A NEW GENUS AND SPECIES OF ANTHRACOSAUR AMPHIBIAN FROM THE LOWER CARBONIFEROUS OF SCOTLAND AND THE STATUS OF *PHOLIDOGASTER PISCIFORMIS* HUXLEY

By A. L. PANCHEN
Department of Zoology, University of Newcastle upon Tyne

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The isolated skull of a Lower Carboniferous anthracosaur labyrinthodont from the Midlothian coalfield was formerly but erroneously attributed to *Pholidogaster pisciformis*. It is now redescribed after 'Airbrasive' development as the holotype of a new genus and species. The anthracosaur agrees in a number of diagnostic cranial characters with the embolomerous forms of the Coal Measures but other characters, particularly those of the braincase and lower jaw, suggest relationship to the Seymouriamorpha. Its cranial anatomy could well be antecedent to that of both these groups and the sparse evidence available suggests close relationship to the American Mississippian anthracosaur *Proterogyrinus*.

A new classification of the Batrachosauria is presented with a major subdivision into Anthracosauria and Seymouriamorpha. The former group comprises the newly proposed infraorder Herpetospondyli to include the Lower Carboniferous forms, together with the infraorders Embolomeri and Gephyrostegoidea. It is concluded that while no batrachosaur with an otic notch could be a reptile ancestor a primitive 'notchless' anthracosaur could be.

The cranial anatomy of *Pholidogaster pisciformis* is then redescribed, after complete 'Airbrasive' preparation of the holotype skull. The holotype, like the anthracosaur, comes from the Gilmerton Ironstone of the Edinburgh region, but the earlier holotype skull of *Otocratia modesta*, long considered to be an ichthyostegid, is also attributed to

Pholidogaster. After redescription of '*Otocratia*' a composite restoration of the *Pholidogaster* skull is presented.

The nature of the dermal ornament, the post-parietal–supratemporal suture, the absence of tabular horns and the nature of the post-cranial skeleton all demonstrate that *Pholidogaster* is an early temnospondyl labyrinthodont in no way closely related to anthracosaurs. It is closely similar to the American Mississippian form *Greererpeton burkemorani* Romer, notably in the presence of large premaxillary fangs and the absence of otic notch and intertemporal. Both may be attributed to the family Colosteidae. It is concluded that there is no strong evidence of close relationship between the colosteids and the Devonian ichthyostegids.

Introduction

The holotype of *Pholidogaster pisciformis* Huxley (1862) consists of an almost complete skeleton of a labyrinthodont amphibian exposed in ventral view. It was acquired by Sir Philip Egerton and the Earl of Enniskillen and donated to the British Museum. The specimen was briefly described by Huxley who gave a figure of the whole skeleton as it then appeared.

The importance of *Pholidogaster* lies in the fact that until recently it was the only articulated skeleton of a Lower Carboniferous labyrinthodont described. The holotype comes from the Gilmerton Ironstone (possibly from the Venturefair pit (Traquair 1903)) of the Midlothian Coalfield, near Edinburgh. The Gilmerton Ironstone is localized in the neighbourhood of Gilmerton, some 2½ km southeast of the centre of Edinburgh and is the equivalent of the Rough Parrot Coal present over much of the west side of the Midlothian Coalfield. This coal lies at about 50 m above the Gilmerton Limestone which forms the base of the Lower Limestone Group (Tulloch & Walton 1958). The whole of the Lower Limestone Group is of P_2 goniatite zone age and is thus uppermost Viséan (Rayner 1967).

Pholidogaster was subsequently described by Watson (1929), who was able to give some detail of the caudal vertebrae, which are essentially rhachitomous but with unusually elongate pleurocentra. The dorsal vertebrae were largely obscured by a covering of gastralia but Watson considered them to be embolomerous.

Little could be made of the skull which was exposed in ventral view, much disrupted, and covered with intractable ironstone matrix. Watson, however, attributed to the same species a somewhat smaller skull from the Royal Scottish Museum, which was without data, but on the nature of the matrix appeared to him to come from the Gilmerton Ironstone.

With more modern techniques of development it was possible to expose most of the skeleton of *Pholidogaster* and after skilled preparation by Mr Arthur Rixon the holotype was redescribed by Romer (1964). He was able to show that the trunk vertebrae bore large but crescentic intercentra and paired elongate pleurocentra, which were much narrower (antero-posteriorly) but extended further ventrally than those of typical rhachitomous labyrinthodonts.

This type of vertebra he described as schizomerous. He also accepted Watson's attribution of the skull in the Royal Scottish Museum to *Pholidogaster*.

This latter skull is certainly that of an anthracosaur. Romer therefore postulated that the 'schizomerous' vertebra was antecedent to the embolomerous vertebra which is typical of the anthracosaurs (Embolomeri) of the Upper Carboniferous and Lower Permian.

In a recent review of the Anthracosauria (Panchen 1970) it was necessary to comment on *Pholidogaster* and I had the opportunity to examine the holotype skull, by then detached and cleaned, except for most of the posterior dorsal region, side-by-side with the Edinburgh skull.

It was immediately obvious that the two were unrelated. Notably the dermal ornament of the *Pholidogaster* holotype was that of a typical temnospondyl and thus of a type which would be unexpected in an anthracosaur. On the other hand that of the anthracosaur, although then only visible over a small area, was closely comparable to that seen in embolomerous anthracosaurs and described in *Eogyrinus* (Panchen 1972*a*).

It thus seems to me highly improbable that *Pholidogaster* was an anthracosaur (Panchen 1970, pp. 61–2). No feature of the postcranial skeleton seemed to indicate anthracosaur affinity or ancestry, and the skull, as then prepared was at best indeterminate. Furthermore, it did not seem very probable, from the appearance of the matrix, that the anthracosaur skull was from the Gilmerton Ironstone. In this, however, Professor Watson's intuition proved correct (see below).

The anthracosaur skull is redescribed here as a new genus and species of batrachosaur labyrinthodont. The holotype skull of *Pholidogaster* is also redescribed together with the holotype skull of *Otocratia modesta* Watson. The latter is referred to *Pholidogaster*.

The holotype of *Otocratia* is the oldest described labyrinthodont skull from the European Carboniferous. The ichthyostegids from Greenland represent the only described labyrinthodont skulls from an earlier horizon. Like *Pholidogaster*, *Otocratia* comes from the Midlothian Coalfield, but from the Burdiehouse Limestone at Burdiehouse near Edinburgh. The Burdiehouse Limestone forms the base of the Upper Oil Shale Group, Calciferous Sandstone Measures (Tulloch & Walton 1958) and thus is Middle Viséan and possibly of B_2 goniatite and D_1 coral-brachiopod age (Westoll 1951; Rayner 1967).

MATERIALS AND METHODS

The anthracosaur skull is now registered in the collections of the Department of Geology, Royal Scottish Museum as number 1950.56.1. A specimen of matrix from the skull was sent for examination to Dr A. H. V. Smith of the National Coal Board at the same time as one from the holotype skull of *Crassigyrinus scoticus* Watson (Panchen 1973*a*). Control specimens of matrix from the Loanhead no. 2 Ironstone (Limestone Coal Group: Namurian A), the Gilmerton Ironstone and the Dunnet Shale, Straiton (U. Oil Shale Group; Viséan) were also enclosed.

The spore assemblage from the anthracosaur matrix, like that from *Crassigyrinus*, was of Upper Viséan or Lower Namurian age and resembled that from Gilmerton rather than tha from Loanhead. It is probable therefore that Watson was correct in assigning both *Crassigyrinus* and the anthracosaur skull to the Gilmerton Ironstone.

The anthracosaur skull has now been cleaned of all surface matrix by the use of an S. S. White Industrial Airbrasive Unit with calcium dolomite powder (Stucker 1961). As in previous reconstructions (Panchen 1964, 1972*a*) a simple model of the skull was made in dental wax as a guide to the final drawing.

The type skeleton of *Pholidogaster pisciformis* Huxley is registered in the Department of Palaeontology, British Museum (Natural History) as R30534. The skull and dermal pectoral girdle are removable as a unit from the rest of the skeleton and their ventral surfaces were cleaned by Mr Rixon (Romer 1964, fig. 2). A part of the dorsal surface comprising the snout region, the dorsal exposure of the right jaw ramus (Romer 1964, fig. 3) and a small area of the left posterior region of the roof were also cleaned. The latter area, however, consisted of a mass of apparently crushed and broken bone. The remaining posterior part of the roof was covered with a hard intractible mass of siderite and no further development was undertaken at that time.

The rest of the skull roof has now been cleaned. Mr Peter Whybrow removed some of the more intractable matrix by mechanical development including cutting with diamond wheels and I have completed the process by removal of the remaining blocks of that matrix and treatment of the whole skull with the Airbrasive machine.

Apart from the holotypes of *Pholidogaster* and *Otocratia* other material referable to *Pholidogaster pisciformis* includes a left clavicle from Gilmerton – Institute of Geological Sciences (Geological Survey) G.S.L. 14, and an interclavicle from Burdiehouse – B.M.(N.H.) (Bryson Collection) R41126. The holotype of *Otocratia* is registered at the Royal Scottish Museum as number 1870.14.440.

No further development has been attempted on the holotype skull of *Otocratia*. It consists largely of the skull roof whose dorsal surface is embedded in a thick block of limestone and whose exposed ventral surface is much eroded. The dangers of development thus outweigh the possible gain in information.

EOHERPETON WATSONI GEN. ET. SP. NOV.

Diagnosis for genus and species. A medium-sized anthracosaur amphibian: skull length to back of skull table (pp length (Panchen 1970)) approximately 130 mm, quadrate length *ca.* 150 mm, tooth row *ca.* 90 mm.

Dental formula (Chase 1963; Panchen 1970): palate 0(?)–2–6, PMX 5, MX (estimated) 24.

Skull table of normal anthracosaur pattern with short blunt tabular horns, pineal foramen large (diameter 5 mm), circular, not on a raised boss. Table-cheek kinetism extends forward to orbit. Orbits large, at midpoint in skull length. External nares large with well-developed naso-labial groove. Well-developed tympanic groove in squamosal but otic 'notch' shallow and ill-defined. No trace of lateral line sulci.

Septomaxillary bone present in naris. Lacrimal just excluded from orbit by prefrontal–jugal contact (or sometimes entering orbit?). Jugal excluded from jaw margin by quadratojugal.

Palate closed, teeth on ectopterygoid subequal in size. Braincase with widely spaced fenestrae ovales: body of parasphenoid extending laterally on each side towards fenestrae. Deep fossae for muscle insertion between midline and fenestrae. Ossified supraoccipital present.

Lower jaw relatively shallow bearing a short retroarticular process. Large meckelian fenestrae of anthracosaur type absent, but three small foramina may be present. Anterior coronoid without denticles, but middle coronoid with small teeth in addition to denticles.

The generic name is proposed to suggest affinity with the Coal Measure anthracosaurs *Palaeoherpeton* and *Eogyrinus*. The specific name is in memory of Professor D. M. S. Watson, F.R.S., who gave the first published account of the holotype.

Holotype. Royal Scottish Museum, Department of Geology no. 1950.56.1. A crushed skull in ironstone including both jaw rami with fragments of the pectoral girdle.

Horizon. No associated data – probably Gilmerton Ironstone (= Rough Parrot Coal), Lower Limestone Group of the Lothian basin (P_2 *Goniotites* zone), U. Viséan, Lower Carboniferous.

Locality. No associated data – possibly Venturefair pit, Gilmerton, Midlothian, Scotland.

The skull (figures 1–4) has been crushed in such a way that the skull table, the right nasal region, the whole right lateral surface of the skull roof and the posterior part of the lateral surface of the right jaw are almost in the same plane. The anterior part of the jar ramus, separated by a small missing area, curves round anteriorly into a more natural vertical plane.

In ventral view almost the whole of the right palatal surface is exposed with the exception of the vomer and the mesial boundary of the pterygoid. The latter bone is flattened into a horizontal plane. The right ventro-lateral surface of the braincase is exposed, together with the incomplete body of the parasphenoid, forward to the level of the basipterygoid articulation.

The mesial surface of the right jaw is also visible in ventral view, but the mesial surface of the dentary is not visible because of the torsion in the ramus already referred to. The lateral surface of the left ramus is also exposed but the articular region is missing on this side. The left ramus is in its natural relation to the left maxillary and lacrimal and part of the cheek region.

In the skull roof only small areas are unrepresented on both sides of the skull and no bone is totally missing on both sides. This is also the case with the lower jaw. Only the vomers, the sphenethmoid region of the braincase and the condylar regions of the exoccipital and basioccipital are completely missing or concealed.

Dermal skull roof

The pattern of dermal bones on the skull table is that normally found in anthracosaurs, and includes a suture between the parietal and tabular, and a large intertemporal bone. The dermal ornament, although somewhat eroded, is very similar to that described in *Eogyrinus* (Panchen 1972*a*).

The parietals are remarkable in being very truncated anteriorly: the parietal–frontal suture, which is easily traced on both sides, is situated only a little in front of the level of the hind margin of the orbit. The parietals enclose an unusually large circular pineal foramen, some 5 mm in diameter, the borders of which are not raised in any way above the general bone surface.

The postparietals are unremarkable: each forms a concave posterior border to the skull roof so that the latter projects backwards in the midline. They have a considerable occipital exposure on either side of a convex, boss-like supraoccipital. In addition to that bone they contacted the exoccipitals on each side in a concave suture and probably also contacted the opisthotics laterally. Their occipital suture with the tabular is mesial to that on the skull roof on the right but vertically below on the left.

Apart from its suture with the post-parietal each tabular contacted the opisthotic on its own side of the occiput. The sutural edge of both tabulars is preserved but the contact, forming the paroccipital brace of the skull, has been disrupted on both sides.

As in other anthracosaurs the tabular bears a characteristic horn, preserved only on the right. As preserved the horn is a short blunt cone, directed postero-mesially, and unlike the elongate blade of Coal-Measure anthracosaurs. It may have been broken off and eroded to this form, but this does not seem probable and its orientation is unlike the laterally divergent horns of Coal-Measure specimens.

The orientation of the tabular–parietal suture also differs significantly from that of embolomerous anthracosaurs. The suture in *Eoherpeton* runs obliquely backwards and laterally, continuing the line of the parietal–post-parietal suture and paralleling the concave border of the back of the skull table. In typical anthracosaurs the suture runs antero-laterally (Panchen 1970) as would be expected for bones of even or elliptical growth (Parrington 1956).

The lateral margin of the skull table, formed by the tabular, supratemporal, intertemporal

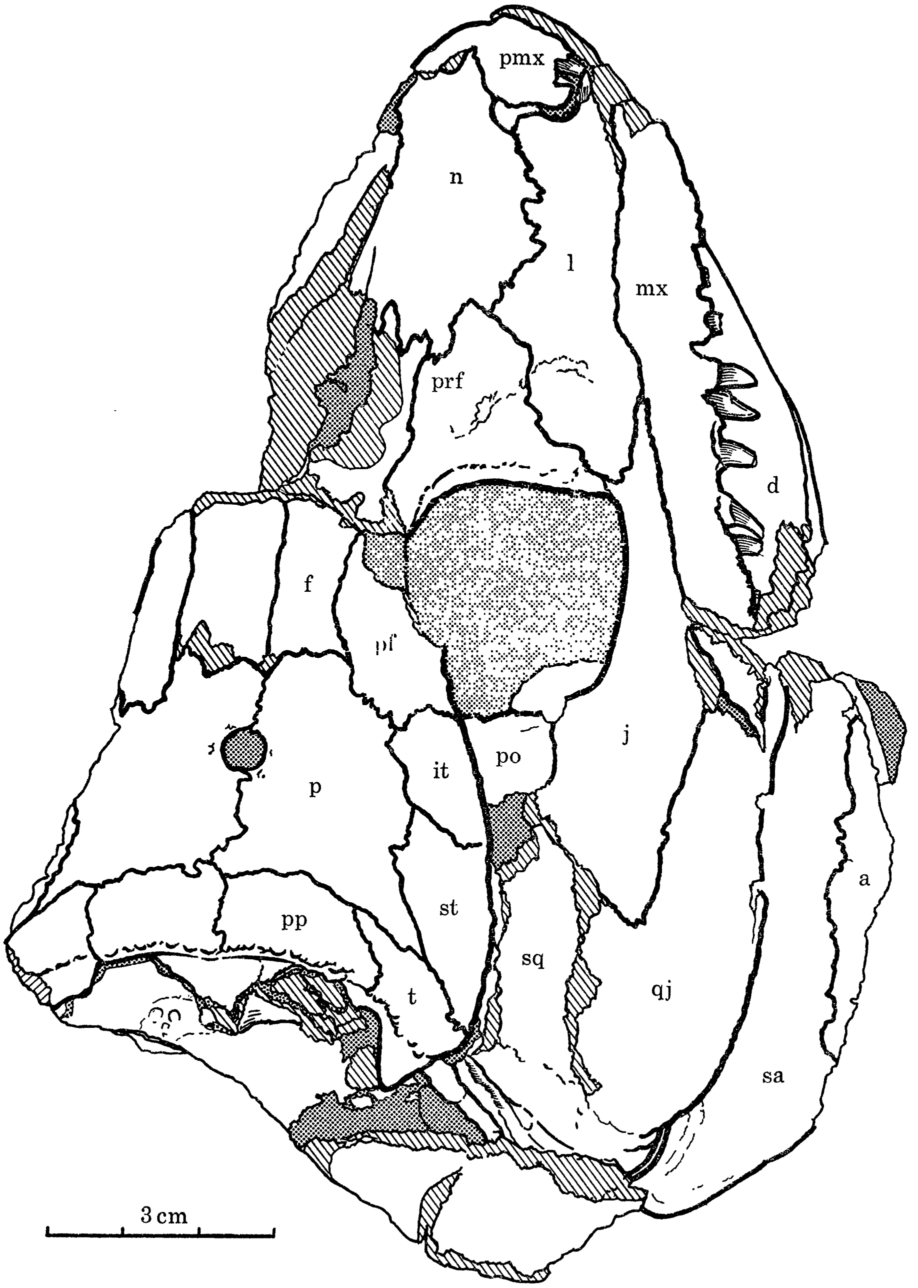

FIGURE 1. *Eoherpeton watsoni* gen. et sp. nov., holotype skull in dorsal view. Natural size. Matrix coarse stipple, broken bone hatched. a, angular; d, dentary; f, frontal; it, intertemporal; j, jugal; l, lacrimal; mx, maxillary; n, nasals; p, parietal; pf, postfrontal; pmx, premaxillary; po, post-orbital; pp, post-parietal; prf, prefrontal; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal; t, tabular.

FIGURE 2

FIGURE 3

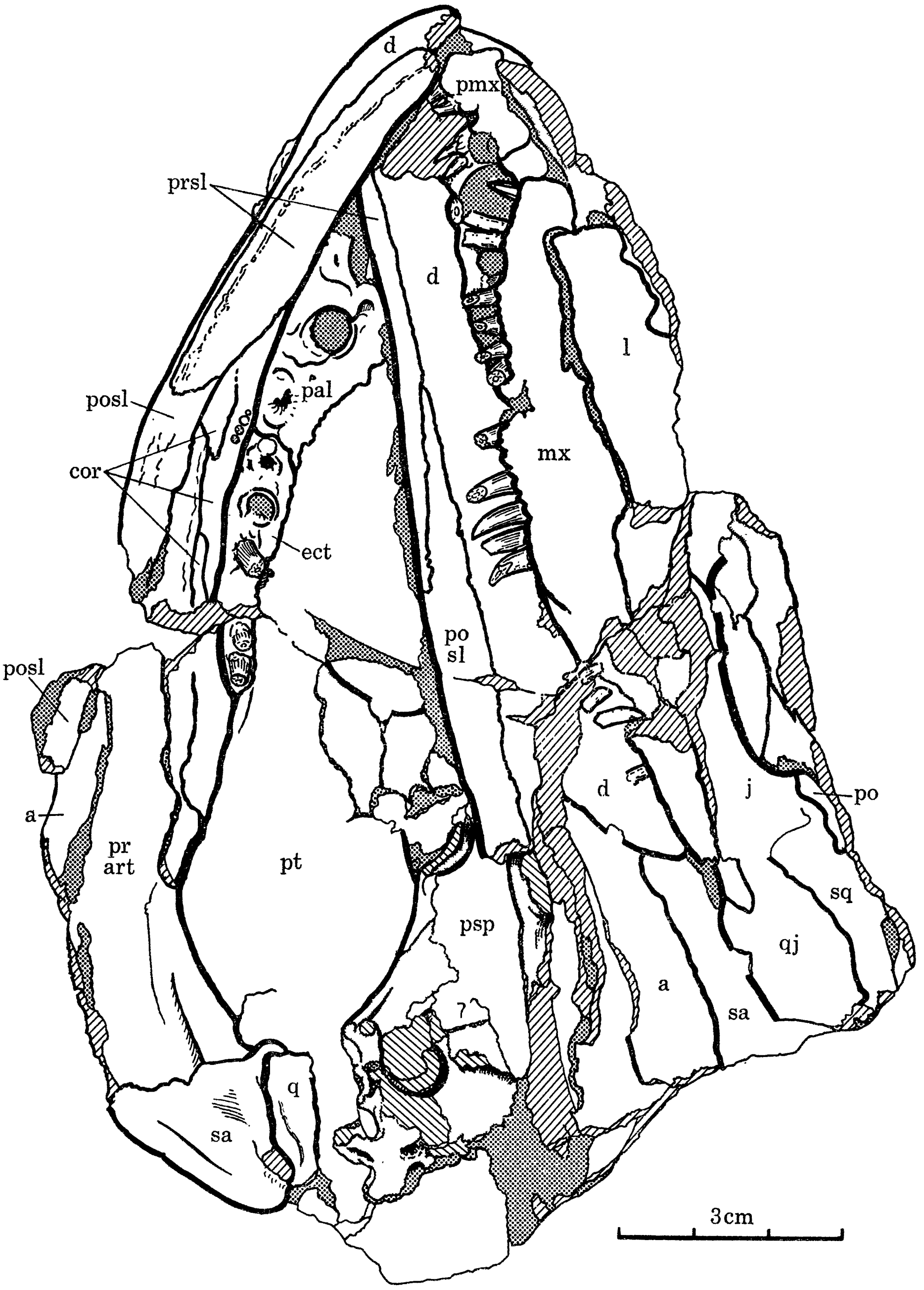

FIGURE 4. *Eoherpeton watsoni*, holotype skull in ventral view. Natural size. Fine stipple, braincase and inner surface of dermal bone. c, coronoids; ect, ectopterygoid; pal, palatine; posl, post-splenial; pr art, prearticular; prsl, presplenial; psp, parasphenoid; pt, pterygoid; q, quadrate; other conventions and abbreviations as in figure 1.

and a considerable post-orbital margin of the postfrontal, is well-preserved on the right but missing on the left. In all embolomerous anthracosaurs and in the related *Gephyrostegus* (Carroll 1970) the supratemporal has a mobile kinetic junction with the squamosal ventro-lateral to it. This junction is retained in many early tetrapod groups (Panchen 1972*b*) and is a remnant of the kinetism present in rhipidistian fish. It is, however, lost in the seymouriamorphs which are close relations of the anthracosaurs.

In *Eoherpeton* it appears that the kinetic junction extended the whole length of the skull table forward to the postero-dorsal corner of the orbit. The evidence for this lies in the form of the edge of the skull table. In the specimen the squamosal and supratemporal are impacted together but with a thin layer of matrix between. They do not appear to have been sutured, however, and it is a reasonable assumption that a normal kinetic joint existed between them. The lateral edges of the intertemporal and postfrontals are, however, exposed in the specimen and it is clear that there was no sutural connexion between them and the squamosal and post-orbital below. The dorsal surface of the postfrontal and intertemporal curves down laterally so that their margin forms a continuous quite sharp edge. In the specimen the lateral part of their ventral surfaces can also be seen sloping up to this edge. Their lateral margin is thus shaped like the leading edge of an aerofoil. The nature of the articulation with the cheek is uncertain, but it is certainly not a suture.

In describing the same region in the skull of *Eogyrinus* (Panchen 1972*a*) it was noted that there appeared to be some mobility between the intertemporal and post-orbital in that genus also.

The orbit of *Eoherpeton*, whose margins are almost complete on the right, is relatively large and almost rectangular in outline. Like the large pineal foramen and the generally open sutures, the large orbit gives the impression of an immature individual.

The pattern of the cheek region contrasts with that of typical anthracosaurs in that the large quadratojugal extends forward below the jugal to a broad contact with the back of the maxillary. The jugal is thus excluded from the margin of the subtemporal fossa. This configuration is primitive and is found in the rhipidistian fish *Eusthenopteron*, in *Ichthyostega* and in *Crassigyrinus* (Panchen 1973*a*, fig. 3). The quadratojugal just reaches the maxillary in *Seymouria* (White 1939).

The right cheek region is somewhat disrupted in *Eoherpeton*. The jugal–quadratojugal suture was traced for virtually its whole length but the quadratojugal–squamosal suture was not, although a conspicuous antero-posterior fracture probably marks its course. A small area of bone is missing in the expected region of the post-orbital–squamosal suture. Virtually no additional information is available from the left cheek.

The cheek region is covered with characteristic anthracosaur ornament, which is more strongly developed than on that of *Eogyrinus*. It is much more comparable to that of *Palaeoherpeton* ('*Palaeogyrinus*', Panchen 1964).

The posterior border of the squamosal is well-preserved on the right and has a gentle S-shaped contour in lateral view. The dorsal concave part of the border slopes obliquely back from under the tabular horn and represents the outline of the otic notch. The thickened posterior edge of the bone in this region bears a sharply incised backward facing vertical groove, which must have held the tympanum. The groove becomes wider and less well defined below the concave part of the edge.

Ventrally the occipital exposure of the squamosal clasps the lateral part of the quadrate.

The snout region is complete on the right of the specimen, except for a fragment missing from the front of the maxillary, and all the sutures were easily traced. On the left the major part of the maxillary is preserved together with most of the lacrimal and a fragment of nasal. The lacrimal border of the external naris is preserved on both sides.

Perhaps the most significant feature of the snout region is the relationship of the lacrimal bone to the orbit. In all adequately described anthracosaurs of the family Eogyrinidae the prefrontal is a broad, often rectangular bone which extends laterally to a long suture with the jugal, thus excluding the lacrimal from the orbital margin. It is probable that with adequate description this will also prove to be the case in the other two embolomerous anthracosaur families, the Anthracosauridae and the Archeriidae (Panchen 1970). In all described Seymouriamorpha, on the other hand, the lacrimal enters broadly into the orbital margin and separates the prefrontal from the jugal (Olson 1965, fig. 5). This is also the condition in *Gephyrostegus* (Carroll 1970).

In *Eoherpeton* there is a suture between the prefrontal and the jugal on the right, but it is very short, and the lacrimal comes to within 3 mm of the orbital margin. The left side is not adequately preserved, but it would be no surprise to find an orbital lacrimal on that side.

The configuration and proportions of the rest of the snout are broadly similar to those of *Palaeoherpeton*, an anthracosaur of similar size. The maxillary is of approximately the same length, extending to just under a centimetre behind the back of the orbit, despite its very different relation to the bones of the cheek region. The dentition, however, is somewhat different.

The maxillary teeth of *Palaeoherpeton* are typically eogyrinid. Individual teeth are slender, recurved and sharply pointed, with a diameter at the base of the crown of less than 2 mm and a crown height of about 5 mm. They are also closely set, at least near the back of the jaw and from the restricted length of maxillary available I estimated the total maxillary count as 30 (Panchen 1970).

In *Eoherpeton* a number of teeth are preserved in each maxillary. The longest is little longer than those of *Palaeoherpeton*, being about 6 mm in crown length. They are, however, somewhat stouter, with a basal diameter of up to 3 mm, are less recurved and, where preserved intact, rather bluntly pointed.

Five more or less complete teeth are preserved in the right maxillary and eight more are represented by crownless stumps. Their position is indicated in figure 1 and in the lateral reconstruction (figure 9). Fourteen teeth are represented in the left maxillary (figure 3, plate 22 and figure 4), all but one by at least a partial crown. On the left the largest teeth are situated in the region below the prefrontal, corresponding to those fully preserved on the right. The teeth diminish both anteriorly and posteriorly from this region. It does not seem probable, therefore, that there was any considerable 'canine peaking', however the second and third teeth preserved on the left appear to have been relatively massive, although now much eroded, and could represent a modest canine peak.

Estimation of the tooth count is difficult. The right teeth seem naturally widely spaced even allowing for lost teeth and replacement phenomena and an estimate of about MX 18 would seem reasonable on that side alone. On the left, however, the teeth are more closely set, though probably not to the degree of *Palaeoherpeton*. An estimated count of MX 24 would seem more reasonable from the evidence of the left maxillary. The reconstructed numbers are illustrated without compromise in the palatal reconstruction (figure 6). The different estimates which could have arisen if each maxillary had been preserved separately demonstrate the danger of sweeping taxonomic conclusions based on incomplete dentitions.

The right premaxillary, which is almost completely preserved, shows only the posterior two teeth in rather poor condition. However, four teeth are represented on the left, visible in ventral view. A replacement pit appears to have been present between the two pairs giving a premaxillary count of five.

The right premaxillary is strongly contoured like that of *Eogyrinus* with a marked posterolateral concavity behind a strong ridge. It does not, however, have the complex deeply pitted ornament seen in the Coal Measure genus. Conceivably its smooth appearance is due to erosion. Almost all its deeply zig-zag suture with the nasal is preserved.

The anterior margin of the external naris, formed by the premaxillary, is also preserved on the right and shows that the bone extended some way into the narial aperture. The naris, even allowing for some crushing, was obviously very high. This is confirmed by its posterior lacrimal border, preserved on both sides. The height of the opening must have been over a centimetre,

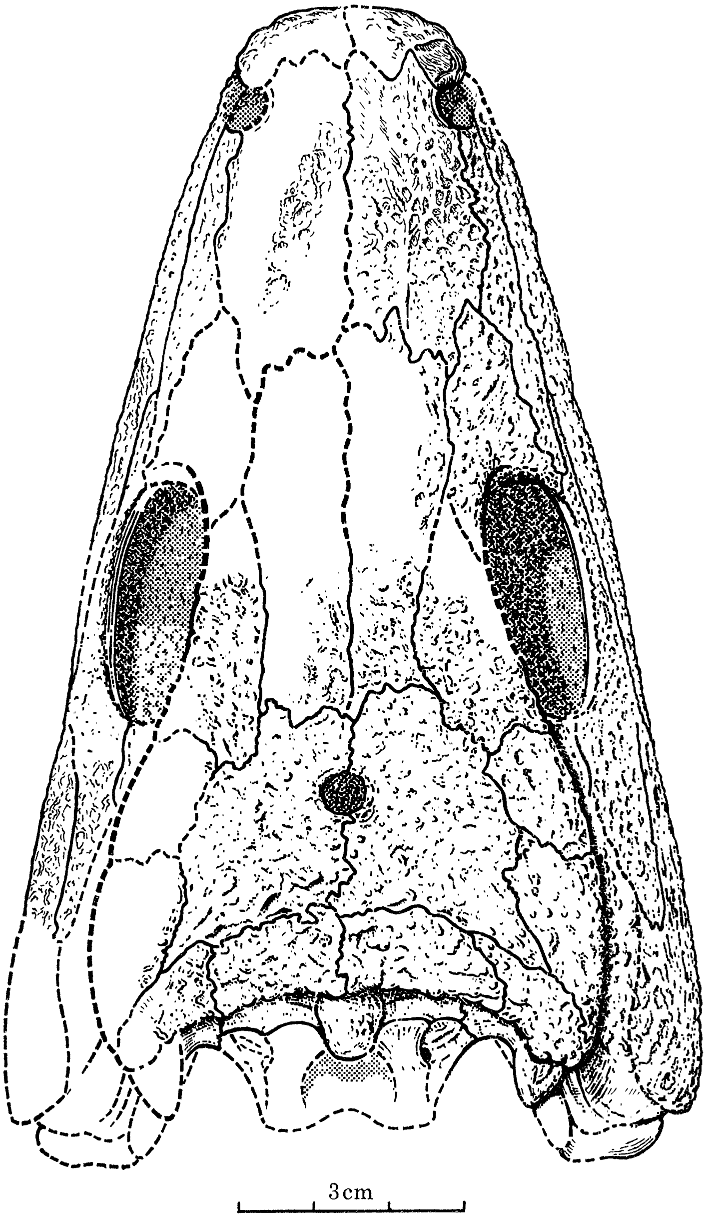

FIGURE 5. *Eoherpeton watsoni*, restoration of the skull, dorsal view. Natural size.

with its upper border formed by a well-preserved concavity in the overlying nasal. On the right the naris is floored in the specimen with rugose and pitted bone distinct from the lacrimal, although the suture between them could not be traced. The narial bone can only be interpreted as septomaxillary, the first to have been described in an anthracosaur (*s.s.*).

The inturning of the base of the premaxillary posteriorly, seen on the right and the similar condition of the front of the left maxillary, make it clear that there was a marked naso-labial groove from the naris to the jaw margin. This is probably a primitive character for tetrapods and occurs in the ichthyostegids, the eogyrinids and other early tetrapods (Panchen 1967*b*).

Nowhere on the generally well-preserved surface of the dermal roof is there any sign of lateral line sulci or canals.

Palate

The configuration of the palate is closely similar to that described in embolomerous anthracosaurs. Although the mesial border of the right pterygoid is hidden there is little doubt that the palate was 'closed', with small interpterygoid vacuities confined to the region of the basal articulation and close apposition or suture between the pterygoids in front.

Nothing is known directly about the form of the vomers: however the anterior edge of the palatine mesial to the choana on the morphological right appears to be 'true edge' and thus defines the shape of the vomer-palatine suture. A small scrap of bone just in front of this in the specimen may be vomer. It is not known whether the vomers were toothless, as in embolomerous anthracosaurs, or bore tusks as in *Gephyrostegus* and some seymouriamorphs. A single vomerine tusk pair is present on each side in *Seymouria* and *Gephyrostegus*, but *Kotlassia* is tuskless (Bystrow 1944).

The right palatine of *Eoherpeton* is completely preserved and its palatal surface fully exposed. The line of the vomerine suture already referred to is convex and inclined backward mesially. Lateral to this the postero-lateral border of the choana is formed by the palatine and is well preserved in the specimen. The palatine extends for about 6 mm dorsally from this border to form a lateral wall to the choana. A small foramen is found in this side wall.

As in other anthracosaurs a tusk pair is situated on the palatine. The anterior tusk site in the specimen is occupied by a very large replacement pit with a diameter of over 6 mm. Its anterolateral border is high and rugose and forms a deep thick wall between the pit and the choana. The second site is also represented by a pit situated near to the lateral edge of the bone and partially closed by post-mortem compression. This has a thickened rugose rim all round but also bears eroded remnants of the tusk. A tusk has therefore been restored there in the palatal reconstruction.

The suture between the palatine and pterygoid and that between the palatine and ectopterygoid were easily traced, except in the case of the anterior end of the former, which is hidden. The palatine–ectopterygoid suture lies in a deep groove with a deeper blindly ending pit separating it from the posterior palatine tusk.

The ectopterygoid probably bore six teeth: the site of the restored fourth is obscured by a fracture in the specimen. The anterior two are represented by pits of which the second is the larger with a diameter of 3–4 mm. Both have thickened rugose margins like those on the palatine. The third site is occupied by a large eroded tooth probably of a similar basal diameter to that of the second pit. The posterior pair of teeth, succeeding the restored one, are present but much eroded in the specimen. Both are somewhat smaller than the second teeth, with a diameter of about 2.5 mm.

The palatal dentition is of considerable interest because of its resemblance to that of *Mauchchunkia bassa* Hotton (1970). *Mauchchunkia* is an anthracosaur of similar size to *Eoherpeton* from an American Mississippian horizon which is probably roughly contemporary with that of Gilmerton (see below). Not only is the tooth count apparently the same, but the raised edge of the replacement pits enhance the resemblance.

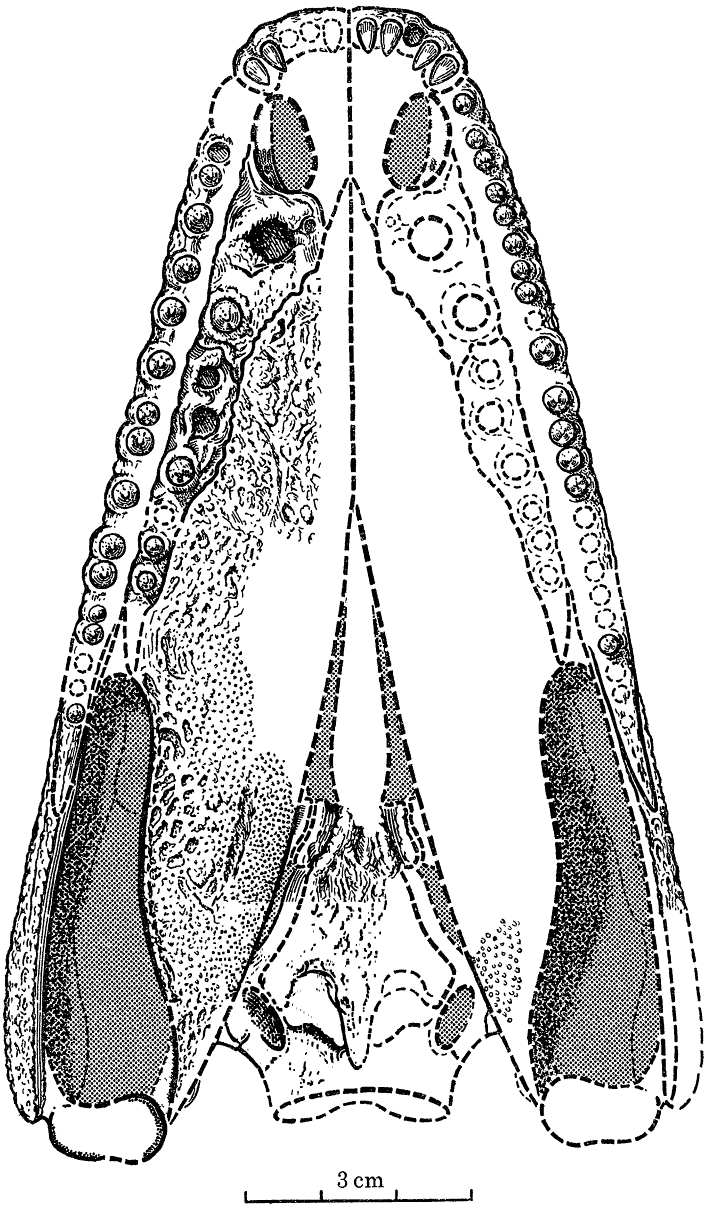

FIGURE 6. *Eoherpeton watsoni*, restoration of the skull, palatal view. Natural size.

The ectopterygoid–pterygoid suture is easily traced except across the fracture noted above and at the posterior end where the ectopterygoid is broken off. The break is just behind the posterior tooth, but the overlying pterygoid bears a deep smooth channel into which the missing fragment of bone fitted. This channel tapers to a point posteriorly at the anterior edge of the subtemporal fossa.

Apart from the concealed mesial border of the pterygoid a small area of that bone is missing between the basal articulation and the area below the back of the orbit. Otherwise the surface of the bone is generally preserved intact although somewhat eroded. The pterygoid is of the type seen in other anthracosaurs, notably *Palaeoherpeton* and *Eogyrinus*. As in these genera, and also probably in *Mauchchunkia*, the free edge of the pterygoid which forms the border of the subtemporal fossa, descended in a smooth curve well below the jaw line, thus following the concave outline of the inner border of the adductor fossa of the lower jaw. This was evidently the case in *Eoherpeton* as the strongly convex edge of the pterygoid occludes the subtemporal fossa to lie along the adductor margin of the lower jaw in the specimen.

The ornament of the pterygoid is closely similar to that in *Eogyrinus* and as far as preserved *Palaeoherpeton*. As in *Eogyrinus* the anterior part of the palatal ramus of the bone, in this case back to about the level of the posterior ectopterygoid teeth, was covered with an irregular dermal ornament. Similarly most of the rest of the bone, including the palatal exposure of the quadrate ramus, was covered with a shagreen of denticles. As in the Coal-Measure genera there is a well-defined area of reticulate ornament just mesial to the border of the fossa, which presumably acted as the origin of a slip of the adductor musculature.

A small area of the epipterygoid, probably that which formed the conical recess for the articulation of the basipterygoid process of the basisphenoid, is exposed over an area obliquely in front of the right process. The articular surface appears to have been broken by crushing but little detail is visible. A fragment of the palatal ramus of the epipterygoid is exposed lateral to the articulation.

Immediately behind the articulation the whole width of the pterygoid is exposed, which gives a useful check on the extent of the bone and hence the depth of the skull as a whole at that transverse level.

Further back the quadrate ramus of the pterygoid is overlain mesially by the braincase in ventral view. The ventro-lateral part of the quadrate ramus is, however, exposed back to the level of the quadrate. The posterior edge of the quadrate ramus is exposed from behind in articulation with the back of the squamosal, paralleling the tympanic groove.

The right quadrate bone is preserved intact, but as it is in natural articulation with the lower jaw the form of its articular surface is hidden. The mesial surface of the quadrate is exposed in the specimen in ventral view. A low but sharp ridge on that surface dorsal to the articular edge probably marks the ventral limit of the investing quadrate ramus of the pterygoid.

The lateral surface of the quadrate lies in its natural relation to the dermal cheek region and projects postero-ventrally, so that the major part of the jaw articulation is visible in lateral view.

A large but featureless plate of bone lies at the back of the specimen and somewhat obscures the back of the articulation. Its mesial end overlaps the left pterygoid in dorsal view. The latter bone has been reflected to the right in post-mortem compression so that in ventral view it is hidden below the left cheek and jaw ramus, while in dorsal view its mesial surface is exposed behind the occiput. The former plate of bone is probably part of the scapulo-coracoid. The left pterygoid provided a useful check of the maximum depth of the quadrate ramus for skull reconstruction. It also demonstrates that, as in *Palaeoherpeton*, the dorsal part of its mesial surface lacked the covering of denticles.

Braincase

Only the right side of the braincase, and of the body of the parasphenoid which covers its ventral surface, are visible in ventral view. The occipital exposure of the braincase, in addition to the opisthotic, is represented by the supraoccipital, noted in the description of the skull roof, and the right exoccipital. Supraoccipital and exoccipital are visible in the specimen in dorsal view. A mass of badly eroded bone lying just below the tabular horn may represent the basioccipital, but no recognizable part of the occipital condyle is preserved.

The ventral surface of the parasphenoid is preserved and visible between the transverse level of the basal articulation anteriorly and the posterior limit of the parasphenoid itself. When the skull is restored this posterior limit lies just behind the level of the back of the fenestra ovalis.

Laterally, in front of the fenestra ovalis, an area of the parasphenoid is missing, thus exposing a part of the ventral surface of the braincase in continuity with its smooth lateral wall. However, the more dorsal part of the braincase wall is concealed and neither the pro-otic foramen nor that for the interorbital vein is visible. These foramina are very large in *Palaeoherpeton* and *Eogyrinus*.

It is not clear whether the lateral wall of the braincase in this region is formed from the pro-otic or from the basisphenoid. There appears to have been considerable fusion between all the separate ossifications of the braincase.

Both basipterygoid processes of the basisphenoid are partially preserved. As in other anthracosaurs a well-defined carotid groove runs ventrally round the circumference of each, just lateral to the parasphenoid. The articular surfaces of both processes are broken or worn away, but it seems probable that the form of the basal articulation was essentially as described in *Palaeoherpeton* and *Eogyrinus*.

As in other anthracosaurs the surface of the parasphenoid is heavily ornamented. Between the basipterygoid processes of the basisphenoid, the parasphenoid is narrow and tapers anteriorly. Its lateral edges in this region are marked by rugose thickening but there is no evidence that the parasphenoid contributed in any way to the articulation itself.

The lateral border of the bone is nowhere preserved behind the articulation but it evidently expanded laterally in normal labyrinthodont fashion under the otic region. More significant is the evidence, from its damaged lateral remnants, that the parasphenoid bore a lateral process on each side extending out towards a relatively laterally situated fenestra ovalis. This situation suggests an incipient stage in the development of the very widely spaced fenestrae, each at the end of an otic tube floored by the parasphenoid, which is characteristic of seymouriamorphs.

Another feature of the *Eoherpeton* parasphenoid suggests the seymouriamorph condition. The bone extends posteriorly to a blunt point in the midline. Immediately lateral to this process the posterior border forms a deep concavity. There appears, however, to be partial fusion with the overlying braincase so that the exact boundary between the two bones cannot be made out.

Behind this concavity a more marked pocket is formed by a deeply descending, sharp-edged ridge of the braincase. Both concavities face postero-ventrally and have an anterior border inclined somewhat laterally. They are presumably for the origin of axial muscles.

Again this condition appears to be a forerunner of that in *Seymouria*. In that genus (White 1939) the parasphenoid forms a pair of deeply descending basal tubera flanking a median posterior process. Each tuber opens posteriorly as a small fenestra which White assumes was filled with a plug of cartilage. The dorso-lateral edge of each fenestra was formed in *Seymouria* by a process of the opisthotic which itself was turned posteriorly at its end to form a shallow pocket above the edge.

The fenestra in *Seymouria* corresponds to the parasphenoid concavity in *Eoherpeton*, while the opisthotic pocket corresponds to that defined in the braincase of *Eoherpeton*. It is probable, therefore, that the ridge and pocket are formed in the opisthotic as in *Seymouria*.

The surface of the braincase is well preserved for nearly a centimetre directly behind the ridge but no opisthotic-basioccipital suture is visible.

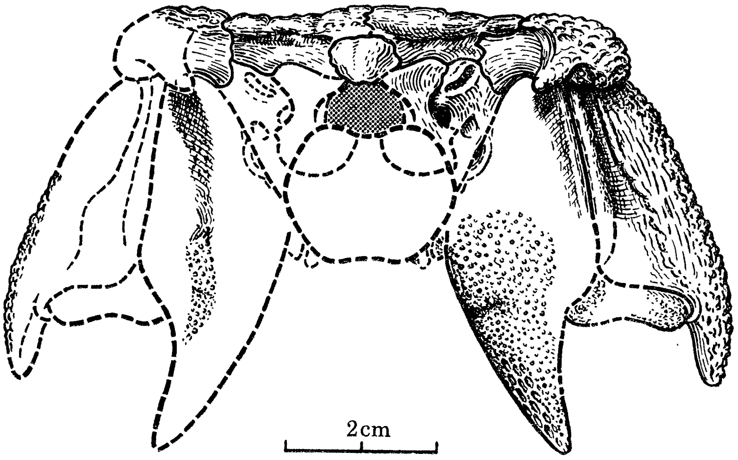

FIGURE 7. *Eoherpeton watsoni*, restoration of the skull, occipital view. Natural size.

Immediately lateral to the basal tuber complex is situated a large fenestra ovalis. This is flattened into a horizontal plane, but in the intact skull must have faced slightly posteriorly as well as ventro-laterally. Its diameter along the longest axis must have been nearly a centimetre by 6 mm across, but in the specimen the fenestra is occluded anteriorly by a small mass of rotted bone which may be a relic of the stapes. Dorso-laterally to the fenestra are preserved the processes for the junction, now disarticulated, of the otic capsule and the skull roof (see below). The bone surface in this region is poorly preserved and no suture could be traced separating pro- and opisthotic.

The occipital surface of the right opisthotic (paroccipital process) has been compressed in the specimen into the same plane as the lateral surface of the bone and is thus visible in ventral view. A sharp ridge, however, indicates that originally the occipital surface was at a right angle to the lateral surface of the bone. Preservation of the occipital surface extends up to the sutural edge for the occipital tabular, but the tabular-opisthotic junction is now disrupted. Just below the tabular contact edge on the opisthotic is situated a shallow pocket, now compressed to a slit about 5 mm long. This pocket is conceivably the remnant of the posttemporal fossa, but this is by no means certain. At about 6 mm below the slit is another blindly ending concavity below which the occipital surface of the opisthotic is no longer well preserved.

The length of the dorso-lateral edge is such that the opisthotic must have contacted the postparietal on the occipital surface as well as the tabular. Further forward, above the fenestra ovalis, the contact between the otic capsule and the skull roof appears to have been similar to that in *Palaeoherpeton* and *Eogyrinus*. Two massive processes, representing the tabular facets on the roof of the braincase, project out of the poorly preserved bone above the fenestra, but the region is too disrupted to make out any further detail.

Part of the right exoccipital is visible in the specimen in dorsal view. It is disarticulated from its original contact with the occipital exposure of the post-parietal and rotated counter-clockwise so that its sutural edge for the post-parietal is now pressed against the lateral margin of the supraoccipital. This sutural edge of the exoccipital is a good fit for the concave ventral border of the post-parietal which is preserved on both sides. Lateral to the exoccipital contact, each post-parietal has a second short contact edge for the opisthotic.

The exoccipitals would have extended down on either side of the foramen magnum from the skull roof to the occipital condyle. The mesial edge of the exoccipital, which formed the border of the foramen magnum, is embedded in the left quadrate ramus of the pterygoid on which the bone now rests and is therefore not visible, but the lateral edge is well preserved.

This lateral edge is strongly concave and formed the mesial border of the large vagus foramen, just as in *Seymouria* and *Kotlassia*. A shallow concavity runs obliquely down in the surface of the opisthotic below the 'posttemporal fossa' to the lateral border of the foramen, which is preserved. Below the foramen edge the exoccipital is broken off laterally but some of the internal body of the bone is visible in front of and below its occipital exposure.

The convex boss-like supraoccipital has been mentioned in describing the occipital exposure of the roofing bones. Its suture with the flanking post-parietals is visible on each side although compression has forced it upwards relative to these bones. Nearly all its lower edge, forming the border of the foramen magnum, is visible.

In *Palaeoherpeton* and other anthracosaurs a massive ridge runs down the occiput in the mid-line from the backwardly projecting skull table to the foramen magnum. In *Palaeoherpeton* this ridge is formed ventrally from the supraoccipital, but the bone extends widely on either side of it (Panchen 1964, figure 2). In *Eoherpeton* the occipital exposure of the supraoccipital is confined to the ridge, while in seymouriamorphs and temnospondyl labyrinthodonts the supraoccipital is lost altogether.

Lower jaw

The lower jaw of *Eoherpeton* is very different from that of Coal-Measure anthracosaurs such as *Eogyrinus*. It is relatively much shallower posteriorly, lacks the enormous meckelian fenestrae characteristic of embolomerous anthracosaurs, and has a short but well-defined retroarticular process. A high surangular crest is also characteristic of the jaw of *Eogyrinus*. This gives a strongly convex dorsal outline to the ramus immediately in front of the articular, and forms a high lateral wall to the adductor fossa. This feature is not so strongly developed in the American eogyrinid *Neopteroplax* (Romer 1963).

In *Eoherpeton* the upper edge of the surangular of the right ramus is concealed by the cheek region. On the left it is concealed anteriorly and missing posteriorly as is the whole articular region. A modest surangular crest has been restored (figure 8).

The jaw rami taper only moderately in front of the adductor fossae, unlike those of *Eogyrinus*, and dorsal and ventral edges of the jaw are almost parallel along the anterior third of its length. The ventral edge in this region, seen in both rami, is marked by a well-defined ridge, although the ramus is elliptical in section.

The dermal ornament which covers the external, lateral surface is quite well preserved on both rami. The symphysial region, partially preserved only in the right ramus, is ornamented externally with small, shallow, but well-defined pits. Between this extreme anterior region and a point about half way along the ramus the ornament is generally shallow and ill-defined, so that most of the dentary and the anterior (pre-) splenial are rather smooth. However, the right dentary shows a short shallow groove (figure 9) at about 2.5 cm from its anterior end which extends back horizontally for about 1 cm. There is no corresponding groove on the left ramus and the groove cannot plausibly be interpreted as a lateral line sulcus. It is perhaps for a nerve or blood vessel. The post-splenial, preserved anteriorly on both sides, is rather more strongly ornamented with net-like pits and ridges, and the back of the dentary, preserved on the left, with a shallow but more ridged ornament.

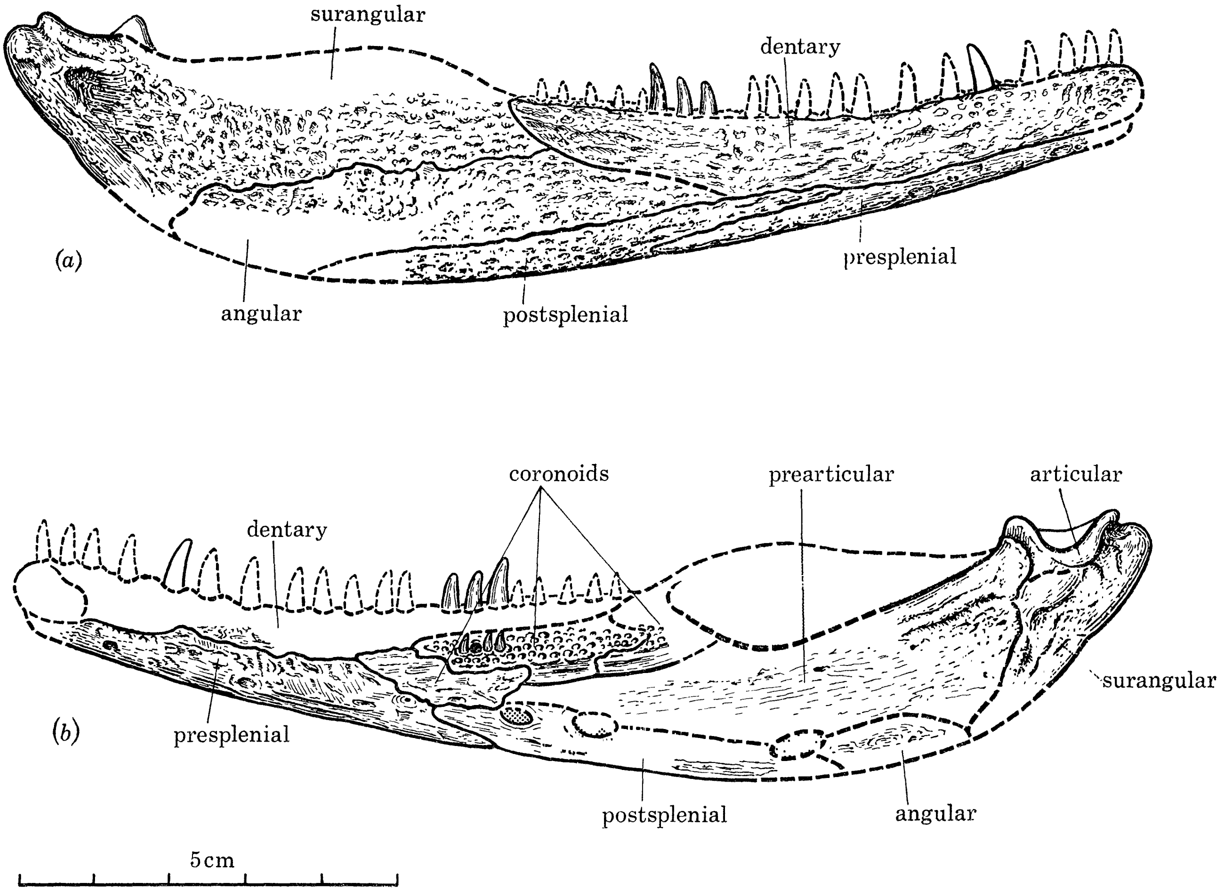

FIGURE 8. *Eoherpeton watsoni*, right jaw ramus, restored. Natural size: (*a*) lateral, (*b*) mesial.

Behind the dentary the ornament is of characteristic anthracosaur type and reflects that on the cheek region which lies above it. It extends back only to the front of the articular region, so that its posterior extension again corresponds to that on the cheek.

As with the skull roof there is nothing which could reasonably be interpreted as evidence of a lateral line system. However, it should be noted that the region which carries the posterior half of the mandibular sulcus in *Eogyrinus* and other anthracosaurs is largely missing on both sides in *Eoherpeton*; and that the anterior part of the sulcus, which runs along the splenial bones, is less well-defined in the Coal-Measure genera.

The ossifications present in the lower jaw of *Eoherpeton* are those typical of primitive tetrapods. On the lateral surface the horizontal suture between the dentary and the two splenials is visible on both rami for almost its complete length, as is the oblique suture between the splenials, which gives a considerable overlap of the post-splenial over the presplenial.

The suture forming the posterior boundary of the dentary above and behind the splenial suture could not be traced on the right, but is in part traceable on the left. Behind the dentary the lateral surface of the ramus is largely formed by the surangular above and the angular below. The anterior part of their horizontal suture is preserved on the left and almost the whole suture on the right.

The surangular forms the retroarticular process, surrounds the articular, except on its anterior and antero-mesial surface, and forms the postero-ventral border of the ramus to a point probably in front of the articular region. This whole region is preserved only on the right.

The junction between the articular and the investing surangular could not be traced as a suture anywhere round the circumference of the former and it is probable that some degree of fusion is present between the two bones. The shape of the articular surface was probably similar to that in *Eogyrinus* but the impacted quadrate contact conceals this. However, the articular surface (glenoid) does not stand above the surangular and the rest of the jaw as it does in the Coal Measure genus.

There is a well-marked lip surrounding the glenoid and below this on the lateral surface of the ramus the unornamented surangular is marked by a large shallow triangular concavity. A thick cylindrical region of the bone extends down behind this to form the back of the ramus. Dorsally this region expands slightly to form the rounded retroarticular process.

On the mesial surface there is a corresponding concavity, somewhat rugose posteriorly, which is continuous dorsally with a broad ill-defined groove separating the retroarticular process from the articular. The process and both concavities presumably acted as areas of insertion for the depressor mandibulae muscle. The rugose area on the mesial surface is dorsal to a similar area in *Eogyrinus*. In the latter genus it is formed from the angular rather than the surangular.

On the mesial surface the surangular has a vertical suture with the prearticular at the level of the front of the articular. The prearticular is a smooth bone which however forms a thickened rim to the adductor fossa. Immediately below the thickest part of the rim is a groove separating it from the body of the bone. The thickened rim expands posteriorly to form a massive buttress to the articular: the line of junction between the two is easily traced.

The ventral edge of the prearticular is missing and the course of its suture with the angular and the post-splenial could not therefore be traced. The mesial exposure of the angular is represented only by a displaced scrap of bone, as is the posterior part of the post-splenial. The sutures between the three bones have been restored in normal labyrinthodont fashion in the obvious absence of the enormous posterior fenestra of embolomerous forms. A posterior meckelian foramen has also been restored at the junction of the three bones.

Further forward the mesial surface of the post-splenial is well preserved and the ventral rims of two other foramina are visible, although crushing has destroyed their dorsal borders and that of the bone itself. Beyond the anterior foramen a process of the post-splenial extends forward between the presplenial and the anterior coronoid. Its bounding sutures were easily traced.

The usual three coronoids were present. The anterior one is a small, relatively ventral bone. In addition to the contacts with dentary, presplenial, prearticular and middle coronoid present in *Eogyrinus* and *Kotlassia*, the anterior coronoid also has a suture (noted above) with the post-splenial. In *Eogyrinus* this contact is prevented by the large anterior meckelian fenestra, while in *Kotlassia* the anterior coronoid is much further forward. The latter is also the case in *Seymouria* in which there is no contact with the prearticular either.

The anterior coronoid is devoid of the shagreen of denticles present on that of *Eogyrinus*, a character which *Eoherpeton* shares with the American eogyrinid *Neopteroplax*. However, the middle coronoid and the small part of the posterior coronoid preserved are denticle-covered except near their ventral border. In addition the middle coronoid bore sites for four small teeth, represented in the specimen by three rather eroded teeth and one replacement pit.

With the small size and posterior position of the anterior coronoid, some 4.5 cm of the mesial surface of the jaw ramus from its anterior end must have been formed from the dentary and presplenial alone. The surface and dorsal edge of the presplenial are visible except at its extreme anterior end, so that the course of the suture between the two bones is preserved. However, only a small ventral area of the mesial surface of the dentary is visible and nothing is thus known about the form of the symphysial surface.

Little is visible of the dentary dentition. The tooth bearing upper margin of the right ramus is concealed below the snout. On the left a solitary crownless root just over 2 mm in diameter is visible anteriorly while three consecutive teeth are preserved much further back. The positions of all four are shown in figure 4 and in the composite reconstruction (figure 8).

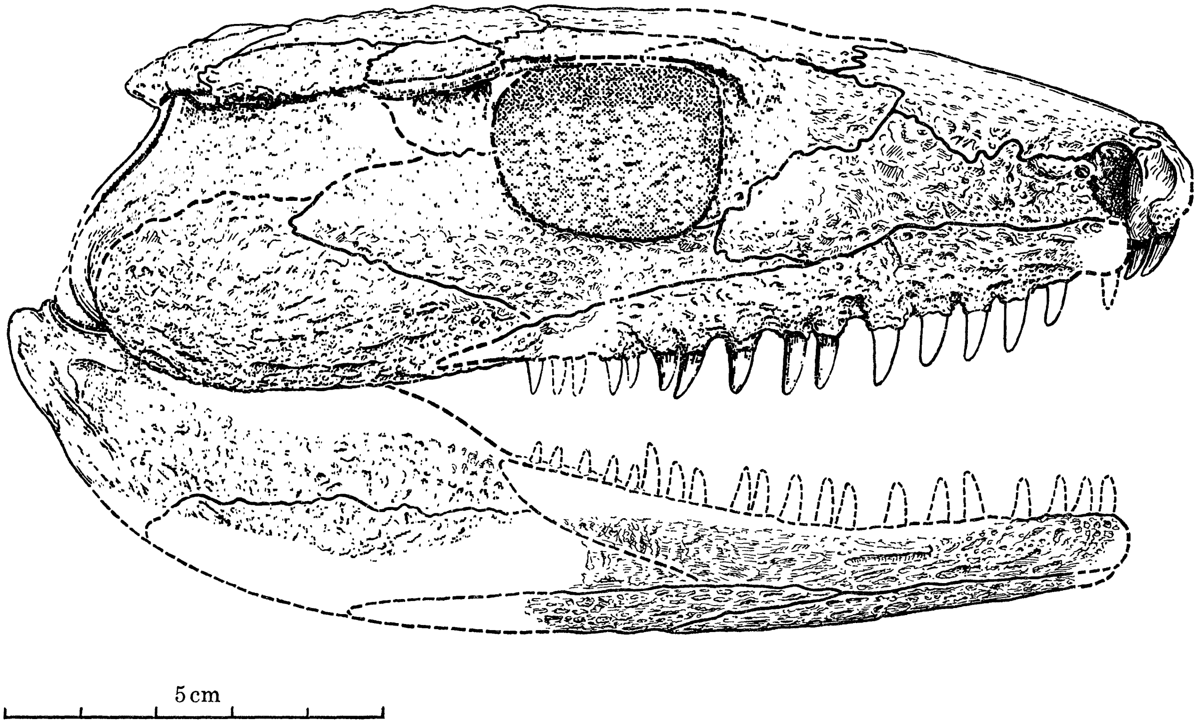

FIGURE 9. *Eoherpeton watsoni*, restoration of skull and jaws, lateral view. Natural size.

Restoration of the skull

Graphic restoration of the skull of *Eoherpeton* in three dimensions was relatively easy and is presented in figures 5–9. In restoring the skull I have attempted to take as little as possible for granted. Bilateral symmetry is not assumed and thus the outlines and sutures drawn as continuous lines are only those visible on the skull. Similarly the shaded areas are confined to what is actually preserved. The lateral view of the skull and jaw (figure 9) is based on the right side of the skull roof. In the case of the lower jaw, however, the data on the lateral external view from right and left are to some extent complementary and the restoration of the jaw alone (figure 8) is 'composite' in lateral view, being based on both rami. Data for the mesial view are only available from the right ramus.

The shape of the skull can be restored with considerable confidence. The skull table is almost certainly undistorted in the specimen. The relative movement of the rest of the skull roof to the table, related to a break across the frontals, is easily corrected by alinement of the margins of the orbit and by the very small adjustment needed between the back of the squamosal and the skull table.

The width of the palatal surface may be estimated without fear of serious error at the transverse level of the two preserved basipterygoid processes. This controls not only the width but also the height of the skull table at that level and hence the slope of the cheek region.

Thus restored the skull of *Eoherpeton* is much more 'reptiliomorph' than the skull of *Palaeoherpeton* ('*Palaeogyrinus*'): Panchen 1964, figures 11–13; 1970, figure 1), an anthracosaur of closely similar size. The cheek is more vertical and less convex in *Eoherpeton* and thus the orbit 'looks' laterally rather than dorso-laterally. The quadrate condyles are very little behind the plane of the occiput. Correlated with this is a relatively short quadrate ramus of the pterygoid and a steep slope to the back of the cheek region in lateral view.

The only wholly conjectural structure in the restoration is the occipital condyle. This has been closely modelled on that of *Palaeoherpeton*. However, the more primitive nature of *Eoherpeton*, together with its much earlier horizon, might suggest that the remnants of a notochordal canal persisted through the condyle and the base of the otico-occipital region of the braincase, as was apparently the case in *Ichthyostega* (Jarvik 1952).

RELATIONSHIPS OF *EOHERPETON*

Eoherpeton watsoni is clearly an anthracosaur labyrinthodont amphibian in the sense in which the term is used below. The features of the skull which make this conclusion inescapable are the presence of a suture between the tabular and parietal on the skull table, the presence of tabular horns, the persistence of the lateral kinetism between the skull table and the flanking cheek regions, the persistent and large intertemporal bones and the form of the dermal ornament. In all these characters it agrees with the embolomerous anthracosaurs of the Upper Carboniferous and Lower Permian (Panchen 1970).

There is also agreement in the retention of a suite of characters that mark both as primitive labyrinthodonts. These include the retention of a discrete supraoccipital ossification, a paroccipital process formed largely from the well-ossified opisthotic, a mobile basal articulation, a closed palate and a high tropibasic skull. The presence of a naso-labial groove from naris to jaw margin is also probably a primitive tetrapod character (Panchen 1967*b*) and one shared with at least the eogyrinid anthracosaurs.

However another series of characters suggest relationship of *Eoherpeton* to the Seymouriamorpha rather than to the embolomerous forms. The 'reptiliomorph' appearance of the skull has already been noted. Reinforcing this are the presence of a (?vestigial or incipient) post-temporal fossa, the widely spaced fenestrae ovales floored by lateral processes of the parasphenoid, the basal tubera of the parasphenoid and their associated invaginations, the relationships of the lacrimal bone, the form of the septomaxillary ossification (cf. *Seymouria*: White 1939; Panchen 1967*b*) and the structure, in most respects, of the lower jaw.

Finally there are several characters of *Eoherpeton* which are diagnostic and do not favour either embolomere or seymouriamorph relationship. The most important of these are the broad quadratojugal–maxillary contact, a primitive feature, the form of the otic 'notch' and tympanic groove and the presence of a retroarticular process. Minor characters include the large orbits and pineal foramen, and the relatively open sutures, suggesting immaturity, the form of the tabular horns, the course of the tabular–parietal suture, the truncated parietals and the presence of true teeth on the middle coronoid.

Until recently the holotype of *Eoherpeton* was the only anthracosaur skull known from the Lower Carboniferous (Viséan or earlier). Recently, however, early anthracosaurs have been described from the Lower Carboniferous of the New World. The most important specimens are from Greer in West Virginia, where numerous labyrinthodont specimens have been collected by the staff of the Cleveland Museum of Natural History. The commonest labyrinthodont, represented by many complete and partial skeletons, is *Greererpeton burkemorani* Romer (1969) whose relationship to *Pholidogaster* is discussed below. In addition two new species of anthracosaur have been named from Greer, *Proterogyrinus scheelei* Romer (1970) and *Mauchchunkia bassa* Hotton (1970).

The horizon from which the Greer specimens were collected is the Bickett Shale, Bluefield Formation (or group), Mauch Chunk Group (or series). Insofar as correlation is possible the horizon is very close to that of the Gilmerton Ironstone from which *Eoherpeton* probably came (Weller *et al.* 1948; Francis & Woodland 1964; Romer 1969; Hotton 1970; Panchen 1970).

Comparison between *Eoherpeton* and the Greer anthracosaurs is difficult for two principal reasons. First there is doubt about the level of taxonomic difference between *Proterogyrinus* and *Mauchchunkia*, and secondly while both Greer holotypes include postcranial material their skulls are relatively poorly preserved, whereas *Eoherpeton* has an almost complete and beautifully preserved skull, but no diagnostic post-cranial remains.

Proterogyrinus and *Mauchchunkia* were placed by their respective authors in different monotypic families of anthracosaurs. The most significant diagnostic difference between the two appeared to be in the structure of their vertebrae. In both cases a vertebra consists of neural arch, pleurocentrum and intercentrum as in all early labyrinthodonts. In *Proterogyrinus* only about eight scattered central elements are preserved in the holotype and no vertebra is in articulation. All the central elements were thin hoops of bone open dorsally and Romer assumed that both intercentra and pleurocentra were represented. In *Mauchchunkia*, on the other hand, the vertebral column of the trunk is almost complete and in articulation. The pleurocentra are similar to the centra of *Proterogyrinus*, if somewhat better ossified, but the intercentra are ossified only ventrally and are thus crescentic wedges. They resemble those of *Gephyrostegus* and, although relatively larger, those of seymouriamorphs and early reptiles.

As Dr R. L. Carroll had pointed out to me, and as I was able to confirm by inspection of the material, all the articulated anthracosaur vertebrae from Greer are of the *Mauchchunkia* type. The principal central element which Romer interpreted as an intercentrum in *Proterogyrinus* is certainly a sacral or caudal pleurocentrum. It was interpreted as an intercentrum because of the presence of a large articular facet for the capitular head of a rib on each side, but this feature is standard in the sacral and early caudal pleurocentra of anthracosaurs. It can be seen in *Eogyrinus* (Panchen 1966), in *Archeria* (Case 1911; Panchen 1970, figure 6*c*; and specimens A.M.N.H. 4552 and M.C.Z. Block No. 3, Geraldine 1939) and even in a Greer specimen (C.M.N.H. 11067).

Although the degree of ossification, particularly of the appendicular elements, is very variable, there are no significant post-cranial differences between *Proterogyrinus* and *Mauchchunkia*. From the material then developed I concluded, as had Dr Carroll, that this applied to all the Greer anthracosaurs.

Hotton notes a number of differences between his restoration of the skull of *Mauchchunkia* and Romer's of *Proterogyrinus*. The proportions of the skulls are said to be different, *Proterogyrinus* having a relatively longer snout and also relatively smaller post-parietal bones. Unfortunately both Hotton and Romer use the ratio of the length of nasals plus frontals to that of the parietals plus post-parietals as a measure of relative snout length. In *Proterogyrinus* the parietals are somewhat truncate as restored, like those of *Eoherpeton*, while those of *Mauchchunkia* each have a mesial process extending forward between the orbits. Also the nasals of *Mauchchunkia* are broken and probably incomplete anteriorly. The relative length of the post-parietals does not seem significantly different. Those of *Mauchchunkia* reach a point in the midline exactly halfway between the back of the skull table and the back of the pineal foramen (from published figures and measurement of the type): this is also the case in *Proterogyrinus*. A small process of the post-parietal extends a little further forward in *Mauchchunkia* but not in *Proterogyrinus*: the right post-parietals seem to be of similar shape and proportions in the two specimens.

The estimated maxillary tooth count of the two specimens is also different, 40+ for *Proterogyrinus*, 26 for *Mauchchunkia*, but the danger of assigning taxonomic significance to such estimates has already been emphasized in describing the dentition of *Eoherpeton*.

Thus the weight of evidence is overwhelmingly in favour of Carroll's original conclusion that there is only one genus and probably species of anthracosaur known from Greer (Carroll *et al.* 1972). There is, however, one small piece of counter evidence. When I was able to study the material (September 1971) five poorly preserved anthracosaur skulls were known from Greer. The *Proterogyrinus* holotype and one other (C.M.N.H. 11035) are of virtually identical size (pp length 86 mm, measured in the former, estimated in the latter), while the *Mauchchunkia* holotype and the other two are again of virtually identical size (estimated pp length 150 mm). This is uncomfortably close to the situation in British eogyrinids (Panchen 1964, 1970, 1972*a*) where *Palaeoherpeton* and *Pholiderpeton* ('*Eogyrinus*': Panchen 1964) are chiefly distinguished by size at the Swanwick locality, and *Pteroplax* and *Eogyrinus* likewise at Newsham.

Subsequently Professor A. S. Romer (personal communication) concluded that only one species of anthracosaur was present at Greer. Provisionally, therefore, the Greer anthracosaurs may be referred to collectively as *Proterogyrinus* (the priority name), with '*Proterogyrinus*' and '*Mauchchunkia*' to indicate the respective holotypes.

Few significant comparisons can be made between the skulls of *Eoherpeton* and *Proterogyrinus*. The median skull roof is preserved in all three holotypes and is essentially similar. (The suture which Romer interprets as the tabular–supratemporal junction in '*Proterogyrinus*' coincides with the supratemporal–intertemporal suture of the other two: the 'supratemporal–intertemporal' suture of '*Proterogyrinus*' is restored.) The tabular horn appears to be different. In *Proterogyrinus* there is a long flat blade, particularly well shown in '*Mauchchunkia*', in contrast to the rounded cone of *Eoherpeton*. It is possible that the form of the tabular in *Eoherpeton* is correlated with the unusual orientation of the tabular parietal suture.

The side of the skull roof in the Greer anthracosaurs is not sufficiently preserved for useful comparison. Hotton restores a small rectangular quadratojugal in '*Mauchchunkia*', without comment, which is very different from that of *Eoherpeton*. The quadratojugal is present only on the left side in '*Mauchchunkia*' and I could not convince myself that the whole bone was preserved.

More important is the condition in *Proterogyrinus* of the otic 'notch'. Two matters of interpretation are involved in deciding this, the position of the quadrate condyle relative to that of the occipital condyle and hence the slope of the cheek, and secondly the forward extent of the 'notch' below the margin of the skull table.

There is little data on the form of the notch in '*Proterogyrinus*'. Part of what is probably the cheek region is preserved but not restored and the slope of the back of the squamosal cannot be inferred. In '*Mauchchunkia*' Hotton restores a squamosal whose posterior edge slopes down at about 45° from a deep notch of which the dorsal border extends forward well into the supratemporal, a condition otherwise unknown in anthracosaurs apart from *Gephyrostegus*.

The only controls on the relative position of the quadrate are the overall length of the disrupted left maxillary and the less broken lower jaw. By extending the restored anterior end of the nasals to correspond to their relative length in '*Proterogyrinus*', the quadrate of '*Mauchchunkia*' would move forward to approximately the same plane as that of *Eoherpeton*. The articular region of the right jaw in '*Mauchchunkia*' is preserved in approximately that plane relative to the back of the skull table.

The lateral edge of the left supratemporal of '*Mauchchunkia*' is shown by Hotton to be divided into two regions which meet at an angle. This angle he assumes to mark the anterior limit of the otic notch. However, the supratemporal of *Eoherpeton* is similarly but not so conspicuously angled and there is little doubt in this case that the notch is nowhere bordered by the supratemporal. Thus the available evidence does not suggest any significant difference between the temporal region of *Proterogyrinus* and *Eoherpeton*.

There is little information on the palate or braincase of *Proterogyrinus*. A pterygoid of normal anthracosaur pattern is preserved in '*Proterogyrinus*'. In '*Mauchchunkia*' the palatal dentition and pterygoid denticles are visible but little else of the palate.

Hotton considers that there were four tusk sites on each palatine ('two tusks and pit pairs') a unique condition for anthracosaurs, but comments on the similarity of the palatal dentition of '*Mauchchunkia*' to that of *Eogyrinus*, which has the usual two. It is not, however, clear either from his restoration or from the specimen that this is the case. The apparent similarity of the palatal dentition to that of *Eoherpeton* has already been commented upon.

Few data are available on the braincase of *Proterogyrinus*. The exoccipital seems to have been similar in '*Mauchchunkia*' and *Eoherpeton* and the fenestra ovalis in a similar position. It is not known, however, whether the American form shared the seymouriamorph characters of the *Eoherpeton* braincase, the basal tubera, the lateral extension of the parasphenoid towards the fenestra ovalis and the (?) posttemporal fossa.

The lower jaw of '*Mauchchunkia*' is visible only in lateral view, so that the condition of the meckelian foramina is unknown. In general shape it appears similar to that of *Eoherpeton*, if somewhat deeper, but there was no apparent retroarticular process.

In summary the skull of *Proterogyrinus* seems on rather limited information to have been essentially similar to that of *Eoherpeton*. Known significant differences are confined to the probable difference in the dentition, with fewer, stouter marginal teeth in the *Eoherpeton*, and the presence of a retroarticular process in that genus.

Both British and American forms probably represent the same group of early and primitive anthracosaurs. It remains to consider their relationship to the embolomerous anthracosaurs, the gephyrostegids and the seymouriamorphs, which together with them constitute the order Batrachosauria. The phylogeny and interrelationships within that group are considered in the next section. However, the significance of the apparently seymouriamorph characters of *Eoherpeton* must be assessed first.

It has already been suggested (Panchen 1970, pp. 13–14) that the exclusion of the labyrinthodont lacrimal from the orbit is a consequence of the backward movement of orbits relative to the bones lateral to them which occurred during the fish-tetrapod transition. This separation has occurred to a variable degree in most labyrinthodonts, except some aberrant or short-faced forms. In the embolomeres, in relation to the long snout, there is a broad prefrontal–jugal contact, whereas in *Gephyrostegus* (Carroll 1970) and in seymouriamorphs (also early reptiles) there is an orbital lacrimal. The condition in *Eoherpeton* could well be an ancestral one for both embolomeres and other batrachosaurs.

The same principle applies to most features of the lower jaw. The lower jaw of embolomeres is specialized. Its unusual depth may be a primitive feature but the enormous fenestrae, perhaps acting as the origin of enlarged intermandibular muscles, may have been specializations concerned with jaw opening in a massive aquatic animal (Panchen 1972*a*). In this respect the more generalized jaw of *Eoherpeton* would then not debar it from either embolomere or seymouriamorph ancestry. This involves the assumption that the ancestral anthracosaurs were relatively terrestrial forms (see below).

The coronoid teeth of *Eoherpeton* may also be regarded as a primitive feature (Nilsson 1944) recalling the coronoid tusks of Rhipidistia (e.g. *Eusthenopteron*: Jarvik 1944), but the retroarticular process needs further discussion.

It is perhaps to be correlated with the form of the tabular horn. I have suggested that the blade-like horn of embolomeres, present also in *Proterogyrinus*, acted as an extension of the origin of the depressor mandibulae muscle (Panchen 1964). The retroarticular process in advanced temnospondyl labyrinthodonts certainly acted as the principal insertion of that muscle.

The tabular horn of *Eoherpeton* may be regarded as intermediate between the condition of embolomeres and *Proterogyrinus* on one hand and gephyrostegids and seymouriamorphs on the other, as noted above. It may also with less certainty be considered primitive and thus the ancestral condition for both other groups. On this or any alternative theory, the retroarticular process would have aided the action of the depressor in a perhaps semi-aquatic animal. In the embolomeres, the presence of the tabular blade (and the fenestral muscles) would have rendered the process superfluous, while in the more terrestrial seymouriamorphs the problems of jaw opening would be much smaller. It may be noted that the presence of a retroarticular process need not be of great taxonomic significance: it is present in the osteolepid rhipidistian *Megalichthys* (Watson 1926) but not apparently in the very closely related genus *Ectosteorhachis* (Thomson 1964).

The basal tubera of *Eoherpeton* and seymouriamorphs may also be related to the relatively terrestrial habit of these animals. *Eoherpeton* and *Seymouria* have skulls of roughly equal size and in both cases quadrate and occipital condyles are in about the same transverse plane. In large terrestrial temnospondyls, notably *Eryops*, the jaw articulation extends well behind the occipital condyle and thus to some extent counterbalances the turning movement of the skull about the occipital articulation with the atlas. In the two batrachosaurs this is not the case and the head must have been held up entirely by powerful dorsal axial muscles. These would have been opposed by ventral muscles inserted on the tubera which flank the occipital condyle, and hence help to maintain the condyle and atlas in articulation and also to rotate the skull in a horizontal plane. In the embolomeres on the other hand the head was probably virtually immobile on the neck (Panchen 1964). They may therefore either have lost the tubera of any ancestor like *Eoherpeton* or never have developed them.

The condition of the posttemporal fossae of *Eoherpeton* is puzzling, assuming that they have been correctly identified and the occiput correctly reconstructed. The 'fossa' in *Eoherpeton* is in the same morphological position as in *Seymouria* and *Kotlassia* except that it is entirely bounded by opisthotic and thus does not encroach into the occipital tabular. This is essentially the condition in temnospondyls such as *Eryops* (Sawin 1941). In *Eryops* the tabular and post-parietal border the 'mouth' of the fossa, but nevertheless the fossa is roofed as well as floored by opisthotic which separates the fossa from the underside of the skull table.

As the posttemporal fossa of early tetrapods is the homologue of the fossa bridgei of their fish ancestors (see, for example, Panchen 1972*b*), that of *Eoherpeton* appears to be vestigial rather than incipient and thus tending towards the embolomere condition in which it has been lost. There is so much uncertainty about the reconstruction of the occiput, however, that I should not like this to be seen as debarring *Eoherpeton* from seymouriamorph ancestry.

Similarly the suggestion of an incipient serymouriamorph condition of the parasphenoid should not debar *Eoherpeton* from embolomere ancestry. Thus the anatomy of the *Eoherpeton* and *Proterogyrinus* gives valuable information on the morphology and habits of primitive anthracosaurs and hence on batrachosaur phylogeny. The condition of the otic notch also has a significant bearing on theories of reptile origin. Both are discussed in the next section.

On the phylogeny and classification of batrachosaur labyrinthodonts

The Batrachosauria, as the term is used here, comprise the primitive and embolomerous anthracosaurs, the gephyrostegids and the seymouriamorphs (Panchen 1970). With the exception of the embolomeres all have reptiliomorph postcranial skeletons with a relatively short pre-sacral vertebral column, well-developed limbs, with (where known) five digits on the manus and pes.

The vertebrae of the batrachosaurs are characterized by a large cylindrical notochordal pleurocentrum to which the neural arch is firmly sutured or, in some seymouriamorphs, fused. In the larger seymouriamorphs, including *Seymouria* and *Kotlassia*, the neural arches are massive and dome-shaped with widely spaced zygapophyses. This development is paralleled in some microsaurs (e.g. *Pantylus*: Carroll 1968) and in early reptiles.

The intercentrum of batrachosaurs is normally ossified as a small crescentic wedge lying in front of the pleurocentrum and below the notochord. *Proterogyrinus*, the gephyrostegids and the seymouriamorphs constitute a chronological as well as a morphological series in the reduction of the relative size of the ossified intercentrum. It is probable that in *Proterogyrinus* and in *Gephyrostegus* (Carroll 1970), the intercentrum was extended dorsally round the notochord in cartilage, but this is less likely in the seymouriamorphs.

Romer (1947) first pointed out that it is probable that the intercentra of embolomeres, which are complete if narrow disks, were secondarily derived from the gastrocentrous type then known only in the seymouriamorphs. This was on the assumption that the batrachosaur vertebra was derived from a proto-rhachitomous condition (Romer 1964). I supported this conclusion and its premises on the assumption that the intercentrum must first have become shortened from the large wedge of rhachitomes to produce the typical batrachosaur condition, before subsequent dorsal expansion to give the embolomerous one (Panchen 1966, 1967*a*).

With the realization that *Pholidogaster* was in no way closely related to the batrachosaurs, it became unnecessary to postulate a proto-rhachitomous ancestor for batrachosaurs and the premises upon which the above argument were based were obviously false (Panchen 1970, and below). However, it now seems even clearer that the distinctive vertebrae of embolomeres, together with their other aquatic specializations, are secondarily derived from a much more terrestrial habit represented by *Eoherpeton* and *Proterogyrinus* (Panchen 1970; Hotton 1970).

The history and, in general terms, the phylogeny of the batrachosaurs from the late Viséan (early Chesterian) onwards is fairly clear. An early and probably ancestral group is represented by *Eoherpeton* and *Proterogyrinus*. These were anthracosaurs of medium size (pp length of skull 80–150 mm) and at least partially terrestrial habit, known only from the Upper Viséan of Europe and North America.

The first embolomeres to appear in the record are of Namurian age. The diagnostic intercentra are associated with other skull and skeletal elements known from the Point Edward formation, Nova Scotia (Romer 1958, 1963; Panchen 1970; Carroll *et al.* 1972). Embolomeres are also less certainly present in the Limestone Coal Group of the Edinburgh district (Namurian A) (E. H. Beaumont & A. L. Panchen, unpublished) and the Hinton Shales of West Virginia which are roughly contemporary (Romer 1941).

A primitive terrestrial batrachosaur has recently been described from a Namurian B horizon in the Ruhr, West Germany (Boy & Bandel 1973), and is classed by the authors, probably correctly, as a gephyrostegid. However, from the base of the Coal Measures until early Westphalian D time batrachosaurs are known only from three areas; from Nova Scotia, from the Coal Measures of Scotland and the Midlands and Northern England, and from the Appalachian region and later the Mid-West of the U.S.A. (Panchen 1970, 1973*b*). The only exception is the large embolomere *Eobaphetes*, but its locality and horizon are not certainly known. All the Coal Measure forms are anthracosaurs (*s.s.*) and the vast majority are eogyrinid embolomeres, which must be regarded as the central stock in embolomere evolution. A second family, the Anthracosauridae, is certainly represented only by the type species *Anthracosaurus russelli* from Scotland and County Durham.

In Westphalian D and Stephanian times the batrachosaurs widen their range taxonomically and stratigraphically. Gephyrostegids are known from the Westphalian D of Bohemia and Ohio, which areas also have embolomeres including some at Linton, Ohio, doubtfully attributable to the Anthracosauridae (Romer 1963).

Gephyrostegid, anthracosaurid and eogyrinid anthracosaurs are not known to have survived the Carboniferous nor certainly to have further extended their range beyond the classic areas of Britain, Nova Scotia, the Appalachians and Bohemia (*Memonomenos* from the Lower Permian of Bohemia is not an anthracosaur). The two remaining taxa of batrachosaurs are principally, and perhaps exclusively, confined to the Permian.

They are the embolomere family Archeriidae, known with certainty only from the Wolfcampian and Leonardian of the southwestern U.S.A., and the suborder Seymouriamorpha. While embolomeres which are certainly archeriid are confined to the Permian and to the single genus *Archeria*, the family may have a much longer history. The distinctive teeth and long narrow snout of *Archeria* are foreshadowed in the tiny embolomere *Calligenethlon* from the

Westphalian B of Nova Scotia (Carroll 1967) which I placed in the Eogyrinidae, and even, arguably, in the anthracosaurs of the Viséan and Namurian of North America.

The Seymouriamorpha are known from the same area of the U.S.A. as *Archeria*, from the Lower Permian of Central Europe and from the Permian of the western U.S.S.R. Seymouriamorph fragments are also reported from the Triassic of the U.S.S.R. by Shishkin (Olson 1965). It is not improbable that the seymouriamorphs are descended from the late Carboniferous gephyrostegids, assuming that the latter shared the incipient seymouriamorph skull characters seen in *Eoherpeton*. The condition of the material is not however sufficiently good to confirm this (Carroll 1970).

Description of the batrachosaurs from the Lower Carboniferous together with the controversy which surrounds the phylogeny and nomenclature of the group make a fresh look at its classification desirable.

Unfortunately the controversy extends to the name to be applied to the taxon embracing all the labyrinthodonts so far discussed. The history of this is reviewed in my recent monograph (Panchen 1970). The recent history is that Säve-Söderbergh's (1934) term Anthracosauria was first used specifically to include the Seymouriamorpha by Romer in 1947, when the latter were otherwise generally but incorrectly regarded as reptiles. While most western European workers used Romer's successive classifications as a framework for their studies his expanded usage of the term Anthracosauria was never really accepted here (see, for example, Westoll 1962, p. 45; Brough & Brough 1967).

At about the same time Efremov (1946) introduced the term Batrachosauria to denote a subclass of tetrapods including only the Seymouriamorpha. Olson (1962) retained the denotation but elevated the group to class status as a 'discrete radiation...in neither a strictly amphibian nor strictly reptilian mode...'. The term Batrachosauria was subsequently extended 'down' to include the embolomerous forms by Tatarinov & Konzhukova (1964) (although in their usage the order Anthracosauria has, superfluously, the same denotation as the subclass Batrachosauria) in much the same way that the term Anthracosauria was extended 'up' by Romer!

Kuhn (1965) used Batrachosauria in the same extended sense and I endorsed this, under his editorship, in my monograph on the Anthracosauria (Panchen 1970). The usage has since been rejected by Kuhn (1967) on (invalid) priority grounds, but Olson (1971) appears to incline towards it. However, both Romer (1972*a*) and Carroll (1972) objected strongly to both the use of Batrachosauria in the extended sense (or at all) and the use of Anthracosauria restricted to the embolomeres. Romer notes (correctly) that the term Embolomeri (Cope 1884 – Embolomera, Cope 1880) has priority over Anthracosauroideae (Watson 1929) and Anthracosauria.

In presenting a revised classification below I have retained the use of the term Batrachosauria to include all the taxa under discussion as one of the four orders (Ichthyostegalia, Palaeostegalia: Panchen 1973*a*, Temnospondyli, Batrachosauria) comprising the subclass Labyrinthodontia.

Division of the Batrachosauria presents problems beyond those of nomenclature. Romer (1966) in his text divided the group (Anthracosauria, *s.l.*) into four suborders: Schizomeri, Diplomeri, Embolomeri and Seymouriamorpha. The first two were proposed following Romer's (1964) account of *Pholidogaster* on the assumption that the latter ('Schizomeri') was an anthracosaur ancestor. Diplomeri included only *Diplovertebron* as a supposed intermediate stage.

For many years considerable confusion surrounded the name *Diplovertebron* but this is hopefully now resolved (Panchen 1970; Carroll 1970). The name properly refers to an embolomere, probably an eogyrinid, but much of the published description refers to specimens of *Gephyrostegus* preserved from the same site (Nýřany, Bohemia) and in some cases in the same block.

Thus the terms Schizomeri and Diplomeri lapse. However, *Eoherpeton* and *Proterogyrinus* cannot be included in the Embolomeri (or Anthracosauria as I defined them) and some new term is required to characterize a primitive group of anthracosaurs to which they both presumably belong: I propose Herpetospondyli to emphasize the reptiliomorph nature of the earliest known batrachosaur vertebrae.

The major taxa of batrachosaurs are then the Herpetospondyli, the Embolomeri, the Gephyrostegoidea and the Seymouriamorpha. Of these the membership of the first three is relatively clear. Enhanced knowledge of the skull of *Proterogyrinus* and discovery of the post-cranial skeleton of *Eoherpeton* would confirm their placement together as a natural group. With our present knowledge this grouping seems reasonable.

Of the embolomeres there is no doubt that the Eogyrinidae and Archeriidae together represent a distinct radiation of long-bodied fully aquatic forms with relatively small limbs and unique vertebrae. *Anthracosaurus russelli* is almost certainly a member of this radiation: I hope in the near future to undertake a full description of all the known material which may be attributed to this species.

Similarly the gephyrostegids represent a natural group of principally late Westphalian and possibly Stephanian forms with a relatively primitive skull but a post-cranial skeleton with significant advanced features.

The skull of these three groups is primitive with respect to that of the seymouriamorphs in retaining the lateral kinetism and in lacking the specialized features of the latter. It seems to me entirely appropriate that they should be grouped together under the name Anthracosauria and thus separated from the Seymouriamorpha within the batrachosaurs. This usage has in fact already been introduced in this paper.

While the denotation and connotation of the term Anthracosauria thus employed are relatively clear those of Seymouriamorpha are not. The seymouriamorph concept now centres on the three families Seymouriidae, Kotlassiidae and Discosauriscidae. The last gives unequivocal evidence of the amphibian status of the group (Špinar 1952). There are, however, a whole series of genera whose attribution to the Seymouriamorpha is doubtful or controversial (Olson 1965; Romer 1968). Notable among the latter are *Nycteroleter* (see, for example, Parrington 1962; Romer 1968) and *Diadectes* (Panchen 1972*b*, and references).

These and other 'seymouriamorphs' may well be more properly referred to the Reptilia, but even allowing their seymouriamorph status it seems even more inappropriate to refer to them as 'anthracosaurs' than it does to use the term for *Seymouria*, *Kotlassia* and *Discosauriscus*.

In the classification that follows I have given a diagnosis of the Seymouriamorpha but have made no attempt to present a classification within the group: recent sub-groupings are set out in Romer (1966) and Olson (1971).

class: AMPHIBIA

subclass: LABYRINTHODONTIA

order: Batrachosauria Efremov

Labyrinthodont amphibia with skulls primitive with respect to the trends shown by the Temnospondyli: intertemporal bone retained, skull tropibasic, interpterygoid vacuities narrow, a movable basal articulation retained between braincase and palatoquadrate, retroarticular process small or absent, a single circular occipital condyle formed from basioccipital and exoccipitals, opisthotic forming an exposed paroccipital process between tabular and exoccipital. Vomers narrow between choanae, tabular contacts the parietal.

Vertebrae with a cylindrical pleurocentrum, always the principal central element, sutured or fused to the neural arch; intercentrum shorter than the pleurocentrum, free, constricted dorsally. Ribs two-headed, lacking uncinate processes and broadened only in the thoracic and proximal caudal region, capitulum usually articulating with the intercentrum, one principal pair of sacral ribs.

Dermal pectoral girdle with clavicles and interclavicles expanded and with ornament externally, interclavicle with long posteriorly directed stem ('parasternal process'), cleithrum splint-like, sometimes expanded at its dorsal end. Ilium of pelvic girdle with a distinct post-iliac process. Humerus normally with an entepicondylar foramen. Manus and pes with five digits, phalangeal formula reptilian: manus 2, 3, 4, 5, 3; pes 2, 3, 4, 5, 3–5.

suborder: Anthracosauria Säve-Söderbergh

Primitive batrachosaurs retaining the lateral kinetism between skull table and cheek regions, tabular bones bear prominent tabular horns. Dentition of marginal teeth on premaxillary, maxillary and dentary, and palatal tusks on at least palatine and ectopterygoid, with or without teeth on ectopterygoid. Fenestrae ovales not markedly lateral in position. Supraoccipital usually ossified.

Vertebrae with neural arch sutured to pleurocentrum, neural spine rectangular in lateral view, neural arch never dome-shaped, intercentrum relatively large, probably always extended dorsally above the notochord in cartilage if not in bone.

Scapulocoracoid ossified as a unit. Post-iliac process of pelvic girdle narrow and distinct. Pes with 5 phalanges on fifth digit.

infraorder: Herpetospondyli nov.

Primitive anthracosaurs well adapted for terrestrial locomotion. Skull only moderately elongate, quadrate condyles at about the same level as occipital condyle, otic 'notch' shallow and ill-defined, not bordered by the supratemporal, kinetism may extend along edge of skull table to orbit. No sign of lateral line sulci, dermal ornament characteristically anthracosaur – an irregular 'pit and ridge' pattern. Lacrimal extends from orbit to septomaxillary, may form part of orbital border. Well-developed naso-labial groove. Posttemporal fossae little developed, basal tubera present in braincase. Palatal dentition of palatine tusks and ectopterygoid tusks and teeth.

Lower jar fairly shallow, without large meckelian fenestrae, teeth as well as denticles on coronoid series.

Less than thirty presacral vertebrae, intercentra ossified to about half the height of pleurocentra, pleurocentra lightly ossified. Atlas-axis complex with some expansion of axis neural arch.

family: Proterogyrinidae Romer: *Proterogyrinus* (? = *Mauchchunkia*), *Eoherpeton*, ?*Papposaurus*

infraorder Embolomeri Cope

Anthracosaurs secondarily adapted for aquatic anguilliform locomotion, limbs relatively small. Skull of crocodilian piscivorous shape, snout elongate, quadrate condyles well behind occipital condyle in large forms, otic notch deep, rounded but not bordered by supratemporal, kinetism at least between supratemporal and squamosal. Lateral line sulci often conspicuous, dermal ornament of normal anthracosaur type. Prefrontal excludes lacrimal from orbit. Naso-labial groove often developed. Posttemporal fossae absent, basal tubera not conspicuously developed. Palatal dentition of tusks on palatine and ectopterygoid, and teeth on ectopterygoid, vomers tuskless.

Lower jaw very deep posteriorly with two large meckelian fenestrae in each ramus, denticles but not teeth on coronoid series.

About forty presacral vertebrae, embolomerous – intercentra complete discs, pleurocentra fully ossified (atlas–axis complex not described).

family: Eogyrinidae: *Eogyrinus*, *Pteroplax*, *Pholiderpeton*, *Palaeoherpeton*, *Neopteroplax*, *Calligenethlon*, *Diplovertebron* (? = *Nummulosaurus*), *Leptophractus*

family: Archeriidae: *Archeria*, ?*Cricotus*, ?*Spondylerpeton*

?family: Anthracosauridae: *Anthracosaurus*, ?*Eobaphetes*

infraorder Gephyrostegoidea Carroll

Small advanced anthracosaurs well adapted for terrestrial locomotion. Skull moderately elongate, quadrate condyles at about the same level as occipital condyle, otic 'notch' shallow but large and well-defined, bordered antero-dorsally by the supratemporal, kinetism extends forward to the orbit. No sign of lateral line sulci, ornament pustular on skull table. Lacrimal extends from septomaxillary to orbital border. Naso-labial groove not apparent. (Condition of posttemporal fossae not known.) Basal tubera not conspicuous. Palatal dentition of tusks on vomers, palatines and ectopterygoids.

Lower jaw fairly shallow, ?without large fenestrae, denticles but not teeth on coronoid series. About 25 pre-sacral vertebrae. Intercentra ossified to about one-third the height of pleurocentra. Pleurocentra poorly ossified, horse-shoe shaped. Atlas–axis complex advanced with broad expansion fore-and-aft of axis neural arch.

family: Gephyrostegidae Romer: *Gephyrostegus*, *Eusauropleura*, ?*Bruktererpeton*

suborder: Seymouriamorpha Watson

Advanced reptiliomorph batrachosaurs, kinetism between skull table and cheeks lost, tabulars without tabular horns. Otic notch typically deeply incised, bordered by the supratemporal. No sign of lateral line sulci in adult specimens, dermal ornament 'pit-and-ridge', more regular than that of anthracosaurs. Lacrimal extends from orbit to septomaxillary or naris. No naso-labial groove. Dentition of marginal teeth on premaxillary, maxillary and dentary, palatal dentition variable, may not include tusks. Fenestrae ovales widely separated at ends of otic tubes which may be floored by processes of parasphenoid, supraoccipital unossified, posttemporal fossae well-developed.

Lower jaw shallow, without large meckelian fenestrae or true coronoid teeth.

Vertebrae with neural arch fused to solidly ossified pleurocentrum, except in small or poorly ossified species. Intercentrum small and neural arch a massive dome in large species.

Scapula and coracoid sometimes separately ossified and sutured together. Post-iliac process short and forming a tapering extension of iliac blade. Pes with 3 or 4 phalanges on fifth digit.

The batrachosaurs have for many years been regarded as the group of early Amphibia from which the reptiles originated. Recently *Seymouria* has been replaced by the earlier and less specialized *Gephyrostegus* as a probable relict of the ancestral group (Carroll 1969, 1970). I have reviewed the evidence on which this claim was based and concluded that it was improbable that any labyrinthodont amphibian, *Seymouria* and *Gephyrostegus* included, showed the anatomical features to be expected in a reptile ancestor (Panchen 1972*b*).

Both Carroll (1971) and I suggested, for different reasons, that the ancestral reptiles were very small animals. We differed, however, in my conclusion that the reptile line had not passed through a much larger labyrinthodont (specifically anthracosaur) stage.

In the rhipidistian ancestors of tetrapods and in the earliest known reptiles the hyomandibular (stapes) is directed ventro-laterally from the otic region (fenestra ovalis) towards the quadrate. In labyrinthodonts on the other hand the stapes is directed dorso-laterally towards a tympanum situated in the otic notch. The similarity between the hyomandibular of Rhipidistia and the stapes of reptiles persuaded me, in agreement with Sushkin (1927) and Parrington (1958) that the labyrinthodont condition was a secondary one. I therefore concluded that it was improbable that the reptile lineage had passed through a stage showing that condition.

The labyrinthodont condition is clearly an adaptation to maintain a small and thus effective sound-conducting stapes in a relatively large skull. However, once established it seems not to have reverted to the fish-reptile orientation of the stapes even in small forms in which the tympanum is relatively large.

However, Dr R. L. Carroll has suggested (personal communication) a hypothetical early 'notchless' anthrocosaur as a reptile ancestor. This concept gives rise to two questions: first whether a notchless anthracosaur is a likely forerunner of the known batrachosaurs (i.e. whether it ever existed), and secondly whether the other characteristic features of the primitive anthracosaur skull are those to be expected in a reptile ancestor.

Both *Eoherpeton* and *Gephyrostegus* are anthracosaurs in which the otic notch is very shallow, but it would be a mistake to regard them as notchless. In *Eoherpeton* the tympanum was evidently dorsally situated at the back of the squamosal and it is probable that the stapes was of labyrinthodont type. This is also the case in *Gephyrostegus.* Furthermore, in the latter genus the exposure of the supratemporal in the margin of the 'notch' suggests descent from a larger anthracosaur with a deeply incised notch like that of a seymouriamorph.

If on the other hand one looks at temnospondyl labyrinthodonts it is evident that either the typical labyrinthodont notch originated within the temnospondyls, possibly more than once, or that the temnospondyls are a polyphyletic group, possibly from the fish level. If one takes the former, more probably hypothesis it is reasonable to assume a similar origin of the notch within the anthracosaurs and thus a primitive notchless anthracosaur.

This probability is enhanced by the lack of any convergence between batrachosaur and temnospondyl lines in the Lower Carboniferous. With the rejection of *Pholidogaster* as an anthracosaur (Panchen 1970, and below) and the description of the vertebrae in '*Mauchchunkia*' there is no reason whatsoever for postulating a rhachitomous ancestor for anthracosaurs. Also the limb bones to be described by Dr Baird from the Tournaisian of Horton Bluff, Nova Scotia, are probably anthracosaur and pre-date all amphibia except the ichthyostegids (Carroll *et al.* 1972).

Thus the hypothetical notchless anthracosaur may well have existed in the Lower Carboniferous or Upper Devonian, but is it necessary to postulate such a stage in reptilian ancestry? The 'reptiliomorph' post-cranial skeleton of early anthracosaurs is equivocal with respect to reptile ancestry, as such a skeleton was probably the common heritage of many if not all early amphibian groups and notably the microsaurs (Carroll & Baird 1968; Panchen 1972*b*). In most respects also the skull of a primitive anthracosaur would be simply that of a primitive labyrinthodont.

Not only the general primitive characters of such a skull, but also many diagnostic ones, such as retention of the kinetism, retention of the intertemporal, an orbital lacrimal and an ossified supraoccipital, would be expected in any very primitive and very generalized labyrinthodont skull. Only the tabular–parietal contact and the presumably correlated tabular horn would be diagnostic at this primitive stage.

It has already been pointed out (Panchen 1964, 1970) that the skull table pattern of anthracosaurs must have passed through the diagnostic temnospondyl condition of separation of tabular and parietal by the supratemporal–post-perietal contact, before the anthracosaur condition was attained. This latter would have been achieved by further backward migration of the parietal–post-parietal junction relative to the flanking temporal series.

In all known reptiles the intertemporal bone has been lost. The only possible exception to this is *Diadectes*, but the presence of an intertemporal and the reptilian status of this form are both in dispute (Panchen 1972*b*, and references therein). In most primitive reptiles, notably captorhinomorphs, the territory of the intertemporal is occupied by a lappet of the parietal, which thus extends laterally to reach the kinetic line between skull table and cheek. In primitive reptiles in which the tabular is retained it lies mesial to the supratemporal rather than behind it and as in anthracosaurs there is a tabular–parietal contact. However, this contact is not necessarily evidence for the anthracosaur ancestry of reptiles.

The reptilian, or more specifically, early captorhinomorph, configuration of the skull table probably arose from the ancestral amphibian one in two main stages (Panchen 1972*b*)

(1) reduction and loss of the intertemporals accompanied by lateral expansion of the parietals to occupy their territory;
(2) truncation of the back of the skull table with reduction of the supratemporals, tabulars and post-parietals.

To achieve the reptilian configuration these events must almost certainly have occurred in the sequence given. Had the sequence been reversed it seems probable that loss of the intertemporal would have resulted, with retention of the kinetism, in a supratemporal–postfrontal contact in the short skull table resulting from truncation. The two cases are paralleled in the microsaurs. In *Microbrachis*, with a long skull table loss of the intertemporal (and supratemporal) has resulted in a parietal lappet, while the microsaurs with short tables have achieved a tabular–postfrontal contact (Panchen 1972*b*).

Thus if the ancestral amphibian was of small size as I have argued (Panchen 1972*b*) and retained a primitive, and thus temnospondyl, configuration of the skull table, loss of the intertemporal could have preceded tabular–parietal contact. The latter would then have inevitably occurred with reduction of tabular, supratemporal and post-parietal under the joint influence of expansion of the parietals and truncation of the table. Only if the tabular–parietal contact was achieved before loss of the intertemporal in the reptilian line would that line have passed through a technically anthracosaur stage, from which later anthracosaurs could also have diverged.

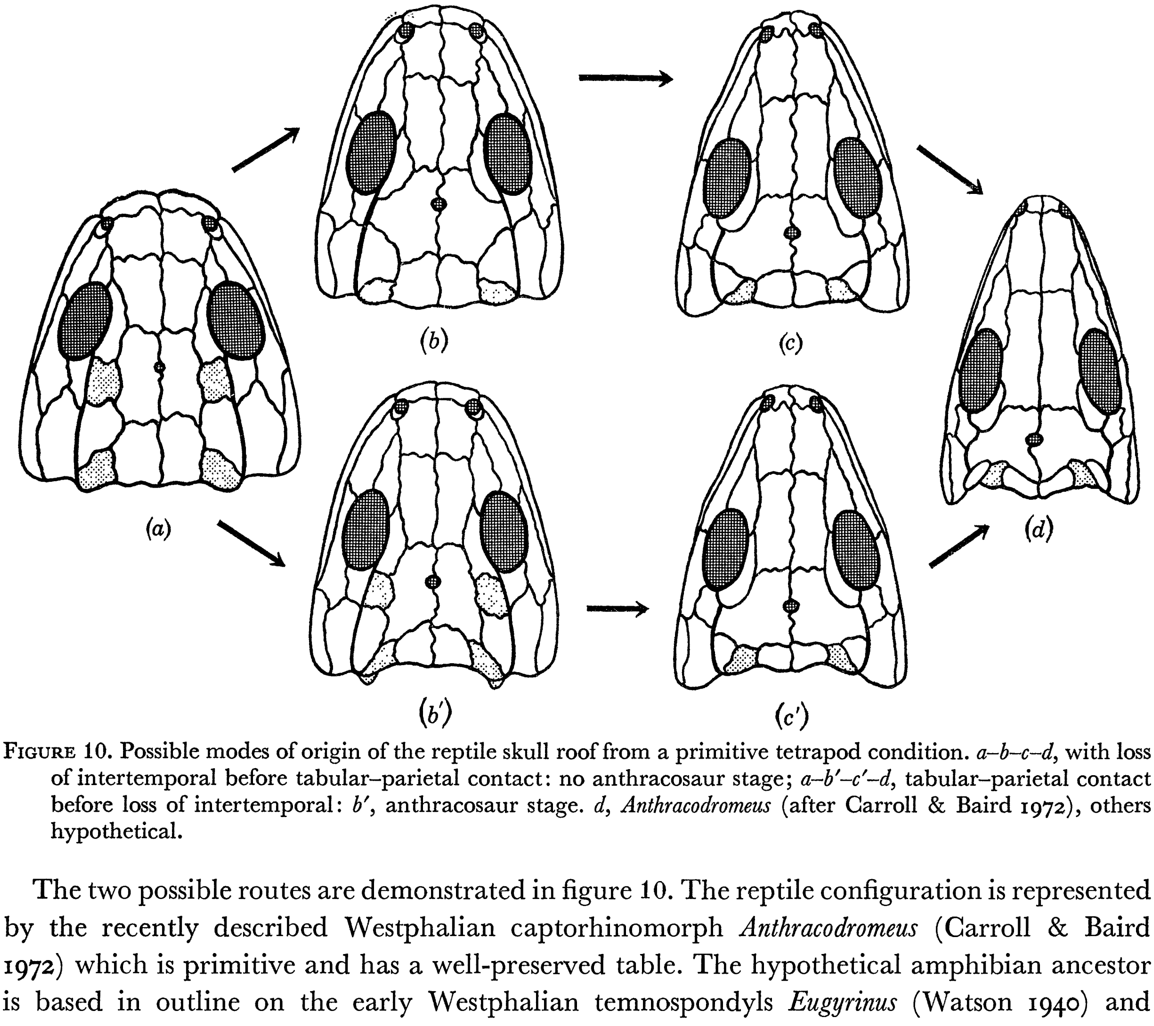

Figure 10. Possible modes of origin of the reptile skull roof from a primitive tetrapod condition. *a–b–c–d*, with loss of intertemporal before tabular–parietal contact: no anthracosaur stage; *a–b′–c′–d*, tabular–parietal contact before loss of intertemporal: *b′*, anthracosaur stage. *d*, *Anthracodromeus* (after Carroll & Baird 1972), others hypothetical.

The two possible routes are demonstrated in figure 10. The reptile configuration is represented by the recently described Westphalian captorhinomorph *Anthracodromeus* (Carroll & Baird 1972) which is primitive and has a well-preserved table. The hypothetical amphibian ancestor is based in outline on the early Westphalian temnospondyls *Eugyrinus* (Watson 1940) and *Dendrerpeton* (Carroll 1967) which are both small and retain the intertemporal. It has, however, been reconstructed as a more primitive form than these relatively late labyrinthodonts by excluding the otic notch and extending the skull table with long post-parietals to bring it nearer to the rhipidistian configuration: the proportions of the table are thus nearer those of *Pholidogaster* and *Greererpeton.*

PHOLIDOGASTER PISCIFORMIS HUXLEY

The main purpose of this section is a redescription of the skull of the species *Pholidogaster pisciformis*. For reasons which are developed below both the holotype of *Pholidogaster* and that of *Otocratia modesta* Watson are here assigned to the temnospondyl labyrinthodont family

Colosteidae Romer (1930). It is further contended that they almost certainly represent the same species, so that *Otocratia modesta* Watson (1929) is a subjective junior synonym of *Pholidogaster pisciformis* Huxley (1862). I am glad to be able to record that Professor A. S. Romer (personal communication) had also independently reached the conclusion that both *Pholidogaster* and *Otocratia* were colosteids.

However, the two holotype skulls will each be described separately so that if further evidence should prove the latter conclusion wrong the purely descriptive accounts will each be self-standing. The two skulls are then used for a composite restoration and the reasons for associating them are presented there. Romer (1964) has given an account of the post-cranial skeleton of the *Pholidogaster* holotype. Thus only new data on the pectoral girdle, which is preserved on the same block as the skull of the holotype and has thus been further cleaned, and a description of other girdle material need be given here. I also include some notes on the significance of other parts of the post-cranial skeleton.

The holotype skull of Pholidogaster

Complete cleaning of the holotype skull shows that its preservation is both much better and much more complete than had been feared (figure 11 and figure 12, plate 23). Every bone of the dermal skull roof is represented in the specimen on one side or the other, and all but the septomaxillary, lacrimal, post-orbital, squamosal and quadratojugal are represented on both sides, albeit by small fragments in the case of some ossifications.

This completeness of preservation also applies to the lateral surfaces of the lower jaw. Only the surangular surface cannot be figured with confidence.

The skull and associated bones have suffered post-mortem distortion and there has been some disruption of the skull table. Compression of the skull has resulted in an oblique flattening so that the dentary of the right lower jaw appears in dorsal view, while the left jugal and a small part of the maxillary appear in ventral view. There has further been a lateral compression of the snout so that on the right, where the bones are probably complete, the lacrimal has overridden the prefrontal, partially obscuring it from view, and the prefrontal in its turn overlies part of the frontal.

In ventral view it is clear that some shortening of the right jaw ramus has taken place post-mortem so that the post-splenial is fractured transversely and there is some overlap. This overlap also reduces the apparent length of the right cheek region. On the left, however, the full length of the jaw is apparent and coincides exactly with the quadrate length of *Otocratia*. Romer gives a largely accurate figure of the ventral view of the *Pholidogaster* skull as preserved, so it is not refigured here from this aspect.

The bones of the skull table are almost completely disarticulated, but all are easily identifiable. Both tabulars, and the right post-parietal and supratemporal are almost complete. The right post-orbital appears to have been rotated counterclockwise through more than a right angle, carrying a fragment of the parietal with it, so that they now obscure the back of the jugal.

After airbrasive development the surface of most of the dermal bones exposed in dorsal view proved to be excellently preserved and to show the characteristic honeycomb ornament. The preservation is in fact better than that of the bones which appear on the ventral surface of the specimen, which were exposed before the whole skeleton was first found.

The further development has confirmed beyond doubt the temnospondyl nature of the dermal ornament of *Pholidogaster* and its difference from that of the anthracosaur *Eoherpeton* (Panchen 1970). The nature of the ornament is shown in the restorations of the *Pholidogaster* skull. The pattern of dermal bones is also that of a primitive temnospondyl. Thus, most importantly, the post-parietals are very long and certainly had an extensive suture with the supratemporals lateral to them. The tabulars were thus separated by this suture from the parietals, the normal temnospondyl condition.

The course of the lateral line system is in part very clear but on other parts of the skull where it would be expected it is vague or apparently absent despite the good preservation of the bone surface. Where best preserved the lateral lines appear as deep narrow sulci. The supraorbital sulcus is sharply incised in both prefrontals but cannot be seen on the posterior part of either bone. The more posterior course of the supraorbital sulcus is therefore unknown but its direction on the prefrontal is quite consistent with it having passed mesially on to the adjacent frontal on its backward course, just as in *Greererpeton* (Romer 1969).

Anteriorly the right sulcus can be seen very clearly as it continues on to the nasal. A short part of its course actually lies along the nasal–prefrontal suture. In the holotype of *Greererpeton* the sulcus could not be traced as far forward as the nasal.

The infraorbital sulcus is visible only on the jugal as it follows its transverse downward course to a junction with the origin of the jugal sulcus. This junction can be seen on both sides of the skull but there is no trace on either side of the forward course of the infraorbital sulcus from the junction.

The most interesting feature of both these regions of the lateral line system is that the sulci are bridged over with bone at several points. There are two such bridges on the nasal and three at the infraorbital junction. This suggests an early stage in the development of the typical labyrinthodont sulcus from the bone-surrounded canals present in Rhipidistia and *Ichthyostega*. It is possible that these bridged sulci might be present in other early labyrinthodonts but probable that only the delicacy of development possible with the Airbrasive machine would reveal the sulci without destroying the bridges.

The sulci on the lower jaw are less obvious. An elongation of the pits of the ornament on the angular and post-splenial marks the course of the mandibular sulcus, while an ill-defined groove separating a dorsal weakly ornamented region of the dentary may represent the oral sulcus.

The dorsal surface of both tabular bones is virtually completely preserved and visible, and the right tabular, although disarticulated, can be seen to fit well into the posterior edge of the supratemporal. It may also be restored alongside the right post-parietal to give the outline of the back of the skull table. Each tabular bears a short conical horn projecting below the edge of the table and very similar to that seen in loxommatids such as *Megalocephalus*. In the left tabular the occipital exposure of the bone can be seen extending laterally from the horn, but this region is obscured on the right.

The length of the supratemporal, almost complete on the right, makes it improbable that the animal had an intertemporal, and the pattern of the skull table was probably identical to that of '*Otocratia*', described below, and closely similar to that of *Greererpeton*. The absence of an intertemporal cannot, however, be confirmed.

Although part of the post-orbital is preserved on the right together with an adjacent scrap of parietal, nothing is known of the total area or shape of these bones. This also applies to the post-orbitals and frontals, although the anterior end of the right frontal, including its whole suture with the nasal and the line of its suture with the left frontal, is well preserved.

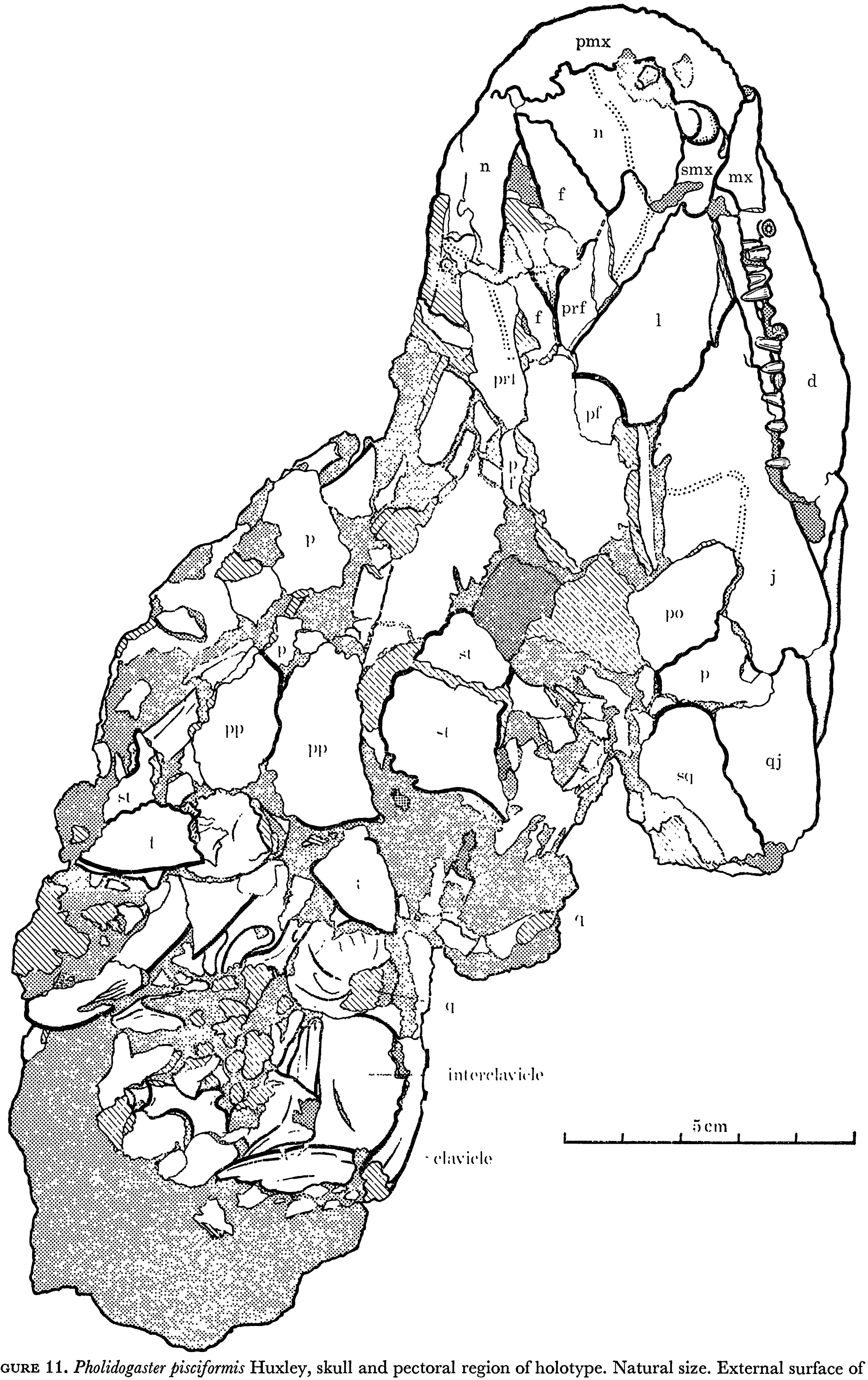

Figure 11. *Pholidogaster pisciformis* Huxley, skull and pectoral region of holotype. Natural size. External surface of dermal bones, white; internal surface and endochondral bones, light stipple; matrix, medium stipple; holes through specimen, dark stipple; broken or eroded bone, hatched. q, quadrate; smx, septomaxillary. Other abbreviations as in figure 1.

FIGURE 12

(*Facing p.* 616)

The rest of the snout can be restored without serious fear of error, except for two points. First there could have been an internasal ossification as Romer shows with less than certainty in *Greererpeton*, but if present it did not extend back to separate the anterior ends of the frontals: the region of the junction between the nasals is distorted and an area of bone is missing so the presence of an internasal cannot be rejected. Secondly it is possible that the skull roof was perforated on each side in the region of the naso-premaxillary suture to accommodate the large parasymphysial tusks of the lower jaw. This occurs in some (?male) individuals of *Megalocephalus* (Tilley 1971) and could have occurred in '*Otocratia*'. In *Pholidogaster* the right tusk perforates the skull but it is not clear whether or not this is a post-mortem effect.

The premaxillary is somewhat disrupted, but its suture with the nasal is preserved in front of the supraorbital sulcus and parts of the sutural edge appear to be preserved both mesially and laterally to this region, although the actual suture is disrupted. Ventrally both premaxillaries can be seen to have borne large tusks at a level just in front of the external nares, although the right tusk is eroded and the left reduced to an eroded root. Their position is exactly that of the corresponding tusks in '*Otocratia*'. No other premaxillary teeth are preserved.

The whole region of the right nostril is well preserved. It is bordered by the premaxillary, the maxillary, a septomaxillary and the nasal. The septomaxillary is well preserved and quite distinct. Not only are its boundaries clear and its surface sunk somewhat below that of the surrounding bones, but its fine irregular surface ornament contrasts sharply with that of those bones. It is unusually long and anteriorly sends a curved ventro-lateral process into the cavity of the nostril. Laterally there is an elongate foramen also bordered by the lacrimal and maxillary.

A similar septomaxillary is apparently present in '*Otocratia*' and probably in *Greererpeton*. In the latter animal Romer describes the prefrontals as extending the whole distance from orbit to naris on both sides. He shows, however, that in the holotype a separate piece of bone is present bordering the naris on each side. He regards each piece as the broken end of its respective prefrontal, but if interpreted as the septomaxillary the pattern of the snout is in accord with *Pholidogaster* and '*Otocratia*'.

In *Pholidogaster* the maxillary and premaxillary meet below the naris. Both are well preserved on the right but the maxillary, which terminates in a pointed process has been 'shunted' forward post-mortem. It seems probable, however, that at least the process overlapped the back of the premaxillary in life. Behind the process the maxillary expands to border the naris and septomaxillary, but is sharply reduced in width from the front of its suture with the lacrimal. Only five maxillary teeth are visible: their disposition is shown in the restoration. Those that are complete are small and bullet-shaped in lateral view.

The lacrimal formed a considerable part of the orbital border; as a result the prefrontal is remote from any contact with the jugal, in contrast to the condition in *Eoherpeton* and the embolomerous anthracosaurs. The lacrimal is thus essentially as Romer figures it in *Greererpeton* except that its suture with the jugal ran obliquely forward and ventro-laterally instead of being transverse. There has been some relative movement between the two bones in the *Pholidogaster* specimen and a small piece of bone, presumably from the palate, has been extruded above the lacrimal at the ventral end of the suture. Anteriorly the border of the lacrimal has a deep concave incision forming the posterior border of the septomaxillary exposure.

The disposition of the lateral line sulci on the large jugal has already been noted. Apart from its general resemblance to that of *Greererpeton* the only other point of importance about the jugal is that it apparently formed a considerable stretch of the jaw margin. The posterior end of the maxillary is not preserved so that the limit of its backward extension cannot be checked, but its taper suggests that it terminated approximately below the junction of the sulci on the jugal. Behind this the ventral edge of the jugal is preserved and appears to have formed the jaw margin. This again contrasts with the condition in *Eoherpeton* but is probably similar to that in *Greererpeton*.

The exposed edge of the right quadratojugal was tentatively interpreted by Romer (1964, fig. 3) as surangular. However, removal of a thick and very hard piece of matrix (bearing what may be the cleithrum and shown in Romer's figure) from the more dorsal surface of the bone confirmed that it was quadratojugal. The small area very tentatively labelled quadratojugal in Romer's fig. 2 proved on development to be very ferruginous matrix, which in many parts of the specimen could only be distinguished with difficulty from poorly preserved bone.

The right squamosal is poorly preserved and sustained some surface damage on removal of the thick piece of matric referred to above. However, a latex cast taken from the natural mould of the matrix has preserved the form of the ornament.

Little can be made of the bones of the palate and braincase in the holotype and as these are largely missing in '*Otocratia*' as well no palatal or occipital reconstruction has been attempted.

In *Pholidogaster* the position of the right quadrate is indicated, probably correctly, in Romer's fig. 2. What appears to be the left quadrate is also preserved immediately behind the right tabular, and is indicated in figure 11. Both include part of the articular surface which, as far as can be judged, was somewhat saddle-shaped.

Romer notes the denticulate right pterygoid in his description and ventral figure and the two somewhat cylindrical blocks of eroded bone which he shows in front of the right quadrate may represent the quadrate ramus of that bone. However, that part of the area which he designates as right pterygoid which lies beside the presplenial does not appear to be denticulate and may include both vomer and parasphenoid. I agree with the identity of the rest of his 'right pterygoid'.

Between this and the right quadrate I find myself unable to interpret anything in ventral view. The bone is badly eroded and saturated with ancient glue which cannot be removed from the surface with the Airbrasive. Its removal by solution would almost certainly result in the disintegration of that part of the specimen.

In dorsal view considerable areas of palatal and neurocranial bone have been exposed. The interorbital septum of the sphenethmoid projects as a thick ridge, broken off along the top, between the lacrimal and post-orbital. Ventrally a projecting eroded mass shown by Romer continuing the line of the left pterygoid, marks its position and presumably includes eroded parasphenoid. To the left of the sphenethmoid in dorsal view a well-preserved part of the dorsal surface of the left pterygoid is now exposed, and part of the left quadrate ramus appears to be exposed to the left of the left quadrate. The presumed dorsal surface of the right quadrate ramus can be seen postero-laterally to the supratemporal and a massive piece of bone presumably pertaining to the braincase but not otherwise interpretable lies between the tabulars and immediately behind the left post-parietal.

The lateral surfaces of both lower jaw rami are mainly well-preserved. Both dentaries are virtually complete. The left, somewhat disrupted, is visible in ventral view, but some of its inner surface appears from above, whereas the right is visible in ventral view only anteriorly, while the main tooth-bearing part of the bone appears in dorsal view. Seven right dentary teeth are more or less completely preserved in addition to three represented by their roots. The dentary teeth are essentially like those of the maxillary but may have been on average slightly larger. It has already been noted that a large tusk appears behind the right premaxillary in dorsal view and is apparently the right parasymphysial tusk. However the alveolar margins of both dentaries are obscured anteriorly, so that this cannot be confirmed, and no other anterior teeth are visible.

A prominent feature of both dentaries, particularly well shown on the left, is a deep recess to accommodate the massive premaxillary tusk when the jaw is closed. Behind this, as already noted, the dentary has a weakly ornamented dorsal strip immediately below the tooth row.

The anterior or presplenial is a considerably smaller bone than Romer indicated in his ventral figure. In fact he shows its true extent as though a fragment on the left, but gives the right presplenial a much greater area. I have managed to trace the bounding sutures of the latter with some airbrasive development and thus can confirm that the left is complete.

The presplenials were thus small bones of only about a quarter of the total jaw length, meeting in symphysis anteriorly behind the dentary symphysis and with little lateral exposure. In these respects they appear to be essentially like those of *Ichthyostega* (Jarvik 1952, fig. 35A).

The post-splenials of *Pholidogaster* were considerably larger. The right is apparently complete, although fractured and overlapped as noted, while the left lacks about a quarter of its area in the mid-region. The lateral exposure of the bone can thus be confidently restored and the bounding sutures, with presplenial, dentary and angular, were traced completely on the right and largely on the left.

The angular is a very large and strongly ornamented bone. That on the right is completely preserved but for the postero-ventral outline behind the jaw angle, while the left has this margin complete but has an area missing immediately in front of it, as indicated in Romer's figure. The ornament radiates from the jaw angle so that the centre of ossification must have been situated near that angle. The dorsal border of the bone appears to be intact, except behind the level of the angle in the right jaw, while this posterior sutural edge can be traced across rotted bone on the left.

Fortunately the posterior edge of the left surangular is preserved although the lateral surface of that bone is much rotted. Thus it is possible to restore the posterior outline of the ramus up to the level of the articulation.

The articular itself appears in the specimen in dorsal view on the left but is too poorly preserved to give any useful data. Morphologically below it the surface of the mesial side of the ramus can also be seen and this again comes into view at the level of the left parietal without however giving enough data to essay a mesial reconstruction.

Otocratia modesta *Watson*

The holotype of *Otocratia modesta* consists of an almost complete and undistorted skull roof embedded in a block of Burdiehouse limestone. Only the ventral internal surface of the roof is exposed and the bone surface is extensively damaged (figure 13). However, most of the sutures in the post-orbital part of the skull could be traced with relative ease, even across damaged bone surface, and agree substantially with those figured by Watson (1929). In addition it has been possible to trace some of the preorbital sutures so that a fairly complete pattern has been revealed.

Little of the skull roof is actually missing. The lateral borders of the skull roof, particularly the maxillary, jugal and quadratojugal regions, have been severely eroded down and only two teeth of the maxillary dentition remain. The premaxillaries on the other hand have suffered much less and the diagnostic dentition is largely preserved. A wedge of rock appears to have been lost adjacent to an oblique fracture across the specimen. This loss has destroyed most of the outline of the (morphological) right orbit with the removal of some bone in front of and flanking the orbit. Relatively little of the true rim of the left is preserved, but the eroded outline is probably close to the shape of the intact orbit.

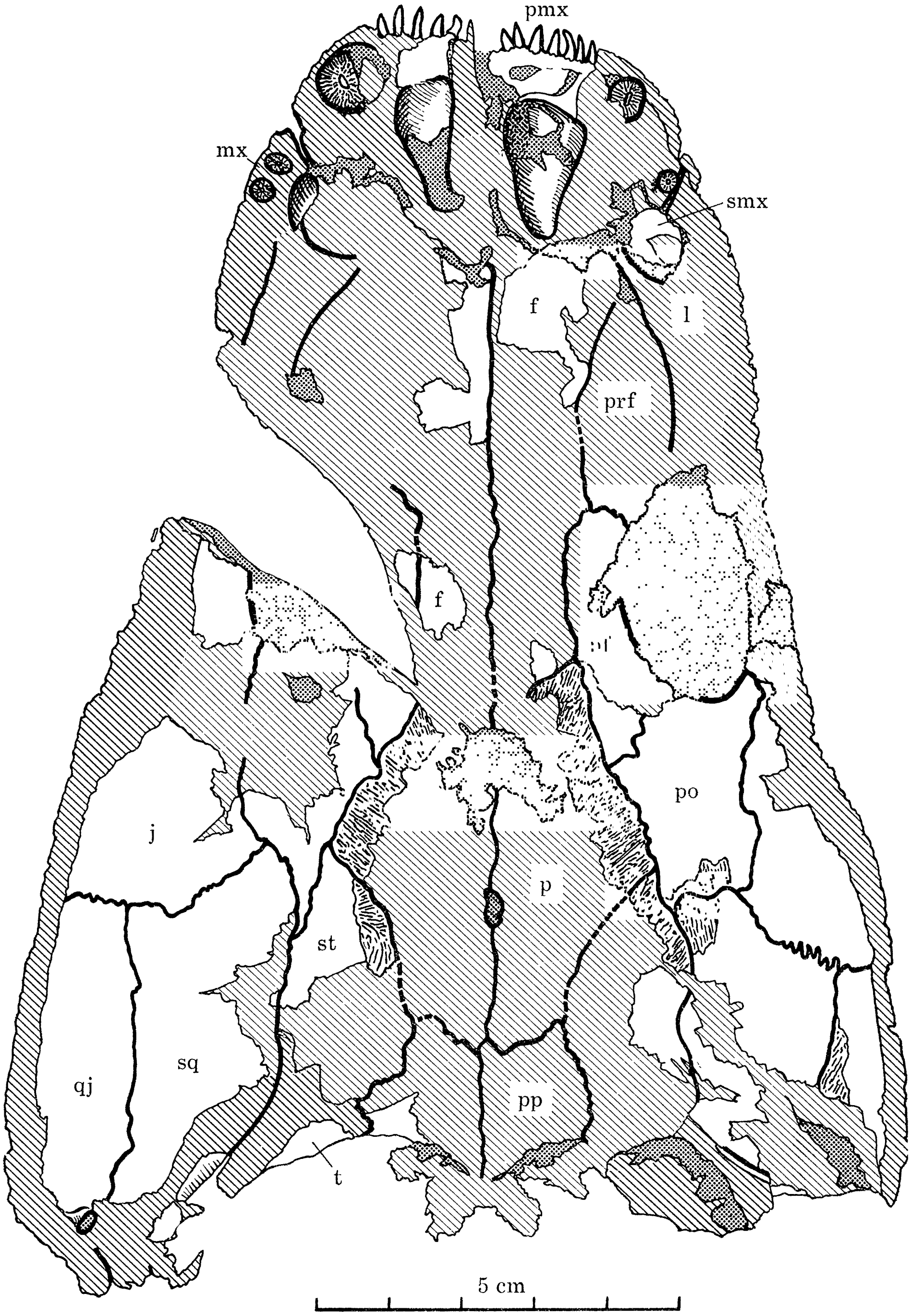

FIGURE 13. *Pholidogaster pisciformis*, holotype of '*Otocratia modesta*' Watson, ventral view. Natural size. Exposed sutural overlaps indicated. smx, septomaxillary. Other abbreviations and conventions as in figure 1.

The skull is virtually identical in size to that of the *Pholidogaster* holotype, with a pp length of 163 mm. The overall length of the specimen is 183 mm and this must be very close to the quadrate length. Thus, allowing for some length behind the post-parietals of the occiput, the occipital condyle must have been very nearly in the same transverse plane as the quadrate condyles. This was also the case in *Greererpeton*, in *Eoherpeton* and probably in *Proterogyrinus*. In *Ichthyostega* there was apparently no true condyle and, as reconstructed by Jarvik (1952), the basioccipital–exoccipital tunnel from which the condyle evolved begins well forward of the quadrates. However, the back of the skull table reaches almost back to quadrate level: this latter condition is probably primitive for labyrinthodonts.

Also primitive in the skull of *Otocratia* is the anterior position of the orbits. Of the 163 mm of pp length nearly 70 mm is post-orbital. The proportions are virtually identical in the holotype skull of *Greererpeton*, which is about four-fifths of the size of that of *Otocratia*.

Otocratia was named by Watson from a unique structure of the otic notch which he reconstructed. Watson claimed that the otic notch was situated unusually posteriorly because of the establishment of a long suture between the tabular and the squamosal. He further claimed that the tabular extended along the dorso-mesial edge of the notch and round behind it to re-establish the tabular-squamosal contact. The otic 'notch' was thus surrounded by a complete 'tympanic ring'.

The critical region in the specimen is very difficult to interpret. Watson is certainly correct in describing a long posterior extension of the tabular, which for most of its length is in close apposition to the squamosal. This can be seen clearly on the morphological right side. Because of this apposition the tabular extension should not perhaps be referred to as a tabular horn as Watson does. It seems probable, however, that the tabular–squamosal junction was a kinetic one rather than a suture. It is further possible that the supratemporal–squamosal junction was kinetic, as in anthracosaurs. Romer notes that this was probably the case in *Greererpeton*.

There is a gap of about 3 or 4 mm between the posterior end of the right tabular 'horn' and the anterior end of the hook of damaged bone which Watson restores as the tympanic ring. In the gap there is a small (here figured) area of undamaged bone surface facing postero-mesially which represents the occipital exposure of the squamosal. Just posteriorly to this another small area of concave bone surface, this time facing ventro-laterally, lies immediately laterally to Watson's 'otic notch'. This latter surface is thus part of Watson's 'tympanic ring', but it seems more probable that the whole hook-shaped piece of bone forming the ring is the distal end of the quadrate ramus of the pterygoid. This conclusion is corroborated by the fact that the 'tympanic ring' is not in the same horizontal plane as the 'tabular horn': as preserved a backward extension of the latter would not meet the former.

The left tabular region is even more difficult to interpret. Watson gives no published account of it, but a note is enclosed by him accompanying the holotype, together with a roughly cylindrical piece of matrix which is in part surrounded by rotted bone. This specimen fits into the tabular region and includes the left tabular horn. It is interpreted by Watson (in the note) as the remains of a bony tube forming the tympanic cavity which opened at the otic 'notch'.

Like the left quadrate region, the left tabular horn is broken off and thus cannot be shown to have extended further posteriorly than that on the right. The bone of the tabular horn, situated dorso-laterally around the matrix cylinder, is at no point in contact with the thin layer of bone situated ventro-mesially. Thus the existence of a tube of bone cannot be inferred. It seems more probable that the latter bone pertains to the occiput and the matrix lumen of the 'tube' may well represent the posttemporal fossa. The bone ventral to it is in continuity with rotted occipital bone behind the skull table and is therefore probably the remains of the paroccipital process.

It therefore seems probable that *Otocratia* had an exceptional backward extension of the tabulars but lacked a definitive otic notch.

Both tabulars extend forward so that their eroded ventral surfaces lie below those of supratemporals. The anterior edge of neither tabular is preserved but it appears that both were probably terminated by an anteromesial facet or facets bracing the braincase as described in *Palaeoherpeton* (Panchen 1964).

The sutures defining the ossifications of the rest of the post-orbital part of the skull roof have been almost completely traced. The pattern is very close to that figured by Watson, and allowing for the fact that the underside of the roof is exposed is startlingly similar to that traced by Romer on the dorsal surface of *Greererpeton.*

In some cases in *Otocratia*, notably the sutures flanking the parietals anteriorly, the overlap surfaces have been exposed by loss of the thin bone covering them ventrally. The sutures are then, of course, traced along the clearly defined edge of the overlap surface, not along the broken edge of the underlying bone. These exposed surfaces are indicated in the figure and apart from demonstrating the extent of overlap in the suture give some idea of the course of the sutures on the dorsal surface.

As in *Ichthyostega* and the holotype of *Greererpeton*, the skull table is advanced in the loss of the intertemporal bone. Its territory is principally occupied by inward extension of the postorbital. There is, however, particularly on the ventral surface, some lateral expansion of the parietal. This is the normal method of sealing of the anterior part of the kinetism on loss of the intertemporal in primitive temnospondyls with a long skull table (Panchen 1972*b*). There is, however, a specimen of *Greererpeton* in the U.S. National Museum (U.S.N.M. 22576) in which a small intertemporal, visible on the left, is retained.

The pineal foramen of *Otocratia* is small and elongate. Its true margin is preserved except perhaps for the anterior third. A clearly defined paraquadrate foramen (Bystrow & Efremov 1940) can also be seen in the right quadrate region. A short extent of suture just behind this appears to separate the back of the quadratojugal from the quadrate itself, but the quadrate–squamosal junction could not be traced.

A number of sutures have been traced in the preorbital region in addition to part of the left fronto-parietal suture. As in *Greererpeton* and *Ichthyostega*, the junction between postfrontal and prefrontal, seen on the morphological left, is far forward on the orbital margin. The latter bone was traced almost completely on the left. Again it extends far forward as a narrow ossification as in *Greererpeton.*

In *Otocratia*, however, there appears to be a separate, roughly circular ossification on each side situated mesially and somewhat posteriorly to the external naris. On the right the naris forms its lateral margin, its posterior margin was traced as suture and its anterior margin probably coincides with a matrix-filled crack across the specimen. On the left the whole circular bone is depressed (dorsally) relative to the surrounding bone. The position of these circular bones, and the 'prefrontal fragments' of *Greererpeton*, corresponds to that of the septomaxillary of *Pholidogaster* (see above).

The suture bounding the prefrontal laterally in *Otocratia* forms the mesial boundary of the lacrimal. This latter bone certainly extends forward to the septomaxillary on both sides and part of its suture with the maxillary can be traced on the left. On the right a thin spur of the lacrimal can be traced extending forward to separate the prefrontal from the septomaxillary. The relation of the lacrimal to the orbital margin could not be traced. It seems more probable, however, that the lacrimal entered the orbit as in the *Pholidogaster* holotype and in *Greererpeton* rather than being separated from it by a prefrontal–jugal contact as in *Ichthyostega.*

The external naris is clearly visible from its ventral, internal aspect on the right, as noted by Watson. As in *Greererpeton* it is a small oval foramen, floored by bone which presumably pertains to the septomaxillary, but showing its aperture quite clearly laterally. On the left the matrix separating the septomaxillary from the maxillary antero-lateral to it presumably represents the aperture of the naris, but its margin is not clear.

On both sides the maxillary–premaxillary suture can be easily seen running obliquely backwards from the jaw margin to the naris. The eroded roots of two maxillary teeth are visible just behind it on the left.

The region of the *Otocratia* skull in front of the narial region is difficult to interpret. The crack which forms the anterior margin of the right septomaxillary continues obliquely inwards to the midline and probably, but not certainly, marks the anterior edge of the right frontal. It is roughly symmetrical with a wider matrix-filled crack on the left. Thus interpreted the naso-frontal suture is similarly placed to that in *Pholidogaster* and *Greererpeton* and not very different from that of *Ichthyostega.*

The margin of bone round the front of the skull is certainly premaxillary. The right premaxillary bears five eroded but full-length small teeth at the front extending to the midline and there are seven on the left. Each tooth is only 5 mm or less in crown length with a basal diameter of less than 1.5 mm. They thus contrast strikingly in size with the enormous premaxillary tusks which confirm the colosteid nature of *Otocratia.*

It is also remarkable that the tips of the small anterior teeth are in the same horizontal plane as the ventral bony margin of the tusk-bearing region of the premaxillary, which is thus separated from the anterior tooth-bearing margin by a marked step.

The right tusk, situated postero-laterally to the anterior teeth is represented only by its root, as it is eroded away to jaw level. Part of its antero-mesial side is missing. Antero-mesially to it there is a pit floored by both bone and matrix, but it is not clear whether this is a replacement pit, as Watson concluded, or merely the enlarged socket of the tusk itself. The maximum diameter of the tusk is nearly 20 mm.

The left tusk is somewhat smaller than the right. The maximum diameter is 14 mm, measured in the plane of the alveolar margin which is not quite horizontal. Again it is difficult to decide whether a replacement pit was present. There is a shallow pit mesial to the tusk in the eroded bone with a small, apparently post-mortem, hole in its floor, but it is by no means certain that it represents a replacement pit. A further tooth, again represented only by the root, is present on the left premaxillary. It is situated right next to the maxillary suture and like the maxillary teeth on the right has a basal diameter of about 3 mm. There is no sign of a corresponding tooth on the left.

The medial region of the snout is dominated by two large elongate, roughly triangular pits, with their long axis running antero-posteriorly and their respective apexes posteriorly. Watson interpreted these pits as choanae, with a narrow longitudinal septum running between them formed from the vomer, but this seems improbable. They are more probably to accommodate large symphysial tusks from the lower jaw. Similar pits occur in many temnospondyls (Romer 1947). In *Ichthyostega* a single bilobed fenestra is present. In the Coal-Measure loxommatid

Megalocephalus this is also the normal condition but one specimen from the Palace Craig ironstone of Lanarkshire has the fenestra divided into two by a median bar formed from the vomers, which runs forward to suture with the premaxillaries (Tilley 1971). This is probably the condition in *Otocratia*, as Watson concluded.

The vacuities are about ½ cm deep with steep, almost vertical sides laterally. The left fenestra or rather pit, has walls and floor of intact bone posteriorly and this may have been the case throughout, but anteriorly much of the floor is missing. The right pit is plugged with a piece of

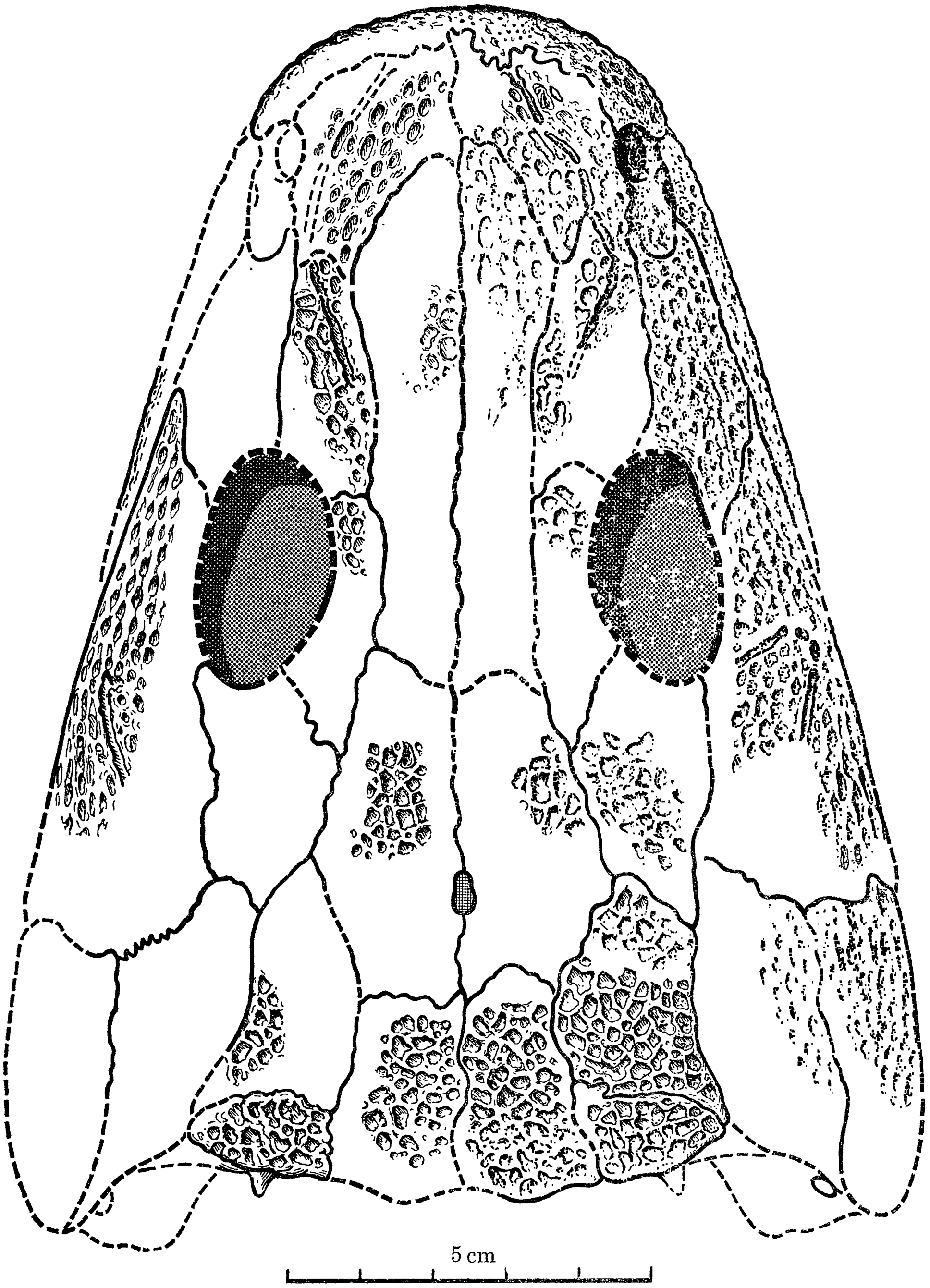

Figure 14. *Pholidogaster pisciformis*, composite restoration of skull, dorsal view. Natural size.

matrix posteriorly, but anteriorly the floor is of intact bone as is all the visible side wall. It is not, however, certain that there is a sutureless transition between the two, nor that the 'floor' (the skull roof) was imperforate.

Thus the pits may be interpreted in three ways: (i) as deep depressions formed entirely from the vomers, (ii) as fenestrae in the vomers with the walls probably formed from those bones, but part at least of the floor formed from the premaxillaries, (iii) as depressions in massive premaxillaries. The second interpretation seems the most probable.

The septum between the pits consists anteriorly of a narrow ridge of matrix with bone preserved on the morphological right. This eroded bone extends forward as a spike to the level of the tips of the anterior teeth and probably consists in part of right vomer and in part of premaxillary. The junction between the two could not, however, be traced.

More posteriorly the septum is eroded down to the level of the rest of the anterior central region. A short median stretch of matrix between the posterior ends of the pits may mark the line of suture between the vomers.

If the whole medial area surrounding the paired pits represents the vomers, it is not possible to reconstruct the pattern of dermal roofing bones of the end of the snout anterior to the frontals. Romer describes short wide nasals between the nares of *Greererpeton*, extending well in front of the narial level. He also, with less certainty, restores an internasal bone. This is figured as extending from between the anterior ends of the frontals to reach the junction of the premaxillaries. It thus separates the nasals throughout their length. This is unlike the situation in *Ichthyostega*, in which the internasal is a small rhomboidal ossification restricted to the nasal-premaxillary junction, or that in *Pholidogaster* (see above).

Restoration of the skull

A series of characters make it probable that the holotypes of *Pholidogaster* and *Otocratia* represent members of the same species. The two skulls are of almost identical size and, despite the disruption of the former specimen, it seems probable that the proportions of the two were likewise very closely similar. Thus the length of the snout can still be accurately estimated in each case.

Where corresponding dermal bones are present and sufficiently well preserved in both specimens they again coincide. This is notably the case with the elongate post-parietals and supratemporals, the backward extent of the jugal and the probable absence of an intertemporal. The left tabular of *Pholidogaster* shows the beginning of the postero-lateral extension so characteristic of *Otocratia.*

The pattern of the snout is also similar. Both skulls show the large septomaxillary and a long prefrontal extending from a point almost at the front of the orbit forward to the level of the septomaxillary, but separated from the latter bone by a process of the lacrimal. The lacrimal of *Pholidogaster* certainly extends from septomaxillary to orbit alongside the prefrontal and most of the suture separating prefrontal and lacrimal can be traced in *Otocratia.*

Finally, both skulls possess the feature which clinches the taxonomic position of *Pholidogaster*: they both show evidence on both sides of massive premaxillary tusks, a very unusual feature among labyrinthodonts.

It is conceivable that the two holotypes represent distinct species of the genus *Pholidogaster.* '*Pholidogaster*' appears to have had smaller tusks than '*Otocratia*', but this is not certain, and, if the case, could be attributed to growth or sexual dimorphism. No other taxonomic difference is apparent. Also both specimens come from the same area and the difference between the two Upper Viséan horizons, while significant, does not make specific separation mandatory. Thus pending further discoveries specific identity will be assumed.

The similarity in size made direct transfer of data possible in producing a composite restoration of the skull (figures 14–15). The *Otocratia* skull gives a good idea of the outline in dorsal view when allowance is made for the missing edges, and it also allows a reasonable restoration of the shape of the orbits. The pattern of sutures is composite, but where present in both skulls I have favoured the '*Pholidogaster*' pattern, which is visible in dorsal view. Allowance for the fact that the sutures are visible only from below is, however, relatively easily made in *Otocratia*, particularly where overlap areas are exposed.

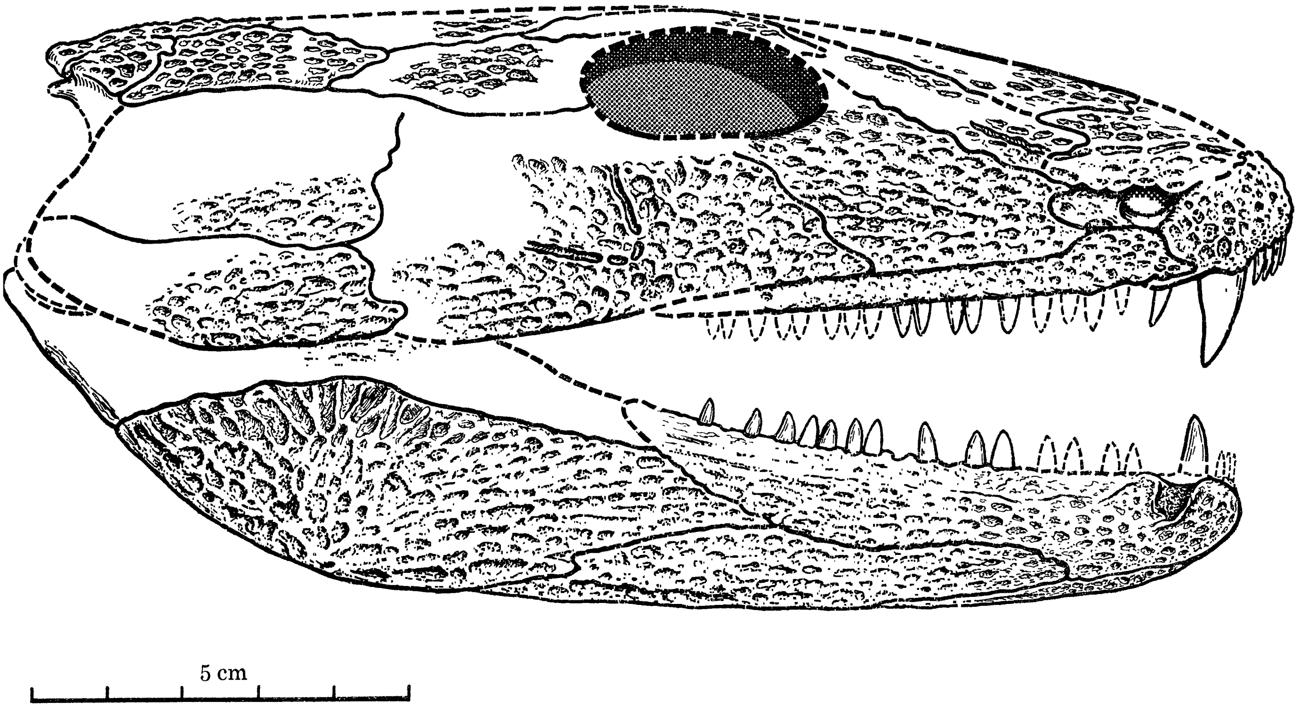

FIGURE 15. *Pholidogaster pisciformis*, composite restoration of skull, lateral view. Natural size.

The dermal ornament and lateral line sulci are only drawn in where they are visible and reasonably preserved in the *Pholidogaster* holotype and, as in the restoration of *Eoherpeton*, bilateral symmetry has not been assumed. However, in lateral view the external surface of the jaw ramus may be regarded as 'composite' as it incorporates data from both rami of the same skull, again as in the *Eoherpeton* restoration. The maxillary and dentary dentition are entirely from '*Pholidogaster*', but the premaxillary dentition is that of '*Otocratia*', including the large size of the premaxillary tusk.

No attempt has been made to restore the skull in palatal or occipital view as the data are insufficient.

Notes on the post-cranial skeleton

The whole of the preserved dermal pectoral girdle is associated with the skull block in the holotype of *Pholidogaster* and some considerable new development has therefore taken place above the girdle.

In ventral view the clavicles are well-preserved and their position is figured by Romer. Compression has resulted in the clavicles being driven together, thus obscuring most of the anterior part of the ventral surface of the interclavicle. The posterior part of that ventral surface is largely missing but a rather poor natural cast of the inner, dorsal surface remains and shows the extent of the bone.

Exposure from above has now revealed the complete ascending process of the right clavicle and in front of it part of the dorsal surface of the interclavicle. The mesial edge of this latter surface is defined by a short thick bony rod, which may represent the right cleithrum or may be part of the ascending process of the left clavicle. Behind it is a massive rectangular piece of bone. This appears to be part of the scapulocoracoid, probably the supraglenoid buttress, and part of the glenoid, but the exposed area is small and the preservation rather poor.

Part of the left cleithrum is also apparently preserved and was visible before the recent development as a fragment of bony rod about 2 cm long and 4 mm thick, lying horizontally behind the left clavicle lateral to the area of the interclavicle.

It has been noted that an irregular and poorly preserved bony rod, figured *in situ* by Romer, was preserved on the summit of a massive piece of ironstone covering the posterior cheek region of the skull. This specimen, some 3 cm long, may also represent cleithrum, as it appears too irregular to be part of a rib.

On the dorsal surface of the holotype, to the left of the girdle bones, a jumble of small bones is now visible. These overlie the left clavicle. They appear to be disrupted anterior vertebrae and one neural arch is clearly visible in right lateral view. Otherwise, however, the bone is poorly preserved and difficult to interpret.

The isolated left clavicle from Gilmerton is certainly to be attributed to *Pholidogaster*. It is exposed in ventral view on a small block of ironstone and is virtually complete except for the ascending process. It is very closely similar in all respects to that of the type: the size is the same and the well-preserved dermal ornament of exactly similar type.

The ornament of the isolated interclavicle from Burdiehouse is again of *Pholidogaster* type and the interclavicle is of the same size as that of *Pholidogaster*. The specimen may reasonably be attributed to '*Otocratia*' and thus on the present hypothesis to *Pholidogaster*. It is preserved with its ventral, external surface exposed on a small block of matrix. The latter appears to be of limestone on the side on which the interclavicle is situated but to merge into ironstone with some interleaving below.

The interclavicle is shown in figure 16 and is used together with the clavicles of the type in a restoration of the dermal girdle. The overlap areas for the clavicles are particularly clear on the ventral surface of the interclavicle. These areas have well-marked boundaries and a very reduced ornament.

I have made no attempt to indicate the cleithra in ventral view in the reconstruction, but the probable cleithrum is shown, as far as preserved, in lateral view. The mode of overlap of cleithrum and clavicle is of standard temnospondyl type, so that the facets for articulation may be seen in ventral view on the clavicles. This is opposite to the situation seen in plagiosaurs (Panchen 1959).

The pelvic girdle of *Pholidogaster* has been described and figured by Romer (1964). Romer shows the mode of preservation in his figure 1 and gives an outline restoration of the pelvic girdle in the reconstruction of the whole skeleton (Romer's plate I). The restoration of the ilium requires comment (Panchen 1970).

In the holotype only the left half of the girdle is preserved and part of the ilium is missing along the line of a break in the specimen. Dorsal to the break the ilium extends postero-dorsally as an elongate rectangular process. This is regarded by Romer as a post-iliac process and is shown in his reconstruction as distinct from the (missing) sacral process of the ilium, a configuration based on that of primitive and embolomerous anthracosaurs (e.g. *Archeria*: Romer 1957; *Proterogyrinus*: Romer 1970). I have pointed out, however, that the ilium of early temnospondyls does not have the two processes as separate entities but that in this case the post-iliac process is a postero-dorsal extension of the sacral process itself (Panchen 1970, p. 35). This type of ilium is typified by that of *Dendrerpeton* (Carroll 1967). It is also present in the segmouriamorphs.

Recognition of the fact that *Pholidogaster* is not an anthracosaur or anthracosaur forebear thus makes it unlikely that it had the anthracosaur type of ilium. It is probable that its ilium was closely similar to that of *Greererpeton* in which the iliac process likewise sloped upwards and

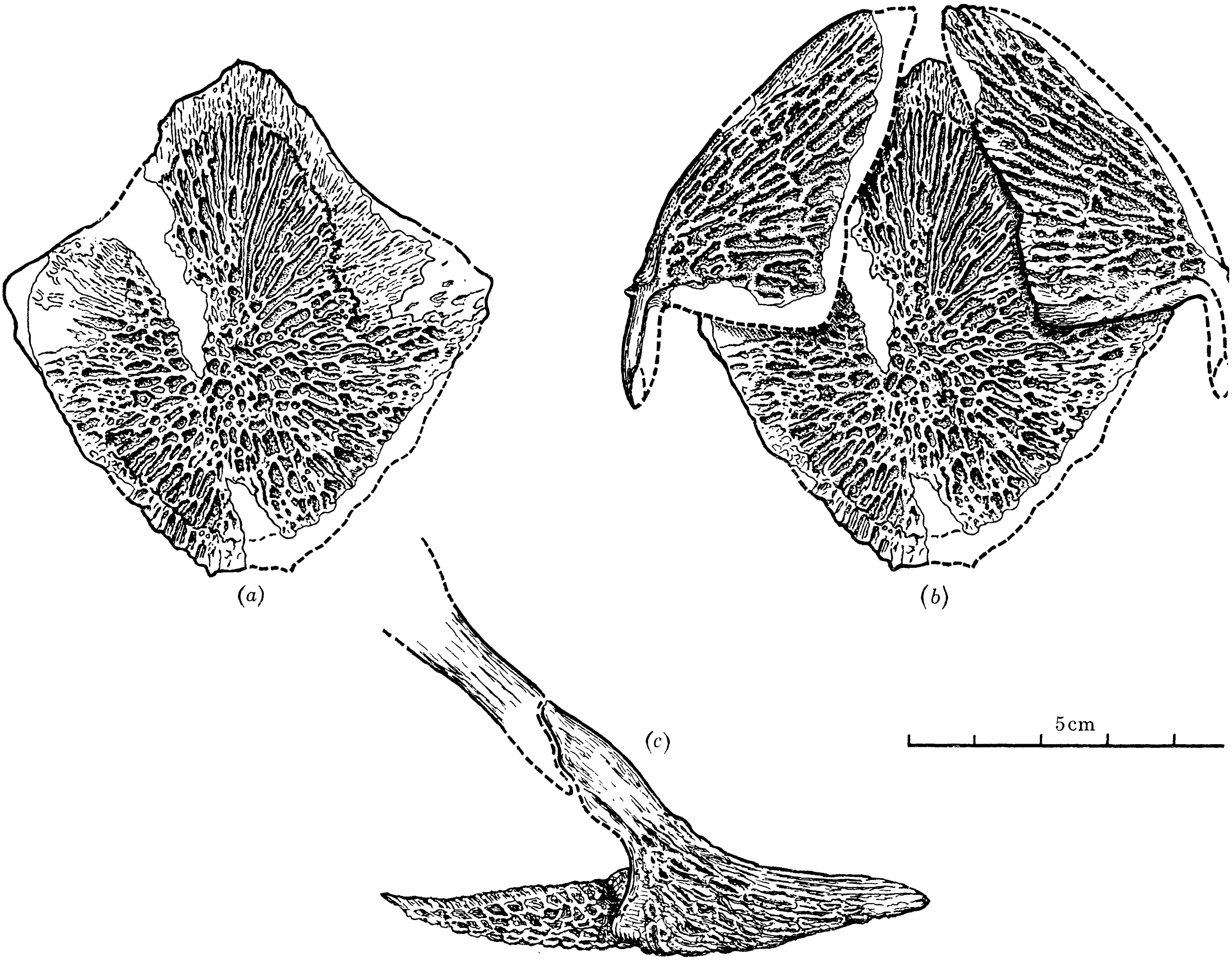

FIGURE 16. *Pholidogaster pisciformis*, dermal pectoral girdle. Natural size. (*a*) '*Otocratia*' interclavicle from Burdiehouse, ventral view; (*b*) and (*c*) composite restoration of girdle, ventral and lateral view.

backwards from the acetabular region (Romer 1969, fig. 7). Romer assumes in *Greererpeton* that the sacral attachment was situated at the top of the iliac process, but only the outer surface of the well-preserved right ilium is figured and the sacral facet cannot thus be seen. This is presumably the case in the specimen. It seems more probable that in both *Pholidogaster* and *Greererpeton* the sacral attachment was just above the 'neck' of the ilium, the normal primitive temnospondyl condition.

The vertebrae of *Pholidogaster* were discussed in my anthracosaur monograph (Panchen 1970). It was concluded that, despite rather elongate pleurocentra, they were essentially of rhachitomous type and closely comparable to those of the temnospondyls *Dendrerpeton* (Carroll 1967) and *Neldasaurus* (Chase 1965). I thus concluded that there was no reason to regard them as representing an ancestral condition to the vertebrae of anthracosaurs. Knowledge of the vertebrae of *Proterogyrinus* makes this even more improbable, as noted above.

However, the vertebrae of *Pholidogaster* are identical in structure to those of *Greererpeton*, as one might expect. Romer (1972*b*) has also recently described the armour of dermal scales and gastralia which covered the whole body of *Greererpeton*, and once again the gastralia of *Pholidogaster* (Huxley 1862; Romer 1964) are closely similar, although the dorsal scales of the latter are little preserved.

Relations of *PHOLIDOGASTER*

It is clear that *Pholidogaster pisciformis* is a primitive temnospondyl labyrinthodont having no close relationship to the anthracosaurs. In fact its anatomical features contrast so strongly with those of its contemporary anthracosaurs *Eoherpeton* and *Proterogyrinus* that any common ancestor must have been structurally and geologically remote from either.

The temnospondyl characters include the nature of the dermal ornament, the presence of a suture between the post-parietal and supratemporal of the skull table, the absence of tabular horns of the anthracosaur type and, correlated with the last two, the profile of the back of the skull table.

Temnospondyl characters of the post-cranial skeleton include the essentially rhachitomous vertebrae, with massive crescentic intercentra and paired pleurocentra, and the short tail. The latter consists of only 31 reconstructed vertebrae (Romer 1964) and contrasts strongly with long tail of embolomeres and primitive reptiles.

The dorsal pectoral girdle of *Pholidogaster*, like the skull, is ornamented externally with characteristic temnospondyl ornament. Its anatomy is typical of early aquatic temnospondyls, with a short rhomboidal interclavicle lacking any parasternal process, broad clavicles and with cleithra reduced to splints, at least ventrally.

Primitive characters of *Pholidogaster* include the absence of otic notches, and the deep, narrow lateral line sulci of the skull roof, which are bridged by bone and thus apparently near the fish condition. They also include the relative length of the skull table and particularly the post-parietals, together with the shortness of the snout, particularly the nasals. The kinetism between skull roof and cheek seems to have been retained and the palate was probably 'closed', with little or no development of interpterygoid vacuities.

The remaining important diagnostic characters of *Pholidogaster* show it to have been closely related to its American contemporary *Greererpeton*. In the skull roof they share the features so far noted, together with the detailed pattern of dermal bones. Notably both have elongate prefrontals flanked by lacrimals which enter broadly into the orbit, and both probably have well-developed septomaxillaries excluding these bones from the margin of the external naris. Both also lack the intertemporal, an advanced feature, although the intertemporal is present in a skull in Washington otherwise indistinguishable from *Greererpeton*.

The most important common feature, however, is the presence of massive premaxillary tusks behind the normal small premaxillary teeth. In describing *Greererpeton* Romer (1969) notes the presence of at least one large tusk in each premaxillary of the holotype, and in discussing its relationships notes the unusual nature of this feature. This and the characters of the dermal skull roof, notably the long table and the configuration of the prefrontal and lacrimal, relate *Greererpeton* to the Pennsylvanian genera *Erpetosaurus* and *Colosteus* from Linton, Ohio (Romer 1930; Steen 1931). There is no doubt that *Pholidogaster* belongs to this assemblage.

In the post-cranial skeleton the resemblances between *Pholidogaster* and *Greererpeton* are also striking. The vertebrae, both from the trunk and tail, are virtually indistinguishable except by size. There also appears to have been a similar number of presacral vertebrae: Romer gives a count of 36 for *Pholidogaster*, to which must be added at least 2 or 3 more to account for those newly exposed above the pectoral girdle, so that a count of 40 is probable. In one specimen of *Greererpeton* (C.M.N.H. 11090) I estimated 42, ± 2.

In the appendicular skeleton the dermal pectoral girdles are similar, that of *Greererpeton* (Romer 1972*b*, fig. 1) having a proportionately somewhat narrower interclavicle. The pelvic girdles are probably of the same type as explained above and the proportions of the limbs to the trunk are also similar. Comparison between the limbs is difficult in that those of *Pholidogaster* are poorly preserved and those of *Greererpeton* not yet fully described.

The femora of *Pholidogaster* are of the same general type as those of *Greererpeton*, but those of *Pholidogaster* are somewhat more fully ossified at the ends, as might be expected in a larger animal.

Significant differences between *Pholidogaster* and *Greererpeton* are difficult to find. *Pholidogaster* is a larger animal. Its skull has a pp length of 163 mm compared to 128 mm for the holotype of *Greererpeton*: all specimens of *Greererpeton* seen by me were of approximately the same size. The post-cranial skeletons of both are in proportion to their skulls. Thus the differences in proportion of the interclavicles, dependent on allometric growth, may be related to size difference as is the difference in degree of ossification of the femora.

Romer restores the orbits of the holotype *Greererpeton* as almost perfect circles in contrast to the ovoid shape seen in '*Otocratia*', but the holotype of *Greererpeton* has a flattened and somewhat disrupted skull roof. Circular orbits in labyrinthodonts are rather unusual. The lateral line sulci seen in *Greererpeton* do not have the distinctive bridges seen in *Pholidogaster* and their apparent distribution is different. *Pholidogaster* shows a well-defined forward extension of the supraorbital sulcus across the nasals, which is not recorded in the holotype of *Greererpeton*, while the latter shows sulci on the supratemporals, post-orbitals in addition to the backward extension of the supraorbital sulci between the orbits. However, most of these differences may be attributed to differences in preservation and preparation between the two holotypes.

A similar argument applies to differences in the respective restoration of the pattern of dermal roofing bones. It is probable that *Greererpeton* had septomaxillary bones occupying the corresponding area to those of *Pholidogaster* and the region in which Romer tentatively restores an internasal in *Greererpeton* is not known in *Pholidogaster* or '*Otocratia*'.

Thus *Pholidogaster pisciformis* and *Greererpeton burkemorani* are closely related temnospondyls of the family Colosteidae Romer (1930). The two Pennsylvanian genera of this family are being revised by Dr John N. Chase and a detailed comparison will be possible when his study is complete. Romer (1969) regards the Colosteidae as in many respects a specialized group and their discovery in the Lower Carboniferous leads to some interesting conclusions about our knowledge of early amphibian evolution.

Pholidogaster, represented by the holotype of '*Otocratia*', has the earliest known intact labyrinthodont skull after the ichthyostegids from East Greenland. Later in the Gilmerton Ironstone it is accompanied by a primitive anthracosaur, *Eoherpeton*, and two very different labyrinthodonts, *Loxomma allmanni*, the earliest known loxommatid, and the strange relict *Crassigyrinus scoticus* (Panchen 1973*a*).

In the succeeding Namurian Limestone Coal Group of Scotland the only labyrinthodonts known are anthracosaurs, represented by an undescribed anthracosaur post-cranial skeleton and possibly the unlocalized femur, *Papposaurus traquairi* Watson (1914), and loxommatids, represented by a normal jaw and the aberrant *Spathicephalus mirus* Watson (1929).

In North America the equivalents of both the Upper Viséan Gilmerton Ironstone and the Namurian Limestone Coals probably lie within the Mauch Chunk Series and are thus Upper Mississippian. At Greer the only labyrinthodonts known are *Greererpeton* and *Proterogyrinus*. Another locality is recorded in the Mauch Chunk Series of the Appalachian Region, U.S.A. The Hinton Shales of West Virginia are situated in the Hinton Group, which lies above the Bluefield Group of the Greer horizon (Panchen 1970, and references therein). Romer (1941) reports labyrinthodont remains from Hinton which include non-diagnostic temnospondyl and possibly anthracosaur remains (D. Baird, personal communication).

Other late Mississippian localities are situated in Nova Scotia and are reviewed by Carroll *et al.* (1972). A number of specimens are known from the Point Edward Formation, Sydney Harbor, which is probably of Namurian A age. These include the jaw ramus described as *Pholiderpeton bretonense* by Romer (1956, 1963) and other anthracosaur material which may represent more than one species. Notable is the fact that the material includes true embolomerous vertebrae, the earliest yet recorded. Also present is a second species of *Spathicephalus*, *S. pereger* Baird (1962) and, notably, a headless temnospondyl skeleton PU 20100 present as a natural mould. The latter, from what little information it yields, appears to be colosteid and closely similar to that of *Greererpeton.*

A second locality in Nova Scotia is also probably Namurian in age but lies above the Mississippian–Pennsylvanian boundary. This is in the Pomquet Formation, Mabou Group at Grand Etang, which like Point Edward is on Cape Breton Island. The labyrinthodont material consists of individual anthracosaur bones, including embolomerous vertebrae, but also a temnospondyl ilium and other appendicular fragments which are comparable to those of *Greererpeton.*

Thus, apart from the ichthyostegids, only three groups of labyrinthodonts are certainly known from pre-Westphalian deposits: (1) the anthracosaurs, possibly known in the Tournaisian at Horton Bluff, N.S., and producing embolomerous forms in the early Namurian; (2) the loxommatids, appearing first in the late Viséan; and (3) the colosteids, appearing first as '*Otocratia*' somewhat earlier in the Viséan. The anthracosaurs and loxommatids continue as the principal labyrinthodonts throughout the British Coal Measures and are recorded at various horizons in the North American Pennsylvanian (Panchen 1973*b*) but the colosteids are apparently absent from the British Coal Measures and do not reappear in America until Westphalian D at Linton, Ohio.

It must be concluded, however, that the anthracosaurs, loxommatids and colosteids are far from being the only Lower Carboniferous labyrinthodonts that existed. In the Westphalian small temnospondyls of edopoid type make an early appearance: *Eugyrinus* is the earliest known temnospondyl in the English Coal Measures and a closely similar skull is known from the Upper Parrsboro Formation at Nova Scotia (Carroll *et al.* 1972). Both these horizons are Westphalian A as is the Jarrow Coal of Ireland in which there are several, as yet inadequately described, small temnospondyls.

Eugyrinus, with a well-developed intertemporal, otic notches and short post-parietals is an unlikely colosteid descendant as is the Joggins, Nova Scotia form *Dendrerpeton*. The latter is the commonest amphibian at Joggins (Westphalian B) and occurs with six microsaurs, one rare anthracosaur and three true reptiles in an undoubted terrestrial fauna.

The ancestors of all three forms were undoubtedly present in the Mississippian but have not been found. Our view of the Mississippian tetrapod fauna is thus largely confined to a few specialized aquatic forms whose environment was favourable to their preservation. It therefore seems not improbable that *Pholidogaster* and *Greererpeton* are to be regarded as secondarily aquatic forms, rather like the embolomerous anthracosaurs, despite their early date.

Several things suggest this. Loss of the intertemporal is an advanced feature defining the colosteids as a separate radiation distinct from that of later temnospondyls. On the other hand they share with later temnospondyls the reduction of the cleithrum to a splint. If they had been primarily aquatic it seems improbable that this reduction of the cleithrum would have taken place. An expanded dermal girdle is usually considered to indicate an aquatic habit and a reduced cleithrum to indicate that the expansion is secondary.

An expanded cleithrum is present in *Ichthyostega* (Jarvik 1955) and is retained in the aquatic plagiosaurs (Nilsson 1939; Panchen 1959). Thus the reduced cleithrum of colosteids and all other labyrinthodonts suggests a terrestrial ancestry.

Furthermore the long presacral vertebral column is probably also secondary, as in embolomeres (Panchen 1966). *Ichthyostega* has only about 24 trunk vertebrae. This is a normal number for labyrinthodonts (Romer 1947) from which both colosteids and embolomeres presumably diverged on assuming an aquatic anguilliform habit. Similarly *Ichthyostega* had sturdy if primitive limbs unlike the reduced appendages of the former groups.

It has been suggested at various times that the colosteids are closely related to *Ichthyostega*. In his original preliminary account of the skull roof Säve-Söderbergh (1932) concluded that the genera *Ichthyostega* and *Ichthyostegopsis* formed a specialized and isolated group, despite their early age, and in 1934 he placed the Ichthyostegalia outside the labyrinthodonts. This isolated position of the ichthyostegids has always been endorsed by Jarvik. Only the genus *Acanthostega*, contemporary with other ichthyostegids, was admitted to the Ichthyostegalia and this with some doubt (Jarvik 1952).

However both Romer (1930) and Steen (1931) placed a number of Carboniferous temnospondyls, including the Linton colosteids, in the order Phyllospondyli. This was held to be characterized, *inter alia*, by precocious development of advanced temnospondyl features, notably an open palate.

Romer (1933) later added the ichthyostegids to this assemblage. He was subsequently able to show that the Phyllospondyli, a group by then collapsing under its own weight, had been founded for a series of larval, neotenous, or ill-known temnospondyls and was not a natural entity (Romer 1939). However, Romer (1945, 1947) retained the connexion between the ichthyostegids and the colosteids. He also retained the idea that the large interpterygoid vacuities of the latter (known only in *Erpetosaurus*) characterized the terminal forms of an early radiation distinct from that of other temnospondyls.

Meanwhile '*Otocratia*', not then known to be a colosteid, had been related to the ichthyostegids by both Westoll (1942) and by Romer (1945, 1947). Both point out, correctly, that the paired median vomerine pits were not choanae, as Watson had interpreted them, and both cite the aberrent occiput of *Otocratia* as suggesting ichthyostegid affinity.

Comparison of the ichthyostegids with later labyrinthodonts is hampered by the paucity of published data on the former. It is now over forty years since the first seven ichthyostegid skulls were collected. Twenty years later the total of ichthyostegid material amounted to about 170 specimens (Jarvik 1952). Now, more than twenty years after that, published accounts are confined to Säve-Söderbergh's original preliminary description, together with a description of the tail, a brief account of a few vertebrae and ribs and annotated reconstructions of the external appearance of the skull (of '*Ichthyostega* sp.') together with a description of the skull roof of *Acanthostega* (Jarvik 1952). Tantalizing glimpses of the post-cranial skeleton of *Ichthyostega* sp. are afforded by a sketch reconstruction and by figures of the pelvic girdle and hind limb (Jarvik 1955, 1965). There is probably no other case in the field of vertebrate palaeontology where our understanding of a critical phase in vertebrate evolution has been retarded for such a long period by lack of information on material already collected.

If the restored skull roof of *Ichthyostega* is compared with that of *Pholidogaster* some similarities emerge. The proportions of preorbital to post-orbital region are almost identical. Common diagnostic features of the dermal roofing pattern include the absence of an intertemporal and the short nasals.

The territory of the intertemporal is occupied by a long suture of the post-orbital and the parietal in both cases. The post-parietals are represented by a single element in *Ichthyostega*, but paired in *Acanthostega*. They are elongate in the ichthyostegids and in *Pholidogaster* and the post-frontal is a relatively small bone in both.

The configuration of the skull table in both ichthyostegids and colosteids is consequent on the loss of the intertemporal in a skull with a primitively elongate post-orbital region and is not therefore necessarily a sign of affinity. In the preorbital region, the lacrimal of colosteids forms a considerable part of the orbital margin whereas that of *Ichthyostega* is excluded from the orbit by a prefrontal–jugal contact as in embolomerous anthracosaurs. In this case the ichthyostegid configuration may be regarded as the more advanced one. Rhipidistia such as *Eusthenopteron* have an orbital lacrimal whereas the ichthyostegid pattern (including *Acanthostega*) is a consequence of the relative postero-dorsal migration of the orbits (e.g. Panchen 1973*a*, fig. 3).

On the other hand I have argued (Panchen 1967*b*) that a marginal nostril bordered above by an anterior tectal, the ichthyostegid condition, is primitive for tetrapods but not for their fish ancestors. In this case the colosteids show a more advanced, typically tetrapod condition. There is also the case with the open lateral line system, the absence of a preopercular bone, the small tabular and the more posterior situation of the pineal foramen: all characters of colosteids.

The lower jaws of both *Ichthyostega* and *Pholidogaster* are of a generalized early tetrapod pattern and thus neither corroborate nor refute relationship between them.

The tabular of *Ichthyostega* is apparently a complex bone with deep descending laminae in the occipital plane. Jarvik regards it as very specialized but only a detailed description can establish its primitive or specialized nature. Possibly the expanded occipital tabular of *Otocratia* may indicate relationship to either *Ichthyostega* or *Acanthostega* as Romer has suggested, but the evidence is slight.

No useful comparison can be made between the palate of *Ichthyostega* and that of early colosteids. It should be noticed, however, that while the restored palate of *Ichthyostega* (Jarvik 1952, fig. 36) has notable primitive features, such as a virtual lack of interpterygoid vacuities and a short parasphenoid confined to the sphenethmoid region, the dentition appears divergent from that of early labyrinthodonts.

In the rhipidistian *Eusthenopteron* (Jarvik 1944) the palatal dentition consists of a row of small teeth on vomers, palatines and ectopterygoids paralleling the marginal teeth on premaxillary and maxillary, but lying of course mesial to the choanae on vomer and anterior palatine. Mesial to the palatal teeth are a row of massive tusks with replacement pits situated on the same palatal bones. An additional row of minute teeth is also present lateral to the palatal teeth and another lateral to the marginal row.

In *Ichthyostega* the principal marginal row and the principal palatal row have been retained but the tusks have been lost. In most early labyrinthodonts on the other hand the palatal dentition appears to be homologous with the tusk row of rhipidistians. Thus typical loxommatids have tusks only on the three palatal bones (Watson 1926, 1929), while anthracosaurs have toothless vomers (except *Gephyrostegus*) and tusks on the palatines: the dentition of the ectopterygoids consists either of one or more tusk pairs followed by smaller teeth or a graded series.

The edopoids *Dendrerpeton* (Carroll 1967) and *Cochleosaurus* Steen (1938) seem to be typical of the early temnospondyl condition. Both retain tusks but not teeth on the palate.

The two Linton colosteids also have palatal dentitions in which the tusks are strongly developed. In *Erpetosaurus* there are tusk pairs only on palatines and ectopterygoids and a small tooth pair on each vomer. A tusk pair in the vomerine region is interpreted as vomerine tusks by Romer but as premaxillary fangs by Steen. This latter interpretation is now accepted by Romer (1969). Conversely a pit situated in front of the palatine is interpreted as palatine by Steen but maxillary by Romer.

In *Colosteus* both Romer and Steen show a series of palatal tusks whose disposition is probably closely similar to those of *Erpetosaurus*.

Thus if the Lower Carboniferous genera *Pholidogaster* and *Greererpeton* had a similar dentition to the Linton forms this would be a significant divergence from the condition in *Ichthyostega*. Later labyrinthodonts, however, show a variety of types of palatal dentition and it is possible that in phylogeny a tusk row could be transmuted to a tooth row or vice-versa.

In conclusion no character of *Ichthyostega* positively demonstrates a close affinity with the colosteids, but an ancestor-descendent relationship is not absolutely ruled out. Ironically the loss of the intertemporal in both, resulting in a similar pattern of the skull table, is the only feature tending to do this. If the Washington skull of *Greererpeton* with its persistent intertemporal shows a relict condition of the immediate ancestry of that genus, *Ichthyostega* cannot represent an ancestral form. Any conclusion about *Ichthyostega*, however, is weakened by the fact that the name may well represent a fauna rather than a taxon.

The material on which this study is based was borrowed from the Royal Scottish Museum, the British Museum (Natural History) and the Institute of Geological Sciences. As on many previous occasions I am pleased to acknowledge my debt to the authorities of these institutions.

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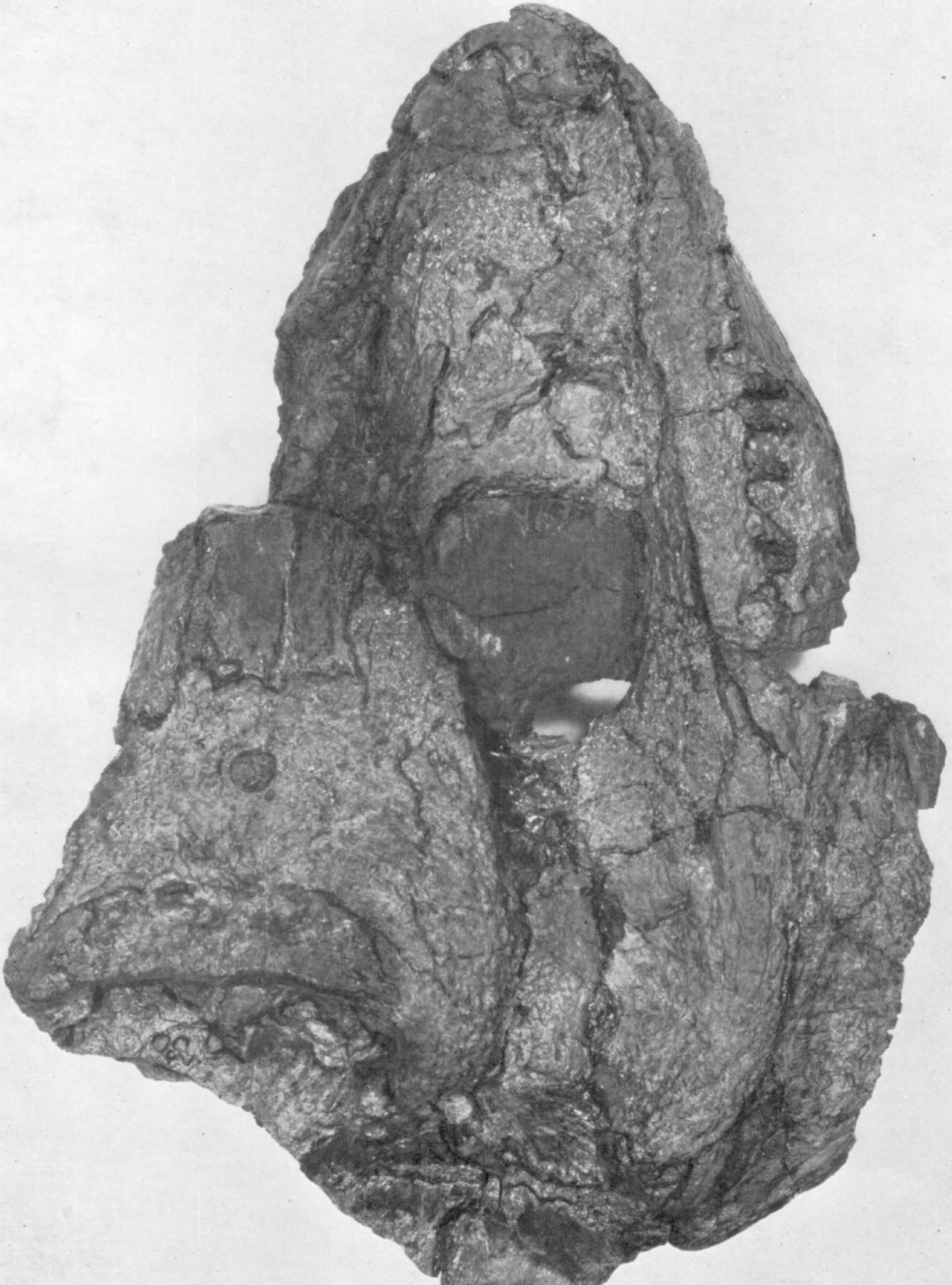

FIGURE 2

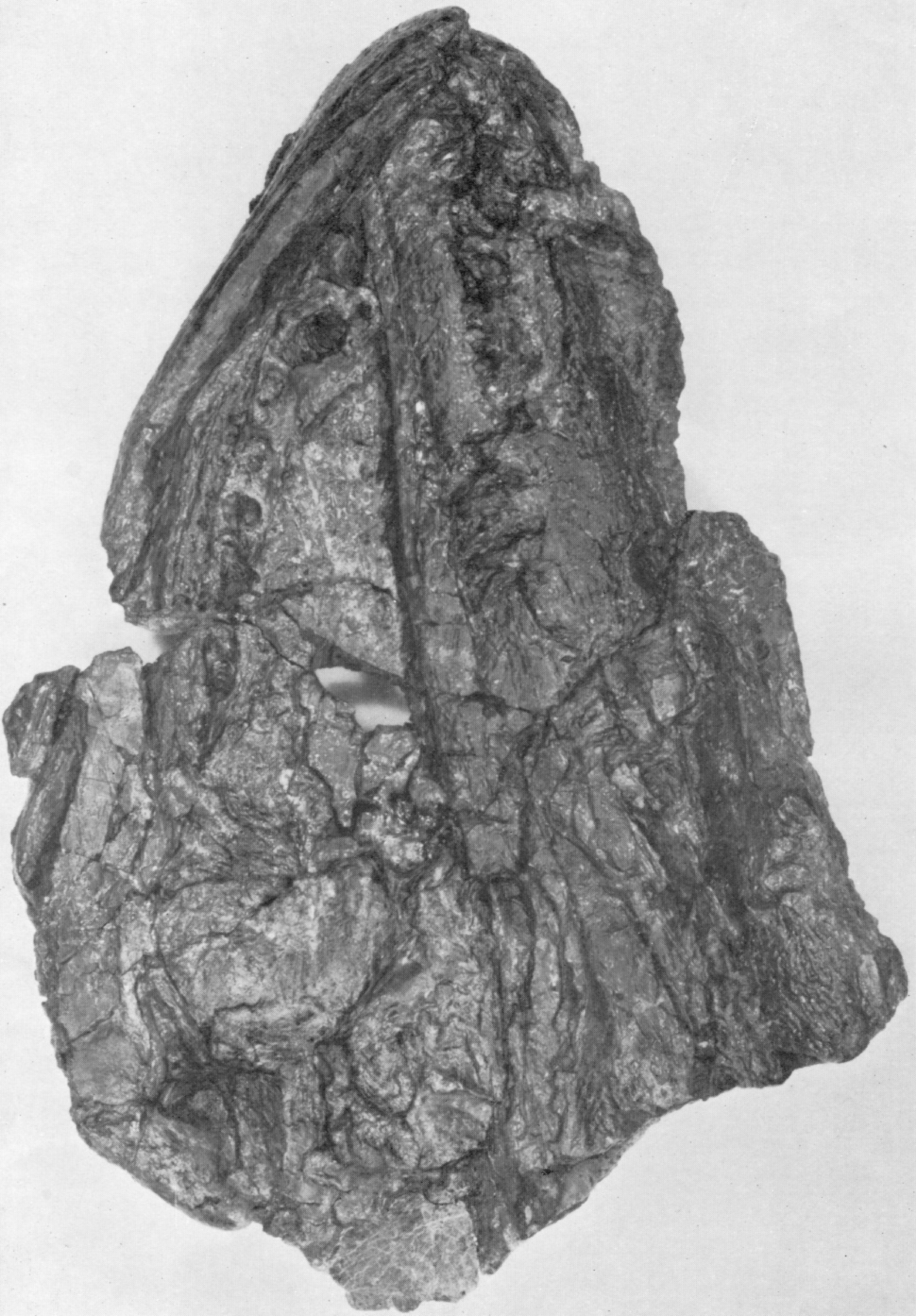

FIGURE 3

FIGURE 12