The Cranial Anatomy of Two Coal Measure Anthracosaurs

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THE CRANIAL ANATOMY OF TWO COAL MEASURE ANTHRACOSAURS

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[Plate 10]

CONTENTS

Amphibian material collected by Mr J. A. Coope from Swanwick Colliery, Derbyshire was developed mechanically and with pyridine. The described remains consist of imperfect skulls of two species of Coal Measure anthracosaurs.

The nomenclature of the anthracosaur-type material in the Hancock Museum is discussed and on the basis of this discussion the two Derbyshire skulls are assigned to the species *Palaeogyrinus decorus* Watson and *Eogyrinus attheyi* Watson.

The *Palaeogyrinus* specimen is described and, with the aid of redescription of critical regions of the type skull, new restorations of the occiput, the braincase, the skull roof and the palate are produced. *Palaeogyrinus* is shown to have an open fenestra ovalis of normal tetrapod type, an external naris which cuts the jaw margin, rather like that of *Ichthyostega*, and an otic notch, which while dorsal in position, is in no sense a continuation of the squamosal-supratemporal joint.

The *Eogyrinus* specimen shows the articular surface of the squamosal and the posterior palatal structure. Removal of the right pterygoid and extensive epipterygoid revealed details of the braincase including a well-preserved basipterygoid process.

The origin of the distinctive anthracosaur pattern of roofing bones is discussed and it is concluded that in this respect these animals are further removed from their fish ancestors than the temnospondyl labyrinthodonts, but that the kinetic separation between squamosal and supratemporal is primitive.

The musculature of the jaws is discussed and it is concluded that the characteristic tabular horn was for the origin of the posterior depressor mandibulae rather than a link with the shoulder girdle. The tabular horn together with the absence of post-temporal fossae in the occiput are therefore seen as secondary characters.

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INTRODUCTION

The new material described in this paper forms part of a collection of Carboniferous vertebrate fossils from a coal mine in Derbyshire. This collection was made by Mr J. A. Coope while an undergraduate at King's College, London, and deposited in the Geology Department of that College.

The whole collection comes from the Swanwick Colliery, near Alfreton, Derbyshire. This is situated at the southern end of the large Yorkshire and East Midlands coalfield. Swanwick Colliery is situated at the horizon of the Black Shale or Silkstone seam which is near the top of the *communis* non-marine lamellibranch zone. The Black Shale is thus in the Lower Coal Measures of Stubblefield & Trotter's (1957) classification, though Yorkian in age (Panchen & Walker 1961).

The fossils were found concentrated in a band of cannel coal overlying the soft Silkstone seam. Apart from the anthracosaurs to be described they include fish remains (preliminary inspection shows specimens of *Megalichthys*, *Sagenodus*, *Gyracanthus* and *Ctenacanthus*) as well as several pieces of loxommid skull and many labyrinthodont fragments.

The specimens to be described belong to two species of embolomerous anthracosaur already known from the Coal Measures: *Palaeogyrinus decorus* Watson and *Eogyrinus attheyi* Watson. The type specimens of both species are in the Hancock Museum, Newcastle upon Tyne.

The pioneer work on the English Coal Measure anthracosaurs and the contemporary loxommids was done in the last century by a devoted group of palaeontologists centred on the Hancock Museum, pre-eminent among whom was Thomas Atthey. The evolutionary importance of these groups has been established largely by the researches of Professor D. M. S. Watson (1912, 1919, 1926, 1929) whose work forms the necessary background for any subsequent consideration of these animals.

The skull of a large American form, *Neopteroplax*, has recently been described by Romer (1963) in a useful review of embolomeres from the American Carboniferous.

PRESERVATION OF MATERIAL, AND METHODS

All the specimens preserved in the Coope Collection were attached to isolated blocks of coal, since the latter had been mechanically cut. For this reason many are indeterminable fragments and many more add nothing to our knowledge of the species they represent.

Like nearly all Coal Measure vertebrate finds the specimens are much compressed and in this case their concentration in lenses makes separation of individual pieces of bone a difficult operation. The amphibian material has been freed from matrix by means of an automatic mallet and mounted needles. In the case of the *Palaeogyrinus* skull (number A1) the palatal surface presented an unrecognizable confusion of scraps of bone, not all of which pertained to the specimen.

Development by solution in pyridine was useful in this case as it dissolves most of the organic constituents of coal, but great care has to be exercised in its use on most Coal Measure material, where the fine cracks in the specimen are filled with pyridinesoluble matrix. In the case of development in acetic acid a solution of Perspex in chloroform may be used to protect the surface of the bone and to hold the specimen together (Panchen 1959): pyridine dissolves Perspex and other plastic substances and thus a different technique had to be devised.

The specimen was set upside down in a block of plaster of Paris to the depth of the roofing bones. The whole was lowered into a covered glass dish and enough pyridine poured on to just immerse the specimen. After about 2 days this was siphoned off and replaced by water for washing. Most of the extraneous bone could then be lifted off but the specimen was in a very delicate state and had to be mended with great care, now using Perspex in chloroform as an adhesive. Small areas of dermal roof in the supratemporal and post-temporal regions were lost, but all significant data from these regions had been recorded.

Rubber latex casts were taken from the dorsal and ventral surfaces, the right basisphenoid region and the right pterygoid of the type of *Palaeogyrinus*, all of which are preserved as natural moulds (Watson 1926). Before casting, the liquid latex was 'filled' with indian ink giving a matt black finish to the casts which makes the detail rather easier to see than in the translucent untreated latex. A wax reconstruction of the type skull roof was used as a basis for the composite restoration of the skull.

Taxonomy of the anthracosaurs in the Hancock Museum

The Coal Measure anthracosaurs are labyrinthodont Amphibia of the order Anthracosauria, and are members of the suborder Embolomeri (Romer 1947; Anthracosauroideae of Watson 1926, 1929) within that group.

Three species of Embolomeri are represented in the Hancock Museum by their type specimens and it is necessary to resolve their taxonomy before the present Derbyshire forms can be classified.

The first species is *Palaeogyrinus decorus* Watson (1926) from the Parrot Coal of Pirnie Colliery Fifeshire. The type consists of a single skull with no postcranial remains. Until the recent discovery no other specimen was known.

The second species is *Pteroplax cornuta* (*sic*) Hancock & Atthey (1868). The type material consists of two isolated skull tables from the Northumberland Low Main Seam at Newsham. The smaller, recently designated as the lectotype by Romer (1963), is beautifully preserved dorsally, the larger very eroded but well preserved ventrally. Both are figured by Atthey (1877).

The third species is *Eogyrinus attheyi* Watson (1926) from the same horizon and locality as *Pteroplax*. The holotype is a large skull complete with both jaw rami and associated with a number of scattered vertebrae, ribs and scutes and a single femur. This was originally described and figured by Atthey (1876) and referred to *Anthracosaurus russelli* Huxley. It was given the reference numbers DMSW 27 (the skull), 28 and 29 by Watson. The second specimen is an isolated braincase (DMSW 30) not certainly referable to *Eogyrinus attheyi*. The third is a fragment of skull (DMSW 31) from the snout region of an animal apparently very similar to the holotype. The only other skull referred by Watson to this species is the larger skull of *Pteroplax cornuta*, which he gave the number DMSW 35.

The remaining material is postcranial. It includes the long vertebral column (DMSW 33) described by Barkas (1873) and Embleton (1889) and referred tentatively by Watson to *Eogyrinus*, and a pectoral girdle (DMSW 34) of very uncertain affinities.

The principal character used by Watson to separate *Eogyrinus* and *Pteroplax* was the shape of the tabular horn. This is present on both sides in the holotype of *Pteroplax* but is missing in that of *Eogyrinus*. In the larger *Pteroplax* skull it is present on one side only and is a slender finger-like process, in contrast to the deep blade of the holotype.

Watson attributed the larger *Pteroplax* specimen to *Eogyrinus* on general form and cited the shape of the horn as diagnostic of the genus *Eogyrinus* (Watson 1929). It is highly probable, however, that the finger-like horn has been eroded to its present form from the blade-like shape, which also occurs in *Palaeogyrinus* and may well be characteristic of all embolomeres.

The general similarity of the *Pteroplax* and *Eogyrinus* material led Romer (1947) to review both as members of the same genus under the name *Pteroplax*, which has priority. However, a further study of the Newsham skulls makes it clear that two forms are represented and that these two generic names may be correctly applied to them. The characteristic differences based on the respective holotypes are tabulated below (table 1).

Table 1

	Pteroplax	*Eogyrinus*
1.	Pineal foramen large, elongate (*ca.* 3–5 mm) on marked median ridge	Pineal foramen small, circular (*ca.* 2 mm) on almost flat surface
2.	Lateral line canals deep and clearly marked between orbits	Line canals shallow and faint between orbits
3.	Skull table ornament of shallow, sharp-edged, flat-bottomed pits, indistinct or absent on parietals and postparietals	Skull table ornament of deeper hexagonal pits between sharp ridges. Developed on parietals and postparietals

The position of the larger *Pteroplax* skull is rather uncertain due to poor preservation of the dorsal surface.

The interorbital region of *Pteroplax* (as in *Palaeogyrinus*) is narrower than that of *Eogyrinus* indicating comparatively larger orbits, but the *Pteroplax* skull table represents a skull of about half the size of the *Eogyrinus* skull. Thus a comparative difference in interorbital width is probably a growth factor of little taxonomic significance.

In the features listed in the table *Palaeogyrinus* agrees with *Eogyrinus* and it is more difficult to find definitive characters separating the two. The most important cited by Watson (1929) is the form of the pterygoid. In *Palaeogyrinus* this is restored as a vertically standing sheet of bone extending, in the region behind the basal articulation, well below the jaw line. In the holotype of *Eogyrinus* there is no apparent extension of the pterygoids below the general level of the palate and the upper jaws.

However, this difference is almost certainly an artificial one due to post mortem distortion in the respective type specimens. The pterygoid of *Palaeogyrinus* has been compressed into a single plane while that of *Eogyrinus* has been flattened laterally in the very depressed holotype skull, making the subtemporal fossa appear abnormally narrow (Atthey 1876, Plate IX).

Other recorded differences are also suspect. The position of the intertemporal bone is essentially the same in both genera. Similarly the condition of the lachrymal, shown as reaching the orbit in *Palaeogyrinus* (Watson 1926) but not in *Eogyrinus* (Atthey 1876) is doubtful in both specimens.

The shape of the orbits in *Eogyrinus* is characteristic (Atthey 1876) and apparently unique amongst anthracosaurs (see, for example, Romer 1947, Figures 44 and 45). It is like that of a playing card heart. The orbits of *Palaeogyrinus* were originally restored with a somewhat different shape, but their outer borders, although not well preserved, are probably like those of *Eogyrinus*.

Undoubtedly one of the chief factors in the taxonomic separation of *Palaeogyrinus* and *Eogyrinus* was the very different geological horizon assigned to their type specimens. The 'Parrot Coal' from which *Palaeogyrinus* comes was thought to be Lanarkian in age, while the Northumberland Low Main Seam, from which comes *Eogyrinus*, is Yorkian. However, the 'Parrot Coal' of Pirnie is also Yorkian (Westoll 1951; Panchen & Walker 1961) and thus it is not surprising to find specimens of both *Eogyrinus* and *Palaeogyrinus* from the same site in Derbyshire, whatever the truth as to their relationship.

The type specimen of *Eogyrinus* represents a very much larger animal than that of *Palaeogyrinus*; the ratio of their skull lengths is approximately two and a half to one. The probability that the *Palaeogyrinus* type skull is that of an adult is supported by the fact that the Derbyshire specimen is of identical size. On the other hand if *Palaeogyrinus* and *Eogyrinus* were considered as growth stages of the same animal the differences in the outline and proportions of their skulls would be satisfactorily explained. Thus the short snout region and comparatively large orbits of *Palaeogyrinus* are very much like those of a small immature labryinthodont which might well grow to have a skull identical with that of *Eogyrinus* (cf. *Benthosuchus*: Bystrow & Efremov 1940).

It is concluded, however, that the existence of two specimens of *Palaeogyrinus* of identical size would be too great a coincidence if they both represented half grown individuals of *Eogyrinus*. Pending the discovery of further material the generic distinction between the two forms will therefore be retained.

PALAEOGYRINUS DECORUS

Watson (1926, pp. 215 to 222, Figures 13 to 17).

The incomplete skull to be described is specimen A1 of the Swanwick collection. It resembles the type in general shape, bone pattern, position, and size of the pineal foramen, and, where visible, the form of the underside of the dermal roof. The skull roof and occiput of the Derbyshire specimen will be described first, followed by a redescription of critical regions of the type, thus allowing new composite restorations of the whole skull.

Skull roof—dorsal

The condition of the bone surface in skull A1 is generally good and most of the sutures were easily traced. The ornament on the surface of the dermal bone is a rather irregular form of the characteristic labyrinthodont 'pit and ridge' type (figure 1).

The ornament of the anthracosaurs is generally much less clear-cut and regular than that of the contemporary loxommids and is also on a smaller scale even in animals of a similar size. In the present specimen the regions where the lateral line grooves are most clearly marked in the type are not represented. However, the supraorbital canal is less defined.

A characteristic feature of both skulls is the small size of the circular pineal foramen, which is about 2·5 mm in diameter and not raised on any sort of boss or prominence.

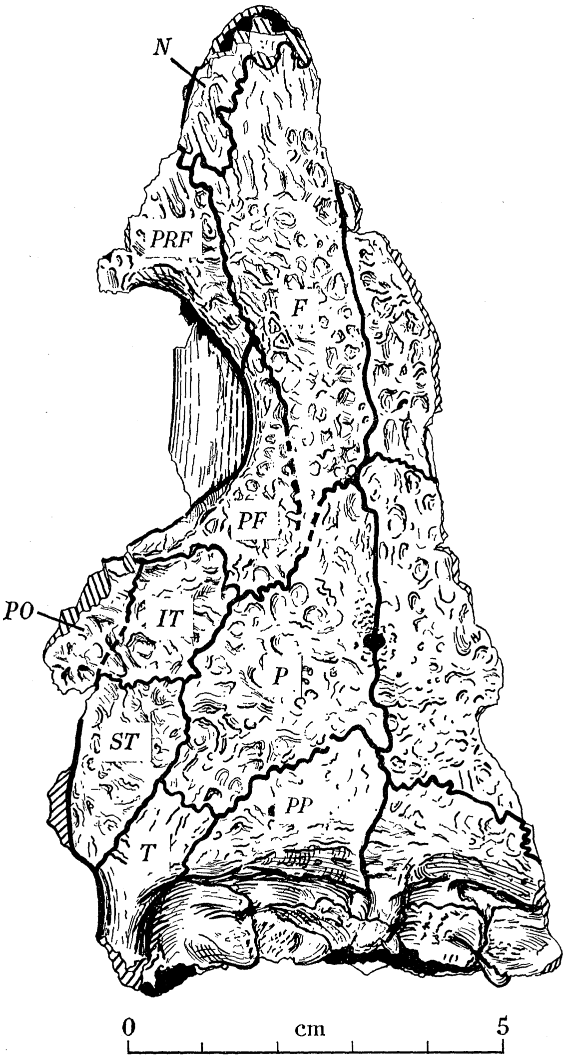

Figure 1. *Palaeogyrinus decorus*: skull A1, dorsal. Natural size. (For explanation of abbreviations used in figures see p. 636.)

Unfortunately the left tabular horn in specimen A1 is broken off at the level of the back of the occiput and the right one is missing. It is clear, however, that the left horn pointed much more directly backwards in this specimen than Watson has figured in the type.

The pattern of sutures traced in this specimen is similar to that figured by Watson and will be clear from figure 1. The rather irregular form of the postfrontal is not absolutely certain at its posterior end. A more complete comparison with the type is given below (Restoration of the skull).

Occiput

Little, if any, distortion of the occiput of skull A1 seems to have taken place (figure 2*a*) but the occipital surface slopes back at about 40° to the horizontal and this very shallow angle may be in part a post mortem effect.

The tabular has a wide occipital exposure and reaches a depth of 1·5 cm in the plane of the occipital surface. Mesially it has a dorsal oblique suture with the postparietal, so that it extends much further towards the midline than on the skull roof, and below this a more vertical but concave suture with the opisthotic. This latter contact terminates ventrally with a finger-like process of the tabular overlapping the opisthotic surface and interlocking with a similar process arising from the lateral surface of the opisthotic.

The paired postparietal bones are confined to a depth of about 8 mm at the maximum. Below this they have a rather irregular suture with the median supraoccipital. The dorsal part of their occipital exposure is formed by the thick rounded overhang of the skull table and in the midline this continues ventrally as a thick rounded rather asymmetrical ridge right down to the foramen magnum. This ridge lies to the right of the suture between the two postparietals.

Particularly important in this specimen is the presence of a clearly defined supraoccipital. Though the region of the synotic tectum is ossified in the braincase of the type specimen, it is, as Watson notes, almost impossible to find any suture separating the bone from the general otic mass, and its occipital exposure is not well preserved. In the present specimen the external bounding sutures, with the postparietals dorsally and with the paired opisthotics laterally, were traced. Although the bone itself is absent similar sutural boundaries are preserved in the two type specimens of *Pteroplax cornuta* (figured Atthey 1877).

On the lower half of the supraoccipital surface are paired cartilage-roughened areas separated by the median ridge already referred to. It seems probable that cartilaginous extensions of the exoccipital overlapped the bone at these points, thus demonstrating an early stage in the encroachment of the area proper to the supraoccipital by the exoccipitals, which occurs in other labyrinthodont groups.

The postero-ventral edge of the supraoccipital forms a more or less flat surface some 2 to 3 mm wide. From this lower surface it extends horizontally into the foramen magnum.

The occipital exposure of the opisthotic bones forms the paroccipital process on each side and acts as a buttress between the exoccipital and the tabular. Dorsomesially each opisthotic has a long oblique suture with the supraoccipital and the specimen confirms, as was noted by Watson, that there is no post-temporal fossa, nor any apparent foramen in its place. The muscles which are usually assumed to have originated in the post-temporal fossa may, in *Palaeogyrinus*, have found origin in a slightly roughened concave area on the tabular whose upper edge is marked by a ridge at the level of the lower edge of the postparietals. Not only is the post-temporal fossa absent but there is no sign of any corresponding foramen. Thus one must assume that the vena capitis dorsalis was not developed in its normal position.

The postero-ventral surface of each paroccipital process forms a cartilage-roughened facet for the exoccipital. At the outer edge of this facet the opisthotic turns sharply forward to form the lateral wall of the otic capsule. It is from this corner that the finger-like process already mentioned extends backwards and upwards to interlock with the corresponding downward process of the tabular.

No trace of either exoccipitals or condylar basioccipital remains in skull A1 and the foramen magnum has been practically closed by compression from below of the parasphenoid region. It is, however, possible to restore the outline of the dorsal part of the exoccipitals from the facets described and this has been done in a complete restoration of the occipital surface with data from the type incorporated (figure 2*b*). It should be noted that the attachment of the exoccipitals to the paroccipital processes and to the supraoccipital must have been cartilaginous. In the type specimen, as Watson notes, the left exoccipital may have become detached and preserved separately as a natural cast. The separation of the exoccipitals in this early anthracosaur is therefore in marked contrast to the co-ossified condition of the occipital arch in crossopterygians (e.g. *Ectosteorhachis* ('*Megalichthys*'), Romer 1937) and emphasizes their serial homology with the pro-atlas and succeeding neural arches. In this connexion Bystrow (1944) notes that the exoccipital-opisthotic suture in the late (and possibly neotenous) seymouriamorph anthracosaur *Kotlassia* is opened by irregular fissures which are asymmetrical and not likely to be nerve foramina. They probably denote the incomplete replacement of cartilage by bone in the suture.

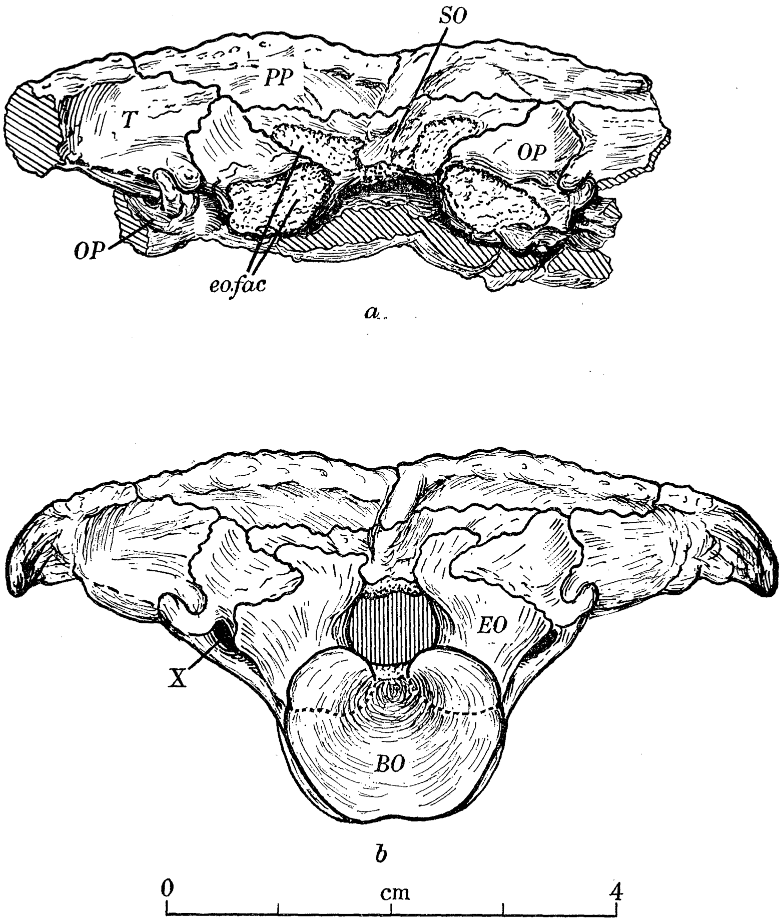

FIGURE 2. *Palaeogyrinus*: occiput (magn. × $1\frac{1}{2}$). *a*, skull A1; *b*, composite reconstruction.

Skull roof—ventral

In the lower slab of the type specimen the ventral surface of the skull table and interorbital region are almost perfectly preserved (figure 3). Only the right tabular horn and the left supratemporal are missing in the cast, but the former is present as bone embedded in the slab. Description of this region is important in reconstruction of the braincase.

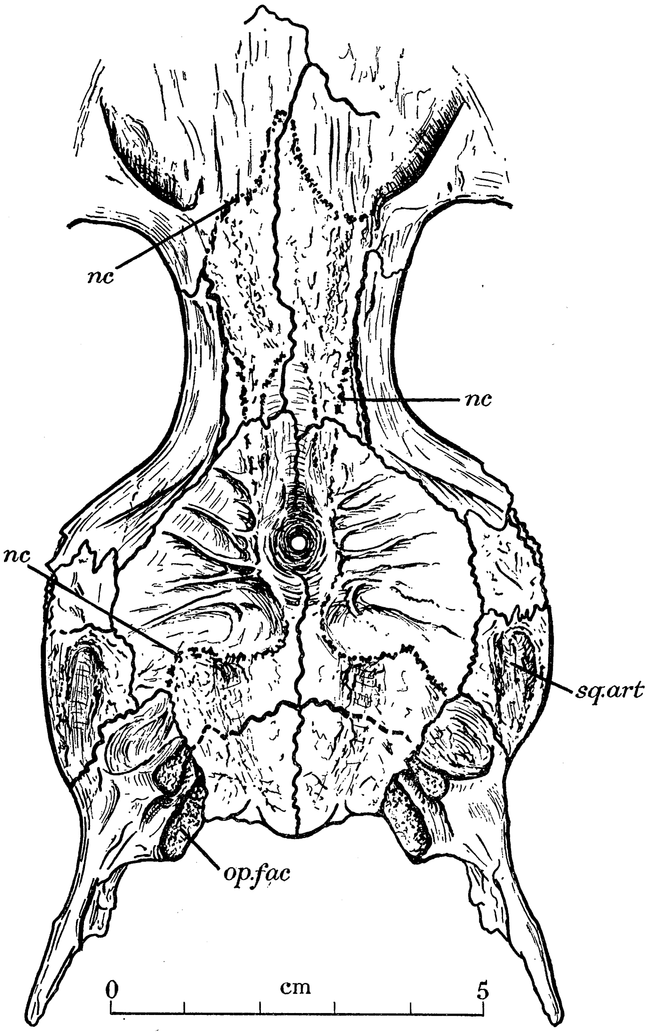

FIGURE 3. *Palaeogyrinus*: skull roof ventral, principally from the type. Natural size. (Not corrected for natural curvature.)

More anteriorly, beyond the interorbital region, and also in the region of the left jugal and snout, the lower slab contains bone covering the natural cast; as thin flakes in the nasal and lachrymal region and as more solid, though badly damaged, bone in the case of the jugal and the maxillary region.

In the Derbyshire skull the underside of the roof is visible as far as the specimen is preserved, where it it not covered by the braincase. Its structure is closely similar to that of the type.

The tabular is a complex bone in ventral view. Mesially it bears a strong facet buttressing the opisthotic region of the braincase. This facet runs for 12 mm almost exactly parallel to the body axis and faces ventrally and mesially. Immediately lateral to the facet the bone is deeply incised by a groove which reaches a depth of about 3 mm anteriorly, but with a reduction in thickness of the bone posteriorly, fades out at the level of the beginning of the tabular horn. Anteriorly the lateral border of the groove forms another facet coplanar with the posterior one. Both are cartilage finished.

The groove appears to have carried the vena capitis lateralis on its forward course from the anterior cardinal vein in the neck region and is continued forward in the dorsal part of the otic capsule.

The two facets are situated on a very thickened region of the bone and anterior to the front one the tabular thins out abruptly and then thickens slightly again for its suture with the supratemporal. The shallow hollow so formed marks the course of the stapes. The interlocking finger-like processes of the tabular below the facet have already been described from the occiput of the Derbyshire skull.

The tabular horn reaches a length of nearly 3 cm beyond the opisthotic facet. In the type specimen, and in Watson's restoration, it is directed outward from the fore and aft plane at an angle of about 35°. This, however, seems exaggerated by the partial dislocation of the bone as a whole (figure 14, plate 10) and an angle of some 20° to 25°, as in the smaller type skull of *Pteroplax*, has been restored in figure 3.

The form of the horn is very similar to that in *Pteroplax*. Its outer surface continues the line of the skull table and, though convex, reaches a sharp edge dorsally and ventrally. Its inner surface, on the other hand, is not continuous: for just over 1 cm it prolongs the surface of the occipital tabular round into an inward-facing plane. It then thins in an abrupt and irregular manner to the blade of the horn.

The rest of the skull table behind the orbits may be considered as a unit: the sutures between the individual bones will be clear from the figure.

In the midline the position of the pineal foramen is a prominent landmark. The bone in this region is thickened strongly round the foramen to form a prominent rim with a diameter of 1 cm. This rim is buttressed on either side by a series of sharp ridges which slope out almost to the edges of the parietals. Beyond them on each side the bone surface is quite smooth.

Behind the pineal the rim merges by a broad roughened ridge into the thickened central region of the posterior part of the table.

The greater part of the posterior central region is roughened like its connexion to the pineal rim and was undoubtedly for the close contact of the braincase. The limits of this contact are very clearly seen in the rubber cast and can be confirmed from the Derbyshire skull. The front of the otic region is seen as a low but sharp ridge running transversely $2\frac{1}{2}$ cm in front of the posterior edge of the skull table.

The contact with the braincase, after running along the pineal rim on either side, broadened out again in the interorbital region 1 cm in front of the pineal foramen.

At the lateral edge of the skull table the underside of the supratemporal bears a shallow but well-defined groove extending from front to back. This groove, which is some 4 mm wide and about 1 mm deep, is separated from the edge of the skull table by 2 mm anteriorly but meets the edge posteriorly. It is for the articulation of the squamosal.

This groove was noted by Watson and a similar groove was described and figured by him on the underside of the larger *Pteroplax* skull ('*Eogyrinus*', Watson 1926, Figure 19).

The orbits are bounded ventrally by well-defined rims formed from the pre- and post-frontal bones and in the interorbital region defining the lateral boundaries of the braincase. In front of the orbits the impression of the braincase tapers to a point in the midline just behind the frontal-nasal suture, but the rims of the orbits, though widening, diverge considerably from this. Along the anterior edge of the orbit these rims flare into broad wedges in ventral view and also thicken to enclose a rounded groove in their antero-mesial surfaces. In the type the left one of these rims is seen to reach the level of the general bone surface about half way along the anterior edge of the orbit, with the turning down of the snout region.

It seems probable that the anterior orbital rim buttressed the cartilaginous anterior extension of the braincase.

Squamosal and otic notch

In the Derbyshire specimen of *Eogyrinus* (below) the facet on the squamosal for articulation to the underside of the supratemporal is seen for the first time as the original bone. This redirects attention to the structure of this region of the skull in *Palaeogyrinus* and its significance in understanding the kinetism of the skull and the structure of the middle ear.

The outer surface and posterior and dorsal edges of the left squamosal are preserved in the upper block of the type and its inner surface and part of the posterior edge in the lower. It retains its natural relations with the quadratojugal and the quadrate. The three bones have been swung round post mortem through 180° and have come to lie over the region of the right tabular horn (figure 14, plate 10). They are slightly disarticulated so that their sutural edges can easily be seen.

The articular facet of the squamosal (figure 4*a*) is very similar to that described below in *Eogyrinus*. It is 1·7 cm in length, corresponding exactly to the articular groove in the supratemporal. Owing to the compression of the specimen the facet appears in the upper block flattened almost into the plane of the outer surface of the bone.

At just over 5 mm it is a little wider than the supratemporal groove and is, as in *Eogyrinus*, concave. The roughened surface does not look like that of a cartilage facet, the roughening being more irregular. The supratemporal groove is also more faintly roughened. The posterior end of the squamosal facet has a well-rounded rim and there is no suggestion that the joint was in any way open posteriorly to form a cleft continuous with the otic notch.

It seems probable, as Watson notes, that there was a considerable mass of ligamentous connective tissue between the concave facets of the two bones. This would give a compressible shock-absorbing joint. It should be noted, however, that the disarticulation of the skull table and cheek region seems to have resulted in the left supratemporal being torn out of the skull table and lost, so that the joint must have been quite resistant to dislocation. The loss of the cheek region in other embolomere skull tables is likely therefore to have been due to post mortem maceration.

The outer surface of the squamosal is ornamented less regularly than the skull table and is marked by lateral line grooves whose disposition is discussed below (Restoration of the skull). Comparison with the Derbyshire *Eogyrinus* suggests that the squamosal sloped down at an average angle of about 40° to the horizontal.

In the type specimen a narrow groove appears just lateral to, and parallel with the supratemporal facet, separating this from the ornamented outer surface. It is difficult to say whether this is a structural feature or due to post mortem damage. No such groove is apparent in the *Eogyrinus* specimen. The groove is indicated in figure 4 but not in the restoration of the whole skull.

The posterior edge of the squamosal is expanded to form the occipital exposure of the bone and faces upwards as well as backwards at about 45°. This occipital surface is, like the dorsal facet, compressed almost into the plane of the lateral surface, but was probably perpendicular to it in life (figure 4*b*).

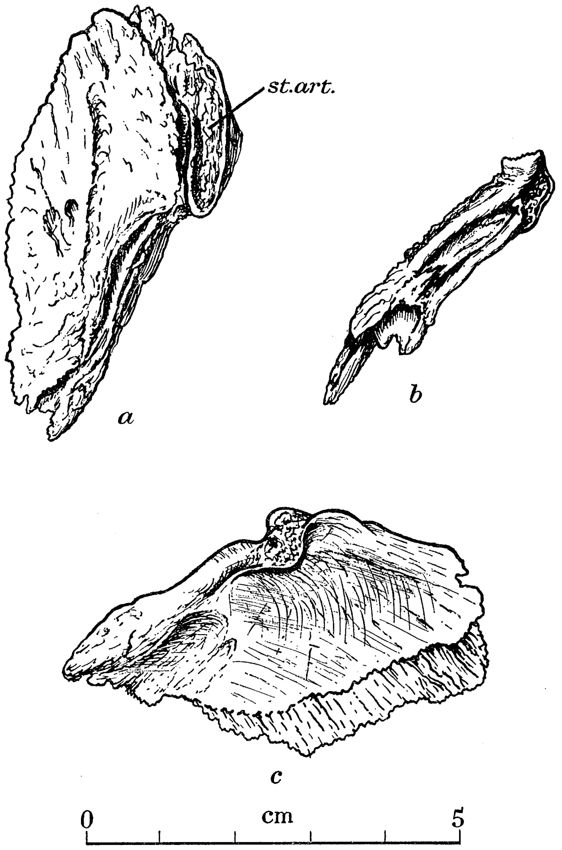

FIGURE 4. *Palaeogyrinus*: squamosal from the type. Natural size. *a*, dorsal; *b*, posterior; *c*, mesial.

The dorsal part of this occipital surface forms the rim of the otic notch and has a mesian longitudinal groove which presumably held the tympanum in place. Below the otic notch the groove widens out so that the occipital surface is concave for most of its length.

In lateral view the otic notch has a curved outline and the squamosal forms part of its antero-dorsal border. The morphological position is therefore the same as in Seymouriamorpha and the diadectomorph cotylosaurs (cf. Romer 1956, Figures 33, 34, 43) as well as the temnospondyls (e.g. *Eryops*, Sawin 1941). This gives support to Parrington's (1959) contention that the characteristic 'labyrinthodont' and 'cotylosaur' positions of the otic notch are merely the result of differential growth of the cheek region, rather than migration of the tympanum from the former position to the latter.

Ventrally the occipital surface of the squamosal broadens out towards its junction with the tabular.

The mesial surface is exposed in the lower block, and appears to be smooth over most of its area (figure 4*c*). The wide sutural surface for the jugal is well preserved antero-ventrally. Postero-dorsally the overlap surface for the pterygoid can be clearly seen just below the otic notch. Dorsally this surface is continuous with a cartilage roughened area, projecting well beyond the plane of the rest of the bone, which forms the antero-lateral wall of the middle ear cavity bordering the otic notch.

Postero-ventrally the sutural surface for the quadrate is visible as a concave area lying alongside the thickened posterior edge.

Pterygoid and epipterygoid

The right pterygoid and epipterygoid are preserved in the type from their posterior limit to a point some 3 cm in front of the basis cranii. The quadrate ramus of the pterygoid has been compressed into a single plane during preservation, but the natural curvature into the horizontal plane of the palatal ramus is largely retained. The bones are preserved as a beautiful natural cast in the lower block and a rather less good impression, with thin flakes of bone adhering, in the upper block.

In mesial view the quadrate ramus of the pterygoid (figure 5*b*) is extremely deep so that the upper edge must have fitted closely under the edge of the squamosal, closing the subtemporal fossa from behind. As Watson notes, the quadrate ramus projects well below the dermal cheek region in lateral view (figure 12), though, when the slope of this ramus (paralleling that of the dermal cheek) is allowed for, together with the convex contour of the latter, this projection was probably not so great as Watson's reconstruction suggests.

The ventral part of the quadrate ramus is ornamented with a shagreen of fine denticles as is often the case in labyrinthodonts. The area thus covered extends to the whole ventro-mesial surface of the palatal ramus. The highest point of the quadrate ramus is buttressed by a marked thickening of the bone from the level of the 'excavatio tympanica' of Bystrow & Efremov (1940) interpreted on the other hand as for muscle insertion by Wilson (1941).

There is no apparent contact area on the mesial surface of the quadrate ramus, so that the lateral surface was probably applied to the squamosal. The posterior extremity forms a very characteristic pointed process which seems to have been inserted in a marked embayment of the mesial edge of the quadrate. The form of this embayment suggests that a large quadrate foramen opened at this point, but it is impossible to confirm this from the natural cast.

The articulation for the basipterygoid process of the basisphenoid, formed from both pterygoid and epipterygoid is very complex. The pterygoid contribution takes the form of a hemispherical recess with a thickened postero-ventral rim. The surface of the recess is roughened in a manner suggesting that it was packed with connective tissue. Above and slightly in front of this is a double facet, the upper part, formed from the epipterygoid, being a convex oval surface facing ventro-mesially. The lower part may be formed either from pterygoid or epipterygoid and faces antero-mesially.

A third articular surface seems to have been the principal one and again is formed from the epipterygoid. Its surface faces postero-dorsally. It is probable that, together with the double facet, it formed a continuous saddle-shaped surface articulating with that of the basipterygoid process, but with the latter incompletely preserved, the actual shape of this articulation cannot be confirmed.

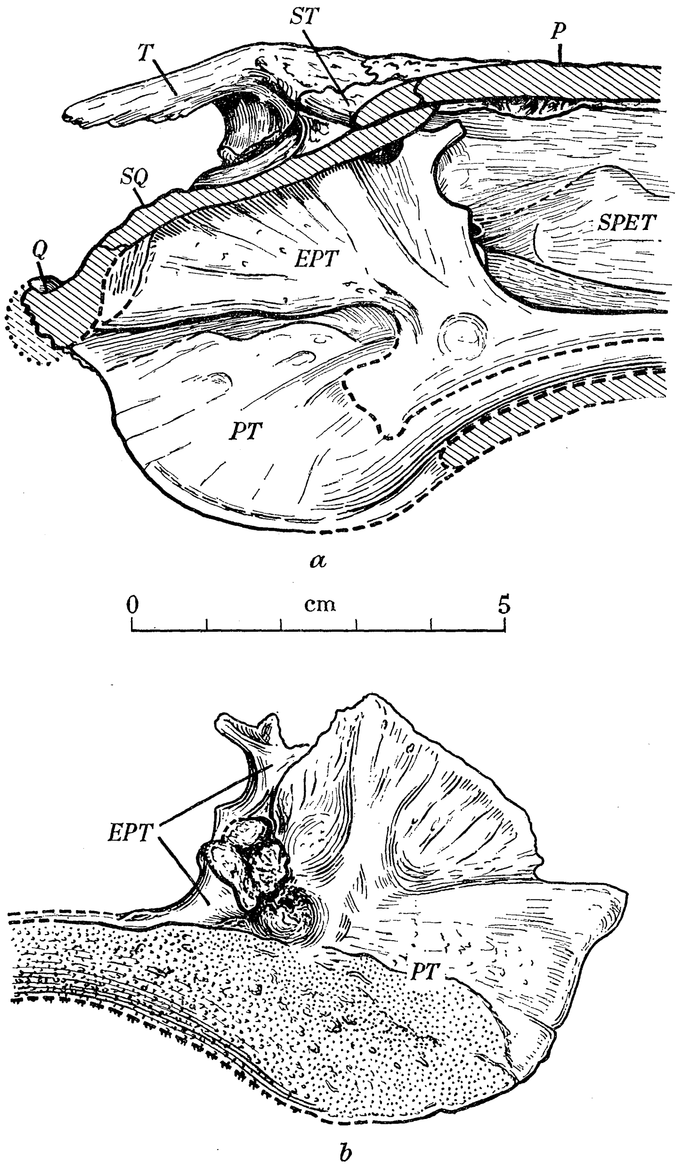

FIGURE 5. *Palaeogyrinus*: from the type. Natural size. *a*, lateral view of suspensorial region, as though sectioned through a plane parallel to quadrate ramus; *b*, mesial view of pterygoid and epipterygoid.

The large anterior facet forms the termination of a massive buttress, shaped like the mouth of a horn, which tapers forward above the ornamented palatal ramus of the pterygoid. This structure, disarticulated from the braincase, is also well seen on both sides of the type of *Eogyrinus* (Atthey 1876, Plate IX).

The columella cranii of the epipterygoid is well preserved in mesial view. It appears as a slender rod extending dorsally from the double facet until it expands to form a forward-projecting process, forming the dorsal edge of a notch for the ophthalmic division of the trigeminal nerve. The dorso-mesial surface of this process is grooved and a second small vertical process probably divided the remaining maxillary and mandibular branches of that nerve.

In lateral view the columella cranii is seen to be continuous with a sheet of bone covering the whole of the upper half of the quadrate ramus of the pterygoid. This is the quadrate ramus of the epipterygoid. Its lower margin runs from the level of the basis cranii to the quadrate condyle. Posteriorly there is a small facet for the overlap of a very restricted quadrate ossification.

The epipterygoid also had a palatal ramus, which appears to have remained in the vertical plane of the quadrate ramus and to have rested on the horizontal palatal ramus of the pterygoid, but its lower edge cannot be made out. The palatal ramus of the epipterygoid gave rise to the horn-shaped buttress and anterior basal facet described in mesial view.

Posteriorly the epipterygoid may have extended as cartilage further down the quadrate ramus of the pterygoid and there seems also to have been a broad epipterygoid process projecting downward and backward from the level of the basis cranii.

An extensive quadrate ramus of the epipterygoid is also described by Romer & Witter (1942) in *Edops* but in this form it is restricted by a much more extensive quadrate ossification. The considerable ossification in the cartilaginous palatoquadrate shown by these forms, and probably by *Eogyrinus* (below), must surely be interpreted as a primitive condition and a progressive reduction of the epipterygoid ossification is to be seen in later labyrinthodonts.

Braincase

One of the most interesting features of the braincase of *Palaeogyrinus* is the distinctness of the various ossifications of which it is formed: this may be due to the presumed neotenous condition of the species as compared with *Eogyrinus* (figures 6 to 9).

The braincase of specimen A1 is not well preserved although it extends from the dorsal occipital region to a point which must be near the anterior limit of ossification. Most of the distortion of this specimen has resulted from the high degree of compression to which it has been subjected and there is also some cracking and erosion of the bone. To expose the braincase in ventral view pyridine development was used (Preservation of material and methods) and pieces of bone apparently pertaining to the cheek region were removed.

The braincase of the type specimen is compressed in the opposite sense, from side to side. It has undergone torsion after death about a longitudinal axis; so that, viewed from behind, the occipital region has been rotated in a counter-clockwise sense in relation to the sphenethmoid region. This rotation has affected the otic region to a lesser extent and resulted in depression of the otic roof on the left. In addition the dorsal otic region has been distorted by rotation about a vertical axis so that the left otic capsule, and particularly its roof, is advanced far beyond the right.

The right side of the otic region has, as it were, been planed off, so that projecting structures such as the basipterygoid process are missing, but there is a natural cast of the right basiphenoid region preserved in the lower slab.

The main part of the braincase is preserved as bone in the upper slab, extending forward to the mid-sphenethmoid region, while the anterior sphenethmoid region is preserved as bone beyond the natural cast in the lower slab.

The condition of the bone surface is not very good, but it is generally possible to distinguish the boundaries of the various ossifications with ease by reference to one side of the specimen or the other, or to the natural cast.

The occipital exposure of the opisthotic and of the supraoccipital have already been described from the specimen A1 and the occipital aspect of the basioccipital and exoccipitals reconstructed by combining these data with those from the type (figure 2*b*). The rest of the otic region has been reconstructed from all three sources (the outline on the underside of the roof of the type, the type braincase, and the Derbyshire specimen).

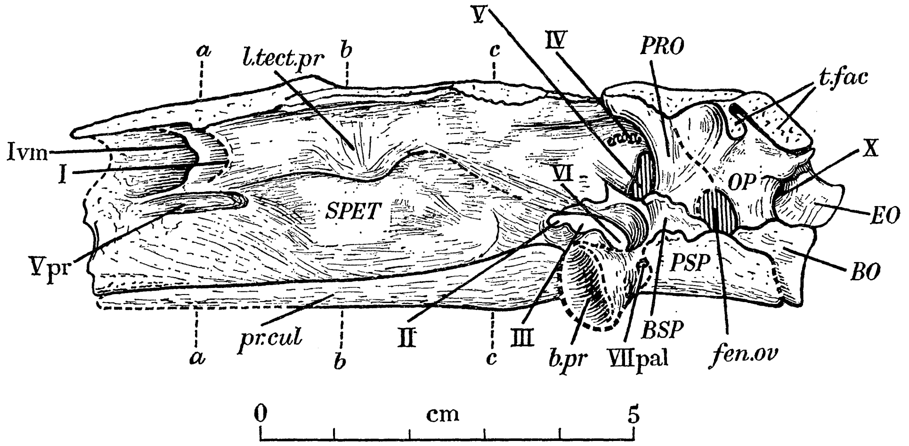

FIGURE 6. *Palaeogyrinus*: braincase, lateral, composite reconstruction. Natural size. (Planes of transverse sections indicated.)

The whole otic and occipital region of the braincase is heavily ossified and there is a complete roof of cartilage bone underlying the dermal roof in this region, as in *Edops* (Romer & Witter 1942) and *Eryops* (Sawin 1941). However, in *Palaeogyrinus* the region of the synotic tectum was ossified from the supraoccipital and not from an extension of the exoccipitals as appears to have occurred in *Eryops*.

In the type the lateral sutures of the supraoccipital are probably represented by two cracks filled with matrix running longitudinally in the expected position: their position corresponds with the inner limits of the otic capsules in the Derbyshire specimen. There is no apparent suture marking the anterior boundary of the supraoccipital and its ossification appears continuous with that of the sphenethmoid region.

The otic capsules are preserved on both sides of the type specimen and their dorsal outline is clear from the natural cast. In the Derbyshire specimen both capsules are preserved, but lack their lateral surfaces, which would include the region of the fenestra ovalis. The ventral surface of the right capsule is exposed by removal of part of the parasphenoid.

The dorsal surfaces of the otic capsules stand slightly above the level of the supraoccipital, which is concave between them. Posteriorly there are two well-defined dorsolateral facets on each side for the tabular bones, whose corresponding facets have already been described. The anterior facet terminates a stout buttress from the side of the capsule and is separated by a deep groove from the posterior facet. This is a continuation of the groove for the vena capitis lateralis already described in the tabular.

From this region the vein probably followed its normal course, running past the antero-dorsal margin of the fenestra ovalis and down to the foramen for the interorbital vein, which is described below.

The roof represents the widest expanse of the otic region and the lateral walls converge towards their ventral junction with the basioccipital, basisphenoid and parasphenoid. The Derbyshire specimen demonstrates that the capsules were fully ossified ventrally and not fused with the underlying bones.

A point of critical importance is the condition of the fenestra ovalis. Watson (1926) described the type as having 'a deep pit whose bottom is shown to be closed by bone on both sides of the specimen'. This pit, which Watson terms the 'pseudo-fenestra ovalis', ... 'lies on the apparent suture between the prootic and paroccipital (opisthotic), the basioccipital forming part of its lower wall'. Thus he concludes that this represents a primitive condition for the tetrapods in which the 'fenestra ovalis' is imperforate. He also attributes a similar condition to the isolated braincase (DMSW 30) ascribed to *Eogyrinus*, but, as Romer (1947) has already pointed out, the large aperture originally identified as the vagus foramen is probably a true fenestra ovalis. Examination of the specimen enables me to confirm this. The side wall of only one otic capsule is preserved and this was described as the right, though crushed into the median plane. However, the smoother, more finished left surface, the curve of its roof and the greater completeness of the adjoining left side of the basiphenoid region suggest that it is the left. This is confirmed by the series of pits in the right surface described and figured by Watson (1926, Figure 18). These are the impressions of the semi-circular canals on the inner surface of the capsule wall. The one in front of the disrupted 'foramen' is the 'pseudo fenestra ovalis', but it corresponds exactly in position with the groove for the anterior vertical semi-circular canal of *Edops* (Romer & Witter 1942; Romer & Edinger 1942). Thus in the '*Eogyrinus*' braincase, as Romer notes, the exoccipital is probably missing, the bone identified as exoccipital is the opisthotic, and the 'vagus foramen' is a true fenestra. It can thus be stated that there is no evidence of such a structure as a pseudo-fenestra ovalis to be derived from this specimen.

The type of *Palaeogyrinus* is therefore the only specimen where such a structure might be present. Watson's figure (1926, Figure 12) of the braincase is a right lateral view and represents, in the otic region, the appearance of the unrestored right side of the specimen. On this side there is a pit corresponding in position to the 'pseudo-fenestra'. The bony surface in and surrounding the pit is very badly worn and immediately below and bordering it there is a wide crack, filled with matrix, extending down to the basioccipital, which may possibly represent the position of the true fenestra. Another similar matrix-filled crack extends obliquely upwards and backwards from the postero-dorsal part of the rim. The pit itself is about 3 mm in diameter by about 2 mm deep and about two-thirds of it is floored by bone. Part of this bony floor appears to be good bone surface and is continuous with the external surface for about half the circumference of the pit.

On the evidence of the right side alone it would be possible to make a *prima facie* case for the existence of a pseudo-fenestra in this species. The relevant region is rather better preserved on the left. Here there is a deep pit some 7 mm × 3 mm in area, with its long axis directed antero-dorsally, and 4 or 5 mm deep. Both long margins and also the postero-ventral edge are good bony edges and in these regions the external bony surfaces are quite good. At least three-quarters of the pit is floored with matrix and no underlying bone was attainable by development until the level of the opposite side of the specimen was reached. The remaining floor of worn bone has no continuity with the sides or edges of the pit, and probably belongs to the opposite side.

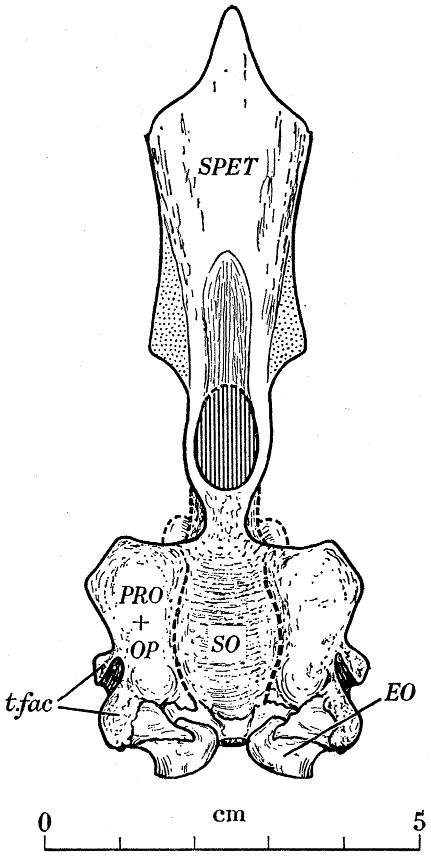

Figure 7. *Palaeogyrinus*: braincase, dorsal, composite reconstruction. Natural size. (Lateral roofing extensions of sphenethmoid stippled: see text.)

It can thus be stated that on the left side of the type braincase of *Palaeogyrinus* there is no evidence whatsoever for the pseudo-fenestra and that the pit described is a normal labyrinthodont fenestra ovalis.

In those forms in which the otic capsule is fully ossified in two regions the fenestra ovalis marks the division into prootic and opisthotic. In *Palaeogyrinus* there is only a doubtful suture separating the two ossifications. This is visible on the right side of the type as a matrix-filled crack running obliquely forward and upward from the 'pseudo-fenestra' to a point near the front of the otic roof.

The ventral margin of the fenestra ovalis is formed by the basisphenoid anteriorly, the parasphenoid in the middle and the basioccipital posteriorly.

The basioccipital is present only in the type and appears to form the bulk of the subcircular condyle. It is more or less complete though the surface is rather worn. The surface of the condyle itself is very deeply concave, the centre point being about 6 mm in front of the rim. The division on the condylar surface between the basioccipital and exoccipitals is not very clear: its apparent position has been restored in the figures.

More anteriorly the lateral exposure of the basioccipital contacts the exoccipital and opisthotic dorsally and forms a small part of the rim of the fenestra ovalis. Ventrally the basioccipital is sheathed by the parasphenoid leaving a small area exposed posteriorly.

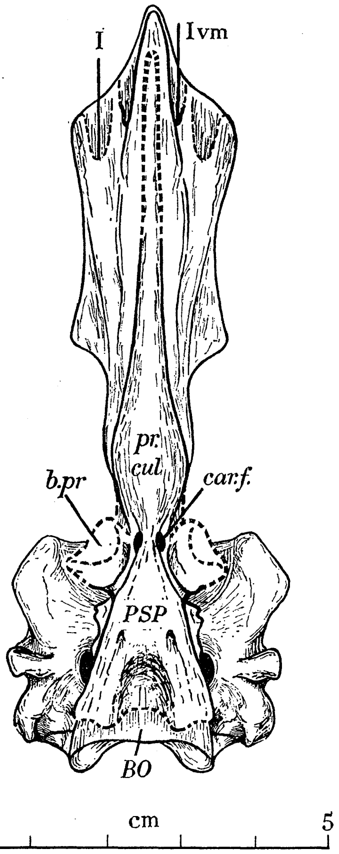

Figure 8. *Palaeogyrinus*: braincase, ventral, composite reconstruction. Natural size.

The exoccipital is apparently complete and in position on the right of the type. Its area of contact with the opisthotic and supraoccipital have been described from the Derbyshire specimen. About a third of the condylar surface was probably formed by the paired exoccipitals and it seems likely, as Watson notes, that they did not meet in the midline. Watson describes a small tubercle on the exoccipital and its postero-dorsal corner, but this appears to be merely the lateral corner of the process which contacted the opisthotic, now separated by distortion.

The vagus foramen is well shown in the right exoccipital and it marks the position of the bottom of the principal opisthotic contact. Watson describes a horizontal groove along the lateral surface of the exoccipital terminating at the foramen: this, however, is very obscure. No trace of a separate foramen for the hypoglossal nerve could be found in the exoccipital.

A bone present as natural cast in both slabs behind the right tabular was thought to be the left exoccipital of the type. The casts are of a spool-shaped bone, whose size and general form agree moderately well with that of the right exoccipital. However, at least the condylar region of the left exoccipital appears to be present in position, although its preservation is poor.

The basisphenoid, with the exception of its basipterygoid processes, is complete in its lateral exposure on both sides of the type. From the lower border of the fenestra ovalis it has a dorsal sutural contact with the prootic, visible on both sides of the type and extending to the front of the otic capsule. The basisphenoid then forms the lower border of a large foramen, through which, as Watson notes, the fifth cranial nerve emerged. This is the prootic foramen.

The prootic foramen has its posterior margin formed by the anterior wall of the otic capsule whose expanded roof extends forward well beyond it. The anterior and dorsal borders are formed by the sphenethmoid. The foramen is probably considerably smaller than Watson describes: its true size is visible on the left of the type, but on the right its walls are broken. There appears to have been a second elongate foramen anterior and dorsal to the first and underlying the projecting roof of the otic capsule.

The latter foramen may have transmitted the fourth cranial nerve and possibly also the ophthalmic branch of the fifth, while the prootic foramen carried the remaining two rami of that nerve.

In the Derbyshire specimen of *Eogyrinus* there is a small foramen in the basisphenoid which may be for the palatine branch of the seventh nerve, and there is a rather indistinct indication of this, on the left side only, in the type of *Palaeogyrinus*. It has been restored in figure 5. The rest of that nerve probably emerged through the prootic foramen.

The basisphenoid extends forward below the prootic foramen to separate the sphenethmoid almost entirely from the upper border of another large foramen. This process of the basisphenoid, well preserved on both sides of the type, is a forward extension of the lateral walls of the dorsum sellae and the relations of the basisphenoid in this region appear to be rather similar to those described by Sawin in *Eryops*.

As in *Eryops* the foramen is formed by the enlargement on each side of the foramen carrying the interorbital vein, which ran transversely behind the sella turcica or pituitary fossa. The enlargement of the foramen provides in its posterior wall a concave anterolateral surface on each side, formed from the basisphenoid. This surface probably served as noted in *Eryops*, *Peltobatrachus* (Panchen 1959) and an unnamed Triassic amphibian (Säve-Söderbergh 1944), for the origin of part of the rectus eye musculature.

In *Palaeogyrinus*, however, the foramen is extended forward to give a total length of some 15 mm, and because of the highly tropibasic form of the sphenethmoid region is seen as an open fenestra from one surface of the braincase to the other. The posterior half of the foramen, forward to the probable position of the sella, has an axis at about 45° to the vertical, anteriorly it is more horizontal. The ventral border of this anterior half is hollowed in a similar manner to the posterior wall and may have formed the origin of the inferior and anterior rectus muscles.

It is probable that the third cranial nerve, the oculomotor, which supplied the inferior and anterior rectus muscles as well as the superior rectus and inferior oblique, emerged from the front, horizontal part of the foramen behind the optic nerve, while the sixth (abducens), supplying the posterior rectus, would have emerged through the posterior half after leaving its foramen in the normal position in the antero-lateral wall of the dorsum sellae.

The optic nerve is assigned to the front of the large interorbital foramen in agreement with Watson, as no other foramen appears on either side in the good bone surface immediately in front.

The basiphenoid is sheathed ventrally by the parasphenoid. The two bones are distinguished, as Watson, notes, by texture, but are not fused. The upper edge of the parasphenoid, with basiphenoid above it, is preserved on the left from the fenestra ovalis forward to the basipterygoid process, where it is eroded somewhat. The junction between the bones can be seen in section on the right.

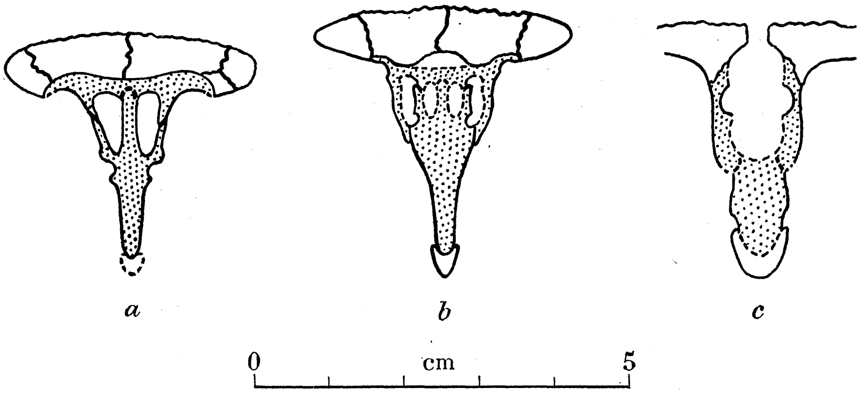

FIGURE 9. *Palaeogyrinus*: braincase, reconstructed transverse sections at planes indicated in figure 6. Natural size. Cartilage bone (sphenethmoid) stippled, dermal bone (skull roof and parasphenoid) blank.

The basipterygoid processes, which lie in the transverse plane of the front of the otic roof, are not well preserved in the type. On the right the process is missing, but it is imperfectly preserved in the natural cast: on the left the articular surface is badly eroded and the process has been bent downwards by the crushing of the whole braincase. The form of the facet has therefore been restored from that of the Derbyshire *Eogyrinus* described below. This saddle-shaped surface is very similar to that of *Edops* and may in fact be general in primitive labyrinthodonts in which a movable basal articulation is retained. In skull A 1 the proximal and posterior part of the right process is preserved together with the adjoining median parasphenoid.

In *Kotlassia* and possibly in *Seymouria* (White 1939) the basipterygoid processes are formed from the basisphenoid alone; but in *Palaeogyrinus*, as in *Edops*, the basipterygoid process consists of a core formed from the basisphenoid surrounded, at least ventrally, by a thin layer of bone continuous with the parasphenoid. Thus the parasphenoid, distinct from the basisphenoid, curves down into the outer layer of the left basipterygoid process of the type: and on the right no clear junction between the parasphenoid and the process can be seen. This is confirmed by the Derbyshire specimen.

This structure of the basipterygoid process may be characteristic of primitive labyrinthodonts in which a mobile basal articulation is retained, the neotenous *Kotlassia* being exceptional. The development of a sutural connexion between the parasphenoid and the pterygoid, seen in more advanced temnospondyl labyrinthodonts, would then mean the locking and strengthening of an existing contact and not the establishment of a new one.

The groove described by Watson, running round the circumference of the base of the basipterygoid process, is clearly marked on both sides of the type, and on the right in the Derbyshire skull. Watson assigns this to the internal carotid artery, but it must also have carried the palatine seventh nerve, if the foramen for the latter has been correctly restored. The carotid foramen, by which the artery entered the basisphenoid-parasphenoid complex, can also be seen on the right in the type in an antero-ventral position on the course of the groove, and on the left of the Derbyshire specimen at the edge of the ornamented parasphenoid. On the right a wide crack obscures the critical region.

The position of the carotid foramina is similar to, though slightly in advance of, that described in *Edops*. In both *Palaeogyrinus* specimens the groove appears to continue forward beyond the carotid foramen, marking the course of the palatine branch of the carotid artery. In neither, however, is this region well preserved.

The parasphenoid occupies the normal labyrinthodont position, sheathing the floor of the braincase. The body of the parasphenoid, from the basioccipital region to that of the basipterygoid processes, is preserved more or less complete, but disrupted and cracked, in the Derbyshire specimen. In the type it is also more or less complete but most of the posterior edge is eroded. It seems to be closely similar to the well-preserved parasphenoid body of the Derbyshire *Eogyrinus*.

The surface of the parasphenoid body is ornamented with a series of longitudinal ridges and striations, though this ornament is not so well defined as in *Eogyrinus*. Ventrally the posterior edge extends back to within 1 or 2 mm of the condylar edge. In this posterior region there is a median ventral concavity about 1·2 cm in length by some 8 mm wide. This is flanked by a low convex region on either side corresponding to the basal tubera for the neck musculature, which are strongly developed in *Seymouria*. A foramen, which probably admitted a minor nutrient branch of the carotid, is visible in the Derbyshire specimen near the front of the concavity.

The parasphenoid body tapers steadily in ventral view with the overall narrowing of the braincase. In lateral view, however, its ornamented surface drops quite suddenly behind the basipterygoid process. This ornamented surface reaches a minimum width of less than 3 mm between the carotid foramina, but is continuous with the anterior, ventral and posterior surface of the basipterygoid processes.

Anteriorly the parasphenoid forms the processus cultriformis sheathing the ventral surface of the sphenethmoid region. This process is present in part in both specimens. In the lower type slab it is preserved either as cast or bony remnants to within 1 cm of the front of the braincase and its ventral outline is present for most of its length.

Immediately in front of the basipterygoid processes the cultriform process expands both dorsally and laterally to form a bowl-shaped investment of the lower surface of the braincase, but it then tapers rapidly to form the narrow sheath characteristic of labyrinthodonts. Its precise width is uncertain as it is visible only in lateral view in the type and not well preserved in skull A1. Throughout its length it is quite distinct from the overlying sphenethmoid; the junction between the two showing as a distinct line either in bone or cast.

The length of the process is unknown. It seems probable that it extended to the anterior limit of the ventral edge of the sphenethmoid. In the type there is a flake of bone extending some 1·5 cm in front of the ossified braincase, restored by Watson as part of the parasphenoid, but it is more likely to be a fragment of vomer.

The sphenethmoid is an even more complex bone than Watson suggests. Essentially it forms an interorbital septum, which expands dorsally towards its contact with the skull roof and posteriorly for its junction with the basisphenoid region, to house the front of the brain and the olfactory tracts.

The dorsal outline shows very clearly as an impression on the underside of the type skull roof (figure 3). In the more heavily ossified Derbyshire specimen there is a rapid widening of the dorsal outline in front of the pineal region, due to the spread of thin sheets of bone laterally along the underside of the skull roof. These contact the rims formed by the underside of the prefrontals. In the type these extensions were probably present as cartilage and are indicated in figures 7 and 8.

Both the braincase specimens and the roof cast suggest that, as with the otic region, there was intimate contact between the sphenethmoid and the skull roof. This, however, was interrupted by a fontanelle in the pineal region and there is no sign of contact in the midline for nearly 2·5 cm in front of the pineal foramen. It seems probable that, allowing an elliptical fontanelle for the pineal, the region in front was roofed but not in close contact with the dermal bone; a condition noted by Romer & Witter in a specimen of *Edops*. The close contact was maintained on either side of this whole region.

The expanded dorsal region of the sphenethmoid enclosed the forebrain posteriorly. This posterior region is exposed on both sides of the type and presents no remarkable features apart from a somewhat hollow area, already noted, in front of the prootic foramen and above this a lateral thickening of solid bone contacting the skull roof.

In front of the braincase proper the dorsal region is tunnelled by two pairs of canals in the same horizontal plane. This region is present in the lower slab of the type and is visible from the left side. The lateral wall, however, is missing, thus exposing the cavity of the left lateral canal. Posteriorly the beginning of the left inner canal is also visible.

In the Derbyshire specimen the lateral wall is present, though somewhat disrupted, on the right side, and it is apparent that the lateral surface in this region has grown down from the braincase roof to meet and overlap the median septum instead of being co-ossified with it. This overlapping lateral wall I shall refer to as the lateral tectal process. It is probable but not certain that this also applies to the wall separating the outer and inner canals on each side. The structure in this respect will be clear from the reconstructed transverse sections (figure 9).

The outer canals probably transmitted the paired olfactory tracts, while the inner pair, as in *Eryops*, may have housed paired vomeronasal nerves.

In such a comparatively small skull both pairs of canals are remarkable for their height. The olfactory canal averages 6 mm and the canal has a pair of internal grooves one dorsal and one ventral, in its medial wall. These may have carried the nervus terminalis and a blood vessel respectively. The inner wall of at least the olfactory canal is quite smooth.

The median septum below the expanded region appears to be solid bone. Its anterior edge is preserved, together with its dorsal extension in front of the canals, in the type, and most of its lateral surface is present as bone or natural cast. The right surface is preserved in the Derbyshire specimen. In the latter there is a well-defined groove extending forward from a point immediately below and just behind the exit of the canals. This is not clear in the less heavily ossified type. It may have transmitted the profundus branch of the fifth nerve forward towards its anterior junction with the superficial ophthalmic.

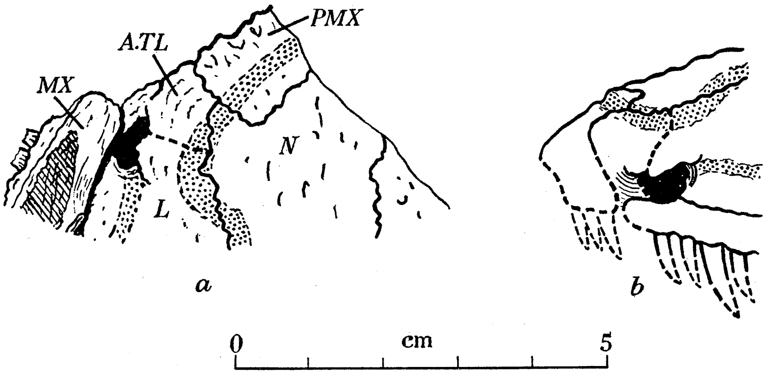

FIGURE 10. *Palaeogyrinus*: snout region from the type. Natural size. Lateral line canals stippled, sutural surface for lacrimal, oblique hatching. *a*, from natural cast, dorsal; *b*, reconstructed lateral view.

Behind this groove the more dorsal part of the septum swells out to a considerable thickness but then tapers again towards the basisphenoid region.

Restoration of the skull

Both the type skull and the Derbyshire specimen A1 were used in the restoration of the skull. The general outline and position of the sutures will be clear from figures 11 to 13. It is only necessary, therefore, to comment on addenda and corrigenda to the original restoration (Watson 1926, Figures 13 to 15).

The labryinthodont 'pit and ridge' ornament is best developed on the skull table forward to a point midway between the orbits. Even here, however, it is not as regular as that of loxommids. Anteriorly in the nasal and anterior frontal region a more elongate and irregular 'pit and ridge' pattern is present. Laterally the pit and ridge appearance virtually disappears and the ornament is an irregular pattern of grooves and depressions defining raised, sometimes scale-like areas.

Posteriorly the dorsal view of the occipital region, with the exception of the condyle itself, is drawn from skull A1. The thickened posterior edge of the skull table is more marked in the Derbyshire specimen than in the type. The orientation of the tabular horns has been corrected as suggested so that they point more directly backwards.

Both intertemporal bones are separated from the orbits by the postfrontals, as shown by Watson, but the left intertemporal reaches to within about 4 mm of the orbit in both the type and the Derbyshire specimen.

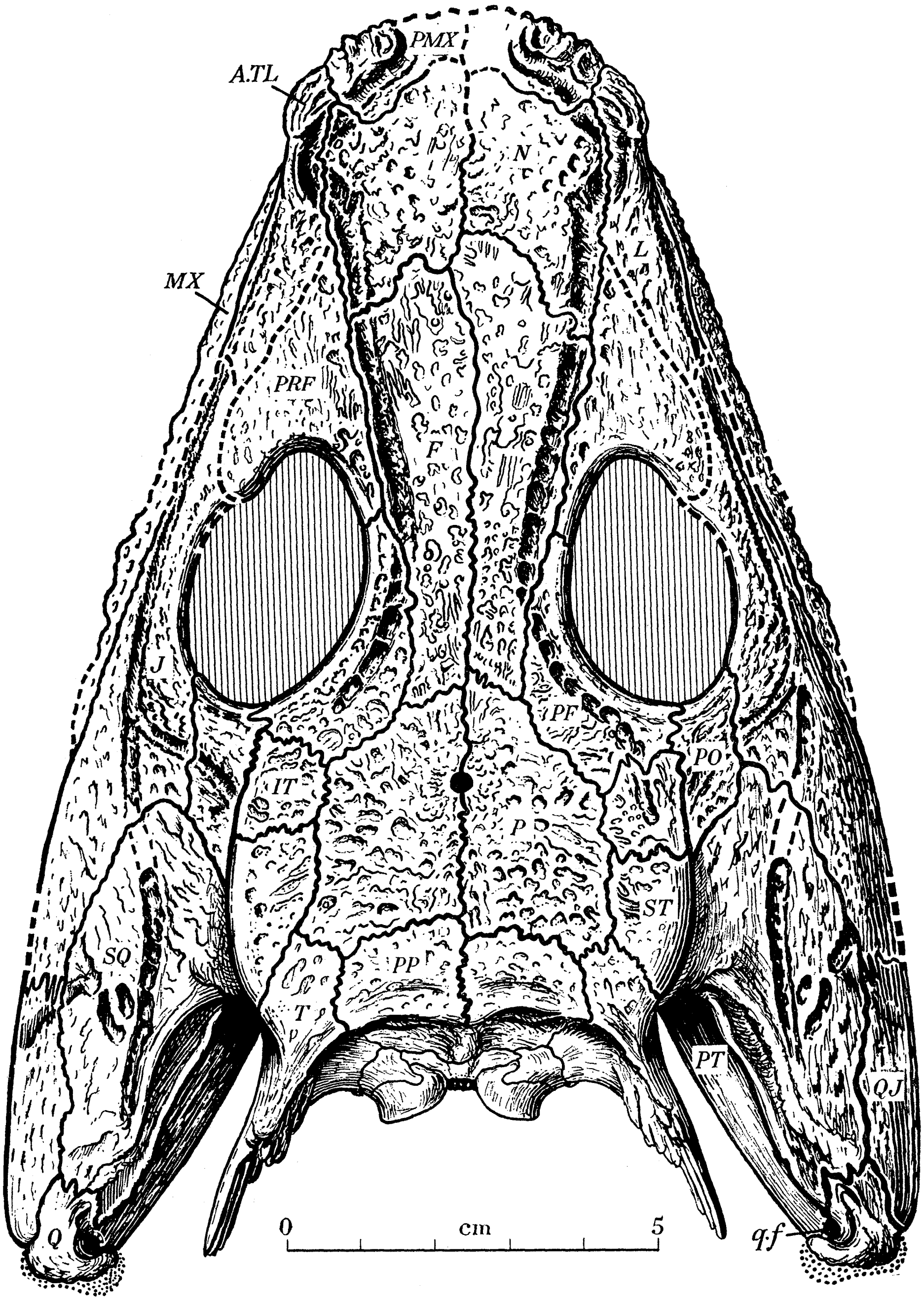

FIGURE 11. *Palaeogyrinus*: composite restoration of the skull, dorsal view. Natural size.

The maxillary was originally figured as a very short bone, not reaching the level of the middle of the orbit; a most unusual condition for the labryinthodonts, in which it frequently contacts the quadratojugal. However, the lower edge of the jugal shows a sutural edge for the maxillary back to a point behind the orbit and the latter bone has been restored extending to this position, where its disarticulated posterior end is situated overlapping the jugal in the type (figure 14, plate 10).

The form of the quadrate suggests that the actual condylar surface was cartilaginous and this has been restored in stipple. A quadrate foramen has also been restored as noted in the description of the pterygoid and epipterygoid.

The nasal-frontal suture was easily traced on both sides of the type specimen and the nasal-premaxillary suture on the left. The former was dotted on the original restoration and the latter taken to be defined by the anterior edge of the specimen. However, it seems that the type includes the lateral part of the left premaxillary and for this reason the present restoration has a slightly shorter snout. The nasal-frontal suture of the Derbyshire specimen, present only on the left, is much further forward than that of the type, as are the frontal-parietal sutures.

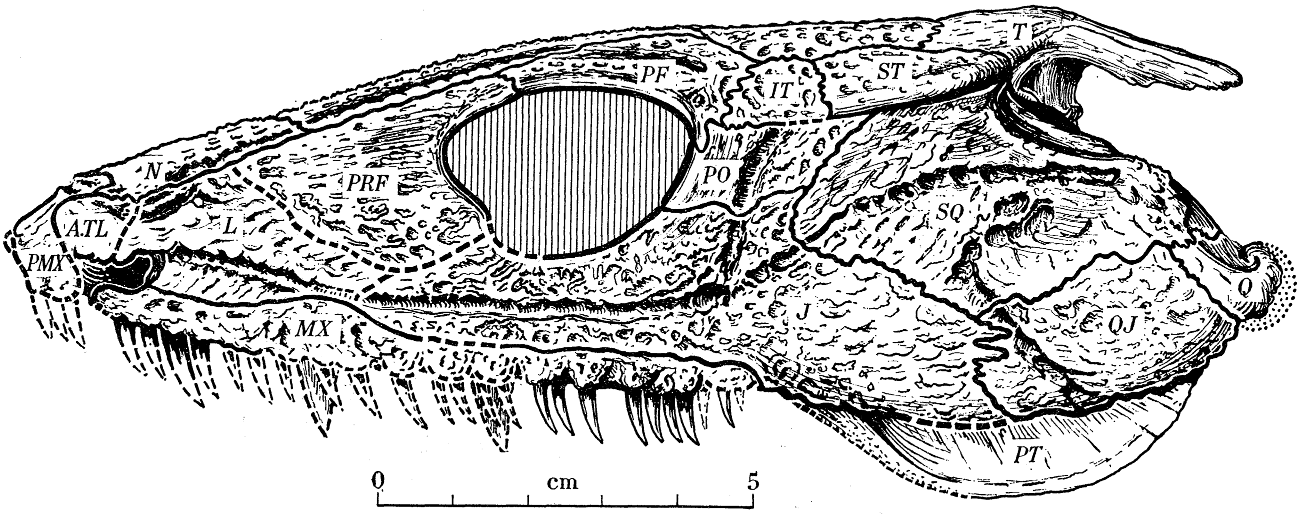

FIGURE 12. *Palaeogyrinus*: composite restoration of the skull, lateral view. Natural size.

Watson restored the lachrymals extending the full distance between the nares and the orbits, thus separating the jugal from the prefrontal in the orbital margin. In the American Permian form *Archeria*, however, the prefrontal contacts the jugal, thus excluding the lachrymal from the orbit (Romer, private communication). This is also probably the case in *Eogyrinus* and possibly so in *Pholiderpeton* (Watson 1929).

On the left of the type specimen there is a well-marked line in this region running back parallel to the axis and cutting the anterior margin of the orbit. This Watson interpreted as the prefrontal-lachrymal suture. The relevant region is missing on the right and in skull A1. The line, however, extends into the matrix of the orbit and seems more likely to be a fracture due to post mortem flattening. No other suture is apparent lateral to this until the now disarticulated region of contact between this preorbital area and the jugal. Thus it appears probable that the prefrontal contacted the jugal, excluding the lachrymal from the orbit.

In the type the external naris was originally restored, on the assumption that the premaxillary was missing, as a complete elliptical foramen, whose postero-medial border only was preserved.

However, it is now established that, as in *Ichthyostega*, the external naris of *Palaeogyrinus* incised the rim of the jaw, being open below, although probably separated from the choana by a process of the maxillary of the ichthyostegid type. The evidence for this is

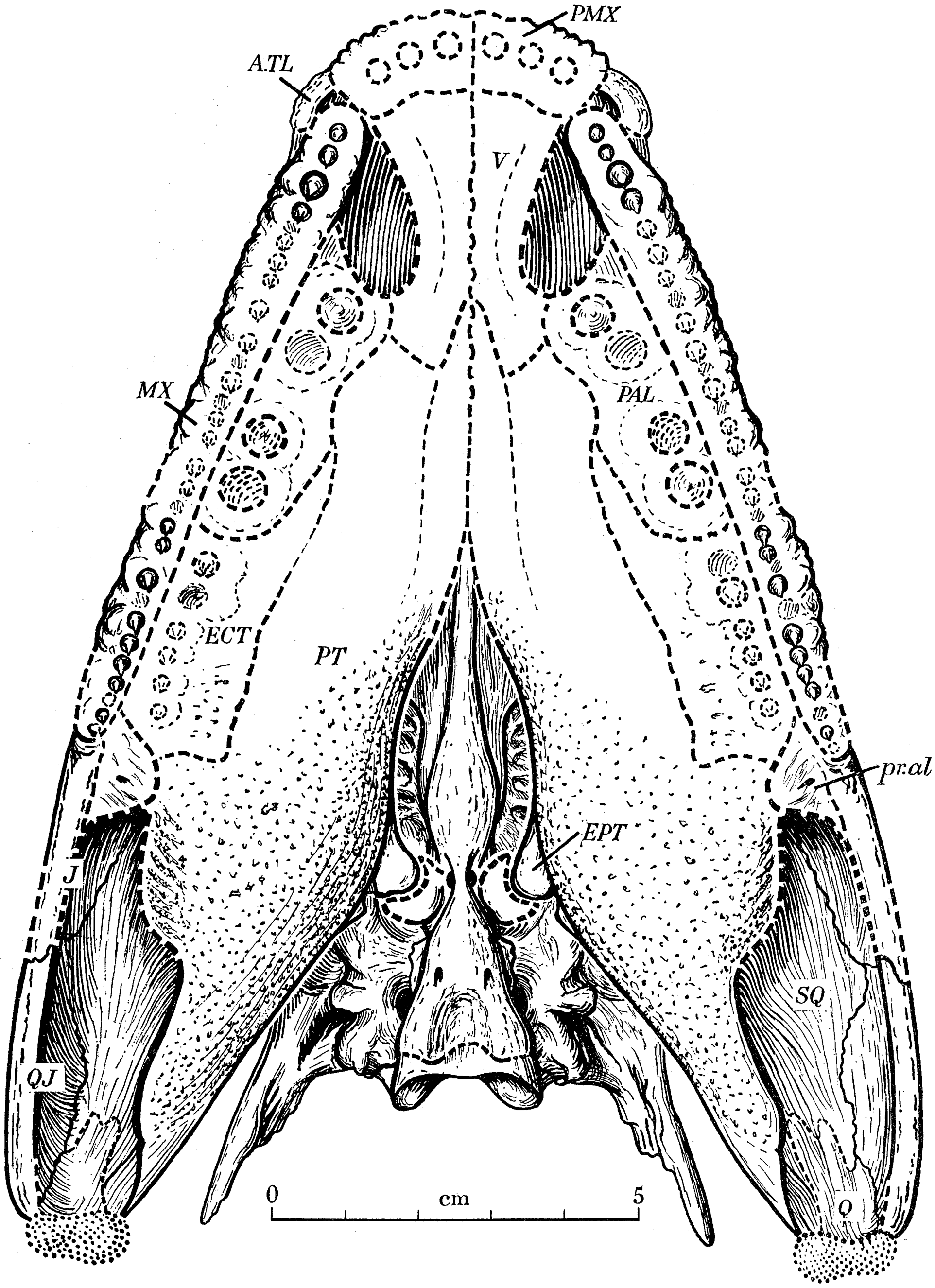

FIGURE 13. *Palaeogyrinus*: composite restoration of the skull, ventral view. Natural size.

derived from the anterior end of the left maxillary of the type, which is preserved with its dorso-medial contact surface for the lachrymal exposed dorsally.

The sutural surface for the lachrymal (figure 10*a*) does not extend to the anterior end of the maxillary, but leaves an area about 5 mm long with no apparent sutural contact.

This area is depressed slightly below the level of the rest of the bone. The anterior end of the maxillary is rounded in dorsal view and, as far as visible in the dorsal cast, does not appear to have a sutural surface for junction with the premaxillary although, as in *Ichthyostega* (Jarvik 1952, Figures 35 and 36) such a contact may have been confined to the palatal aspect.

The aperture of the left naris itself is visible, consistent with the front of the maxillary forming its lower border, on both upper and lower slabs of the type. In the lower slab, however, where the surrounding ossifications are preserved as bone, the borders are very eroded. In the upper slab, preserved as a natural mould, the posterior and dorsal edges are well shown, the nostril being in the form of an inverted triangle, and the ventral apex is formed by the anterior end of the maxillary. The anterior border is formed by a process which appears to slope into the aperture itself, so that in natural cast its true edge is not certainly preserved.

This process is a ventral prolongation of a bone distinct from the surrounding nasal, lachrymal and premaxillary bones. Its suture with the nasal was traced crossing the deepened loop in the supraorbital lateral line canal and its suture with the premaxillary to the anterior limit of both bones. Its posterior suture, with the lachrymal, is less certain, though visible as an irregular groove. This bone corresponds to the 'anterior tectal' shown by Jarvik in *Ichthyostega*.

The relations of the bones surrounding the nostril are similar to the condition in *Ichthyostega* in all but two respects. In *Ichthyostega* there is no descending process of the anterior tectal, but a small rod of bone, called by Jarvik the lateral rostral, projects forward into the nostril from the lachrymal and bears an anterior extension of the suborbital canal. This bone could not be found in *Palaeogyrinus*.

Westoll (1937, 1940, 1943) has criticized the use of the term 'lateral rostral' on theoretical grounds. This bone is present in *Eusthenopteron* (Jarvik 1942, 1944*a*) and *Megalichthys* as well as *Ichthyostega* and is termed by Westoll the 'prenarial' from its antero-ventral position with respect to the nostril in *Megalichthys*. The term 'anterior tectal', to which theoretical objections can also be made, is then replaced by 'postnarial'. However, the bone in *Palaeogyrinus* has been named 'anterior tectal' to avoid the anomaly of a 'postnarial' forming the anterior border of the naris.

It seems probable that the condition of the naris cutting the jaw margin is primitive for tetrapods, but, in spite of its occurrence in *Diplopterax* (Westoll 1943), the evidence seems less clear in the osteolepid fish (Säve-Söderbergh 1932; Westoll 1943; Romer 1947; Jarvik 1952), and the condition in *Palaeogyrinus* and *Ichthyostega* may be paedomorphic rather than primitive with respect to the osteolepid condition, as suggested to me by Dr R. S. Miles. This would be consistent with the ontogenetic development of the face in tetrapods, including mammals, cited by Westoll, where the external nares in the embryo are in communication with the jaw margin.

The tetrapod septomaxillary is normally homologized with the anterior tectal or postnarial (e.g. Romer 1947), but by Jarvik (1937, 1942, 1952) with at least part of the lateral rostral (prenarial). Westoll (1943) has noted that the homologues of both elements may be confused under the name septomaxillary in tetrapods: a study of the snout in primitive forms may throw light on this problem.

FIGURE 14. *Palaeogyrinus decorus* Watson: type specimen. Latex cast taken from upper block (dorsal view). Natural size.

The distribution of the lateral line grooves of the skull has been amended from that of the original restoration. The supraorbital groove on the right could be traced over half way back along the intertemporal. The posterior regions of the supraorbital grooves, forward to the level of the front of the orbit appear as exaggerations of the pits of the dermal ornament. Beyond this they become progressively deeper and wider until they cross from the nasals onto the lachrymals.

At this point the grooves are very deeply incised forming a characteristic semi-circular detour. This detour includes parts of the nasal, lacrimal and 'anterior tectal'. The groove then passes mesially across the snout in the premaxillary and turns forward again, presumably to terminate at the front of the premaxillary.

The suborbital groove terminates anteriorly at the external naris, as in *Ichthyostega*, and is very clearly marked over most of the lachrymal, jugal and postorbital, as figured by Watson. It is also possible to trace a connexion between the point of flexure of the suborbital groove on the jugal and the well-marked groove running dorsally on the squamosal: this is not very clearly marked along the first centimetre of the latter bone. Thus the jugal groove ('preopercular canal' of Stensiö) is complete almost to the back of the squamosal, as restored by Stensiö (1947). It may be presumed to have continued down to the quadrate region and thus on to the lower jaw.

Below the jugal groove on the squamosal is a series of irregular lateral line pits and a more consistent groove which curves downward and slightly back over the quadratojugal. The groove becomes fragmented again towards the edge of that bone: nevertheless it appears to 'run off' the edge rather than turning back into the horizontal plane as originally figured. This complex below the jugal canal has been homologized by both Westoll and Stensiö with the pit lines on the cheek of osteolepid fish.

For the sake of completeness an attempt has been made to portray the skull in palatal view (figure 13). The restoration of the skull roof, braincase and pterygoids give most of the necessary data for the posterior half of the skull. The anterior ossifications of the palate are mostly derived from the condition in other anthracosaurs, notably the closely related *Eogyrinus*.

The large choanae, separated by narrow toothless vomers, follow the pattern seen in *Pholiderpeton* and *Anthracosaurus* (Watson 1929), personally observed in *Eogyrinus* and generally taken as characteristic of the embolomerous anthracosaurs. In the type of *Eogyrinus* the dorsal roof of the choana runs out to the antero-lateral margin of the snout and is continuous with the external naris (Atthey 1876, Plate IX) and it has been assumed that in both *Eogyrinus* and *Palaeogyrinus* the anterior end of the maxillary formed a bridge defining the two cavities.

EOGYRINUS ATTHEYI

Watson 1926, pp. 222 to 238, Figures 18 to 25.
Anthracosaurus russelli Huxley–Atthey 1876.
Pteroplax cornutus Atthey–Romer 1947.

The incomplete skull specimen to be described is specimen A2 of the Swanwick collection. It is attributed to this genus and species on resemblances to the holotype which include the shape of the skull table and its constituent bones, the proportionate size of the pineal foramen and its situation on a slightly raised area, the form and ornamentation of the bones of the palate, the dentition (as far as preserved) and other features noted in the description.

Separation from *Palaeogyrinus decorus* is subject to the reservations noted in the above taxonomic discussion. The size of specimen A2 exceeds that common to both specimens of *Palaeogyrinus* though it is not nearly as large as the holotype of the present species. Direct comparison of specimen A1 with specimen A2 is unsatisfactory because of the absence or poor preservation of palatal structure in the former and apart from size the only significant difference between the two is the completely flat pineal region of *Palaeogyrinus*. This difference is, however, a slight one.

Skull roof

Preservation of the bone surface is generally good and the ornament is of the distinctive anthracosaur type (figure 15). In the cheek region the ornament is much less marked, consisting of little more than an irregular roughening bearing occasional tiny pits. This seems to be a common condition in anthracosaurs and a similar ornament in this region occurs in the type specimens of *Eogyrinus* and *Palaeogyrinus*.

The sutures on the skull table, with the exception of parts of the midline suture, were fairly easily traced, and the pattern of dermal bones in this region will be clear from figure 15; their relations are not distinguishable in any major feature from those of *Palaeogyrinus*. Unfortunately the tabular horn is broken off, but there is no reason to suppose that it was not of the form found in *Palaeogyrinus* and *Pteroplax*. The pineal foramen is small, and unlike that of *Pteroplax*, which is elongate, is somewhat widened transversely. It is not borne on a marked median ridge, as is that of *Pteroplax*, though the general midparietal region is inconspicuously raised.

The skull table is preserved intact along its left lateral edge as far as the inner border of the orbit. Compression and shearing forces have, however, disrupted the relations of the table and the adjacent left cheek region and forced a piece of bone, probably epipterygoid, between them. The postorbital bone appears to have swung round about a point midway along its suture with the intertemporal so that its front end lies beneath the orbital edge of the postfrontal, and posteriorly it has become separated from that bone. The proximal edge of the squamosal is likewise separated from its original contact with the supratemporal and the whole preserved cheek region has been flattened into a horizontal plane. The squamosal and jugal have also separated along the line of their joint suture, though traces of their suture interdigitations remain on each side.

The articular surface of the squamosal is exposed and is preserved for well over three-quarters of its length. The tangential plane of the articular surface lies at something over 30° to the plane of the squamosal. Allowing for some flattening this angle would represent the approximate slope of the cheek region from the skull table. The width of the concave articular surface is just under 1 cm.

As in *Palaeogyrinus* the surface at the edge of the squamosal must have been overlapped by the edge of the supratemporal so that the edge of the latter fitted along the outer edge of the former. This outer edge, though slightly disrupted in the specimen, forms a more or less straight line, and it seems very unlikely that the slight gap between the two bones widened posteriorly to form an otic notch.

The concave articular surface itself forms a deep hemicylindrical groove. This suggests that there must have been a considerable amount of packing material between it and the corresponding groove under the supratemporal, if this latter took the form of that in *Palaeogyrinus* and the larger *Pteroplax* skull (Watson 1926, Figure 19). The surface of the squamosal groove, where well preserved, does not suggest that the packing material was cartilage. A bone surface formerly covered with cartilage has a very characteristic appearance best likened to a series of minute interlocking sausages: the squamosal groove on the other hand has a surface irregularly pitted in a manner which recalls the dermal ornament, though the surface appears rougher and less finished.

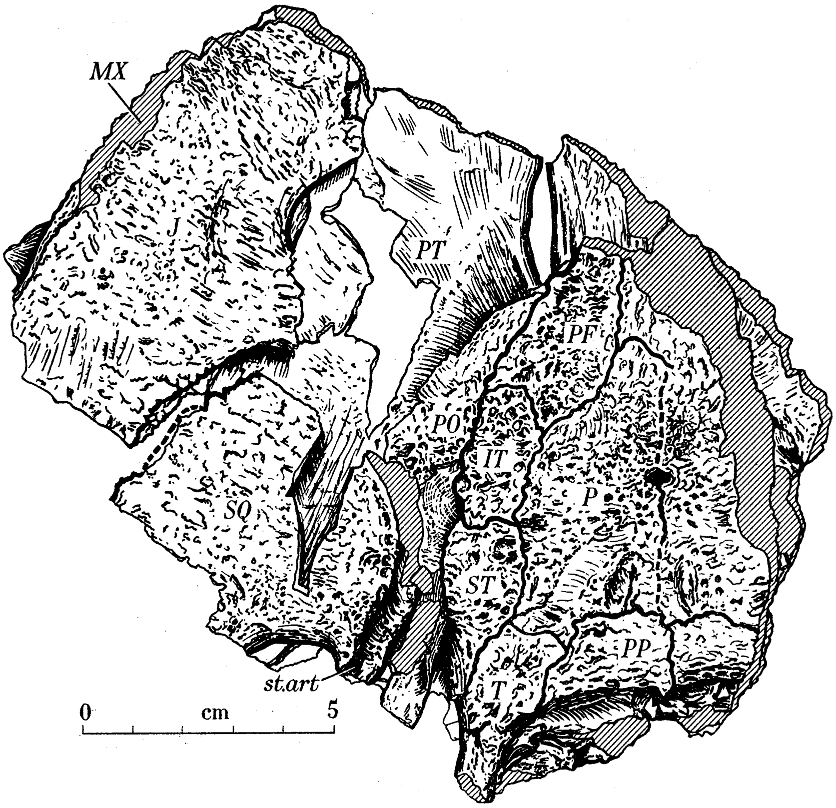

FIGURE 15. *Eogyrinus attheyi*: skull A2, dorsal. Two-thirds natural size.

The posterior edge of the squamosal is preserved for about 2 cm from its corner with the articular edge. Dorsally the posterior edge is thickly rounded and concave forming part of the border of the otic 'notch'.

Below the level of the otic notch and at 1 cm from the corner an unornamented shelf of the squamosal runs back at 45°. The mesial edge of this shelf forms a deep vertical flange for the support of the tympanum and to define a channel for the stapes.

The shelf itself represents the preserved part of the occipital exposure of the squamosal, whose edge contacted the quadrate ramus of the pterygoid.

The jugal bone is almost completely preserved, lacking only a small part of its posterior extension towards the quadratojugal and of its anterior extension to suture with the lachrymal. Its lack of strongly defined dermal ornament and the absence of any apparent lateral line canal, suggests that the bone lay somewhat below the surface of the skin in life. Mesially part of the orbital border is preserved representing about 2·3 cm of the antero-lateral edge of the orbit.

Laterally the jugal is bordered by the slender maxilla, which is present in part in this specimen. It is however, much eroded and devoid of teeth. At the level of the back of the orbital edge, but at the lateral edge of the jugal, there is developed a massive triangular processus alaris (Bystrow & Efremov 1940) descending from that bone and lying in a vertical longitudinal plane. It projects 1·4 cm below the general lower surface of the jugal, is about 3 cm from front to back and reaches a thickness of over 1 cm.

Anteriorly it would have been overlapped in the undamaged skull by the posterior end of the tooth-bearing ectopterygoid and would have bordered the anterior end of the subtemporal fossa. Probably correlated with the depth of the pterygoid, the process is in the vertical plane, even when the slope of the cheek region is allowed for. A similar process, with the tip broken off, is present in the holotype on the right side and the base of the corresponding process may be seen on the left. The process is figured but not commented upon by Atthey (1876, Plate IX).

Palate

The palatal surface of the specimen is very well preserved (figure 16), but compression has been accompanied by horizontal shear, so that posteriorly the midline of the parasphenoid lies under the middle of the left tabular-postparietal suture of the skull roof.

The posterior 2·5 cm of the palatine is preserved and is chiefly occupied by a very large palatal tusk together with its root and socket. As far as preserved, it is separated from the pterygoid by the ectopterygoid.

The palatine tusk corresponds in position to a cavity in the right palatine figured by Atthey in the type. This cavity appears to have been the site of a posterior palatine tusk distinct from the anterior one represented on the left. Thus it seems probable that each palatine of *Eogyrinus* bore two tusks, each with a replacing pit.

The tusk in the Derbyshire specimen measures just under 1·5 cm in diameter at the base and tapers to 0·8 cm at 1·3 cm distally, where it is broken off. The palatine bone is swollen and pitted at the base of the tusk. Elsewhere it is irregularly swollen and ornamented with small pits. There is no certain sign of a replacing pit posterior to the tusk.

The ectopterygoid is almost complete, lacking only the termination of its anterior process inside the palatine and a fragment from its inner border. Compression of the whole specimen has torn it, together with the palatine, away from its original suture with the maxilla. Like the palatine the bone surface is irregularly swollen and pitted.

Laterally it bears a series of teeth of considerably smaller size than the palatine tusk. The anterior of these is by far the largest, having a basal diameter of 6 mm. It is placed at a distance of 2 cm from the anterior edge of the bone, and between the two there lies a replacing pit for a similar sized tooth.

The remaining four smaller teeth are of similar size, about 2·5 mm basal diameter: two are complete and are about 5 mm long. All the teeth, including the tusk, are of typical labyrinthodont type and are longitudinally striated with fine grooves.

The left pterygoid is almost complete but for its extension anteriorly beyond the level of the ectopterygoid and its extension posteriorly as the quadrate ramus. The general surface of the bone is ornamented as in *Palaeogyrinus* with tiny closely packed tubercles. Laterally, however, where the bone borders the subtemporal fossa the ornament becomes more like the pitted type of the ectopterygoid. This lateral border, preserved for 7·5 cm, tapers down to a smoothly curved edge.

To give an adequate width to the subtemporal fossa this skull would have to be restored with the pterygoid inner wall of the fossa in a similar vertical plane to that of *Palaeogyrinus*. This is also the case in the type specimen (Atthey 1876, Plate IX).

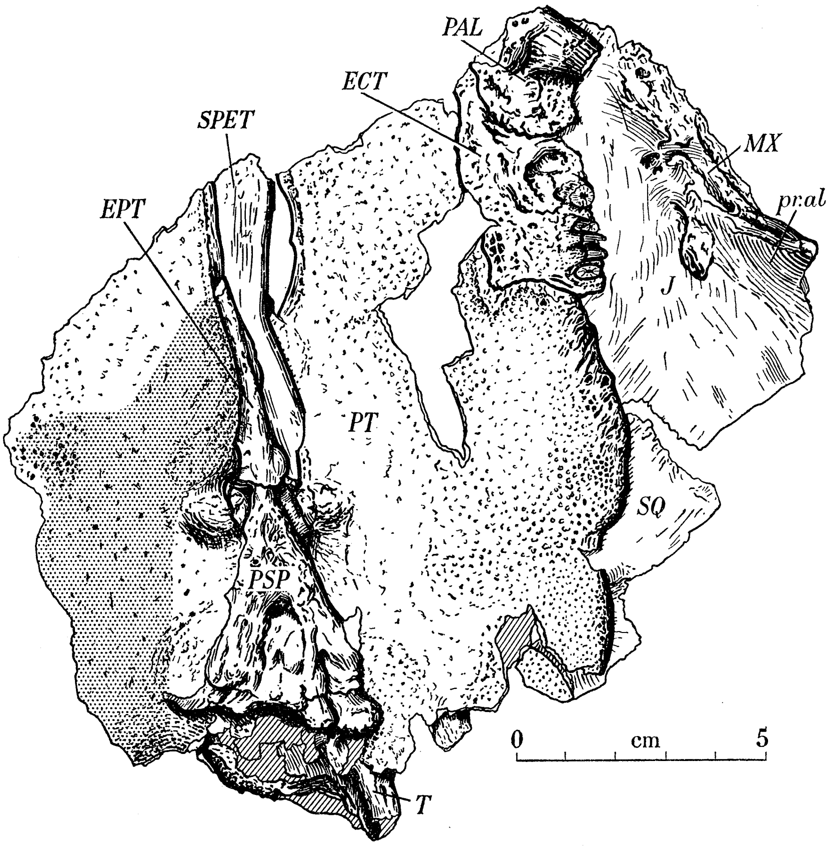

Figure 16. *Eogyrinus*: skull A2 ventral. Two-thirds natural size. (Area of epipterygoid preserved below (dorsal to) right pterygoid, fine stipple.)

The inner border of the left pterygoid is preserved intact for nearly 3 cm from the front of the specimen and again for some 2 cm backwards from the region of the basicranial junction. Anteriorly for 0·5 cm the edge is cut back ventrally some 3 mm, presumably for the ventral overlap of the edges of the processus cultriformis of the parasphenoid, but further back this evidence of overlap disappears and the edge becomes smoothly rounded as it is behind the basicranial junction. The anterior stretch of preserved edge is markedly concave in ventral view suggesting the presence of small interpterygoid vacuities behind the overlap region.

On the right the true edge of the pterygoid was present from the front of the specimen back to the level of the basipterygoid process and the bone appeared very little modified below this process. Subsequent dissection, although the pterygoid was somewhat disrupted at this point, suggested that the basicranial articulation was formed chiefly between the epipterygoid and the basipterygoid process of the basisphenoid and parasphenoid as in *Palaeogyrinus*. This view is supported by the condition in the type in which the principal articular surfaces of the epipterygoids project into view at the end of massive processes from above the smooth edges of the pterygoids (Atthey 1876, Plate IX, labelled 'u').

Removal of the right pterygoid established that, as in *Palaeogyrinus*, there was an extensive ossification of the epipterygoid. This lay as a solid sheet of bone between the pterygoid and the braincase, behind the level of the basicranial articulation. Unfortunately the bone itself was in poor condition due to crushing of the specimen and showed no morphological detail. The area occupied by this quadrate ramus of the epipterygoid is indicated in figure 16.

More anteriorly a columella cranii of the type seen in *Palaeogyrinus* but considerably more massive was preserved, but again the details are difficult to make out.

Braincase

Removal of the right pterygoid and most of the epipterygoid exposed the right lateral surface of the braincase. Preservation of the braincase extends forward to a point on the sphenethmoid some 6 cm in front of the basal articulation, but the anterior 3 cm are relatively undifferentiated sphenethmoid and are not included in figure 17.

The occipital region is closely similar to that of *Palaeogyrinus*. The paired opisthotic facets, for the articulation of the exoccipitals, are well preserved. Little or nothing of the condylar region of the exoccipitals remains, but part of the condylar basioccipital appears behind the parasphenoid.

In the otic region the vagus foramen is present bordered by a remnant of exoccipital postero-ventrally. The anterior edge of the otic capsule is concealed below the disrupted columella cranii of the epipterygoid. The fenestra ovalis is not visible, but seems to have been concealed by the post mortem dorso-lateral shift of the edges of the parasphenoid and basiphenoid.

The basiphenoid seems to have been very similar to that of *Palaeogyrinus*. That part which invests the base of the prootic can be seen projecting above the edge of the parasphenoid and the complete ventral half of the basipterygoid process is well preserved and has been dissected out. The articular surface of this process terminates a massive cylindrical column some 120 mm in diameter with its axis horizontal and at about 45° forward of the transverse plane. The articular surface itself faces antero-laterally and is saddle-shaped with the axis of its main concavity vertical.

Posteriorly a flange of bone extends back from the body of the process to contact the otic region of the basiphenoid, but is broken off on the specimen. A foramen is situated between the body of the process and this flange: this may be for the palatine branch of the seventh nerve.

The parasphenoid is preserved from its posterior limit forward to the basicranial region. Like that of *Palaeogyrinus* it is ornamented, this ornament being particularly strongly developed anteriorly. Again as in *Palaeogyrinus* there is a well-marked median concavity posteriorly; the two convex bony areas flanking this form the basal tubera. A foramen terminating a posterior groove is clearly seen in this region on the left.

Because of the condition of the specimen the corresponding one on the right is less clear. These foramina are in a considerably more posterior position than the similar pair in *Palaeogyrinus*, but like them are probably for a nutrient branch of the carotid artery.

Laterally, on the right, most of the upper boundary of the parasphenoid is visible and, as in *Palaeogyrinus*, it borders the basioccipital and is distinct from the basisphenoid. The ornamented part of the parasphenoid is distinct from the basipterygoid process, but at one point the two appear confluent and it is probable that the parasphenoid formed an outer core to the process.

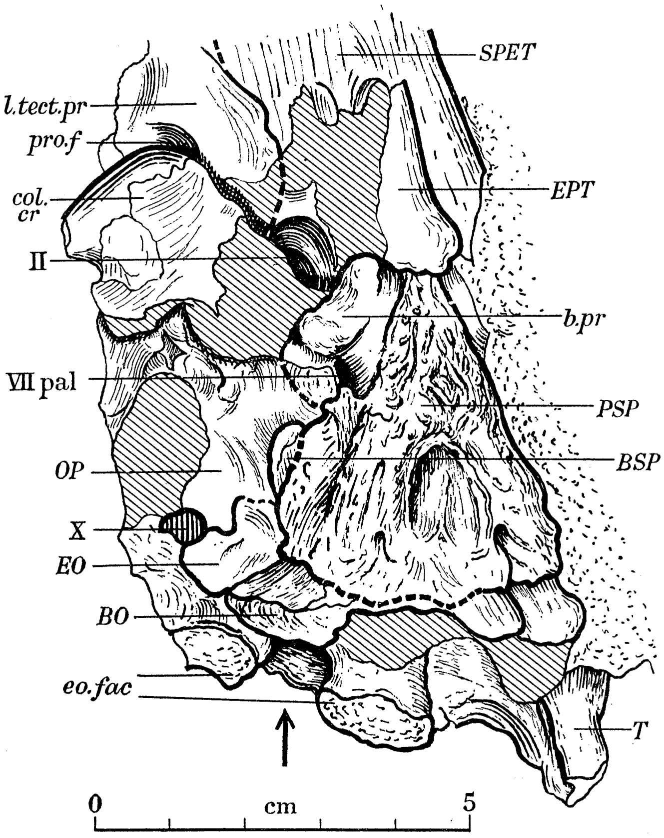

FIGURE 17. *Eogyrinus*: skull A2 ventral. Natural size. Right pterygoid and most of epipterygoid dissected away to show braincase. (Arrow indicates displaced axis of skull roof.)

In front of the process and the disrupted remains of the columella cranii may be seen part of the anterior margin of the interorbital foramen, showing, as in *Palaeogyrinus*, the clearly defined concavity for the origin of the anterior and inferior rectus muscles of the eye. Above this the front of the general concave area of the sphenethmoid in which the prootic foramen was situated is also visible, but the latter is concealed by the columella cranii.

The sphenethmoid region has been distorted so that the narrow interorbital septum has been flattened to the left and the processus cultriformis of the parasphenoid lost. Part of the articular region of the anterior epipterygoid remains in this area. The lateral tectal process of the sphenethmoid can clearly be seen overlapping the top of the interorbital septum, just as in *Palaeogyrinus*.

A transverse section of the sphenethmoid is exposed at the front of the specimen but the canals are indistinct because of crushing.

A thorough account of the braincase of *Eogyrinus* must await a new description of the type skull. It may be stated, however, that no important difference has yet been found between the braincases of *Palaeogyrinus* and *Eogyrinus*.

The evolution of the anthracosaur skull

The subdivision of the Labyrinthodontia into two major sub-groups, the Temnospondyli and the Anthracosauria (Romer 1947) was first proposed by Säve-Söderbergh (1935). The two groups are defined by very different evolutionary trends, but a detail of dermal roof pattern provides a useful clue for their separation. In the tabular region two mutually exclusive patterns occur.

The temnospondyl pattern, characteristic of typical rhachitomous and stereospondylous forms as well as the early ichthyostegids and loxommids, has the postparietal (interparietal, 'dermo-supraoccipital') suturing with the supratemporal, thus separating the tabular and parietal (figure 18*b*). This pattern, together with some of the characteristic temnospondyl trends, also occurs in the aberrant plagiosaurs, which are probably to be regarded as a group distinct from the temnospondyls (Nilsson 1946; Panchen 1959).

The anthracosaur pattern, on the other hand, reverses the situation. The tabular is an elongate bone directed antero-mesially and suturing with the parietal. It thus separates the supratemporal and postparietal (figure 18*c*). In the Coal Measure embolomerous anthracosaurs the tabular is also produced backwards to form a projecting horn. The anthracosaur pattern occurs in the Anthracosauroideae (Watson 1929, Embolomeri of Romer 1947) and in the Seymouriamorpha, a group very close to the most primitive reptiles.

One apparently primitive feature is retained in the skull roof of embolomerous anthracosaurs, but is lost in all described seymouriamorphs with the exception of *Gephyrostegus* (*Diplovertebron*). The skull table and cheek region, or more specifically the supratemporal of the former, and the squamosal of the latter, have no sutural contact and were probably united by connective tissue in the manner described above. This is reasonably assumed to be a relic of the common osteolepid fish condition in which the postparietal shield (postparietals, supratemporals, tabulars and the extrascapulars behind them) had no firm suture with the rest of the skull roof (figure 18*a*).

In the osteolepids, however, this separation of skull table from cheek and more anterior skull region is typically related to a kinetic separation of the neurocranium into two regions, a posterior otico-occipital region lying under the skull table and an anterior ethmosphenoid region (e.g. Romer 1937). In typical labyrinthodonts this division of the neurocranium, if it was ever present, has disappeared and the parasphenoid bone, originally underlying the ethmosphenoid region only, extends back to sheath the otic region and the anterior part of the basioccipital. This condition has been reached by all described anthracosaurs.

A more primitive condition of the parasphenoid and braincase is seen in *Ichthyostega*. Though there is no gap between the two regions of the braincase the division present in the ancestral fish is represented by a transverse suture and the parasphenoid has not grown back to underlie the otic region, but is situated entirely in front of this suture (Jarvik 1952, 1955). In ichthyostegids, however, the skull table is firmly sutured to the parietals in front and to the cheek region on both sides, and its former lateral boundaries are no longer represented by a straight line (figure 18*b*).

In the embolomerous anthracosaurs it is only the lateral edges which remain free. Inspection of the pattern of dermal bones shows that not only is the former anterior edge of the table now firmly sutured to the parietal-intertemporal region, but that there has been a greater degree of rearrangement of the original fish pattern than in temnospondyls.

The osteolepid postparietal shield terminates anteriorly with the front edges of the postparietals and supratemporals (Westoll 1938, 1943) and thus these edges form an approximately straight line, as do the corresponding back edges of the parietals and intertemporals. In primitive temnospondyls a comparative reduction in the length of the postparietals and expansion backwards of the parietals results in the parietal-postparietal suture coming to lie behind the intertemporal-supratemporal sutures on either side of it. Loss of the intertemporal, which occurs in most temnospondyls including *Ichthyostega*, distorts the original straight line even further. In the anthracosaurs, however, this backward movement of the parietal-postparietal suture reaches a condition in which the suture has passed beyond the supratemporal altogether and gives the distinctive sutural contact of parietal and tabular. This, as Westoll (1962) has noted, completely 'locks' the original transverse weakness.

Thus it may be concluded, if saltatory rearrangements of bones are excluded, that the ancestors of the anthracosaurs must have passed through a temnospondyl condition of the bones of the skull table. The distinctive anthracosaur skull pattern must therefore be regarded as a secondary one within the Amphibia, though the lack of sutural contact with the squamosal in the embolomeres must equally be regarded as primitive.

It is often assumed (e.g. Romer 1947) that the junction between the skull table and cheek region, though derived from the osteolepid junction, represents a forward extension of the anthracosaur otic notch and thus that the primitive position of the tympanum is between the lower edges of the tabular and supratemporal dorsally and the upper edge of the squamosal ventrally. It is known to have occupied this position in temnospondyls as demonstrated by the direction of the stapes towards the dorsally placed otic 'notch', a rounded emargination between tabular and squamosal.

However, as first pointed out by Sushkin (1927) the position of the hyomandibular in the crossopterygian fish is very similar to that of its homologue the stapes in early reptiles, with its main axis directed ventro-laterally towards the quadrate. This idea has recently been very fully developed by Parrington (1958, 1959) who notes that in none of the amphibian groups characteristic of the Carboniferous, or the earlier ichthyostegids, is the stapes known. Also none, with the exception of the loxommids, has a well-defined otic notch of the temnospondyl type.

Thus the temnospondyl otic notch may reasonably be regarded as a secondary condition characteristic of that group and its descendents alone. Furthermore, the rounded form of the otic 'notch' in temnospondyls does not suggest formation by the closure from the front of a slit between the table and cheek (Parrington 1959). Consideration of the seymouriamorphs and those primitive reptiles which bear an external otic notch leads to a similar conclusion. The otic notch of *Seymouria*, usually regarded as being in the 'amphibian' position, has the squamosal forming part of its upper border (White 1939) and is very similarly placed to those of the reptilian Diadectidae and Procolophonidae (e.g. Romer 1956, Figures 33, 43).

Turning to the captorhinomorphs, a group of very primitive reptiles in which no external otic notch is apparent, *Limnoscelis* retains the loose junction between squamosal and supratemporal at least as a point of sutural weakness (Romer 1946), but it is likely, from the form of the occiput, that the stapes in this form, like that in the related *Captorhinus*, was situated in the typical reptilian position. Nor is there any apparent reason for believing that the ancestors of *Limnoscelis* had a tympanum placed between the squamosal and supratemporal, which was subsequently, in its evolutionary history, squeezed out backwards and then either dropped down to a reptilian position or lost altogether.

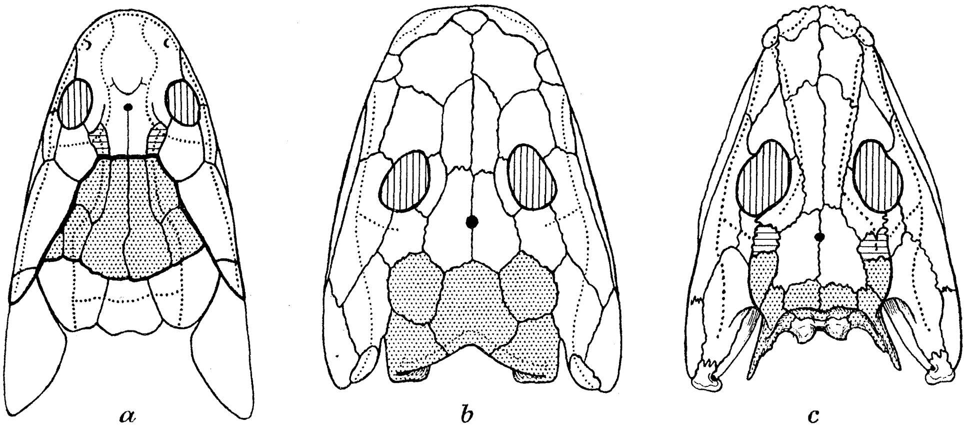

FIGURE 18. Skulls in dorsal view, not to scale, *a*, *Osteolepis*; *b*, *Ichthyostega*; *c*, *Palaeogyrinus*. Bones of postparietal shield (*PP*, *ST*, *T*) stippled, *IT* hatched. (*a* and *b* after Jarvik.)

Thus it may be assumed that the persistent lack of sutural contact between squamosal and supratemporal in embolomeres has no necessary connexion with the position of the tympanum, although the position of the latter has been described in this region from the skulls of both *Palaeogyrinus* and *Eogyrinus*.

It seems probable, therefore, that a limited degree of kinetic movement was retained in the embolomere skull, though this must have been different in kind as well as in degree from that present in the ancestral osteolepids. In the latter the snout region of the skull, together with the palatoquadrate and dermal jaw and cheek region must have moved as a whole on the posterior braincase and skull table, the whole system being braced by the notochord which extended forward to the basisphenoid region.

With the complete disappearance of the division of the neurocranium in anthracosaurs the only remaining movable articulation within the skull is that between the basisphenoid region and the palatoquadrate on either side of it. Thus the palatoquadrate on either side and the dermal jaw and cheek region to which it is attached is potentially capable of rotating about the neurocranium at the basipterygoid process of the basisphenoid.

This is the basic kinetic articulation of the tetrapod skull and the movable articulation is retained in seymouriamorphs, primitive reptiles and a few temnospondyls, as well as in the embolomeres.

The movement about this articulation, especially in groups other than the embolomeres, must have been very limited indeed. It seems possible, however, that the retention of a partially loose cheek region in the latter may have been related to it.

The chief purpose of kinetic movement of the skull in vertebrates seems to be to protect the brain from shocks received by the jaw mechanism in feeding. In the embolomeres such shocks and also considerable mechanical stresses would arise chiefly as a result of the action of extremely powerful adductor mandibulae (temporalis) musculature. Any component of this which took origin from the braincase or the underside of the roofing dermal bones would tend to produce rotation of the palatoquadrate, represented by the pterygoid and quadrate bones posteriorly, about the braincase. Muscles whose line of action between skull and jaws lay in front of the basipterygoid articulation, such as the pterygoideus, would tend to stretch the region between quadrate articulation and skull table, whereas the more posterior components of the adductor mass would tend to compress it. The latter effect might also be produced by the action of a powerful depressor mandibulae, which, because of the lack of a well-developed retroarticular process, was inserted very close to the quadrate condyle (figure 19).

It seems probable that the effect of this expansion or compression would be minimized by presence of a shock absorber at the point of greatest stress. Thus if the slit between the skull table, to which the neurocranium was attached, and cheek region, which transmitted the stress, was filled with strong but elastic connective tissue, the results on the braincase of either compression or expansion of the cheek region would be minimized.

It is possible also that there was some muscular control retained to brace the junction itself: the levator palatoquadrati, lost in most tetrapods with akinetic skulls, would brace the pterygoid and quadrate, and thus the cheek region, to the cranium and skull table, and thus prevent complete disarticulation.

The tabular horns have been characterized by Watson (1926) as the first link in a primitive bony chain connecting the skulls with the dermal shoulder girdle, a connexion occurring in most groups of bony fish. In the osteolepids the connexion takes place by means of a post-temporal bone which attaches to the skull anteriorly and to the supracleithrum of the dermal girdle posteriorly. Watson assumed that a similar connexion occurred in embolomerous anthracosaurs and described as a post-temporal a small bone associated with the type of *Pholiderpeton scutigerum* Huxley. He also associates with *Eogyrinus* a shoulder girdle from Newsham bearing a broadly expanded clavicle and cleithrum and topped by a supracleithrum.

It seems probable, however, that neither specimen is correctly placed. Romer (1947, 1957) has noted that the 'post-temporal' is very similar to the cleithrum of the American embolomere *Archeria* and that the girdle of the latter is similar to that of temnospondyls such as *Eryops*, with reduced cleithrum and no supracleithrum and quite unlike that associated with *Eogyrinus*. It should also be noted that *Archeria*, in which no bony connexion between skull and girdle seems probable, also bears tabular horns (e.g. Romer 1947, Figure 44).

Thus it cannot be assumed that any bony connexion occurred in *Archeria* and its existence in other embolomeres is equally unlikely. Romer (1947, p. 262), however, notes the possibility of a ligamentous connexion, presumably as a relic of the fish condition. Even if this were the case, the tabular horn must be regarded as a neomorph as the post-temporal in osteolepids articulates with the extrascapular series and the opercular bone and has no bony connexion with the tabular, nor has the latter any horn (Jarvik 1944*a*, *b*).

The description of the well-preserved dermal girdle of *Archeria* (Romer 1957) makes no mention of any scar or process on any of the dermal elements (it would presumably be expected on the antero-dorsal edge of the cleithrum); so it must be concluded that there is no direct evidence for even a ligamentous connexion with the skull and other possible functions of the tabular horn must be considered.

The most likely function would seem to be that of a process for muscle insertion. An important muscular system originating, at least in part, from the occipital tabular region is that of the depressor mandibulae.

The bodily form and mode of life of these animals must have been, as noted by Watson, very crocodile-like. If, like crocodiles, they captured swimming prey in the water a powerful depressor would be necessary to affect a positive and rapid opening of the jaws while swimming.

In the crocodiles the degree of development of the depressor is obvious in the skull from the substantial retroarticular process. Its absence in the embolomeres has already been noted, but the articular region of the mandible is very deep in those forms in which it is known and would provide an extensive insertion for the muscle running down behind the jaw articulation.

In modern amphibia the depressor mandibulae originates partly from the posterior dorsal edge of the skull and partly from the fascia of the epaxial muscles and this may have been the case in most labyrinthodonts. In most modern reptiles, however, this insertion is confined to the skull (Adams 1919). It seems possible that in embolomeres we have the retention of an intermediate condition in which the tabular horn, extending back along the neck region, provided a firmer origin for the posterior part of the depressor mandibulae than the fascia in which the horn was probably partially embedded. Thus the skull in the reptilian descendants of the early anthracosaurs would have 'captured' the posterior part of the muscle with a reduction of the tabular horn.

This theory assumes the presence of a tabular horn in the early anthracosaurs ancestral to reptiles, and if this were the case would explain the distinctive pattern of the bones of the skull table. For a horn to develop it is probable that the growth of the tabular was 'elliptical' (Parrington 1956) with an axis representing the maximum growth rate running obliquely to the fore and aft plane so that the horns diverged somewhat posteriorly.

Once the characteristic parietal contact had been established it would be retained if the growth rate of the tabular and postparietal were both reduced. This would result in loss of the tabular horn if the growth of the tabular also became radially symmetrical.

The post-temporal fossa is a characteristic of almost all labyrinthodont skulls, other than those of embolomeres, occurring even in the related Seymouriamorpha, although only as a narrow slit in *Seymouria* itself (White 1939). It may also be homologized with the supraotic fossa of osteolepids (Romer 1941) and with the fossa Bridgei of actinopterygians (Säve-Söderbergh 1936; Romer 1947). The function of the post-temporal foramen is to carry the vena capitis dorsalis, but posteriorly in the above groups it is widened out to form the fossa, a deep pocket to house the origin of some of the occipital musculature (Säve-Söderbergh 1936; Romer 1941, 1947).

The assumption that the tabular horns of embolomeres lay on and strengthened the fascia of the axial muscles from which the posterior depressor mandibular originated implies that there could have been very little movement of the head on the neck. This implication is also inherent in Watson's assumption of a bony connexion of the skull to the shoulder girdle. This lack of mobility might well correlate with the loss of the post-temporal fossae, but the fact that these fossae are present in fish and thus probably in the ancestors of the embolomeres suggests that their loss is correlated with a secondary rearrangement of the occipital musculature and that the whole arrangement of the neck region has diverged from the fish condition.

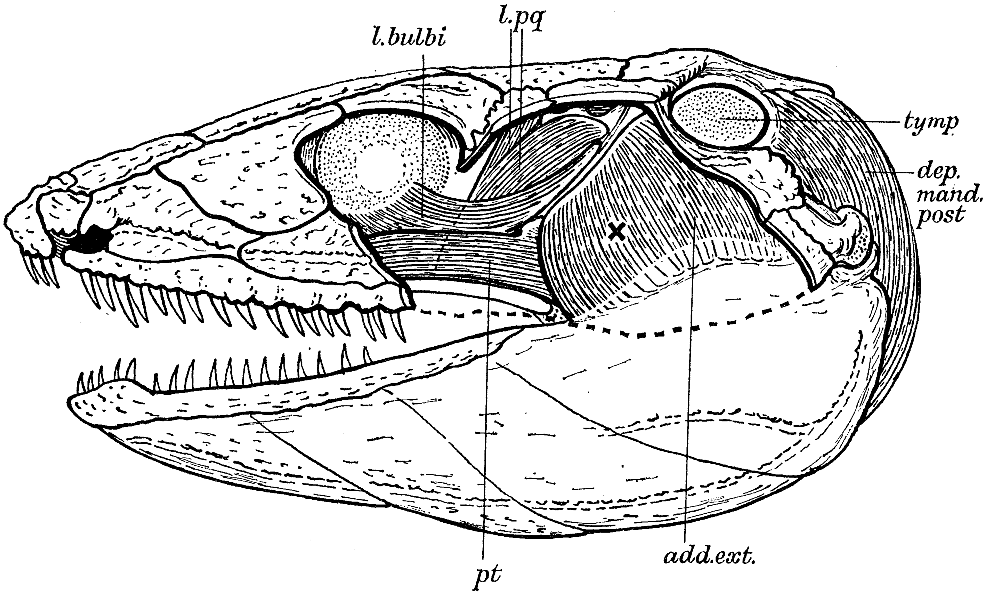

FIGURE 19. *Palaeogyrinus* skull in lateral view. Two thirds natural size, reconstructed with jaw musculature: bones of cheek largely removed. (Lower jaw modified from that of *Eogyrinus*.) Axis of basal articulation indicated by X.

In primitive temnospondyl labyrinthodonts such as *Eryops* the occipital condyle is already functionally double and movement of the head on the neck must have been virtually confined to the vertical plane. Powerful muscles, inserted in the post-temporal fossae, probably assisted in this movement.

There is, however, no sign of a trend towards a double condyle in the embolomeres and the simple concave surface of the condyle, just like that of a vertebral centrum, together with the possible loose articulation of the exoccipitals and the presence of tabular horns, all suggest very limited movement of the head on the atlas and thus, presumably, little need for the post-temporal fossa. This, like so many characters of the embolomeres, emphasizes their exclusive adaptation to an aquatic environment and in this, as in other respects such as the character of the vertebrae (Romer 1947), their divergence from the line that led to seymouriamorphs and reptiles.

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Explanation of abbreviations used in figures

A.TL,	‘anterior tectal’
BO,	basioccipital
BSP,	basisphenoid
ECT,	ectopterygoid
EO,	exoccipital
EPT,	epipterygoid
F,	frontal
IT,	intertemporal
J,	jugal
L,	lachrymal
MX,	maxillary
N,	nasal
OP,	opisthotic
P,	parietal
PAL,	palatine
PF,	postfrontal
PMX,	premaxillary
PO,	postorbital
PP,	postparietal
PRF,	prefrontal
PRO,	prootic
PSP,	parasphenoid
PT,	pterygoid
Q,	quadrate
QJ,	quadratojugal
SO,	supraoccipital
SPET,	sphenethmoid
SQ,	squamosal
ST,	supratemporal
T,	tabular
V,	vomer
add.ext,	external adductor
b.pr,	basipterygoid process
car.f,	carotid foramen
col.cr,	columella cranii
dep.mand.post,	posterior depressor mandibulae
eo.fac,	exoccipital facet
fen.ov,	fenestra ovalis
l.bulbi,	levator bulbi
l.pq,	levator palatoquadrati
l.tect.pr,	lateral tectal process
nc,	neurocranium (impression)
op.fac,	opisthotic facet
pr.al,	processus alaris
pr.cul,	processus cultriformis
pro.f.	prootic foramen
pt,	pterygoideus
q.f.	quadrate foramen
sq.art,	articular groove for squamosal
st.art,	articular groove for supratemporal
t.fac,	tabular facet
tymp,	tympanum

Nerve foramina in skull indicated by Roman numerals I, olfactory; Ivm, vomeronasal; II, optic; III, oculomotor; IV, trochlear; V, trigeminal; Vpr, profundus; VI, abducens; VIIpal, palatine; X, vagus.

FIGURE 14. *Palaeogyrinus decorus* Watson: type specimen. Latex cast taken from upper block (dorsal view). Natural size.