in the slab and could be etched out further if required. The orientation of the flange may have been altered by crushing but, in the holotype of *Anthracosaurus russelli*, similar flanges just touch over the foramen magnum, showing what is probably their natural position. Dorsomesially is a facet, probably for a proatlas. In *Proterogyrinus* (Holmes 1984) the exoccipitals are produced dorsomesially but do not meet in the midline.

Irregular bosses, perhaps for attachment of ligaments, rise from the neck of the exoccipital in both *Pholiderpeton* and *Palaeoherpeton*, one of the latter noted by Watson (1926). One of them, on the anteroventrolateral surface in *Pholiderpeton*, might have articulated with the digitiform process of the opisthotic.

Foramina are absent from the exoccipitals of *Pholiderpeton* and *Palaeoherpeton*. The vagal foramina described by Watson (1926) and Panchen (1964) in *Palaeoherpeton* and *Anthracosaurus* are more likely to be deep grooves. The anterior face of the exoccipital between the opisthotic and condylar facet in both *Palaeoherpeton* and *Pholiderpeton* are covered in smooth finished bone, implying a substantial canal between the exoccipital and the otic bones, and the nerve probably ran through here as in *Proterogyrinus* (Holmes 1984).

There was no dorsomesial buttress of the exoccipitals in *Pholiderpeton* and *Palaeoherpeton*, of the kind reconstructed by Panchen (1964). Specimen A1, on which this reconstruction is based, is peculiar in having an area of finished bone lining the region usually described as a supraoccipital. It is distinctly separate from the more lateral facets for the exoccipital. As in *Seymouria*, the loxommatids and reptiles, the exoccipital did not contact the skull table in embolomeres, a primitive feature in contrast to the usual condition in temnospondyls and microsaurs (Smithson 1982).

The parasphenoid is well preserved in *Pholiderpeton*, except just anterior to the basipterygoid process, where it is crushed. The processus cultriformis shows few differences from that described in *Eogyrinus* or *Palaeoherpeton* (Panchen 1972, 1964). Its junction with the sphenethmoid is obvious in section, and can be inferred from the character of the ornament in lateral view. Just anterior to the basipterygoid process its section is almost an equilateral triangle whose base fits the sphenethmoid. More anteriorly it becomes first shallower and then deeper and of a narrow V-shape in section (figures 16 and 38). It is preserved in contact with the ossified portion of the sphenethmoid but in contrast to most other described embolomeres it continues forward, fragments of it being present for a distance of about 175 mm in front of the basipterygoid processes (figure 38). This is at least as far forward as the anterior end of the pterygoids in the reconstructed palate. Posteriorly the parasphenoid of *Pholiderpeton* resembles that of other embolomeres, but all features are more sharply defined. The dorsal extent of the parasphenoid remains unknown. The posterior part forms the basal tubera, with an obvious gap between it and the basioccipital. Crushing prevents an estimate of their depth. Longitudinal grooves and pits are found where the parsphenoid merges with the basioccipital, as in the Swanwick specimen A2 (Panchen 1964).

The side walls of the sphenethmoid have been 'concertina'd' by crushing (figures 10*b* and 14). The sphenethmoid was firmly sutured to the skull roof, and has retained its natural

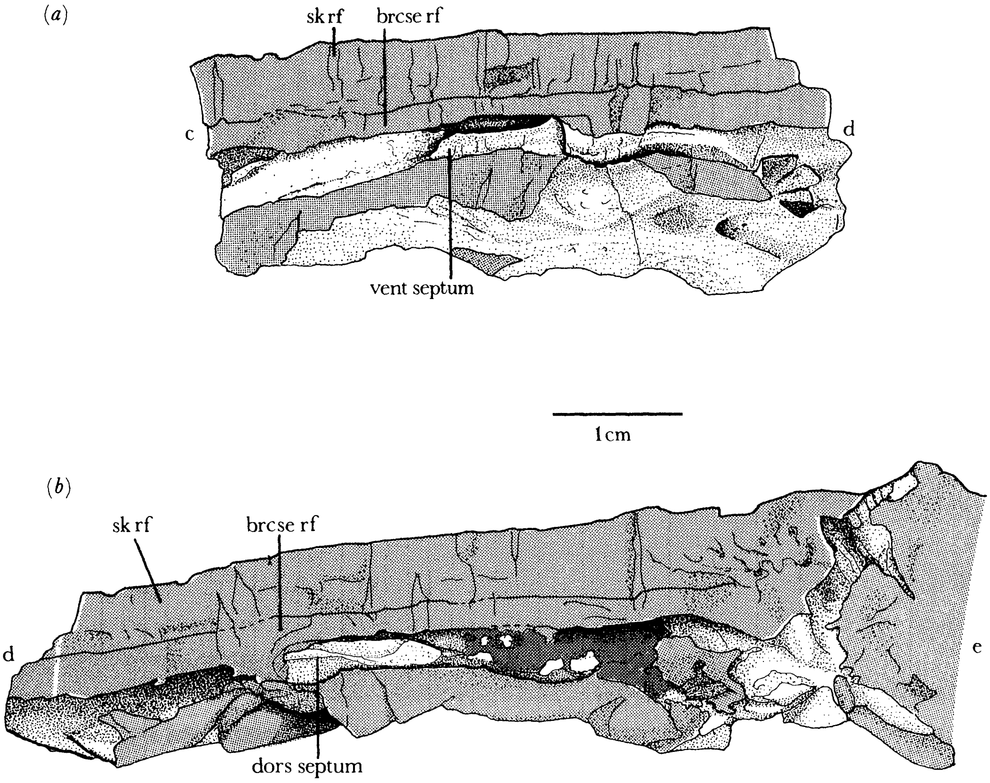


FIGURE 14. *Pholiderpeton scutigerum* holotype, section through sphenethmoid region: (*a*) c–d, view of morphological left side of section; (*b*) d–e, view of morphological right side of section.

relations with the dermal bones. Just anterior to the basipterygoid processes (as preserved) the sphenethmoid is swollen but the walls are thin, enclosing a substantial cavity. Anteriorly buttresses run out dorsolaterally under the skull roof, almost to the parietal–frontal suture as seen on the right. The parietal–sphenethmoid suture has almost been eliminated here. Anterior to the buttresses the sphenethmoid runs parallel to the postfrontal–frontal suture, as in the Swanwick specimen of *Palaeoherpeton*. On the left side, the sphenethmoid wall appears to form a lateral tectal process, as described by Panchen in *Palaeoherpeton* (specimen A1) (figures 10*b*, 14 and 16). I am satisfied that it is not an artefact of preservation, because finished bone in the Swanwick specimen appears both lateral and mesial to the process, being confluent over its ventral margin when viewed in section.

The lateral tectal process might result from ossification of the orbital cartilages. These paired structures form the dorsal part of the interorbital septum during embryological development of many gnathostomes, being completed by upgrowths from the ventral trabecular plate. In the typical tropibasic skulls of living amniotes and most fossil amphibia, these elements are compressed together in the midline. Posteriorly the orbital cartilages send down processes of the pila antotica to meet the basal plate, separating an anteroventral orbitonasal fissure from a posterodorsal prootic fissure. This is represented by the sphenethmoid–basisphenoid buttress in the ossified braincase of embolomeres and other tetrapods. The orbital cartilages (as the taenia marginales) are also responsible for forming the roof of the braincase over the prootic fissure, closing it dorsally. In reptiles, the orbital cartilages ossify as the planum supraseptale

(Goodrich 1930; de Beer 1937). This structure thus appears homologous with the lateral tectal process, although the appearance of both as distinct ossifications is variable. Holmes (1984) reports no ossified roof to the sphenethmoid in *Proterogyrinus* and no obvious lateral tectal process in *Archeria* (personal communication). In the living *Natrix* the only interorbital ossification is formed by dermal bone (de Beer 1937). This region of the braincase is thus highly variable and the lateral tectal process, with its sporadic appearance, should be accorded no taxonomic significance.

On the right, the side wall is crushed into an oval concavity (figure 38). However, the walls seem complete, and although they are broken there is no evidence of a foramen. The anteroventral margin of the concavity is well marked and regular. The bone is thick here and the margin is formed by a hollowing out of the solid sphenethmoid body. Dorsally, where the sidewall is thin, the concavity is apparently exaggerated where the bone has been crushed into the sphenethmoid cavity. The anterior margin is probably determined by the point at which the median septum becomes ossified (see below). This feature seems to correspond best with the more posterior of the two depressions labelled 'profundus' on the lectotype of *Eogyrinus* (Panchen 1972), likewise without a foramen present. Anteroventral to the concavity a V-shaped groove, possibly perforated at its apex, may correspond either to the more anterior of the two 'profundus' depressions on the lectotype of *Eogyrinus* or to the 'stepped ridge' in that specimen (Panchen 1972). However it is more ventral than the former and more anterior than the latter. There is nothing comparable to the rectangular roughened patch of bone described in *Eogyrinus* as the origin of the m. levator palatoquadrati, nor to the foramen which pierces the sphenethmoid body in G 13.74. This foramen appears to be unique to this specimen and may represent simple failure of ossification of the orbital cartilages and be of no morphological or taxonomic significance.

The anterior end of the ossified sphenethmoid extends about 95 mm in front of the parietal foramen (figure 38). The median septum extends further anteriorly than the side walls. The margin curves a little posteriorly, then strongly anteriorly to meet the median septum and the walls are covered throughout in finished bone. A similar condition exists in other described embolomeres such as *Palaeoherpeton* and *Eogyrinus*, though in the latter the median septum extends relatively much further forward. The anterior margin of the septum is unfinished, suggesting extension of the sphenethmoid in cartilage, perhaps to the full length of the processus cultriformis.

The longitudinal sections available from *Pholiderpeton* and *Palaeoherpeton* reveal that the sphenethmoid was fully roofed by bone independent of the skull roof (figures 10 and 14). In *Pholiderpeton* the former is about 3–4 mm thick. In the section illustrated in figure 14*a* a thin, fragile septum rises from the midline of the floor of the sphenethmoid canal. On its counterpart (figure 14*b*) a more substantial septum grows down from the roof of the sphenethmoid. Although it is broken and folded over it is evidently continuous with the sphenethmoid roof and the median septum anteriorly. Presumably the two septa were joined in cartilage in life to give two parallel chambers, and were co-ossified anteriorly. There is no evidence of a septum in *Palaeoherpeton* (A1) and *Eogyrinus* (G 13.74), because the sections available are posterior to the point at which the septum became fully ossified. I can find no evidence from the sections of the holotype of *Pholiderpeton* of either a vertical or a horizontal septum subdividing the sphenethmoid canals as Panchen described in *Palaeoherpeton* (1964) and *Eogyrinus* (1972). As I interpret the type of *Palaeoherpeton*, the lateral tectal process has been pushed mesially into the canal. There is no bone on the counterpart to correspond to the lateral tectal process, as would be necessary if the visible wall in this specimen were a vertical septum subdividing the left-hand canal. The grooves dorsal and ventral to the canal probably represent the courses of nerves IV and III as seen in G 13.74, which Panchen interpreted as running dorsal and ventral to the lateral tectal process.

The thin-walled region of the pineal and pituitary body has suffered much damage. Posteriorly an irregular canal, lined with finished bone, runs through the sphenethmoid roof, presumably for the 'pineal' stalk (figure 10*b*). However the pineal foramen itself it not well defined because of the poor preservation of the parietals dorsally. There is no obvious gap in the roof as suggested for *Palaeoherpeton* (Panchen 1964) but the section here does not run exactly on the midline, where a small gap may have existed.

The section in figure 10*a* shows a most unusual feature. In the wall of the sphenethmoid roof anterior to the 'pineal' canal is a circular foramen about 1.5 mm in diameter, surrounded by dense perichondral bone, not represented on the counterpart. The foramen leads into a duct (figure 10*a*, duct) in the sphenethmoid roof, to join the brain cavity. Distortion prevents certainty as to whether this duct ran transversely over the brain cavity or longitudinally from the cavity into the 'pineal' canal. It is unlike anything described previously. One possible explanation is that the parapineal stalk ran through it rather than up the wide canal for the pineal. There is much confusion in the literature between 'pineal body' or epiphysis and pineal or parietal 'eye', properly called 'parapineal body', and primitively both were present in the brain. The more anterior of the two, the parapineal, is the body which forms the parietal eye in such reptiles as *Sphenodon* (Romer 1962). It is possible that embolomeres possessed both bodies in a well-developed state and that the epiphysis occupied the wider canal, with the parapineal occupying the duct and entering the pineal canal above the epiphysis.

Reconstructions of the braincase of *Pholiderpeton*, supplemented by information from *Palaeoherpeton* and *Eogyrinus*, are given in figures 15 and 16. Several of the foramina for the cranial nerves can be identified with some confidence, others with much less. The olfactory nerve (I) clearly passed from the brain cavity through the large canals in the dorsal part of the sphenethmoid on either side of the median septum. In most tetrapods, the profundus branch of cranial nerve V also passes through the olfactory canal, running as a rule lateral to the olfactory nerve (Goodrich 1930). In *Pholiderpeton* it may have exited through the small foramen somewhat posteroventral to the olfactory foramen. There is no apparent separation of olfactory and profundus canals as there is in *Eryops* (Romer & Witter 1942) or in modern amphibia. Posteriorly the foramina for nerves IX (glossopharyngeal) and X (vagus) can be recognized. Nerves IX and X usually issue through the remains of the fissura metotica (Goodrich 1930) in the occipital region, and in *Pholiderpeton* they probably left through the large foramen between the exoccipital and opisthotics. Although these nerves often leave the braincase independently, they pass through a common foramen in amphibians and mammals. Romer & Witter (1942) adopt this interpretation for *Edops*. Cranial nerve XII exits in the occipital region anterior to the embryonic occipital arch in most gnathostomes. It may have a varying number of roots (Goodrich 1930) and some may have left through the common foramen for IX and X as in *Eryops*. In later temnospondyls, in which the exoccipitals increased in size and came to form the major portion of the occipital condyle, the hypoglossal foramina were enclosed within the exoccipital.

Interpretation of the nerve foramina in the orbitotemporal region of the skull is more

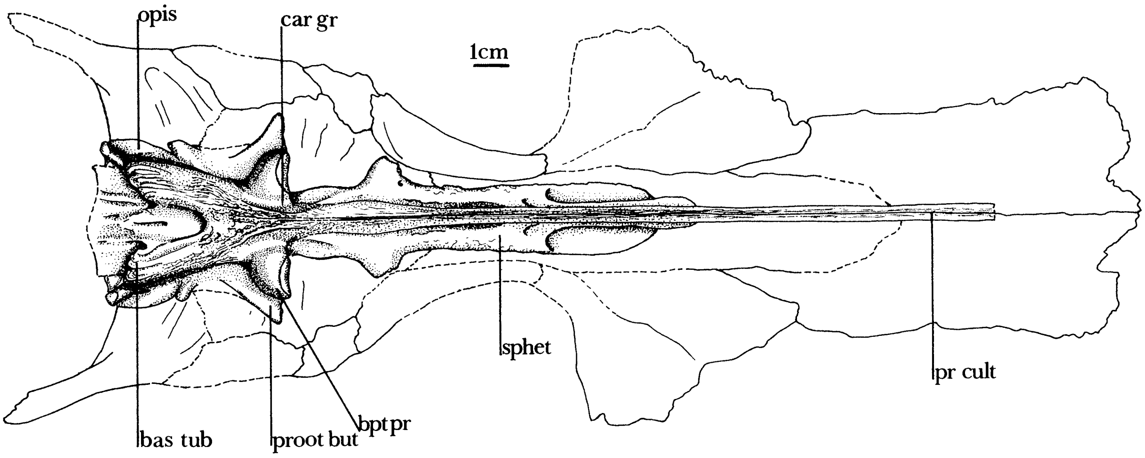


FIGURE 15. *Pholiderpeton scutigerum* holotype, reconstruction of braincase in ventral view.

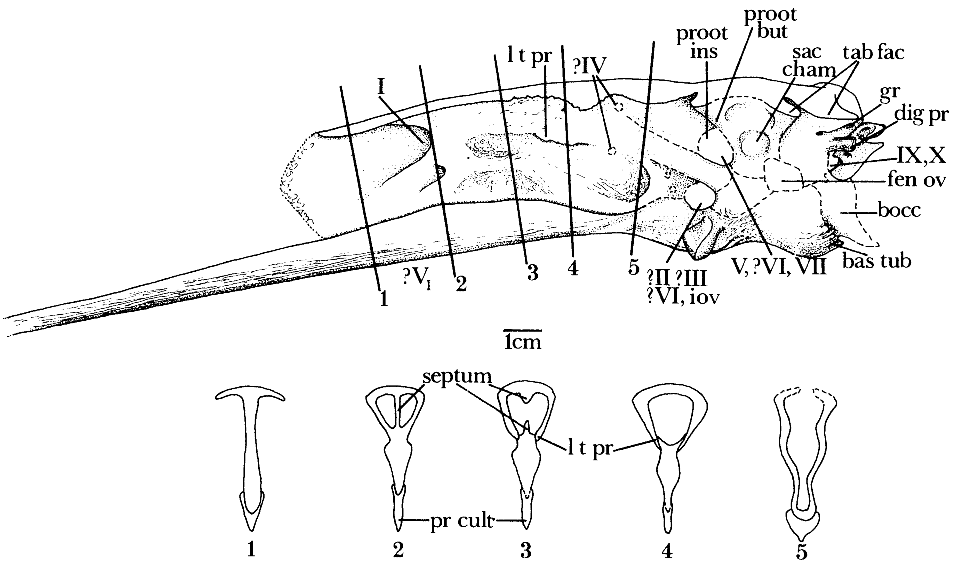


FIGURE 16. *Pholiderpeton scutigerum* holotype, reconstruction of braincase in lateral view; 1–5, sections through sphenethmoid region.

difficult, because they show some variation in living forms and in fossil amphibia the region is frequently poorly preserved. Two large foramina are, however, characteristic of embolomeres: a posterior prootic foramen, separated by the sphenethmoid–basisphenoid buttress from a more anterior foramen. These probably equate to the prootic and orbitonasal fissures separated by the pila antotica joining the basal plate in embryonic development. The profundus (which crosses the fissure to enter the sphenethmoid anteriorly), the trigeminal (V), abducens (VI), and lateral-line branches of the facial (VII) primitively issue through the prootic foramen, whereas the optic (II) and oculomotor (III) primitively leave through the orbitonasal or oculomotor foramen. In most tetrapods, the prefacial commissure, joining the basal plate to the otic capsule, separates the facial (except the lateral-line branch), from the trigeminal, though the commissure may be lost in some fish. In embolomeres likewise there is no evidence of a commissure separating these nerve roots, although the region is usually poorly preserved. The prootic foramen appears large in embolomeres examined, but its dorsal margin is frequently destroyed during preservation and is not certainly known. The orbitonasal foramen allows the interorbital vein to pass across the braincase in addition to providing for nerve exits. In many tetrapods the orbitotemporal region of the braincase may be so completely developed that the cranial nerves issue through separate foramina. In *Eogyrinus*, there are several small foramina here which Panchen (1972) has interpreted as carrying nerves II, III and IV. None of these foramina can be certainly identified in *Pholiderpeton*, but they have been added tentatively in the reconstruction.

The fenestra ovalis of embolomeres is not well known for in no specimen is it adequately preserved, and *Pholiderpeton* provides little more information. All trace of the borders of the fenestra have been destroyed. The saccular chamber of the otic capsule of *E. attheyi* bears a segment of finished bone posteriorly, concave dorsally. Comparison with *Edops* suggests that this could represent part of the anterodorsal rim of the fenestra. On the right in *Pholiderpeton* may be a remnant of this rim of finished bone. Evidence from all embolomere braincases suggests that ossification between the posterior part of the otic capsule and the basioccipital region (the region of the metotic fissure) was minimal, making the margin of the fenestra ovalis very ill defined. The size of the footplate of the stapes may give a minimum size for the fenestra ovalis.

Watson (1926) considered a supraoccipital to have been present in the anthracosaur occiput and thus to be a primitive tetrapod feature; Romer (1947), noting its absence in temnospondyls, suggested it as unique to anthracosaurs and reptiles. Watson described a supraoccipital in the loxommatid '*Orthosaurus*' (= *Megalocephalus* (Beaumont 1977)) but when Beaumont (1977) redescribed the loxommatids she found a clear midline suture between paired opisthotic bones in *Baphetes*. She concluded that a separate midline ossification was absent in this animal. Having examined the material, I accept her conclusions. The condition is moreover identical to that which I find in the occiput of *Pholiderpeton* and I likewise conclude that a supraoccipital was absent. Although the neurocranium in embolomeres was clearly roofed by bone, the origin of the bone is in doubt. In *Pholiderpeton* the evidence suggests that it was provided by medial ingrowths of the opisthotics. This is supported by the fact that in specimen G 15.71 the otic capsule has split longitudinally in the midline. The interpretation of both the holotype of *Palaeoherpeton* and specimen A1 may be disputed; neither shows evidence of a midline suture. Specimen A1 is the only embolomere to have areas of finished bone associated with the occiput. I believe it is the existence of these areas of the opisthotics which creates the appearance of a separate midline region, but that this was in fact also part of the opisthotic.

The absence of a supraoccipital in embolomeres and loxommatids would suggest that it was not a feature primitive for tetrapods. A separate midline ossification, whether it originates from the otic capsules or the occipital arch, appears consistently only in reptiles. Among microsaurs, for example, an ossified supraoccipital may appear in some genera (e.g. *Pantylus*) (Romer 1969) and not in others (e.g. *Microbrachis*) (Carroll & Gaskill 1978).

The reconstructed skull

A reconstruction of the skull of *Pholiderpeton* is presented, based on previous work on other eogyrinids (Panchen 1964, 1972), dimensions which can be derived from the specimen with confidence, and three-dimensional models made with wax sheets or modelling clay. Information from one side of the skull has been freely duplicated for the other, asymmetry between sides being considered of minor significance.

Asymmetry in the final reconstruction derives from use of the preserved shape of the skull table and snout roofing bones. This effect could result from distortion during fossilization, but is equally likely to reflect an asymmetry present in the living animal. Reconstructions of the whole skull are presented in figures 17–19.

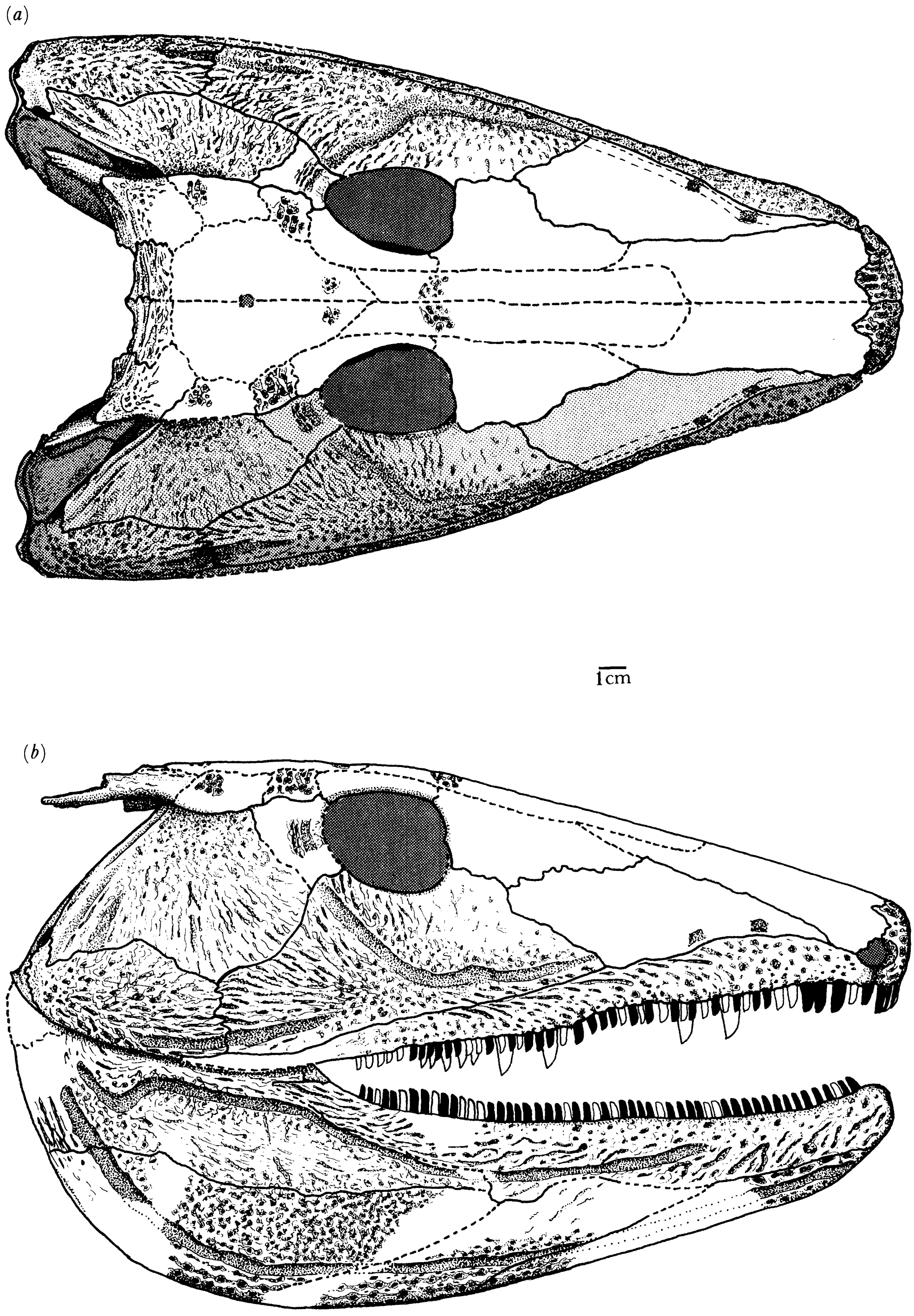


FIGURE 17. *Pholiderpeton scutigerum* holotype, reconstructions of skull: (*a*) dorsal view of skull roof; (*b*) lateral view of skull roof and lower jaw.

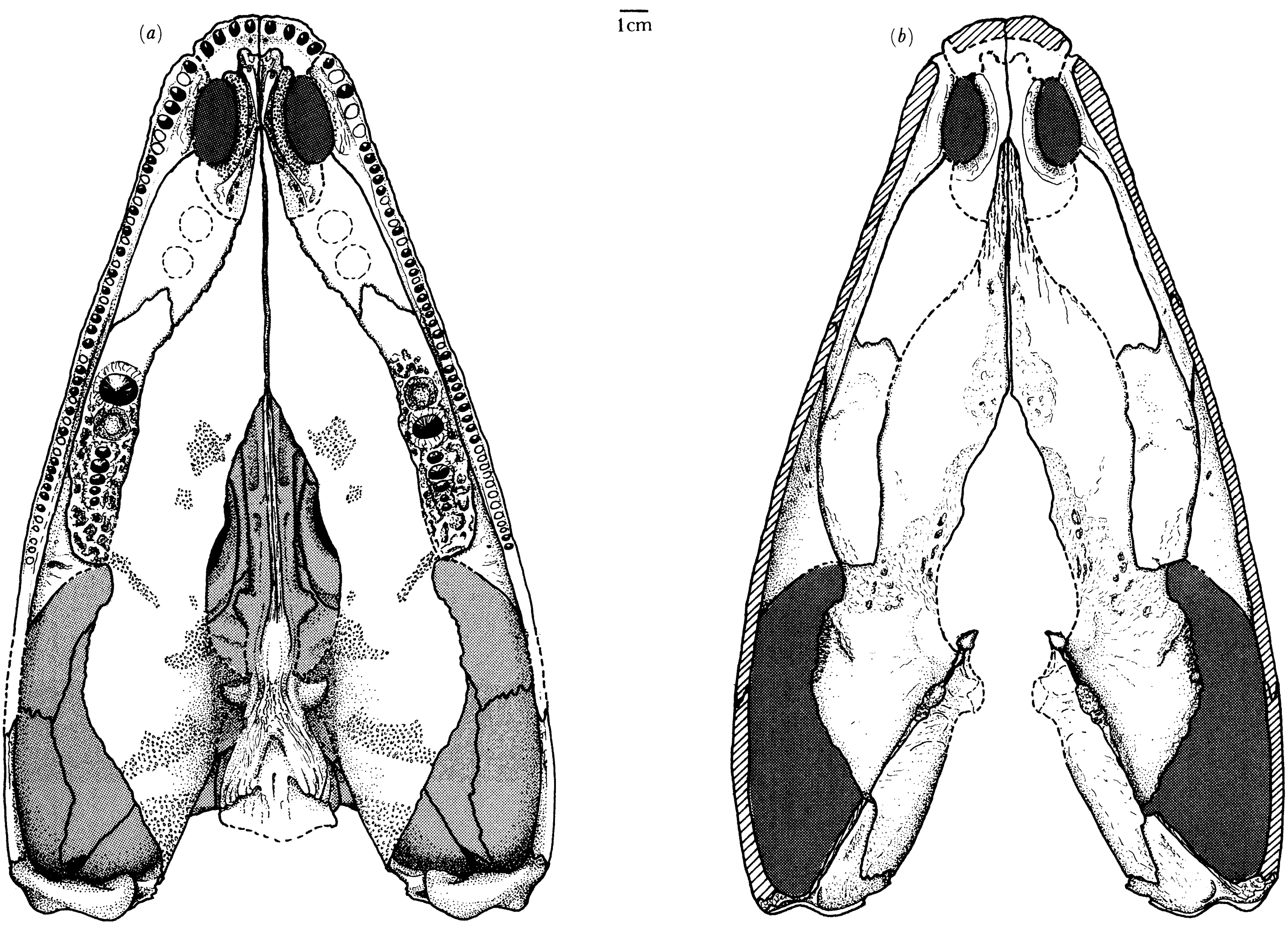


FIGURE 18. *Pholiderpeton scutigerum* holotype, reconstructions of skull: (*a*) ventral view of palate; (*b*) dorsal view of palate (roofing bones removed). Hatching indicates sectioned bone.

The reconstructed skull of *Pholiderpeton scutigerum* bears a strong resemblance to that of *Eogyrinus attheyi* (Panchen 1972). The ornament, lateral-line canal courses where known, and suture patterns closely resemble those of the larger animal as described under individual bones. Several features of the reconstructed skull, however, deserve further comment.

The proportions of the skull in the two genera can be compared by expressing them as percentages (table 1). In *Pholiderpeton* the length of the snout has been reconstructed with some confidence, as has the position of the anterior margin of the orbits. The same features can be measured in *Eogyrinus*; the snout anterior to the orbits is proportionately longer than it is in *Pholiderpeton*, but the parietal foramen has a similar position in each animal. This would be expected from simple allometric growth. As pointed out by Bystrow & Efremow (1940) for *Benthosuchus*, such size differences can have no taxonomic significance taken alone.

The condition of the nares is similar in basic form to that found in many other tetrapods, such as loxommatids, (Beaumont 1977), *Greererpeton* (Smithson 1982) and *Ichthyostega* (Säve-Söderbergh 1932) and is usually taken to be primitive for tetrapods (Säve-Söderbergh 1932; Westoll 1943; Panchen 1967*a*). *Crassigyrinus* (Panchen 1985) provides an intriguing exception.

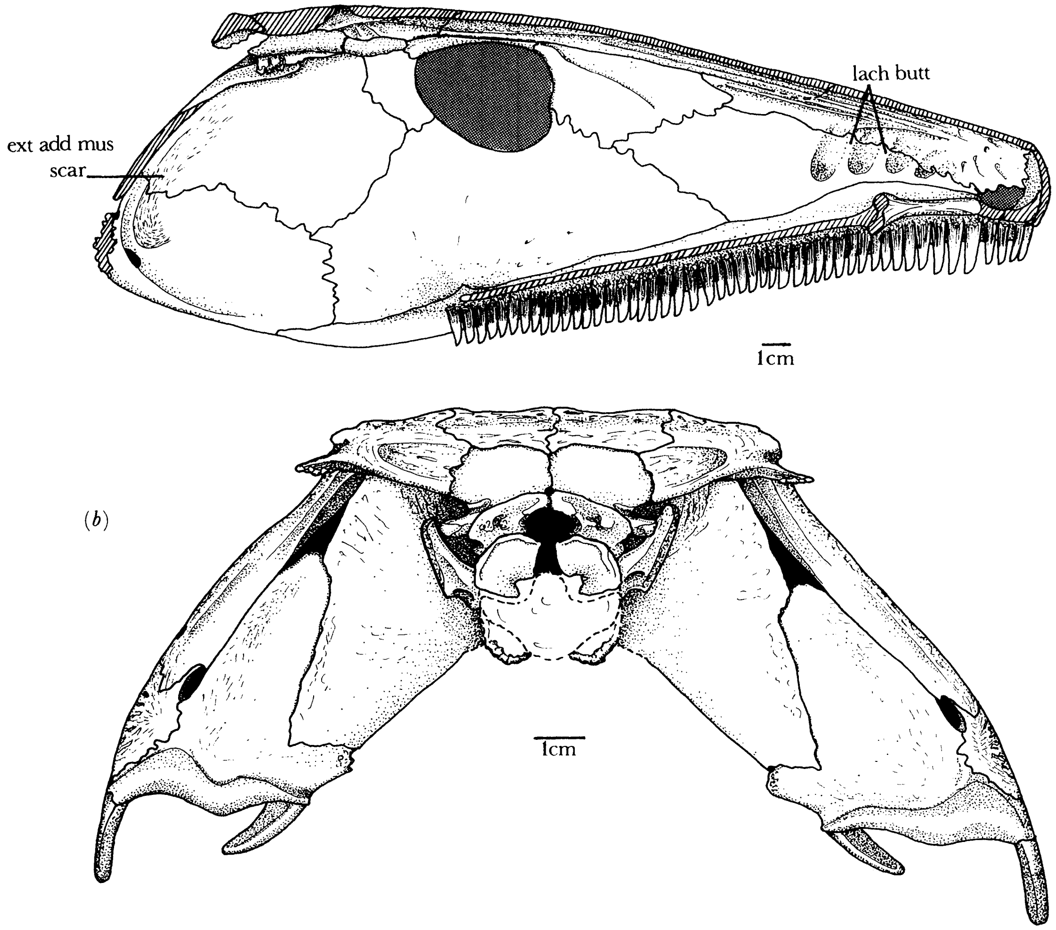


FIGURE 19. *Pholiderpeton scutigerum* holotype, reconstructions of skull: (*a*) internal (mesial) view of skull, quadrate removed; (*b*)occipital view. Hatching indicates sectioned bone.

TABLE 1. *EOGYRINUS* AND *PHOLIDERPETON* SKULL MEASUREMENTS (MILLIMETRES)

	a	*A*	*C*	*a*/*A* (%)	*a*/*C* (%)
Pholiderpeton	45	230	275	19.5	16.3
Eogyrinus	55	285	340	19.2	16.1
	b	*B*	*C*	*b*/*B* (%)	*b*/*C* (%)
Pholiderpeton	110	165	275	66.7	40
Eogyrinus	112	218	340	51.4	33

Lengths: *a*, postparietal–parietal foramen; *A*, parietal foramen–snout; *b*, postparietal–orbit; *B*, orbit–snout; *C*, postparietal–snout.

The rounded margin of the maxilla anteriorly might support the suggestion by Panchen (1967*a*) that a nasolabial groove was present laterally. A nasolabial groove is found in plethodontid salamanders (Panchen 1967*a* and references therein), highly specialized and lungless animals which use exclusively cutaneous respiration through the skin of the body and buccal cavity. The nasolabial groove is used to clear water from the external naris and to prevent it from entering the buccal cavity. Muscles which originate on the septomaxilla operate the valvular mechanism controlling this, and it carries muscles controlling narial aperture in other living amphibia. Panchen suggested that early tetrapods might likewise have had a nasolabial groove to keep the buccal cavity free of water, by analogy with plethodontids. However, being lungless and employing cutaneous respiration exclusively, plethodontids are totally unlike large-bodied early tetrapods such as embolomeres. The latter probably relied on costal ventilation of the lungs, although they possible excreted carbon dioxide through the skin (see below). Cutaneous respiration was probably of minor importance for obtaining oxygen. Pressure from the lungs would have been available to 'blow off' water from the buccal cavity, diminishing the need for a nasolabial groove. In addition, embolomeres did not possess a septomaxillary, so that even if a nasolabial groove were present it must have operated rather differently from that in plethodontids.

A functional nasolabial groove may be unlikely, but nevertheless a 'pinching-in' at the suture between the premaxilla and maxilla is a common phenomenon in early tetrapods. It is found in loxommatids and *Ichthyostega*, and has been recently described in *Eoherpeton* (Panchen 1975) and *Proterogyrinus* (Holmes 1984). The latter resembles *Ichthyostega* in that the choana is separated from the external nostril only by a very narrow process of the maxilla which just touches the premaxilla but fails to make a firm suture. The arrangement may be primitive for tetrapods. In the recently described *Crassigyrinus*, however (Panchen 1985), the nostrils are placed high up on the snout as in *Eusthenopteron*. Thus the polarity of its character is equivocal. *Crassigyrinus* does, however, exhibit a groove at the premaxillary–maxillary suture. The origins and significance of this groove remain obscure; it is absent in the colosteid *Greerepeton* (Smithson 1982). Smithson (1985) suggests a connection between the 'nasolabial groove' and the kinetic junction which existed here in osteolepiforms.

The relations between the pterygoids along the midline is of some interest. Recently Rosen *et al.* (1980) noted the occurrence of a midline palatal suture in *Ichthyostega*. They postulated not only that such a condition was primitive for tetrapods, but also that it was a character which they shared uniquely with dipnoans. In *Pholiderpeton* the pterygoids met in an unsutured junction anteriorly but did not clasp the processus cultriformis, which probably reached forward as far as the vomers. It probably lay above the pterygoid junction, as Panchen suggested for *Eogyrinus* (1972). The midline pterygoid junction varies in embolomeres, being fused in *Anthracosaurus* and sutured anteriorly in *Archeria*.

The overall pattern of the dermal palate in *Pholiderpeton* and other embolomeres is similar to that in the colosteid *Greererpeton* (Smithson 1982). In *Eusthenopteron* (Jarvik 1954), by contrast, the pterygoids never meet in the midline, being separated anteriorly by the vomers and the parasphenoid. Thus the pattern is different from that in many early tetrapods. The pattern in early dipnoans such as *Griphognathus* (Miles 1977) differs from both that of the majority of tetrapods, and that of *Eusthenopteron*, in having the pterygoids sutured along the whole of their long common junction; where they separate, each is sutured to the parasphenoid. The parasphenoid and associated sphenethmoid, however, continue dorsally above the pterygoids as appears to be the case in tetrapods. If the primitive tetrapod pattern is for the pterygoids to meet in a midline suture anteriorly but to be separated posteriorly, it represents a condition intermediate between that of osteolepiforms and that of dipnoans, and could, without other evidence, be equally easily derived from either. Although a midline palatal suture could be a feature shared uniquely between tetrapods and dipnoans, it could also be related to the acquisition of autostyly and consequent sealing and strengthening of the skull which has occurred in each group. There seems ample evidence that this was independently derived in each, being quite different in character in the two. In dipnoans the palate is firmly fused to the braincase in even the earliest members; in the earliest tetrapods, the basal articulation remains unsutured or possibly even mobile, a character retained in some living representatives such as *Sphenodon*. The apparent similarity between the autostyly of dipnoans and urodeles is almost certainly convergent (assuming tetrapods to be monophyletic).

The paraquadrate foramen, found in many early tetrapods, is usually interpreted as carrying the mandibular branch of the seventh cranial nerve and associated blood vessels into the subtemporal fossa (see, for example, Beaumont 1977). In *Pholiderpeton* the course of this nerve is interpreted by comparison with living forms as continuing into a foramen in the mesial face of the prearticular. However, as in the loxommatid *Megalocephalus* (Beaumont 1977), the paraquadrate foramen is linked by a canal to a more lateral foramen in the thickened margin of the quadratojugal adjoining the quadrate. Thus a nerve which must subsequently enter the mesial face of the lower jaw must have taken a circuitous route to do so. In living tetrapods, the chorda tympani passes over the posterior face of the quadrate (Goodrich 1930) to the inner surface of the lower jaw. Thus the paraquadrate foramen looks an unlikely entry point for this nerve, and was probably associated only with blood vessels. The nerve probably followed a course similar to that restored by Smithson & Thomson (1982) for *Greererpeton*.

In contrast to previously described embolomeres, the quadrate ramus of the pterygoid in *Pholiderpeton* would not be visible in lateral view projecting below the jaw margin in the reconstructed skull. The complete unit is preserved flattened into a single plane in the holotype. Even in this state, it is less deep than the reconstructed cheek region, which is restored with some confidence. Although the cheek would appear foreshortened in lateral view, the quadrate ramus would at the same time have been shortened dorsoventrally as a result of its curvature. Holmes (1984) restored the quadrate ramus in *Proterogyrinus* as projecting below the jaw margin and it apparently did so in *Palaeoherpeton*, but the significance of the difference is uncertain.

Many early tetrapods exhibit an emargination at the back of the skull, usually in the region between the tabular and squamosal bones. In the past this has generally been construed as an 'otic notch' housing a tympanum. It is most convincingly displayed in many temnospondyl groups, where it is found in association with a rod-like stapes which is directed dorsally towards its centre. Its presence in seymouriamorphs and in anthracosaurs led most early workers to believe not only that the 'otic notch' was a consistent feature of 'labyrinthodonts', but that the tympanum was primitive for tetrapods. The reconstruction of the 'otic notch' in *Pholiderpeton* was discussed in more detail by Clack (1983) in which it was concluded that a tympanum was probably absent in this animal. A detailed reconstruction of the region will be found in figure 17*b*. However, although the notch might be regarded as simply a V-shaped space between the tabular and squamosal, in other related animals not only is the lateral margin of the tabular smooth and rounded, as indeed it is in *Pholiderpeton*, but that of the supratemporal is likewise smooth and embayed. This can be seen in *Proterogyrinus* (Holmes 1984) and is also true of *Crassigyrinus* (Panchen 1985), both earlier and more primitive than *Pholiderpeton*. The notch here seems clearly to have had some functional significance, although unfortunately the stapes is unknown in both these forms. Panchen and Holmes regard the embayment as probably having housed a functional spiracle in *Crassigyrinus* and *Proterogyrinus* respectively. The idea was first suggested by Carroll at an informal lecture to the Society of Vertebrate Paleontology in 1980, and is increasingly seen as likely by workers on early tetrapods. Ideas about what function such a spiracle might have had remain speculative.

The tabular horn is a characteristic feature of the anthracosaur skull and is particularly well developed in embolomeres. Its function was first considered by Watson (1926), who proposed that it articulated with the bone he interpreted as the post-temporal. He noted that this is indicated by the 'presence of an articular surface on the inner side of the tabular horn'. The 'post-temporal', however, is now identified as the cleithrum (Romer 1947, 1957, 1963). In 1964, Panchen proposed an alternative function for the tabular horn. He envisaged it as a process for muscle attachment and suggested that the most likely muscle to attach here was part of the depressor mandibulae. In modern amphibians this muscle originates partly on the posterior dorsal edge of the skull and partly from the fascia of the epaxial musculature. In reptiles, however, it is confined to the skull (Adams 1919). Panchen restored part of the depressor mandibulae originating from the ventral surface of the horn, which would thus provide a firmer attachment than muscle fascia. He extended the hypothesis to suggest the development of the tabular horn, possibly resulting from elliptical growth of the bone (Parrington 1956), was correlated with the acquisition of tabular–parietal contact, also characteristic of anthracosaurs. Further, with axial muscles supported and strengthened by the tabular horn, Panchen suggested the resulting limitation to movements of the head correlated with loss of the post-temporal fossae, typically absent in anthracosaurs.

New information from *Pholiderpeton* and related specimens prompts alternative suggestions. In embolomeres the posterior aspect of the tabular horn is very complex. Its most delicate component is the posteriorly directed blade growing from the ventral surface of the tabular. This is often lost or distorted during fossilization and its original attitude not always determinable. However in *Pholiderpeton* its ventral aspect is preserved intact. The central surface extended almost exactly horizontally from the skull table. It is this delicate, horizontal ramus to which, according to Panchen, the depressor mandibulae would have attached. As it contracted, it would have imparted a strong tangential force to the tabular blade. The blade appears poorly adapted to resist such a force. On the other, its elongate growth seems designed to accommodate tensional forces along its length.

Attachment of the depressor mandibulae to the dorsal fascia is unique to modern amphibia, being confined to the back of the skull, particularly the squamosal in reptiles (Adams 1919). The condition in modern amphibia would well result from the extensive loss of ossification which has occurred in the skulls of these creatures. The dorsal fascia may substitute for the original bony attachment. Adams restored the depressor mandibulae of *Eryops* attaching to the back of the skull; Rose (1980) restored it originating along the posterior margin of the squamosal. Its attachment here in embolomeres could account for the presence of a groove in this position. It remains possible that part of the muscle originated on the tabular anterior to the blade.

Dorsally the tabular blade bears longitudinal striations and a deep rugose pit is present above the base of the blade in many embolomere specimens. As Watson suspected, it seems quite certain that something attached here. Although it was clearly not a post-temporal, it seems most likely to have been a ligament, attaching within the pit, supported by the blade and possibly augmented by fleshy muscle attachments running along the length of the blade. These could have been muscles of the epaxial system, supporting the head and stiffening the neck, but an alternative is that part of the trapezius group attached here. The somewhat laterally directed orientation of the tabular blades supports the latter possibility. The trapezius muscle derives from the hyoid arch levators (Romer 1962) and is frequently large in tetrapods. It originates on the occiput and has slips which insert onto the shoulder girdle, primitively to the dermal elements of cleithrum and clavicle. The sternomastoid, cleidmastoid and other anterior and ventral slips may differentiate. One of these slips could have originated on the tabular, inserting on the blade of the substantial cleithrum found in *Pholiderpeton*. Rose (1980) restored the sternocleidomastoideus as attached in a similar position on the tabular of *Eryops*; and Howie (1970) also restored a cleidomastoid on the tabular of '*Parotosaurus*' (= *Parotosuchus*; see Kozur 1977). It is unlikely to have restricted head movement and may indeed have assisted if the girdle were to have been held rigid. It may also have had a role in raising the head, as it did in *Parotosuchus*.

The delicate, elongated tabular blade found in *Pholiderpeton* is seen in other eogyrinids, but in other anthracosaurs some variation is apparent. In *Anthracosaurus russelli* there are two elongated blades, the upper apparently homologous with the boss above the pit for ligament insertion. This may be correlated with greater development of the trapezius, associated with the obviously different habits of this genus. In *Proterogyrinus*, which in many respects is an ideal protoembolomere, in place of the typical blade-like horn is a relatively short and thin cylindrical process (Holmes 1984). There is a boss developed above it as in other embolomeres, and the two are separated by a notch. The tabular 'horns' in *Eoherpeton* (Panchen 1975) and *Crassigyrinus* (Panchen 1985) are each undifferentiated knobs, probably homologous to the complete embolomere unit, and to the tabular 'buttons' seen in loxommatids and *Greererpeton*.

Functional morphology of the embolomere skull

Anatomical evidence for jaw muscles is confined to those already mentioned on the pterygoid, quadrate, quadrotojugal and squamosal. Elsewhere distinguishable muscle scars are absent.

Adductor muscle may be broadly divided into an external group (the capitimandibularis) and an internal group (the pterygoideus). The muscle scar found on the squamosal, quadratojugal and quadrate in *Pholiderpeton* was probably the site of origin of a superficial division of the capitimandibularis, which may be inserted on the internal surface of the surangular crest, effectively a 'coronoid process', as it is seen to do in other forms. The degree of development of the muscle scar and the surangular crest suggest that this muscle may have been a substantial one. Slips of the capitimandibularis originate in different places in different groups; being modified according to the feeding mechanism of the animal, they are necessarily extremely fluid. It is likely that the muscle was differentiated into several slips in *Pholiderpeton*. An insertion in and around the adductor fossa, medial to the superficial slip, is usual, but the site of the origin remains in doubt, and the degree of development quite unknown. There has been some debate in the past as to whether part of the capitimandibularis originated on the underside of the skull table or was confined to the palate and cheek. In 1964, Panchen noted that any component of the external adductor which took its origin on the braincase or dermal roofing bones would have the effect of producing a rotation of the braincase with respect to the palatoquadrate and that the 'kinetic' line' between the squamosal and supratemporal, consisting of ligamentous tissue, acted as a shock-absorber to minimize this effect. In 1970, however, he assumed that the main adductors originated only on the palatoquadrate and cheek, because only then could the skull table be kinetically isolated from the cheek. This has been (Thomson 1967; Jarvik 1980) inferred to be so in rhipidistians, presumably for similar reasons. Kinetism apart, however, there seems no reason for suggesting that the adductor muscles were excluded from insertion on the skull table in embolomeres, and a possible argument against their insertion on the palatoquadrate is the thinness of the bone in the region of the quadrate ramus. In terms of jaw function alone the argument is relatively unimportant. Attachment to the skull roof or to the palatoquadrate lying directly below it would in fact make little difference to the relative position of the origin with respect to the insertion.

The internal adductor or pterygoideus probably arose from the dorsal surface of the pterygoid and appears to have had two or possibly three divisions judging from the muscle scars. No certainly identifiable muscle scars are found on the anterior parts of the pterygoid, although it remains possible that a slip ran forward anteriorly as postulated, for example, by Beaumont for loxommatids (Beaumont 1977). Although the muscle scars on the pterygoid are well developed, indicating that the muscle may have been large and important, no muscle scar for its area of insertion can be demonstrated. Absence of a muscle scar is no indication of absence or poor development of a muscle (D. S. Brown, personal communication). The pterygoideus muscle in other forms usually inserts around the adductor fossa, medial to the capitimandibularis. In *Pholiderpeton* as in *Eogyrinus* (Panchen 1972) the processus alaris of the jugal formed a smooth edge over which the pterygoideus may have run as a pulley. In crocodiles, a 'stem tendon' (Iordansky 1964) is formed by a tendon of the pterygoideus which runs over the pterygoid in an analogous position. Panchen postulated such an arrangement for *Eogyrinus*.

A muscle is most efficient when it is acting at right angles to a line between its point of insertion and the jaw articulation. The efficiency of muscles which may be restored in *Pholiderpeton* can be investigated to find at which point in the jaw action the muscles produce their greatest effect. To do this, representative muscle fibres were drawn for two probable divisions of the capitimandibularis and for slips of the pterygoideus. It is apparent that the external division of the capitimandibularis, attached to the posterodorsal margin of the surangular crest, would be acting most efficiently as the jaw approached closure. The situation is much less clear for the remaining muscles. The anterior slips of the pterygoideus may be considered as originating at the processus alaris. Points of insertion may have been at any point surrounding the adductor fossa. A fibre restored with its point of insertion on the posterior margin of the adductor fossa would be acting most efficiently with the jaws fully adducted, whereas another with its point of insertion restored at the centre or more anteriorly in the fossa would have the opposite effect. For other fibres which may be restored, for example one which originated at any point vertically above the deepest part of the jaw, the efficiency of the muscle may not alter significantly during jaw closure.

Olson (1961) identified two basic arrangements of jaw-closing musculature in tetrapods; one adapted towards the static pressure system, an arrangement in which muscles were most efficient at jaw closure, allowing a powerful grip on prey, the other adapted towards the kinetic inertial system, an arrangement in which muscles were most efficient at initiation of jaw closure, giving a powerful bite but little grip. There are examples of animals at the extremes of these adaptations which may be placed in one or other of these categories, but for many other less specialized animals this system is probably oversimplified. To judge whether an animal is adapted to one system or the other, it is necessary to know not only the type of any muscle restored but also the relative size. In *Pholiderpeton*, for example, muscles with potential for each system can be plausibly restored but the size and proportional effect of each cannot be ascertained. Further, there appear to have been muscles which fit into neither category and others which may have had the potential to belong to both, for example the pterygoideus, which may have had a broad area of insertion including both types of fibre. Thus, although embolomeres have usually been interpreted as adapted to the kinetic inertial system (see, for example, Panchen 1972), the findings of this study do not fully support such an interpretation.

The relation between the skull table and the cheek in embolomeres has been of some interest since the time of Watson (1926). He envisaged it as being intermediate in condition between the kinetic junction in osteolepids and a fully interdigitating suture. He described a groove in the supratemporal of G 13.78 and the holotype of *Palaeoherpeton* which would match a concave facet on the squamosal, the gap between them being filled by a pad of ligament. Later Panchen (1964) accepted this idea, although he suggested that very little movement could have been possible at this junction and that it would have been rather different from that in osteolepids. He viewed the dermal skull kinetism as related to that found at the basal articulation, suggesting that the purpose of the kinetism was to protect the brain from shocks received by the jaw mechanism in feeding. Any component of jaw musculature which took origin from the braincase or underside of the roofing dermal bones would tend to produce rotation (or more accurately dorsoventral movement) of the palatoquadrate. This would be mimimized by the presence of a shock-absorber at the point of greatest stress, hence the presence of ligamentous tissue between the supratemporal and squamosal. Later (1970, 1972) he revised this assessment and suggested that no adductor muscle arose on the skull table or braincase, and that these were thus kinetically isolated from the jaw mechanism.

Both Watson and Panchen accepted the occurrence of some movement at the supratemporal–squamosal junction, the movement being a dorsoventral 'squeezing' absorbed by the ligamentous tissue. However, for such movement to occur, some compensatory movement must have occurred elsewhere in the dermal roof. A consideration of the structure of the rest of the skull roof, however, reveals no point at which this could occur. Both Watson and Panchen noted that the 'kinetic line' in embolomeres extended only part way along the cheek–skull-table junction, the intertemporal and postorbital being apparently joined in a normal interdigitating suture. The rest of the skull is a firmly sutured unit. The skull table and snout bones are rigidly joined to the cheek anteriorly, and thus in effect to the cheek posteriorly. The cheek region takes the form of an L- or U- shaped girder, with the palate beneath sutured to it laterally, and would thus have been totally incapable of bending either laterally or dorsoventrally. At what might appear to be its weakest point, below the orbit, the processus alaris forms a powerful buttress which appears ideally situated to prevent any such movement. The only other possibility allowing movement at the supratemporal–squamosal junction must be bending at some point on the skull table, presumably at the narrowest point, which is between the orbits. However, the postfrontals are among the thickest bones of the skull table, forming strong ridges on the underside of the bone over the orbits, and the sutures between the bones between the orbits are arranged so as to interlock to form the strongest possible structure. This plus the suturing between cheek and skull table posterior to the orbits make the possibility of bending of the table extremely unlikely.

Bending of the skull table at any point is also effectively ruled out in embolomeres by the close apposition below it of the solidly ossified braincase which essentially acts as an I-beam, a structure which would resist any bending. It is thus impossible to see how movements could have occurred at the supratemporal–squamosal junction. It also seems unlikely that the short section of 'cushioned' junction could have provided an effective 'shock-absorber' to the braincase when the remaining parts of the cheek–skull-table junction were conventionally sutured. The structure of this region must be reinterpreted.

Although the squamosal of embolomeres clearly bore a dorsal facet, and *Pholiderpeton* is no exception in this respect, the relation of this to the supratemporal may have been misunderstood. Close examination of the margin of the supratemporal in *Pholiderpeton* indeed shows a groove, as noted both by Watson and Panchen in *Palaeoherpeton* and G 13.78 (and also R 8425). However this does not run exactly laterally, as Panchen noted in *Palaoeherpeton* (except at the extreme posterior end). Laterally the margin is very much pitted and roughened, and in cross-section is *convex* (see figure 38, s, and inset). The width of the convexity matches the width of the squamosal facet. If the squamosal fitted exactly laterally, leaving no overhang of the supratemporal, a convex surface would meet a concave one, their pitted and roughened surfaces meeting. Figure 38, inset (a) shows the previous interpretations of the position of the squamosal; (b), the current proposal. Thus the occurrence of a ligamentous filling is ruled out.

Examination of the surfaces of the squamosal facet and the margin of the supratemporal shows that they resemble most closely the surfaces of the anterior part of the lachrymal bone where it sutures with the maxilla. Here is an essentially broad horizontal surface, pitted and roughened but not interdigitated, above the canine peak. It occurs where great stresses must be encountered and where a vertical surface (the maxilla) meets an angled one (the lachrymal). It appears that at points of such stress, rather than the more common interdigitating suture, a broader surface has been developed to resist vertical compression (an idea first informally suggested by Dr M. J. Heaton in 1980). The broad surface distributes the vertical forces more evenly over the bones. It seems significant that the squamosal facet lies above the point at which the lower jaw is deepest and where presumably the greatest forces occurred. At this point the steeply sloping cheek meets the horizontal skull table. It appears that the junction at this point is providing the best type of suture both to resist vertical forces and for a point at which a sloping surface meets a horizontal one.

The degree of sculpturing on the supratemporal varies, apparently between genera of embolomeres, although with the little which is known of them this could result from individual variation. Thus G 13.78 shows very little sculpturing, whereas elsewhere (Clack 1987) I attribute this skull table to *Anthracosaurus*. In *A. russelli* the 'kinetic line' has apparently been sealed (Panchen 1977). Some skull tables show that a slight overhang of the supratemporal was present (e.g. in *Pteroplax*) by exhibiting a slightly incurled margin. However, I do not believe these differences represent fundamental differences in structure. I suggest that in none was the skull table functionally 'kinetic', but that, from a primitively unsutured condition, the supratemporal–squamosal junction in eogyrinids was developed as a suitable one to resist vertical forces and possibly correlated with the deep lower jaw. The groove on the supratemporal was probably occupied at least in part by a component of the external adductors. The broad butt-joint would only have been necessary if muscles originated above it on the skull table.

In the recently described primitive embolomere *Proterogyrinus* (Holmes 1984) and in the early anthracosaur *Eoherpeton* (Panchen 1975; Smithson 1985) the intertemporal has a non-interdigitating junction with the postorbital. These animals thus appear to show a more primitive condition than the later embolomeres, assuming that this type of junction is a remnant of the kinetism found in osteolepids and other early bony fish. The pre-maxillary–maxillary suture was also unconsolidated in *Proterogyrinus*; this might also represent a remnant of the kinetic mechanism found in the skulls of fish. It is nevertheless difficult to attribute a functional significance to the 'lateral kinetism' in this animal or in *Eoherpeton*. The snout roofing bones (nasals, prefrontals) were firmly sutured to the anterior cheek bones (lachrymals, jugals) and therefore the skulls were almost as solidly constructed as they were in the eogyrinids.

The distinction between 'kinetic' and 'akinetic' amphibian skulls may not be as clear-cut as has been generally believed in the past. Fossil amphibian skulls often disarticulate along the skull-table–cheek junction, for example *Dendrerpeton* (Steen 1934) and *Greererpeton* (Smithson 1982). The latter animal was taken to have a 'kinetic' skull by Panchen (1975) but was shown by Smithson to have been fully sutured at this junction. Some juvenile temnospondyls (*Saurerpeton*)show a separation of skull table and cheek regarded as a 'kinetic line' by Milner (1982). This may represent retention of the primitive condition in a juvenile rather than any functional mobility.

Because the skull table of embolomeres was rigid, and the braincase fully ossified and firmly attached beneath it, it follows that the braincase was immobile with respect to the dermal skull roof. The nature of the basipterygoid junction is thus puzzling. The surface of the basipterygoid process is strongly suggestive of a synovial joint and its shape leads to the inference of some form of rotatory or dorsoventral movement. The palatal complex is firmly sutured anteriorly, laterally and posteriorly to the rigid skull roof. Thus, if it occurred at all, movement must been restricted to distortion of the palatal bones, which are relatively thin except in the region of the basipterygoid. In loxommatids an apparently synovial basal articulation is combined with a skull in which the supratemporal and squamosal are united by a broad area of overlap, precluding all possibility of kinesis here. Beaumont explained this by postulating movement at the pterygoid–ectopterygoid and pterygoid–palatine sutures and a quadrate which was mobile with respect to the quadratojugal and squamosal. As has been described, no such movement can be postulated for embolomeres, because the palatine–pterygoid and quadrate–quadratojugal sutures are firm. However, the ectopterygoid–pterygoid suture is a simple overlap as in loxommatids. This may have permitted a very small amount of bending of the palate. Indication of the presence of an m. levator palatoquadrati suggests that some movement may have occurred, although its purpose is unknown.

Axial skeleton

The eogyrinid vertebral column is represented only by incomplete sections of column and isolated elements, described by Panchen for *Eogyrinus* (1966, 1972) and by Boyd (1980) for *Pteroplax*, following earlier descriptions of the same material (Atthey 1884; Embleton 1889; Watson 1926). The presacral count is uncertain (Panchen 1966) and the cervical region completely unknown. New material from *Pholiderpeton* provides helpful information about both. Comparisons can be made with the recently described protoembolomere *Proterogyrinus* (Holmes 1984) and so far undescribed material from the Permian embolomere *Archeria*. I have included descriptions of the atlas vertebra of the latter to aid comparison.

Atlas vertebra of Archeria crassidisca

The atlas intercentrum is visible on AMNH 4550, a complete skeleton; other specimens include MCZ 2046 (part) MCZ 2047 (part) and AMNH 16203 (figure 20*a–e*). Its anterior face is markedly convex to match a concave occipital condyle (J. A. C., personal observations). The bulbous surface flattens slightly dorsally to provide seating for the exoccipital portions of

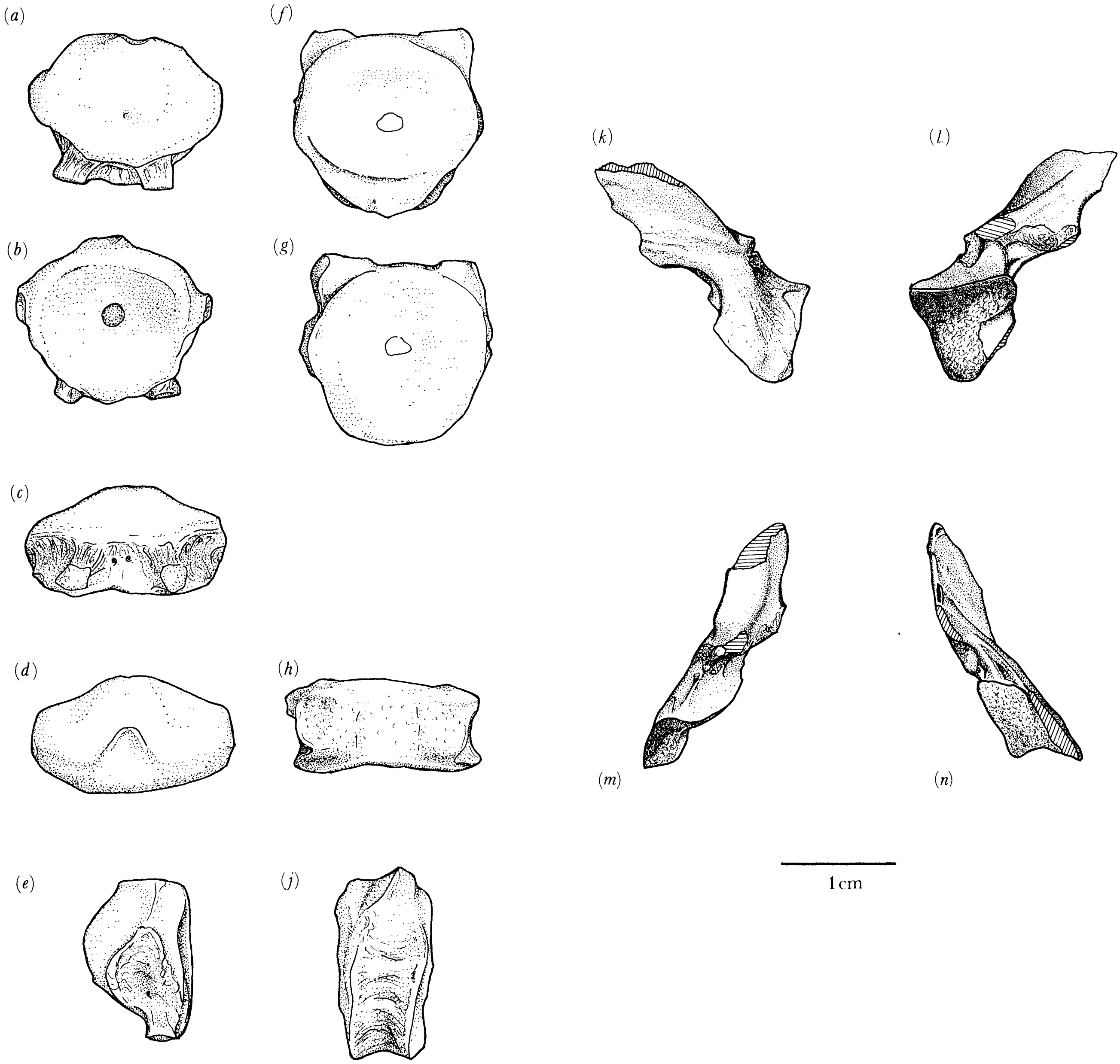


FIGURE 20. *Archeria crassidisca*, atlas vertebral elements: (*a*–*e*) AMNH 16206 intercentrum, anterior, posterior, ventral, dorsal and lateral views respectively: (*f*–*j*) MCZ 6989 pleurocentrum, anterior, posterior, dorsal and lateral views respectively: (*k*–*n*) MCZ 2047 neural spine, lateral, mesial, anterior and posterior views respectively.

the condyle, which can be seen *in situ* in MCZ 2046. A small dimple marks the original position of the notochord. The posterior face is amphicoelous, as in a pleurocentrum, with a small notochordal pit at the centre. An amphicoelous profile is reported on the atlas intercentrum of *Proterogyrinus* (as *Mauchchunkia* (Hotton 1970; Holmes 1984)).

Periosteal bone sheaths the ventral surface reaching upwards laterally to just over half the height of the centrum. The posterior margin is drawn out laterally in some specimens around an articulatory facet. Two projections (probably parapophyses) grow out ventrolaterally on either side of the midline, covered with striated periosteal bone, terminating in depressions of unfinished bone.

The atlas pleurocentrum represented by specimens MCZ 2046 (part) and MCZ 2047 (part) (figure 20*f–j*) is essentially similar to a normal embolomere pleurocentrum, but the ventral margin is produced into a blunt keel which articulates with the following intercentrum.

The anterior face has an intercentrum-like profile, slightly amphicoelous near the notochordal foramen, but convex nearer the perimeter, except along the anteroventral edge. Here a somewhat depressed rim forms a flange which merges further dorsally into the body of the centrum. The atlas intercentrum and pleurocentrum articulate in a relation opposite to that of other central elements. Here the intercentrum provides the 'socket' and the pleurocentrum the 'ball' rather than vice versa as in other vertebrae. A similar reversal also occurs in *Proterogyrinus* (Holmes 1984) and dissorophids. DeMar (1968) suggested that it was equivalent to the odontoid process seen in higher vertebrates. The posterior face of the pleurocentrum is more fully amphicoelous, so that normal relations between inter- and pleurocentrum are restored thereafter. Dorsally the surface is unfinished, and provides facets for the neural arch, set at an angle of about 45° to the vertical. A flattened area between them forms the floor of the neural canal. The ventral and lateral surfaces of the pleurocentrum are covered in periosteal bone which covers the neural arch facets laterally.

The right half of the atlas neural arch is preserved in MCZ 2047 (figure 20*k–n*). The pedicel has a large concave trapezoid ventral facet for articulation with the pleurocentrum. Part of this surface is covered with periosteal bone which presumably marks the base of the poorly differentiated transverse process, the tip of which has broken off. Anteriorly the articular surface forms a lip which clearly contacted the atlas intercentrum.

The neural spine is small, tapering and covered laterally and mesially with periosteal bone. It clearly did not meet its fellow except possibly by a cartilaginous junction just over the neural canal. A small rough patch on the anterior surface could indicate the articulation point for a proatlas, though none has been found. The posterior zygapophysis is not developed. The atlas arch of *Archeria* closely resembles that of *Eryops* in general structure.

Axial skeleton of Pholiderpeton scutigerum

Associated with the holotype are a total of 47 vertebral centra: 25 intercentra, 21 pleurocentra, 1 indeterminate. There are a maximum of 48 ribs and 20 neural arches (see Appendix 1). Postcranial elements in the holotype are shown in figures 42 and 43 and are numbered from the left of the specimen, except for those on the small block and those on R 2396, which have been numbered last.

Centra

Most centra of the holotype have been compressed anteroposteriorly. Three isolated specimens have been subjected to shearing and lateral compression and have segments missing. Two have neural arches still in articulation. The preservation of these specimens is different from that of the majority of specimens; although the matrix suggests that they formed part of the original block, it is not obvious with which part they should be associated. They give the impression that there was more of the animal present than was collected or that some has subsequently been lost. Preservation prevents reliable measurements of centrum length in most cases. Measurements of the best preserved are tabulated below (tables 2 and 3).

Table 2. Measurements of intercentra of *Pholiderpeton scutigerum*, holotype

	length/mm		diameter/mm		diameter of notochordal foramen/mm (max. and min.)
intercentrum	dorsal	ventral	less rim	plus rim	
i	10	—	25	31	6.0–6.5
ii	9	11	25	30	5.0–6.5
iii	—	7	26	30	4.0–4.7
iv	—	—	26	31	5.0–5.7
v	—	8.5	26	30	6.0–10.0
vi	9	11	26	30	5.5–6.0
vii	—	—	25	30.5	6.0–6.5
viii	—	—	25	30	6.0
ix	—	9	26	30.5	6.0–6.5
x	4–4.5	6	26.5	31	5.0
xiv	—	7	19.5	24	3.0–4.0
xv	—	—	26	29	4.5–7.0
xvi	–	7	22	26	3.5–7.0
xxi	–	–	19	–	4.0–8.0
xxii	–	–	–	26	5.0–6.0

Table 3. Measurements of pleurocentra of *Pholiderpeton scutigerum*, holotype

pleurocentrum	length/mm	diameter/mm	diameter of notochordal foramen/mm (max. and min.)
a	12	35	3.0–4.5
b	14	32	4.5–5.0
c	—	26	3.0–3.5
d	—	33	3.5–5.0
e	—	33	4.0
g	12–13	33	4.0–4.5
m	—	32	2.5
p	9	17–24	3.0–4.0
q	10	24	4
r	—	24	—
s	—	30	—

Pleurocentra, virtually circular in outline, were measured across the diameter, discounting the facets for the neural arch. They are approximately rectangular in outline laterally so that length is more or less uniform throughout.

Intercentra are more complex (figure 21*a–f*). The main body of the centrum consists of a disc of spongy bone, its anterior and posterior faces convex except for the notochordal foramen which lies at its centre. The ventral half of the centrum is surrounded by a compressed rim which thickens dorsally to merge into the rest of the centrum. It forms shoulders in anterior and posterior views which bear facets for the rib articulation. Measurements were taken including and excluding this rim where it was sharply defined. Length was measured both dorsally and ventrally for intercentra where possible. Maximum and minimum diameters of the notochordal foramen were taken.

Although generally similar to those of other embolomeres, a few differences exist particularly in the intercentra. Where visible, the intercentra do not taper in lateral view as described for *Eogyrinus* by Panchen (1966), but are more nearly rectangular, as seen in *Pteroplax* (Boyd 1980) and *Archeria* (Case 1911). Pleurocentra are slightly longer than intercentra, although the

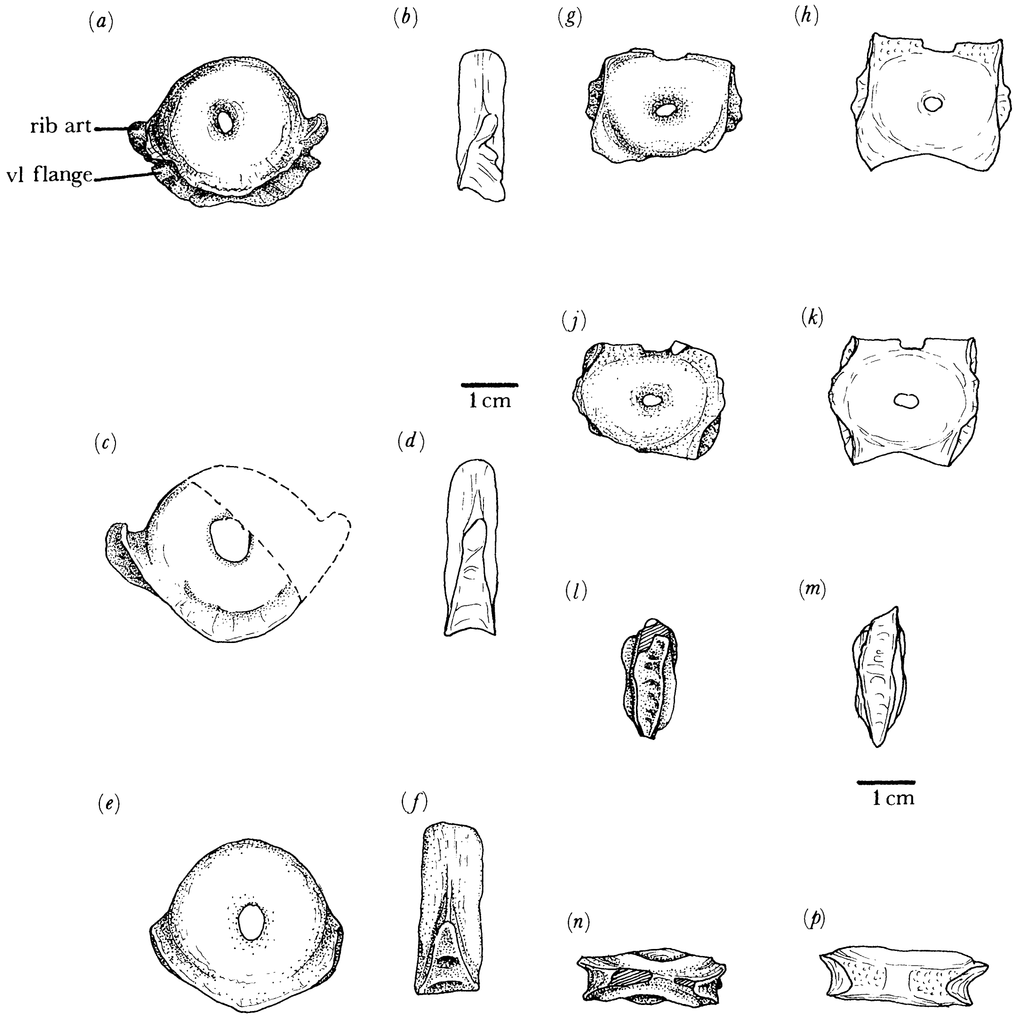


FIGURE 21. *Pholiderpeton scutigerum* holotype, centra. (*a*–*f*) Intercentra: (a) intercentrum xiv (cervical), anterior view; (*b*) lateral view, restoration; (*c*) intercentrum v (midtrunk), anterior view; (*d*) lateral restoration; (*e*) intercentrum ii (posterior trunk), anterior view; (*f*) lateral restoration. (*g*–*p*) Atlas pleurocentrum: (*g*) anterior view; (*h*) restoration; (*j*) posterior view; (*k*) restoration; (*l*) lateral view; (*m*) restoration; (*n*) ventral view; (*p*) dorsal view, restoration.

difference is difficult to measure accurately. The discrepancy varies along the length of the column, being greatest in the lumbar and sacral regions and least in the cervical and caudal regions.

In *Pholiderpeton* the notochordal foramen is always significantly larger in the intercentra. This was not described by Panchen for *Eogyrinus* but Boyd notes it in *Pteroplax* on specimen G 83.69. The effect may result from delay of ossification of the intercentra during the ontogeny of the animal, reflecting the predominance and more complete ossification of the pleurocentra in the phylogeny of anthracosaurs.

One pleurocentrum (s) (figures 41 and 43) has a partially occluded notochordal foramen. Occluded centra have been reported previously in embolomeres (Panchen 1977) associated with *Eobaphetes*, and others tentatively attributed to *Anthracosaurus*. Panchen suggested that this feature could either be age-related, occurring in only large mature animals, or a feature which could be used to distinguish *Anthracosaurus* centra from those of *Eogyrinus*. Its discovery in *Pholiderpeton* and also in an *Archeria* centrum (from a box of isolated specimens, YPM 5773) rules out any taxonomic significance for this character.

Several small centra of *Pholiderpeton* are presumably cervical. The best preserved is pleurocentrum p (figures 21*g–p* and 43) and it has been removed intact from the matrix. Comparison with *Archeria* identifies it as the atlas pleurocentrum. Neural arch facets are visible dorsally. Periosteal bone appears laterally but not ventrally. The centum tapers ventrally in lateral view and the profiles of both faces resemble those of intercentra. This must mean that the next cervical intercentrum was amphicoelous anteriorly, normal relations between centra thus being restored more posteriorly than in *Archeria*.

In *Proterogyrinus*, the atlas pleurocentrum remains a paired structure, as in temnospondyls such as *Eryops*. Holmes interprets this as correlated with the possibility of independent movement between two atlas arch halves, a device for ensuring that the spinal nerve was not obstructed during rotatory movements at the occipitocervical joint (Kemp 1969). However, he noted that the atlantal pleurocentrum was unitary in *Gephyrostegus* (Carroll 1970), as it is now known to be in the two later embolomeres *Pholiderpeton* and *Archeria*, the three exhibiting a morphocline of increasing ossification. The incomplete ventral periosteal bone in *Pholiderpeton*, however, contrasts with its completion in *Archeria*, the paired structure in *Proterogyrinus* presumably representing the primitive condition.

Intercentrum xxi (figure 43) has an enormous notochordal foramen, as large as that of some of the largest intercentra, and probably derives from the second or third cervical vertebra. Intercentrum xiv (figures 40 and 43) has a well-developed rim of periosteal bone between the rib articulations, drawn out into two ventrolateral flanges (figure 21*a*, *b*). It is probably also a cervical element. Unfortunately, no atlas intercentrum has been identified in *Pholiderpeton*. Intercentra i, ii and iii (figures 39 and 42) represent anterior trunk centra, judging from *Eogyrinus*. There are lateral bosses for the articulation of the rib capitulum and a pit ventral to them, as described for *Eogyrinus* (Panchen 1966) (figure 21*c*, *d*). They have enormous notochordal foramina and the bosses are relatively larger than those figured for *Eogyrinus*. Intercentra ii and vi (figures 39 and 42) compare closely with those of vertebrae R–W (Watson 1926; Panchen 1966) on specimen G 13.77 (DMSW 33), that is to say, posterior trunk. They were probably situated no more than 10 vertebrae anterior to the sacrum. They are broader anteroposteriorly and the periosteal covering is less extensive than in anterior trunk intercentra. Although the centrum is produced laterally into sloping 'shoulders' there is no development of a distinct boss. The ventrolateral pit, common to all intercentra, is evident, however (figure 21*e*, *f*).

No trace of an arterial groove compared to that noted by Panchen on on intercentrum x of G 13.77 has been identified, but few of the intercentra are preserved in such a way that it would be visible had one been present.

Neural arches

Two specimens of the left half of an atlas arch are available for *Pholiderpeton*, one associated with the holotype (NA 11) (figures 40 and 43), and one with MCZ 6977. The latter has been extracted from the matrix, but the former is inextricably crushed onto the specimen. However, it agrees exactly with MCZ 6977 and the detail on the bone is slightly better preserved (figure 22). A prominent finger-like process arises from the anteromesial corner of the otherwise

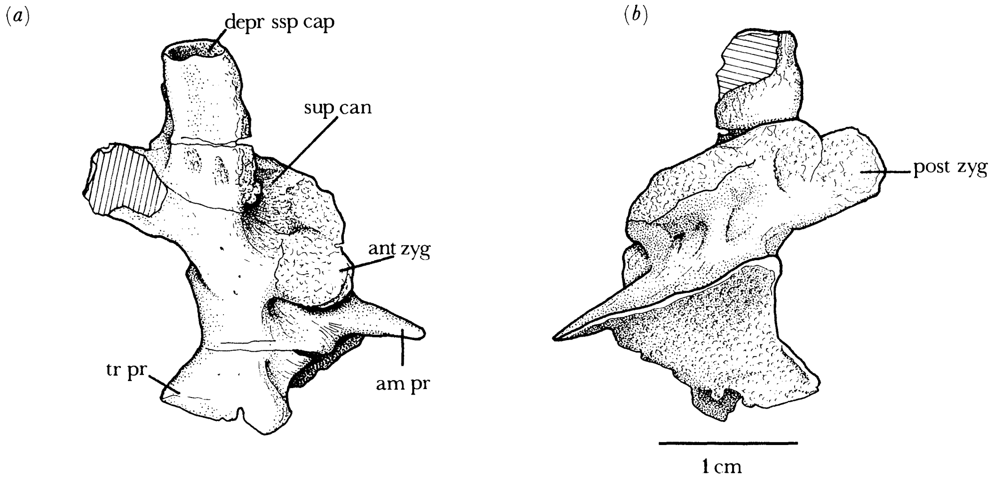


FIGURE 22. *Pholiderpeton scutigerum* MCZ 6977, specimen drawing of atlas arch: (*a*) approximately dorsal view; (*b*) approximately ventral view.

trapezoid articular surface. This would presumably have articulated with the atlas intercentrum, more or less in the midline. An anterior lip of the articulating surface contacted the atlas intercentrum. The transverse process is very reduced, being represented only by a slight production laterally of the pedicel. It seems unlikely to have borne a diapophysis for a rib. The neural spine is also very small, being a rectangular process about 11 mm high and 6 mm wide. MCZ 6977 shows an unfinished facet dorsally which could have been for a tendinous insertion of the semispinalis capitis muscle, which usually inserts in this region in tetrapods (Evans 1939; Rose 1980). The development of an anterior zygapophysis indicates the presence of a proatlas. The posterior zygapophysis is about half the size of a normal zygapophysis. Unfinished bone above the neural canal in both examples indicates the area of attachment between the two halves of the arch, either by cartilage or a ligament. In MCZ 6977 there is a mesial groove of finished bone, below the spine, which probably formed the supraneural canal (figure 22*a*). The atlas arch of *Proterogyrinus* (Holmes 1984) is different in proportion from that of *Pholiderpeton*, having larger zygapophyses; the spine is shorter dorsally but longer anteroposteriorly, and the body more elongate. It lacks the anteromesial process seen in *Pholiderpeton*. The atlas arch of *Archeria*, by contrast, shows a reduced neural spine, transverse process and proatlantal facet.

Neural arch 15, the axis arch (figures 23*b*, *c*, 40 and 43) has been compressed almost exactly laterally so that its left side is visible. The neural spine is relatively short and poorly ossified with a pitted and striated surface. The posterior margin rises vertically for a short distance and then curves anteriorly at an oblique angle, the spine curving forward over the reduced anterior zygapophysis. The latter has a small articulatory surface and a weakly buttressed base. The posterior zygapophysis is somewhat more substantial and the transverse processes are extremely short. The reduced anterior zygapophysis would have accommodated the postzygapophysis of the atlas arch; above it is an area of heavily pitted and striated bone, somewhat recessed, which probably accommodated the neural spine of the atlas arch.

A forward-curving axis spine is seen in *Kotlassia* (Bystrow 1944), *Proterogyrinus* (Holmes 1984), *Eryops* (Moulton 1974) and *Ophiacodon* (Romer & Price 1940). Such a modification of

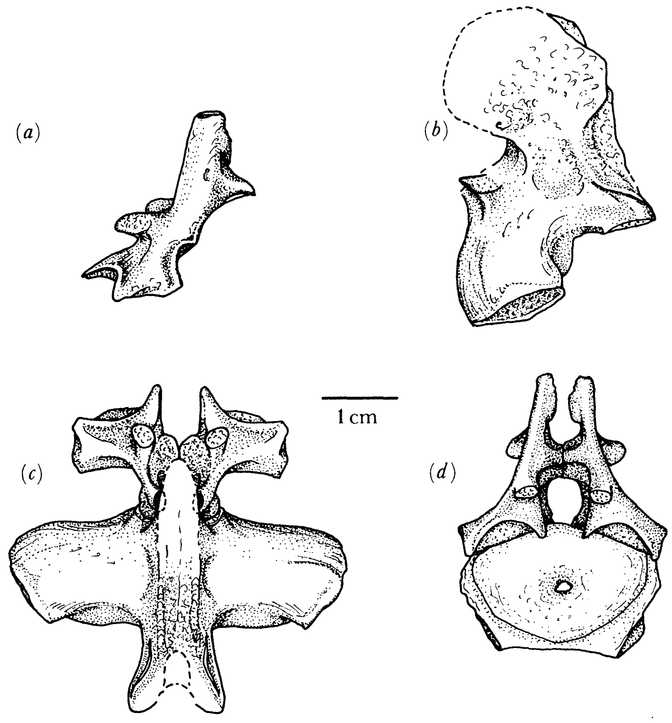


FIGURE 23. *Pholiderpeton scutigerum*, restorations of atlas–axis complex from holotype and MCZ 6977: (*a*) atlas arch in left lateral view; (*b*) axis arch in left lateral view; (*c*) atlas and axis arches in dorsal view; (*d*) atlas arch and pleurocentrum in anterior view.

the spine prevents fouling between the axis and the adjacent third cervical spine when the head is raised.

Several of the remaining arches are preserved adequately enough to merit further description. Arches 8 and 16 (figures 40 and 43) show robust spines, relatively undistorted and preserved in lateral view. They are short, hatchet-shaped and bear unfinished facets dorsally and a horizontal ridge across the base of the spine. Arch 9 is broken across the base of the spine to reveal the supraneural canal. The supraneural canal is now known in several embolomeres: *Archeria* (Case 1915), *Pteroplax* (Boyd 1980) and *Carbonoherpeton* (Klembara 1985) as well as the primitive temnospondyl *Greererpeton* (Smithson 1982). It is probably primitive for tetrapods, being present in osteolepiforms (Andrews & Westoll 1970*a*). The transverse processes associated with these arches are moderately long and narrow, and they probably originated from the anterior trunk, resembling arches illustrated by Panchen (1966) for *Eogyrinus*.

Arches 1 and 10, although widely separated on the specimen, are similar to each other and probably derive from the posterior trunk. Each is crushed anteroposteriorly. The spines of each have been subject to breakage and plastic deformation, making reconstruction difficult. The rest of the surface is ridged, folded, and broken. The posterior face of arch 1 is illustrated (figure 24) to show a deep groove running dorsoventrally. This almost certainly marks the course of the segmental artery. The course of this artery has been inferred from grooves and ridges preserved on the vertebrae of both *Eogyrunis* and *Eryops*. In *Eogyrinus*, Panchen (1966) noted a groove on the posterior margin of an intercentrum, and Moulton (1974) noted a groove running down neural spines of *Eryops* in three caudal neural arches. The artery is assumed to

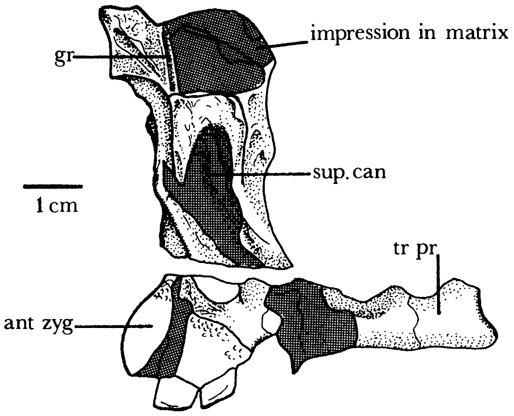


FIGURE 24. *Pholiderpeton scutigerum* holotype, neural arch (NA) 1, from reverse of specimen, to show groove (gr) for segmental artery.

follow the segmental boundary, which Panchen suggested (1967*b*) marked the dividing line between inter- and pleurocentrum. There is no other evidence of segmental artery grooves in *Pholiderpeton*.

Ribs

Most of the ribs associated with *Pholiderpeton* conform to the pattern of typical embolomere ribs from the 'thoracic' region as described by Panchen (1966) for *Eogyrinus* and by Boyd (1980) for *Pteroplax*. Others exhibit regional differentiation. Rib 8 (figures 39 and 42) resembles those from the lumbar region described by the above authors. It is short, only slightly curved, and tapers to a blunt recurved tip, surrounded by small knoblike projections. The tuberculum and capitulum are more or less confluent. The distal end of another such rib is present on the specimen R 2396 (R47, figure 42). These ribs are significant because they are among the most posterior elements to be preserved on the specimen and help to 'key in' the vertebrae to those of G 13.77 described by Panchen (1966). Comparison with G 13.77 and Panchen's (1972) reconstruction suggests, as with intercentra ii and vi, a position no more than 10 vertebrae anterior to the sacrum.

Several ribs associated with the more anterior parts of the specimen are of interest. Rib 39 (figures 41 and 43) is much the smallest rib preserved and could well be associated with an anterior cervical vertebra. The head is largely obscured but there seems little separation being tuberculum and capitulum, which would be expected of a rib articulating with the very short transverse process of the axis arch. Distally the rib narrows sharply and flattens, the tip being striated for about 14 mm. Short first cervical ribs are known from *Seymouria* (White 1939), *Eryops* (Moulton 1974) and indeed a large number of early tetrapods.

Ribs 16 (figures 39 and 42) and 35 (figures 40, 41 and 43) are also short by comparison with thoracic ribs. They expand gradually distally, 34 and 35 ending in an almost fan-shaped tip. Unfortunately the heads of all these ribs are obscured to some extent, although apparently the tuberculum and capitulum were not greatly separated. Short expanded ribs are associated with the cervical and pectoral regions in many tetrapods, for example *Proterogyrinus* (Holmes 1984), *Kotlassia* (Bystrow 1944), *Seymouria*, *Eryops*, *Gephyrostegus* (Carroll 1970) and *Pantylus* (Carroll 1968). This is presumably associated with the muscular attachment of the pectoral girdle.

Rib 38 (figures 40, 41 and 43) is unusual in having a thin but distinct flange produced from its dorsal margin at about its mid point. The tuberculum and capitulum are well differentiated, and the shaft is weakly curved and expanded. Pectoral ribs with dorsal flanges are known from *Eogyrinus*, *Pteroplax* and *Gephyrostegus*, the last preserved more or less in articulation. The flange probably represents a poorly developed uncinate process. It lies roughly in series with the point at which rib 39 narrows; this point on rib 39 could therefore also be interpreted as an incipient uncinate process. Uncinate processes provide attachment points for muscles supporting the shoulder girdle, and for the iliocostalis muscle which runs anteriorly along the vertebral column from the pelvic girdle.

Cervical region of Pholiderpeton

Figure 23 shows reconstructions of the atlas–axis complex of *Pholiderpeton* and figure 25 gives an attempted reconstruction of the whole cervical region on which some comments are necessary. The atlas intercentrum has been restored by reference to that of *Archeria*, which also possesses fully embolomerous trunk centra. In the related but earlier *Proterogyrinus* (Holmes 1984) the atlas intercentrum is wedge-shaped and the remaining vertebrae are not fully embolomerous. However, it is possible that the atlas intercentrum of *Pholiderpeton* was more strongly notochordal than that of *Archeria*.

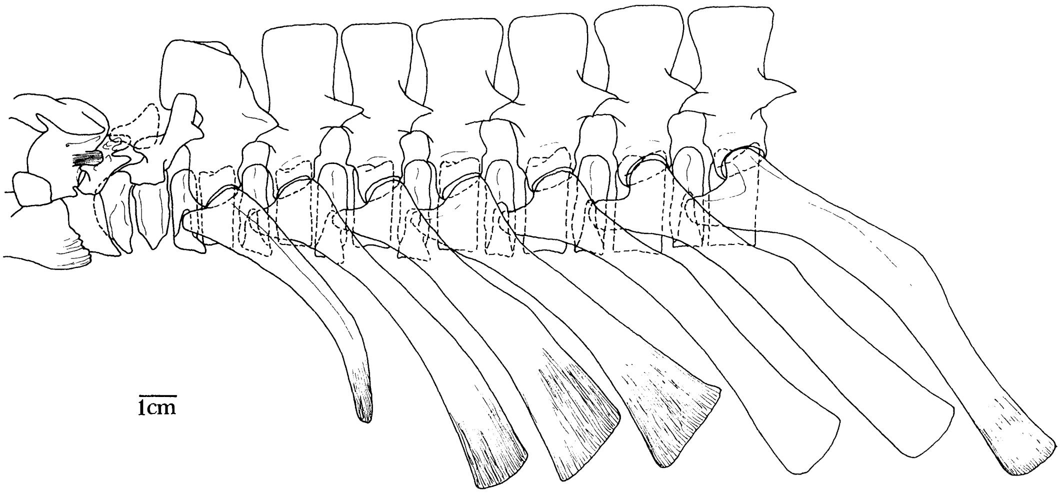


FIGURE 25. *Pholiderpeton scutigerum*, reconstruction of cervical region from holotype and MCZ 6977 (atlas intercentrum from *A. crassidisca*).

At least 6 or 7 cervical vertebrae were present in *Archeria* (AMNH 7117 (J.A.C., personal observations)); Carroll (1970) restores six in *Gephyrostegus*. The atlas vertebra has been restored without a rib, the atlas arch having only a very reduced transverse process. Atlantal ribs were apparently absent in *Eryops*(Moulton 1974) and were omitted from Carroll's reconstruction of *Gephyrostegus*. In *Seymouria*, where they are found, they are associated with an almost undifferentiated atlas arch. Holmes (1984) infers their presence in *Proterogyrinus*. The small rib (39) is restored as the axial. Ribs with expanded ends are restored on vertebrae 3–6, although as only 4 such ribs are represented on the specimen, their actual number and arrangement is conjectural. The least modified is placed first in accordance with the similar arrangement found in *Gephyrostegus*, *Kotlassia* and *Seymouria*. Rib 38 may be the first pectoral or last cervical and is restored on vertebra 8. Between it and the sixth cervical a hypothetical intermediate has been restored to avoid too abrupt a change in the morphology of the series. Rib heads are not well known except on rib 39. In this they are well separated but in the more anterior ones they were apparently closer together. A cervical rib is described for *Calligenethlon* (Carroll 1967) and here the heads are almost confluent. The ribs have been restored as rather more posteriorly directed than trunk ribs, as in *Gephyrostegus* and *Kotlassia*.

The atlas–axis complex of *Pholiderpeton* shows characters such as the retention of a substantial proatlas, a finger-like process on the atlas arch restricting movement between arch and centrum, and an atlas neural spine in articulation with the axis arch. These all suggest restriction of movement. However it is of interest to compare these regions in *Pholiderpeton* and *Proterogyrinus*. In *Proterogyrinus* the atlantal zygapophysis for the proatlas is almost half as long as the entire arch, and the arch itself is elongated anteroposteriorly. The atlas neural spine broadly overlaps the anteriorly directed axis arch. A relatively larger proatlas and a more restricted range of movement than in *Pholiderpeton* is indicated. In *Archeria* reduction or loss of the proatlas and reduction of the neural spine with consequent restriction of contact between atlas and axis spine suggest a trend towards increased mobility of the neck region.

The presacral count of embolomeres

No embolomere other than *Archeria* is represented by a complete articulated skeleton, the presacral count of the earlier and larger species being unknown. Watson (1926) published a reconstruction of *Eogyrinus* based on the length of articulated column G 13.77 (DMSW 33), in which 26 vertebrae are preserved including the sacrum. Because the most anterior of these show no specializations expected of cervical vertebrae, he allowed a total of 32 for the presacral count.

In 1966, Panchen concluded that a presacral count of 40 was likely for *Eogyrinus*, based on a comparison with *Archeria*; in 1972 he published a complete reconstruction of the postcranial skeleton based on *Archeria* as a model. This was done with some reservations, for although *Archeria* provides the only real clue to the presacral count of embolomeres, its skull shows specializations and it could be atypical in the length of its vertebral column. The 1966 analysis was based on the use of orthometric linear units to compare the proportions of the vertebral column and femora in the two animals. Panchen acknowledged the possible sources of error associated with this method.

A minimum of 25 vertebrae is represented on the holotype of *Pholiderpeton*, the total number of intercentra present. Unfortunately the preservation of the specimen does not usually allow differentiation between left and right ribs; otherwise the maximum number present from one side might have provided a complementary estimate of vertebrae represented.

The state of the specimen gives little indication of how much is missing, but it is clearly incomplete. However, the most anterior parts of the column, the atlas and axis are represented. By comparison with G 13.77 it has been possible to identify the most posterior parts which are represented and show that they probably originated from a position no more than 10 vertebrae anterior to the sacrum, and probably closer. Had they been in reality as close as five to the sacrum and if only two were missing from the rest of the column, a presacral count of 32 would be possible. This would give the embolomeres a body shape similar to *Proterogyrinus*, but the hypothesis seem unlikely, judging by the state of preservation of the specimen. A more realistic proposal is that the posteriormost elements are the seventh or eighth anterior to the sacrum and that seven or eight vertebrae are missing from the rest of the column, resulting in a presacral count of 40. These hypotheses rest on two assumptions which are both made with reservations. The first is that G 13.77 did in fact belong to an eogyrinid; although its attribution is likely, it is not certain. The second is that presacral counts of 32 and 40, by analogy with *Proterogyrinus* and *Archeria* respectively, are the only alternatives. Although a count of 32 does seem the minimum allowable, counts of between 33 and 39, and even over 40, are in theory possible.

Although the postcranial skeleton of *Greererpeton* is currently being redescribed, available information suggests that it resembles *Pholidogaster* (Romer 1964; Panchen 1975). In this animal the intercentrum is horseshoe-shaped and the pleurocentra paired crescents elongated dorsoventrally. This condition is also seen in *Kourerpeton* (Olson & Lammers 1976) in which the presacral column consists of about 40 vertebrae. It is possible that such a condition results from adaptation of the standard rhachitomous pattern along lines parallel to that of embolomeres and that in both it is connected with aquatic locomotion, and particularly with long-bodied forms. This gives more weight to the argument that the fully embolomerous eogyrinids were long-bodied.

Appendicular skeleton of *Pholiderpeton*

Shoulder girdle

The right scapulocoracoid (figures 26*a*, *b*, 40 and 41) has lost its anteroventral portion, but its outline has been restored by reference to those of *Archeria* (Romer 1957) and *Proterogyrinus* (Holmes 1980), which this element otherwise resembles.

The glenoid is an elongate oval resembling those of *Archeria* and *Proterogyrinus*. Its anterodorsal end is carried on a thickened buttress strengthening the posterior margin of the scapular blade. The glenoid was probably obliquely orientated, differing from those of *Eoherpeton* (Smithson 1985) and *Seymouria* (White 1939) in which it is more nearly horizontal. This difference, noted by Smithson, could be related to aquatic locomotion and the low degree of torsion seen in the humerus. The articulatory surface shows little curvature except for the anterodorsal corner, which faces posterolaterally. Compression may have reduced the curvature, but *Archeria* also lacks a conspicuously spiral glenoid and *Pholiderpeton* was probably similar. The maximum length of the glenoid is about 44 mm, whereas the distance measured around the humeral head is about 52 mm; thus the glenoid is significantly smaller than the humeral head. The short scapular blade is striated and terminates in unfinished bone dorsally, indicating the presence of a cartilaginous suprascapular area.

An elongate depression runs up the buttress on the posterior margin, as in other early tetrapods. This has been interpreted, for example by Romer (1922), Miner (1925) and Holmes (1980), as being the point of origin for part or all of the subcoracoscapularis muscle. The patterns of ossification of the pectoral region of early amphibia are closely comparable with those of early reptiles such as *Captorhinus* (Fox & Bowman 1966) and *Dimetrodon*. These in turn are easily homologized with those of living reptiles, such as *Sphenodon* and *Iguana*, the whole arrangement being essentially conservative. The musculature associated with this structure in early amphibia can therefore be restored with some confidence. The conclusions of the above authors for *Eryops* and *Captorhinus* (Holmes 1977) are largely accepted here.

The remaining scapulocoracoid plate is very thin, in places less than 1 mm thick. It shows no evidence of more than one centre of ossification, like those of other early amphibia. The three major scapulocoracoid foramina – supraglenoid, supracoracoid and glenoid – are all present. The specimen is broken across the posterior margin a little above the glenoid and the

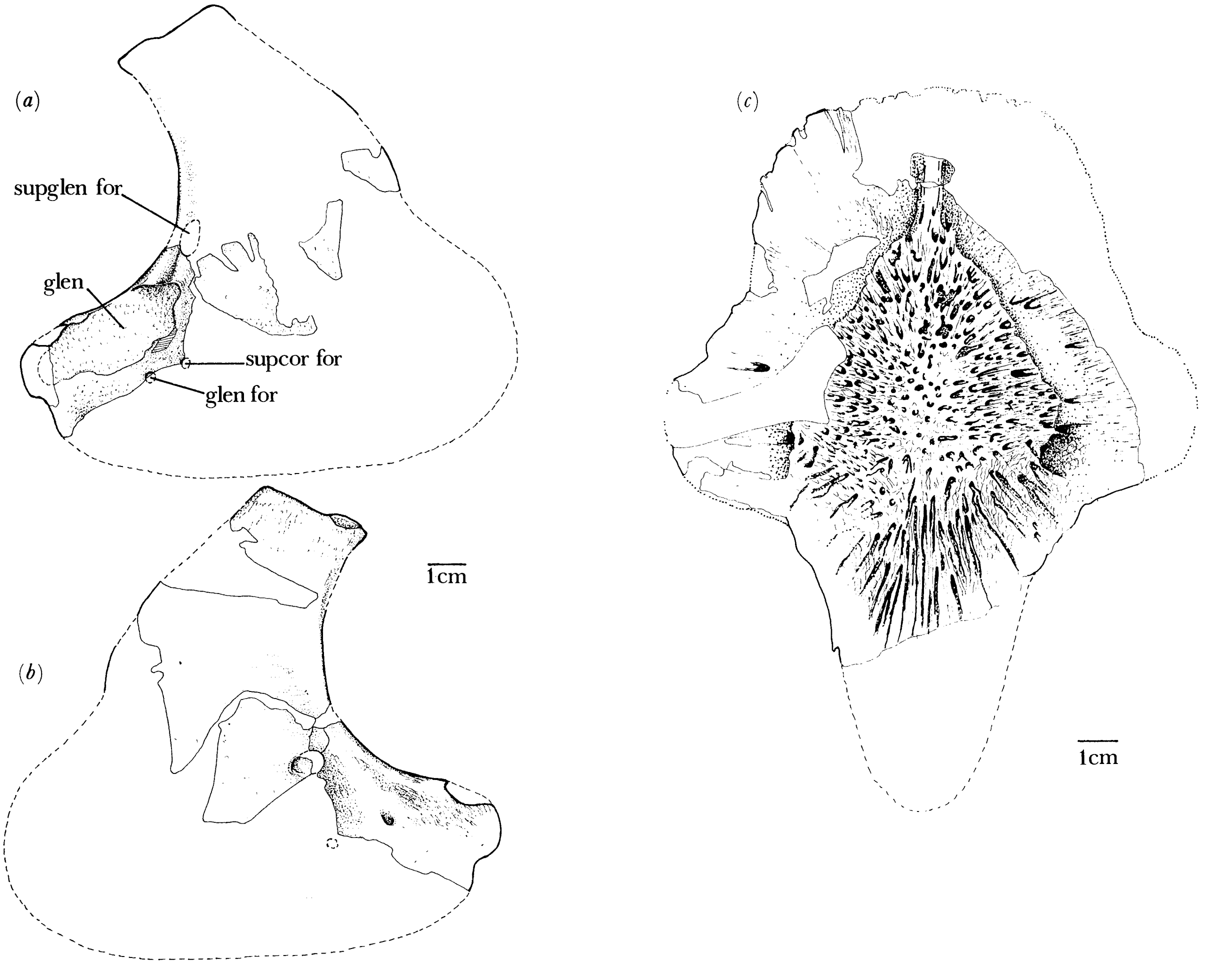


FIGURE 26. *Pholiderpeton scutigerum* holotype: (*a*, *b*) restorations of scapulocoracoid in (*a*) lateral and (*b*) mesial views: (*c*) restoration of interclavicle in ventral view.

break continues anteroventrally to disrupt the supraglenoid foramen. This large foramen is situated with the mesial opening on a level with the anterior end of the glenoid. Part of its ventrolateral margin can be seen 10 mm dorsal to the glenoid. This is unusually low by comparison with *Archeria* or *Proterogyrinus*, but only a series of specimens could show whether this is significant or results from simple individual variation. The foramen pierces the supraglenoid buttress as in *Seymouria* and most other anthracosaurs except *Eoherpeton* (Smithson 1985) which more closely resembles early reptiles. In *Dimetrodon*, for example, the foramen is small and situated anterior to the glenoid.

The glenoid foramen pierces the coracoid plate running ventrolaterally, emerging on the lateral surface just posterior to the midpoint of the glenoid and about 7 mm below it, similar to its counterpart in *Archeria*, though more posteriorly placed than in *Proterogyrinus*. The supracoracoid foramen opens laterally in a similar position to *Archeria*, but nothing more of it is preserved.

The scapulocoracoid of *Pholiderpeton* shows none of the reduction of ossification often seen in thoroughly aquatic animals, for example *Dvinosaurus*, *Trimerorhachis*, *Greererpeton* and *Microbrachis*. In *Archeria* it is slow to ossify but older animals attain the degree of ossification seen in *Pholiderpeton*; this suggests a greater degree of terrestriality in the latter.

The interclavicle is beautifully preserved (figures 26*c* and 40) showing the finest detail of the ornament. It is about two thirds complete, allowing restoration of most of the outline with confidence. Only the length of the 'parasternal process' is uncertain. The overall similarity of the preserved parts to those of other anthracosaurs such as *Archeria*, *Proterogyrinus* and *Gephyrostegus* (Carroll 1970) allow it to be restored as a moderately long process (figure 27*a*, *c*, *e*, *f*).

The bone has been flattened during preservation to eliminate the original curvature seen in the interclavicle of *Proterogyrinus*. The diamond-shaped raised central interclavicular area bears ornament, as do those of other anthracosaurs. Superimposed on the pit and ridge ornament (illustrated in figure 26*c*) is a tracery of extremely fine striations. Ornament is much better developed than on the interclavicle of *Proterogyrinus* or that attributed to *Eogyrinus* (Panchen 1972).

Anteriorly the interclavicular area is developed into a ridge, indicating that the clavicles did not quite meet in the midline but remained narrowly separated, as they were in *Archeria*. Posteriorly the interclavicular area merges smoothly into the parasternal process. The interclavicular area is relatively broader than in *Archeria*, although narrower than in *Proterogyrinus*.

The area of clavicular overlap is almost uniformly wide round the anterior margin, forming a broadly rounded outline anteriorly and smaller rounded wings laterally. On the overlap areas just posterior to the widest point of the interclavicular areas are shallow depressions with a pitted surface. Ligaments to the clavicles possibly originated here. The anterior margin of the bone is crenellated as in many other fossil amphibian interclavicles.

The most remarkable feature of this bone is its size. It is easily the largest embolomere interclavicle described, certainly much larger than that attributed to *Eogyrinus* by Panchen (1972). Because *Pholiderpeton* has a skull about one third smaller than that of the lectotype of *E. attheyi*, the attribution must be doubted. The attributed bone (G 15.81) (figure 27*b*) might after all pertain to *Pteroplax*, an idea considered but rejected by Panchen. Indeed the ornament on G 15.81 is rather different in character from that on the isolated skull table that forms the only dermal material pertaining to that genus.

The shape of G 15.81 is also significantly different from that of *Pholiderpeton*. If *Pholiderpeton* and *Eogyrinus* are generically distinct, G 15.81 could conceivably be the interclavicle of a juvenile *Eogyrinus*, but the evidence suggests that they were congeneric (see below). A further possibility is that interclavicle shape changed during the ontogeny of anthracosaurs, rendering attribution of G 15.81 impossible without further information.

No reasonably complete growth series of anthracosaur interclavicles exists at present; however, some evidence of a radical change in shape during ontogeny derives from *Gephyrostegus bohemicus* (Carroll 1970). If they are conspecific, the interclavicles of the larger, type specimen and MB 1901 1378 are remarkably different from that of the smaller specimen T 107 (DMSW B 65) from the Watson collection at Cambridge. The former, (figure 27*e*) has an essentially kite-shaped outline like that of other anthracosaurs, with obliquely orientated clavicular overlap areas, a diamond-shaped interclavicular area and a tapering stem. By contrast that of T 107 (figure 27*f*) has an almost reptiliomorph T-shaped outline with transversely orientated clavicular overlap areas, a short, broad central area and a narrow, parallel-sided stem. Although they are very different at first sight, faster rates of growth along the diagonal axes than along the transverse and longitudinal axes could produce such a

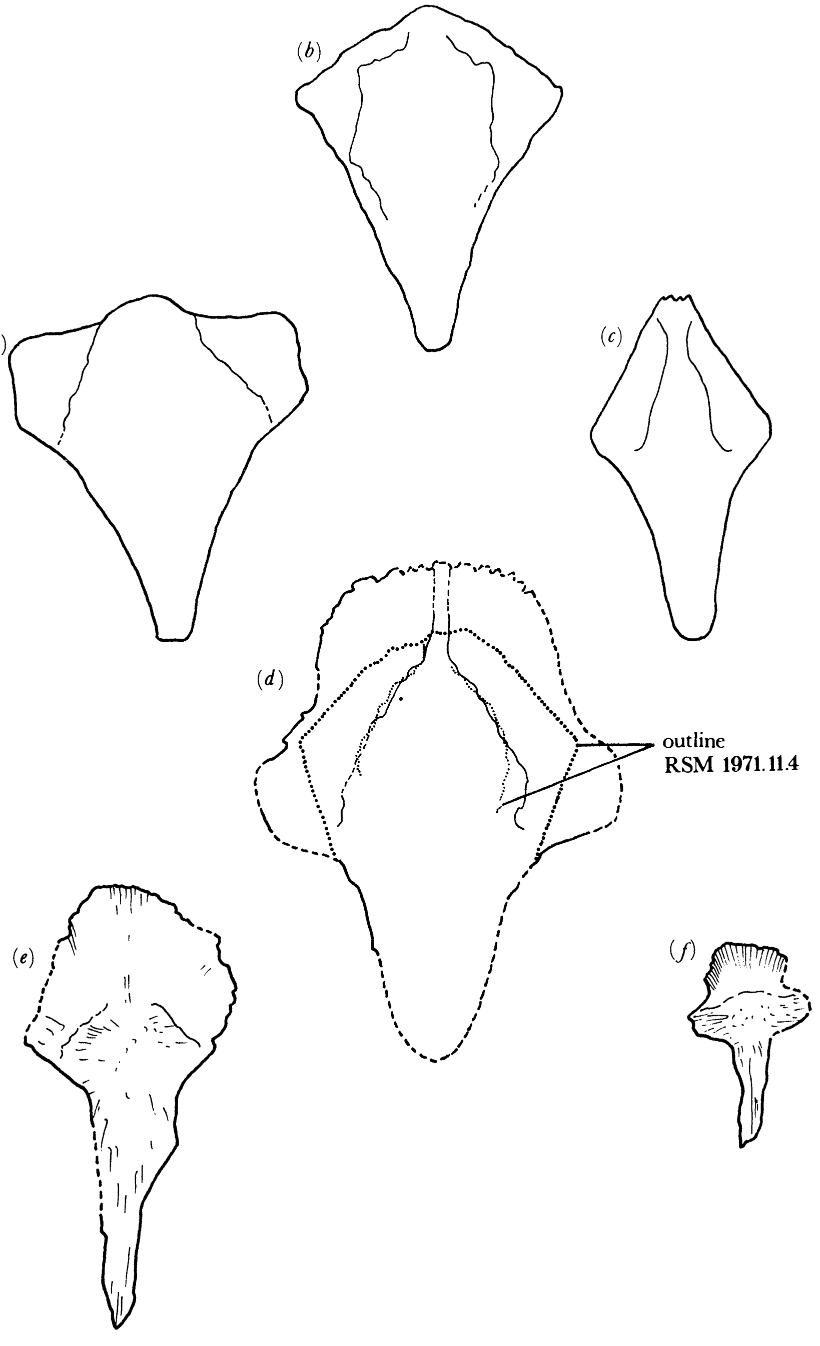


FIGURE 27. Embolomere interclavicles: (*a*) *Proterogyrinus scheeli* (from Holmes 1980); (*b*) G 15.81 (from Panchen 1972); (*c*) *A. crassidisca* (from Romer 1957); (*a*–*c*) reduced to same anteroposterior dimension; (*d*) *P. scutigerum* holotype with outline of RSM 1971.11.4 superimposed (dotted lines). (*e*, *f*) *Gephyrostegus bohemicus*: (*e*) MB 1901.1378 (from Carroll 1970); (*f*) T 107 (from Carroll 1970). (*e*, *f*) To same scale; (*a*–*d*), not to scale.

transformation. This sort of change could not convert an interclavicle like G 15.81 into one like that of *Pholiderpeton* and the attribution of G 15.81 must remain in doubt. Change of shape may occur in the interclavicle of *Crassigyrinus* (A. L. Panchen, personal communication).

The interclavicle RSM 1971.11.4 which Panchen (1977) attributed to *Anthracosaurus* is almost identical to that of *Pholiderpeton* in both ornament and in the size of the interclavicular area. The maximum width of this area is a little less in RSM 1971.11.4 but could easily fall within the limits of individual variation. The clavicular overlap of RSM 1971.11.4 is narrower than in *Pholiderpeton* and is not produced laterally into rounded wings. The outlines of the two are superimposed in figure 27*d*). The provenance of RSM 1971.11.4 is uncertain but appears to be from the Airdrie Blackband Ironstone (Panchen 1977), which is upper *modiolaris* zone, Westphalian B, well within the range of the genus *Pholiderpeton* (see below) to which genus I believe this bone should be attributed.

The right clavicle (figures 40 and 41) shows ornament similar in character to that on the interclavicle, the elongated pits converging at a point just below where the shaft arises.

In dorsal (internal) view (figure 28*a*) the surface is smooth over most of its surface except for fine striations which run radially in a band 20–30 mm along the medial margin. Presumably this marks the area of overlap with the interclavicle. On the anterolateral margin about 35 mm posterior to the anteriormost point is a raised rugose area, perhaps the point of origin of part of the sternohyoid muscle, which inserts on the hyoid apparatus. This muscle apparently originates on the anterior margin of the clavicle in *Captorhinus* (Holmes 1977) Alternatively, a ligament to the interclavicle or scapulocoracoid might have been inserted here. The anterior edge of the clavicle has a crenellated margin like that on the interclavicle.

The outline of the clavicle can be restored by reference to the overlap area on the interclavicle. The thickness of the broken bone at any point also provides a guide, the margin being reconstructed by extrapolation from the degree of taper in cross section.

The clavicular stem is directed posterodorsally, but its tip and posterior margin are damaged and this prevents assessment of its length and mode of articulation with the cleithrum. There was apparently a lamina of bone continuous with the posterior part of the triangular area, as in *Archeria*, rising up along the posterior margin of the stem, and its extent has been extrapolated as above. A pitted area on this lamina at the base of the stem perhaps indicates the insertion of a ligament to the interclavicle. A shallow groove begins about 30 mm above the base of the stem, running up its anterior margin.

The clavicle of *Pholiderpeton* proves to be much more like that of *Archeria* than that of *Proterogyrinus*, in having a relatively elongate ventral part with the clavicular stem arising posteriorly and directed posterodorsally. *Proterogyrinus* (Holmes 1980) has a short broad ventral part and the broad clavicular stem arises anterolaterally. Its lateral surface bears pits like the ventral part, whereas in *Archeria* it is narrow and the lateral surface is unornamented. In *Pholiderpeton* the narrow stem resembles that of *Archeria*, with its lateral surface striated but otherwise unornamented.

Holmes (1980) suggests that the massive nature of the clavicular stem in *Proterogyrinus* represents the primitive condition. However, the clavicular stem of *Ichthyostega* (Jarvik 1980) is also narrow and tapering; this observation suggests that this is the primitive condition, with the broad shape in *Proterogyrinus* derived perhaps in association with the limb movement which Holmes describes.

Together, the cleithra give an almost complete picture of the bone (figures 28*b*, *c*, 41 and 42). The shape, consistent with those of other primitive tetrapods, most closely resembles that of *Archeria* (figure 28*b*, *c*). The dorsal blade is elongate and less expanded anteroposteriorly than in *Archeria*. It is slightly convex laterally in cross section. The anterior edge is thin and waved, but the posterior is strengthened by a buttress seen in the cross section (figure 25*d*). The

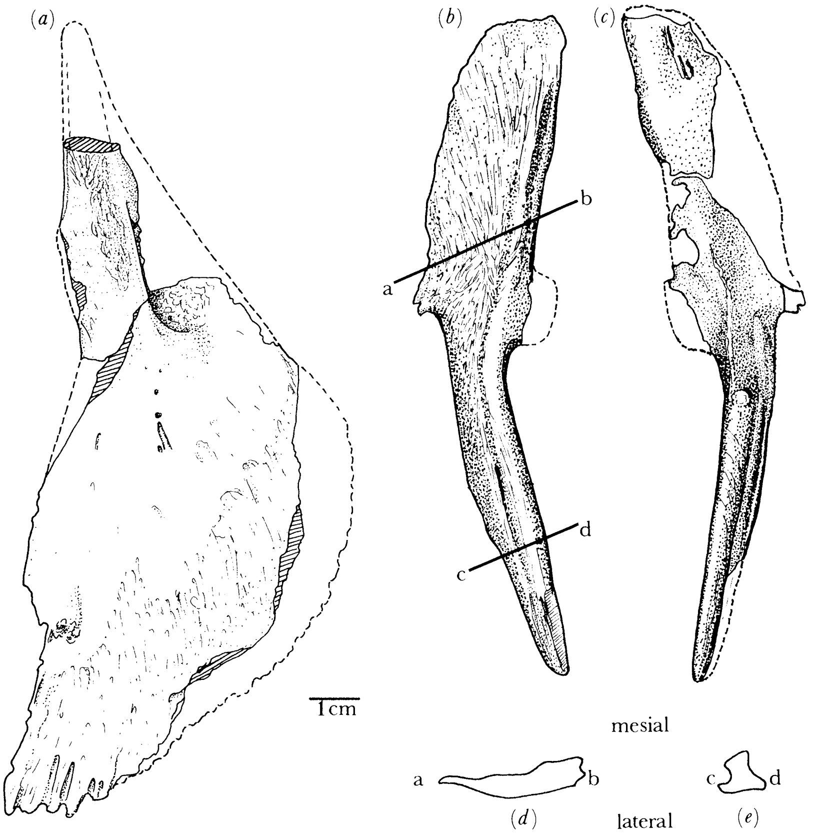


FIGURE 28. *Pholiderpeton scutigerum* holotype. (*a*) Right clavicle, internal (dorsal) view. (*b*–*e*) Right cleithrum: (*b*) lateral view; (*c*) mesial view; (*d*) section across a–b; (*e*) section across c–d.

posterior margin bears two shallow, parallel, longitudinal grooves which terminate at the base of the blade. The more mesial and deeper of the two grooves presumably housed the anterior margin of the cartilaginous suprascapular blade. The anteroventral corner of the blade is drawn out into a recurved bifurcate point, where a smooth margin is found in *Archeria* and other anthracosaurs. A similar feature is, however, found in the small temnospondyl *Dendrerpeton* (Carroll 1967).

The shaft is more complex than that of *Archeria*. In both, a posterior groove clasped the scapulocoracoid. Anteromesially, however, a second much deeper groove, not described in *Archeria*, runs from the ventral tip of the shaft dorsally to the point where the bone expands into the blade (figure 28*e*). This groove was apparently continuous with that on the anterior margin of the clavicular stem and may have housed a ligament linking the two bones. Posteriorly at the point where the shaft meets the blade is a conspicuous boss, where posterior face is largely broken and obscured in both elements, but some unfinished surface can be seen here on the left element. It presumably clasped the dorsal margin of the scapular blade at the point where the suprascapular arose. No equivalent structure has been described on the cleithrum of *Archeria*.

According to Romer (1922), Miner (1925) and Holmes (1977), the cleithrum provided the point of insertion of the levator scapulae muscles in primitive tetrapods. Miner restored the levator scapulae muscles in *Eryops* as having only a single insertion, by comparison with the urodele '*Megalobatrachus*' (= *Andrias*). However, urodeles are unsuitable as models for primitive tetrapods. In particular, the shoulder girdle is much reduced and resembles those of early reptiles and amphibia much less than does that of, for example, *Sphenodon*. In *Sphenodon*, the levator scapulae is differentiated into a superior slip inserting on the suprascapular blade and an inferior slip inserting on the scapular. Holmes restored the muscle in *Captorhinus* as likewise differentiated into two slips, inferring the presence of the superior slip on the scapular or on a splint-like cleithrum which may have been present. In *Pholiderpeton*, and also in *Eryops*, a dual insertion for the muscle seems likely. In both animals, the cleithrum was relatively large and differentiated into blade and shaft. The blade in *Pholiderpeton* capped a cartilaginous suprascapular, whereas in *Eryops* the suprascapular region was coossified with the scapular. It is likely that differentiation into superior and inferior slips is the primitive condition for the insertion of this muscle. Reconstructions of the shoulder girdle are presented in figure 29 and a reconstruction of head, cervical region and shoulder girdle in figure 37.

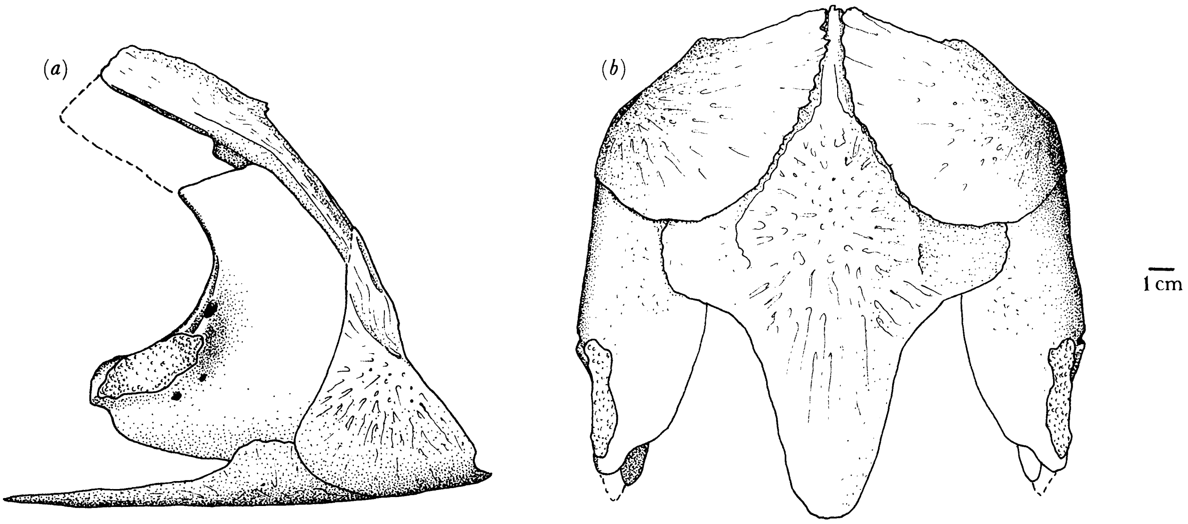


FIGURE 29. *Pholiderpeton scutigerum* holotype, reconstructions of pectoral girdle in (*a*) right lateral view, (*b*) ventral view.

Pectoral limb

Both humeri of *Pholiderpeton* are preserved, (figures 38 and 41) but the exposed parts do not complement each other completely (figure 30*a*–*c*).

The humerus, closely similar to those of *Archeria* (Romer 1957) and *Proterogyrinus*, (Holmes 1980) is essentially a broad L-shape with an expanded rectangular entepicondyle and an entepicondylar foramen. It measures 95 mm from the apex of the proximal articulation to the most distal point of the entepicondyle. It is shorter and broader than that of *Archeria* with a somewhat less expanded entepicondyle than that of *Proterogyrinus*.

The articular surface on the humeral head of *Pholiderpeton* has a narrow crescentic outline, curving though about 160°. It extends anteriorly almost to the deltopectoral crest. The articulatory surface is barely differentiated into two facets by a ridge running proximally along the apex of the surface. The surface curves from anteroventral over the condyle to terminate posterodorsally, the reverse of the situation in *Eoherpeton* (Smithson 1985). This could be the result of compression. The posterodorsal corner of the head just below the rim bears a pitted depression. Bounded more posteriorly by two rugose areas, almost confluent and forming a longitudinal ridge, the area is comparable with those in *Proterogyrinus* (Holmes 1984) marking the insertions of the subcoracoscapularis muscle proximally and latissimus dorsi distally. More anteriorly the humeral head in *Pholiderpeton* is shallowly concave with a pitted surface perhaps for the insertion of the scapulohumeralis muscle as in *Proterogyrinus*.

The entepicondyle is roughly rectangular as in *Archeria* and *Proterogyrinus*. Relatively thin, with a thickened posterior margin, it is unfinished distally and the rest of the surface is sculptured where the muscles controlling flexion of the epipodials and manus originated. The entepicondylar foramen is present, a feature which *Pholiderpeton* shares with many early tetrapods such as other anthracosaurs, *Greererpeton* (Holmes 1980), *Ichthyostega* (Jarvik 1980) and early reptiles. Absence of this foramen was once taken to be characteristic of fossil amphibia (Romer 1957) being lost in many later temnospondyls, but its presence now seems likely to be primitive for tetrapods, as it occurs in osteolepiforms (Andrews & Westoll 1970*b*). The foramen lies in the fork of a Y-shaped ridge strengthening the ventral surface of the humerus in *Pholiderpeton*, *Archeria* and *Proterogyrinus*.

The ectepicondyle lies at the end of a tall ridge whose course can be inferred from the fractures in the bones overlying it. The ectepicondyle is lined with finished bone except for a small pit at the extreme distal point. It does not project significantly over the distal margin as it does in the most heavily ossified *Archeria* specimens, but it is better ossified than in *Proterogyrinus*.

On the anteroventral margin of the humerus, an almost circular ridge surrounding a deep pit marks the visible portion of the deltopectoral crest. Although this area is better ossified than in *Proterogyrinus* or the majority of examples of *Archeria*, no other regions of the deltopectoral crest are visible. The conspicuous anterior flange, so characteristic of other anthracosaurs, has been inferred in the restoration. The flange was interpreted by Holmes as providing the insertion of the deltoideus.

The articulatory facet for the ulna is terminal like that in *Archeria*, rather than ventral as in *Proterogyrinus*. Holmes suggests that the differences between the latter may result from the low degree of ossification in *Archeria*. The terminal position in the better-ossified *Pholiderpeton* argues against this explanation. The ulna articulation, although distorted by compression, follows a shallow sigmoid curve in dorsal view, running from just beneath the ectepicondyle to a point midway along the distal edge of the entepicondyle. Its concave anterior portion bears a low ridge dividing the surface into dorsal and ventral facets as in *Eoherpeton* (Smithson 1985).

Neither radial condyle of *Pholiderpeton* is acccessible. *Archeria* and *Proterogyrinus* differ from each other here and it would have been valuable to determine which animal *Pholiderpeton* resembled. In *Proterogyrinus* the facet is bulbous and more ventrally placed than in *Archeria* (Romer 1957). However, examination of a series of *Archeria* humeri shows some variation in the position of the radial condyle. In some the condyle is at least as much ventral as terminal (T 104, MCZ 2473) and in others (MCZ 5957) it is even bulbous.

Compression prevents a reliable estimate of the original angle between the plane of the proximal articulation and the plane of the entepicondyle. As preserved it is about 23°, although a low value is expected by comparison with *Archeria* and *Proterogyrinus* where it is usually shallow, 30° and 37° respectively.

The *Archeria* humerus (T 104) in the Cambridge collection shows an unusually high degree of 'twist', about 57° (bicondylar axis). This specimen is also unusual in the positions of the radial condyle and the deltopectoral crest. The latter is placed rather centrally, well away from the anterior flange. Its unfinished surface is almost confluent with the poorly ossified articular surface. It also exhibits an incipient supinator process, unusual for an anthracosaur and otherwise found only in *Eoherpeton* (Smithson 1985). This specimen illustrates the degree of individual variation which can occur within the genus and emphasizes the danger of drawing general conclusions from a single specimen.

A 'twist' of 30°–37°, found in the majority of embolomere humeri, is much less than that found in tetrapods such as *Eryops*, where it is about 88° (Andrews & Westoll 1970*b*) or that in the terrestrial anthracosaur *Eoherpeton* (Smithson 1985). Figures by Jarvik (1980) show an angle of about 50° in the humerus of *Ichthyostega*, intermediate between the aquatic anthracosaurs and the terrestrial temnospondyl.

Descriptions of several early tetrapod humeri are now available which seem to confirm Romer's suspicion that the 'tetrahedral' type of humerus with a high degree of twist, found in *Eryops*, other terrestrial temnospondyls, *Seymouria* and other 'cotylosaurs', may not be primitive but convergently derived in each. Humeri of the anthracosaurs *Calligenethlon* (Carroll 1967), *Gephyrostegus* (Carroll 1970), *Brukterpeton* (Boy & Bandel 1973), *Proterogyrinus* (Holmes 1980) and *Eoherpeton* (Smithson 1980, 1985) all conform to the L-shaped pattern seen in *Archeria*, with only minor variations. In isolation this might mean that the simple L-shaped humerus is a shared derived character uniting anthracosaurs. However, several non-anthracosaurian humeri share many of the same features. The humerus of *Greererpeton* figured and briefly described by Holmes (1980) bears a striking resemblance to an immature humerus of *Proterogyrinus*. They both have a low degree of 'twist' and an anterior flange. The latter was regarded by Romer (1957) as an adaptation to aquatic locomotion, although in what way was not discussed. Discovery of the flange in *Greererpeton*, admittedly aquatic but otherwise very differently adapted, persuaded Holmes that it was likely to be a primitive feature for labyrinthodonts, retained in anthracosaurs but lost in later temnospondyls. It is now known in both the terrestrial anthracosaur *Eoherpeton* (Smithson 1985) and the recently described *Crassigyrinus* (Panchen 1985). The entepicondylar foramen, found in *Greererpeton* and all known anthracosaurs, is lost in most later temnospondyls, pointing out the primitive nature of the *Greererpeton* humerus. An anterior flange on the humerus may prove primitive for all tetrapods, homologous as Holmes suggests to the preaxial process of the osteolepiforms such as *Sterropterygion*.

Recently published figures of the humerus of *Ichthyostega* by Jarvik (1980) show great similarity to an anthracosaur humerus. However, Jarvik's interpretation is at odds with that conventional for early tetrapod humeri. Despite this similarity, Jarvik comments that the 'humerus in *Ichthyostega* is a most peculiar structure, difficult to interpret in the terms used for *Eusthenopteron* and *Eryops*'. By comparison with anthracosaur humeri, however, that of *Ichthyostega* is seen to conform to that of a primitive tetrapod (Panchen 1985). Even if the detailed interpretation is disputed, it at least suggests that the broad L-shape with rectangular head is primitive with the 'twisted' tetrahedral type as derived. Use of the term 'tetrahedral' for this L-shaped form is misleading and should be abandoned.

The ulna (figures 30*l* and 40) measures 60 mm, discounting the olecranon process. It is virtually identical to that of *Archeria* but relatively longer and thinner than that of *Proterogyrinus*. The olecranon region is fairly well ossified, although not as complete as that of MCZ 2045

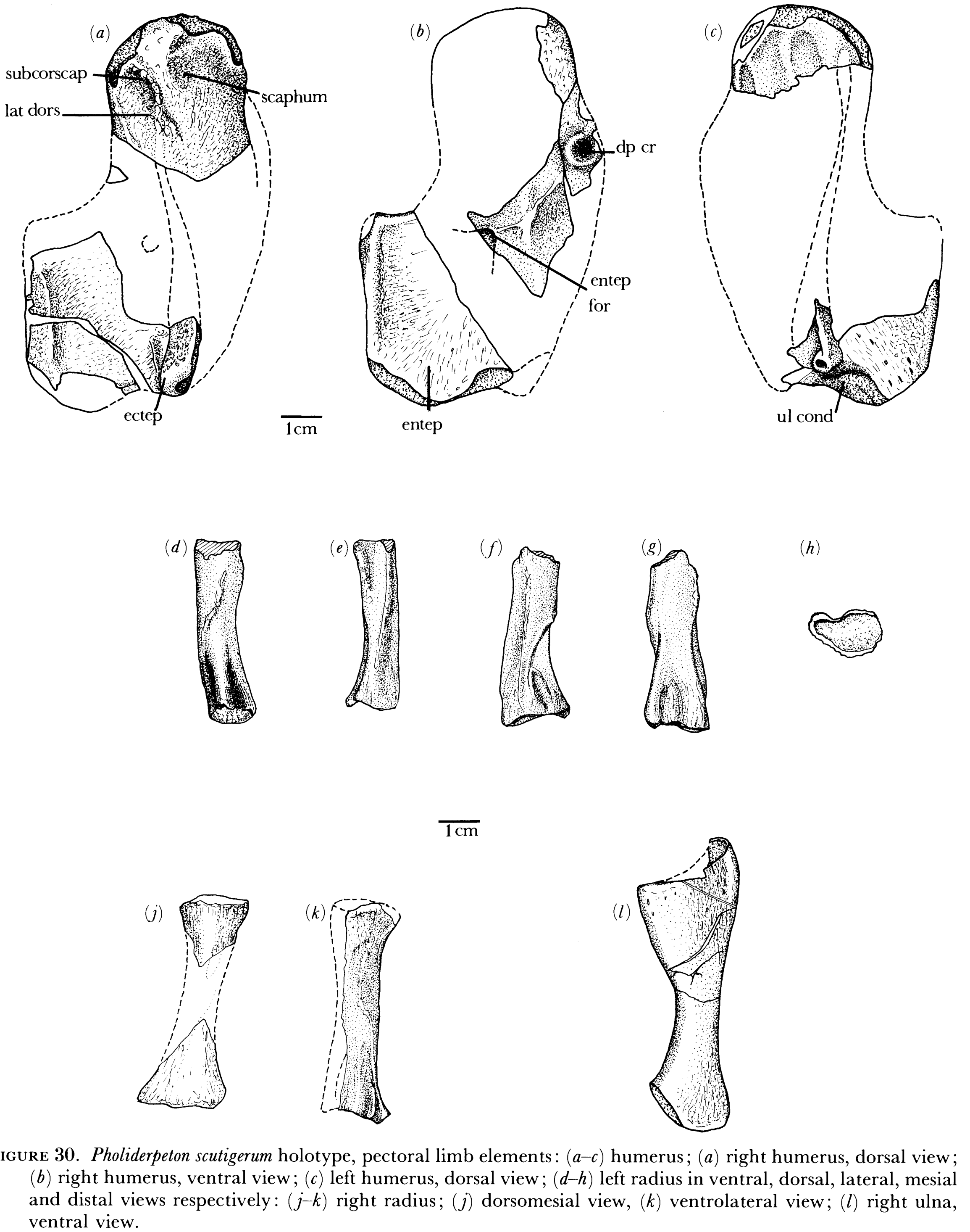


FIGURE 30. *Pholiderpeton scutigerum* holotype, pectoral limb elements: (*a*–*c*) humerus; (*a*) right humerus, dorsal view; (*b*) right humerus, ventral view; (*c*) left humerus, dorsal view; (*d*–*h*) left radius in ventral, dorsal, lateral, mesial and distal views respectively: (*j*–*k*) right radius; (*j*) dorsomesial view, (*k*) ventrolateral view; (*l*) right ulna, ventral view.

(*Archeria*), figured by Romer (1957). The articular surfaces are not sufficiently well preserved for comment. The olecranon and proximal part of the shaft are striated for attachment of the triceps muscle.

The left radius has been removed intact from the matrix and it is complete except for the proximal end (figures 30*d–h* and 39). The right radius is complete and measures 50 mm. Both elements have suffered a certain amount of compression, but generally resemble those of *Archeria*. The proximal articulation is not visible, but the distal is pear-shaped in ventral view (figure 30*h*). The apex, on the ventral (flexor) surface, represents the termination of a stout buttress which runs up the bone to merge into the shaft about 15 mm away from the articular surface. Distally the buttress separates two concavities, perhaps for tendon or ligament attachments. As in *Archeria* a keel, rugose initially, is developed on the ventral surface, just proximal to the middle of the shaft and curves onto the lateral surface, continuing to the distal end. A second rugose ridge placed dorsomedially begins at the proximal end and continues distally, losing height to merge into the shaft. The ridge is separated by a shallow groove from a third, less well developed ridge running the whole length of the bone on the dorsal (extensor) surface, and a fourth poorly developed ridge runs almost parallel with it on the dorsolateral surface. These ridges are all present on *Archeria* but are much less well developed in *Proterogyrinus*.

Phalanges, including unguals, and metacarpals have been identified in *Pholiderpeton*, but as they are totally disarticulated they add little useful information. No carpal bones have been identified in *Pholiderpeton*.

Limb function

Function of the shoulder joint in *Pholiderpeton* can best be compared with that in the related anthracosaurs *Archeria* (Romer 1957) and *Proterogyrinus* (Holmes 1980). Romer suggested that in *Archeria* there was probably a great deal of cartilage at the articular surfaces. The material consists of a large number of isolated specimens plus some articulated skeletons, showing different degrees of ossification, of which he figured the most complete. Certainly in immature animals much cartilage must have persisted and have been relatively slow to ossify, consistent with the aquatic habits which he envisaged for the animal. Romer noted consequent difficulty in placing the bones in their proper articulation. He nevertheless made some broad generalizations based on the most complete specimens. He suggested that, because it lacked the spiral surface seen in the glenoid humeral head of many other early tetrapods, movement of the humerus at the shoulder joint in *Archeria* was probably restricted to a simple fore-and-aft swing. This picture is probably oversimplified. Muscles for abduction and adduction, acting in combination with those for protraction and retraction, would inevitably produce some degree of rotation. As the glenoid moves forward during the power-stroke, the manus must remain in position. If the limb is to remain articulated, rotation must occur, either at the elbow joint, or at the shoulder as Romer (1922) himself suggested. For an effective limb it seems more probable that some component of rotation occurred at each joint. It is impossible to see how a fore-and-aft swing would allow the arm to be 'turned back along the body' as Romer suggested, without dislocating the shoulder completely.

The humeral head of *Pholiderpeton* is significantly longer than the glenoid by a factor of about 16%, within the range of 15–20% given by Jenkins (1971) for *Dimetrodon*. The condylar surface is an arc which subtends an angle of about 160°, not far short of the figure of 180° in *Captorhinus* (Holmes 1977). From its point of maximum retraction, with the posterior ends of the glenoid and condyle adjacent, to the point of maximum protraction with anterior ends of glenoid and condyle adjacent, the humerus moves through 90°, a figure similar to that in *Eryops* (Miner 1925) and greater than the 60° which Holmes quotes for *Captorhinus*. Clearly in this respect movement of the humerus of *Pholiderpeton* was subject to no greater restrictions than those of the terrestrial tetrapods. The figures are, however, strikingly different from those which Holmes (1980) gives for *Proterogyrinus*, in which the condylar arc was about 80° and the humeral head was only slightly longer than the glenoid. (His statement (1980, p. 356) that 'the glenoid is only slightly longer than the corresponding surface on the humerus' is contradicted later (p. 370) and is presumably an error.) Holmes interprets the figure to mean a very restricted range of movement for the humerus of *Proterogyrinus*, which could achieve a total arc of a mere 27° during the stroke. This figure seems unreasonably small. The similarity and close relationship between *Proterogyrinus* and *Pholiderpeton* suggests that the low figure in *Proterogyrinus* is more likely to be a result of poor ossification rather than a reflection of a major difference in functional anatomy between the two. It is difficult to believe that *Pholiderpeton* is more similar to the terrestrial reptiles and temnospondyls in this respect than it is to *Proterogyrinus*. Holmes himself described the surface of glenoid and humeral head as incompletely ossified. Low condylar arcs can be seen in immature *Archeria* humeri, for example MCZ 2053, T 104, but in the most complete the arc is comparable with that in *Pholiderpeton*. It is therefore probably unwise to infer too much regarding the range of movement in the incompletely ossified humerus of *Proterogyrinus*.

According to Holmes, the orientation of the ulna of *Proterogyrinus* was rather unusual. When fully extended, the long axis of the ulna made an angle of no more than 90° with the long axis of the humerus. The long axis of the articular surface of the ulna lay more or less along the entepicondyle. The ulna apparently underwent a degree of rotation during flexion and extension. Holmes notes that although the glenoids of *Proterogyrinus* and *Archeria* are similar, with the humerus of *Proterogyrinus* orientated in a similar manner to that given for *Archeria*, owing to the unusual articulation of the ulna, the forearm would lie in an anterodorsal orientation. A simple fore-and-aft swing would allow the hand to contact the surface only with the humerus fully retracted, a most unlikely situation.

Because Holmes stresses that the ulnar and radial condyles were well preserved with this unusual orientation the best fit for the bones, he suggested that the fault must lie with the interpretation of the glenoid. He therefore proposed a cartilaginous ridge-and-groove arrangement similar to that proposed by Romer (1922) for *Dimetrodon* and as is found in *Captorhinus*, which he assesses would result in a more realistic orientation for the forearm.

It is difficult to reconcile Holmes's recognition of the low degree of ossification of the humeral head in *Proterogyrinus*, plus his proposal for this extensive cartilaginous development, with his cautious interpretation of the range of movement of the humerus based on the low degree of curvature found in the head. Whether such a ridge-and-groove system was present in *Proterogyrinus* must remain in doubt in the absence of osteological evidence.

It appears that the glenohumeral joint of all early tetrapods was helical in structure to a greater or lesser degree. In *Eoherpeton* (Smithson 1985) the humeral condyle is markedly spiral with an incipient groove-and-ridge arrangement on condyle and glenoid. This suggests that some facility for rotation was present in this very early tetrapod forelimb. Even in embolomeres such a structure is apparent, although only weakly developed. The development in *Eoherpeton* may well represent the primitive state for the tetrapod glenohumeral joint, which became more highly developed in later more fully terrestrial animals. In the aquatic embolomeres, the structure may have been more weakly developed in response to aquatic or anguilliform locomotion, or could simply have been unossified as Holmes suggested.

The long-bodied embolomeres, using anguiliform location, are likely to have used girdle rotation (i.e. rotation about a vertical axis) as a means of progression, because this is most effective when the vertebral column is strongly bent (Edwards 1977). Being less reliant on limb retraction or humeral rotation, they presumably lost the helical joint which is usually associated with these modes of progression. Conversely, short-bodied animals probably relied more heavily on these two modes, because these are most effective when the vertebral column is a straight rigid rod, achieved more easily with a short column. Thus short-bodied animals may show correspondingly more strongly helical glenohumeral joints.

The terminal position and essentially flat surface of the radial condyle in *Archeria* led Romer to suggest that the arm was inefficient as a limb for walking on land. In most primitive terrestrial forms the condyle is ventral, transmitting forces vertically to the humerus without excessive use of muscular power. A terminal condyle does indeed suggest that the radius was unlikely to have borne the weight of the animal. However, in long-bodied animals like embolomeres, it may not have been required to do so; like most other elongated vertebrates, they were probably habitually belly-crawlers. The radius would be in a suitable position to transmit a thrust along its length from the laterally positioned manus to the humerus which was pushed sideways rather than lifted.

Archeria humeri show a range of variation in the form and position of the radial condyle, including some in which it is more ventral than terminal and others in which it is rounded, even 'bulbous'. Individual differences in degree of ossification could explain the apparent inconsistency of a ventral radial condyle in the anthracosaur *Proterogyrinus* which, although not as elongated as later embolomeres, could well have been a belly-crawler, and the terminal condyle in *Eoherpeton* which, with its long legs and short trunk, seems likely to have been a terrestrial 'walker'.

Embolomere limbs appear adapted to assist and direct anguilliform locomotion which the animals almost certainly employed. They acted as struts against which the body could push and added a certain amount of their own forward thrust. Anguilliform locomotion can only function on land if the body can brace itself against resistances acting normally to the body surface (Gray 1968). The animal's body itself may assist by bracing against the undergrowth. In high-speed locomotion the legs, although making the same movements as in slow progression, may have taken no part in propulsion. This is apparently the case in some species of salamander (e.g. *Triturus* and *Ambystoma*) (Evans 1946). Similarly, long-bodied lizards, for example the skink (*Scincus scincus*) propel themselves through the undergrowth or soft sand by serpentine movements of the body (Gray 1968).

Scutes

Scutes lie in a thick but much disturbed layer ventrally on the specimen; the original arrangement has been represented as faithfully as possible in figures 39 and 41. Intact dermal armour of *Archeria* (AMNH 4550) and an embolomere specimen from Linton (MCZ 2161) shows the arrangement of scutes in internal and external view. *Pholiderpeton* resembles *Eogyrinus* (Panchen 1972) in the range of size and shape of scutes. Figure 31 shows a representative selection, of which the types in figure 31 *a*, *b* and *k* are the most numerous. These are elongate wedges, bearing a strong, shallowly sigmoid ridge curving across the internal surface, defining a broad spatulate depression at one end and a second narrower depression running to the tapering tip. The ridge possibly formed the area of attachment to the underlying dermis, as in the dermal scales of *Polypterus* (Pearson 1981).

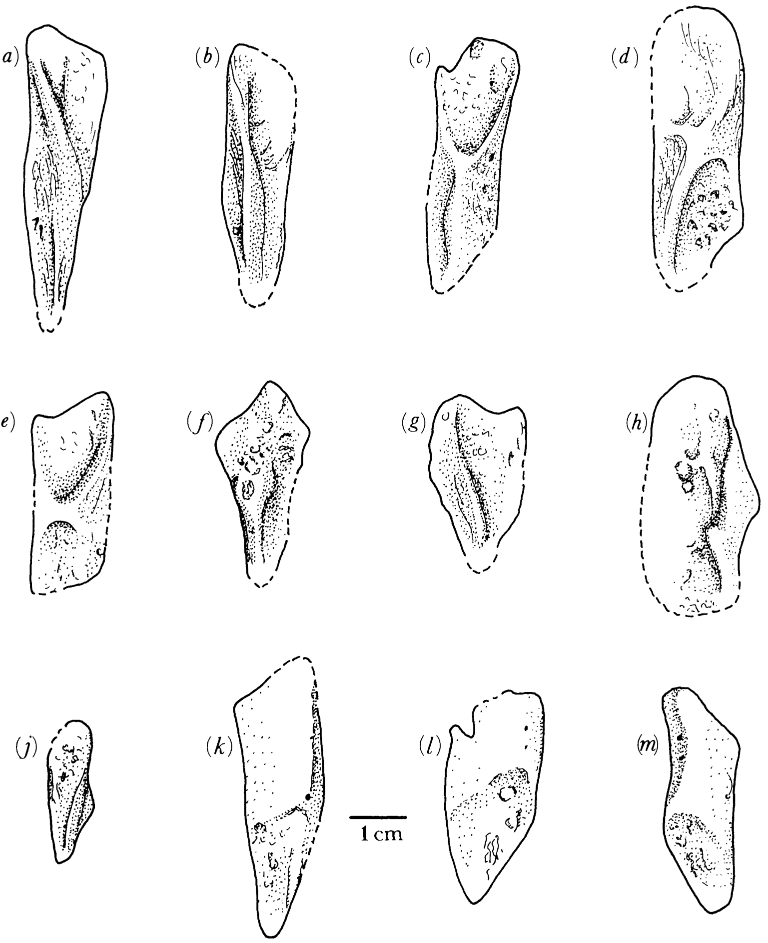


FIGURE 31. *Pholiderpeton scutigerum* holotype, scutes: (*a–j*) internal views; (*k–m*) external views.

The smooth external surface bears a concave, lightly sculptured area at the tapering end, to receive the broader end of the succeeding and more ventral scute. The broad depressed area on the internal surface received the tapering end of a more dorsal scute. Scute-rows overlapped minimally. Holmes's figure shows the scute-rows in *Proterogyrinus* to be arranged at an angle of 45° to the long axis of the body: this angle would allow locomotor-generated shear to occur between them (McN. Alexander, in Pearson (1981)), but would prevent torsion. Thus it would allow both the lateral movement necessary for a scute-covered amphibian using anguilliform locomotion (Pearson (1981) for *Polypterus*) and the movement required during costal ventilation.

Comparison with *Proterogyrinus* suggests that scute *f* (figure 31) originated from the midline. No V-shaped or boomerang-shaped scutes have been found in *Pholiderpeton* nor in MCZ 2161 at the ventral midline. Cope & Matthew (1915) illustrate this type of scute associated with *Archeria* although I could not confirm this. Irregularly shaped scutes may originate from rows just posterior to the interclavicle, filling an area between anteriorly and posteriorly directed scute-rows.

Externally, above the ridged margin, many scutes show one or a series of several small pores, not noted in *Eogyrinus* (Panchen 1972), but subsequently found there. Serial sections show that the pores were in contact with the blood-spaces within the bone of the scute and were probably entry or exit points for blood vessels. Pits in dermal bone have been reported in the skull and girdle-bones of some temnospondyls (Bystrow 1947) and were thought to indicate the presence of a rete vasculosum, a network of blood vessels used in cutaneous respiration. The animals in which the pits were discovered were large, predominantly aquatic animals (e.g. *Benthosuchus*), but cutaneous respiration is most effective only when the skin is in contact with air and decreases in importance with increase in the size of animal (Schmalhausen 1968). Bystrow (1947) suggested that cutaneous respiration was used to assist oxygen exchange when the primarily aquatic animals were on land; totally aquatic forms, such as *Dvinosaurus*, lacked the system and may have relied entirely on gills. No pits are seen in the dermal skull or girdle bones of *Pholiderpeton*, but the scute pores could be equivalent. In *Pholiderpeton* the ribs were well developed and pulmonary respiration by means of costal ventilation probably provided the main source of oxygen. However, in modern amphibia and in air-breathing fish, the lungs are not used in excretion of carbon dioxide, which is lost through the skin or the gills (Randall *et al.* 1981). This may have been true of early tetrapods. The pore system and associated blood vessels may have been used in the excretion of carbon dioxide.

UNIDENTIFIED BONE

One bone remains unidentified in the holotype of *Pholiderpeton*. Lying over the right jaw ramus, and originally covered by scutes on the obverse of the specimen, is an approximately rectangular plate of thin bone. Part appears on the reverse. The bone is only about 1 mm thick and bears no ornament (figures 32 and 41, X) except for fine striations. Two edges of the bone are roughly straight; the remaining two are irregular, the short edge being fluted. Part of the postsplenial has been pushed up through the bone to form an artefactual ridge. Part of a second similar bone lies just posterior to the right jaw ramus, on the reverse of the specimen (figure 40, X2).

The bone apparently does pertain to *Pholiderpeton*, sandwiched as it is between other bones

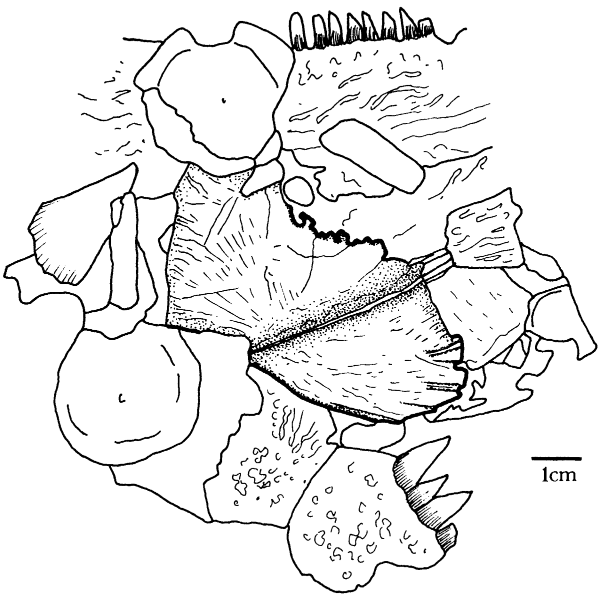


FIGURE 32. *Pholiderpeton scutigerum* holotype, unidentified bone, after preparation.

of the same animal. It does not pertain to a fish (P. L. Forey & S. M. Andrews, personal communication). It is clearly not a dermal bone, and possibilities for its true identity are limited. The ossified tympanic membrane of *Diadectes* was described by Watson (1954). It is found *in situ* in several specimens and thus its identity, although not its function, is certain. Its description matches that of the unidentified bone. An ossified tympanic membrane in *Pholiderpeton* would present a number of problems. First, it appears to be rather large and unsuitably shaped to fit the 'otic notch' (figure 17*b*). Secondly, embolomeres are considered to be primitively tympanumless (Clack 1983). The only animals known to possess ossified or heavy cartilaginous tympana are aquatic diving forms such as mosasaurs and turtles (Wever 1978). It is difficult to visualize *Diadectes* as belonging to the category. An ossified tympanum in *Pholiderpeton* might suggest that not only was a tympanum primitive for embolomeres but that the stapes of *Pholiderpeton* was adapted primarily to underwater hearing and thus convergent upon that of *Greererpeton*. However in his recent (1985) discussion of ear function in *Crassigyrinus*, Panchen suggests that here, the middle ear was adapted for aquatic audition, but that it was not necessarily derived from a more terrestrially adapted one. An ossified tympanic membrane might also have been uniquely evolved from the dermis.

The unidentified bone might also have been an ossification either of the normally cartilaginous palatoquadrate or of Meckel's cartilage; thin laminae of bone have already been described from the lower jaw sections. Smithson (1986) recently suggested that the fenestrae in the lower jaws of embolomeres resulted from persistent incomplete ossification of the mesial surface. These unidentified bones are similar in size to the larger of the two Meckelian fenestrae in *Pholiderpeton* and could represent ossifications of Meckel's cartilage in this position. An ossification within the dermis beneath the lower jaws (equivalent of a gular plate) or a neomorph element of the shoulder girdle are other possibilities.

STRATIGRAPHY, PALAEOECOLOGY AND TAPHONOMY

The Black-bed Coal, from which the holotype of *Pholiderpeton* derives, lies within the *communis* zone, near to the base of the productive Coal Measures of Yorkshire. It occurs widely in West Yorkshire round the areas of Leeds and Bradford. Toftshaw was a minor colliery and no sections of it are immediately available. Nearby was the larger and more productive Low Moor Pit, of which a section pit is given in Green *et al.* (1878) (table 4). In both these pits, the Black-bed Ironstone lies immediately above the Black-bed Coal, separated by 'a few inches of shale' (Davis & Lees 1878); further west, they become more widely separated. Miall (1869) knew the

Table 4. Section at low moor pit (from Green *et al.* 1878)

	thickness	total
Crow Coal	1′6″[a]	—
Measures*	27′6″	—
Black-bed Ironstone	4′6″	33′7″
Black-bed Coal	2′10″	—
Measures	27′6″	—
Sandstone 'Thick Stone'	27′0″	—
Measures	63′1″	117′7″
Better-bed Coal	2′3″	—

[a] 1 foot = 12 inches; 1 inch = 2.54 cm.

* Unproductive strata, a contemporary mining term.

shales overlying the Black-bed Coal as fossiliferous but gave no list of genera. Green *et al.* (1878) recorded the occurrence of plant remains (*Lepidodendron*, *Ulodendron* and *Calamites*) as well as teeth, scales, and coprolites of fish and occasional labyrinthodont remains.

Because both Black-bed and Better-bed seams and associated shales occur at Low Moor, they are often confused. Davis (1876) quotes the 'Better Bed' as lying about 130 feet below the Black-bed, with the 'Better Bed bone-bed' immediately above it. This varies from 'a quarter to five eighths of an inch thick' (Davis 1876), and is composed of comminuted bones, principally of fish but with some amphibian remains. The matrix is brownish-black argillaceous shale. Davis (1876) and Davis & Lees (1878) gave a list of the genera of fish which had been found there, which includes sharks, acanthodians, actinopterygians (rare), rhipidistians, coelacanths (abundant) and dipnoans (rare); he also mentioned the occurrence of '*Loxomma*'. The material from Harvard, originally labelled MCZ 2550, includes material from the Better-bed bone bed, which occurs as whitish bone in irregular matrix containing comminuted fish scales and teeth. Other fragments of MCZ 2550 may derive from either seam. To compound the confusion, Miall (1870, p. 19) refers to the holotype of *Pholiderpeton* as 'the Low Moor fossil'. A precise faunal list is thus unavailable for the Black-bed shale, although eroded *Megalichthys* scales are associated with the holotype of *Pholiderpeton*.

The taphonomy of the holotype of *Pholiderpeton* was commented on in 1929 by Watson, who suggested that 'the animal had entered a cylinder or cortex of a decayed *Lepidodendron* trunk and had there died and been much disturbed either by the attacks of fishes or by currents and finally buried whilst still being completely concealed by the plant'. In fact the specimen was covered ventrally only by a thin layer of shale, which has now been removed. The fossilized wood with its characteristic marking lies only dorsal to the animal. The wood does represent the compressed trunk cortex of a lepidodendroid tree fern, both upper and lower surfaces bearing leaf-scars, and infilled with featureless matrix. Many *Spirorbis* tubes occur at one point near the braincase; these might indicate aerobic conditions. Rather than indicating aerobic conditions of deposition, the worms were more probably associated with the wood before deposition, as it floated on the surface (C. T. Scrutton, personal communication). The body does not seem to have been disturbed as Watson suggested; the bones are excellently preserved and show no signs of attack.

Lack of any sacral or postsacral material may indicate disruption of the body by decay of the contents of the hind-gut. Build-up of gases within the abdominal cavity, rupturing the body-wall, probably caused disintegration at its weakest point (Shäfer 1972; Milner 1980). The presacral parts of the body were then deposited, ventral side down. Although disturbed, the elements still retain something of their original positional relation, with most of the skull elements anteriorly, limbs and girdles some distance behind and presacral elements posteriorly. The animal apparently lay with its head facing into a water current. Elements were detached and carried downstream, one of the first elements to do so being the skull table and its associated snout bones. While the braincase was still attached, and possibly therefore at an early stage in decomposition, the whole unit was lifted and turned over lengthways through 180°.

The body appears to have been lying chiefly on its right side. All elements of the left-hand side are consistently more disturbed than those of the right. The left cheek elements are scattered among the remaining skull bones, often rotated through 180°. The left ectopterygoid has floated further downstream than the right. Elements of the right limb are preserved almost entire and in close association, whereas those of the left, except for the cleithrum, are far removed or lost altogether. The interclavicle, although a ventral element, is also disturbed, having been turned over and rotated. Its large surface area and flat shape probably facilitated its being picked up and moved by a current. The most disturbed and scattered elements are the dorsalmost (centra and neural arches).

Distribution is consistent with disturbance by a current carrying parts of the dissociated skeleton downstream, and somewhat attenuating it. Moving waters are generally better oxygenated than stagnant pools; however, the good preservation of the bones suggests rapid burial after disturbance, the bone being protected from further decay. It seems likely that the lepidodendroid trunk settling on the bones could have been the fortunate coincidence directly responsible for this protection.

Archeria crassidisca: *analysis of the skull table*

The most abundant embolomere remains belong to the genus *Archeria*, relatively common in the Lower Permian of North America. A series of *Archeria* skulls was studied to establish the range of variation present within one species of embolomere (*A. crassidisca*), thus assisting with embolomere systematics generally. Skull tables constitute the most commonly preserved elements of embolomeres, but by themselves have proved difficult to deal with taxonomically. Eleven of the best preserved *Archeria* skulls were studied.

From the Museum of Comparative Zoology, Harvard: MCZ 2121, 2046, 2047, 2049, 2052, 2053, 2063, 2072, from the Geraldine Bone Bed, Lower Admiral Formation, Wichita Group.

From the American Museum of Natural History: AMNH 4550 from 'North fork of the Little Wichita River', (formation unknown, Lower Permian); AMNH 4551 from Baylor County (Admiral or Belle Plains Formation); AMNH 7117 from the Putnam Formation, Wichita Group.

The skulls are remarkably consistent in size and pattern, with paired parietals forming a characteristic arrowhead or dart shape, which dominates the skull tables and imparts an almost uniform shape. In undisturbed skull tables, the margins are smoothly rounded, with the widest point posteriorly placed. To quantify this similarity the proportions of the parietals were analysed. The length from the parietal–frontal–postfrontal junction to the posterior margin at the midline (f) was measured and calculated as a percentage of the width measured at the parietal–supratemporal–tabular junction (g) to give f/g (%) (figure 33 and table 5). The parietals are subject to less damage in preservation than the skull table as a whole and are useful in comparative studies. The skulls varied between 60 and 75% for f/g; this variation presumably represents individual variation in *A. crassidisca*.

Parietal ornament is consistent throughout with small discrete pits at the centre, radiating towards the margins where the pits become elongated. The underside of the skull table is often available but has been ignored in previous analyses. Special attention was therefore paid to this area. Several characters were found which differed consistently and markedly from known eogyrinid skull tables, such as the poor development of ridges of the internal surface of the parietals, the pits for the columella cranii, and the lack of development of the anterior tabular facet. These have been described in the text and are enumerated below.

Absolute sizes were also compared by using the following reference points: interorbital width, parietal foramen–postparietal length, width of skull table at midpoint of supratemporal

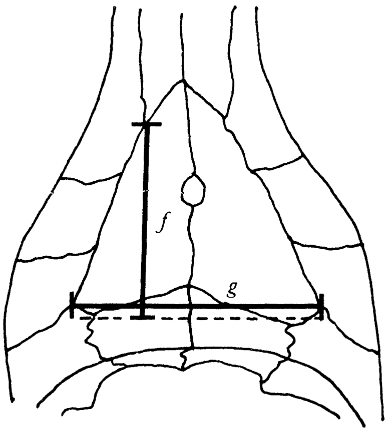


FIGURE 33. Diagram to illustrate positions at which measurements *f* and *g* were taken.

margin, width of parietal foramen, and (where available) snout–postparietal length (table 5). The subjective similarity of the skull tables was borne out in the analysis. With one exception they fall into two size groups.

Group 1 skulls:	MCZ 2121, 2047, 2052, 2053, 2063, 2072. AMNH 4550, 7117.
Group 2 skulls:	MCZ 2046, 2049.

The greatest differences between the groups occur in the skull table and interorbital width. It is tempting to read into this the existence of two distinct size-groups, perhaps representing sexual dimorphism or year groups. However, the complete snout–postparietal length is known in only two specimens (MCZ 7117, 2046) with a minimum length for one (MCZ 2072). The sample is not large enough to warrant any definite conclusions. A surprising inconsistency of parietal foramen size is not accountable for by differential preservation. Holmes (1984) reports a similar inconsistency in *Proterogyrinus*.

The remaining skull, AMNH 4551, is much larger, approaching the size of *Pholiderpeton scutigerum*. Its relationships to other *Archeria* specimens will remain unclear until a detailed taxonomic study is conducted on the genus. *Archeria* appears to be longer-snouted than eogyrinids. The four *Archeria* skulls of known snout–postparietal lengths (MCZ 2046, 2072; AMNH 4551, 7117) were compared with the British embolomeres *Pholiderpeton*, *Palaeoherpeton* and *Eogyrinus*. The British embolomeres seem to form an allometric series (Panchen 1970). Panchen plotted parietal foramen–postparietal length and other parameters against snout–postparietal length, although he was using incomplete data. An underestimate of snout–postparietal length was used for *Palaeoherpeton* (Panchen 1964, 1972); a revised estimate of 150 mm is used here. Orbit–postparietal length plotted against the former parameters shows straight-line relations when plotted on a simple linear scale rather than the logarithmic scale used by Panchen. For the low values involved this is probably not significant. *Archeria*, plotted on the same graph, clearly seems to belong to a different series with a greater snout–postparietal length. AMNH 4551 appears from these data to belong to the same series as the other *Archeria* specimens, but only further data could confirm this (tables 5 and 6; figure 34).

The following diagnosis may be given for *Archeria*, based on the single species *A. crassidisca*.

TABLE 5. *ARCHERIA* SKULL MEASUREMENTS (MILLIMETRES)

number	width of parietal foramen	parietal foramen–post-parietal	snout–post-parietal	width of skull table at mid supra-temporal	inter-orbital (minimum)	length of parietal (f)	width of parietal (g)	f/g (%)	Orbit[a]–post-parietal
2121	5.5	22.5	—	58.0	23.0	30.0	40.0	75	—
2047	4.5	22.5	—	56.0	24.0	30.0	50.0	60.0	—
2052	4.0	22.0	—	58.0	23.0	25.0	38.0	65	—
2053	6.0	23.0	—	56.0	24.0	29.0	40.0	72	—
2063	4.0	24.5	—	56.0	22.5	29.0	40.0	72	—
2072	5.5	24.5	min. 173	56.0	23.5	25.0	38.0	65	64.0
4550	4.5	22.5	—	54.0	21.5	27.0	43.0	62	—
7117	—	24.0	172	—	23.0	—	—	—	62.0
2046	4.0	21.0	143	48.0	17.0	23.0	36.0	63	60.0
2049	4.0	21.5	—	48.0	17.5	22.0	34.0	64	—
4551	6.0	35.0	240	74.0	37.0	—	—	—	79.0

[a] Orbit measured from anterior margin.

Table 6. Embolomere skull measurements (millimetres)

	parietal foramen–post-parietal	Snout–post-parietal	width of skull table at mid supra-temporal	inter-orbital (mini-mum)	length of parietal (*f*)	width of parietal (*g*)	*f*/*g* (%)	orbit[a]–post-parietal
Pholiderpeton (holotype)	45.0	275.0	90.0	35.0	56.0	64.0	87	105.0
Pholiderpeton (A2)	39.0	—	85.0	—	51.0	60.0	85	—
Palaeoherpeton (holotype)	32.0	150.0	67.0	27.0	38.0	50.0	76	80.0
Palaeoherpeton (A1)	27.0	—	80.0[b]	32.0[b]	40.0[b]	60.0[b]	67[b]	—
Eogyrinus (lectotype)	48.0	340.0	90.0[b]	44.0	72.0[b]	62.0[b]	116[b]	112.0
R 8426	50.0	—	102.0[b]	—	70.0[b]	80.0[b]	87[b]	—
G 13.78	43.0	—	97.0	42.0	50.0	69.0	72	—
Anthracosaurus (holotype)	46.0	295.0	120.0	62.0	62.0	88.0	70	128.0
Pteroplax (holotype)	35.0	—	75.0	27.0	57.0	43.0	130	—
Eobaphetes (holotype)	37.0	250[b]	89.0	40.0	48.0	65.0	73	96[b]

[a] Orbit measured from anterior margin.

[b] Adjustments made for incomplete or highly asymmetrical skulls.

Embolomeres with:

1. Underside of parietals with fluting present but poorly developed.

2. Deep pits (for columella cranii) on underside of parietals, posterolateral to parietal foramen.

3. Pits on underside of postparietals, approximately at centre of exposed portion (function uncertain).

4. Underside of supratemporal smooth, very little pitting at margin.

5. Massive posterior buttress on tabular for reception of opisthotic, but very small anterior facet, not placed at mesial end of strongly developed ridge.

6. Parietals approximately dart-shaped, corners forming an almost equilateral triangle in many cases; parietal proportions (*f*/*g*) 60–75 %. Table increases steadily in width posteriorly, forming a truncated triangle.

7. Ornament on parietal consisting of discrete pits at the centre, tending towards elongation at the margins, but with elongation not confined to the margins.

8*. Skull elongate in snout region.

9*. Teeth numerous, about 60 per marginal tooth row.

10. Teeth even, cylindrical except for laterally flattened and slightly recurved chisel-shaped tips; no canine peak.

11. Jugal narrow below orbit (MCZ 2046, AMNH 4550, 4551, 7117).

12. Jugal enters jaw margin (AMNH 7117, 4551).

13. Surangular crest flat-topped.

No tabular horn examined was sufficiently complete to be diagnostic but MCZ 2063 has the

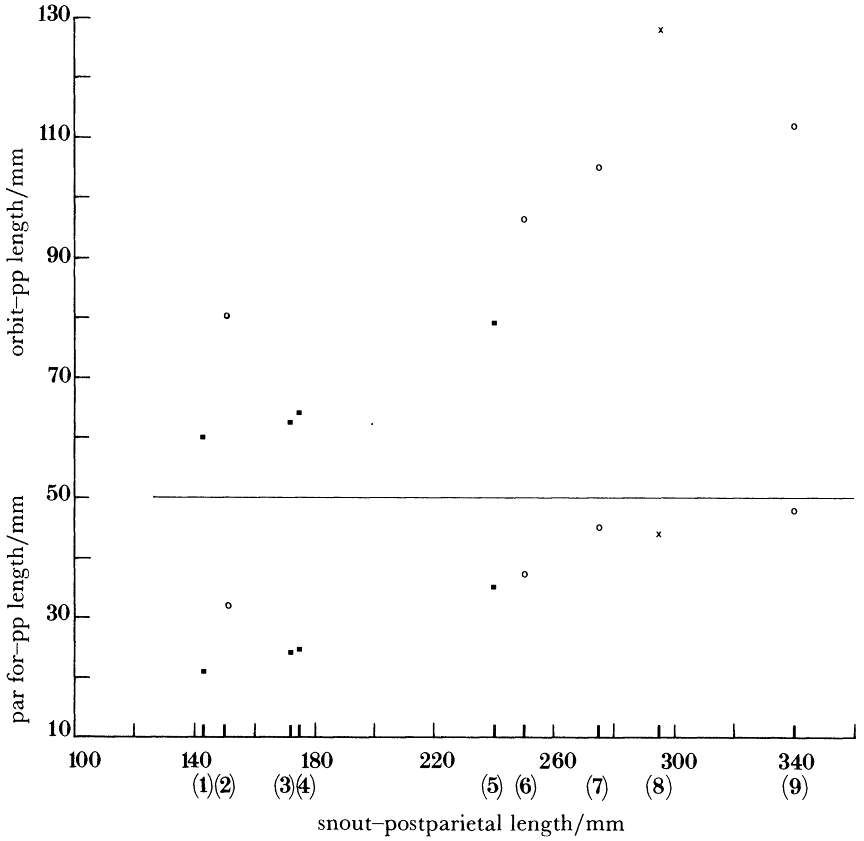


FIGURE 34. Graph of embolomere skull measurements: (1) *Archeria crassidisca* MCZ 2046; (2) *Palaeoherpeton decorum* holotype; (3) *A. crassidisca* AMNH 7117; (4) *A. crassidisca* MCZ 2072; (5) *A. crassidisca* AMNH 4551; (6) *Eobaphetes kansensis* holotype; (7) *Pholiderpeton scutigerum* holotype; (8) *Anthracosaurus russelli* holotype; (9) '*Eogyrinus*' *attheyi* lectotype. Symbols: filled squares, *A. crassidisca*; open circles, eogyrinids; cross, *Anthracosaurus russelli*.

characteristic pit above the horn found in other embolomeres. The palatal dentition is not preserved in any specimen examined. Asterisks in the above diagnosis represent autapomorphies of *Archeria* used in the final cladogram.

TAXONOMY AND RELATIONSHIPS OF *PHOLIDERPETON SCUTIGERUM*

The holotype of *Pholiderpeton scutigerum* has provided much new information about an eogyrinid. Together with information from *Archeria* this information allows a fresh assessment of the taxonomy of the Eogyrinidae and the embolomeres as a whole.

Study of *Archeria* skulls demonstrates the uniformity of skull-table characters in one species of this genus. Such uniformity is thus inferred to exist within the closely related, although earlier, British and North American embolomeres. Although they are often badly or incompletely preserved, such features as the ornament, proportions of the skull tables, especially the parietals, and characteristics of the underside of the skull table, may be taken as diagnostic rather than resulting from individual variation or differential preservation.

Skull-table characters, particularly of the underside, thus contribute in large measure to the taxonomy presented below. Measurements of skull tables are presented in table 6.

A strictly cladistic methodology is not entirely feasible in assessing relationships within this group, both because of the incompleteness of the material and the difficulty of assessing which condition of many of the characters is primitive and which derived (Boy 1981). Therefore no cladistic analysis within the Eogyrinidae is presented.

Throughout this study it has become clear that, apart from size and details of the dentition, *Pholiderpeton scutigerum* shows few cranial characters which could distinguish it from *Eogyrinus attheyi*. Only differences in the dentary tooth count appear significant. Their parietal proportions (f/g) differ somewhat but the significance of this is difficult to assess. The difference (about 20 %) falls outside the range seen in a single species of *Archeria*. R 8426 is very similar to *P. scutigerum*, whereas in the lectotype of *E. attheyi* the skull table is incomplete and measurements must be estimated. The differences between them do not merit generic separation, but a higher dentary tooth count in a smaller skull suggests a specific distinction. *Pholiderpeton*, the older name by some 60 years, takes priority, the genus *Eogyrinus* Watson becoming a subjective junior synonym of *Pholiderpeton* Huxley. The family name Eogyrinidae is maintained because the International Rules of Zoological Nomenclature prohibit changing the name of a family-group taxon in the event that the type genus is synonymized (Stoll *et al.* 1964, article 40).

A maxilla of about the same size as that of *Pholiderpeton scutigerum* (G 40.28), and the skull table R 8426 with similar parietal proportions to the latter, although of larger size even than '*Eogyrinus*', both occur at Newsham. This serves to blur the distinction between the two species. I am however reluctant to synonymize them further without more evidence. The specimen from Airdrie (GS 28318, L 11614) has a different tooth shape from either *Pholiderpeton scutigerum* or *P. attheyi* (figure 8*e*). This may be indicative of real but otherwise undiagnosable specific differences, or possibly, as Panchen (1972) suggested, evidence of sexual dimorphism. It is placed in the genus *Pholiderpeton*, *incertae sedis* as to species. The specimen of *Pholiderpeton sp.* occurring at Swanwick (*P. scutigerum*, Panchen 1970) differs from the holotype in bearing no lateral-line canals on the skull roof, in effect on the jugal owing to its preservation. The parietal ornament appears to be somewhat finer but the impression is subjective. Fragments of a (probably single) embolomere jaw ramus, perhaps from the same individual, bears lateral-line canals in the normal positions. Absence of lateral-line canals on the skull roof may well result from individual variation.

The two lower jaws attributed to *P. bretonense* from the Point Edward formation are probably those of embolomeres, as Romer (1963) suggested, although the internal surface is concealed in each. However, each has the characteristic surangular crest and numerous marginal teeth in a strongly tapering ramus. Many embolomere fragments occur at Point Edward, including some small forms, but there is nothing to suggest their attribution to *Pholiderpeton* or indeed to the family Eogyrinidae. The material is largely undiagnostic. Their removal from the genus *Pholiderpeton* is thus advisable, and they should stand as undetermined embolomere remains.

The genus *Pholiderpeton* may be diagnosed as follows.

Embolomeres with:

1. Underside of parietals with fluting present and well developed.
2. Depressions or facets on underside of parietals for columella cranii.
3. Underside of supratemporal pitted and roughened.

4. Massive posterior buttress on tabular for reception of opisthotic, with an anterior facet placed at mesial end of a well-developed ridge.
5. Parietal proportions (f/g) 85–116%.
6. Ornament on parietals consisting of pits of varying sizes, coalescing; elongation confined to margins; well defined.
7. No strongly defined midline ridge or depressions on skull table.
8. Intertemporal excluded from or just entering orbit.
9. Tabular horn not bifurcate, upper boss small, not significantly developed.
10. Marginal teeth numerous (40–53), even, closely spaced, canine peak on maxilla at 2–5; slight development of anterior crest to give chisel-shaped tip.
11. Ectopterygoid with 2 tusks plus several (4–7) smaller teeth.
12. Jugal deep below orbit.
13. Jugal does not enter jaw margin.
*14. Single poorly defined lateral-line canal on squamosal, at posterior margin; lateral line section over jugal–quadratojugal suture, parallel to jaw margin.
15. Lachrymal excluded from naris by nasal–maxillary suture.
16. Rounded surangular crest.
17. Attaining large size, snout–postparietal length up to 350 mm.

The asterisk indicates an autapomorphy of the genus *Pholiderpeton*. The most significant difference between the two recognized species is the dentary tooth count. Premaxillary and ectopterygoid teeth show discrepancies between left and right sides in one individual (the lectotype of *P. attheyi*).

The two species may be diagnosed as follows:

P. scutigerum

1. Maxillary tooth count: maximum 47.
*2. Dentary tooth count: maximum 53.
3. Premaxillary tooth count: 4.
4. Ectopterygoid formula: 2(4–5).

P. attheyi

1. Maxillary tooth count: 40+ (? < 50).
2. Dentary tooth count: 40+ (? < 45).
3. Premaxillary tooth count: 3.
*4. Ectopterygoid formula: 2(6–7).

Asterisks indicate autapomorphies of the two species.

The smaller genus *Palaeoherpeton* differs from *Pholiderpeton* in several points: the course of the lateral-line canals on the squamosal and quadratojugal, the form of the jugal and in the proportions of the parietals in additions to the obvious disparity in size. The contrast in lateral-line canal pattern is illustrated in figure 35 and described in the text. That of *Pholiderpeton* is unusual among early tetrapods; *Palaeoherpeton* exhibits a more typical pattern for tetrapods. The pattern in *Pholiderpeton* may be used as an autapomorphy of the genus, and is a valid character on which to distinguish it from *Palaeoherpeton*.

The jugal contributes to the jaw margin in the smaller embolomeres *Palaeoherpeton*, *Archeria* and *Proterogyrinus*, whereas it is usually excluded in larger ones. The larger *Archeria* specimen, AMNH 4551, is a possible exception, as is *Neopteroplax* in Romer's (1963) tentative restoration. This character may be size-related and its status is doubtful. The jugal in

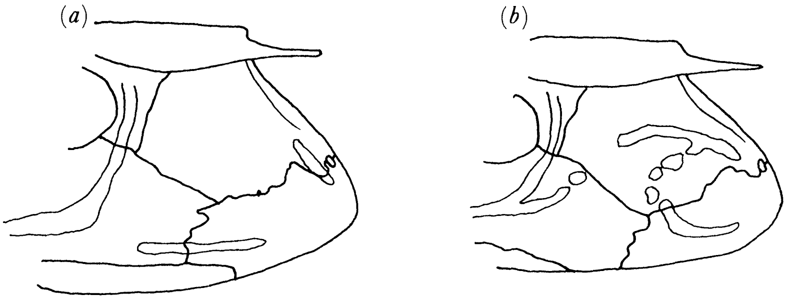


FIGURE 35. Dermal cheek bone and lateral-line canal patterns in (a) *Pholiderpeton* and (b) *Palaeoherpeton*.

Palaeoherpeton is much shallower than in *Pholiderpeton*. In *Archeria*, even the largest specimen has a narrow jugal and the character may be indicative of more than simple growth in the two former animals. The configuration of the lachrymal–postfrontal–jugal sutures is uncertain around the orbit in *Palaeoherpeton*. Watson (1926) interpreted the lachrymal as having a broad exposure in the orbital margin; Panchen (1964) restored it as excluded as in other eogyrinids. If Watson was correct, either the diagnosis (below) of the Eogyrinidae must be modified, or *Palaeoherpeton* removed from the family.

The teeth of *Palaeoherpeton* are poorly preserved but the crowns appear to taper more than those of *Pholiderpeton*. Panchen (1964, 1970) estimated a tooth count of about 30, although the revised interpretation (1972) of the snout of *Palaeoherpeton* might allow a higher count than this.

The most obvious difference between the two genera is that of size. I accept Panchen's assessment (1964) that occurrence of two independent specimens of almost identical size suggests that they may not represent a mere growth stage of a larger species. Two separate genera are thus maintained. The diagnosis of the genus *Palaeoherpeton* and only species, *P. decorum*, is as follows.

Embolomeres with:

1. Underside of parietals with fluting present and well developed.

2. Depressions on underside of parietals for ?columella cranii.

3. Underside of supratemporal pitted and roughened.

*4. Well-developed facets on postparietals for opisthotic.

5. Massive posterior buttress for reception of opisthotic, with an almost equally large anterior facet placed at mesial end of greatly developed ridge.

6. Parietal proportions (f/g) 67–76%.

7. Ornament on parietals consisting of pits of various sizes, coalescing; elongation confined to margins; well defined.

8. No strongly defined midline ridge or depressions on skull table.

9. Intertemporal excluded from orbit.

10. Tabular horn not bifurcate, upper boss very small (or broken in type?), not significantly developed.

11. Marginal teeth numerous ($>$ 30?) closely spaced; even; tapering and slightly recurved tips, no anterior keel.

12. Jugal shallow below orbit.

13. Jugal enters jaw margin.

14. y-shaped lateral-line groove on squamosal; quadratojugal grooves continue anteriorly onto squamosal, not jugal.

?15. Small animals; snout–postparietal length *ca.* 150 mm.

Unknown characters include: marginal tooth count, ectopterygoid tooth count, condition of surangular crest, entry of lachrymal into naris. Asterisk indicates an autapomorphy of the genus.

The isolated skull table which constitutes the only certain skull material pertaining to *Pteroplax cornutus* has caused taxonomic problems in the past (Watson 1926; Romer 1947, 1963, 1966; Panchen 1964, 1970, 1972). However, development of the underside of the skull table has shown additional characters by which it can be distinguished from other British embolomeres. They are as follows:

1. Underside of parietals with fluting very weakly developed.
2. Round deep pits on underside of parietals for ?columella cranii.
3. Underside of supratemporal smooth; margin also smooth.
4. Round, though small, pits on underside of postparietals.
5. Double tabular facets weakly defined, separated by shallow groove.

*6. Parietal proportions (*f*/*g*) *ca.* 130%; markedly elongate.

7. Ornament on parietal well defined, pits discrete, almost uniform in size, elongated even near centre of parietals.
8. Tabular with upper boss somewhat produced posteriorly.
9. Parietal foramen on distinct midline ridge, bounded by grooves.

Asterisk indicates an autapomorphy of the genus.

The parietal proportions fall outside the range in *Pholiderpeton*, the genus with which it has been most often compared. If the proportions of *P. attheyi* represented a low value for the species, that of *Pteroplax* could (just) fall within the 15% range seen in one species of *Archeria*. It could likewise, on this character alone, be a third species of *Pholiderpeton*. However, in many other skull characters it differs significantly. In characters 2, 4, 5, and 7 it most closely resembles *Archeria*; in character 9 it resembles *Proterogyrinus*.

In 1970 Panchen estimated the postparietal–snout length of *Pteroplax* to be a maximum of about 170 mm. This assumed that it fitted into the allometric series formed by the better known embolomere skulls. Bearing in mind its distinction on skull-table characters from both *Pholiderpeton* and *Palaeoherpeton*, *Pteroplax* may not belong to this series. Had it been a long-snouted genus like *Archeria*, it could have a snout length of as much as 240 mm. A specimen from Newsham (G 24.40), comprising nasals and premaxilla attributed by Boyd (1978) to *Pteroplax* on the character of the ornament, bears teeth which are distinctly different in shape from any specimen of *Pholiderpeton* (figure 8*f*), and I find merit in the attribution. If long-snouted, the elongate skull table of *Pteroplax* is quite unlike the short, broad table of *Archeria*.

I agree with Panchen's original assessment (1964) that a parietal foramen on a distinct midline ridge could be a taxonomically useful character. The centre of the skull table, being greatly thickened in embolomeres, is the part least likely to suffer from *post mortem* distortion. The midline ridge is almost certainly a feature of the intact skull. Holmes (1984) has recently used this character as an autapomorphy of *Proterogyrinus*. Its presence in *Pteroplax* invalidates this unless *Pteroplax* is also a proterogyrinid with this feature characteristic of the family. The ornament of *Pteroplax* is clearly distinct. Both *P. attheyi* and *Pteroplax* are preserved in the same matrix and differences are unlikely to be due to differential preservation. *Pteroplax* also differs from eogyrinids not so much in the shape of the tabular blade (Watson 1926) but in the greater development of the upper boss. The genus rests in the Embolomeri *incertae sedis* as to family.

A second isolated skull table from Newsham (G 13.78) has usually been attributed to *Pholiderpeton attheyi* (as *Eogyrinus*), for example by Watson (1926), Panchen (1970, 1972). However, the current study, drawing attention to characters of the underside of the skull table, suggests that it may be distinguished from that genus on a number of characters. Several other characters suggest that it is more correctly attributed to *Anthracosaurus*, which is now known to occur at Newsham (Panchen 1981). This skull table, and an isolated jugal of *Anthracosaurus*, will be described and discussed in a separate paper (Clack 1987).

The large North American embolomere genera from the Pennsylvanian present a problem for diagnosis. Few of the skull table characters used to define the British genera are available for study. None is available for *Leptophractus* specimens AMNH 6830 and 6831 or the Columbia University specimen (Panchen 1977). *Eobaphetes* is preserved with the skull table visible only in dorsal view and *Neopteroplax* is so heavily restored that very little can be gained from it. It does, however, have strongly fluted parietals. Many of the sutures given by Romer (1963) from the unrestored skull were tentative. In its present condition, it impossible to distinguish original fossil from restoration, a situation that should be rectified as as matter of some importance.

In 1977 Panchen suggested the possible synonymy of *Leptophractus* and *Neopteroplax* and/or *Leptophractus* and *Eobaphetes*. All three have massive anterior dentition, similar in character to *Anthracosaurus*. *Neopteroplax* and *Leptophractus* have, or are inferred to have, a high marginal tooth count with relatively smaller teeth than *Eobaphetes*. In *Eobaphetes* the surangular crest is flat-topped, whereas in *Neopteroplax* the surangular slopes strongly down from the articular to the dentary without forming a crest. Both genera apparently have smaller and more circular orbits than the British genera. None has well-developed lateral-line canals. The parietals of *Neopteroplax* and *Eobaphetes* exhibit the typical irregular pit-and-ridge ornament with coalescing pits of unequal sizes seen in *Pholiderpeton*, although in *Eobaphetes* it is (at least subjectively) finer. In *Eobaphetes* the tabular horn is incipiently biramous, with the upper boss drawn out posteriorly, but the preservation is insufficiently good to compare it with, for example, those of *Anthracosaurus* or *Pteroplax*. The tabular horn is missing in *Neopteroplax*. The three genera show only a few characters to distinguish them from the British eogyrinids or from one another; tooth count and shape of surangular crest. I believe them all to be eogyrinids; although they may eventually emerge as synonymous, until further discoveries are made and *Neopteroplax* is de-restored, I concur with Panchen (1977) and maintain *Eobaphetes* as generically distinct from *Neopteroplax*. I likewise agree that *Leptophractus* is too poorly known to replace *Neopteroplax* as the type of a genus including both animals (as it would if synonymized, having nomenclatural priority). Some material referred to *Leptophractus* represents a large form (AMNH 6830) which may belong to a separate taxon (Hook & Baird 1986) although still an eogyrinid. I do not consider the British and North American eogyrinids to be separable into two subfamilies. Another embolomere specimen from Linton has recently been discovered in the Humboldt Museum (Specimen MB AM 17, A. C. & A. R. Milner, personal communication). This shows a partial skull roof of a small individual, which exhibits an orbital lachrymal. It probably represents a proterogyrinid (Agnew 1984) or an archeriid (Hook & Baird 1986) rather than an eogyrinid.

Although there is now a little more evidence that the British embolomeres were long-bodied, I maintain *Archeria* in a separate family on the grounds of its long-snouted skull and specialized cervical region. The family Eogyrinidae may be diagnosed as follows. Although all the characters are diagnostic, only number 3 is unique to the family and can thus be regarded as an autapomorphy.

1. Skull an elongate triangle in shape, maxillae essentially straight, no lateral flare.
2. Skull proportions fit into allometric series shown in figure 34.

*3. Parietals with well-defined fluting on underside.

4. Double tabular facets for otic capsule well developed, separated by a deep groove.
5. Ornament on parietals well defined, pits unequal in size, coalescing, elongate only near margin.
6. No strongly defined midline ridge or depressions on parietals or postparietals.
7. Tabular horn with lower element blade-like.
8. Lachrymal excluded from orbit by prefrontal–jugal suture (see below).
9. Lachrymal excluded from naris by nasomaxillary suture, or barely reaching naris by a narrow process.
10. Pterygoids denticulate (as compared with *Anthracosaurus*).
11. Two large subequal Meckelian fenestrae.
12. Dentition variable: ectopterygoid with 2 or 3 tusks plus a variable number of smaller teeth, at least 25 marginal teeth.

The revised classification resulting from this study is as follows.

Family Eogyrinidae
  Pholiderpeton scutigerum Huxley
  P. attheyi (Watson)
  Palaeoherpeton decorum (Watson)
  Eobaphetes kansensis Moodie
  Leptophractus obsoletus Cope
  Neopteroplax conemaughensis Romer
  N. relictus Romer
Family Archeriidae
  Archeria crassidisca Cope
  A. victori Stovall
Family Anthracosauridae
  Anthracosaurus russelli Huxley
Genera *incertae sedis* as to family
  Calligenethlon
  Cricotus
  Diplovertebron
  Pteroplax
  Spondylerpeton

Relationships of the embolomere families

The mutual relationships of the anthracosaur families Eogyrinidae have been discussed in a number of recent papers including those by Holmes (1984), Panchen (1985), and Smithson (1985). Holmes included the Proterogyrinidae within the infraorder Embolomeri. Although the vertebrae were not the fully ossified rings as in embolomeres *sensu stricto*, he noted that the intercentra of *Proterogyrinus* were almost certainly completed in cartilage dorsally to produce effectively embolomerous units. Although this was probably also the case in the anthracosaurs *Gephyrostegus* (Carroll 1970) and *Eoherpeton* (Smithson 1985), other similarities unite them with fully embolomerous forms and the present author, Panchen and Smithson accept this grouping, even though it renders the term 'embolomere' somewhat ambiguous. The term Herpetospondyli (Panchen 1975, 1980) lapses (Holmes 1984; Panchen 1985). The three above authors agree in placing the Eogyrinidae as the sister-group of the Archeriidae, but there is disagreement concerning the relationships of the Anthracosauridae. Two of the authors (Holmes, Smithson) place the Anthracosauridae as the sister-group of the two former families with the Proterogyrinidae as the sister-group of all three; the third (Panchen) places the Anthracosauridae as the sister-group of the other three embolomere familes. The conclusions drawn by the three previous authors must now be reassessed in the light of new information from *Pholiderpeton*.

First I shall examine the autapomorphies of each group, and if necessary propose alternatives which I feel are more secure. Holmes and Smithson used chisel-shaped teeth as an autapomorphy of *Archeria*, although this shape is found incipiently in *Proterogyrinus* (Holmes 1984) and in the Eogyrinidae (above). The characters of elongate snout and numerous marginal teeth are preferable to define *Archeria*. Smithson used a deep descending flange of the quadrate ramus of the pterygoid to characterize the Eogyrinidae, but this character is also found in *Proterogyrinus* (Holmes 1984). Panchen used the number of premaxillary teeth (3–4) to characterize the Eogyrinidae but four are also found in *Archeria* (AMNH 7117; J.A.C., personal observations). Holmes used the intertemporal–postorbital suture as a character uniting the eogyrinids, but this character is also found in *Anthracosaurus*. The supraneural canal is present in *Pholiderpeton* so that its loss cannot be used to unite eogyrinids, as Holmes did. I have employed fluting on the underside of the parietals as an alternative. The skulls of eogyrinids form a uniform growth series, expressed in figure 34. This is clearly distinct from that of *Archeria* and *Anthracosaurus*. More information about other embolomere skulls in the future might make this statistically significant, and an autapomorphy which could be defined mathematically.

I have used three characters as autapomorphies of *Proterogyrinus*. The finger-like lower blade of the tabular horn is distinguishable from the flattened blade in other embolomeres, although this is arguably the primitive condition of this element in all embolomeres. Only further discoveries of embolomere tabular horns could confirm this. Although the expanded cleithrum was regarded by Holmes (1980) as a primitive character, by comparison with other anthracosaurs (e.g. *Gephyrostegus*) (Carroll 1970) I believe the expansion to be unique to *Proterogyrinus*. The nasals are excluded from the naris in *Proterogyrinus*, a character not seen in any other embolomere. Holmes also used coronoid dentition (present on anterior coronoid, but absent on the posterior two) and the character of the parietal foramen (situated on a midline ridge) as autapomorphies of *Proterogyrinus*. The latter, as noted above, is found in *Pteroplax* and is therefore invalid. Coronoid teeth are absent in *Gephyrostegus* (Carroll 1970); thus their presence in *Proterogyrinus* is likely to be a primitive retention (as in *Anthracosaurus*) rather than the loss from the posterior two being a derived character.

Several autapomorphies define *Anthracosaurus russelli*, including the consolidated palate lacking denticles, single large Meckelian fenestra and others documented in Panchen (1977, 1984). I have added the development of a lateral surangular shelf (Panchen 1981) to those listed by Holmes, Panchen and Smithson, but have omitted others. The biramous tabular horn used by Panchen is incipient in all embolomeres. The greater development of the upper component is matched by that in *Pteroplax* and probably *Eobaphetes*; at the same time, if I am correct in my attribution of skull table G 13.78 to *Anthracosaurus* (Clack 1987), it is restricted to *A. russelli*. The dorsally expanded quadrate cited by Holmes is also seen in *Pholiderpeton*.

Next follows an examination of the characters used by the three authors to define each node in turn. All three authors pair the Eogyrinidae and Archeriidae as sister-groups, though the characters which they use differ somewhat. Smithson used a single character: long prefrontal–jugal suture excluding the lachrymal from the orbit. To this Panchen added two: trunk vertebrae fully embolomerous (i.e. intercentra fully ossified into rings), and about 40 presacral vertebrae. The first of these three is reasonably secure, although as mentioned in the text, *Palaeoherpeton* may be an exception. Specimen MB AM 17 certainly is if it pertains to either of these two families. Of the postcranial characters cited by Panchen, the first is known to be true of both, and the second has a high probability. However, neither is known in *Anthracosaurus*. Holmes's characters do not necessarily constitute synapomorphies to unite the two families. He did not present a cladogram but a character distribution, and of five, cited three characters which he recognised as paralleled by other groups. Coronoids lacking tusks are found in *Gephyrostegus*. The lachrymal is excluded from the orbit in *Eoherpeton*. This character is similar to that cited by Smithson and Panchen, but by their more precise definition (long prefrontal–jugal suture) it is rather different from that in *Eoherpeton*. The reservations noted above still apply. A jugal exposed in the jaw margin is now known not to be characteristic of eogyrinids; its appearance is confined to *Palaeoherpeton*.

Holmes's fourth character, a jaw which is deep at the angle, is on investigation, somewhat subjective. By comparison with *Proterogyrinus*, the description seems justifiably applied to *Pholiderpeton*, in particular *P. attheyi* which possesses a massive lower jaw. To assess the character more objectively, however, I made a series of measurements of all the known complete embolomere jaws, calculating depth (maximum depth of a line at right angles to one joining the anterior margin of the adductor fossa and the back of the articular, i.e. excluding the surangular crest) as a percentage of length (maximum length along the jaw ramus between symphysis and the back of the articular). The figures were as follows, in order of size: *Proterogyrinus* (Holmes 1984), 19.2%; *Neopteroplax* (Romer 1963), 22.35%; *Archeria* (personal observations) 23.3%; *Pholiderpeton scutigerum*, 25.7%; *Eobaphetes* (Panchen 1977), 25.8%; *P. attheyi* (Panchen 1972), 26.5%. The eogyrinids *Pholiderpeton* and *Eobaphetes* thus form a consistent group, but the eogyrinid *Neopteroplax* falls some distance from them, being about half way between *Proterogyrinus* and *Pholiderpeton* in these terms. *Archeria* may represent a special case in that, because it is long-snouted, its skull proportions are rather different from those of eogyrinids and a proportionately longer jaw would be expected. This makes the relative depth of the jaw more difficult to assess. It is probably safer to omit this character from any cladogram of the embolomeres. Loss of the ventral ramus of the tabular horn, used by Holmes (1984), is now known to be untrue of both eogyrinids and archeriids. The characters used by Panchen and Smithson are thus the most secure of those used to unite these two families, although each is subject to some reservations.

At the next node, Smithson and Holmes agree in placing *Anthracosaurus* as sister-group of the other two, whereas Panchen placed *Proterogyrinus* in this position. Smithson used two characters to support his scheme; 40 presacral vertebrae and tuskless vomers. The first is unknown in

Anthracosaurus, and the second unknown in *Archeria*, *Proterogyrinus* and *Eoherpeton*. It may thus be characteristic of all embolomeres, or of all embolomeres plus *Eoherpeton*. It may conceivably be restricted to the Eogyrinidae and Anthracosauridae. Holmes cited five characters, three of which he recognized as paralleled elsewhere. A fully ossified braincase also occurs in loxommatids and its taxonomic status is doubtful. Absence of parasymphysial tusks is now known to be untrue of *Pholiderpeton*. Two postcranial characters (intercentra ossified dorsally to form rings, and a dorsal suture absent from the pleurocentra) cannot now be confirmed in *Anthracosaurus*. The final character of dentition absent on coronoids one and two is found in *Gephyrostegus*.

Panchen used three characters to unite the Proterogyrinidae with the Eogyrinidae and Archeriidae. Presence of a surangular crest is true for all three and is absent in *Anthracosaurus*; thus it is secure. The descending flange of the pterygoid, as defined, is untrue of *Pholiderpeton scutigerum*, but if the character is redefined as 'quadrate ramus of pterygoid expanded ventrally' it might be employed in this way. Unfortunately for this scheme, the character is also found in *Eoherpeton* (Panchen 1975) and may be characteristic of all embolomeres plus *Eoherpeton*. An oblique glenoid of the scapulocoracoid is true of all three but is unknown in *Anthracosaurus*.

All three authors have made certain assumptions about the postcranial skeleton of *Anthracosaurus*. Because nothing is known about it, I suggest that postcranial characters be omitted from this part of the analysis and I have produced a new cladogram based on the skull and braincase alone. When this is done, the eogyrinids are found to share three characters uniquely with *Anthracosaurus*, the first two of which are unusual and found nowhere else either among embolomeres, anthracosaurs or other fossil amphibians. They are: (i) a digitiform process of the opisthotic; (ii) a mesially directed flange on the exoccipital; and (iii) postorbital–intertemporal suture. Thus a sister-group relationship between the Eogyrinidae and Anthracosauridae is supported by a greater number of more secure characters than one between the Eogyrinidae and Archeriidae, which is supported by only one which requires no qualification.

In the past (Romer 1963; Panchen 1970), two genera were included within the Anthracosauridae which are now placed within the Eogyrinidae (Panchen 1977). These are *Leptophractus* and *Eobaphetes*, and they were placed among the Anthracosauridae primarily because of their massive dentition and reduced tooth count. *Neopteroplax*, an eogyrinid, has large premaxillary teeth, a conspicuous canine peak and reduced tooth count, but with the full description of *Anthracosaurus* (Panchen 1977, 1981), it was clear that neither *Leptophractus* nor *Eobaphetes* possessed any of the unique characters which define the Anthracosauridae. It seems likely that the potential for enlargement of the teeth with reduction of tooth count was present in both families and a sister-group relationship could help to explain why they have been confused in the past. Consolidation of the skull-table–cheek 'kinetism' at the postorbital–supratemporal suture has occurred in both, but has been elaborated to include the squamosal–intertemporal suture in some anthracosaurids. It is possible that this has also occurred in *Neopteroplax*; Romer's (1963) drawings and description give no hint that the skull roof was 'kinetic' or that the squamosal–intertemporal suture was not an interdigitating one. Consolidation of the skull roof could well be linked with enlargement of the teeth.

Archeria is placed at the next node. This relationship is supported by one character and may be regarded as the weakest link in this arrangement. It is supported by the character of the lower component of the tabular horn, which is blade-like. This relationship implies either a reversal to an orbital lachrymal in *Anthracosaurus*, or its parallel development in eogyrinids and archeriids. Further discoveries may confirm the embolomerous condition of the vertebral column of *Anthracosaurus* and would help to support the grouping (as in Smithson's scheme), but it must be omitted from consideration at this stage. The same argument must be applied to tuskless vomers, used by Smithson at this node.

To unite the four embolomere families into a monophyletic group, two characters can be used without qualification. These are: (i) tabular horns differentiated into upper and lower components, separated by a notch or pit; and (ii) two large Meckelian fenestrae, or a derivation thereof. The first is essentially the same as one used by Holmes at the same node. The second was employed by Holmes, Panchen and Smithson. Others may be added, but in each case exceptions can be found or qualifications noted. Some may be explained by reversals to a more primitive condition; in others, the character is unknown for some of the animals in question.

Two characters are found in all but *Anthracosaurus*: (i) development of a surangular crest; and (ii) a ventrally expanded quadrate ramus of the pterygoid. A shallow lower jaw and unexpanded quadrate ramus are seen in other more primitive tetrapods, such as *Megalocephalus*, and the shallow lower jaw also in *Crassigyrinus* and the anthracosaur *Eoherpeton*. In *Anthracosaurus*, both character reversals could be associated with the comparative shallowness of the skull as compared with other embolomeres, which I interpret as a derived condition. The opisthotics bear free lateral processes in *Proterogyrinus*, *Pholiderpeton* and *Anthracosaurus*. In the latter two they are characteristically digitiform, whereas in *Proterogyrinus* they are broad-based, but presumably gave rise to the digitiform condition. The condition in *Archeria* is unknown at present. In all except *Archeria* the tabular bears double facets for reception of the opisthotic. In *Archeria* the anterior facet is not developed and the tabular resembles that of *Eoherpeton* (Smithson 1985). Double tabular facets are, however, also seen in *Crassigyrinus* (Panchen 1985) and may thus be characteristic of a larger group or developed convergently in *Crassigyrinus*. The state of the vomers has been commented on above as a possible synapomorphy at this level and it has been included in parentheses until further information is available.

Three characters of the postcranial skeleton are also included here but with the caveat that all are unknown in *Anthracosaurus*. They are, however, known and consistent in each of the other three groups. They are: (i) pleurocentra complete or almost completely ossified rings; (ii) oblique glenoid of the scapulocoracoid (as in Smithson 1985); and (iii) humerus with a low degree of twist and only slightly helical condyle (Smithson 1980). These three may be developed in association with primarily aquatic locomotion and would perhaps be unexpected in *Anthracosaurus*, with its rather terrestrial mien (see also Panchen 1977).

If *Anthracosaurus* were found to have been embolomerous with both pleurocentra and intercentra ossified as complete rings, the above scheme of relationships would be supported. However, even if it were found to possess incompletely ossified centra, the relationship may not necessarily be refuted. In all the genera of anthracosaur in which the vertebrae are known, the configuration is gastrocentrous, and in each case the centra were probably completed in cartilage to give what would be, in effect, an embolomerous unit (Panchen 1985). Discovery of this condition in *Anthracosaurus* would perhaps show more about the usefulness of vertebral characters in taxonomy than about the relationships of embolomeres. The fully embolomerous condition could easily be derived by increased ossification from the configuration found in *Proterogyrinus*. It may easily have developed, along with the elongated presacral column, in parallel in the eogyrinids and archeriids. Similar reasoning may be applied to the characters of the pectoral limb, cited above, which may be associated with anguilliform locomotion.

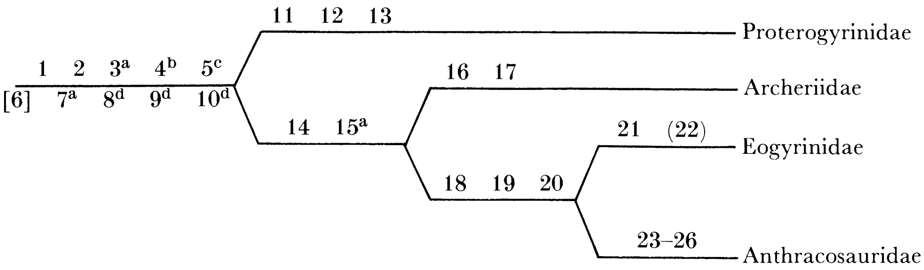


FIGURE 36. Cladogram of embolomere families (for characters, see text).

The cladogram derived from these characters is presented in figure 36, and the characters listed below.

1. Tabular horns biramous, differentiated into upper and lower components, separated by a notch or pit.

2. Two large Meckelian fenestrae, or a derivation thereof.

3^a. Surangular crest usually developed.

4^b. Tabular with double facets for reception of opisthotic.

5^c. Opisthotic with free lateral processes.

[6. Vomers tuskless.]

7^a. Processus alaris of jugal contacts pterygoid.

8^d. Pleurocentra ossified as rings.

9^d. Oblique glenoid of scapulocoracoid.

10^d. Humerus with low degree of twist; condyle only slightly helical.

11. Tabular horn with lower component short, distinctively narrow and finger-like.

12. Expanded cleithrum.

13. Nasals excluded from naris by premaxillary–lachrymal suture.

14. Lower component of tabular horn blade-like.

15^a. Lachrymal excluded from orbit by long prefrontal–jugal suture.

16. Skull elongate in snout region.

17. Numerous marginal teeth, about 60.

18. Digitiform process of opisthotic.

19. Medially directed flange of exoccipital.

20. Postorbital–intertemporal suture.

21. Parietals strongly fluted on underside.

(22. Skulls fit into growth series detailed in figure 34)

23. Massive dentition, reduced in number; two premaxillary teeth.

24. Single large Meckelian fenestra, produced from confluence of two.

25. Palate reinforced; pterygoids fused in midline; pterygoids cover palatines; pterygoids lacking denticles.

26. Lateral shelf on surangular.

Key:
[a] Implied reversal in *Anthracosaurus*.
[b] Implied reversal in *Archeria*; also present in *Crassigyrinus*.
[c] Character unknown in *Archeria*.
[d] Unknown in *Anthracosaurus*.
[ ] Character distribution uncertain.
( ) Definition of character incomplete (see text).

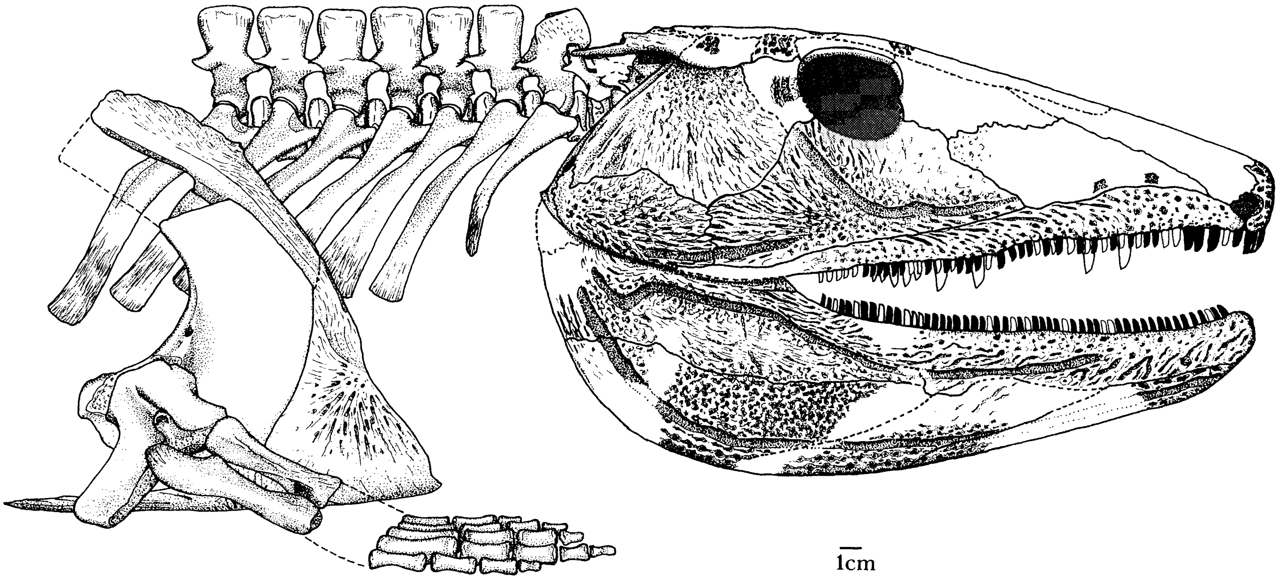


FIGURE 37. Reconstruction of head, cervical and pectoral region of *Pholiderpeton scutigerum*, from holotype.

This work would not have been possible without the cooperation and patience of the staff of Cliffe Castle Museum, Keighley, who allowed me to borrow the holotype of *Pholiderpeton scutigerum* for the duration of the work. I also thank the staffs of the following institutions for permission to borrow and, where necessary, prepare specimens in their care: the Hancock Museum, Newcastle upon Tyne; the Museum of Comparative Zoology, Harvard University; the British Museum (Natural History); and the American Museum of Natural History.

Dr A. L. Panchen has been a most patient and helpful guide and supervisor during the completion of this work and my particular thanks go to him, Dr T. R. Smithson and Dr A. R. Milner for invaluable and stimulating discussion.

During my visit to the United States in 1980, I was shown courtesy and kindness by numerous people, including Dr D. Baird of Princeton University; Dr D. Brinkman, then of the Museum of Comparative Zoology, Harvard; Dr R. Carroll of the Redpath Museum, McGill University; Dr E. Gaffney of the American Museum of Natural History; D. N. Hotton III of the Smithsonian Institution, Washington, D.C.; and Dr K. Thomson, of the Peabody Museum, Yale University, all of whom allowed me unlimited access to their collections.

Dr R. Holmes, Dr A. L. Panchen and Dr T. R. Smithson generously allowed me to have copies of the relevant parts of the manuscripts of their most recent papers before publication, and Mr M. J. Boyd and Dr P. A. Rose gave their permission to quote from their unpublished

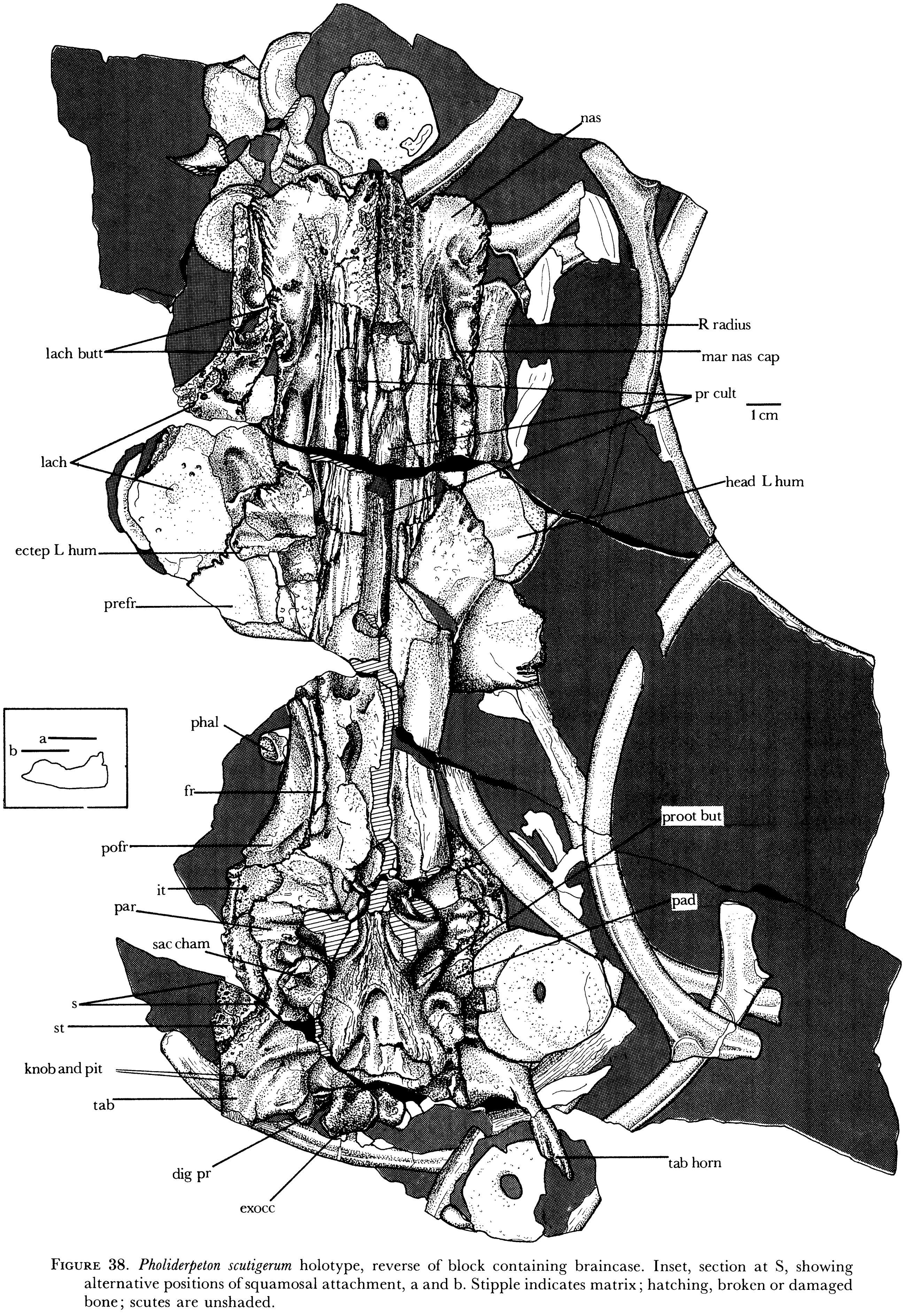
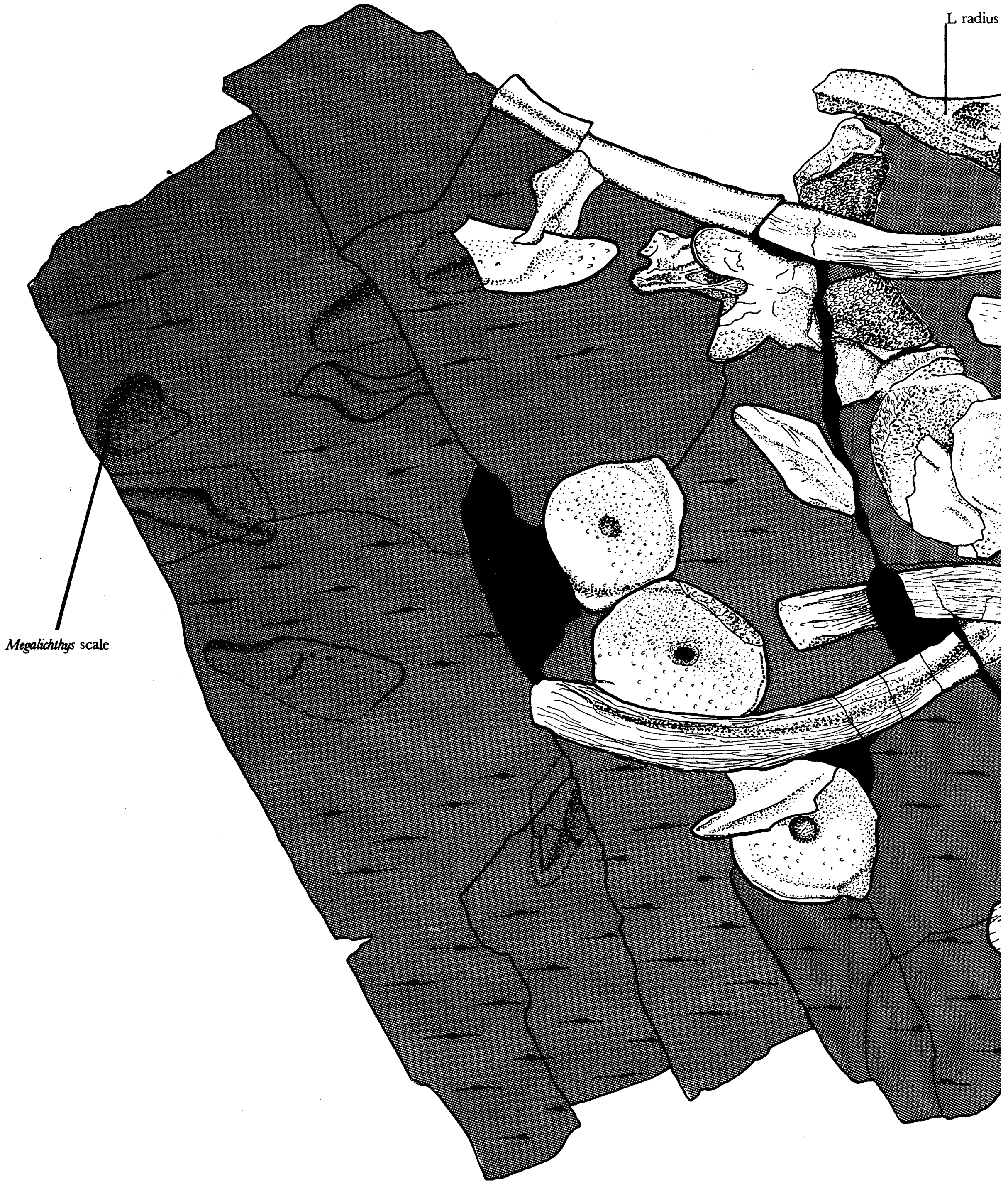


FIGURE 38. *Pholiderpeton scutigerum* holotype, reverse of block containing braincase. Inset, section at S, showing alternative positions of squamosal attachment, a and b. Stipple indicates matrix; hatching, broken or damaged bone; scutes are unshaded.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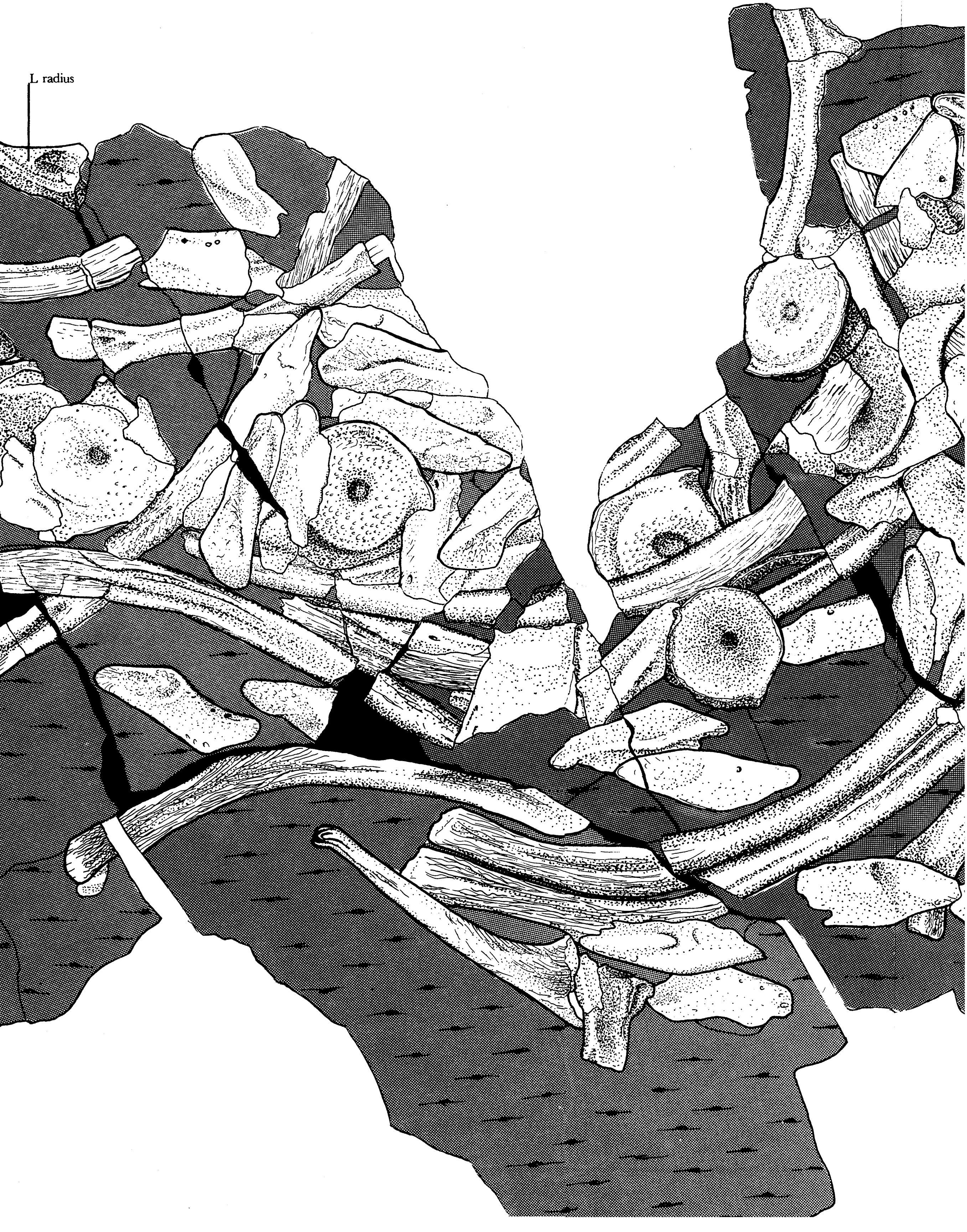
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FIGURE 39. *Pholiderpeton scutigerum* holotype, obverse of block containing braincase and small isol
Stipple indicates matrix.

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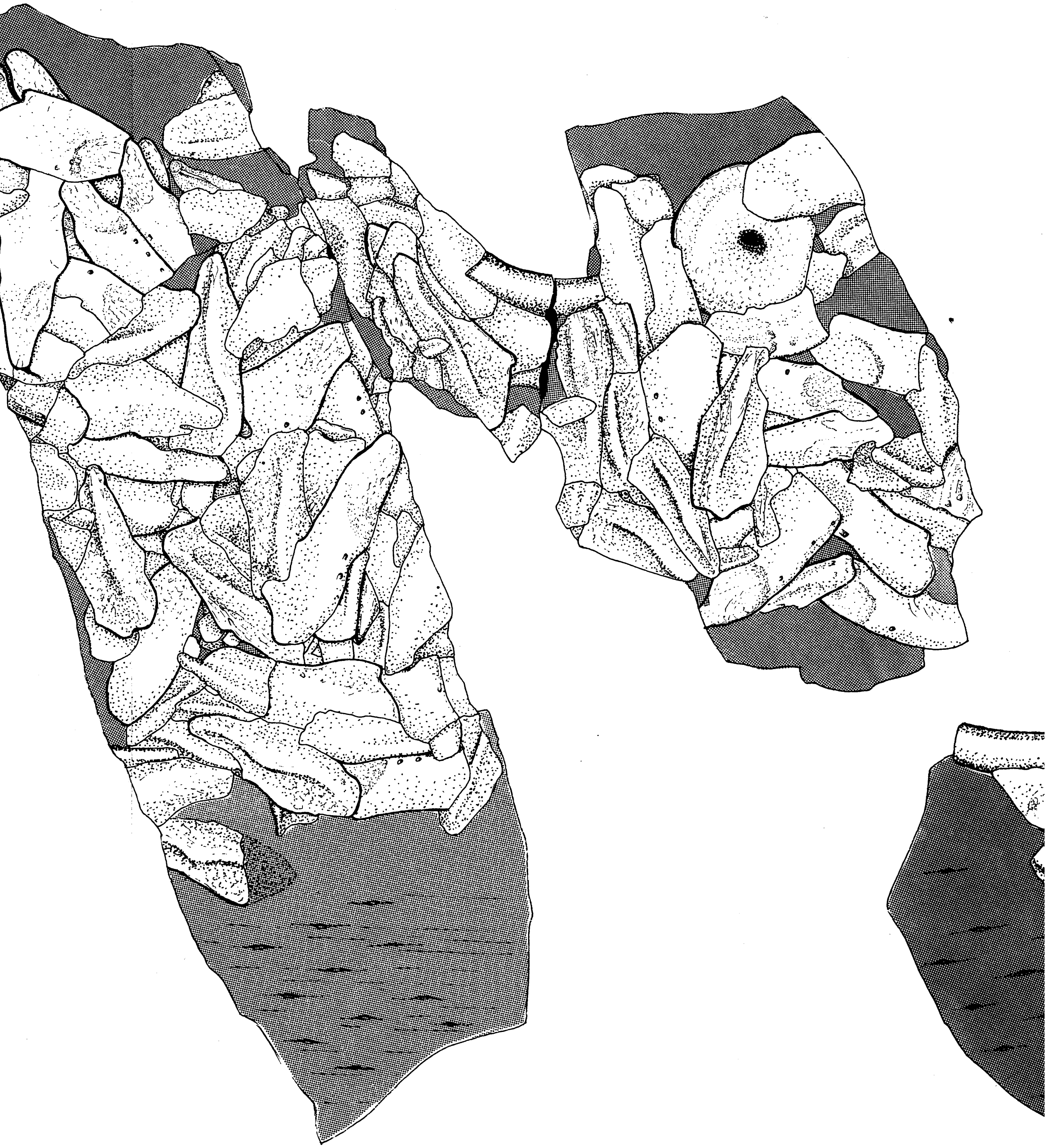

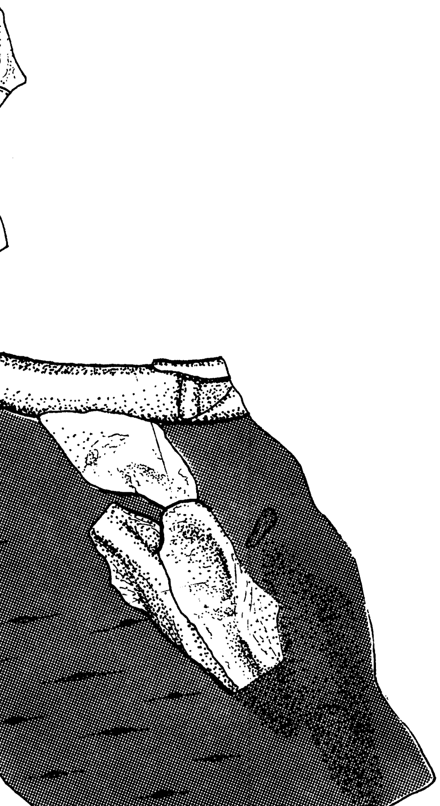

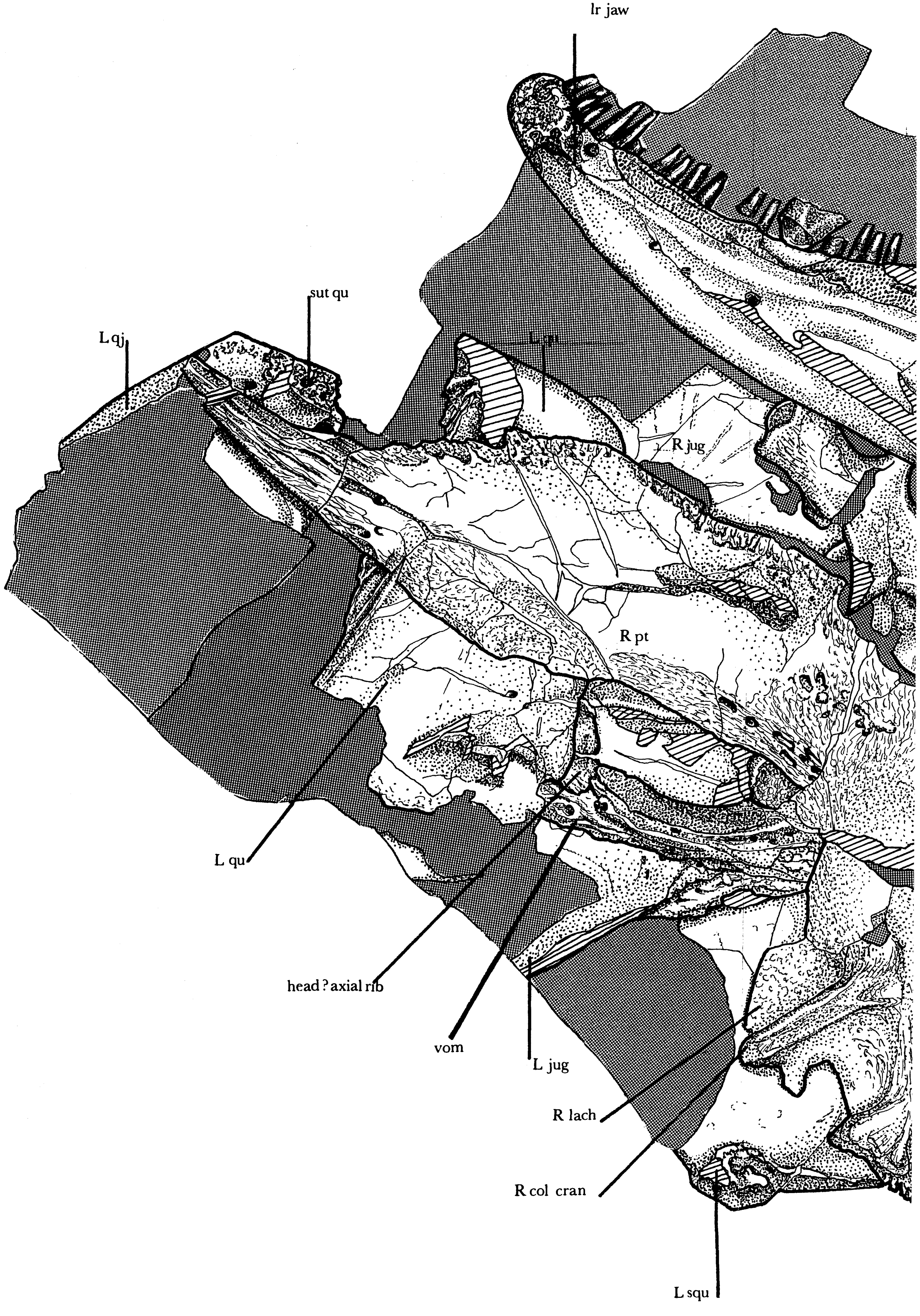
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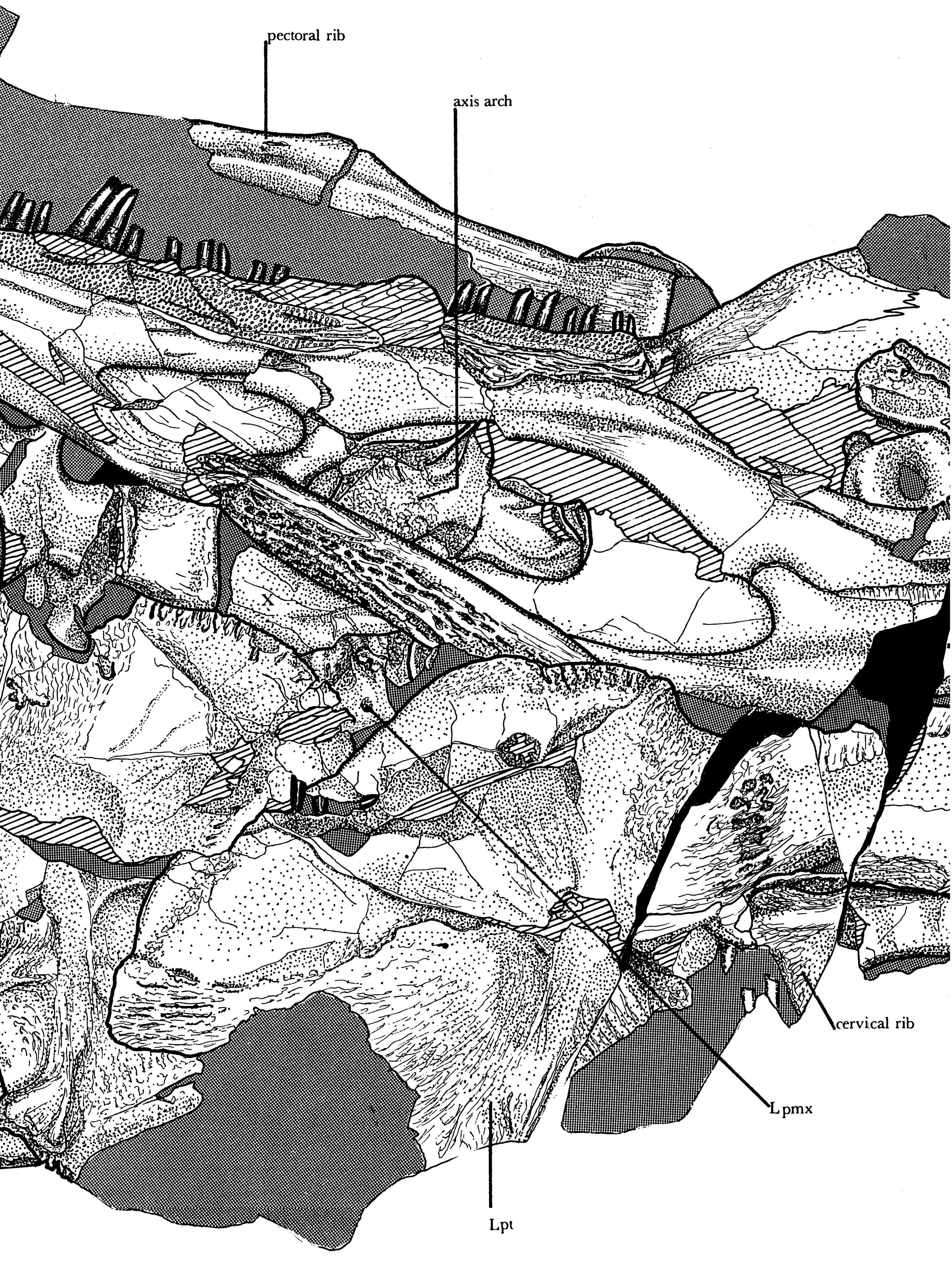
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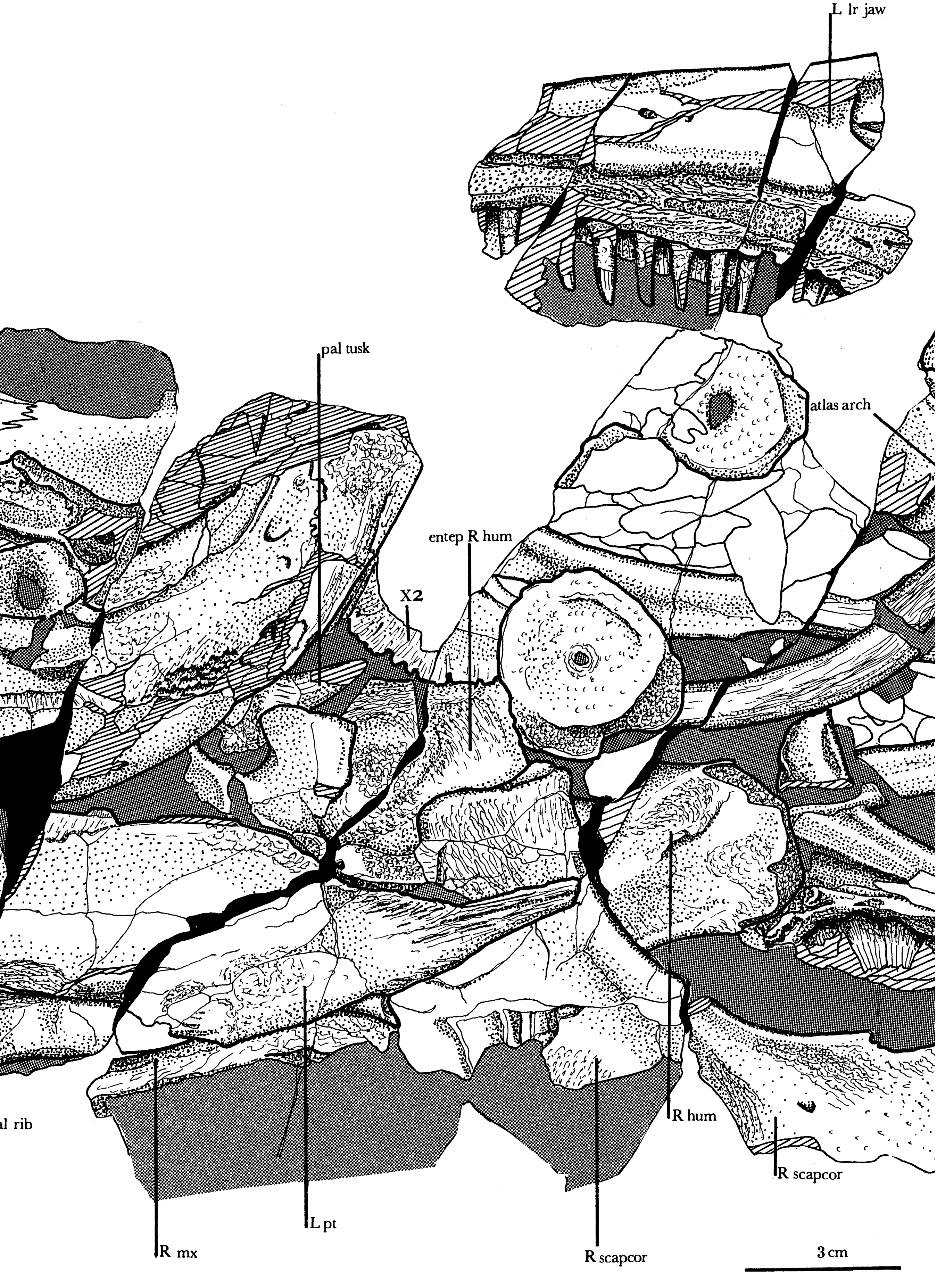
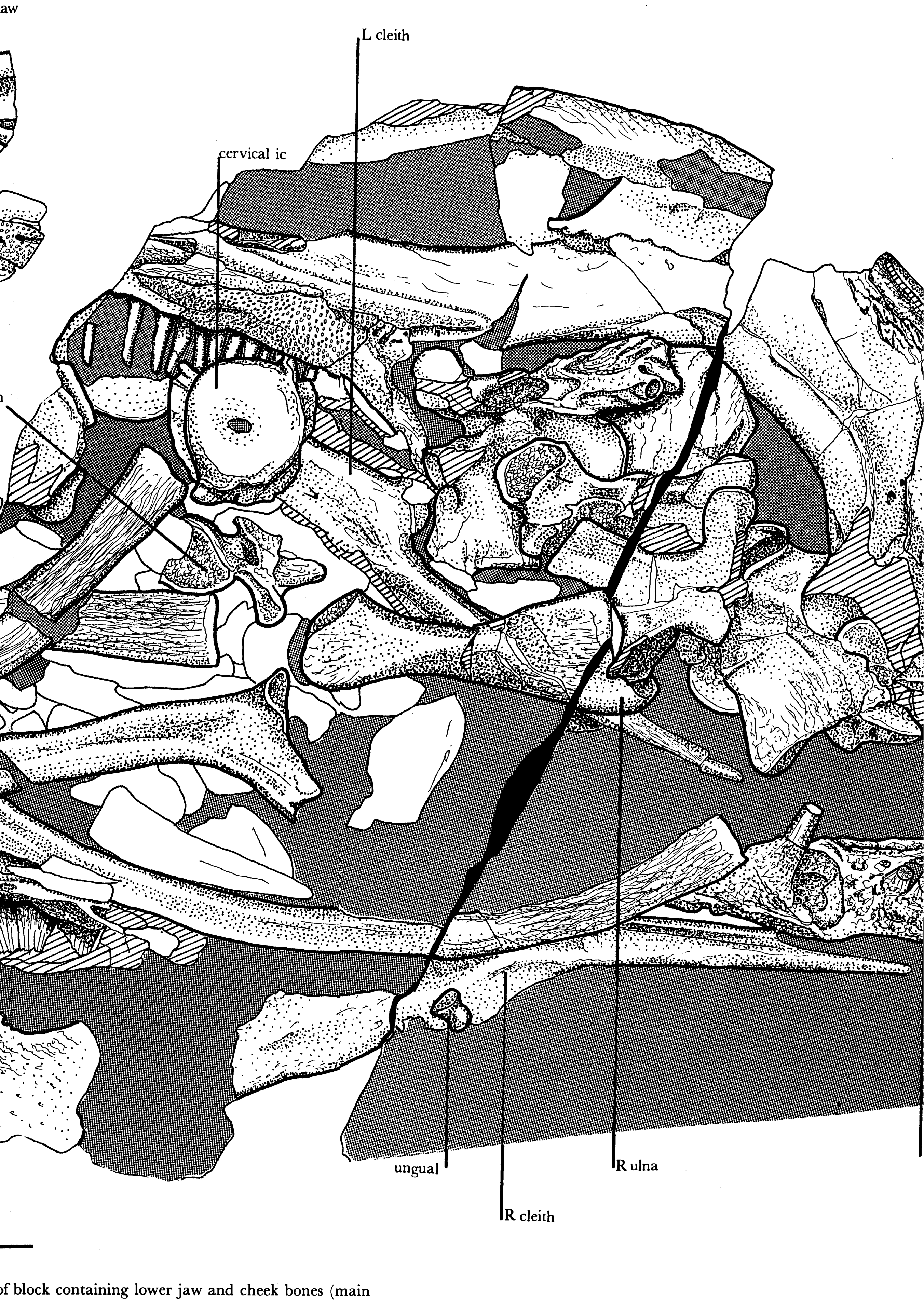


FIGURE 40. *Pholiderpeton scutigerum* holotype, reverse of block c
skull block). Stipple indicates matrix; hatching, broken o



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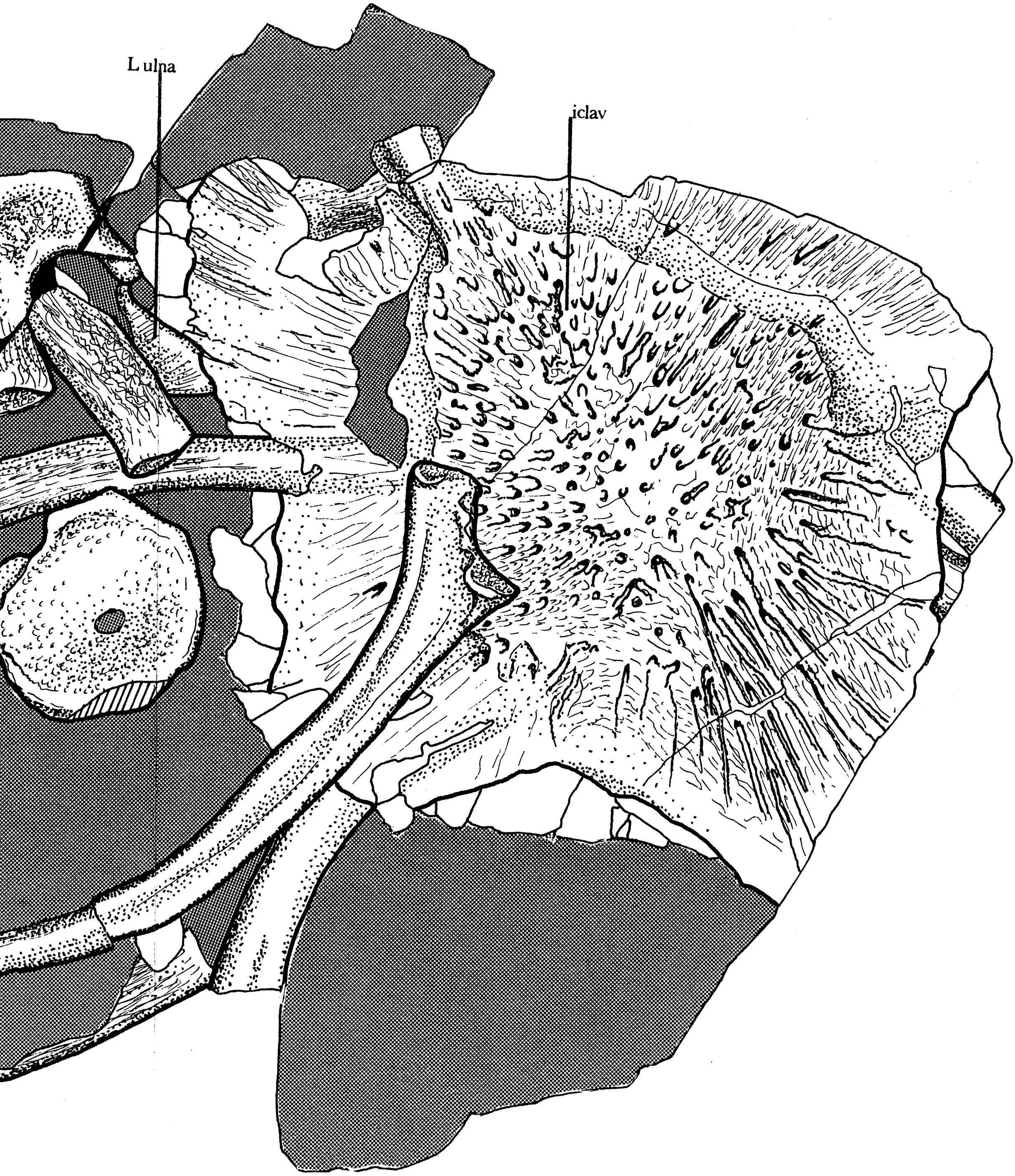
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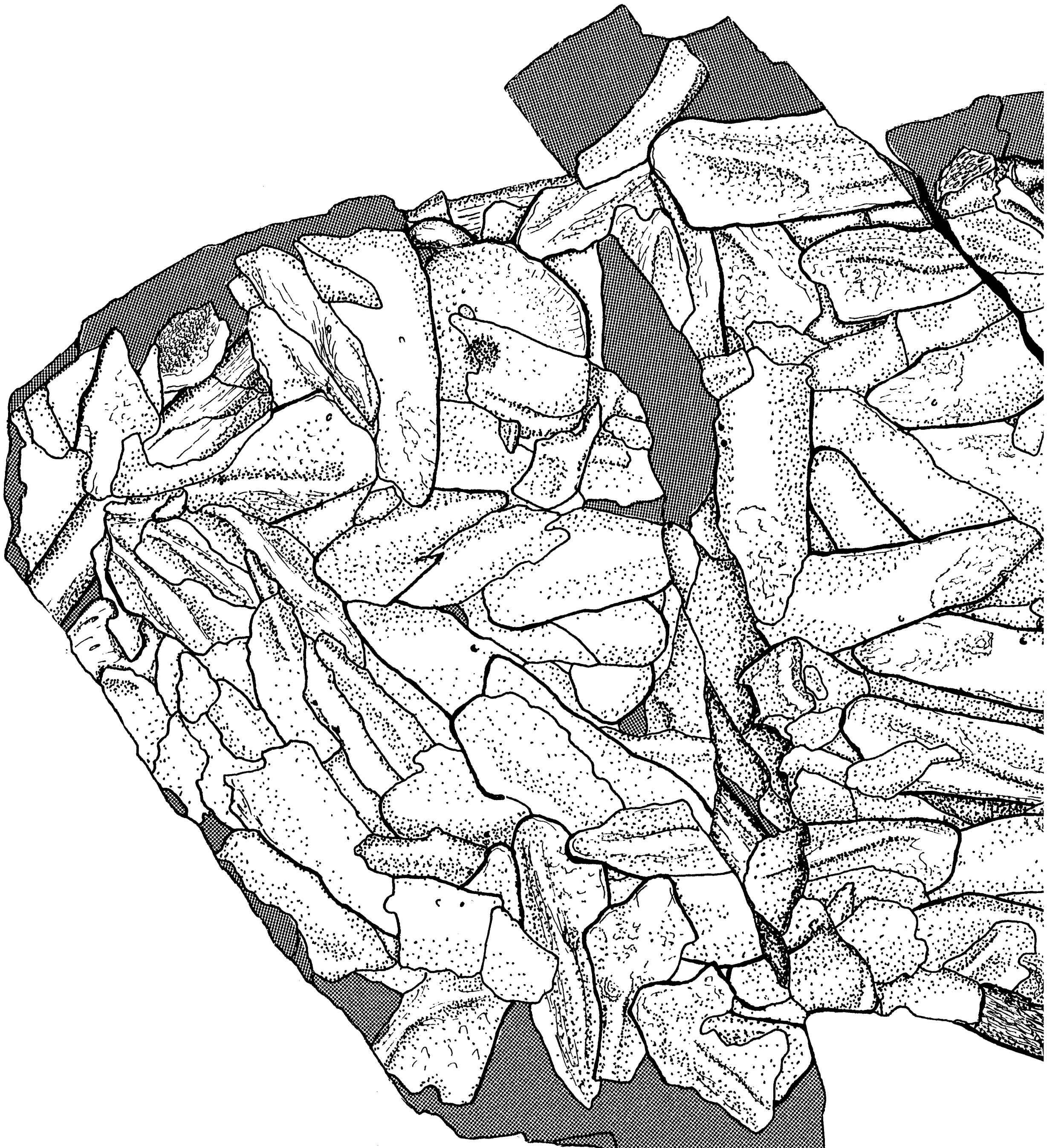

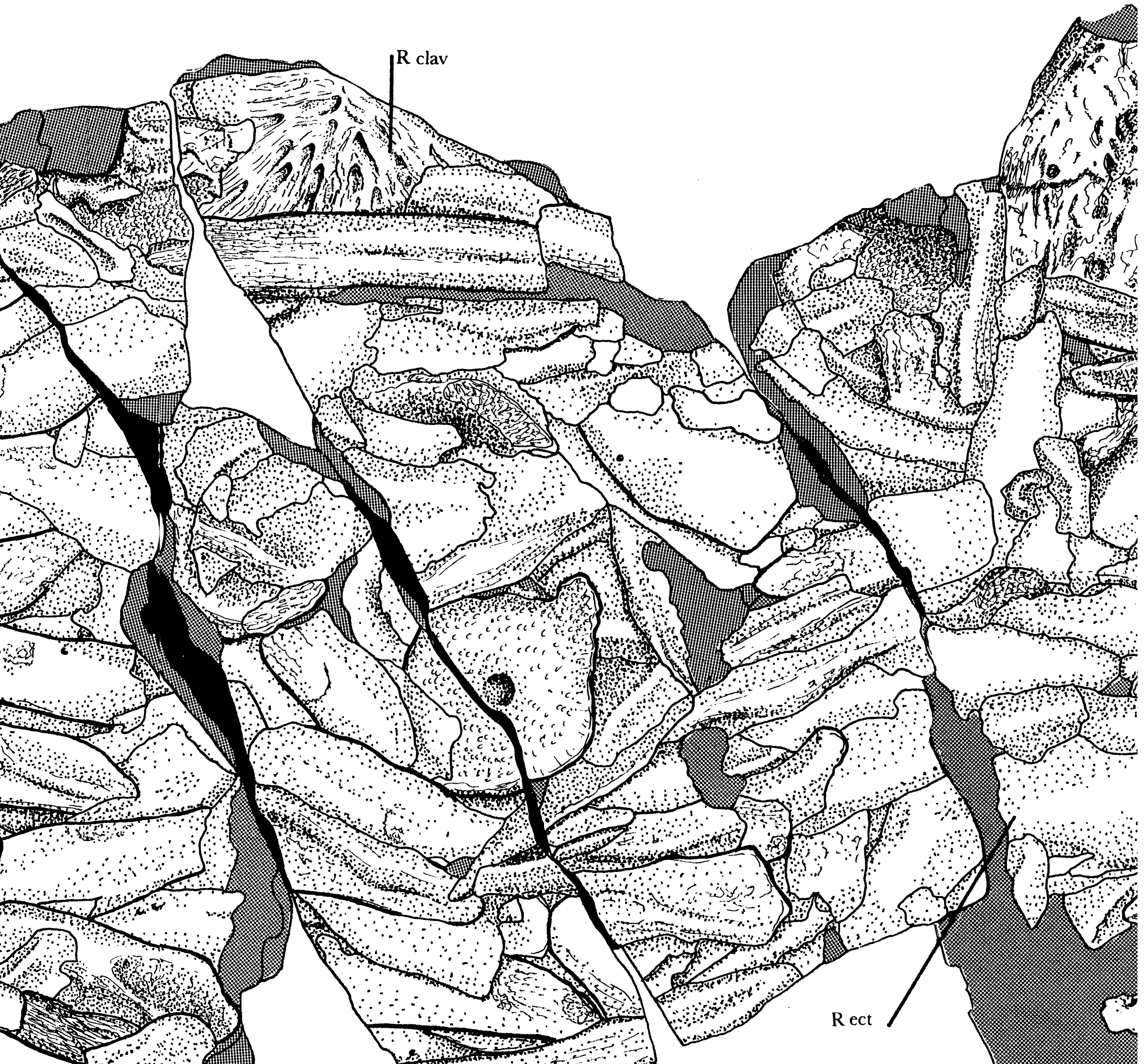
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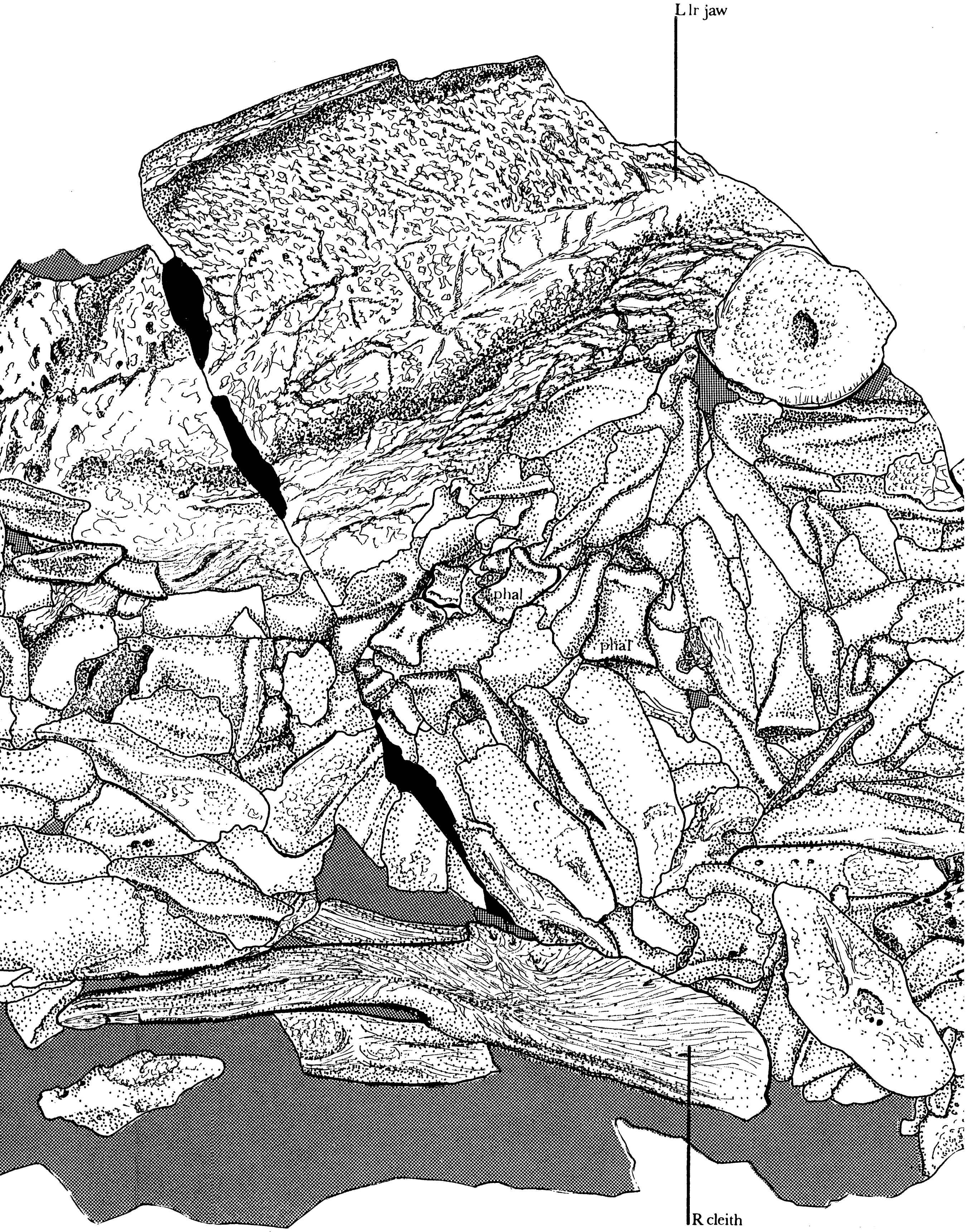
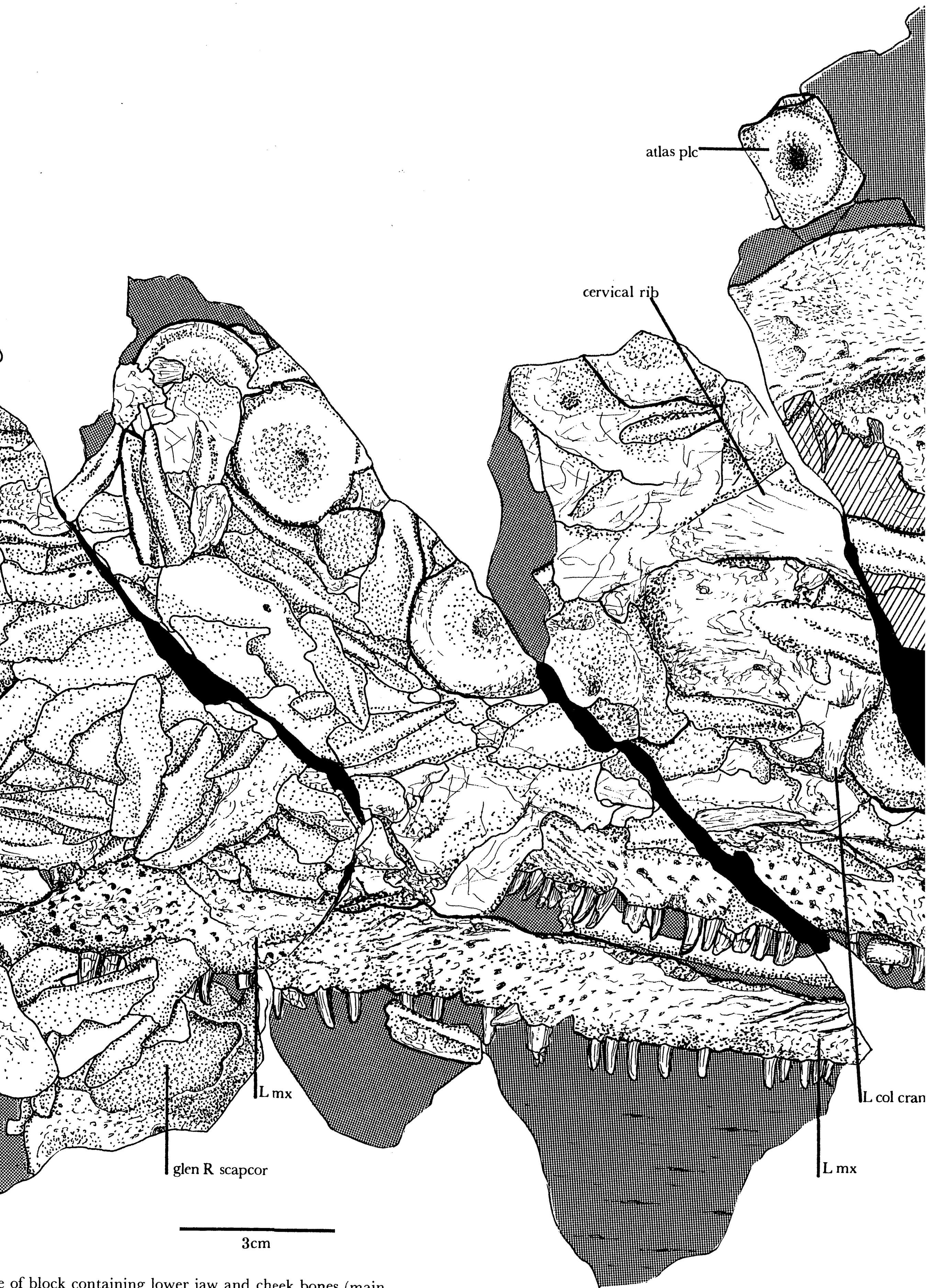


FIGURE 41. *Pholiderpeton scutigerum* holotype, obverse of block
skull block). Stipple, matrix; hatching, b



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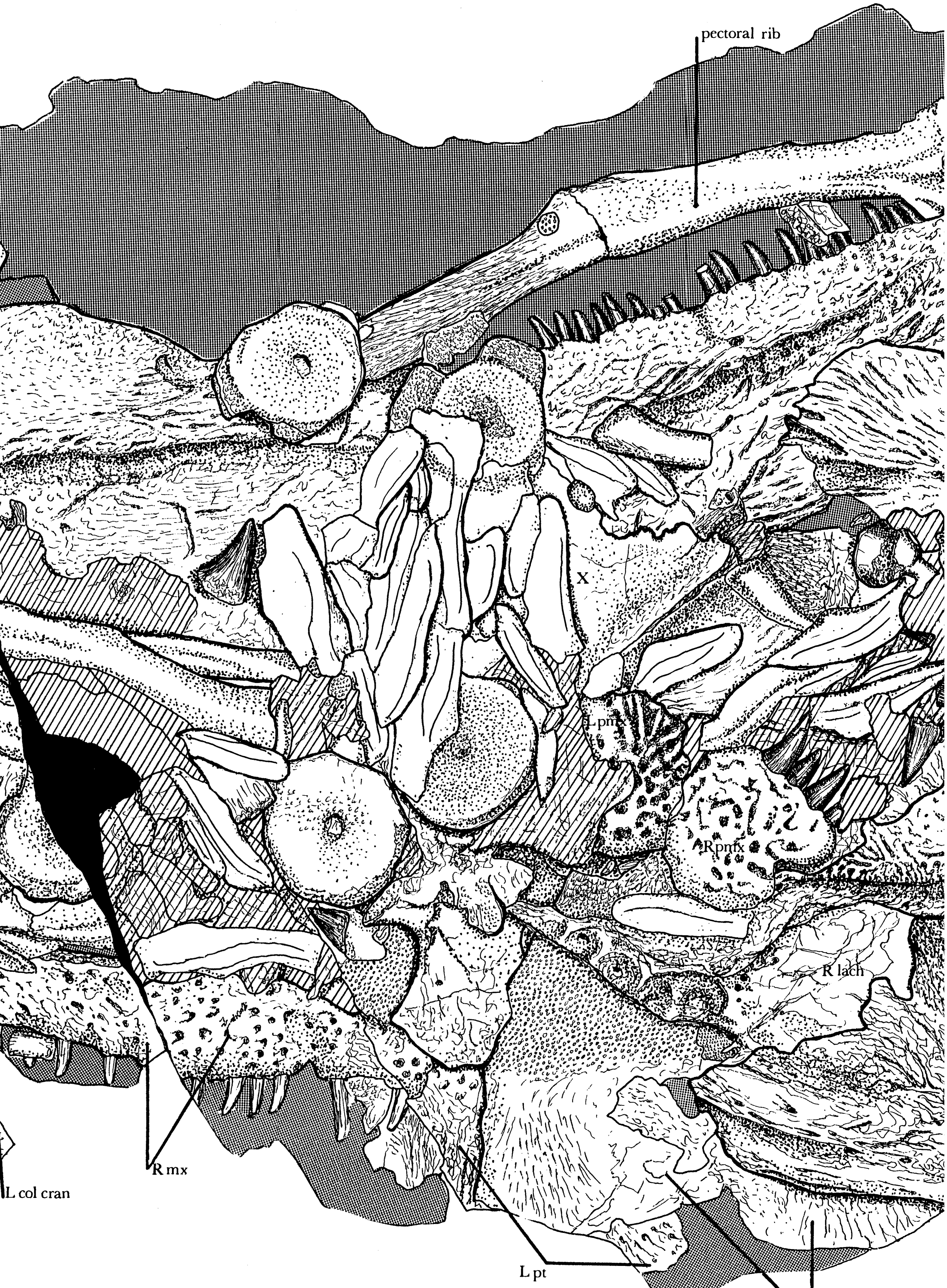
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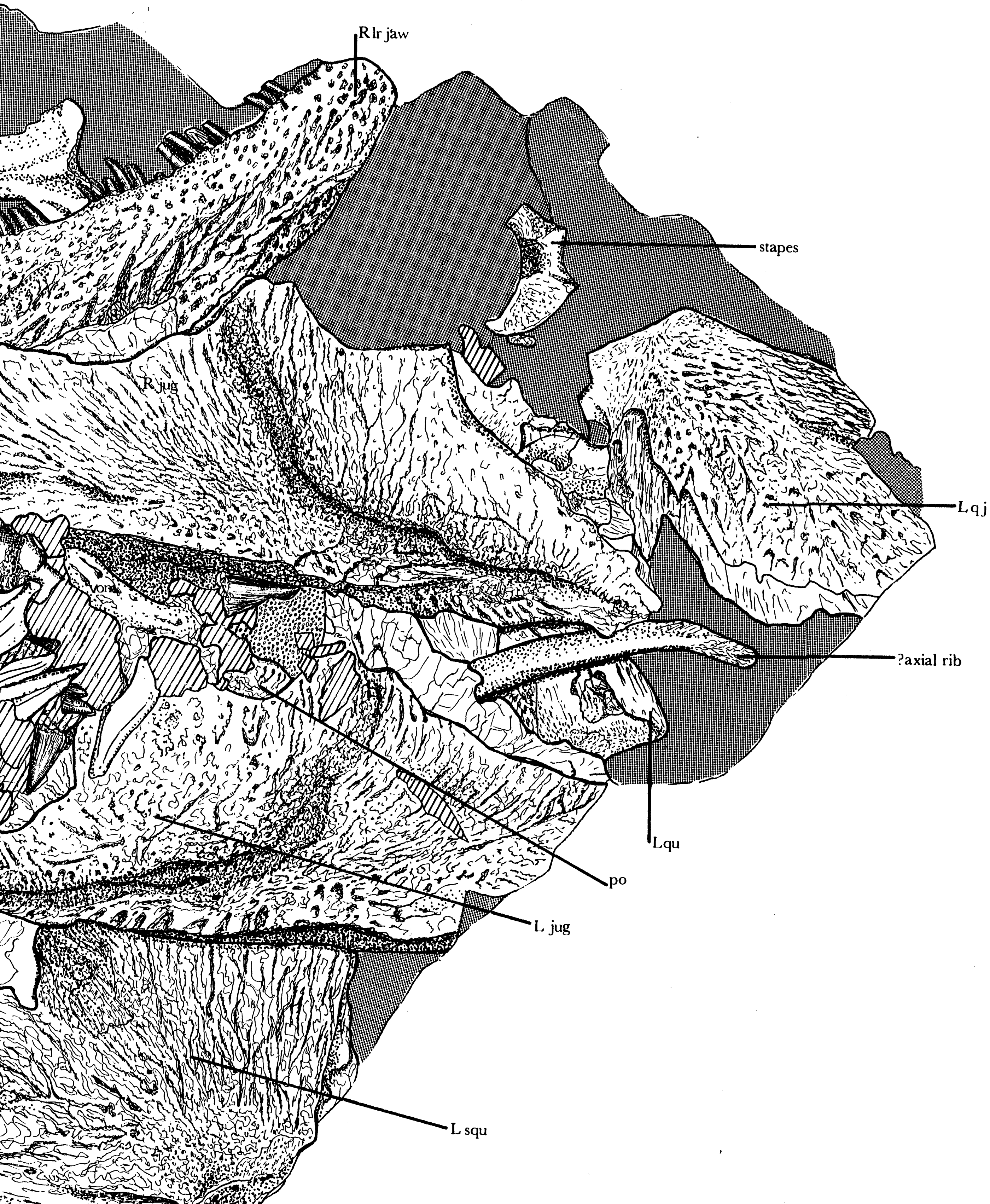
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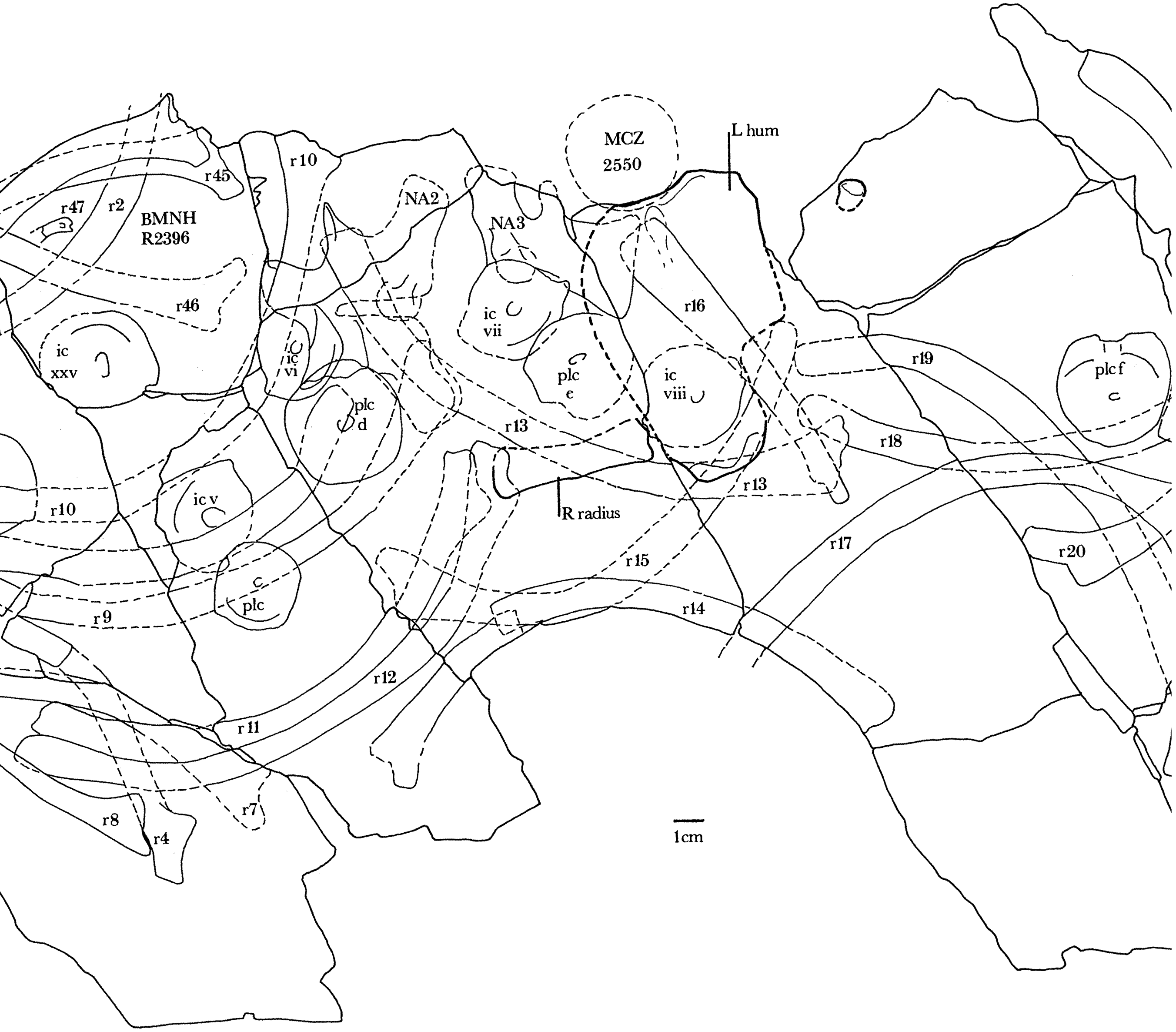
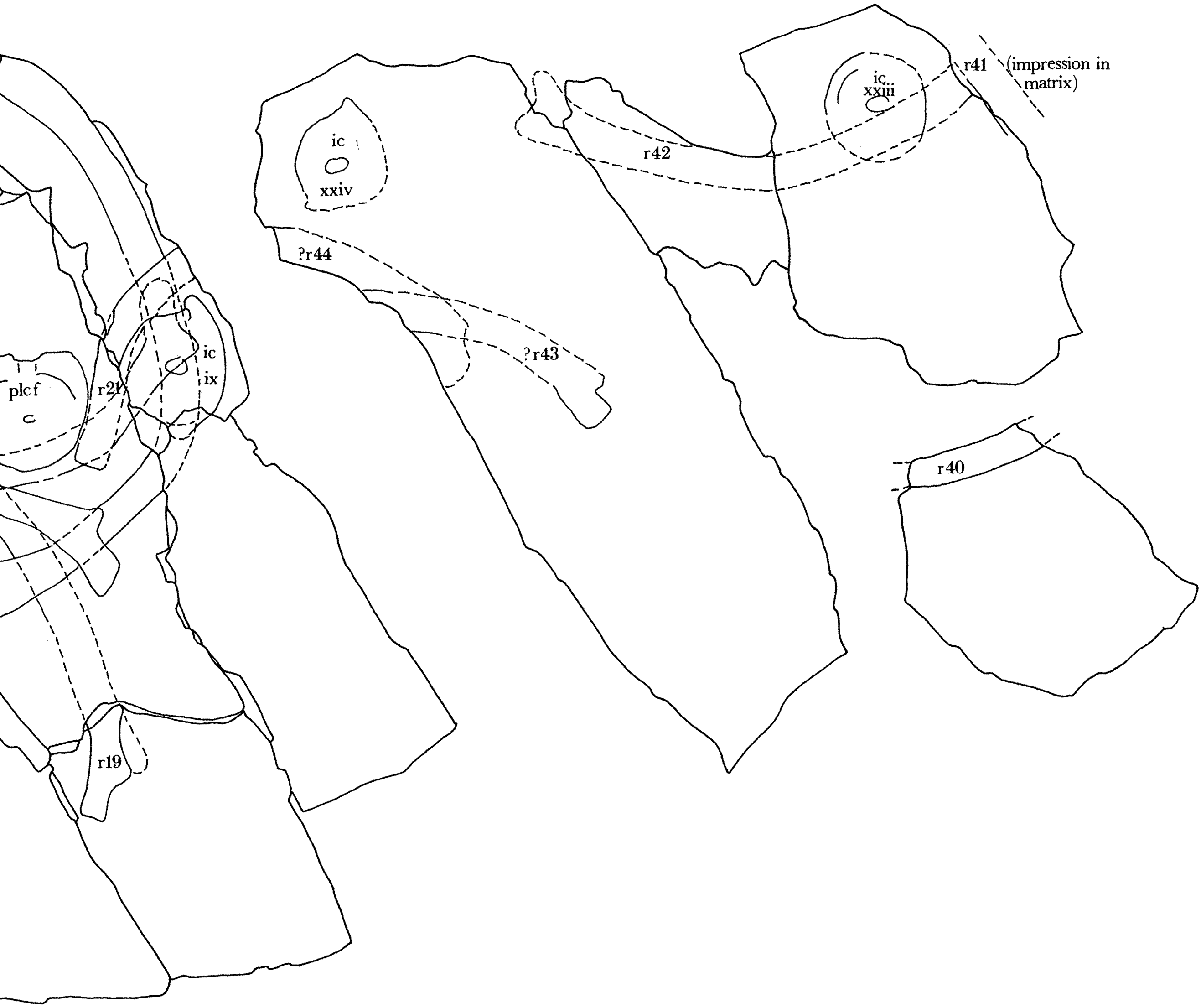


FIGURE 42. *Pholiderpeton scutigerum* holotype, diagram of braincase block and small isolated block to show position of postcranial elements. Heavy lines indicate pectoral limb elements.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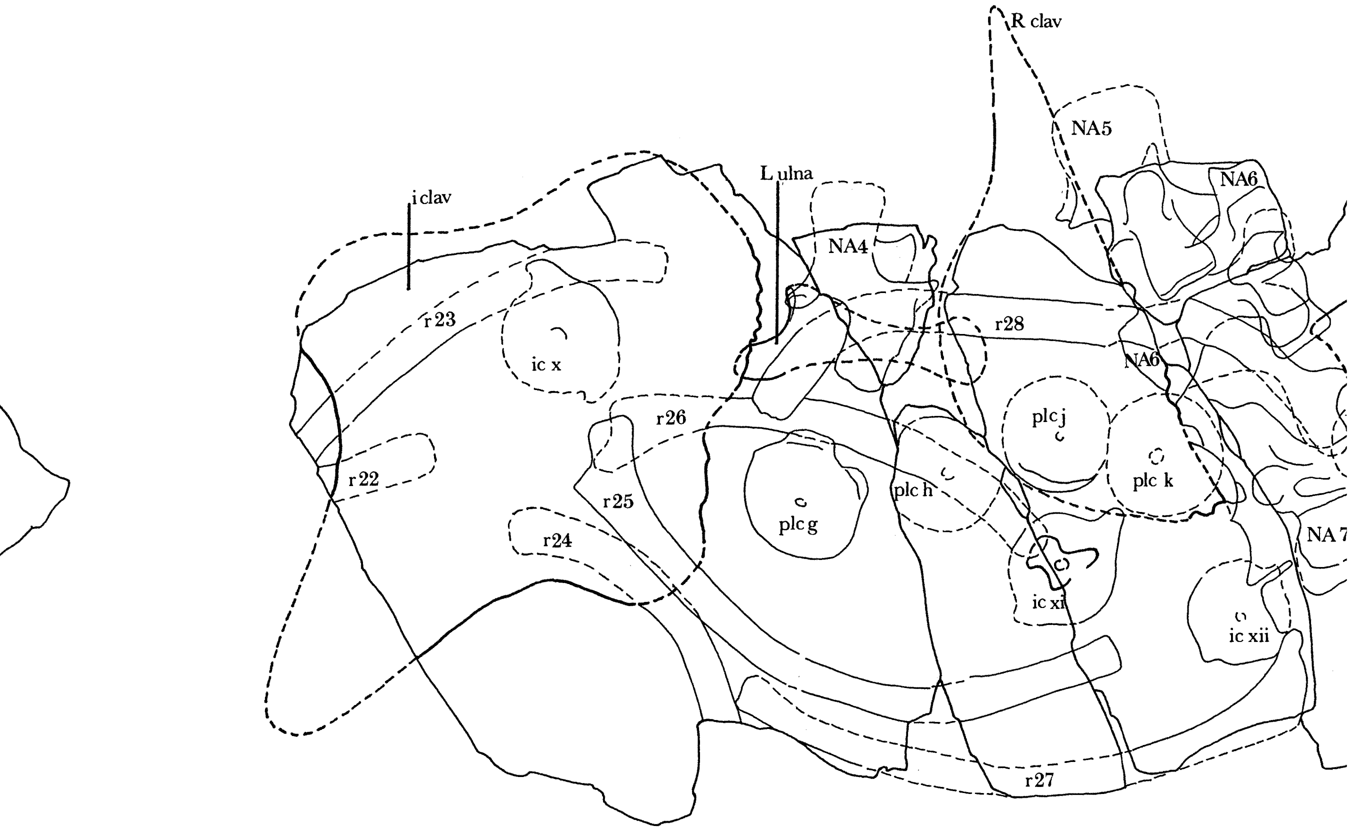
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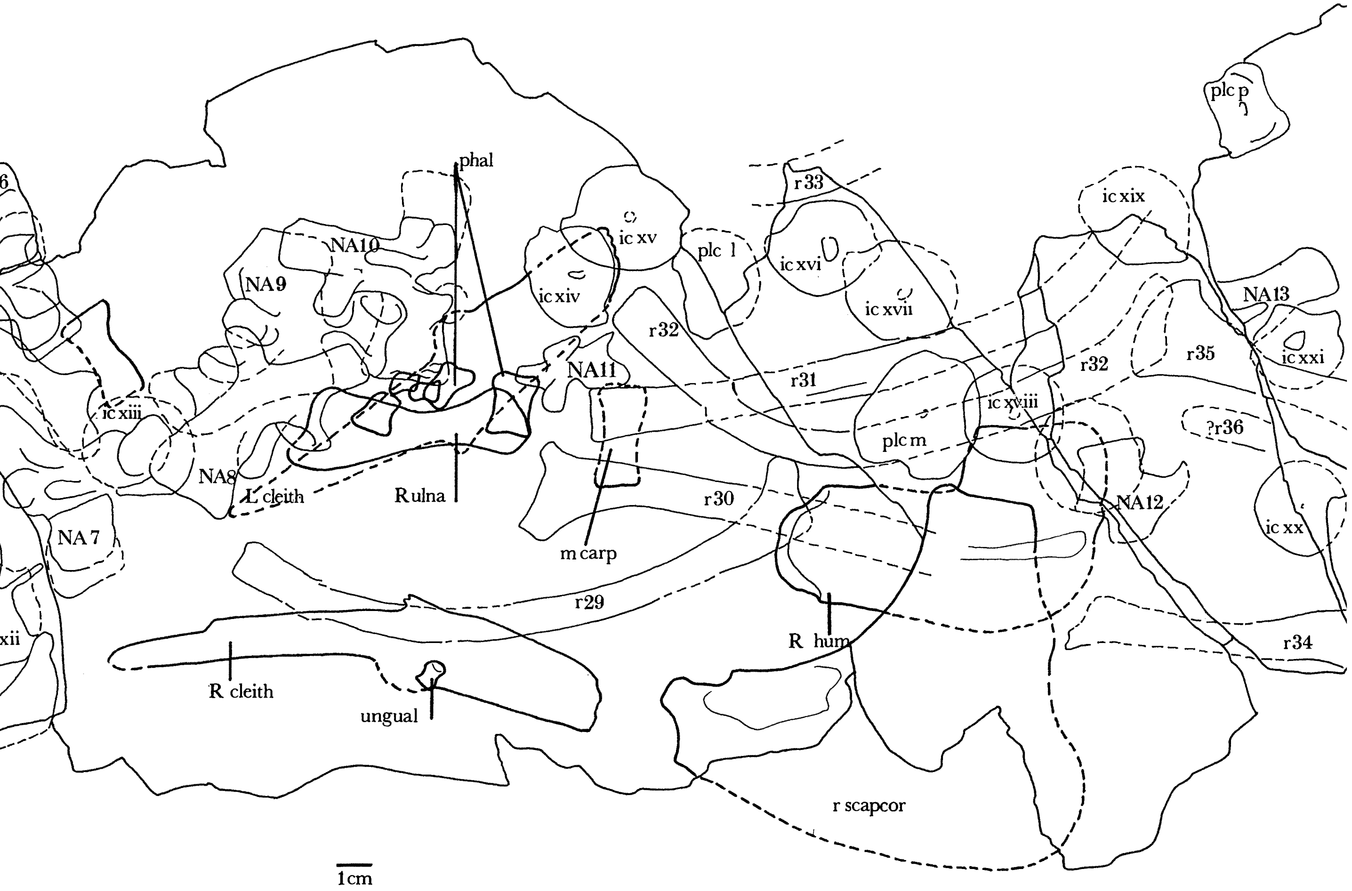
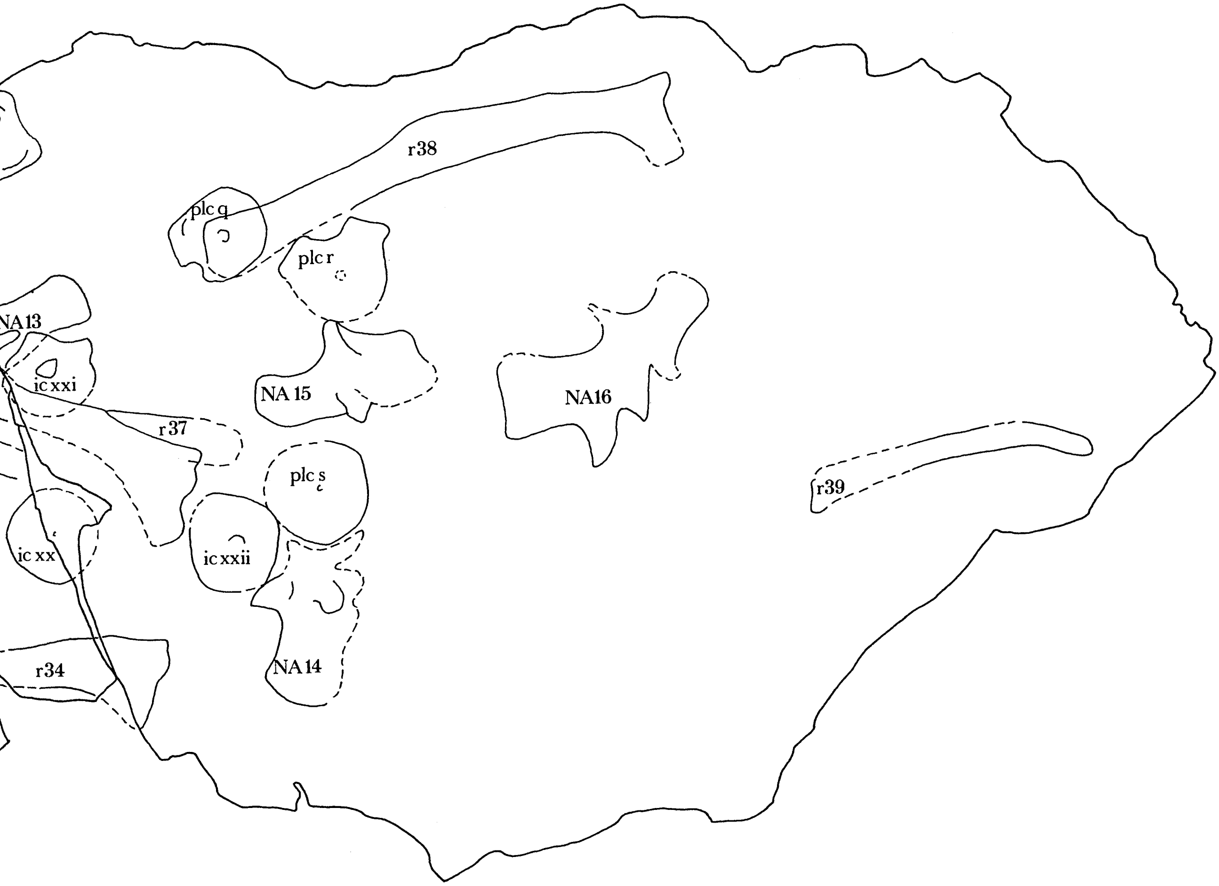


FIGURE 43. *Pholiderpeton scutigerum* holotype, diagram of main skull block to show position of postcranial elements. Heavy lines indicate pectoral limb and girdle elements.


r38
plc q
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ial

theses. I am indebted to Mr G. E. Howson of the University of Newcastle upon Tyne and to Mr M. R. Ashby of the University Museum of Zoology, Cambridge, for technical assistance, and I was greatly assisted by Dr C. P. Ellington of the Department of Zoology, University of Cambridge, in discussion of the functional morphology of the skull and jaw muscles of *Pholiderpeton*, and by Mrs Ann Maxwell who relieved me of typing much of the manuscript. Finally I thank my husband Robert for his constant support and encouragement.

This study was funded for the first two years by a Science Research Council 'Instant Award', without which the work could not have begun; the S.R.C. also subsidized the visit to the United States. The Department of Zoology, University of Newcastle upon Tyne, also contributed to the cost of this visit, without which this work would have been much the poorer.

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ABBREVIATIONS USED IN THE FIGURES

add	adductor
am	anteromedial
ant	anterior
bas tub	basal tubera
bocc	basioccipital
bptpr	basipterygoid process
brcse	braincase
bsph	basisphenoid
butt	buttress
car	carotid
ch ty	chorda tympani
clav	clavicle
cleith	cleithrum
col cran	columella cranii
cond	condyle or condylar
cor	coronoid
dent	dentary
depr ssp cap	depression for m. semispinalis capitis
dig	digitiform
dp cr	deltopectoral crest
dors	dorsal
ect	ectopterygoid
ectep	ectepicondyle
entep	entepicondyle
ext	external
exocc	exoccipital
fac	facet
fen ov	fenestra ovalis
fl	flange
for	foramen
fr	frontal
glen	glenoid
gr	groove
hum	humerus
ic	intercentrum
iclav	interclavicle
ins	incisure
iov	interorbital vein
it	intertemporal
jug	jugal
L	left
l t	lateral tectal
lach	lachrymal
lat dors	m. latissimus dorsi scar
lev pter	m. levator pterygoideus scar
lig att	ligamentous attachment point
lr	lower
mag	magnum
mar derm orn	margin of dermal ornament
mar nas cap	margin of nasal capsule
mcarp	metacarpal
med	medial
mus	muscle
mx	maxilla
NA	neural arch
nas	nasal
olf can	olfactory canal
opis	opisthotic
pal	palatine
par	parietal
phal	phalanx
plc	pleurocentrum
pmx	premaxilla
po	postorbital
pofr	postfrontal
pofr–fr sut	postfrontal–frontal suture
pospl	postsplenial
post	posterior
pp	postparietal
pr	process
pr cult	processus cultriformis
prefr	prefrontal
prespl	presplenial
proatl	proatlas
proot	prootic
prot pr	prootic process
prt pr	paratemporal process
psph	parasphenoid
pt	pterygoid
pt–epipt	pterygoid–epipterygoid complex
pt–epipt sut	pterygoid–epipterygoid suture
pq	paraquadrate
qj	quadratojugal
qu	quadrate
R	right
r	rib
rf	roof
sac cham	saccular chamber
scapcor	scapulocoracoid
scaphum	m. scapulohumeralis scar
scu	scutes
sk	skull
sphet	sphenethmoid
squ	squamosal
ssc	semicircular canal
st	supratemporal
subcorscap	m. subcoracoscapularis scar
supcan	supraneural canal
supcor	supracoracoid
supglen	supraglenoid
surf	surface
sut	suture with
tab	tabular
tr	transverse
ul	ulna
vent	ventral
vl	ventrolateral
vom	vomer
zyg	zygapophysis
I-XII	cranial nerves

Appendix 1. List of specimens pertaining to *Pholiderpeton scutigerum*

Housed in Cliffe Castle Museum, Keighley:

NS 111.81	Disarticulated skeleton comprising most of the skull and presacral elements. Holotype (Huxley 1869). Black Bed Coal, Toftshaw, near Bradford, Yorkshire. (Miall 1870; Watson 1926, 1929; Panchen 1970.)
	Attributed specimens:
NS 62.78/5	Neural arch. Low Moor or Toftshaw, near Bradford, Yorkshire.
NS 62.78/14	Pleurocentrum. Low Moor or Toftshaw, near Bradford, Yorkshire.
NS 63.78/25	Two pleurocentra and one neural arch. Probably part of holotype. Black Bed Coal, Toftshaw, near Bradford.
NS 63.78/26	Several fragments of neural arches, centra, ribs etc. Probably part of holotype. Black Bed Coal, Toftshaw, near Bradford, Yorkshire.
NS 63.78/52	Rib fragment. Low Moor or Toftshaw, near Bradford, Yorkshire.
NS 63.78/496	Two pleurocentra from sacral region of an embolomere. Unprovenanced, probably Low Moor or Toftshaw, near Bradford.

Housed in the British Museum (Natural History):

R 2396	Scutes, ribs and vertebrae, part of holotype. Black Bed Coal, 'Topshaw' (sic.), near Bradford. Purchased J. Ward 189?.
R 2397	Three fragments labelled 'scutes of *Pholiderpeton scutigerum.*' 'Boyd's Coal, Topshaw' (sic.), near Bradford. Purchased J. Ward 189?. 1 (scutes plus rib-head), part of holotype; 2 others possibly, but not certainly, part of holotype.
R 2398	Lower jaw fragment, part of holotype. 'Boyd's Coal, Topshaw' (sic.) near Bradford. Purchased J. Ward 189?.
R 2647	Anterior caudal intercentrum and haemal arch. Low Moor, near Bradford. Purchased 1895.
R 2648	Isolated left articular. Low Moor, near Bradford. Purchased J. W. Davis 1895.
R 2649	Isolated right articular (waterworn). Low Moor, near Bradford. Purchased J. W. Davis 1895.

Housed in the Museum of Comparative Zoology, Harvard University:

MCZ 6976	Centrum and part of prefrontal and lachrymal. Part of holotype (ex MCZ 2550). Black Bed Coal, Toftshaw, near Bradford, Yorkshire.
MCZ 6977	Left squamosal, quadrate quadratojugal and atlas neural arch (ex MCZ 2550). Low Moor, near Bradford, Yorkshire; probably Better Bed Coal. Purchased W. P. Sladen 1875.

APPENDIX 2. LIST OF SPECIMENS ATTRIBUTED TO *P. ATTHEYI* (WATSON 1926).

From the Low Main Seam, Newsham, Northumberland; U. *modiolaris* zone, Westphalian B.

Housed in the Hancock Museum, Newcastle upon Tyne:

G 13.71	Nearly complete skull with both jaw rami and rib fragments. Figured by Atthey (1876), (as *Anthracosaurus russelli*), Watson (1926), (as *Eogyrinus attheyi* type specimen) and Panchen (1970, 1972) (as *E. attheyi*). Designated lectotype of *E. attheyi* by Romer (1963).
G 13.72	At least twelve vertebrae, six ribs, a number of dermal scutes and a ? femur. Figured in part by Atthey (1876) (as *A. russelli*) and Panchen (1966), (in part), (1972) (in part, as *E. attheyi*). Associated with G13.71.
G 13.74	Isolated neurocranium (no data attached; presumed to be from Newsham). Figured by Watson (1926) and Panchen (1972) (as *E. attheyi*).
G 13.75	Part of snout. Hancock & Atthey (1869) (as *A russelli*). Watson (1926) (as *E. attheyi*). Panchen (1972) (as *E. attheyi.*)
G 13.76	Slab with caudal centra and ribs, scutes, etc. Panchen (1972) (as *E. attheyi*).
G 13.77	Articulated length of vertebal column, including 24 presacral vertebrae, the sacrum and a number of proximal caudal vertebrae. Figured by Barkas (1873), Embleton (1889), Watson, (1926) and Panchen (1966), (as *E. attheyi*).
G 13.79	Isolated right articular condyle. Panchen (1972) (as *E. attheyi*).
G 13.80	Articular, including condyle of left lower jaw ramus. Panchen (1972) (as *E. attheyi*).
G 13.83	Isolated neural arch. Figured Watson (1926) (as *E. attheyi*).
G 15.83	Isolated palatine with tusk pair. Panchen (1926), (as *E. attheyi*).

G 15.84	Slab bearing intercentrum and neural arch of dorsal vertebra, plus five dermal scutes. Figured (in part) by Panchen (1972) (as *E. attheyi*).
G 15.88	Left quadrate and jaw fragment, now know to pertain to G 13.71 (Boyd & Turner 1980). Figured by Panchen (1972) (as *E. attheyi*).
G 24.24	Isolated quadratojugal, possibly that described by Atthey (1876), (as *A. russelli*).
G 40.28	Isolated maxilla, right, with tooth row. Barkas (1873) (as type of '*Leptognathus*').

Housed in the British Museum (Natural History):

R 8426	Isolated skull table, formerly in the collection of Leeds City Museum. Figured by Atthey (1876) (as *Pteroplax*), Watson (1926) (as *Eogyrinus*) and Panchen (1970, 1972) (as *E. attheyi*).

In addition to these, a large number of isolated postcranial elements and dermal scutes are catalogued as *E. attheyi* in the Hancock Museum (Boyd & Turner 1980). These should now be attributed to *Pholiderpeton attheyi*.

APPENDIX 3. LIST OF SPECIMENS ATTRIBUTED TO *PHOLIDERPETON* SP.

Housed in the British Museum, (Natural History):

R 2377	Posterior part of left lower jaw of large embolomere. New Ironstone Shale, Fenton, Staffordshire. J. Ward Collection. Hancock & Atthey (1871) (as *Anthracosaurus*).

Housed in the collections of King's College, London University:

A2	Partial skull with skull table, braincase and part of lower jaw. Black Shale, U. communis zone, Westphalian A. Swanwick, near Alfreton, Derbyshire. J. Coope Collection. Figured by Panchen (1964) (as *Eogyrinus*). Figured by Panchen (1970), (as *Pholiderpeton scutigerum*).

Also from this collection are a number of uncatalogued fragments: dentary with surangular and coronoid, three lower jaw fragments, left articular and left quadrate.

Housed in the British Geological Survey, Keyworth, Nottingham (formerly at Leeds):

GS 28318	Preorbital region of skull with anterior right jaw ramus. Airdrie, Lanarkshire, Scotland. Probably Palace Craig Ironstone, L. *similis–pulchra* zone, or possible Airdrie Blackband Ironstone, U. *modiolaris* zone (both are Westphalian B). Figured by Watson (1929) (as *Pholiderpeton scutigerum*). Figured by Panchen (1972) (as *Eogyrinus attheyi*).

Housed in the Manchester Museum, Manchester:

L 11614	Anterior left jaw ramus of GS 28318; data as above. Figured Watson (1929) (as *Pholiderpeton scutigerum*). Figured Panchen (1972) (as *Eogyrinus attheyi*).

Housed in the Royal Scottish Museum, Edinburgh:

RSM 1897.112.23–4	Incomplete skull lacking the snout region but including part of the braincase and right basal articulation. Virtuewell Coal shale, U. *modiolaris* zone, Westphalian B. Newarthill, Lanarkshire, Scotland. Panchen (1972) (as *E. attheyi*).
RSM 1957.1.5806	Caudal vertebra. Splint Coal, L. *similis–pulchra* zone, Westphalian B. Wishaw, Lanarkshire, Scotland. Panchen (1972) (as *E. attheyi*).
RSM 1971.11.4	Interclavicle. Probably Airdrie Blackband Ironstone, Lanarkshire, Scotland. Figured Panchen (1977) (as *Anthracosaurus russelli*).

FIGURE 39. *Pholiderpeton scutigerum* holotype, obverse of block containing braincase and small isolated block. Stipple indicates matrix.

FIGURE 40. *Pholiderpeton scutigerum* holotype, reverse of block containing lower jaw and cheek bones (main skull block). Stipple indicates matrix; hatching, broken or damaged bone; scutes are unshaded.

FIGURE 41. *Pholiderpeton scutigerum* holotype, obverse of block containing lower jaw and cheek bones (main skull block). Stipple, matrix; hatching, broken or damaged bone.

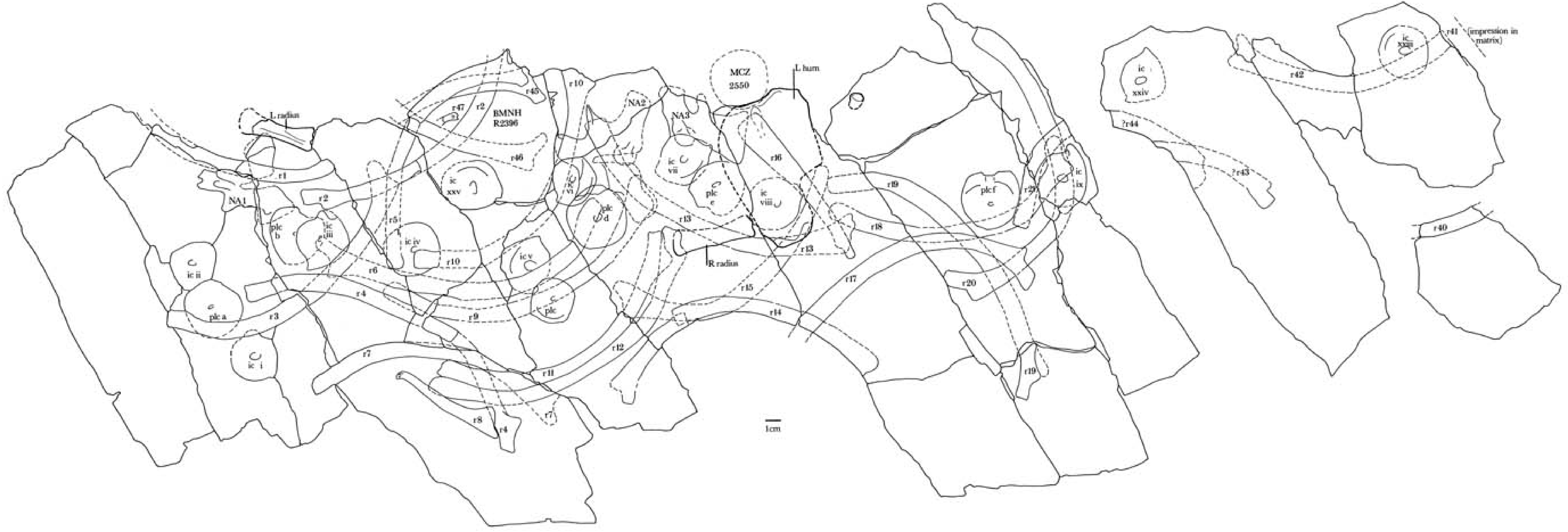

FIGURE 42. *Pholiderpeton scutigerum* holotype, diagram of braincase block and small isolated block to show position of postcranial elements. Heavy lines indicate pectoral limb elements.

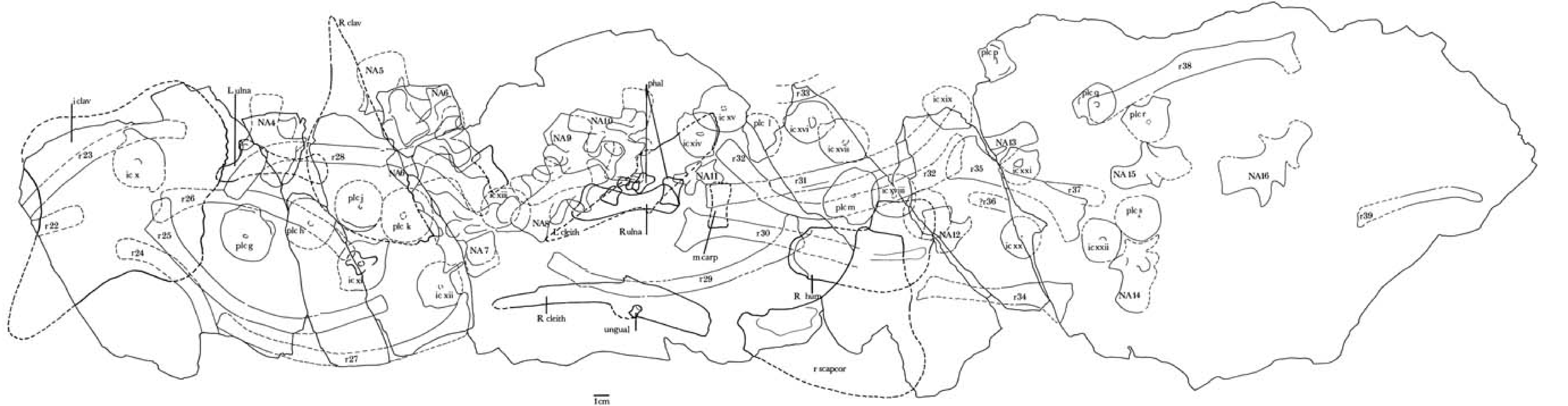

FIGURE 43. *Pholiderpeton scutigerum* holotype, diagram of main skull block to show position of postcranial elements. Heavy lines indicate pectoral limb and girdle elements.