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The Skull and Skeleton of Eogyrinus attheyi Watson (Amphibia: Labyrinthodontia)

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THE SKULL AND SKELETON OF *EOGYRINUS ATTHEYI* WATSON (AMPHIBIA: LABYRINTHODONTIA)

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[Plates 24 and 25]

CONTENTS

As a preliminary to the redescription of the anatomy of *Eogyrinus attheyi* Watson, an account is given of the problems of nomenclature of British members of the anthracosaur family Eogyrinidae to which it belongs. There is no evidence to show that the four named genera of British eogyrinids differ from one another in any significant feature not explicable by allometric growth. Reconstruction of a series of allometric curves based on known skull specimens allows estimation of the dimensions of incomplete specimens. The skulls then fall into four size groups which correspond, with some stratigraphical backing, to the four named genera.

The lectotype skull of *Eogyrinus*, from the Low Main Seam, Newsham, Northumberland, has been cleaned using an 'Airbrasive' unit and is used as the basis of a new description of the skull. Additional information is provided by other Newsham specimens and two skulls from the Middle Coal Measures of Lanarkshire. The skull is completely known and is typical of anthracosaurs. The skull roof is closely similar to that of the eogyrinid *Palaeoherpeton* ('*Palaeogyrinus*'), but no anterior tectal bone is present above the naris in *Eogyrinus*. The nature of the dermal ornament is fully described.

The palate is typically anthracosaur, with toothless vomers, a 'tusk-pair' on each palatine and ectopterygoid, and additional small ectopterygoid teeth. The pterygoids descend below the level of the jaw line posteriorly as in *Palaeoherpeton*.

The braincase is reconstructed from an isolated Newsham specimen, originally attributed by Watson, from the lectotype and from one of the Scottish skulls. The isolated specimen shows the course of the semicircular canals as well as the fenestra ovalis. Most of the cranial nerve foramina are present. A complete reconstruction of the lower jaws is possible both as single rami and in articulation. Description of the jaw articulation allows a reconstruction of the relative movements of the rami in opening and closure.

The only associated material of the appendicular skeleton is the lectotype left femur, but an interclavicle from Newsham is certainly eogyrinid and probably pertains to *Eogyrinus*. Isolated ventral scales are described and their pattern of articulation reconstructed.

The material described in this paper is combined with that used in an earlier account of the axial skeleton to give a reconstruction of the whole skeleton of *Eogyrinus* in articulation, together with a restoration of the appearance of the living animal.

Introduction

Eogyrinus attheyi Watson (1926) is, judging from the dimensions of the skull, the largest anthracosaur amphibian known. The lectotype skull was described by Atthey (1876) from the Low Main Seam, of Newsham, Northumberland, and referred by him to *Anthracosaurus russelli* Huxley. Associated with the skull, and presumably from the same individual, are a number of vertebrae and ribs, scales and a femur.

In addition to Atthey's description of the type a number of other specimens from Newsham were described by Atthey (1877) and Hancock & Atthey (1868, 1869*a*, *b*) and referred either to *Pteroplax cornutus* H. & A. or to *Anthracosaurus*.

Several specimens, almost certainly pertaining to *Eogyrinus*, were described under various generic names (all *nomina oblita*) by Barkas (1873). Notable amongst these is a length of articulated vertebral column subsequently prepared and described by Atthey (1884) and later by Embleton (1889) and Watson (1926). I have recently used this, together with the type and other material to give an account of the whole axial skeleton (Panchen 1966).

In 1912 the lectotype skull was reconsidered by Watson and placed by him in the genus *Pteroplax*. *P. cornutus* is the only other anthracosaur occurring in Newsham, and the lectotype consists of an isolated skull table. For this reason it was thought probable by the authors of the genus that the 'cheek' regions of the skull were unossified. They had attributed two other similarly preserved skull tables to *Pteroplax* in spite of their larger size and rather different form.

In 1926 Watson separated *Eogyrinus* from *Pteroplax* and referred the two larger skull tables to the former genus. In naming *Eogyrinus* he gave an account of an isolated braincase which is correctly attributed, but did not redescribe or figure the lectotype skull. He also attributed to *Eogyrinus* a mysterious specimen from Newsham consisting of two blocks with large plates of dermal bone. These had been attributed to *Pteroplax* by Hancock & Atthey (1868). They were reconstructed by Watson as an extremely fish-like pectoral girdle and attributed to *Eogyrinus* partly on the character of the dermal ornament, partly on the presence of an interclavicle, then unknown in fish. He also attributed a small isolated interclavicle. It is highly unlikely, however, that the large pectoral girdle pertains to *Eogyrinus* (Romer 1947, 1957; Panchen 1964; Andrews 1972) and the isolated interclavicle is more probably that of a loxommatid (E. Beaumont: personal communication). There is, however, an interclavicle from Newsham which almost certainly pertains to an anthracosaur which was described but not figured by Hancock & Atthey (1868) and first referred to an unknown labyrinthodont 'reptile', and then tentatively to *Anthracosaurus* (H. & A. 1869*a*).

Specimens of *Eogyrinus* are known from a number of other localities apart from Newsham.

A jaw specimen described by Hancock & Atthey (1871) came from Fenton in Staffordshire, and an undescribed skull from Newarthill, Lanarkshire, is probably also *Eogyrinus*. A skull from Airdrie in Lanarkshire, referred by Watson (1929) to *Pholiderpeton*, is also to be referred to *Eogyrinus* (Panchen 1970, and below).

The lectotype (and that of *Pteroplax cornutus*) was so designated by Romer (1963).

Classification of British eogyrinids

I have recently produced a comprehensive systematic account of the Anthracosauria (Panchen 1970) and discussed the special taxonomic problems concerned with the status of *Eogyrinus*. They will be summarized here.

Eogyrinus is placed in the family Eogyrinidae comprising usually Carboniferous anthracosaurs with at least three premaxillary teeth and a total marginal tooth row of some 40 to 50 teeth. The palatal dentition of eogyrinids consists of a 'tusk pair' on each palatine and ectopterygoid followed by four or more ectopterygoid teeth. The dental formula (Chase 1963; Panchen 1970) for *Eogyrinus attheyi* is 0–2–2 (7); pmx 3 or 4, mx 45. The teeth of Eogyrinidae show mild 'canine peaking' in large species and are roughly cylindrical with conical crowns.

Two other families of anthracosaurs are distinguished by their dentition. In the Anthracosauridae the dental formula is markedly lower, 0–2–2 (2), pmx 2, mx 20 for *Anthracosaurus russelli*. In the Archeriidae the marginal tooth count is similar to that of Eogyrinidae, but the teeth, situated in a long spatulate snout, are of very distinctive form with longitudinal chisel-shaped crowns slightly hooked back from the cylindrical body of the tooth and very close-set. Canine peaking is very marked in the Anthracosauridae but unknown in the Archeriidae.

Thus distinguished, four taxa of British eogyrinids have been named, *Palaeoherpeton* ('*Palaeogyrinus*') *decorum* (Watson), *Pholiderpeton scutigerum* Huxley, *Pteroplax cornutus* H. & A. and *Eogyrinus attheyi* Watson. Only the skulls of *Palaeoherpeton* and *Eogyrinus* are known with reasonable completeness. Cranial material of *Pteroplax* is confined to the lectotype skull table and it is thus not absolutely certain that it is an eogyrinid, while the holotype of *Pholiderpeton*, not available for study at the time of writing, has enough of its dentition exposed to view to ensure that it is an eogyrinid, but requires considerable preparation and study before its validity as a taxon is certain.

In 1964 I noted that there seem to be no significant differences between the type skulls of *Palaeoherpeton* and *Eogyrinus* not explicable as a result of allometric factors resulting from their considerable difference in size. I also attempted to establish valid differences, apart from size, between the two eogyrinids from Newsham, *Pteroplax* and *Eogyrinus*. These concerned: (1) the shape of the pineal foramen, elliptical and situated on a ridge in *Pteroplax* but circular on a flat surface in *Eogyrinus*; (2) the definition of the lateral line canals between the orbits, strongly marked in *Pteroplax*, ill-defined in *Eogyrinus*; and (3) the form and disposition of the dermal ornament. The differences are real and marked, but I now feel less happy about their taxonomic significance. All three could be interpreted as due to differences in preservation, while the character of the lateral line grooves seems also to be size-related. Small eogyrinid skulls such as those of *Palaeoherpeton* and *Pteroplax* have much more closely defined grooves than large skulls such as the various specimens of *Eogyrinus*.

It therefore became necessary to establish some criteria to produce at least a provisional classification of British eogyrinids and a combination of size range and stratigraphic range was decided upon, with the use of any secondary characters which might be available. To look at size range in the four named taxa it became necessary to estimate the dimensions of the skull in very incomplete specimens. In order to do this the assumption was made that all the British eogyrinids differed in proportion only in direct allometric relation to their absolute size,

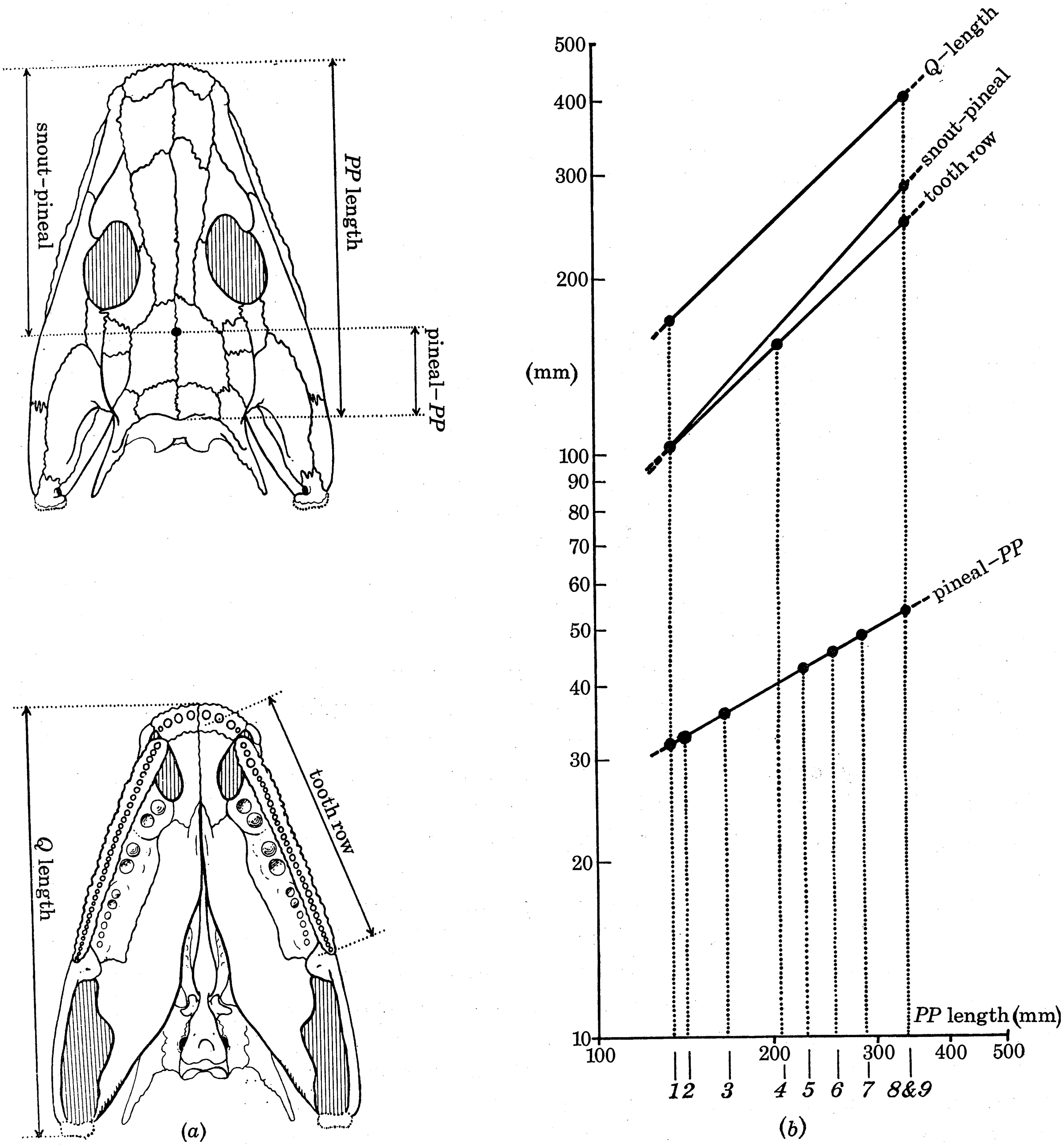

FIGURE 1. Taxonomy of British eogyrinids. (*a*) Dorsal and palatal view of *Palaeoherpeton* skull with indices; (*b*) 'allometric graph': numbers below abscissa refer to table 1.

i.e. that the skulls, if complete, would form an allometric 'growth' series with the type skulls of *Palaeoherpeton* and *Eogyrinus* as the smallest and largest respectively. It was also necessary to assume that the skull specimens used in the study were adult or near adult. This assumption is reinforced by the rarity of the discovery of growth stages of Palaeozoic amphibia except under specially favourable circumstances (Romer 1963) which do not seem to have occurred in the British Coal Measures. It is vindicated in the case of *Palaeoherpeton* by the closely similar size of the only two known skull specimens and strengthened for the other taxa by their stratigraphical distribution.

Nine skull specimens, all of which had been attributed to one or other of the four genera, were used in the study (Panchen 1970). The dimensions used are shown in figure 1*a* and the data tabulated as table 1. Figure 1*b* is a logarithmic plot based on the allometric equation $y = bx^k$. The variable standard of comparison (x) is the postparietal length which is plotted on the abscissa. The other indices are plotted as separate curves against this. All the indices used are accessible on the *Palaeoherpeton* and *Eogyrinus* skulls, and on the assumption that the series is allometric the corresponding indices for the two skulls are connected by straight lines. The available indices for the remaining skulls could then be plotted on the appropriate straight line curve and the estimate of the missing dimensions obtained.

Using this method the nine skulls fall into four size/geological horizon groups so that there is no overlap in geological range between adjacent size groups. It is a lucky coincidence that each group contains one of the four type specimens. The type skull of *Pteroplax cornutus* is a 'group' of one member in agreement with Watson. Its skull table differs somewhat in proportion from that of all the others. As this difference concerns the width:length ratio it need not prejudice the inclusion of *Pteroplax* in a series based only on longitudinal measurements.

Only two revised assignations of specimens to species result from the study and both are supported by stratigraphy in addition to size. These are the skull from Airdrie G 28318, which was referred by Watson (1929) to *Pholiderpeton*, which is now placed as *Eogyrinus* and the specimen from Swanwick (A 2) described (Panchen 1964) as *Eogyrinus* which is now assigned to *Pholiderpeton*.

The geological horizons of the specimens used in the graph are set out below in terms of British Coal Measure stratigraphy (Panchen & Walker 1961) together with their localities and taxonomic grouping:

M. Coal Measures:		
Similis-pulchra Z:	Airdrie: G 28318†	*Eogyrinus attheyi*
	Newsham: Lectotype	
	Newsham: DMSW 35	
	Newsham: R 8426	
	Newsham: Lectotype	*Pteroplax cornutus*
Modiolaris Z:	Pirnie: Holotype	*Palaeoherpeton decorum*
L. Coal Measures:		
U. Communis Z:	Swanwick: A 1	
	Swanwick: A 2	*Pholiderpeton scutigerum*
L. Communis Z:	Toftshaw: Holotype	

The specimens noted above from Fenton and Newarthill extend the range of *Eogyrinus* up into the Philipsii zone of the Upper Coal Measures and down to the upper Modiolaris zone respectively.

It is of course doubtful whether the four species named, even if valid, should be placed in four monotypic genera, but pending further information, notably the development and study of *Pholiderpeton*, the generic distinction will be maintained.

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† Horizon not certain (see below).

With the exception of very early anthracosaurs, including specimens from the Mississippian of West Virginia recently described by Romer (1970), and Hotton (1970), no valid postcranial distinctions were known, either within the Eogyrinidae or within the anthracosaurs (Embolomeri *sensu* Romer) as a whole.

Table 1. Indices in British eogyrinids

Numbers after specimen references refer to graph, data in square brackets estimated (after Panchen 1970).

	PP length	Q length	pineal -*PP*	tooth-row upper	tooth-row lower	snout-pineal
Palaeoherpeton, holotype: Pirnie (*1*)	135	170	32	103	—	103
Coope Coll., A1: Swanwick (*2*)	—	—	33	—	—	—
Pteroplax, lectotype: Newsham (*3*)	—	—	36	—	—	—
Coope Coll., A2: Swanwick (*4*)	—	—	43	—	—	—
Pholiderpeton, holotype: Toftshaw (*5*)	—	—	—	—	[155]	—
DMSW 35 (H.M. G13.78): Newsham (*6*)	—	—	46	—	—	—
B.M.(N.H.) R8426: Newsham (*7*)	—	—	49	—	—	—
G.S. 28318: Airdrie (?Palace Craig I. stone) (*8*)	—	—	—	[240]	[260]	—
Eogyrinus lectotype: Newsham (*9*)	340	410	[54]	250	250	285

The following provisional diagnosis is thus based entirely on the skull:

Genus *Eogyrinus* Watson 1926.

Large anthracosaurs from the British Middle and Upper Coal Measures (postparietal length: 250 to 350 mm). Pineal foramen small, not on marked median ridge. Lateral line sulci shallow, not sharply incised. Dentition: probably three maxillary teeth, more than 40 maxillary teeth with strong 'canine peaking'; dentary teeth in excess of 40. Denticles on anterior coronoid (contrast *Neopteroplax* Romer 1963). Palatal dentition, where known, 0–2–2 (7). Surangular region strongly expanded dorsally (contrast *Neopteroplax*).

MATERIALS AND METHODS

The specimens used in the description of the skull and postcranial remains of *Eogyrinus* are listed below. The following abbreviations are used for the institutions owning the material:

B.M.(N.H.)	Department of Palaeontology, British Museum (Natural History).
G.S.	Institute of Geological Sciences (British Geological Survey – 'Museum of Practical Geology').
H.M.	Hancock Museum, Newcastle upon Tyne.
M.M.	Department of Geology, the Manchester Museum.
R.S.M.	Department of Geology, Royal Scottish Museum.

Specimens in the Hancock Museum used by Watson (1926) in his description were given a reference number preceded by the initials DMSW but are also registered in the Museum's collections.

From the Low Main Seam, Newsham, Northumberland, England. L. Similis-pulchra zone, Middle Coal Measures (Westphalian B) (Panchen & Walker 1961).

H.M.: G13.71 (DMSW 27). Nearly complete skull with both jaw rami and rib fragments; figured by Atthey (1876, plate VIII, fig. 1; plate IX; plate X, figs. 1, 2) as *Anthracosaurus russelli*, by Watson (1926, fig. 20) as *E. attheyi* type specimen; lectotype (Romer 1963).

H.M.: G 13.72 (DMSW 28). Over 12 vertebrae, 6 ribs, scutes, femur; figured in part by Atthey (1876, plate X, fig. 3) as *A. russelli*, in part by Panchen (1966, fig. 6*a*) as *E. attheyi* holotype. Associated with the lectotype skull.

H.M.: G 13.74 (DMSW 30). An isolated braincase, no attached data but presumably from Newsham; figured by Watson (1926, fig. 18).

H.M.: G 13.75 (DMSW 31). Part of a snout; as *A. russelli*, Hancock & Atthey (1869*a*), *Eogyrinus*, Watson (1926).

H.M.: G 13.76 (DMSW 32). A slab with caudal centra and ribs, scutes, etc.

H.M.: G 13.78 (DMSW 35). An isolated skull table, figured Atthey (1877, plate XIII, fig. 1) as *Pteroplax*, Watson (1926, fig. 19) as *Eogyrinus*.

H.M.: G 13.79 (DMSW 36). Right jaw articulation (articular and quadrate regions).

H.M.: G 13.80 (DMSW 37). Articular end of left jaw, probably the specimen referred to *A. russelli* by Hancock & Atthey (1871).

H.M.: G 15.81 (?*Eogyrinus*). An interclavicle, referred to *A. russelli*, Hancock & Atthey (1869*a*).

H.M.: G 15.82. Counterpart (natural mould) of the previous specimen.

H.M.: G 15.83. An isolated palatine with tusk pair.

H.M.: G 15.84. Dorsal vertebra, ?rib and scutes, probably Newsham.

H.M.: G 15.88. An isolated left quadrate and jaw fragment, no data but almost certainly Newsham.

H.M.: G 25.51–60. Scutes.

B.M.(N.H.): R 8426. An isolated skull table formerly in the Leeds Museum; referred to *Pteroplax*, Atthey (1876), *Eogyrinus*, Watson (1926).

In addition to these specimens a number of specimens of ribs and vertebrae from Newsham are listed in the account of the axial skeleton (Panchen 1966) and used here in the reconstruction.

From Airdrie, Lanarkshire, Scotland. No data on horizon, from the nature of the matrix probably Palace Craig Ironstone, L. Similis-pulchra zone, but could be Airdrie Blackband Ironstone, U. Modiolaris zone; both are Middle Coal Measures, Westphalian B.

G.S.: 28318 (Charlesworth Coll.). Preorbital region of skull with anterior right jaw ramus, referred to *Pholiderpeton scutigerum* Huxley by Watson (1929, fig. 2).

M.M.: L 11614 (Ormerod Davies Coll.). Anterior left jaw ramus of G.S. 28318 (Watson 1929).

From Virtuewell Coal shale, Newarthill, Lanarkshire, Scotland. U. Modiolaris zone, Middle Coal Measures, Westphalian B.

R.S.M.: 1897/112/23–24. An incomplete skull lacking the snout region, but including a part of the braincase and right basal articulation.

From Splint Coal, Wishaw, Lanarkshire, Scotland. L. Similis-pulchra zone, Middle Coal Measures, Westphalian B.

R.S.M.: 1957.1.5806. A caudal vertebra.

The account of the skull roofs and lower jaw is based principally on the lectotype. This was developed by Atthey to the greatest possible degree obtainable by the use of mounted needles. Further treatment to remove the remaining thin layer of black shale from the bone surface was therefore only possible with recent techniques. This final development was largely accomplished using an S.S. White Industrial Airbrasive Unit with calcium dolomite as the abrasive powder

(Stucker 1961). Dental mallet and Airbrasive development was also used on the Newarthill specimen and for the final cleaning on several of the Newsham specimens.

In reconstructing the skull roof a simple three-dimensional model was made by bending a sheet of dental wax traced with a drawing of the flattened lectotype skull into shape. Photographs of this model were used as a guide in the final drawings.

The skull

Dermal skull roof

The skull roof of the lectotype is virtually complete (figure 2, plate 24) and it probably represents the most fully preserved as well as the largest anthracosaur known. Its principal dimensions have been set out in table 1. Like all coal shale specimens it is considerably flattened: the skull roof has thus been depressed into a single horizontal plane while the two jaw rami are separated and flattened from side to side. The left maxillary bone has been displaced from the skull roof but is preserved, almost complete, in the same block with its anterior end overlying the articular region of the left jaw and the remainder visible on the ventral surface of the specimen.

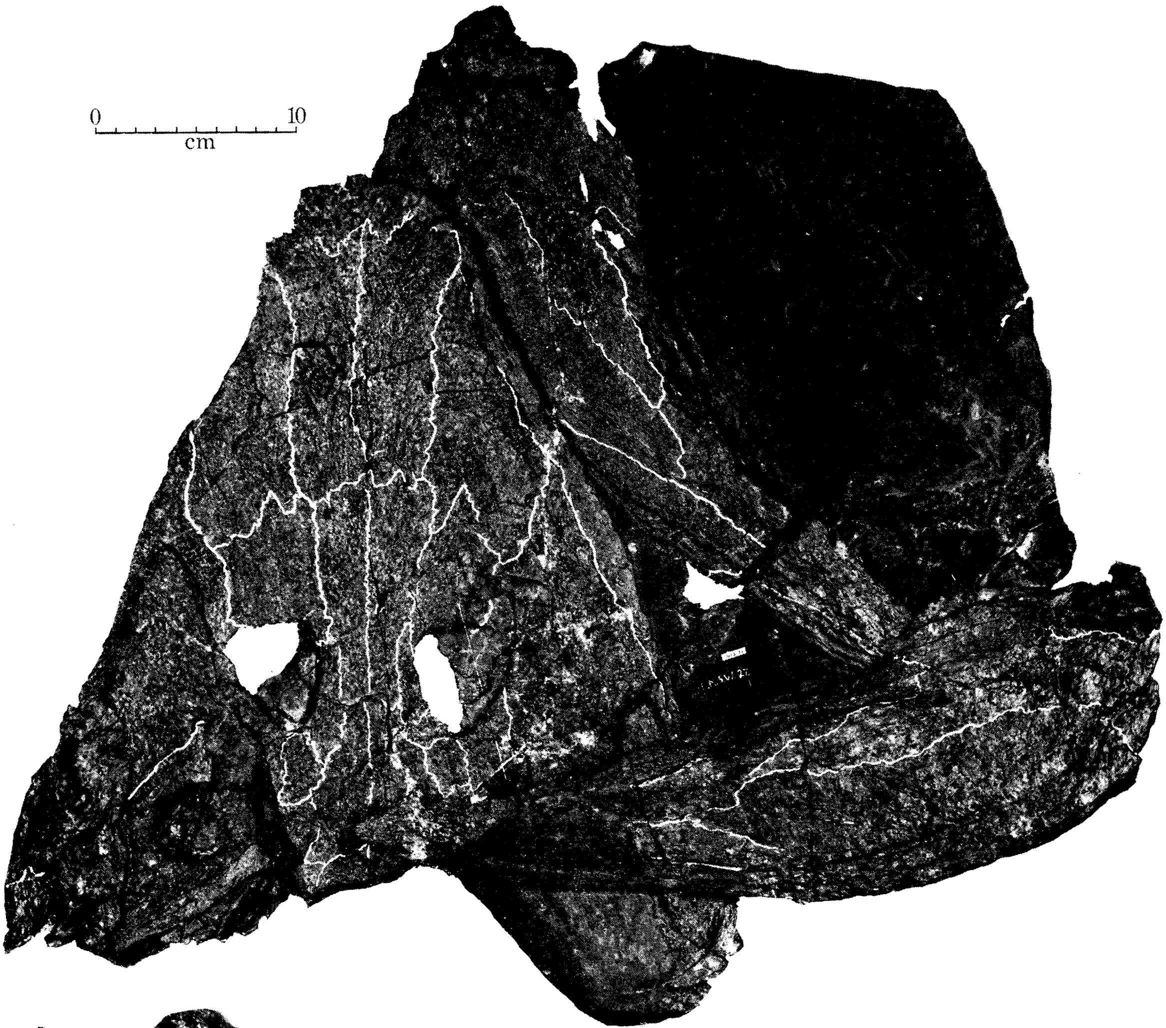
Only a few areas of the skull roof are missing or obscured. The left quadrate region is lacking and part of the cheek, including the squamosal–quadratojugal junction, is obscured by the displaced left ectopterygoid. Unfortunately most of the right squamosal is also missing or covered by the front of the left jaw ramus. A small section of this ramus and most of the squamosal region under it have been restored in a sand-based mastic at some time for display purposes. Thus the squamosal–quadratojugal suture cannot be seen on either side. However, most of the quadratojugal–quadrate suture is preserved on the right and is further described in describing the quadrate (Palate, see below).

The extreme back of the skull table and occiput are missing in the lectotype, but the two isolated Newsham skull tables both show the complete postparietal and tabular, except for the end of the tabular horn, and include the occipital exposure of those bones. In the Hancock Museum specimen they are preserved on both sides; in the British Museum specimen, on the right only. Both specimens show the undersurface of the skull table well: the former was accurately figured by Atthey (1877) and Watson (1926). Both specimens are strikingly similar to the skull table of *Palaeoherpeton* in ventral view (Panchen 1964, fig. 3) and show the same surfaces of attachment for the braincase and lateral articular surfaces for the squamosal.

The skull from Airdrie ('*Pholiderpeton*': Watson 1929) gives a particularly good lateral view of the right maxillary and corresponding lower jaw with their dentition (figure 3).

As flattened, the lectotype skull forms an isosceles triangle with remarkably straight sides: restored in the round it is very reminiscent of that of a crocodile (figure 4). The fronts of the orbits are at about two-thirds of the postparietal length of the skull from the snout. The orbits themselves were somewhat heart-shaped and the plane of their openings probably lay at about forty-five degrees to the vertical so that they 'looked' dorso-laterally. The snout was relatively narrow but truncate and the external nares nearly terminal.

The form of the nares is clear from the type and the Airdrie skull. Each nasal bone has a highly ornamented and indented antero-lateral edge which forms the upper border of the naris. Below this border lies the premaxillary-maxillary suture so that the lower border is formed in part by the premaxillary and in part by the maxillary. The outline of the snout in



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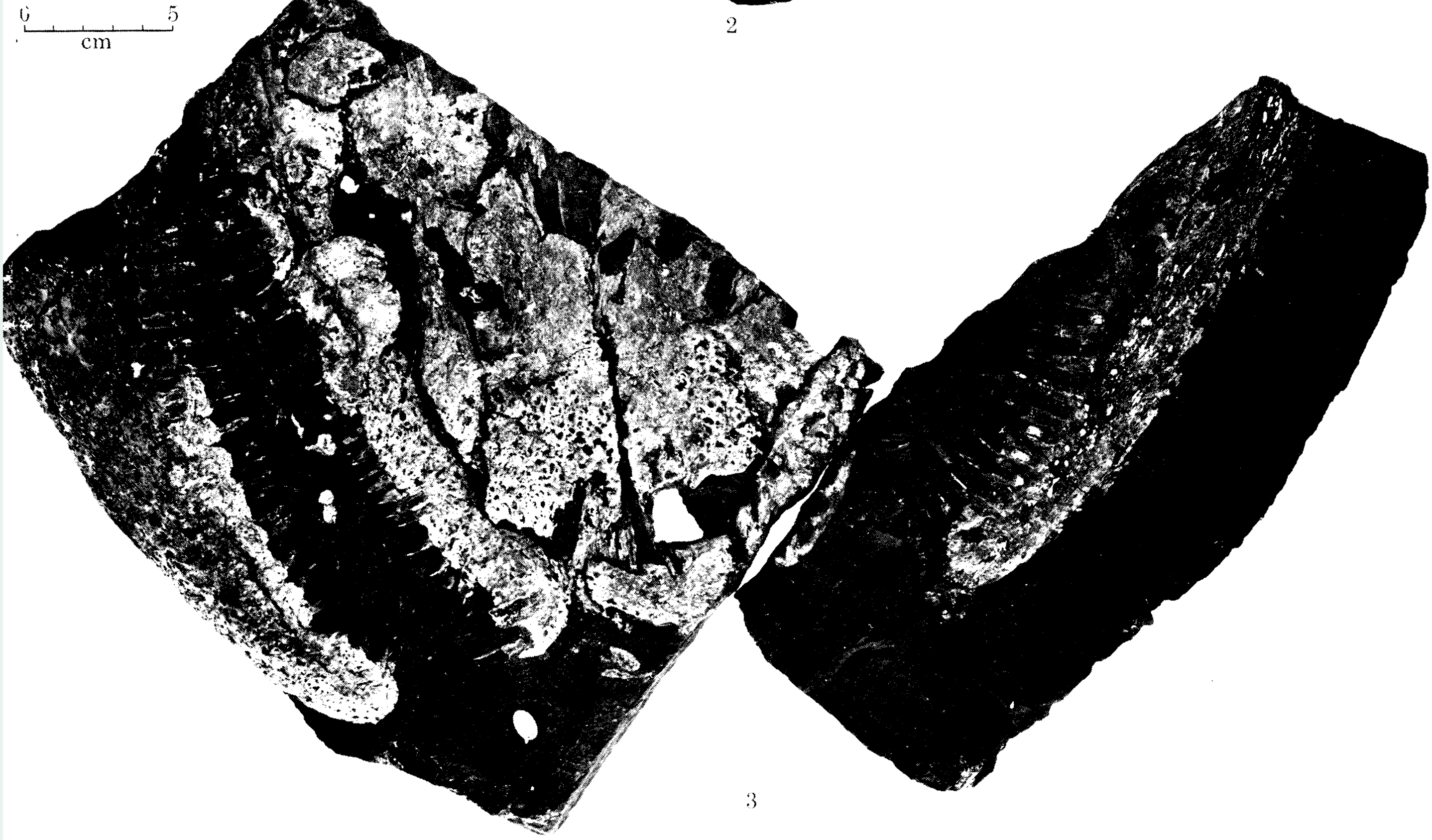

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FIGURE 2. *Eogyrinus attheyi* Watson, skull of lectotype in dorsal view.

FIGURE 3. *E. attheyi* Watson, the Airdrie skull in dorsal view.

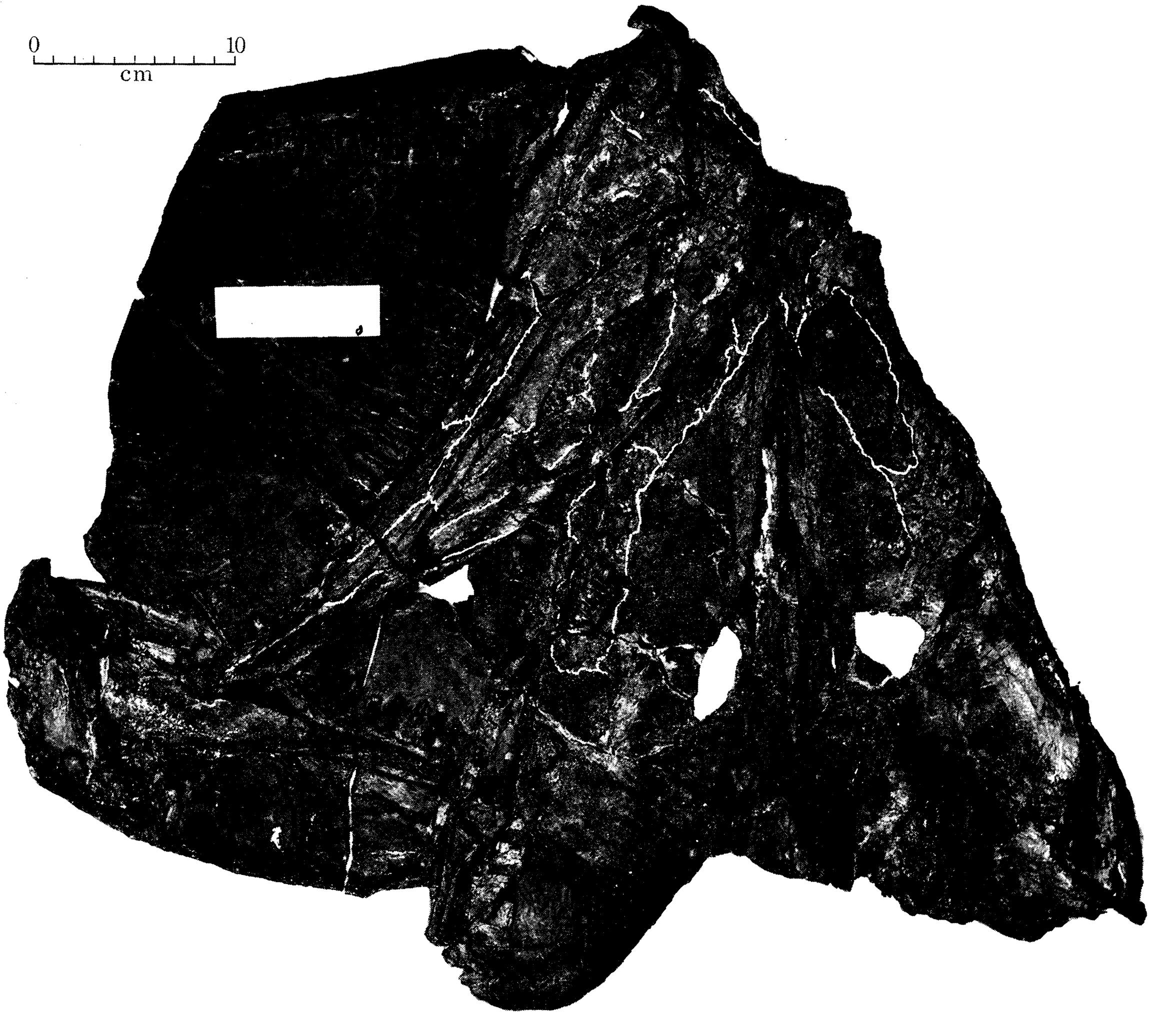

Figure 5. *E. attheyi* Watson, skull of lectotype in ventral view.

dorsal view is strongly constricted at this suture so that a naso-labial groove (Panchen 1967*b*) runs from the naris down to the jaw margin.

Thus the nostrils of *Eogyrinus* are large, antero-laterally directed and 'flared' in a manner reminiscent of a thoroughbred stallion. There is no sign in either specimen of a septomaxillary bone, nor is one described in any anthracosaur.

In restoring the snout of *Palaeoherpeton* from the natural mould of the type specimen I reconstructed an anterior tectal bone overlying the external naris (Panchen 1964). The anterior tectal is certainly absent in *Eogyrinus* and in *Anthracosaurus* (Panchen 1967*b*, 1970), and study of the better preserved material of these two genera makes it necessary to admit that I was wrong in my interpretation of *Palaeoherpeton*. As far as can be judged the nares of *Palaeoherpeton* and their surrounding ossifications are essentially the same as those of *Eogyrinus*.

The pattern of dermal bones of the skull roof will be clear from the restoration and is that which is probably characteristic of all anthracosaurs (Panchen 1970). There is a full complement of the bones found in primitive tetrapods without any additional ossifications. Notably extra unpaired median ossifications are lacking. Nearly all the sutures can be traced easily from the lectotype and, with information from other specimens, only the course of the quadratojugal–squamosal suture is uncertain. It should be particularly noted that a large rectangular prefrontal bone forms almost the whole anterior edge of the orbit and has a long lateral suture with the jugal, thus excluding the lacrimal from the orbit.

This corresponds to the condition restored in *Palaeoherpeton* (Panchen 1964). It appears to be an anthracosaur feature not found in related batrachosaurs. Thus in *Gephyrostegus* (Carroll 1970), *Discosauriscus* (Špinar 1952), *Seymouria* (White 1939), *Kotlassia* (Bystrow 1944) and other seymouriamorphs the lacrimal extends into the orbital border.

The lacrimal bone is also excluded from the border of the external naris in *Eogyrinus* by a short nasal–maxillary contact, but this is not the case in the holotype of *Anthracosaurus russelli* (Panchen 1970) and is probably a variable character.

As in all anthracosaurs there is a large intertemporal bone flanking the skull table on either side immediately behind the orbits. In the lectotype both intertemporals have a point contact with the orbital border, but it is likely that this is a variable character as is the lacrimal–naris relationship.

One of the most characteristic features of the anthracosaur skull is the kinetic skull table, which is characterized by a mobile articulation on each side between the supratemporal and the cheek region, represented by the squamosal (Watson 1926; Panchen 1964, 1970). In the lectotype the nature of the articulation cannot be seen. It is obscured on the left by a wide matrix-filled crack and on the right by the jaw ramus. However, both isolated skull tables show the hemi-cylindrical articular surface under the supratemporal, as was noted by Watson, and the nature of the contact has been described in *Palaeoherpeton* and *Pholiderpeton* ('*Eogyrinus*') (Panchen 1964).

There was certainly some mobility between the supratemporal and squamosal, therefore the nature of the junction between the intertemporal and postorbital is of some interest as it is a direct continuation forward of the articulation. The junction is seen on both sides of the lectotype as a rather wavy suture which would suggest immobility. However, the suture also shows an overlap of the intertemporal on the postorbital in that there is a drop in the bone level across the sutural line. Also in DMSW 35 the sutural surface of intertemporal is preserved on both sides and takes the form of a concave cylindrical surface. Thus there may have been limited mobility between the intertemporal and postorbital continuing the mobile supratemporal-squamosal junction forward.

The pineal foramen in the lectotype is a small hole, some 2 mm in diameter, on a flat surface. However, in DMSW 35 it appears as a large oval foramen with a minimum diameter of 5 mm and it is similar but disrupted in the other isolated skull table. There seems little doubt that the difference is due to erosion in the latter two specimens as the foramen opens into a hemispherical depression seen from below and the bone is therefore thin around its border. Thus differences in the form of the foramen are unreliable as taxonomic characters.

In 1964 I suggested that the oval foramen on a median ridge, seen in the type of *Pteroplax cornutus*, should be contrasted with the small round foramen on a flat surface in *Palaeoherpeton* and *Eogyrinus* as a taxonomic feature, but this is obviously suspect.

The form of the tabular horn was used by Watson (1929) as a taxonomic character to separate *Eogyrinus* from *Pteroplax*. It is not preserved in the lectotype of *Eogyrinus* but is present on the left of DMSW 35 as a slender fingerlike process in contrast to the ovoid blade present in *Palaeoherpeton* and *Pteroplax*. I have already noted, however (Panchen 1964), that the difference appears to be due to erosion in the *Eogyrinus* specimen. This is confirmed by the other skull table and the Newarthill skull, both of which have the right horn partly preserved. In both cases, although broken, it appears to be of the *Palaeoherpeton–Pteroplax* type.

The form of the otic notch in *Eogyrinus* is very similar to that in *Palaeoherpeton*. The ventro-lateral border of the notch is formed from the squamosal: the occipital exposure of that bone held the tympanum as described in *Palaeoherpeton*. The otic notch region of the pterygoid is well preserved on the left of the lectotype of *Eogyrinus*, where roofing and occipital squamosal are separated by a sharp ridge which forms the border of the notch.

The dermal ornament of the anthracosaurs is distinctive but very difficult to characterize in words. It has already been noted (Panchen 1964) that it is less regular than in the contemporary loxommatids. In the latter, e.g. *Megalocephalus* from Newsham, the whole skull is ornamented with rounded pits of usually subcircular outline separated by a web of ridges. The pattern is an almost ideal illustration of labyrinthodont ornament as illustrated by Bystrow (1935, 1938*a*).

The nearest approach to this ornament on the skull of *Eogyrinus* occurs on the postfrontal, intertemporal and supratemporal bones. It is well preserved on the latter two bones in the lectotype and the British Museum skull table and on the postfrontal on both sides of the lectotype. Even on these bones, however, while there is a similar system of pits to those of the loxommatids, the ridges vary irregularly in height and in many places fade out altogether. On the rest of the skull roof the pattern is even more irregular.

Comparison of the eogyrinid specimens available to me suggests, however, that there is a fairly standard distribution of different types of ornament on the various bones of the skull roof. The specimens include both known skulls of *Palaeoherpeton*, the Swanwick skull of *Pholiderpeton* and the lectotype of *Pteroplax*, in addition to the various *Eogyrinus* skulls. A similar range of types of ornament is also shown by Romer (1963, fig. 1) on the skull of *Neopteroplax*. It is perhaps therefore worth attempting to describe this ornament distribution and some attempt has been made to illustrate it in the reconstructed figures.

Of the paired midline bones the postparietals of *Eogyrinus* have an irregular pit-and-ridge system in which the pits tend to be transversely expanded and the transverse components of the ridge system somewhat more prominent. On the flanking tabulars a similar ornament is directed in the plane of the tabular horn. The parietals have, behind the pineal foramen, more rounded pits, but the ridges have their posterior edges more strongly defined than their anterior ones when transversely orientated and the longitudinal part of the ridge system is weaker. Thus the whole is reminiscent of a ripple-marked beach. In front of the pineal the British Museum skull table shows a series of diverging granular ridges which are indicated in the reconstruction. The lectotype is somewhat worn in this region.

The frontals are well preserved in the lectotype and show a change to another type of ornament, more strongly developed on the nasals, in which the general contour of the bone has a series of slightly divergent rounded ridges and furrows like a newly ploughed field and the pits become a less marked feature as one moves forward. At the front of the nasal bones, however, there is a sharp change already noted. Here there is a close and irregular ornament of pits and ridges in high relief and this type of ornament extends laterally to the extreme anterior end of the lacrimals. The ornament of the premaxillaries, except where they form the floor of the external nares, is also extremely complex and irregular, giving a ragged profile to the front of the snout.

The ornament on the bones lateral to the orbit is generally much less strongly defined. The prefrontals on both sides of the lectotype show a sharp change at about the level of the middle of the orbit from an irregular but well-defined ornament mesially to an ill-defined ornament laterally. A more uniform change takes place over the short extent of the postorbital. Jugal and squamosal show a low relief diffuse ornament, which is particularly ill defined on the squamosal. This may in part be due to poor preservation of the surface but is paralleled by *Pholiderpeton*, *Palaeoherpeton* and *Neopteroplax*.

The quadratojugal, seen in the latter two, has a more strongly defined ornament and in *Eogyrinus* the bone has scattered but strongly defined small pits. Finally the maxillary has an irregular ridge and furrow ornament with marked pitting anteriorly where it adjoins the nasal.

The degree of ornamentation of the bone is presumably inversely correlated with the thickness of dermis and epidermis that lay over it in life, strong ornament indicating a thin cover, weak ornament a thicker one. The same principle applies to the imprint of the lateral line system on the skull roof which is much less well defined in *Eogyrinus* than in the smaller *Palaeoherpeton* and, where preserved, *Pteroplax*.

As in *Palaeoherpeton* the most posterior trace of the supraorbital sulcus appears as an exaggeration of the dermal ornament. In *Palaeoherpeton* the sulcus can be traced right back along the postfrontals and beyond the junction with the infraorbital sulcus on the right intertemporal. In *Eogyrinus*, however, the supraorbital sulci cannot be traced with certainty behind the front of the orbits where they probably crossed from the frontals to the postfrontals. On the frontals they pass forward as broad furrows irregularly broken into long shallow pits following exactly the course seen in *Palaeoherpeton*.

For most of their course along the lateral edges of the nasals the sulci of *Eogyrinus* retain the same appearance as they do on the frontals. Anteriorly, however, when they reach the heavily ornamented part of the nasals, they become less obvious. At the corresponding point in the skull of *Palaeoherpeton* the supraorbital sulcus on each side expands into a broad deep groove and is deflected laterally across the tip of the lacrimal (including that part misinterpreted as the anterior tectal – Panchen 1964, figs. 10, 11) and back on to the nasal to form with its fellow the characteristic labyrinthodont 'lyrae'. In *Eogyrinus* the grooves at this point are much less clear but appear to follow a similar course, so that the anterior centimetre of the nasal–lacrimal suture lies laterally in the groove. The latter then turns back on to the nasal and terminates at the border of the naris.

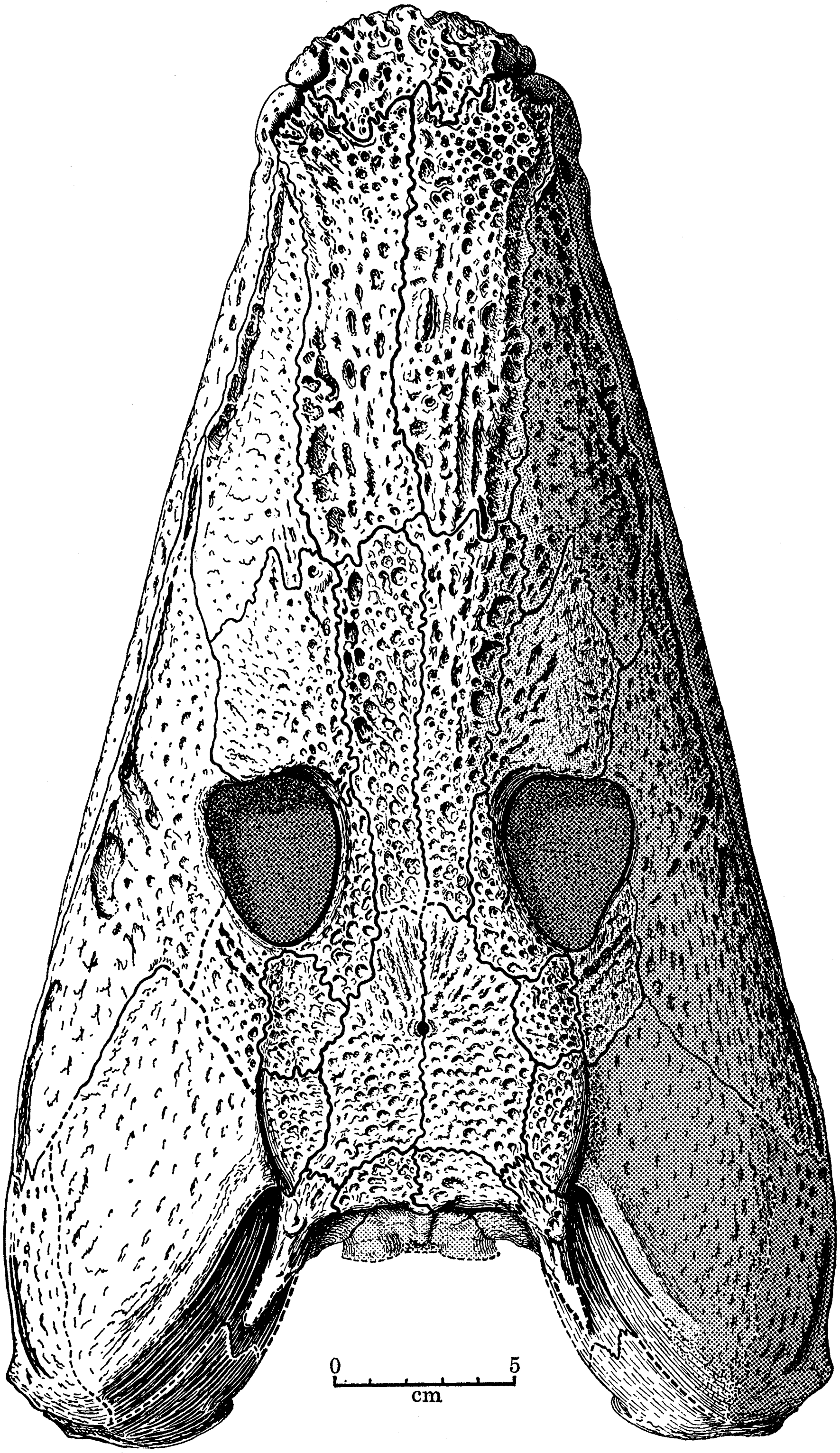

FIGURE 4. *Eogyrinus attheyi* Watson, composite restoration of the skull, dorsal view. Half natural size.

Most of the course of the infraorbital sulcus can be traced. It can be seen crossing the right postorbital in the lectotype as in *Palaeoherpeton*, but its course from the lateral edge of the postorbital across the jugal to the lateral edge of that bone is less clear. The right jugal is disrupted in that region: the left is well preserved, but the sulcus can only be seen as a wide shallow groove across the distal half of the bone. Once the jugal border is reached the infraorbital sulcus can be seen clearly on both sides running forward through the jugal and the lacrimal just mesial to their suture with the maxillary.

At the extreme anterior end of the lacrimal, the groove again becomes less well defined but it passes so close to the supraorbital sulcus that an anastomosis between the two might have been present. Just below the tip of the lacrimal, in the maxillary, there is a large pit on the right of the holotype which may mark the end of the infraorbital sulcus. However, the displaced left maxilla is not well enough preserved to show this and the right maxillary of the Airdrie skull shows no such pit, so it may be due to post-mortem damage. The rest of the surface of the Airdrie skull is not well enough preserved to show lateral-line grooves.

Other parts of the system are visible on the lectotype of *Eogyrinus*. The anterior end of the jugal sulcus may be seen on the left as it extends posteriorly from the angle of the infraorbital sulcus. However, after about 2.5 cm it is obscured by the displaced ectopterygoid. It is much less distinct on the right. The sulcus is not seen again on the left until it reappears rather obscurely following its normal course parallel to the posterior edge of the squamosal.

Another groove is very prominent running along the lateral margin of the jugal and just crossing the jugal–quadratojugal suture. Anteriorly it is first seen on the right some 6 cm behind the angle of the infraorbital sulcus. It may be seen crossing the suture on the left. Much further back on the right, behind the overlying jaw ramus, a groove runs parallel to the edge of the quadratojugal to terminate posteriorly above the quadrate. It is probably a continuation of the more anterior groove but the connecting region is missing on both sides.

The whole groove presumably corresponds to the pits and groove found below the jugal sulcus on the cheek of *Palaeoherpeton* but its orientation is different. In *Palaeoherpeton* the groove runs ventro-posteriorly from the squamosal to the quadratojugal and 'runs off' the quadratojugal ventrally.

It is not possible to tell, because of the nature of the ornament, whether either supraorbital sulcus or infraorbital sulcus extended on to the premaxillary. The primitive condition, represented by the rhipidistian forerunners of tetrapods, is for the infraorbital canal to pass forward below the nostril, usually through the lateral rostral bone and to anastomose with the supraorbital canal on each side in the premaxillary. A transverse commissure then connects the two anastomoses across the snout (e.g. Panchen 1967*b*). This arrangement is clearly developed in *Ichthyostega* (Jarvik 1952) and a well-developed commissure is present across the snout of *Megalocephalus*, the loxommatid contemporary of *Eogyrinus* (Watson 1926).

Palate

Most of the data used in the restoration of the palate of *Eogyrinus* are derived from the lectotype. In that specimen the palatal surface is almost completely preserved back to the level of the front of the orbits, although, as noted, the left ectopterygoid has been displaced on to the dorsal surface of the specimen. Also parts of the right vomer and palatine, together with the anterior right maxillary, are obscured in palatal view by the overlying right jaw ramus (figure 5, plate 25).

Behind the level of the front of the orbits, both pterygoids are preserved mesially to a point well behind the basal articulation; also those parts of the epipterygoid which form the palato-quadrate contribution to that articulation can be clearly seen on both sides. Preservation of the right pterygoid extends back laterally to a point midway along the border of the subtemporal fossa and, while the left pterygoid is largely missing posteriorly, an isolated piece includes a more posterior part of that border.

Part of the right quadrate is preserved in the lectotype: the rest is represented by the isolated quadrate specimen from the Hancock Museum.

The basal articulation is disarticulated on both sides in the lectotype, but can be seen in articulation on the right in the Newarthill skull.

Thus the whole palatal surface can be restored in some detail without fear of serious error.

The palate of *Eogyrinus* (figure 7, p. 297) is typically that of an embolomerous anthracosaur (Panchen 1970). It has narrow toothless vomers, palatines with a single tusk pair on each side and ectopterygoids each bearing a tusk pair and accessory teeth. The whole dentition is discussed in detail below.

The palate is that of a primitive labyrinthodont in that the palatines suture with the vomers, the interpterygoid vacuities are very small, the basal articulation mobile and the quadrate ramus of the pterygoid long (Watson 1926).

The vomers form the mesial borders of the choanae and suture with the pterygoids and palatines posteriorly. Anteriorly they butt against the posterior edge of the premaxillaries, but on the left there is a small piece of bone flanking the vomer anteriorly which appears to be a palatal process of the premaxillary. The choanal border of the vomer is well preserved on the left and the sutures with the other palatal bones easily traced, but the midline suture between the vomers cannot be made out. Posteriorly its presumed course is covered by a displaced palatal tusk.

In describing the Airdrie skull as *Pholiderpeton*, Watson (1929) described the dorsal surface of the vomer and claimed evidence of the presence of Jacobson's organ. Dorsally the right vomer is as he described it, being divided into two broad longitudinal channels separated by a ridge. The inner channel of the two appears to be roofed by bone posteriorly, so that the structure could be interpreted as a backwardly directed tunnel. The left vomer is not sufficiently preserved for corroboration, nor is it possible to decide whether the roofing derives from the vomer or the nasal.

On the ventral surface Watson describes a pair of openings, one on each vomer, as openings of the vomerine tunnels and interpreted these as for Jacobson's organ. However, the ventral surface of the vomers in the Airdrie specimen are very poorly preserved, apparently having been damaged in clearing parts of the palate of the very intractable ironstone, and the openings are difficult to make out with certainty. Nothing corresponding to them can be seen on the well-preserved lectotype vomers.

The ventral surfaces of the latter are irregularly grooved and in the left vomer there are three nerve or nutrient foramina situated in a line. Several irregular tiny foramina are present on the right.

As the left maxillary is displaced the roof of the nasal cavity, formed by the nasal bone, is exposed between the choana and the margin of the external naris. In ventral view the roof is strikingly smooth. There is a small rounded diverticulum, bounded postero-mesially by the palatine which was presumably floored by the maxillary in the intact skull.

The left palatine is dominated by the large tusk and its replacing pit. There is a large oval foramen formed by the edge of the palatine lateral to the tusk just behind the nasal diverticulum. Behind the tusk and its pit ('tusk pair') the surface of the palatine has a strong irregular ornament rather like that on the dorsal surface of the premaxillaries. The bounding sutures of the left palatine and, as far as exposed, the right were easily traced.

Lateral to the left palatine the ventro-lateral sutural surface for the maxillary is seen on the lacrimal. The surface is strongly but irregularly roughened with scattered foramina and contrasts with the corresponding surface behind it on the jugal. Here the anterior part of the maxillary sutural surface is marked by a series of longitudinal ridges while more posteriorly the maxillary fitted into a smooth groove in the jugal.

Both ectopterygoids are complete and their ventral surfaces fully exposed. The bounding sutures are easily traceable on the right while the displaced left ectopterygoid has left an anterior fragment sutured to the palatine but is otherwise intact to its edges.

It has already been pointed out (Panchen 1970) that the second tusk pair on each side is situated on the ectopterygoid and thus that my tracing of the palatine-ectopterygoid suture behind the tusk pair in the Swanwick *Pholiderpeton* skull ('*Eogyrinus*' – Panchen 1964) is incorrect. My original restoration of the palate of *Palaeoherpeton* with that arrangement has therefore been corrected (Panchen 1970).

As I interpret them from the lectotype the ectopterygoids form a very asymmetrical pair. Their anterior bounding sutures are, allowing for distortion, roughly at the same antero-posterior level; but while the centre of the right tusk is some 2 cm from the suture that of the left must have been about 3 cm. As the left ectopterygoid is displaced there is an element of uncertainty but 3 cm represents a minimum figure.

In addition to the tusk pair each ectopterygoid bears a row of accessory teeth and as if in compensation for the asymmetry there are seven on the right and six (including one empty socket) on the left. As on the palatine the ornament on the surface of the ectopterygoid is strongly incised and not dissimilar to that on the premaxillaries. The left ectopterygoid also shows the mesial sutural surface for the pterygoid. The latter overlaps the former in ventral view and the width of this sutural overlap surface as preserved increases posteriorly to over a centimetre. The nature of the sutural surface does not suggest that there was any mobility between ectopterygoid and pterygoid.

Posteriorly, as in *Pholiderpeton*, the ectopterygoid was separated from the subtemporal fossa by a massive processus alaris of the jugal. The process is almost complete on the right of the lectotype and its basal part is preserved on the left. The form of the process is a narrow elliptical cone projecting ventro-mesially from the jugal and meeting the pterygoid to form the anterior rim of the fossa.

The large pterygoids form most of the palatal area. As in other primitive labyrinthodonts and rhipidistians the major part of the palatal surface of the pterygoids is covered with a shagreen of fine denticles, each one of which is a minute tooth with a pulp cavity. However, this is not the case with that part of the anterior pterygoid which sutures with the palatines and vomers, and the palatine-ectopterygoid suture is at the approximate level of the front of the denticle-covered area on the left, while that area extends a little further forward on the right.

In this anterior region the pterygoids were sutured together, but in the lectotype compression has opened this suture up to reveal deep sutural surfaces bearing longitudinal ridges. In the region of the suture each pterygoid projects ventrally as a sharp mesial ridge. The ridge from each bone may either have diverged from the other as two blades (as restored) or formed a common median ridge. The sutural surfaces extend posteriorly only as far as the back of the palatine tusk pair dorsally and less far at palatal level. Posteriorly they are transformed into smooth surfaces at a point roughly corresponding to the preserved anterior end of the parasphenoid. Thus the parasphenoid and the braincase above it were apparently clasped by upturned vertical edges of the pterygoids. These smooth mesial edges of the pterygoids continue to be visible from below to about the level of the last ectopterygoid tooth and were probably in contact with the braincase throughout. It is only at the level of the back of the ectopterygoids that the pterygoids begin to diverge to produce small interpterygoid vacuities and to allow room for the basal articulation.

Somewhere at about this level the plane of the pterygoids, almost horizontal anteriorly, started to turn into the vertical plane to form deep mesially facing quadrate rami. There is no doubt that, as in *Palaeoherpeton*, the ventral edge of the quadrate ramus must have plunged well below the level of the margin of the skull roof along the border of the subtemporal fossa. This is shown on the right of the flattened lectotype skull, where unless this were the case, the fossa would have to be restored as impossibly narrow. There is along the border of the fossa an area of pterygoid surface where the denticles give way to a shallow but sharply defined pit-and-ridge ornament which may have acted as origin for a slip of the adductor mandibulae musculature. A similar area is much less conspicuously developed in *Palaeoherpeton*.

Apart from the fragment noted the posterior part of the quadrate ramus is missing in the lectotype: it has been restored as in *Palaeoherpeton* with a dorsal area of the mesial surface lacking denticles.

A more dorsal part of the quadrate ramus would appear in dorsal view contacting the occipital squamosal dorso-laterally and the quadrate posteriorly. Part of the dorsal region is preserved on the left in the lectotype but is disrupted and shows no remarkable features. The contact with the quadrate is discussed below.

In early tetrapods the only endochondral ossifications of the palatoquadrate are the epipterygoid and quadrate. Both are represented in the material of *Eogyrinus*.

That part of the epipterygoid which contributes to the basal articulation is well preserved and visible from below on both sides of the lectotype (figure 8, p. 299). It strikingly resembles that seen in the separated pterygoid–epipterygoid of the *Palaeoherpeton* type. As in *Palaeoherpeton* the main articular surface ('conical recess') is born on the postero-mesially directed terminal surface of a massive horn-shaped process of the epipterygoid. Anteriorly this process can be seen running forward along the edge of the pterygoid as a palatal ramus of unknown extent. In *Palaeoherpeton* the articular surface was described as a large facet on the buttress combined with a double facet behind it. The condition in *Eogyrinus* shows that the whole is a large single saddle-shaped surface for articulation with the basipterygoid process of the basisphenoid.

In *Palaeoherpeton* an additional articular recess was described lying postero-ventral to the epipterygoid articulation and apparently formed in the pterygoid. This region is exposed in *Eogyrinus* and is clearly seen on the right. Instead of a conical cavity there is a slightly roughened area bordered postero-ventrally and antero-dorsally by parallel thick ridges.

Part of the anterior edge of the columella cranii can also be seen on the same side of the lectotype in the expected position. It is flattened into a horizontal plane and exposed to view between the conical recess and the braincase. Again the structure is similar to that in *Palaeoherpeton*. The columella is not sufficiently exposed to view to see the notches for nerve exits seen in *Palaeoherpeton*, but the boundary between the columella cranii and, posterior to it, the dorsal part of the quadrate ramus of the pterygoid can be clearly seen, just as in *Palaeoherpeton*. There is every reason to believe that the columella was continuous with an extensive quadrate ramus of the epipterygoid, applied to the hidden (dorso-lateral) surface of the pterygoid as in *Palaeoherpeton* and *Pholiderpeton* (Panchen 1964).

The dorsal part of the quadrate ramus of the pterygoid immediately behind the columella cranii is marked by a very deep 'excavatio tympanica' (Bystrow & Efremov 1940) situated just as in *Palaeoherpeton* but much more strongly defined.

The isolated quadrate specimen (H.M. G 15.88) was recognized because of the very accurate fit of its condyle with the glenoids of the articulars in the various lower jaw specimens. This is particularly striking in the case of DMSW 37. The condyle is obscured laterally by an impacted piece of bone, but the lateral end of the right condyle, together with the suture between the quadrate and quadratojugal, is preserved in the lectotype.

The quadrate condyle is slipper-shaped in ventral view and convex in parasagittal section throughout its width. The edges of the condylar surface are sharply defined, particularly mesially. The whole shape of the articular surface may be judged not only from the preserved quadrates but from the articular glenoids. The nature of the jaw articulation is considered with the description of the lower jaw.

Some information is preserved on the attachment of the quadrate to the surrounding ossifications. In the lectotype the quadratojugal-quadrate suture is preserved in part on the right and has been opened by compression. The suture, visible above the lateral end of the condyle, is parallel to the posterior margin of the condyle and leaves only a little of the lateral part of the quadrate visible in dorsal view. Mesially where it contacts the quadrate ramus of the pterygoid the quadrate has an extensive dorsal exposure, seen in the isolated specimen. Here wide, deep sutural interdigitations can be seen at 3 to 4 cm along the postero-dorsal surface from the rim of the condyle. These interdigitations of the quadrate stand above the bone in front of them, yet in ventral view the transition across the suture is quite smooth, suggesting that the bone in front of the quadrate is the epipterygoid and that at that point the pterygoid is missing. Just laterally there is a small area where a double layer of bone is present. Thus this specimen endorses the probability that there was an ossified quadrate ramus of the epipterygoid extending back to the quadrate as in *Palaeoherpeton*, *Pholiderpeton* (Panchen 1964), *Edops* (Romer & Witter 1942) and loxommatids (E. Beaumont, personal communication).

Ventrally part of the quadrate-epipterygoid suture can be traced in the same specimen but there seems to be some fusion between the two endochondral ossifications mesially. It should be noted that if the interpretation of the bone as epipterygoid is correct that bone would be exposed to view from below in the intact skull in the dorso-mesial roof of the subtemporal fossa.

The paraquadrate foramen (Bystrow & Efremov 1940) is very clearly seen ventrally on the left of the lectotype, but appears to have been closed by compression on the left. On both sides a conspicuous oval pit is situated just in front of the foramen. The paraquadrate foramen perforates the quadratojugal but there appears to be a second foramen or pit perforating the quadrate itself. This is seen as a pit ventrally just in front of the condyle on the right of the lectotype and a compressed slit rather more mesially situated may represent it in the isolated quadrate. It has been indicated in the reconstruction.

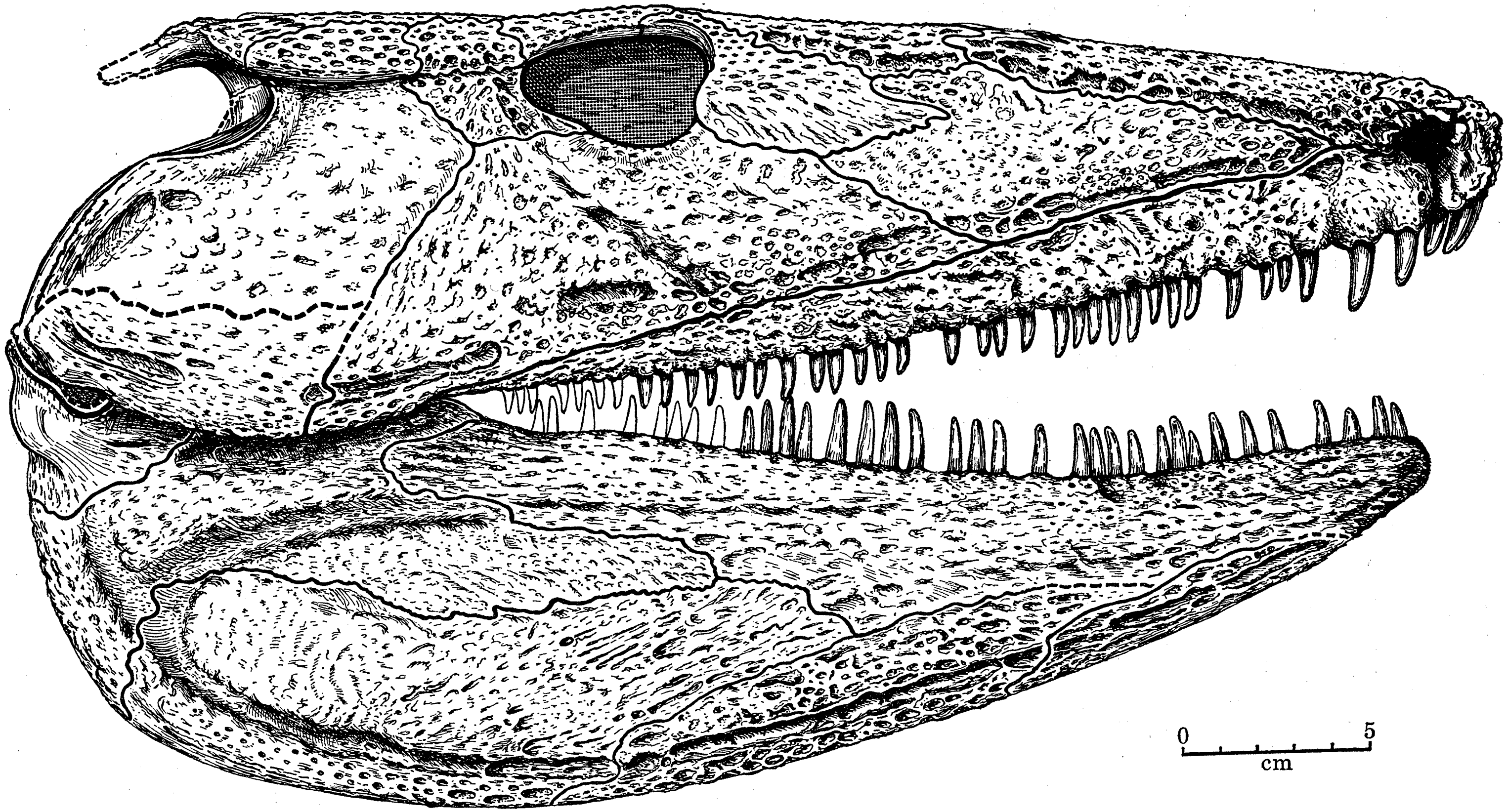

FIGURE 6. *Eogyrinus attheyi* Watson, composite restoration of the skull and jaws, lateral view, maxillary and dentary dentition from Airdrie skull except unshaded teeth. Half natural size.

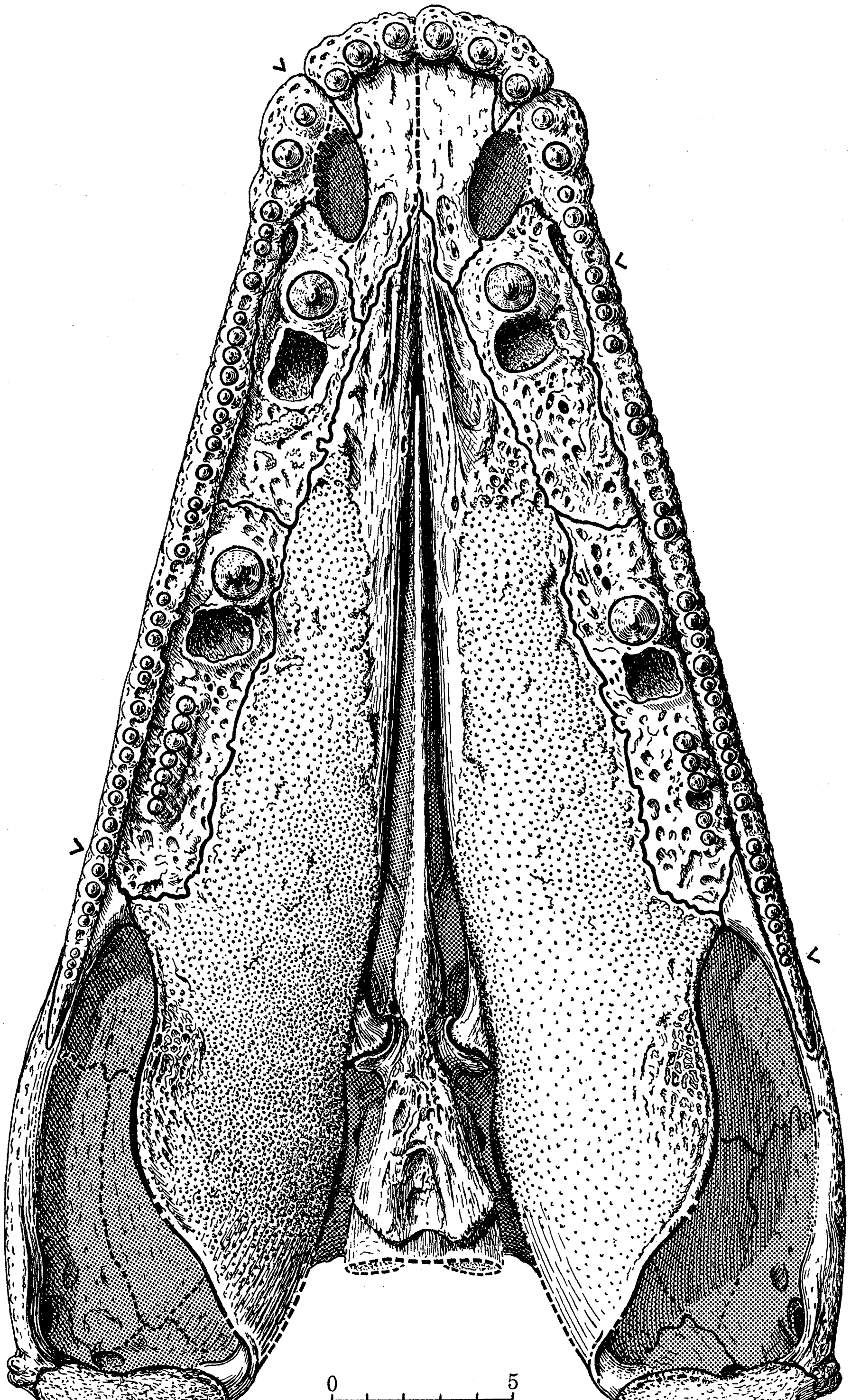

FIGURE 7. *Eogyrinus attheyi* Watson, composite restoration of the skull, palatal view; maxillary dentition between arrow heads on morphological left from lectotype, on right from Airdrie skull. Half natural size.

Braincase

The braincase of *Eogyrinus* is represented by that of the lectotype, preserved *in situ*, by the isolated 'DMSW 30' (Watson 1926) and by part of the left posterior region in the Newarthill skull. Nothing is visible of the braincase in the Airdrie skull. The braincase of the type, where accessible, has been completely cleared of matrix but is still rather difficult to decipher. The posterior region of the sphenethmoid has sheared horizontally so that the ventral part, and the whole anterior region, are displaced to the morphological right of the dorsal part.

Behind the basal articulation the region of the fenestra ovalis is obscured by eroded bone, particularly a rotted piece on the left which may represent the only known anthracosaur stapes. However, information in this region is available from DMSW 30 and the two specimens to some extent complement one another's deficiencies. The form of the basipterygoid process of the basisphenoid in ventral view is well shown in the Newarthill skull. All three specimens, however, lack the occipital condyle. The lectotype has been sheared off obliquely, as was noted in the description of the skull roof, so that only a small part of the lateral exposure of the basisphenoid is visible on the left, although the bone is visible in section on the sheared surface. In DMSW 30 it is completely missing, as is the exoccipital, and in the third specimen only a little of the left lateral exposure is visible.

Apart from the basioccipital and exoccipital and the dorsal part of the anterior sphenethmoid region a complete composite restoration of the external appearance is possible from the three specimens and in addition the inner wall of the left otic region is visible in DMSW 30. The latter, however, is from a somewhat smaller skull than the lectotype. The restorations of the braincase are based principally on DMSW 30 and thus represents a slightly smaller braincase than that shown in the restoration of the palatal view of the whole skull (figures 9 and 10, pp. 302 and 305).

The otic region of one side only is visible in DMSW 30, which is strongly compressed from side to side. Watson described the left surface of this otic wall as the inner one and the right as the outer. One of several deep pits in the right surface was described as a 'pseudo-fenestra ovalis' and an open fenestra as the vagus foramen. However, Romer (1947) pointed out that the latter was probably the true fenestra ovalis and I have suggested (Panchen 1964) that the 'pseudo-fenestra' housed the anterior vertical semicircular canal, while other pits mark the situation of other parts of the labyrinth. Thus it is certainly the wall of the left otic capsule which is preserved.

As Watson noted the braincase of *Eogyrinus* is essentially similar to that of '*Palaeogyrinus*' and all important differences are probably to be attributed to allometric size-related differences in proportion between the two and to a greater degree of ossification in *Eogyrinus*. As both basioccipital and exoccipital are virtually absent in all cases and there is no preserved occipital surface no attempt has been made to restore the skull in occipital view. It was, apart from differences in proportion, undoubtedly similar in this aspect to the skull of *Palaeoherpeton* (Panchen 1970). In the composite reconstruction of the braincase the basioccipital and exoccipital have been restored to give a condyle whose diameter corresponds to that of the vertebral centra. The condyle would thus have been relatively as well as absolutely larger than that of *Palaeoherpeton*, giving a rather different configuration of the occiput in which the foramen magnum must have been largely sunk within the condylar area.

The wall of the otic capsule is quite complex and is well preserved in the isolated braincase.

Its roof, which was closely applied to the underside of the skull roof, is very closely similar in lateral outline to that of *Palaeoherpeton* with a double tabular facet in which the two areas are separated by a deep indentation for the vena capitis lateralis. Behind the level of the fenestra ovalis the otic roof is extraordinarily thick as seen in section on the inner (right) surface of the specimen (figure 9*a*) but is less so anteriorly. The front of the otic roof is marked by a clear oblique suture, seen on both outer and inner surface with a thick semicircular piece of roofing bone, which is either the anterior part of the supraoccipital, the back of the sphenethmoid or a fragment of skull roof. The first explanation seems more probable. This 'supraoccipital' forms the antero-lateral corner of the roof of the otic mass.

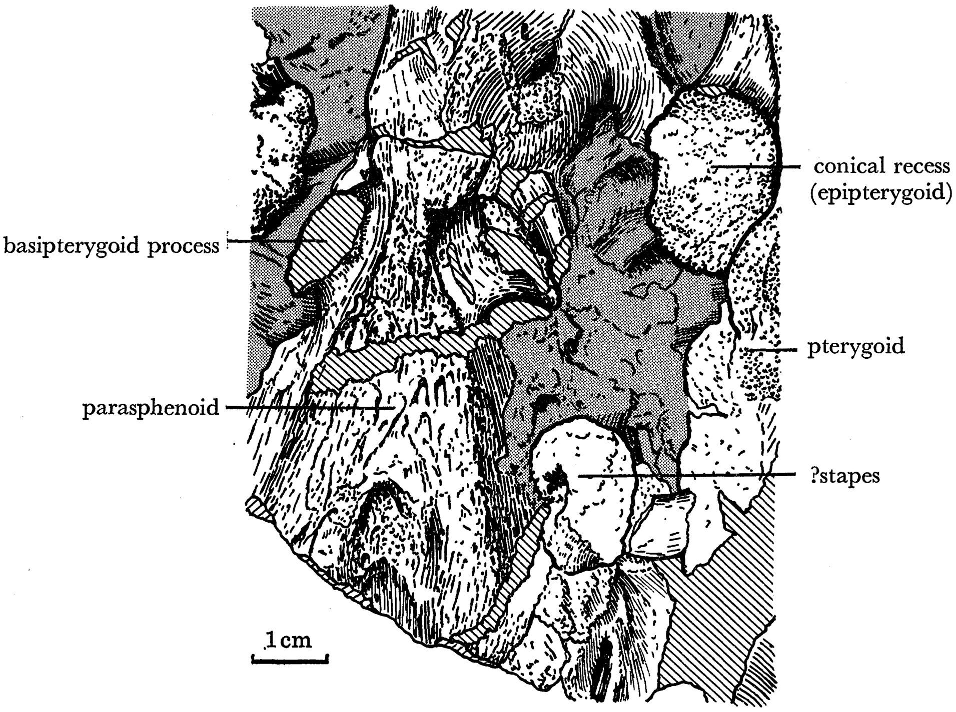

FIGURE 8. *Eogyrinus attheyi* Watson, lectotype; palatal view of the region of the basal articulation drawn slightly obliquely from right latero-ventral aspect. Natural size.

In describing the occiput of *Palaeoherpeton* (Panchen 1964), it was noted that the occipital tabular and the opisthotic had interlocking finger-like processes. The corresponding process of the opisthotic of *Eogyrinus* (which may be termed the digital process) is quite massive and is directed backwards horizontally below the otic roof and separated from the latter by a deep, sharply defined groove. Anteriorly this groove widens into a large triangular concave area whose anterior boundary is formed by the buttress which terminates dorsally in the anterior tabular facet. In front of the buttress the otic wall forms a large spherical depression dorsally.

Below the digital process that part of the otic capsule between the fenestra ovalis and the posterior margin of the whole otic region was described by Watson as the exoccipital. Its posterior edge, seen in side view, is smoothly concave and has been restored as the anterior margin of the vagus foramen. This part of the otic capsule, together with the digital process and probably the thickened roof above them constitute the opisthotic but there is no traceable suture between opisthotic and pro-otic. The combined bone, the periotic, formed all but the ventral and probably a small part of the posterior rim of the large fenestra ovalis. A part of the basioccipital has been restored entering the margin of the fenestra in the latter position, corresponding to the position in *Palaeoherpeton*.

The lateral surface of the periotic surrounding the fenestra shows a series of expanded swollen areas which are either of unfinished or eroded bone. In front of the digital process and below the triangular concavity referred to above is a convex roughened area extending forward to the buttress. Also the antero-dorsal and postero-dorsal edges of the fenestra are of thickened and roughened bone. Reference to the type suggests that these latter surfaces were concerned with articulation of a massive stapes (figure 8). The large rotted piece of bone in the type, referred to above, is closely applied by its base to the roughened areas surrounding the fenestra. Very little can be made of the structure and orientation of the stapes, if such it is. It appears as a massive eroded pyramid with its apex directed ventrally and a cavity which may be due to post-mortem damage near its base in the mesial surface. As preserved its apex is directed neither towards the otic notch nor towards the quadrate but erosion and distortion have obviously obscured its relationships.

An additional roughened area below the spherical concavity is more probably involved in the articulation of the epipterygoid together with a well-marked boss antero-ventral to it on the basisphenoid. Mrs Beaumont informs me that a similar articulation is present in loxommatids and a corresponding crista parotica is present in *Edops* (Romer & Witter 1942).

The mesial wall of the periotic has an unfinished bone surface throughout and is marked by a number of pits concerned with the labyrinth (figure 9*a*). A series of large pits almost certainly housed the semicircular canals. The largest pit (Watson's 'pseudo-fenestra ovalis') situated antero-dorsal to the true fenestra ovalis proves after some cleaning to have two large foramina opening from its inner wall. It is probable that the canal from one of these emerged from the otic mass in a large pit (pit A) immediately above the 'pseudo-fenestra' and thus housed the anterior vertical semicircular canal, while the second re-emerged in a pit above and behind the fenestra (pit B) in line with the digitiform process and thus housed the horizontal semicircular canal. The course of the posterior vertical canal is more obscure but it may have entered the bone at pit B and emerged from pit C above pit B. Alternatively, the latter may mark its whole course. Above the pits for the semicircular canals two small deep pits in the otic roof probably mark the course of endolymphatic sacs as in *Edops* (Romer & Witter 1942; Romer & Edinger 1942).

The general disposition of the basisphenoid is similar to that in *Palaeoherpeton*, but it does not seem to have entered the border of the fenestra ovalis. Dorsally the boundary of the bone at its suture with the periotic can be clearly seen on both sides of DMSW 30 as can the dorsal part of the vertical suture separating its posterior edge from the body of the parasphenoid. Just below the oblique periotic-basisphenoid suture and anterior to the parasphenoid suture is the boss for epipterygoid articulation already referred to.

A large, strongly developed basipterygoid process of the basisphenoid is present ventrally on each side below and slightly anterior to the boss. The processes are much damaged in DMSW 30.

In describing the basipterygoid processes in *Palaeoherpeton* I considered that they were formed in part by the parasphenoid, but this later seemed unlikely (Shishkin 1968; Panchen 1970). In *Eogyrinus* it is clearly not the case, for while, as Watson notes, the basisphenoid and parasphenoid are difficult to distinguish in DMSW 30, their bordering suture can be seen clearly passing mesially to the process in the Newarthill specimen.

Only the ventral part of the articular surface and rim of the process is known from the *Eogyrinus* specimens and while it has been restored with a saddle-shaped surface as in *Edops* it is possible that there was a division of the articulation by a ridge into a dorsal and ventral area as occurs in loxommatids (E. Beaumont, personal communication).

The carotid groove, which passes round the ventral part of the circumference at the base of each process, is clearly seen in all three specimens and the carotid foramen can be seen clearly on the right in the lectotype and, although closed by crushing, on the right of DMSW 30. The foramen is situated on each side just in front of the basipterygoid process. As in *Palaeoherpeton* the course of the groove can be seen continuing forward below the foramen. Thus the foramen received the intercranial branch of the internal carotid artery while the palatine branch continued forward externally in the groove. It was also suggested in the description of *Palaeoherpeton* that the groove also transmitted the palatine seventh nerve forward after its emergence from a small foramen just behind the basipterygoid process. This foramen can be seen clearly only on one side of the Derbyshire specimen of *Pholiderpeton* ('*Eogyrinus*': Panchen 1964). Its presence in *Eogyrinus* is uncertain as none of the specimens demonstrate it and the critical region is not well preserved either in the type, where it is obscured by a wide crack, or in the Newarthill specimen where it is not completely exposed. In DMSW 30 the foramen appears to be absent on the left but the area is damaged on the right. A recent reference to its presence in the type of *Eogyrinus* (Panchen 1970, p. 16) is in error and should refer to the Derbyshire '*Eogyrinus*'.

Above the basipterygoid process the basisphenoid extends forward as a stout buttress, which is particularly well preserved on the left in DMSW 30, separating the two large foramina apparently characteristic of the anthracosaur braincase. Above the buttress is the pro-otic foramen through which emerged the fifth (trigeminal) nerve and possibly at least the non-palatine branches of the seventh. Posteriorly the pro-otic foramen was bordered by the otic capsule and antero-dorsally by the sphenethmoid. In DMSW 30 the sphenethmoid border of the foramen is eroded on the left and is missing on the right as is part of the otic capsule, so that the specimen gives an exaggerated idea of the size of the foramen.

The lower surface of the buttress of the basisphenoid is an extension forward and upward of the dorsum sellae and as in *Palaeoherpeton* it forms the postero-dorsal border of a large fenestra opening from one side of the braincase to the other. This is probably an enlargement of a foramen carrying the interorbital vein, as originally suggested for *Eryops* by Sawin (1941). Again as in *Eryops*, *Peltobatrachus* (Panchen 1959) and *Palaeoherpeton* recesses in the posterior wall of the fenestra, formed by the dorsum sellae, served as the origin of the rectus eye muscles. The floor of the fenestra is deeply concave and formed the sella turcica for the hypophysis.

In *Palaeoherpeton* the fenestra extends obliquely forward and upward for some distance but it is relatively smaller in the braincase of *Eogyrinus*. In *Palaeoherpeton* it seemed probable that not only the sixth cranial nerve emerged on each side through the dorsum sellae, but also that the third and anteriorly the second (optic) nerve emerged through the fenestra.

In DMSW 30, however, the fenestra has two foramina situated in the concave area of sphenethmoid immediately in front of it. These are very clearly seen on the right of the specimen but disruption has obscured them on the left. Comparison with the restorations of *Edops* and *Eryops* suggests that the smaller postero-ventral one transmitted the third nerve while the optic nerve emerged through the other.

Several other foramina can be seen in this posterior sphenethmoid region. The contour of the basisphenoid buttress is continued forward by the sphenethmoid as a wide rounded ridge. Just above this ridge at about 17 mm in front of the buttress is situated a foramen seen on both sides of the specimen, which is probably for the fourth (trochlear) nerve. In the braincase of *Palaeoherpeton* a large trochlear foramen was tentatively restored immediately above the pro-otic foramen but this was probably incorrect. Below the rounded ridge, at roughly the level of the trochlear foramen, a pair of small foramina can be seen clearly on the left of DMSW 30 and less clearly on the right. Analogy with Romer & Witter's account of *Edops* suggests that these may have been for the optic and ophthalmic arteries.

Before describing the morphology of the sphenethmoid an account may be given of the parasphenoid. The general form of the body of the parasphenoid is closely similar in all anthracosaurs in which it is preserved. The whole ventral part of the otic region is encased by the parasphenoid which forms at least the ossified lower border of the fenestra ovalis, and contacts the pro-otic in front of it. It is not known whether it also had a contact with the opisthotic behind the fenestra. The critical region is obscured by the stapes in the type and the basioccipital which probably separated opisthotic and parasphenoid is missing in DMSW 30.

In front of the fenestra, as already noted, the lateral part of the parasphenoid body terminates abruptly to expose the side of the basisphenoid and the parasphenoid continues forward as a narrow ventral strip between the basipterygoid processes. Posteriorly the parasphenoid body

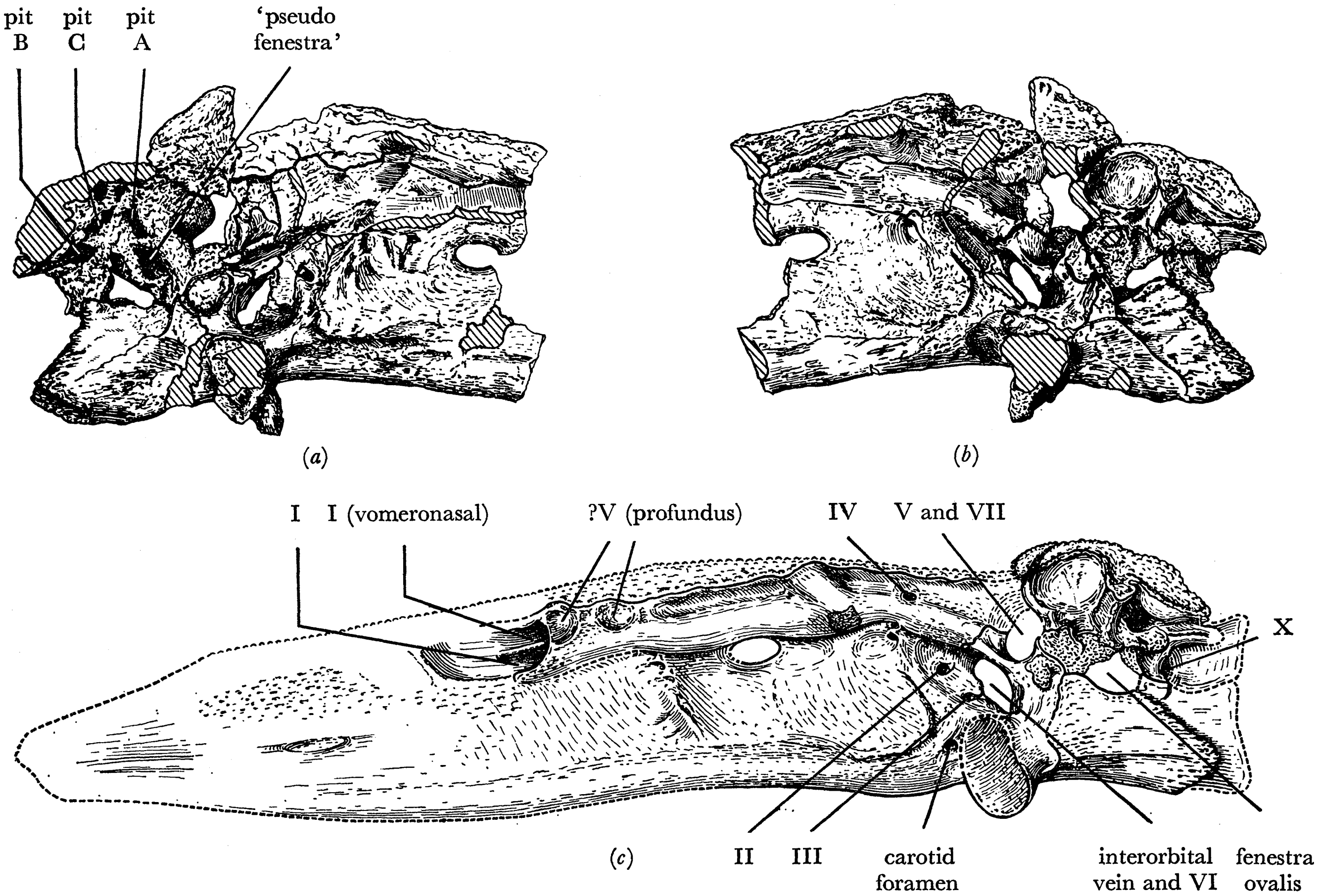

Figure 9. *Eogyrinus attheyi* Watson, braincase, two-thirds natural size. (*a*–*b*) DMSW 30 as preserved, right and left lateral views; (*c*) composite restoration, left lateral.

has a concave outline medially so that it projects back ventro-laterally on each side. In the complete braincase the basioccipital would have been exposed behind it.

The form of the parasphenoid body is well preserved in the type (figure 8) and shows the characteristic median fossa extending forward some 2 cm from the posterior edge. The areas flanking this fossa correspond to the basal tubera of *Seymouria*. No clear foramina corresponding to those in *Palaeoherpeton* and *Pholiderpeton* (Panchen 1964) are visible in this region. The fossa is ornamented by a light pitting and the basal tubera by longitudinal striations. In front of the fossa a strong irregular rugose ornament extends forward ventrally to a point between the basipterygoid processes while regular ridges are present ventro-laterally.

In front of the basipterygoid processes the parasphenoid forms the processus cultriformis. There is no clear suture between the processus cultriformis and the sphenethmoid above it either in the type or in DMSW 30. However, in the latter the region of the process immediately in front of the basipterygoid articulation has a fine striated ornament distinguishing it from the sphenethmoid and their junction is confirmed by the section exposed at the broken end of the specimen in which the parasphenoid is seen as a deep trough whose upper edges coincide with the groove.

The processus cultriformis is expanded laterally immediately in front of the basipterygoid processes just as is that of *Palaeoherpeton* and in the same region there is a dorsal expansion. The carotid foramen is almost certainly situated in the junction between the parasphenoid and the true neurocranium. It is probable that the processus cultriformis extended forward to at least the point at which the braincase is covered by the junction of the pterygoids anteriorly but this cannot be confirmed from the type which is the only specimen in which this region is preserved.

Data on the sphenethmoid are available from both the type and DMSW 30. As in *Palaeoherpeton* it consists of a solid interorbital septum extending right forward to the pterygoid junction with a more complex dorsal region housing the forebrain and olfactory tracts. The junction of sphenethmoid and basisphenoid is clearly marked at the end of the basisphenoid buttress but ventrally in the region of the basal articulation it is impossible to decide where the boundary comes. Dorsally the sphenethmoid extends back to, if it does not include, the bone described as supraoccipital.

Postero-ventrally the interorbital septum is very thick corresponding to the widest part of the processus cultriformis. Further forward at the anterior limit of preservation of the isolated specimen there is a large oval fenestra in the septum, not apparently represented in *Palaeoherpeton*, which possibly allowed communication between paired orbital blood sinuses. The lateral surface area between this fenestra and a point just antero-dorsal to the carotid foramen forms a shallow concavity bounded postero-ventrally by a stepped ridge. At about 1.5 cm in front of the fenestra the septum again reaches a wide point seen laterally in the type as a rather complex vertical ridge. It is probable that the part of the septum in front of this ridge contacted the pterygoids on each side in a loose sliding articulation. The only other remarkable feature of the septum, seen in the type on the left only, is an elongate concavity which, as in *Palaeoherpeton*, may mark the course of the profundus nerve. It is, however, relatively much smaller and much further forward in *Eogyrinus*.

As in *Palaeoherpeton* the sphenethmoid above the septum is both complex and difficult to interpret. In DMSW 30 this region has been subjected to very strong lateral compression, thus closing the internal cavities and crushing the sphenethmoid roof and with it the pineal fontanelle. Thus it is not discoverable whether the latter was as large as in *Palaeoherpeton.*

The internal cavity of the sphenethmoid was obviously developed in the region where the bone was perforated by nerve foramina, but in front of this it is confined to a convex region above the septum which appears as a continuation of the contour of the sphenethmoid buttress. The section exposed at the anterior end of DMSW 30 shows only a double wall representing the compressed cavity, so that at the transverse level of the fenestra in the septum only a single median cavity was present, with solid septum below and thick solid roof above. No other sections of the dorsal sphenethmoid are available.

Reference to the type, however, shows that a lateral tectal process was present in the sphenethmoid as in *Palaeoherpeton.* This is a vertical sheet of bone, formed on each side from the sphenethmoid as a downgrowth of its roof. It forms the lateral wall of that part of the sphenethmoid above the septum and thus of the cavity housing the forebrain and the canals for the olfactory tracts. It was distinguished as a process in *Palaeoherpeton* because it overlapped the septum on each side rather than merging with it.

In DMSW 30 this region of overlap of the lateral tectal process appears to have been broken off on both sides along the line of the top of the septum so that the region of overlap is lost, but in the type the overlap can be seen very clearly for most of its length. A small well-defined cartilage-roughened rectangle is situated ventrally on the tectal process just in front of the small arterial foramina. This area may have acted as part of the origin of the levator palatoquadrati (l. arcus palatini) muscle. It is situated below a rounded oblique thickening of the bone to provide strengthening of the bone against the pull of the muscle. There is also an oblique extension of the roughening on to the septum below.

Anteriorly the lateral tectal process extends forward to the point at which the olfactory tracts emerged from the braincase. In *Palaeoherpeton* as in *Eryops*, but not in *Edops*, two pairs of canals pass anteriorly through the sphenethmoid. The inner pair were assigned by Sawin to the vomeronasal nerves and the outer to the olfactory tracts in *Eryops* and I followed this interpretation in *Palaeoherpeton.* The type of *Eogyrinus* required meticulous cleaning with Airbrasive and mounted needles to resolve the structure there. A large single anteriorly directed foramen marks the emergence of the sphenethmoid canals and is clearly seen on the left in the type. However, cleaning of the cavity of the foramen and the forward continuation of its inner wall demonstrates that it is divided into two channels by a somewhat distorted but horizontal septum. This septum continues forward beyond the foramen and is represented by a short ridge, somewhat broken, which is visible in lateral view. It seems probable that the ventral channel was for the olfactory tract and the dorsal one for the vomeronasal nerve.

Immediately behind the joint foramen the lateral tectal process is marked by two hemispherical depressions one behind the other. These correspond exactly in position with two foramina in *Edops* forming the entrance and exit to a short bridge of bone, which Romer & Witter reasonably suggest marked the course of the profundus nerve. In *Eogyrinus*, however, after cleaning there appeared to be no canal connecting them, both being closed pits. There is, however, a line of junction between the bony lining of the cavity of the anterior one and its inner wall which may indicate closure by compression of a narrow channel.

In the interests of completeness an attempt has been made to reconstruct the dorsal and ventral views of the braincase (figure 10). As in the reconstruction of *Palaeoherpeton* the outline of the roof of the braincase in dorsal view may be drawn from its impression on the underside of a skull roof specimen. The impression is present in the two isolated skull tables, but poorer preservation makes it less well defined than in the type of *Palaeoherpeton*. The outline used for the *Eogyrinus* reconstruction is from DMSW 35, the Hancock skull table.

The principal differences in dorsal view from *Palaeoherpeton* are the large area of 'supraoccipital' already referred to, which the impression shows to have extended forward to the level of the front of the basipterygoid processes, and a wide lateral expansion of the sphenethmoid roof just in front of the pineal fontanelle. The latter expansion may be confirmed from the type in which the braincase may be seen to extend out to within about 1 cm of the margin of the orbit. There it meets a smooth orbital rim. This expansion reaches its widest immediately above the buttress for the levator palatoquadrati and is paralleled by a similar expansion in the heavily ossified Derbyshire specimen of *Palaeoherpeton*.

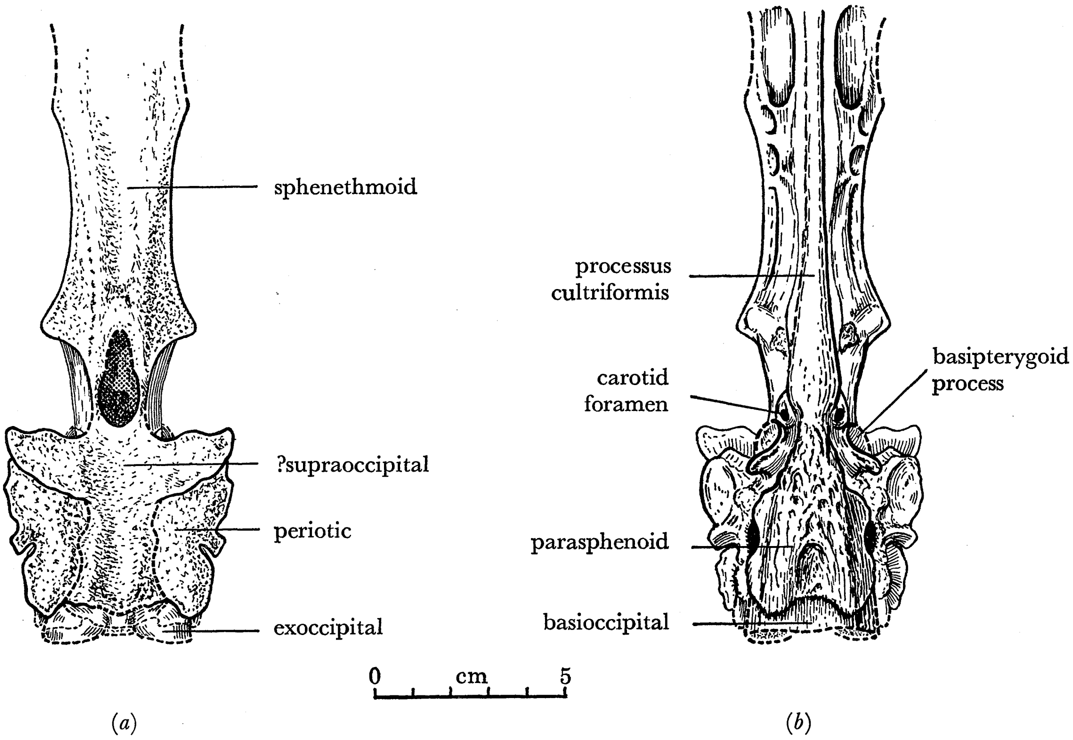

FIGURE 10. *Eogyrinus attheyi* Watson, braincase, composite restoration, half natural size: (*a*) dorsal, (*b*) ventral.

Nothing is known of the dorsal outline of the braincase beyond about 2 cm in front of the level of the exit of the olfactory tracts. The skull table specimens are not preserved forward to that region and beyond it the dorsal edges of the braincase are obscured by the pterygoids in the type. Therefore no attempt has been made to restore the outline in dorsal and ventral view in front of that level.

Lower jaw

The lower jaw of *Eogyrinus* is represented by very good material. Both rami are virtually complete in the lectotype. The left ramus has a section, averaging about 6 cm in length, missing in the region of the external suture between pre- and postsplenial, which in the specimen has been restored in the same mastic as the underlying region of the skull roof (figure 2, plate 24). The right ramus is, however, complete. The symphysial region of the right ramus is obscured in external view by the overlapping left ramus but the corresponding region is visible in front of the break in the latter. Similarly, the mesial view of the front of the left ramus is obscured by the skull roof but that of the right is completely exposed (figure 5, plate 25). Thus every part of the lower jaw can be reconstructed by reference to one or other of the rami.

Information from the lectotype is supplemented and reinforced by data from the other specimens. G13.80 (DMSW 37) has an articular region less distorted by compression than those of the lectotype, and the lower jaw of the Airdrie skull, while adding nothing of importance on jaw structure, shows an almost complete right dentition in relation to that of the upper jaw.

In giving an account of the general osteology of anthracosaurs (Panchen 1970) I have given a full description of the form of the jaw ramus and the arrangement of the bones of which it is composed based on the lectotype of *Eogyrinus*. Only additional notes need therefore be given here. For completeness, however, I include the restorations of the lateral and mesial aspects of the jaw ramus previously published (figure 11) together with a new reconstruction of the whole mandible in dorsal view (figure 12).

The mandible of *Eogyrinus* is of characteristic anthracosaur form reaching a depth of over 10 cm behind the dentary tooth row but tapering to only about 2.5 cm just behind the symphysis. The glenoid fossa of the articular is terminal: no retroarticular process is developed. Below the articular the postero-ventral edge of the ramus descends steeply to a rounded angle giving the great posterior depth.

In front of the articular the dorsal edge of the ramus, forming the lateral wall of the adductor fossa, is strongly convex forming a high surangular crest which is strengthened by a longitudinal thickened region just below its margin. This thickening projects strongly on the mesial surface.

The surangular crest is particularly strongly developed in the jaw of *Eogyrinus*, especially in comparison to *Neopteroplax* (Romer 1963) a form of almost equal size. Also in contrast to *Neopteroplax* is the development of a well-defined raised area with denticles on the anterior coronoid, like that on the other two coronoids.

Lateral line grooves are clearly visible on the lateral surface of both lectotype jaw rami. The mandibular sulcus forms the continuation of the jugal sulcus of the skull roof. It first appears in the lower jaw on the surangular as a broad, shallow and rather indistinct groove parallel to the posterior margin of the jaw. It then continues forward near the ventral margin of the angular and of the two splenial bones, becoming progressively narrower, deeper and more well-defined anteriorly. With the narrowing of the jaw towards the front the distance between the groove and the ventral edge of the jaw also diminishes.

As Watson notes, there is a well-defined oral sulcus whose junction with the mandibular sulcus occurs at the angular-surangular suture. From this point the oral groove extends antero-dorsally on the surangular but becomes indistinct at the level of the back of the tooth row. However, it appears to continue forwards on the dentary, parallel to the upper margin of that bone.

The dermal ornament on the lateral surface of the jaw rami varies characteristically in different regions as does that of the skull roof. The articular is not ornamented and the ornament on the surangular is shallow and ill-defined. There are, however, scattered pits on the latter bone postero-ventral to the mandibular groove.

The ornamentation of the angular is similar to that on the surangular. Below the mandibular groove it consists of scattered pits, but more regularly arranged and well defined than those of the surangular, while above the groove the pits are extended, particularly anteriorly, into shallow grooves. These radiate, presumably from the centre of ossification, in an antero-dorsal direction. On the two splenials the pit-and-ridge system is even more sharply defined below the groove with a tendency for the pits to coalesce into grooves on the presplenial. Above the groove a similar ornament is present, tending to fade out dorsally on the postsplenial.

Finally the dentary has only an ill-defined ornament below the presumed continuation forward of the oral groove, but above it, and thus lateral to the roots of the teeth, the whole bone is swollen laterally and has an ornament of scattered pits which are very ill-defined posteriorly but increase in definition towards the front.

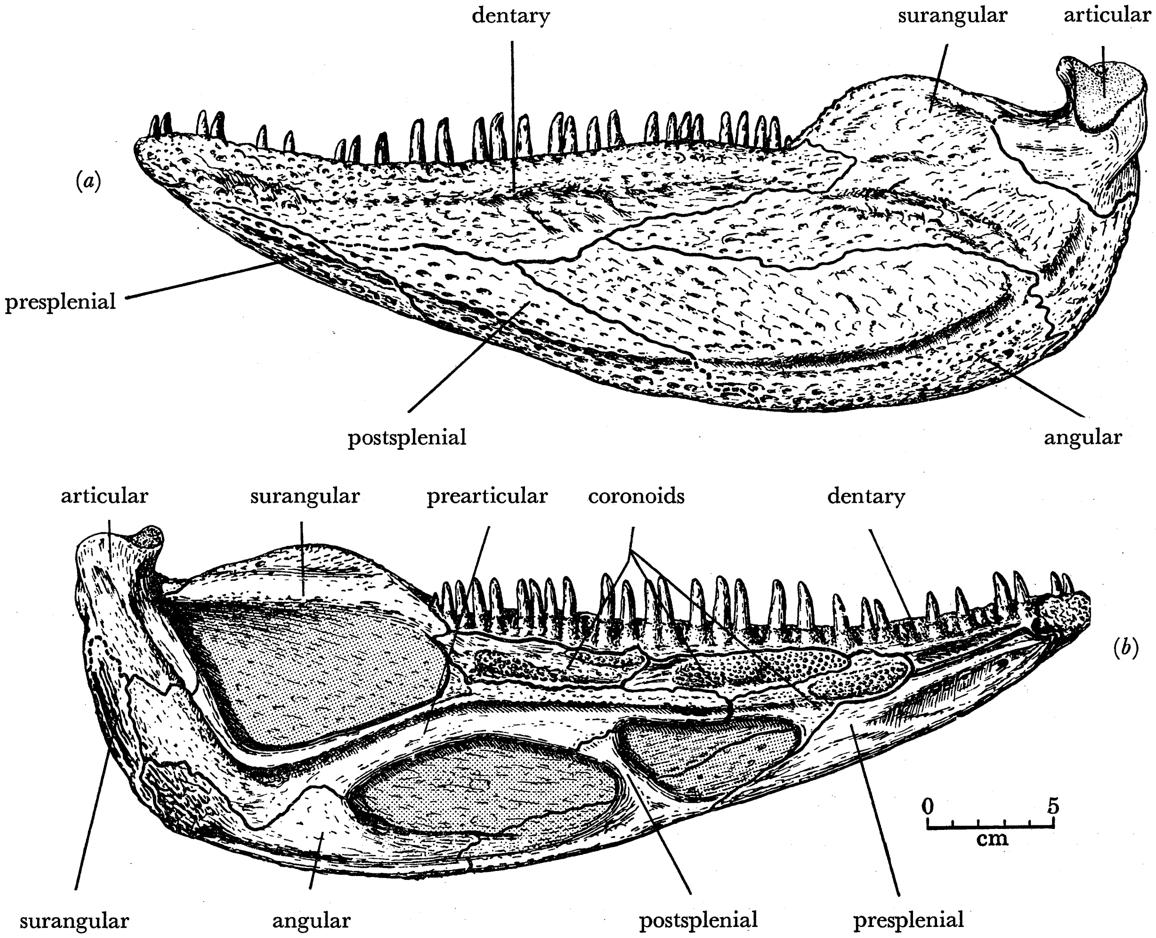

FIGURE 11. *Eogyrinus attheyi* Watson, left jaw ramus, composite restoration in the plane of the ramus. One-third natural size: (*a*) lateral, (*b*) mesial.

In general terms the ornamentation of the jaws mirrors that of the skull roof. The pitted ornament below and surrounding the mandibular groove parallels that of the median roof out to the supraorbital sulcus and, like it, becomes more defined towards the muzzle, while the area between the mandibular and oral grooves parallels the cheek region and the side of the snout. Finally and predictably the ornamentation of the dentary mirrors that of the maxillary.

The form of the jaw articulation merits some discussion. The outline of the glenoid surface of the articular in dorsal view (figure 12) closely mirrors that of the quadrate condyle with which it articulates. Because of the complex shape of their respective surfaces and the close fit between them, the articular glenoid could not 'roll around' the condyle about a simple horizontal transverse axis.

The shape of the articulation differs from a simple roller hinge in three principal ways. First, the surface of the glenoid is toroidal or 'saddle-shaped', being concave from front to back but convex upwards for most of its length from its lateral to its mesial end. Secondly, the long axis of the glenoid is not a transverse straight line in dorsal view, but an arc of a circle, being convex backwards. Both glenoids probably lay roughly on the same arc.

Thirdly, the glenoid is 'screw-shaped' like that of the shoulder girdle of most primitive tetrapods, so that the plane connecting the anterior and posterior edges of the glenoid rotates from a horizontal orientation mesially to one inclined at about 45° anteriad laterally. The quadrate condyle is in all respects a natural cast of the mould formed by the glenoid.

It seems apparent therefore that as the lower jaw opened the glenoid moved laterally along the condyle so that the articulars of the two rami diverged. This was effected by the 'screw-shaped' articulation, while the second factor, the common arc, allowed them to diverge about the centre of rotation, presumably the symphysis. This does not mean, however, that the two jaw rami diverged as a whole: the first factor, the saddle shape of the glenoids, imparted a rotational movement to each ramus about a longitudinal horizontal axis. Thus while the articulars and tooth-bearing upper margins of the rami diverged their ventral edges converged and the overall separation of the rami remained the same.

As the jaw closed a rotation on the opposite sense occurred: the ventral edges of the jaw diverged, the articulars moved mesially along the quadrate condyles and the upper margins of the jaw converged, thus swinging the points of the teeth in opposite rows towards one another.

It is the last effect which possibly explains this rather complicated mechanism. If there was a certain amount of 'play' in the jaw articulation it would be possible on rapid closure of the jaw for the maxillary and dentary tooth rows to meet in the same plane on one side, instead of the dentary teeth fitting inside the maxillary ones as they should. Thus complete closure would be blocked. If, however, each dentary tooth row were rotating inwards towards that of the opposite side as the jaw closed, the chances of collision with the tips of the maxillary teeth would be minimized. If it happened, further closure would move the tips of all the dentary teeth mesially, thus releasing the blockage. It is also possible that, if the symphysis of the jaw were either relatively immobile between rami or strongly elastic, the release of torsional stress along the length of the jaw imposed when opening the mouth would assist in jaw closure.

The symphysis was probably elastic rather than immobile. The symphysial surface is visible only in the right ramus of the lectotype where it appears as an ovoid area of roughened bone somewhat raised in the middle but more heavily pitted round the periphery. Thus there must have been a considerable amount of cartilage and possibly ligamentous tissue between the two symphysial surfaces. Behind the symphysis there is a clearly defined shallow concave area on the presplenial which may mark the origin of an intermandibular muscle. As the area is below the midline a muscle between the two sides with that origin would both restrain disarticulation at the symphysis and promote the torsion of the rami which accompanied jaw opening.

It is also possible that the two large meckelian fenestrae which characterize the mesial view of the anthracosaur jaw ramus were concerned, at least in part, with the origin of massive more posterior components of the intermandibular musculature. A massive ventrally situated muscle between the rami would, by promoting the same torsion, act as a powerful auxillary muscle in jaw opening, thus compensating for the lack of a retroarticular process in these primitive labyrinthodonts.

The depressor mandibulae, which in more advanced labyrinthodonts inserts on the retroarticular process, has a strongly rugose insertion just dorsal to the jaw angle in *Eogyrinus* and is situated on the mesial surface of the angular (figure 11 *b*). The muscle must have run from its origin on the occiput and tabular horn (Panchen 1964) behind the tympanum and middle ear cavity, down the occipital surface of the squamosal and behind the jaw articulation. Its course across the articular is marked by a tapering concave area on the posterior surface of that bone and a shallow groove on the mesial surface of the surangular immediately above the insertion of the muscle.

Something of the function of the adductor muscles of the jaw has been considered in an extended discussion of the skull kinetism of anthracosaurs (Panchen 1970). The adductor muscles of *Eogyrinus* were obviously extremely massive. The origin of the main external adductor was probably only on the palatoquadrate so that it was kinetically isolated from the braincase. In the closed position of the jaw the muscle must have been virtually completely encased in bone. The descending lamina of the quadrate ramus of the pterygoid would have fitted close to the deeply depressed margin of the adductor fossa of the jaw on the mesial side, while laterally the surangular crest extended into the subtemporal fossa of the palate. It is probable therefore that on jaw closure there was a mesial component of the pull of the muscle between pterygoid and surangular flange which would have assisted the torsion of the jaw ramus required for closure.

The probable strong development of the pterygoideus has already been discussed (Panchen 1970). The very deep jugal region in anthracosaurs allowed plenty of space above the palatal bones for the origin of this muscle and a slip probably also originated on the ornamented part of the quadrate ramus described above. Thus the bulk of the pterygoideus lay mesial to the external adductor in the wider posterior part of the subtemporal fossa. It seems possible, however, although not so certain as I implied in the previous discussion, that a component of the pterygoideus emerged at the front of the fossa running under the pulley-like surface of the processus alaris of the jugal.

The insertion of the main pterygoideus mass is probably marked on the jaw ramus by the shape of the strongly depressed inner margin of the adductor fossa. In the mesial view (figure 11 *b*) this margin has two main regions at right angles: the posterior one which is almost vertical has a well-marked surface for muscle insertion, bounded by a sharp posterior edge, which extends well up on to the antero-mesial surface of the articular. The same surface continues round as a rim to the antero-ventral border of the fossa and its edge continues forward along the jaw ramus defining the somewhat recessed area below it in which the meckelian fenestrae are situated.

The insertion area on the posterior margin of the fossa is perpendicular to the direction of pull of the pterygoideus and presumably acted as its insertion while the mesial part of the external adductor may have extended its insertion on to the antero-ventral border.

Dentition

The teeth of anthracosaurs are taxonomically important in their shape, their internal structure and in the overall pattern of the dentition. The internal structure of *Eogyrinus* teeth was figured by Atthey (1876) who shows a series of transverse sections. Their histology, apparently typical of anthracosaurs, may also be compared with that of the loxommatids *Megalocephalus* ('*Loxomma*': Embleton & Atthey 1874). In each case, when sectioned near the base of

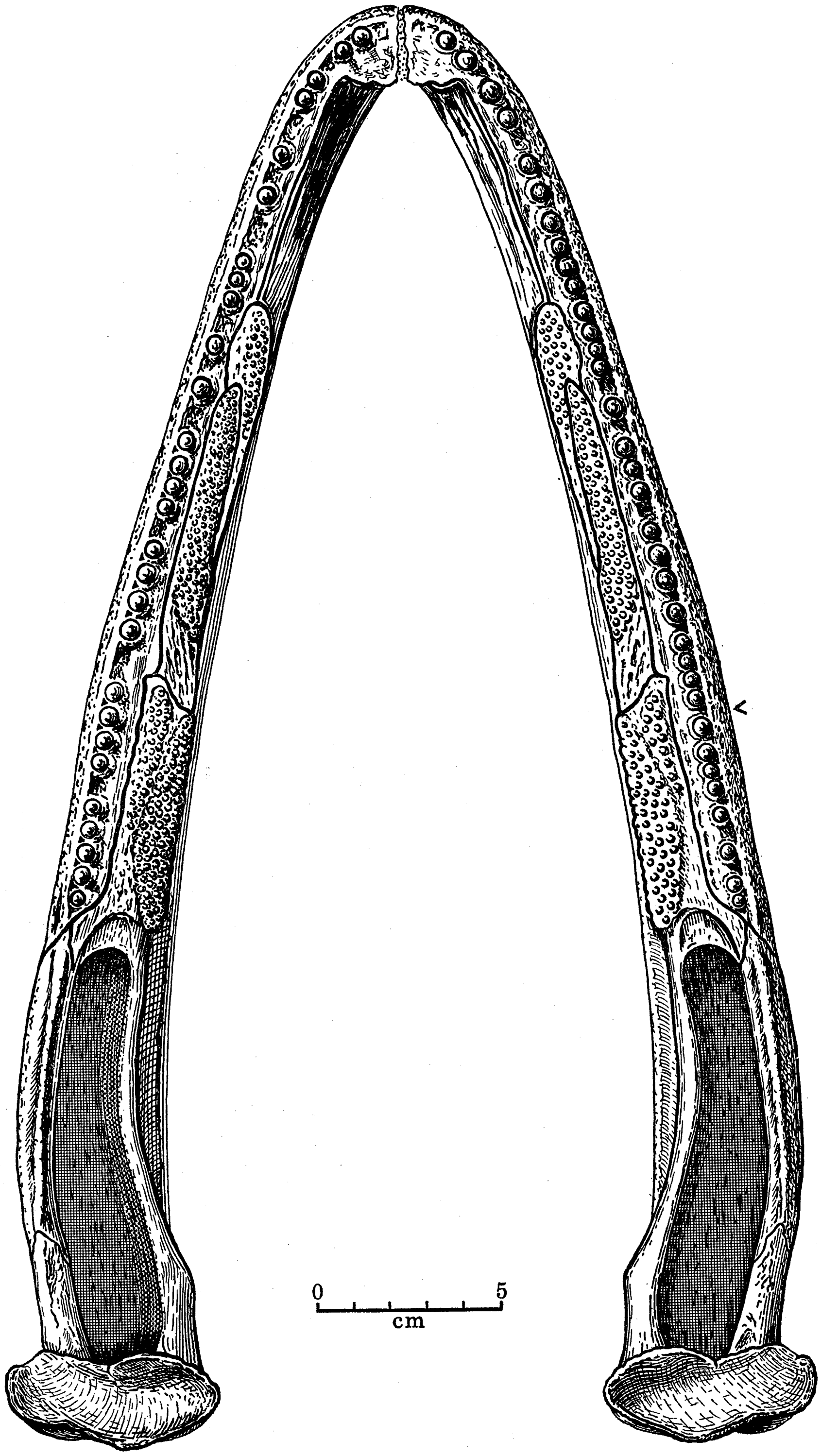

FIGURE 12. *Eogyrinus attheyi* Watson, lower jaws in articulation, composite restoration in dorsal view. Half natural size. Dentition of right dentary back to arrowhead from Airdrie skull.

the crown, the teeth show the characteristic labyrinthodont infolding of the dentine. In the anthracosaurs the radial infoldings of the external primary dentine (Bystrow 1938*b*; Globulärzone: Schultze 1969), while more tortuous, appear as single lines, whereas in the loxommatid there is a short side branch at each angle (Panchen 1970, fig. 4).

In an extensive recent review of tooth structure in rhipidistians and early tetrapods Schultze demonstrates that the loxommatid type of tooth is very similar to the type of tooth (polyplocodont) found in some osteolepiform Rhipidistia and thus presumably represents the primitive labyrinthodont type. The polyplocodont tooth also occurs in *Ichthyostega*. In primitive temnospondyls (Edopoidea, Trimerorhachoidea, some Eryopoidea) an intermediate condition occurs, while the advanced type of tooth seen in anthracosaurs also occurs in advanced temnospondyls, plagiosaurs and seymouriamorphs.

The form of the teeth in the Eogyrinidae, typified by *Eogyrinus*, distinguishes them from the other two families of anthracosaurs (Panchen 1970). The teeth are tall and slender, particularly on the dentary, and taper very little over most of their exposed length. The tip of the crown tapers to a blunt point and is often hooked back slightly. In the family Archeriidae the teeth are close set and more markedly hooked back and terminate in a longitudinal chisel-like blade. The teeth of *Anthracosaurus russelli*, representing the Anthracosauridae, are about twice the size of those of *Eogyrinus* in a slightly smaller skull and are massive fluted cones.

The small palatal teeth of *Eogyrinus* are similar to the marginal dentition, but no complete palatal tusk is well enough preserved for description.

The palatal dental formula of *Eogyrinus* has been quoted in the generic diagnosis as 0–2–2–(7) and the position of the teeth noted in describing the palate. The left palatine tusk has only 2 or 3 mm of crown preserved and is sheared off horizontally exposing a good transverse section. The section is a circle with a basal diameter of 14 mm. Two displaced tusks are partly visible on the right. One has its damaged root covering part of the midline suture between the vomers, while the tip of the crown is concealed by the underlying right jaw ramus: about a centimetre of crown is exposed. The other tusk lies along the edge of the same ramus. The jaw ramus thus conceals about half the width of the tusk and the exposed part is badly eroded. It has a minimum crown height of over 2 cm and appears to be strongly recurved.

As it is situated in the region of the front of the right palatine it may pertain to that bone while the other displaced tusk is from the right ectopterygoid. The left ectopterygoid tusk is present *in situ* on the displaced bone, but is severely squashed and eroded.

Thus all four tusks are preserved and each pair site bears a clear sharp-edged replacement pit.

There is a residual doubt about the number of premaxillary teeth present in *Eogyrinus*. The right premaxillary is obscured in ventral view by the jaw ramus. The left shows two preserved teeth, one near the midline, the other right beside the maxillary suture. Half-way between the two the crushed remnant of a third tooth can be seen: so that three widely spaced teeth were certainly present. However, the edge of the bone is somewhat turned under in ventral view and there is a remote possibility that another tooth or pair of teeth, or their replacing pits, might have been present between those visible. However, inspection of the Airdrie skull, which is difficult to interpret in that region, also suggests that there were three premaxillary teeth.

The mesial premaxillary tooth in the lectotype has a basal diameter of 6 mm and a minimum length of 15 mm, the outer one a diameter of 5 mm.

The maxillary tooth count has been given in the diagnosis as in excess of forty. In the lectotype the anterior part of the right maxillary is again obscured by the right jaw ramus so that only the posterior teeth are visible. The left maxillary is displaced but appears almost complete. Only the anterior end, comprising the first 5 cm and the extreme, and probably toothless posterior end, are missing.

In the palatal reconstruction (figure 7) the disposition of the teeth on the left maxillary between the marker arrows is exactly that on the displaced lectotype maxillary. The replacement sites representing teeth lost post-mortem as well as true replacing pits are however conjectural and may be too numerous in the longer gaps.

The right maxillary dentition in both palatal and lateral reconstructions is drawn directly from the Airdrie skull in which the complete dentition is preserved back to the level of the marker arrow in the palatal drawing. Allowing not more than one site in each of the major gaps this gives a count of 39 teeth to the limit of preservation, with perhaps seven or eight to be restored to give the full length of the tooth row.

The first two maxillary teeth in the Airdrie skull are large and represent a canine peak. The first has a basal diameter of 5 mm and a crown length of 15 mm while the figures for the second are 7 and 18 mm respectively. The third tooth, almost certainly separated from the second by a replacement pit, was probably as large or larger than the first, but is not well preserved.

Thereafter apart from a diminution at the extreme posterior end there seems little systematic regional variation in size along the tooth row, individual teeth varying according to the growth stage they have reached.

In the lateral reconstruction of the whole skull the dentary dentition is again drawn directly from the Airdrie skull as far as it is preserved. This includes some 30 teeth or replacement pits with perhaps a dozen more to be restored in the missing part of the dentary.

The arrangement shown in the previously published restoration (figure 11) is derived from both jaw rami and is thus an impression of the tooth arrangement and not the preserved dentition of one ramus. In the dorsal reconstruction of the mandible (figure 12) the right dentition is from the Airdrie skull, consistent with the lateral reconstruction of the whole skull, while the left is drawn from the reconstructed jaw.

There is some regional variation apparent in the dentary dentition. There is no canine peak. The anterior teeth are small, rarely exceeding a crown height of 12 mm for the first 10 cm of the ramus. The left ramus of the Airdrie skull shows, however, that they were exceptionally deeply rooted, reaching an overall height of 30 cm. Behind this region there is a gradual increase in average crown height in the lectotype to a maximum of nearly 20 mm at some 16 cm from the symphysis. This regional variation is much less marked in the Airdrie skull which, while apparently representing an animal of similar size, is much more lightly built. The difference conceivably indicates sexual dimorphism.

Little can be said about the occlusion of the upper and lower dentitions. The dentary teeth fitted between the maxillary teeth and the palatal series but the regional variations in the dentary teeth do not seem to be reflected in the marginal or palatal dentition. Mrs Beaumont informs me that this is the case in the loxommatids, dentary teeth of almost tusk size occupying the gaps between successive palatal tusks. Nor in *Eogyrinus* are there any symphysial tusks on the lower jaw so that a palatal vacuity between the vomers to accommodate them is unnecessary.

An attempt was made on the Airdrie skull to study tooth replacement as Edmund (1960*b*) has done with part of the dentition of *Archeria* using his own principles (Edmund 1960*a*). No simple pattern of replacement emerged, but the dentition shown in the lateral reconstruction of the skull represents the data for such a study.

The final component of the dentition of *Eogyrinus* is the covering of denticles on the pterygoid of the palate and the three coronoids of the lower jaw. This is characteristic of Rhipidistia (e.g. *Eusthenopteron*: Jarvik 1954) as well as labyrinthodonts. In *Eusthenopteron* it is supplemented by denticles on the parasphenoid, absent in *Eogyrinus*, and denticle-covered bony plates between the pterygoids behind the otic region and covering the gill bars. The whole must represent a mechanism for retaining slippery prey in the mouth.

APPENDICULAR SKELETON

Interclavicle

The anthracosaur interclavicle from the Hancock Museum is preserved on a slab of shale with only its ventral surface exposed and is also represented by a counterpart slab bearing a natural mould of the bone surface. The areas preserved as bone and as impression are almost but not quite coincident. The right antero-lateral region is missing from the bone beyond an oblique break, but the counterpart extends somewhat beyond the break. If the right side is restored from the left only a small part of the anterior border in the midline is totally unrepresented (figure 13).

The interclavicle is completely isolated but may be attributed to an anthracosaur for a number of reasons. Its shape is similar to that of the *Archeria* interclavicle (Romer 1957) with a broad spatulate process ('parasternal process'; Brough & Brough 1967) extending well behind the region of clavicular overlap. This feature is characteristic of, but not exclusive to, anthracosaurs. The ornament on that part of the surface not modified for overlap is of characteristic anthracosaur type.

The specimen could conceivably pertain to a loxommatid were it not for the very different interclavicle which also occurs at Newsham and is probably to be attributed to the loxommatid *Megalocephalus*. The latter specimen, to be described by Mrs Beaumont, bears ornament of a much more loxommatid type in spite of Watson's original attribution to *Eogyrinus*.

Thus the present specimen is almost certainly to be referred either to *Pteroplax* or to *Eogyrinus* but there is some doubt as to which.

Its estimated overall length is 120 mm, almost exactly the size shown by Romer (1957, fig. 1) for what, from his data, seems an average specimen of *Archeria crassidisca*. This dimension would favour attribution to *Pteroplax* but on rather tenuous evidence. The specimen on which Romer bases his reconstruction of the *Archeria* pectoral girdle (M.C.Z. 2045) has femora of length 87 and 84 mm. A published basis for comparison with *Pteroplax* is given by the syntypes of *A. crassidisca* (Cope) (Case 1911: '*Cricotus*'; Panchen 1970). The slightly larger of these has a femoral length of 70 mm and the smaller a skull with postparietal length of 150 mm. Vertebral diameters for the species, presumably from these specimens, are given by Cope (1884 – also Case 1911) as 25 mm.

The estimated postparietal length of the *Pteroplax* lectotype skull is 167 mm and that of the smallest known *Eogyrinus* skull (DMSW 35) is 255 mm. The above data suggest that the specimen on which Romer based his description of the interclavicle of *Archeria* would have had a skull of postparietal length *ca.* 185 mm. Bearing in mind the difference in proportion of the skull between archeriids and eogyrinids of similar size (Panchen 1970, fig. 11) Romer's *Archeria* and the lectotype of *Pteroplax* probably represent individuals of very similar size. However, a series of vertebrae in the Hancock Museum which are almost certainly attributable to *Pteroplax* have an average diameter of about 20 mm, suggesting a somewhat smaller individual than the syntypes of *A. crassidisca* and a considerably smaller one than Romer's specimen.

The case for the attribution of the Hancock interclavicle to *Eogyrinus* depends on its width and proportions. While its estimated length is the same as that of the *Archeria* interclavicle its widest point is relatively further forward; at about 90 mm from the posterior border of the parasternal process measured along the midline in *Eogyrinus* and some 75 mm (from Romer's figure) in *Archeria*. Thus the Hancock specimen could be regarded as an effectively larger bone

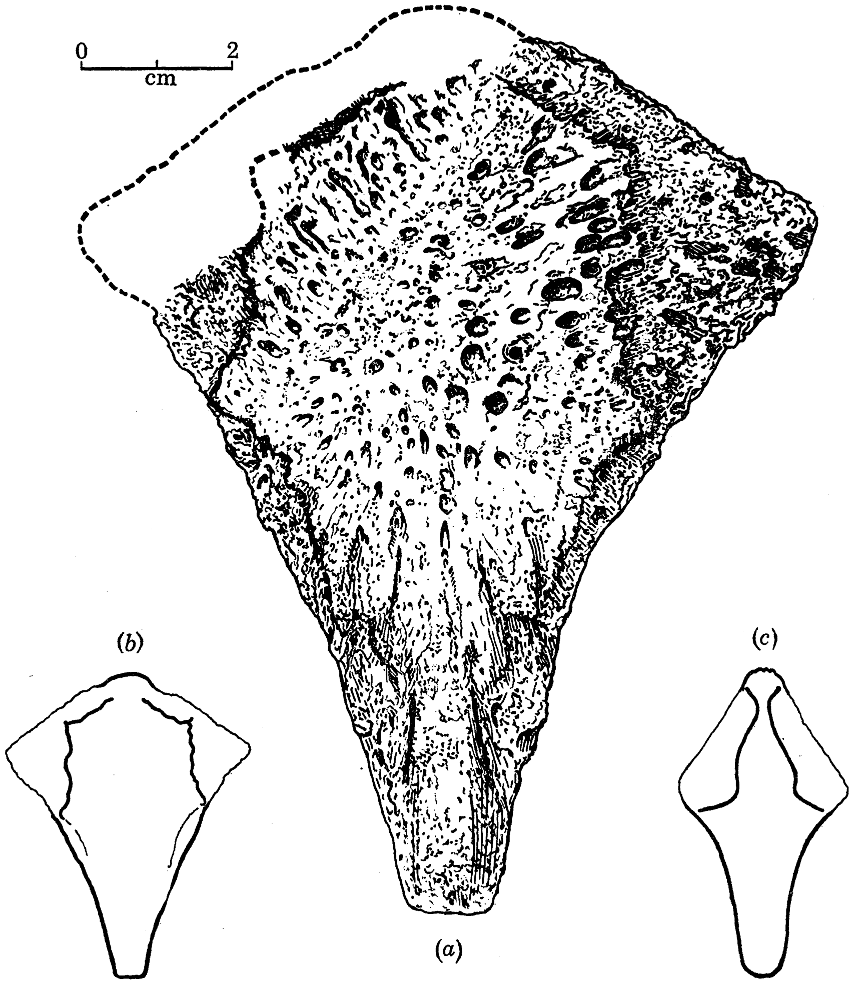

FIGURE 13. Anthracosaur interclavicles, ventral view. (*a*) Newsham interclavicle (?*Eogyrinus*), natural size; (*b*, *c*) comparison between the Newsham specimen and *Archeria* (*c* after Romer).

in which the anterior region is less strongly developed or, conceivably, which should have been restored with a more extensive clavicular region.

The width at the widest point is nearly 100 mm compared to nearly 70 mm in *Archeria* and significantly the width of exposed bone between the overlap areas for the clavicles is much greater, averaging 50 mm between the parallel edges compared with 20 mm for a tapering surface in *Archeria* (Romer's figure 10*b*, *c*).

Thus the Hancock interclavicle suggests an animal of greater girth than *Archeria*. It could represent a small individual of *Eogyrinus* and, whether *Eogyrinus* or *Pteroplax*, is almost certainly the interclavicle of an eogyrinid.

The ornament of the median ventral surface of the interclavicle is similar to that of *Archeria* in being 'punctate': its most distinctive feature being a series of fairly widely spaced pits with a general radial arrangement. The median centre of ossification is situated towards the back of the clavicular region. The ornament is, however, more irregular than Romer's account suggests is the case in *Archeria*. In the Hancock specimen the pits become shallow, elongate and rather ill-defined on the parasternal process and the surface between the major pits is irregularly pitted and striated.

As preserved the bony surface between the clavicles is more or less flat but the process is convex ventrally with a particularly prominent region in the midline about half-way along its length.

The area of overlap for the clavicles is well-defined and clearly seen on the left and has a complex ornament of small irregular pits and ridges with occasional larger shallow pits. As already noted the main inner border of the overlap area is roughly parallel to the midline, in contrast to *Archeria*, but anteriorly the border turns sharply towards the midline and is parallel to the antero-lateral edge of the bone. The area between the two is a continuation of the main overlap area but it does not seem very probable that the anterior area was covered by the clavicle.

If the interclavicle is that of *Eogyrinus* it seems likely that the whole shoulder girdle was relatively smaller than that of *Archeria*. The reduced anterior region of the interclavicle restricts the area of overlap of the clavicles antero-posteriorly and it is also restricted laterally, suggesting relatively much smaller clavicles. This agrees with the weak development of the femur described below and suggests that *Eogyrinus*, despite its enormous size (an estimated 4 to 5 m in length: Panchen 1966) had very feebly developed limbs.

An incomplete anthracosaur interclavicle (R.S.M. 1971.11.4) is preserved in the Royal Scottish Museum. Only the anterior half is present and the lateral edges are broken, but it probably represents a somewhat larger individual than the Hancock specimen, with an estimated overall width of 105 to 110 mm compared with 100 mm for the latter. In most respects they are similar but the edges of the clavicular overlap areas in the Scottish specimen are more nearly parallel straight lines. The ornament is very different: in the latter it is in very low relief consisting of very small pits with fine grooves radiating laterally from them.

Unfortunately there is no specific data on locality or horizon, but the specimen is known to be from the William Grossart collection. Grossart was a Lanarkshire surgeon who collected principally within that county (I am indebted to Dr C. D. Waterston for this information) and the specimen is preserved in a matrix that closely matches the Airdrie, Lanarkshire, Blackband Ironstone. Thus attribution to that horizon somewhere in the Scottish Central Coalfield is not too improbable. This, together with the nature of the ornament, suggests that the specimen is more probably to be assigned to *Anthracosaurus russelli* than to an eogyrinid and it will be described and figured in the projected description of that species.

Femur

A left femur is the only limb bone certainly associated with *Eogyrinus*. It was preserved in a block of shale together with numerous vertebrae and ribs as part of the lectotype skeleton. When *in situ* the dorsal surface was exposed but not completely free of matrix, while a central part of the shaft was visible ventrally through an excavation that had been made in the shale. The distal (not proximal as in Panchen 1966) end of the bone is missing beyond an oblique break corresponding to the end of the block.

Careful development has made it possible to remove the femur intact from the block and the specimen has been completely cleaned of matrix with the Airbrasive machine. Preservation is quite good apart from the effects of compression, which has flattened the concave intertrochanteric fossa and its margins into a single horizontal plane and somewhat crushed the shaft.

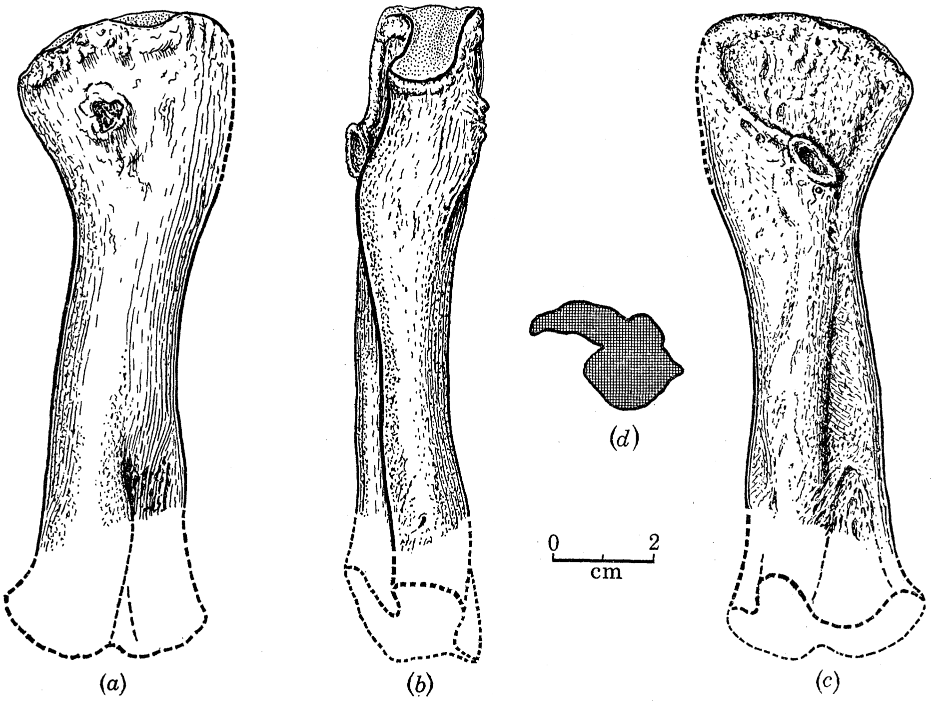

FIGURE 14. *Eogyrinus attheyi* Watson, lectotype left femur corrected for crushing and restored. Two-thirds natural size: (*a*) dorsal, (*b*) anterior, (*c*) ventral, (*d*) section exposed at broken end of specimen, distal axial view.

There are surprising differences from the femur of *Archeria* (Romer 1957), but judging from Carroll's figures there is a closer resemblance to that of *Calligenethlon*.

The femur will be described in the conventional orientation, with the axis horizontal and at right angles to the axis of the trunk.

The outline in dorsal view is very distinctive. The head is expanded in the normal way and this is exaggerated in the specimen by the compression referred to. The shaft, however, has a sinuous S-shaped curve so that when the head is placed in the same position as that in the figure of *Archeria* the shaft has a strong forward inclination proximally. The distal end then moves back with the curvature into a transverse plane in front of that of the head (figure 14). The anterior and posterior margins of the shaft are almost parallel but diverge slightly along its length so that the shaft is at its narrowest proximally.

The convex, terminal articular surface for the acetabulum is much compressed in the specimen, but was apparently closely similar to that of *Archeria*. The dorsal surface of the expanded head region is strongly roughened. This is due principally to post-mortem erosion of the surface, but one feature, absent in *Archeria*, is very prominent. This is a rectangular pit, with raised edges, situated at about 2 cm from the terminal edge and not much more than a third of the antero-posterior width from the anterior edge. Analogy with femora such as that of *Dimetrodon* (Romer 1956) suggests that it is for the insertion of the puboischiofemoralis internus muscle. The corresponding area in the *Archeria* femur is smooth. In the latter, however, there is a rugose area directly posteriorly for the ischiotrochantericus muscle. It is impossible to say whether this was present in *Eogyrinus*, as a fragment of bone is missing from the posterior edge.

The dorsal surface of the shaft beyond the proximal expansion of the head was probably cylindrical, but is somewhat crushed in the specimen. At the distal end of the specimen the shaft is apparently beginning to divide to define the intercondylar groove before it is broken off. There is a striated rugose area posterior to the beginning of the groove. At the distal end posterior to this area the hind margin of the bone is produced into a sharp ridge somewhat bowed outwards and downwards. The whole of the anterior margin of the bone also appears as a sharp edge but this is certainly exaggerated by crushing.

In anterior view the femur is closely similar in its general outline to that of *Archeria* with the dorsal surface of the shaft very slightly concave and rising towards the proximal end and towards a gently convex distal end.

The most striking differences from *Archeria* are seen in ventral view. Although the compression and erosion of the ventral surface of the head makes it somewhat uncertain, there seems to have been no development of an internal trochanter or of the massive anterior border of the intertrochanteric fossa which buttresses it in *Archeria*. The fossa itself is even more restricted in distal extent than that of *Archeria*, in striking contrast to the condition in *Seymouria* (White 1939).

On the other hand, the fourth trochanter in *Eogyrinus* is exceptionally strongly developed. In *Archeria* it takes the form of an elongate pit bordered by anterior and posterior rugose ridges and extending distally from the anterior surface of the anterior border of the fossa, almost to the ventral midline of the shaft. In *Eogyrinus* it is confined to a more normal position distal to the fossa and somewhat anterior to the midline. It is, however, situated on the ridge which forms the posterior border of the fossa, as in *Eryops*, and not on the anterior (internal trochanter) ridge, as in *Archeria* and *Diadectes*. The fourth trochanter takes the form of an oval pit bordered by a raised rim which surrounds its whole circumference. Its form thus suggests a powerful tendinous insertion of the caudifemoral muscle, which agrees with the strongly developed origin seen on the centrum of the seventh caudal vertebra (Panchen 1966).

The ventral surface of the shaft is generally well preserved and shows one important difference from that of *Archeria*: there is no distinct rugose adductor crest. In *Archeria* the two surfaces, anterior and posterior, on either side of the crest meet at about a right angle in the crest itself which runs obliquely, from a point in the ventral midline just distal to the fossa, to terminate below the posterior tibial condyle behind the popliteal space. In *Eogyrinus* the ventral surface of the shaft is divided into two areas, a massive cylindrical region terminating in the posterior condyle. and a flat or concave area which terminated in the popliteal space and the anterior condyle. Thus the cylindrical part follows the course of the adductor crest but is not at any point thrown into a crest. The beginning of the popliteal space, concave and rugose, just appears before the specimen is broken off.

The distal section exposed by the break (figure 14*d*) is not dissimilar to the distal view of the *Archeria* femur. The posterior part of the shaft appears cylindrical corresponding to its shape in ventral view. It is separated from the thinner anterior part of the shaft by the beginning of the intercondylar groove dorsally. Ventrally the separation, at the margin of the popliteal space, is a little further forward.

The most important differences between the *Eogyrinus* femur and that of *Archeria* are in the development of the adductor ridge and the trochanters. The lack of a strongly developed adductor ridge in *Eogyrinus* suggests a relatively weak development of the muscles concerned with the ridge, particularly as the shaft is relatively slender. Thus the adductor femoris was presumably even more weakly developed than that in *Archeria*, which in turn had a weaker adductor ridge than *Eryops* (Romer 1922, 1957). This suggests that the hind limb of *Eogyrinus* was particularly ill-developed for terrestrial locomotion.

The lack of a well-defined internal trochanter in *Eogyrinus* together with the position of the fourth trochanter are perhaps best interpreted as primitive characters. *Archeria* is in this respect reptiliomorph, with an anteriorly situated fourth trochanter and marked internal trochanter, while *Eogyrinus* resembles *Eryops* with a strongly developed fourth trochanter on the posterior border of the fossa and little or no apparent development of the internal trochanter.

In both *Eogyrinus* and *Archeria* contraction of the caudifemoral muscles, which inserted on the fourth trochanter, must have pulled the femur strongly backwards; but in the case of *Archeria* a more powerful rotational movement would also be imparted due to the position of the trochanter. In swimming this would rotate the extended (and presumably webbed) foot into a vertical plane, the best position for a rowing power stroke.

In walking pose the same combination of rotation and retraction would be adaptive to the power stroke which is presumably the reason for the position of the fourth trochanter in early reptiles. The rotation is also produced by the ilio-femoralis and the adductor, both of which insert on areas defined by the adductor ridge (Romer 1922). Thus the femur of *Eogyrinus* is both more primitive and less efficient either for walking or swimming than that of *Archeria* despite the much greater size of the Carboniferous form.

Scales

Isolated presumably ventral dermal scales, probably pertaining to *Eogyrinus*, are common in the Hancock collections from Newsham. They are preserved with the lectotype vertebrae and femur, with vertebrae and ribs in DMSW 32 (G13.76), and with a vertebra in G15.84. A few scales are also associated with other *Eogyrinus* material, thus supporting their identification. A series of much smaller scales associated with scattered limb bones probably pertain to *Pteroplax*.

The associated scales of *Eogyrinus* are of the same general type as those figured by Atthey (1876). They are elongate, varying between 40 and 60 mm in length and between 12 and 20 mm in maximum width. There is some variation in shape, but in general they are lanceolate in outline with the maximum width near one end and a blunt point at the other (figure 15).

Typically one surface, probably the inner, visceral one, shows a variably shaped, spoon-like depression at the broad end and a marked ridge forming the (?)anterior border of the depression and continuing down the midline of the scale to the point. The opposite (?external or ventral) surface is convex and bears a strong median ridge throughout. Some specimens, however, show on their exposed surface a pair of low converging ridges with a concave area between them. It is uncertain whether in this case the 'internal' or 'external' surface is exposed, but the former is more probable.

A second general type of scale (figure 15*f*, *g*) is also preserved from Newsham and probably pertains to *Eogyrinus*, but not so certainly as the first. It is not associated with any other skeletal remains of *Eogyrinus*, but both types of scale are preserved together on a small block of shale as G25.51 and the second type is associated with one of intermediate shape (figure 15*e*) on G25.52. In this second type both ends are bluntly rounded so that there is no marked taper in either direction although there is some constriction between the ends. On the exposed surface one end has the overlap depression while the other end presumably had a similar depression on the opposite surface. None of these scales shows a marked median ridge but in one example there are parallel lateral ridges with a concave area between them.

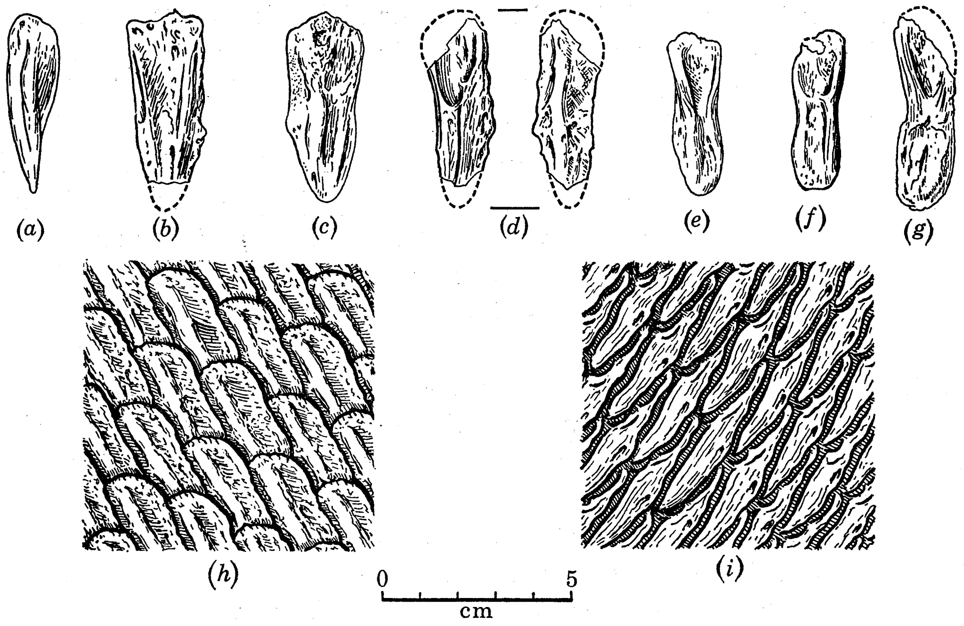

FIGURE 15. *Eogyrinus attheyi* Watson, ventral scales one-half natural size. (*a* to *g*) Single scales, (*a*) G25.54 external; (*b*, *c*) both from G15.84 – ?internal; (*d*) G25.60 internal and external views of same scale; (*e*, *f*) from G25.52; (*g*) G25.55; (*h*, *i*) reconstruction in external and internal view respectively, of an area of squamation (based on (*d*)).

The probable mode of overlap of the first type of scale can be seen from two isolated and matrix-free scales (G25.60) one of which is probably the specimen figured by Atthey. Assuming, as in the description, that the depression is internal and that the ridge forms its anterior border, and further assuming that the depression is at the medial end of the scale, the overlap can be reconstructed from the fit of the scales. Thus the anterior border of the posterior scale of an adjacent pair overlies (is internal to) the posterior border of the one in front, so that the front edge of the posterior scale rests against the ridge of the latter. The depression obviously accommodates the point of a more medial scale so that the point of each scale lies internal to the one distal to it in the same lateral row. Finally the best fit between the two isolated scales is when the depression of the posterior one is somewhat distal to that of the one in front. This would result in an overall staggering of the boundaries of the scales in successive rows like courses of bricks in a wall.

Presumably, as in other labyrinthodonts, the ventral scales or gastralia were arranged in a chevron pattern with the median angle of each row directed forwards. The general pattern of

Eogyrinus would then be closely similar to that figured by Cope (Cope & Matthew 1915; Panchen 1970) in *Archeria*. It seems probable that the ventral armour of scales was both flexible and to some extent could contract or expand in area. The best fit between scales as seen in 'internal' view appears to correspond to a greater degree of overlap between successive transverse rows than the best fit in 'external' view. Thus variations in trunk volume due to respiration as well as deformation in swimming would be possible. In figure 15 the reconstruction of an area of squamation is 'expanded' in presumed external view but 'contracted' in internal view.

RECONSTRUCTION OF THE SKELETON

In order to summarize our knowledge of the anatomy of *Eogyrinus* an attempt has been made to reconstruct the whole skeleton, together with a highly speculative reconstruction of the living animal (figure 16). The restoration of the skull, of course, follows that already given, but that of the postcranial skeleton requires some comment.

The axial skeleton of the trunk and the proximal region of the tail can be restored with some confidence. In my account of the axial skeleton (Panchen 1966) I gave reasons for believing that the number of trunk vertebrae was similar to that in *Archeria*. *Archeria* has some 40 presacral vertebrae (Romer 1947; Carroll 1970), 39 have been restored for *Eogyrinus*. The last 24 trunk vertebrae of *Eogyrinus*, or rather the regional variation they show along the series, are well known from the length of articulated column preserved in the Hancock Museum (G13.77 – DMSW 33). However, more anterior vertebrae are known from the lectotype and, apart from the nature of the axis-atlas complex, the whole trunk column may be restored without fear of serious error. The sacral vertebra and rib and the first seven caudals with the first four caudal ribs are also known from DMSW 33.

The trunk rib series is known in much the same way as the vertebrae. Seven ribs from various parts of the trunk were figured in reconstructed anterior–posterior sequence in the account of the axial skeleton and there are a large number of isolated ribs in the Hancock Museum which fill the morphological gaps in this series. The first member of the series was one in which the postero-dorsal edge of the shaft was prolonged as a blade proximally and it was suggested that this was a pectoral rib underlying the girdle: a second rib of this type is also known. Four such ribs from one side of the body have been drawn in the reconstruction, in contrast to the higher number in related amphibia such as *Kotlassia* (Bystrow 1944), because of the presumed small size of the girdle.

The reconstruction of the tail beyond the seventh caudal vertebra is conjectural but not completely without evidence. It has been drawn with roughly the same length as the trunk as in Romer's (1956) sketch restoration of *Archeria* and is largely based on data from that genus. As well as in *Archeria* caudal vertebrae have been figured in *Diplovertebron*, *Nummulosaurus* (Fritsch 1901; Panchen 1970) and *Spondylerpeton* (Romer 1930; Panchen 1970).

The most noteworthy feature of the tail of anthracosaurs, judged from this material, is the form of the more posterior neural spines. They are set very far posteriorly relative to their respective pleurocentra and are slender and inclined backward at about 45 degrees. A figure of some posterior vertebrae of *Archeria* given by Case (1911; Panchen 1970, fig. 6*h*) also shows them to have been very elongate and Romer's restoration of *Archeria* shows the presence of a tail fin supported either by these spines or possibly by supraneural spines articulating with them. He notes, however, that the details are uncertain.

An isolated caudal vertebra in the Royal Scottish Museum (R.S.M. 1957.1.5806) may give limited support to a similar structure of the tail in *Eogyrinus*. The specimen consists of an almost perfect caudal pleurocentrum bearing a fused neural arch with a spine, unfortunately broken off just above the postzygopophyses, which are apparently just like those of *Archeria* or *Nummulosaurus*. It comes from the Splint Coal, Wishaw, Lanarkshire, which is of Lower Similis-pulchra zone age and thus within the recorded time span of *Eogyrinus*. The only other species to which it could pertain is *Anthracosaurus russelli* which has, however, not been recorded quite so late in the Coal Measures and is a much rarer form.

The posterior part of the tail of *Eogyrinus* has, therefore, been restored with elongate, fin-supporting spines but it is probable that these did not extend proximally to very near the sacral region. An isolated vertebra from farther down the tail than the seven proximal caudals is preserved in DMSW 33 (Panchen 1966, fig. 10*c*). This is slightly smaller in diameter than the Wishaw specimen, but is thicker antero-posteriorly suggesting that it is from a more proximal part of the tail of a somewhat smaller animal. Only the base of the neural arch is preserved, but it appears to be like that of the trunk and proximal caudal vertebrae and not like those of the slender-spined distal caudals.

Another problem concerns the extent of the caudal ribs. The proximal caudal ribs are of very distinctive shape. The first four right ribs are preserved in association with their vertebrae (Panchen 1966, fig. 8) and it seemed from the form of the vertebrae that only one or at the most two more pairs of ribs could have been present, the seventh vertebra (and the more distal one) lacking any clear transverse process. However, the Wishaw vertebrae appears to have transverse processes. Only six pairs of ribs have been drawn in the reconstruction.

Unfortunately but inevitably the restoration of the appendicular skeleton is unsatisfactory. The femur is the only appendicular element certainly associated with *Eogyrinus*, although the interclavicle described is certainly eogyrinid. The rest of the pectoral girdle is based on Romer's figures of that of *Archeria* as are the humerus, the radio-ulna and the hand.

The ilium and part of the ischium are based on an actual specimen. It has been pointed out (Panchen 1970, p. 53) that one of the two ilia referred by Romer (1945) to the genus *Memonomenos* as *M. simplex* (Fritsch) is that of a large anthracosaur. Unfortunately the other specimen is Fritsch's type and is certainly not the same species and probably not anthracosaurian. The anthracosaur specimen has therefore no specific designation. It was originally part of Fritsch's *Macromerium schwartzenbergii*, which name, however, is properly applied to a pelycosaur (Romer 1945).

The specimen (Fritsch 1889, Plate 66, figs. 1, 2) consists of a complete ilium with a strongly developed post-iliac process and a large part of the ischium. Its structure appears from Fritsch's figure to be very similar to that of *Archeria*, although correlated with its larger size it is more massively built. I have already pointed out that its size is such that it is well within the *Eogyrinus* range, but by comparison with the proportions of *Archeria* perhaps representing a slightly smaller individual than the *Eogyrinus* lectotype femur.

The probability of Fritsch's specimen being an eogyrinid is very high: archeriids are unknown in Europe and anthracosaurids, apart from their rarity, are known only from the Lower and Middle Coal Measures of the British Isles, apart from two doubtful American species (Panchen 1970). Fritsch's specimen is from the Upper Stephanian of Kounová, Czechoslovakia. Although considerably later than the Upper Coal Measure specimens of *Eogyrinus* it is not unlikely that it should be referred to the same genus. It is used in the reconstruction after Fritsch's figures with a very slight size adjustment.

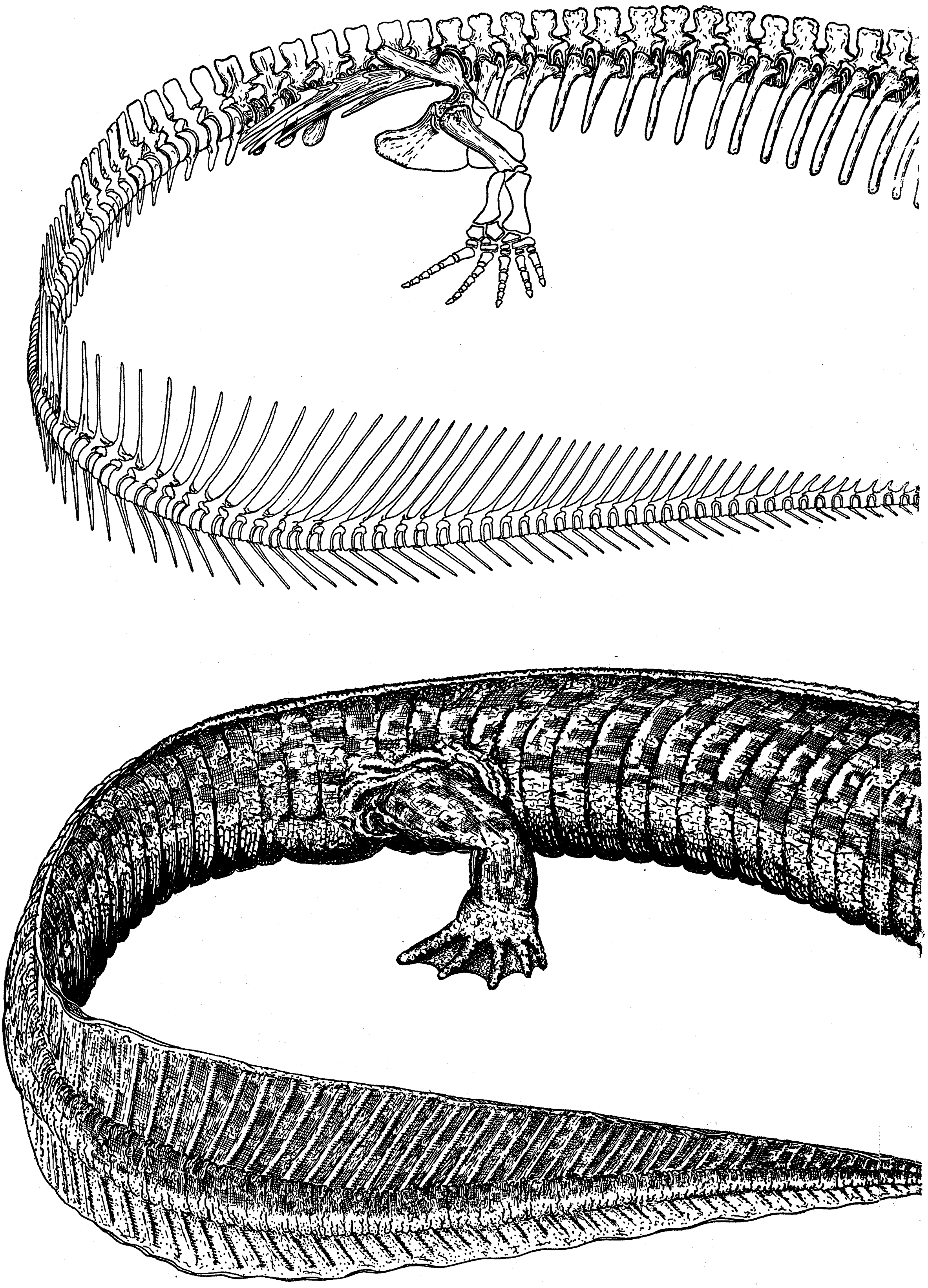

FIGURE 16. *Eogyrinus attheyi* Watson: composite restoration of the skeleton and the living animal. Estim

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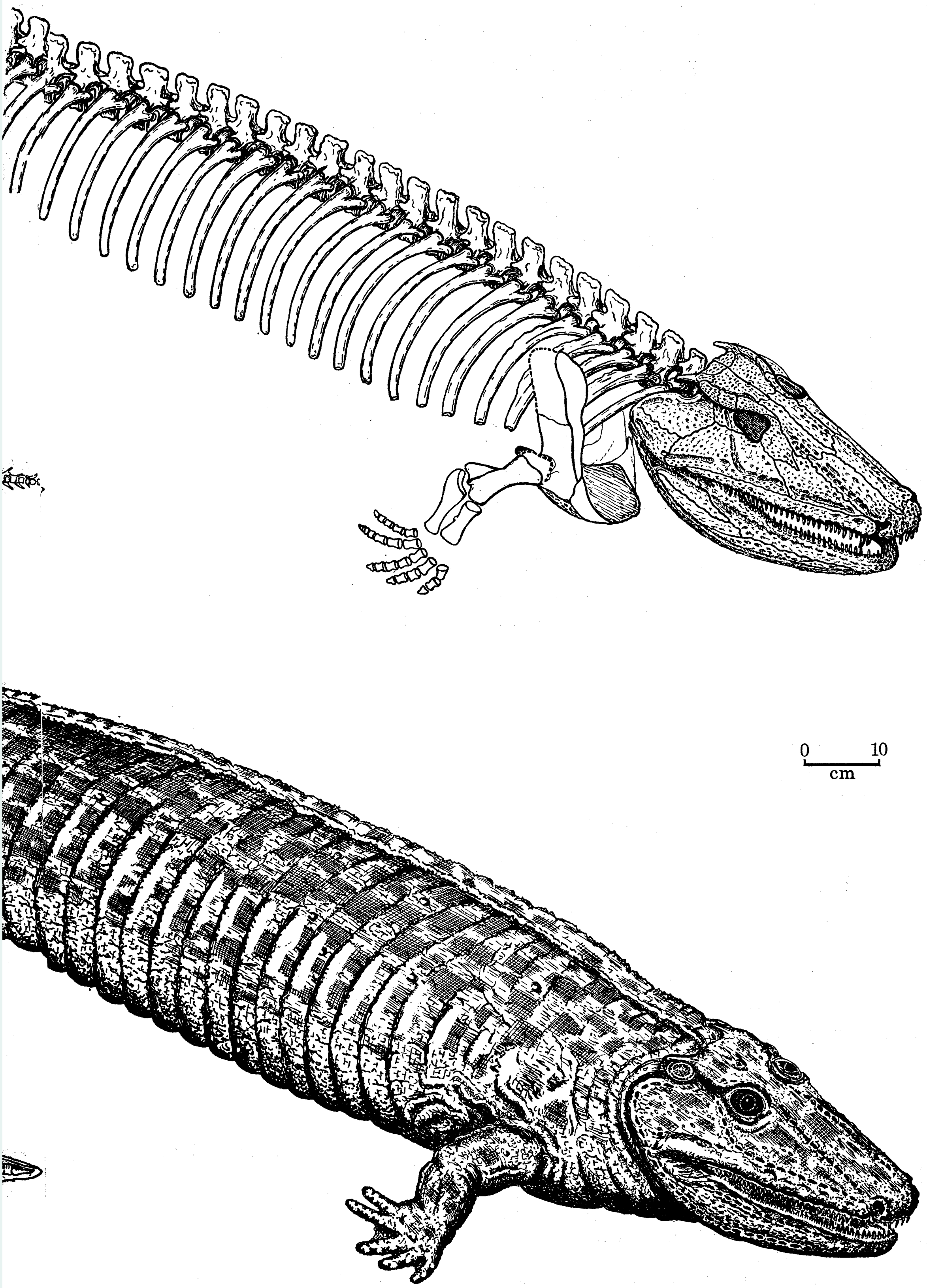

ed overall length of the original animal about four metres. Conjectural regions of the skeleton unshaded.

As in the forelimb, the distal elements of the hind limb are based on those of *Archeria*. It should be noted, however, that the considerable differences in the two genera between their respective femora and, if correctly assigned, the interclavicles, would lead one to expect differences in the distal parts of the limbs as well. It is probable, however, that the restoration of five digits in both the manus and the pes is correct, as this is a character common to all batrachosaurs in which the feet are known.

Little need be said about the 'flesh' reconstruction. The ventral scales are not shown with the skeleton but are suggested in the whole animal. Nothing further is known of the integument: if dorsal scales were present they were probably small dermal 'squamulae' of bone like those of *Eryops* (Romer & Witter 1941), but may not have been visible from the surface. The only standards of comparison for the external appearance are the larger living urodeles, but they are taxonomically remote.

Functional considerations determined the reconstructed body form. It is generally agreed that the long-bodied anthracosaurs were anguilliform swimmers in which the trunk as well as the tail produced propulsive lateral waves (Parrington 1967; Panchen 1970). In fish locomotion the amplitude of these waves increases from head to the end of the tail so that in *Eogyrinus* the trunk would taper from front to back as well as the tail to produce the necessary increase in flexibility. This is not taken into account in Romer's restoration of *Archeria*.

In *Eogyrinus* the dimensions of the thoracic region are set by the large hoop-like ribs. It is also very probable that these marked the course of persistent well-developed myosepta (Panchen 1967*a*) and that the segmental divisions were obvious externally. Thus the body rings have been drawn with their boundaries corresponding to the position of the ribs in the trunk. The pose of the feet is similar to that commonly seen in urodeles when they are floating passively below the surface.

The majority of the material on which this study is based is in the collections of the Hancock Museum: I am therefore particularly indebted to the Curator, Mr A. M. Tynan, and to the Council of the Natural History Society of Northumberland, Durham and Newcastle upon Tyne for the opportunity to study the unique material in their care. I am also grateful to the authorities of the British Museum (Natural History), The Royal Scottish Museum, the Institute of Geological Sciences and the Manchester Museum for the loan of the remaining specimens.

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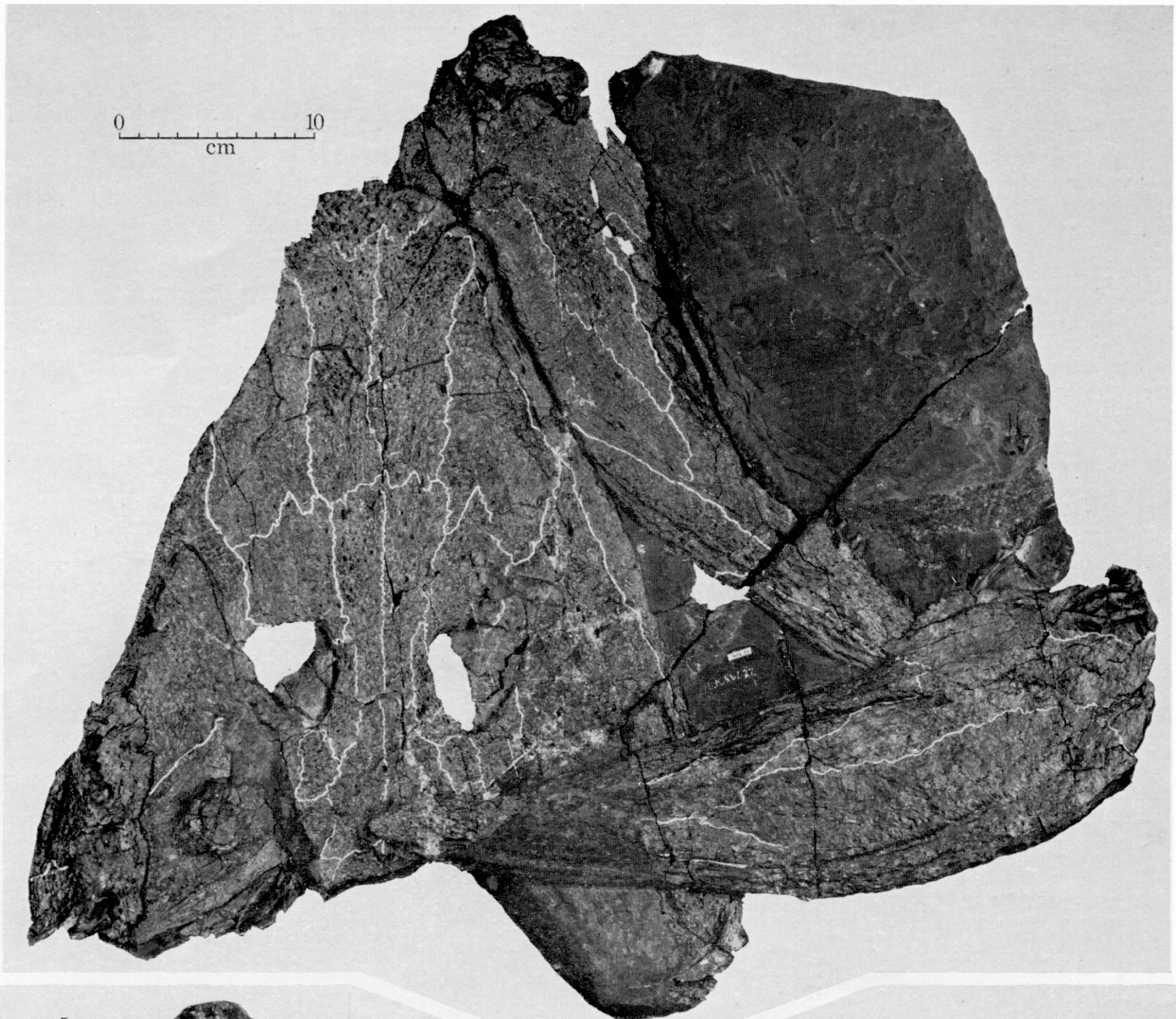

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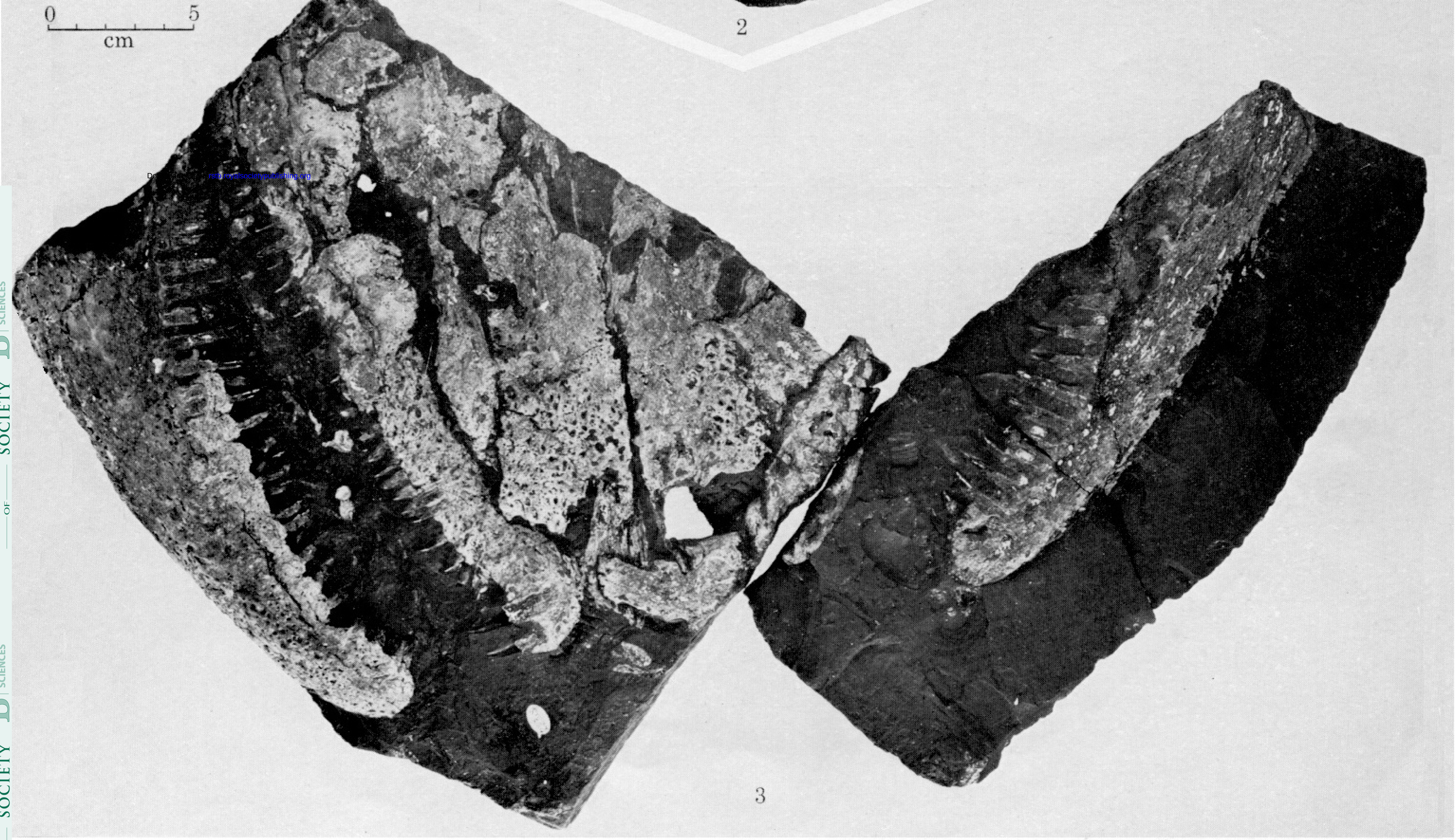

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FIGURE 2. *Eogyrinus attheyi* Watson, skull of lectotype in dorsal view.

FIGURE 3. *E. attheyi* Watson, the Airdrie skull in dorsal view.

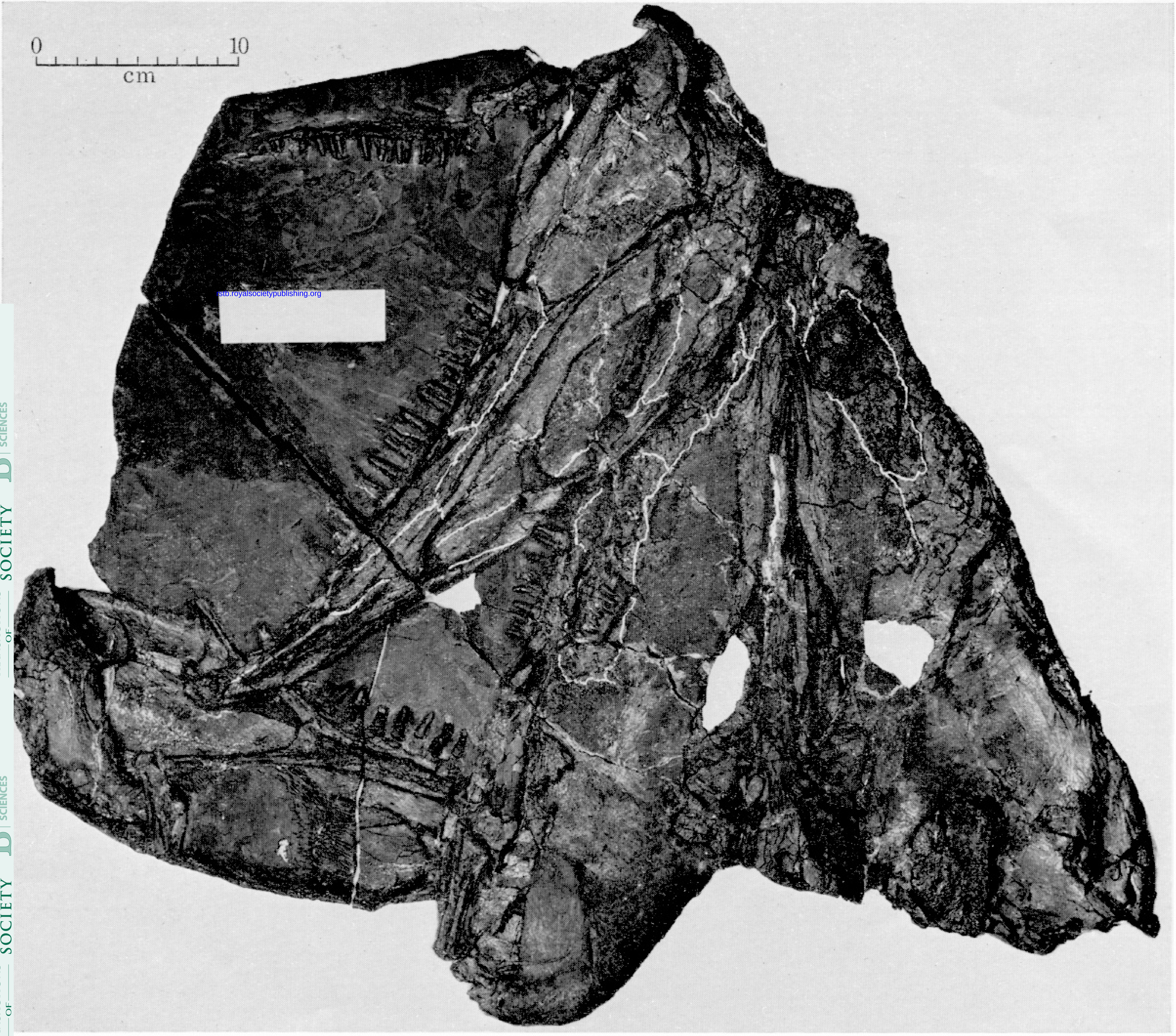

FIGURE 5. *E. attheyi* Watson, skull of lectotype in ventral view.