ON *ANTHRACOSAURUS RUSSELLI* HUXLEY (AMPHIBIA: LABYRINTHODONTIA) AND THE FAMILY ANTHRACOSAURIDAE

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[Plates 1 and 2]

CONTENTS

A complete description is given of all the known material attributable to *Anthracosaurus russelli* Huxley. Apart from one skull specimen from Usworth Colliery, Washington, Tyne and Wear, England, all known specimens come, or are thought to come, from the Blackband Ironstone of Airdrie, near Glasgow, Scotland. Both horizons are of Coal Measure age, the former Westphalian A, the latter Westphalian B.

Complete preparation of the holotype allows a reconstruction of the skull roof and occiput and, together with the Usworth specimen, the palate and a series of skull sections. Two lower jaw specimens are described for the first time. The cranial anatomy of *Anthracosaurus* is that of a massive embolomerous anthrocosaur which differs from eogyrinid embolomeres, notably *Eogyrinus attheyi*, in a number of important features. These include loss of the skull table/cheek kinetism and presence of an orbital lacrimal, biramous tabular horns and a wide dorsal exposure of the quadrate. Features of the palate are correlated with the distinctive dentition of relatively few very large marginal teeth and long palatal tusks: they include broad plate-like pterygoids, whose anterior rami meet in a median suture and extend laterally to the palatine tusks (thus largely concealing the palatine bones from ventral view) and whose quadrate rami lack a deep descending flange. The lower jaw is unique in having confluent meckelian fenestrae.

Vertebrae attributed to *A. russelli* are of normal embolomerous type except that the notochordal canal is occluded by a bony plug in the centra. An interclavicle of distinctive shape is also attributed.

Several North American embolomere specimens are presently placed within the family Anthracosauridae. Of these the most complete is *Eobaphetes kansensis* Moodie consisting of three blocks, the original holotype and paratype and a third block not before described. As was first demonstrated by Dr Donald Baird these comprise a single skull, here described in its entirety.

Description of *Eobaphetes* is preceded by a discussion of its provenance. This was originally recorded as 'Coal Measures', Washington County, Kansas, which is improbable but not more so than its current attribution to the Namurian of Washington County, Arkansas. Coal and spore analysis, supported by palaeogeography, suggest a late Pennsylvanian, probably Stephanian, horizon.

In most respects the anatomy of skull roof and lower jaw of *Eobaphetes* suggests relationships with *Eogyrinus* rather than *Anthracosaurus*. This is also the case with the closely related *Leptophractus obsoletus* from Linton, Ohio, to which species '*Anthracosaurus lancifer*', also from Linton, is referred. However, *Eobaphetes* and *Leptophractus*, together with *Neopteroplax conemaughensis*, share a number of distinctive features. These include a flat-topped surangular crest to the jaw and, importantly, a dentition of massive palatal tusks and anterior marginal teeth but numerous small posterior teeth in maxillary and dentary. Tooth shape is also distinctive.

It is thus proposed to retain the family Anthracosauridae for *A. russelli* alone, while placing the American species within the Eogyrinidae, but as a new subfamily the Leptophractinae, distinct from the Eogyrinidae. A diagnosis of each of these taxa is given.

INTRODUCTION

The holotype of *Anthracosaurus russelli* Huxley (1863) consists of a massive skull, almost completely preserved but lacking the lower jaw. The specimen was discovered by workmen on the estate of the Monkland Iron and Steel Company, near Airdrie, Lanarkshire, about 12 miles east of Glasgow, in 1861. The skull was eventually sent to Huxley for study by a Mr James Russell, mineral surveyor.

It was originally enclosed in a large nodule from the Airdrie or Mushet's Black Band Ironstone. The ironstone is of Middle Coal Measure age and lies near the top of the Modiolaris zone in the Scottish Central coalfield. It is thus middle Westphalian B in European terminology (Westoll 1951; Panchen & Walker 1961; Panchen 1970). With one exception all known specimens of *Anthracosaurus russelli* are believed to have come from the same locality and horizon.

The exception is an incomplete skull discovered several years ago at Usworth Colliery, near Washington, County Durham. This specimen, again lacking the lower jaw, is enclosed in a sandstone matrix from the roof of the Top Busty seam and is thus of Lower Coal Measure age (U. Communis zone: Westphalian A) (Panchen, Tilley & Steel 1967; Panchen 1970).

The palatal surface of the holotype was originally cleared of almost all of its investing matrix by Huxley, but because of the intractible nature of the ironstone matrix and the crude methods of preparation of the time the surface is considerably damaged. Subsequently the occipital surface and the extreme back of the skull table were prepared with greater skill by Professor Dr M. S. Watson, F.R.S., who gave a revised account of the specimen in his review of Scottish

Carboniferous Amphibia (Watson 1929). I later cleared most of the dermal skull roof and gave a preliminary figure and reconstruction in a monograph on the Anthracosauria (Panchen 1970). Preparation of the whole skull is now complete (see below – Materials and methods).

No anatomical account of the lower jaw of *A. russelli* has been previously given and both Watson and, until recently, I were unaware of the existence of two incomplete jaw rami from Airdrie. The first of these has been on exhibition in the public galleries of the British Museum (Natural History) as an example of a Coal Measure fossil for many years (!) and was presented to the Museum in 1921. The other is the property of the Glasgow City Museum and Art Galleries at Kelvingrove and was sent to me for identification in September 1973 by Dr W. D. I. Rolfe of the Hunterian Museum, Glasgow University.

Little is known of the postcranial skeleton. Huxley described a pleurocentrum and neural arch from a trunk vertebra together with a rib from a block containing three other ribs and two intercentra. Watson rightly pointed out that these specimens were not then diagnostic within the embolomerous anthracosaurs and could be attributed to *A. russelli* only on locality and horizon.

An anthracosaur interclavicle from the Royal Scottish Museum may also tentatively be referred to *A. russelli*. It is apparently from a large anthracosaur and differs significantly from that of *Eogyrinus attheyi* Watson (Panchen 1972*a*), the only other British anthracosaur of comparable size. There is also some reason to believe that it is from Airdrie (see below).

An account has recently been given of the history of the discovery and classification of embolomerous anthracosaurs (Panchen 1970). *Anthracosaurus russelli* was placed in the family Eogyrinidae by Watson (1929), but separated from *Eogyrinus* and other British anthracosaurs by Romer (1945*b*, 1947, 1963, 1966). In the last edition of his text Romer (1966) included *Anthracosaurus* (with *Eobaphetes*, *Erpetosuchus* and *Leptophractus* as probable synonyms) together with *Crassigyrinus* (doubtfully) as members of the family Anthracosauridae. I have been able to show that *Crassigyrinus scoticus* Watson (1929), the only described species of that genus, is not an anthracosaur, but a unique and relict form with several fish-like features (Panchen 1970, 1973).

With elimination of *Crassigyrinus* the following nominal species have been attributed to the family Anthracosauridae:

Anthracosaurus russelli Huxley (1863)
Anthracosaurus lancifer (Newberry) (Romer 1963)
Leptophractus obsoletus Cope (1873)
Eobaphetes ('*Erpetosuchus*') *kansensis* Moodie (1916)

In the present work all the material attributable to *Anthracosaurus russelli* is redescribed and a reconstruction of the whole skull is presented. An account is also given of the holotype of *Eobaphetes kansensis* together with two other specimens. As Dr Baird first concluded all three are parts of the same individual and together allow a reasonably detailed account of the cranial anatomy. Unfortunately there is still considerable doubt as to the provenance of *Eobaphetes* and a full account is given of the evidence of its locality and horizon.

Like *Eobaphetes*, *A. lancifer* and *Leptophractus* are both North American anthracosaurs, but both came from the famous cannel coal underlying the U. Freeport Coal at Linton, Ohio (Romer 1963; Panchen 1970). The relationship of the three North American forms to *A. russelli* and thus their membership of the family Anthracosauridae is considered in the final section.

MATERIALS AND METHODS

The specimens that have been referred to the family Anthracosauridae are listed below. The following abbreviations are used for the institutions owning the material:

A.M.N.H.	Department of Vertebrate Paleontology, American Museum of Natural History, New York.
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.G.	Hunterian Museum, Glasgow University.
K.M.	Department of Natural History, Glasgow City Museum and Art Galleries, Kelvingrove.
O.S.U.	Geological Museum, Ohio State University.
R.S.M.	Department of Geology, Royal Scottish Museum.
S.M.	Central Library, Museum and Art Gallery, Sunderland, Tyne and Wear.
U.S.N.M.	Division of Vertebrate Paleontology, U.S. National Museum (Smithsonian Institution) Washington, D.C.

Anthracosaurus russelli Huxley (1863)
(non Atthey 1876, Hancock & Atthey 1869)

From the Mushet's or Blackband Ironstone, Airdrie, Lanarkshire (now Strathclyde Region); Upper Modiolaris zone, Middle Coal Measures, Westphalian B, Upper Carboniferous. *N.B.* While it is reasonably certain that the Airdrie specimens come from the Modiolaris zone horizon, another horizon, the Palace Craig Ironstone (L. Similis–Pulchra zone, U. Westphalian B: Westoll 1951; Panchen & Walker 1961), has yielded fossil labyrinthodonts near Airdrie. The Palace Craig is sometimes referred to as the 'Palace Craig Blackband' and also as Mushet's Ironstone. Dunlop (1907, 1910) states that the holotype was found in the Palace Craig.

G.S. 28313. Nearly complete skull lacking the right suspensorial region, no associated mandible. HOLOTYPE Huxley (1863), also figured Watson (1929), Panchen (1970).

B.M.(N.H.) R4822 (presented by Catherine A. Raisin, D.Sc. in 1921). Anterior half of left jaw ramus, exposed in mesial view.

K.M. G73–87QA. Anterior half of left jaw ramus, exposed in mesial view but badly eroded. Figured McNair (1912). Probably from Carnbro Pit (Mr E. N. Cambell – in litt.).

H.M.G. V.2014. Fragment of maxillary and ?ectopterygoid with teeth and tusk embedded in ironstone.

H.M.G. V.2015. An isolated tusk, the tip of the crown as natural mould, the rest exposed as a longitudinal section.

B.M.(N.H.) 37324. A block of ironstone surfaced with shale containing a pleurocentrum with articulated neural arch and associated intercentrum, another intercentrum and four incomplete ribs: figured in part Huxley (1863).

G.S. 56580. Natural mould in ironstone shale of three neural arches in articulation, right lateral view; from Airdrie: matrix probably Blackband Ironstone.

G.S. 56581. Natural ironstone mould as above – three embolomerous vertebrae in articulation, left lateral view.

G.S. 54119–54120. Two isolated embolomerous pleurocentra with remnants of ironstone matrix. Both registered as 'Carboniferous Limestone series, Airdrie, *Anthracosaurus*'.

R.S.M. 1971.11.4. (Grossart Collection: originally lot 1893.20 (256)) an incomplete interclavicle, exposed in ventral (external) view.

The last specimen is labelled 'Labyrinthodont scale'- horizon 'Lower Carboniferous'- locality '?Loanhead'. However, other specimens of *A. russelli* from Airdrie, including the holotype and the above centra, were originally labelled as Lower Carboniferous or 'Carboniferous Limestone', and the matrix appears to be from the Airdrie Blackband, rather than from the (Limestone Group, but U. Carboniferous) Loanhead No. 2 Ironstone from which fossil amphibia have been recovered near Edinburgh. Dr C. D. Waterston informs me that the collector obtained most of his material from Lanarkshire.

From a sandstone overlying the Top Busty Seam, Usworth Colliery, near Washington, County Durham (now County of Tyne and Wear); U. Communis zone, Lower Coal Measures, Westphalian A, Upper Carboniferous.

S.M. 193/1966a–f. An incomplete jawless skull, exposed mainly in palatal view, in three blocks, together with blocks containing teeth from the same individual. Figured Panchen *et al.* (1967).

Anthracosaurus lancifer (Newberry) comb. Romer (1963).

All specimens from a canneloid shale below U. Freeport Coal, Linton Diamond Mine (Yellow Creek), Jefferson County, Ohio, U.S.A.; Allegheny Group or series, Middle Pennsylvanian equivalent to Westphalian D, Upper Carboniferous.

O.S.U. 4500. An isolated lanceolate tooth preserved as a natural cast. HOLOTYPE of *Rhizodus lancifer* Newberry (1856, 1873), as *Anthracosaurus lancifer*: Romer (1963).

A.M.N.H. 6830. Two counterpart slabs showing anterior snout and lower jaw, mostly as natural moulds. Figured Cope (1875, pl. 38) as *Leptophractus obsoletus*, Romer (1963) from casts made after etching by Dr D. Baird, as *A. lancifer*.

A.M.N.H. 6969. Two counterpart blocks showing three vertebral central elements and two neural arches, all in articulation as natural moulds. One block tentatively associated with *L. obsoletus* and figured Cope (1875, pl. 39) since lost, the other as ?*A. lancifer* by Romer (1963), specimen labelled '*Spondylerpeton*'.

A.M.N.H. 6939. Natural mould of incomplete shoulder girdle with scales, figured Romer (1963).

Leptophractus obsoletus Cope (1873) from Linton.

A.M.N.H. 6831. Natural mould of jaw ramus with part of maxillary region, with teeth and tusk, SYNTYPE. Figured Cope (1875, pl. 39, fig. 1).

Columbia University specimen: Natural mould of jaw ramus and maxillary region, with teeth and tusks, SYNTYPE. Figured Cope (1875, pl. 39, fig. 2) [not seen].

Eobaphetes kansensis Moodie (1916) (*Erpetosuchus kansensis* Moodie 1911). Horizon and locality in dispute (see below).

U.S.N.M. 6699. Incomplete skull originally exposed in ventral view; including braincase and part of palate with skull table and left suspensorial region together with two vertebral centra; overlain by incomplete right jaw ramus in lateral view. HOLOTYPE of *Erpetosuchus* (preoccupied) *kansensis* Moodie (1911). Figured Moodie (1916) as *Eobaphetes kansensis* (jaw ramus as left maxilla and nasal in errore), *vide* also Romer (1930, 1963), Panchen (1970).

U.S.N.M. 6680. An almost complete left jaw ramus, from the same individual as U.S.N.M 6699. PARATYPE.

N.S.N.M. unregistered ('the Bassler block' – Baird in litt. 1962). Left suspensorial region in dorsal view, in continuity with holotype, with part natural moulds of both jaw rami.

The nodule in which the holotype skull of *A. russelli* was enclosed was of typical blackband ironstone structure, with thin concentric, but not continuous, layers of coal of about 1 mm thickness scattered through it. The presence of the coal made development easier than it otherwise might have been, as the matrix covering the skull roof was up to 3 cm in thickness. The outer layers of matrix were taken off with hammer and very sharp quarter-inch chisel: then a dental mallet was used and final development was by an S. S. White Industrial Airbrasive Unit with calcium dolomite powder.

The bone of the left (complete) cheek region roofing the subtemporal fossa had been reduced by the original development to a thickness of about 2 mm in many places. Over most of this area the ventral periosteal bone had been completely stripped off and the whole was very fragile. It was therefore reinforced ventrally by the application of numerous coats of a solution of polystyrene in toluene (Thurmond 1974) before final cleaning of the dorsal surface was attempted. No attempt was made to clean the incomplete left cheek region which is distorted and disrupted in addition to having similar developmental damage ventrally.

Development of the other Airdrie specimens was, where necessary, entirely by Airbrasive unit, followed by coating with a very dilute solution of Perspex in chloroform. The County Durham skull was also cleaned by Airbrasive unit on the palatal surface but the dorsal surface is covered with an intractable sandstone which would not yield to development by mallet or Airbrasive. The chief value of the specimen is to give detail of the anterior region of the palate.

The Linton specimens were studied during a visit to the U.S.A. in 1971 both as the original natural moulds and as casts prepared by Dr Baird. In addition plastic casts of A.M.N.H. 6830 (left counterpart: Romer 1963, fig. 12), A.M.N.H. 6969 and A.M.N.H. 6831 were kindly prepared for me in the American Museum of Natural History, and of O.S.U. 4500 in the Ohio State University Museum.

Some preparation has been carried out on the specimens of *Eobaphetes*. The dorsal surface of the holotype block has been completely cleared of matrix by using the same techniques employed on the holotype of *Anthracosaurus* and some surface cleaning has been done with the Airbrasive unit on the paratype jaw ramus. The Bassler block, however, was judged too delicate for any but slight cleaning of the exposed dorsal surface and was left intact.

Virtually all matrix developed from the *Eobaphetes* specimens has been retained for spore and other analysis.

The matrix of both the holotype and the Bassler block includes informative natural moulds of missing regions of the jaw rami, particularly those of the paratype (left) jaw articular and surangular region. Casts of these were taken by brushing on successive layers of indian ink filled 'Rubberlin' latex. (Jim Robbins Co., Troy, Michigan, U.S.A.). After drying the casts stripped off without damage to give an excellent impression.

ANTHRACOSAURUS RUSSELLI HUXLEY

Dermal skull roof

The skull roof of the holotype is virtually complete except for the right suspensorial region, as noted above (figure 1). Because of the extreme massiveness of all the cranial bones, and also no doubt because it was enclosed in a nodule, compression has not affected the skull to the degree that it has in the lectotype of *Eogyrinus attheyi* Watson, the only other complete British anthracosaur skull of comparable size (Panchen 1972*a*).

The snout region of the *Anthracosaurus* skull retains its original outline in dorsal view and very little 'spreading' of the skull appears to have taken place due to compression in the preorbital region. Compression has, however, forced down the median bones of the skull roof, together with the underlying braincase, relative to the skull margin. As a result the lacrimal and anterior part of the jugal bones are distorted and somewhat disrupted, particularly immediately in front of the orbit.

The left cheek region and suspensorium are complete but have been flattened post-mortem into an almost horizontal plane. On the right the cheek region is preserved only to the transverse level of the back of the skull table and has suffered disto-mesial compression as well as flattening. As noted above the dorsal matrix has not been removed from this right cheek region but the skull roof is visible ventrally.

All the sutures of the skull roof may be traced with ease and there is little or no scope for alternative interpretation, even in the disrupted preorbital region. Apart from the right cheek region all the dermal ossifications and their bounding sutures are matrix-free and visible on both sides of the skull.

The most striking feature of the skull of *Anthracosaurus*, particularly when compared with that of *Eogyrinus*, which is of similar size, is the extreme massiveness of the former. This is particularly correlated with the enormous teeth which are characteristic of *Anthracosaurus*. The roots of the marginal teeth are set in unusually deep maxillary and premaxillary bones so that the snout is very deep anteriorly.

The external nares are well preserved on both sides and are very large, but that part of each nasal bone which roofs them has been depressed together with the back of the premaxillary on both sides, post-mortem, to close the narial aperture almost completely. There is some constriction of the skull margin below the naris in the plane of the maxillary-premaxillary suture in lateral view, and some constriction of the snout in this plane in dorsal view. However, there is no clearly defined naso-labial groove like that of eogyrinid anthracosaurs and other primitive labyrinthodonts (Panchen 1967). The nares are also somewhat more dorsally situated and relatively closer together as well as being larger than those of *Eogyrinus*.

The orbits are somewhat larger than those of *Eogyrinus* and in the undistorted skull would have 'looked' more laterally (rather than dorsally) than those of the latter. The orbits are also more widely separated than in *Eogyrinus* and behind the orbits the skull table of *Anthracosaurus* is nearly 30 % wider. The circular pineal foramen, like that of *Eogyrinus*, is small (4 mm diameter) and not conspicuously raised.

The back of the skull table in dorsal view is more deeply concave in *Anthracosaurus* and the cheek/suspensorial region extends considerably further behind the posterior edge of the table. This latter feature was regarded by Romer (1947) as characteristic of the family

Anthracosauridae and was used to include the unrelated relict *Crassigyrinus* within that family (Panchen 1970, 1973). However, the long suspensorium of *Anthracosaurus* is simply a measure of the length behind the skull table. The orbit-quadrate distance is not very different from that of *Eogyrinus*.

Significant dimensions of *Anthracosaurus* and *Eogyrinus* are compared in table 1. The standard indices (Nos. 1–5) are those adopted in comparing eogyrinid skulls (Panchen 1970, 1972*a*). All measurements except those of tooth row (no. 5) and suspensorium (no. 12) are in a sagittal, parasagittal or transverse plane.

TABLE 1. *ANTHRACOSAURUS RUSSELLI* AND *EOGYRINUS ATTHEYI* TYPE SKULLS

		Anthracosaurus/mm	*Eogyrinus*/mm
1	overall length (Q length)	400	410
2	median length (PP length)	295	340
3	snout-pineal length	250	285
4	pineal-back of skull table (pineal-PP)	45	*ca.* 54
5	tooth row length	230	250
6	snout width (at pmx–mx suture)	75	70
7	min. internarial width	42	57
8	length of naris (ant.-post.)	30	17
9	min. interorbital width	62	45
10	min. width, orbit-jaw margin (in plane of dermal bone)	32	67
11	length of orbit	68	50
12	back of orbit to quadrate	170	160
13	max. width of skull table	114	90

The dorsal surface of the dermal roofing bones has been freed of matrix with little or no apparent surface damage and yet the dermal ornament appears to be very little developed. This is in striking contrast to the condition in eogyrinid anthracosaurs (Panchen 1964, 1970, 1972*a*). The premaxillary is ornamented with small, widely spaced pits and there is shallow more closely-spaced pitting around the dorsal borders of the orbits. Elsewhere there has been an extreme reduction of the characteristic anthracosaur ornament (assuming that the ornamented condition is the primitive one: Panchen 1975), in scale, density and relief.

The reduction of the ornament is coupled with an almost complete absence of lateral line sulci (see below). These two features, together with the massive reptiliomorph appearance of the skull and the large teeth give the impression that *Anthracosaurus russelli* was a more terrestrial animal than the eogyrinid and archeriid embolomeres.

In most respects the pattern of dermal bones is typical of embolomerous anthracosaurs and similar to that of *Eogyrinus*. Thus the horned tabular contacts the parietal on each side, there is a persistent and large intertemporal bone on each side at the front of the skull table and the supratemporal forms little of the border of the otic notch. Two important features of the skull, however, distinguish *Anthracosaurus* from all described embolomeres. These are an orbital lacrimal and the absence or extreme reduction of any kinetic joint between the skull table and cheek region.

Although disrupted, the lacrimal bone is present on both sides of the skull. Anteriorly it is bordered along its mesial edge by the antero-lateral part of the nasal, which forms the roof of the external nostril. In this region the lacrimal tapers anteriorly to form a truncated process, intact on the right, broken but complete on the left, which just enters the posterior

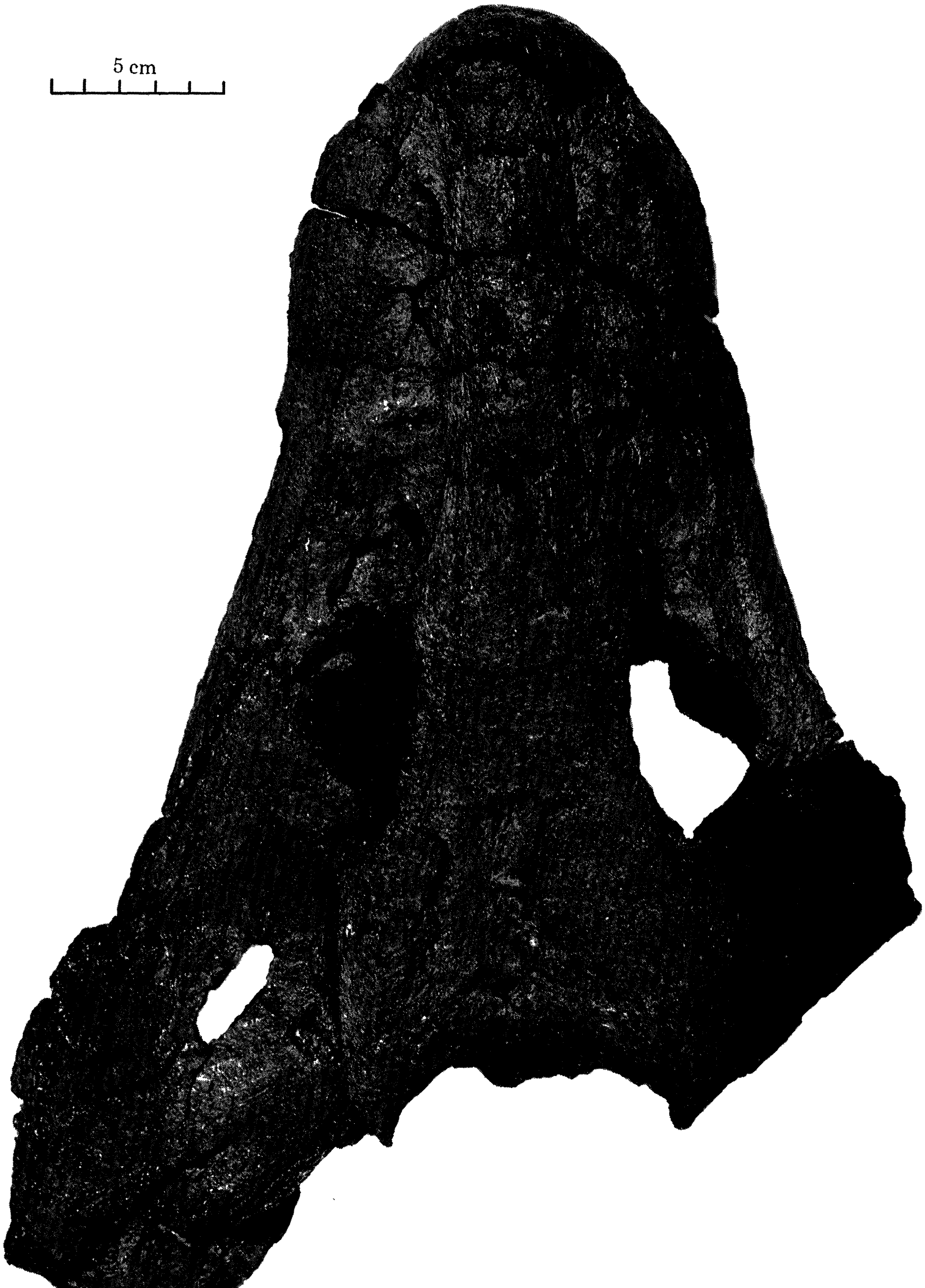

FIGURE 1. *Anthracosaurus russelli* Huxley, holotype skull in dorsal view. Half natural size.

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FIGURE 2. *Anthracosaurus russelli* Huxley, holotype skull in ventral view.

FIGURE 3. *Anthracosaurus russelli* Huxley, Usworth Colliery specimen in ventral view.

margin of the nostril. This contrasts with the condition in *Eogyrinus*, in which the corresponding process tapers to a point and is excluded from the naris by the junction of nasal and premaxillary. As in *Eogyrinus* no septomaxillary ossification is preserved.

In *Anthracosaurus* each lacrimal extends backwards from the narial process as an elongate bone with nearly parallel sides. On the right post-mortem compression has forced the lacrimal to override the prefrontal and nasal bones, whereas on the left there is limited post-mortem overlap of the lacrimal by the nasal.

The right lacrimal shows the orbital contact clearly: a process of the bone extends backwards, between the prefrontal dorso-mesially and the anterior end of the jugal laterally, for a distance of some 2 cm, to enter the orbital margin. On the left the lacrimal is more disrupted posteriorly but appears to be virtually complete. Once again it has a broad orbital exposure, but the flanking jugal is somewhat broken.

If the left side of the skull alone was preserved a doubt as to the orbital extension of the lacrimal would be possible. With both sides preserved as they are, the nature of this region is unequivocal.

A lacrimal approaching or entering the orbit is the primitive condition for batrachosaur labyrinthodonts. It is present in the Lower Carboniferous form *Eoherpeton* (Panchen 1975), and retained in the terrestrial anthracosaur *Gephyrostegus* (Carroll 1970) and the seymouriamorphs. In other described embolomeres, however, the lacrimal is broadly excluded from the orbit by a lateral expansion of the prefrontal which sutures with the jugal. This appears to be a consequence of elongation of the snout.

The dorsal part of the squamosal, which contacts the supratemporal and has a suture with the postorbital, is present and matrix free on the right as well as the left of the skull, as is the dorsal part of the postorbital. Thus the nature of the skull table–cheek contact can be seen on both sides.

The postorbital sutures dorsally with both supratemporal and intertemporal. It also has an anterior process extending round the orbit to suture with the postfrontal. The dorsal border of the postorbital, forming its suture with the three skull table bones, is far removed from a straight line and is closely similar on both sides of the skull. Also the postorbital-supratemporal part of the suture is somewhat convoluted and shows small interdigitations. It is unlikely therefore that relative kinetic movement was possible between the postorbital and the skull table as it was in *Eoherpeton* and possibly in *Eogyrinus.*

Furthermore, in *Anthracosaurus* the squamosal and supratemporal also meet in an apparently immovable suture, which is very slightly disrupted on the left of the specimen but intact on the right. The sutural line on both sides is convex upwards and somewhat irregular.

Thus the kinetism of the skull table, considered primitive for batrachosaurs and other early tetrapods (Panchen 1972*b*), and characteristic of embolomerous and gephyrostegid anthracosaurs, has been obliterated in the holotype of *Anthracosaurus russelli.* However, closure of the skull table kinetism also takes place in some individual osteolepiform crossopterygian fish (Jarvik 1937; Thomson 1967). It is possible, therefore, that this is an age character, or, while characteristic of *Anthracosaurus*, is of little taxonomic significance.

Nevertheless, in a recent classification of batrachosaurs (Panchen 1975) the presence of the kinetism was one of the features used to separate the suborder Anthracosauria (comprising primitive batrachosaurs, embolomeres and gephyrostegids) from the suborder Seymouriamorpha, the members of which show the derived condition of loss of the kinetism. Amendment of that classification in the light of the structure of *Anthracosaurus* is discussed in the last section of this paper.

The region of the otic notch is preserved, at least in part, on both sides of the skull. The notch itself, as in other anthracosaurs, is bounded by the tabular bone dorsally and by the squamosal anteriorly and ventrally. The supratemporal just enters the antero-dorsal 'corner' of the notch in the form of a small process extending posteriorly below the tabular in lateral view. This process is visible on both sides.

The notch itself has been closed by post-mortem compression to a narrow slit on both sides of the skull, but was probably of the ovoid rounded form seen in anthracosaurs and other large labyrinthodonts.

The tabular bone overlying the notch is in general form like that of other anthracosaurs. Thus in dorsal view it is a somewhat rectangular bone extending obliquely forward and inward, between the supratemporal and postparietal, to its characteristic suture with the parietal. Like that of other anthracosaurs it also has an extensive occipital exposure, to be described below, and terminates in a massive tabular horn. The horn itself, however, has a structure not before described in an anthracosaur.

Essentially the tabular horn is biramous, with a short stout upper and mesial ramus extending posteriorly as a continuation of the body of the bone and also continuing the downward and inward curvature of the posterior part of the tabular. The upper ramus is preserved on both sides of the skull, but is more complete on the left. In the left tabular the ramus has curved round into a downward vertical plane and is then broken off. It does not seem probably, however, that it extended much further in the intact skull.

The lower, lateral ramus extends ventrally and laterally, at about 45° to both planes, from the ventral surface of the upper ramus. It also has a backward direction at about the same angle to the transverse plane. Anteriorly its lateral surface is continuous with the lower part of the exposed lateral surface of the tabular. It is not known how far the lower ramus extended as it was broken off along a roughly horizontal plane on the left and is present only proximally on the right. Its principal function was probably the enclosure and support of the back of the tympanum. It is also probable that, together with the upper ramus, it acted as origin for part of the depressor mandibulae musculature, as originally suggested for the tabular horn of the embolomere *Palaeoherpeton* ('*Palaeogyrinus*': Panchen 1964).

This form of tabular horn may not be unique to *Anthracosaurus*, as few known anthracosaur skulls have the horns intact. The stout upper ramus is very similar to the horn of *Eoherpeton* (Panchen 1975) while the elongate finger-like lower ramus is more like that of embolomeres, notably *Eogyrinus*. In *Palaeoherpeton* and *Pteroplax* (Atthey 1877) the distal part of the horn is more blade-like, but proximally it is thickened suggesting the lower and upper ramus of the *Anthracosaurus* horn respectively.

Ventrally the otic notch is bordered by the squamosal, which is complete and well preserved on the left. As in *Eoherpeton* there is a well marked groove on the dorsal surface of the squamosal close to and paralleling its posterior edge. Again as in *Eoherpeton* the groove is relatively deep and well-defined anteriorly, where the squamosal forms the border of the otic notch, but becomes wide and ill-defined posteriorly after some 25 mm. It may be concluded that, as in *Eoherpeton* it housed the lower edge of the tympanum. This is corroborated by an irregular ornamentation in the groove anteriorly, presumably for the attachment of connective tissue.

The pattern of bones of the cheek region is in general similar to the eogyrinid anthracosaurs

Eogyrinus and *Palaeoherpeton*. It differs, however, in one important respect. The quadratojugal extends forward to contact the maxillary and exclude the jugal from the jaw margin. This undoubtedly represents the primitive condition, in contrast to that of these eogyrinids. It is present not only in *Eoherpeton* but also in *Crassigyrinus*, *Ichthyostega* and crossopterygian fish such as *Eusthenopteron* (Panchen 1973, fig. 3). The exact nature of the quadratojugal-maxillary overlap, seen only on the left, is not entirely clear. There has been some disruption at this point but the boundary suture of the jugal is clear throughout and its exclusion unequivocal.

The only possible sign of the lateral line system of *Anthracosaurus* is a shallow but clearly defined pit on the surface of the jugal. It is situated at the level of the maxillary-quadratojugal overlap with its lateral boundary along the suture with those bones. The pit opens anteriorly into an ill-defined groove which almost immediately fades out. It corresponds in position to part of a well-defined sulcus in *Eogyrinus*.

A curious feature of the cheek of *Anthracosaurus* is the presence of a long ovoid fenestra perforating the skull roof in the plane of the squamosal-jugal suture. It has been completely developed on the left and is visible from below on the right, and cannot be artefact or due to post-mortem damage as Watson suggested. The left, undistorted fenestra is 35 mm long and has a maximum width of 10 mm.

The quadrate in *Anthracosaurus* is unusually large and massive and its wide dorsal exposure constitutes a major part of the long cheek region. At the back of the skull cheek region the quadratojugal extends 40 mm posteriorly beyond the squamosal and their joint suture is continued backward as a suture between the quadratojugal and the quadrate. Anteriorly the quadrate is overlain by the somewhat truncated squamosal, but mesially the exposure of the quadrate continues anteriorly for at least a further 25 mm. At the level of the truncated edge of the squamosal a large (8 mm), shallow pit, square in outline, is exposed on this mesial surface of the quadrate. It is separated by a rugose ridge from a second smaller pit which is situated immediately posterior to the postero-mesial corner of the truncated squamosal.

It is probable that these pits are for the insertion of a quadrate process of the stapes. A similar but single pit was described by Watson (1926) in the Coal Measure loxommatid labyrinthodont *Megalocephalus* and again it is probable that its function was the insertion of a stapedial process (White 1939; Parrington 1948). In *Megalocephalus* the pit is situated at the quadrate-pterygoid junction, but its situation in *Anthracosaurus* merely reflects the much more extensive ossification of the quadrate along the palatoquadrate cartilage.

The ventral aspect of the quadrate and the form of its condyle are described below with the rest of the palate.

Reconstruction of the skull roof of *Anthracosaurus* from the holotype presents few difficulties (figures 4 and 5). In the preorbital region distortion is relatively slight and easily corrected. The right maxillary region appears to have retained its natural contour and the sections exposed by transverse breaks across the specimen allow one to estimate the degree to which the right lacrimal has overridden the nasals due to depression of the latter. This allows restoration of the true depth of the whole snout.

The skull is remarkably shallow in the region of the orbit compared to that of *Eogyrinus*, but there is little or no latitude for error in reconstructing this region as the dermal bone ventrolateral to the orbit is intact on both sides. This suborbital region, formed from the jugal and maxillary, has a minimum transverse width in the plane of those bones of less than 35 mm compared to nearly 70 mm in *Eogyrinus* (table 1). Also little 'opening-up' of the palate due

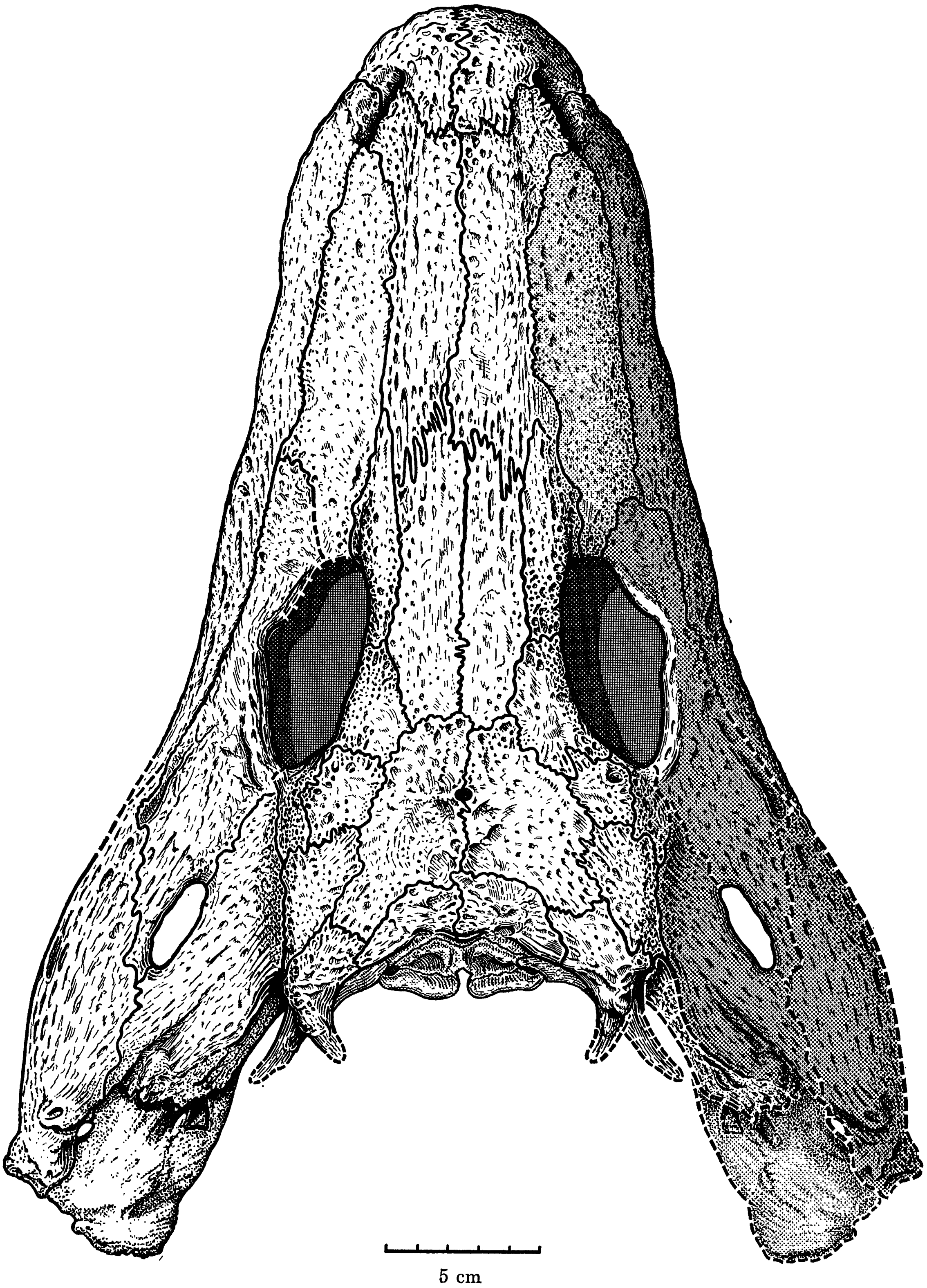

FIGURE 4. *Anthracosaurus russelli* Huxley, restoration of the skull from the holotype, dorsal view. Half natural size. Quadrate, light stipple on both sides.

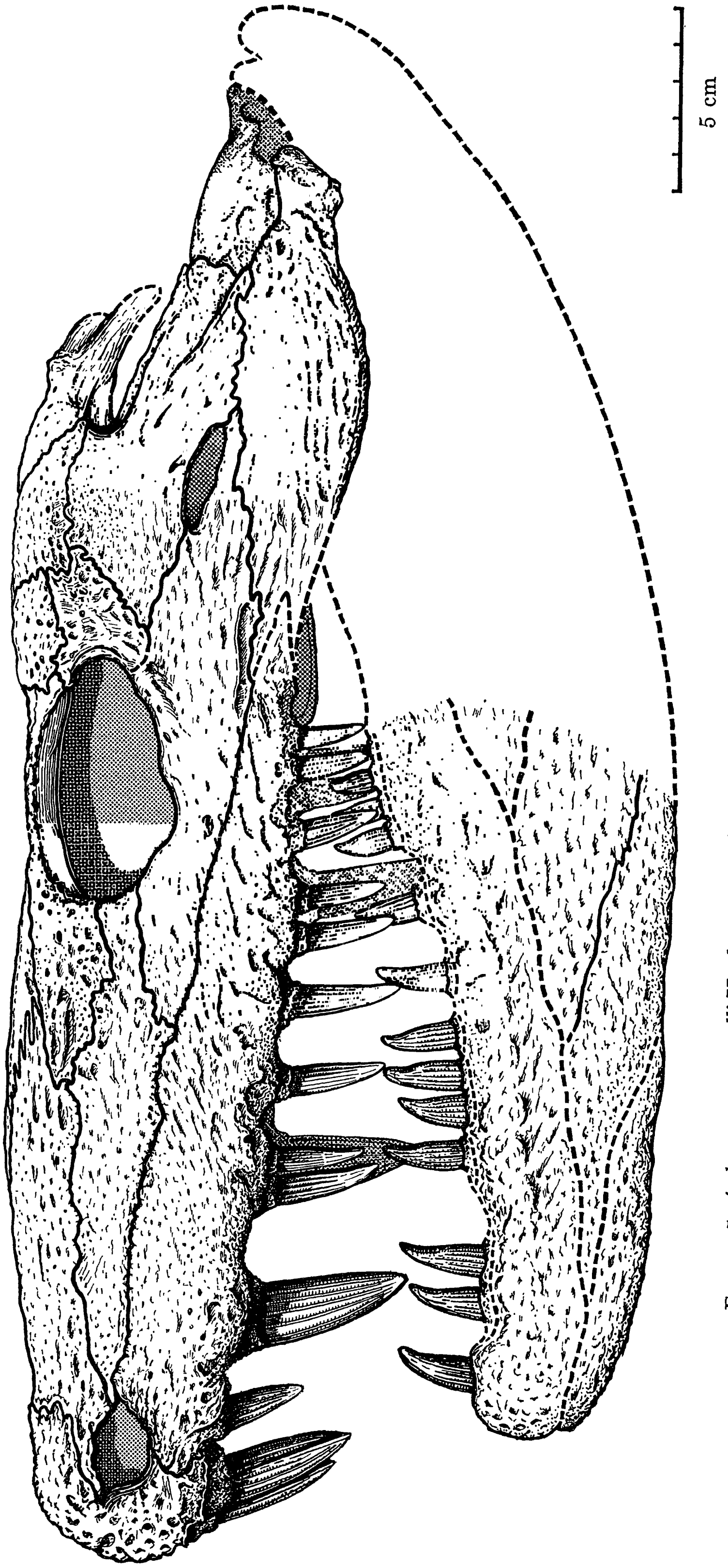

FIGURE 5. *Anthracosaurus russelli* Huxley, composite restoration of the skull, lateral view. Half natural size.

to spreading by compression appears to have occurred in *Anthracosaurus*, so that the transverse width of the skull cannot be seriously in error in the orbital or pre-orbital region.

Behind the orbits, however, the skull roof is underlain by the subtemporal fossa in the cheek region, so that post-mortem compression was no longer resisted by the palate. It is here that the cheek has been flattened into a horizontal plane and judgement thus had to be exercised in restoring its original contour. It is possible that I have restored the cheek region as too wide and too shallow, thus exaggerating the characteristic flare in dorsal view. However, any drastic reduction of this flare would have given a cheek region whose lower edge dropped suddenly and in an unnatural manner behind the orbit in lateral view.

Thus the skull of *Anthracosaurus russelli* is remarkably shallow posteriorly compared to that of *Eogyrinus*, which forms a deep uniform wedge in lateral view. This, combined with the long suspensorium, gives a very shallow slope to the dorsal outline of the cheek behind the occiput, formed by squamosal and quadrate.

Thus the depressor mandibulae muscles must have had an almost horizontal line of action from occiput and tabular horns to lower jaw. It therefore seems probable that a small retroarticular process, like that seen in *Eoherpeton* (Panchen 1975), was present in *Anthracosaurus*.

The shallow cheek region of *Anthracosaurus* also makes it impossible that there was a high surangular crest on the lower jaw like that of *Eogyrinus*.

Apart from reconstructions of four external views of the skull it has been possible to reconstruct three transverse sections, by taking advantage of natural breaks in both the holotype and the County Durham specimen (figure 8). These are further described and points of reconstruction explained in describing the palate and braincase. The planes of these sections and the breaks on which they are based are indicated in figure 9.

The most distinctive feature of the dermal roofing bones in these sections is the extreme massiveness of the maxillary bone. In the first section, at a level behind the nares, but at about half way along the choanae, the bone above the maxillary is also massively thick. This thickness is produced by a ventral extension of the nasals (seen in the holotype) for most, if not all of the depth of the lacrimal. It is probable that this extension reached the maxillary, as shown in the reconstruction, but compression of the specimen and consequent damage makes this uncertain.

At the level of the top of the lacrimal the nasal is considerably thickened to form the dermal roof to the unossified olfactory capsule on each side.

In the plane of the second section, seen in both skulls at approximately the reconstructed level, the ventral extension of the nasals below the top of the lacrimal has disappeared except for a short thickened overlap region. In this plane, however, the lacrimal itself is massively thickened ventrally for its contact with maxillary and palatine. At this level the paired thickenings of the nasals, seen in the first section, appear as hook-like processes in section. With paired vertical processes from the palate they separate a median chamber, containing the braincase, from lateral cavities flanking it.

The course of the naso-lacrimal duct has been restored in the first two sections. This is clearly seen perforating the lacrimal on both sides of the holotype in the break on which the second section is based. The evidence for the first section is, however, less satisfactory, as the section of the duct can be seen, rather doubtfully, only on the left.

The third section is reconstructed in a plane near the front of the orbit and is based on evidence from a nearly transverse break in the holotype, supplemented by some data on the median palate from the County Durham specimen.

Once again the dermal roofing bones are notable for the massiveness of the junction of the maxillary with the palate and dorsally with the lateral roofing bone, in this case the jugal.

Palate

The palatal area of the holotype is complete except for the right suspensorial region, but was badly damaged in its original development. Thus little of the periosteal bone surface remains, except posteriorly on the left quadrate ramus of the pterygoid and the quadrate itself. It is therefore impossible to tell in this specimen whether the surface of the bone was ornamented in the way characteristic of other anthracosaurs.

However, despite the poor condition of the surface, with bone missing or hidden in some places, the palate is undistorted and the general shape is clear (figure 2). Also the dentition is very well preserved with almost every tooth represented by at least the stump of its crown, and a series of right maxillary teeth, as well as the left premaxillary teeth, complete and intact. The dentition is described in detail in a later section.

A few palatal sutures are traceable on the holotype. The ectopterygoid-maxillary suture was traced throughout its length on the left, as were parts of the anterior and mesial suture of the ectopterygoid with the pterygoid.

Fortunately the County Durham specimen yields important detailed information on the anatomy of the anterior palatal region as well as retaining, again on the left, part of the inner border of the ectopterygoid.

The area preserved in the County Durham specimen extends, in palatal view, from the anterior, premaxillary border of the choana to the back of the ectopterygoid. Anteriorly the specimen is broken off almost along a transverse plane, but the break is slightly oblique so that the anterior border of the right choana only is preserved. On the left preservation includes most of the maxillary to the level of the back of the ectopterygoid, parts of the latter bone, and the region of the palatine.

Preservation of the pterygoids extends almost to posterior ectopterygoid level in the midline, but laterally both pterygoids are preserved back to a transverse level only about 20 mm behind the posterior palatine tusk. The right maxillary is preserved back to a level corresponding to that of the anterior tusk.

There has been considerable disruption of the bone in the vomerine region but most of the palatal surface of the right vomer is intact and has been fully developed. Behind the vomerine region a transverse break across the specimen, roughly parallel to the anterior broken surface, passes through the level of the missing anterior palatine tusk on the right and the preserved posterior tusk on the left.

The nearly transverse section so exposed extends to the skull roof and yields evidence on the unique structure of the palatine region. It has been used together with that from the holotype in the reconstruction of the second of the three restored sections (figure 8*b*). Behind the transverse break the County Durham specimen is split longitudinally and thus gives further evidence on the interior structure, used for the third reconstructed section.

The surface of all the exposed palatal bones in the County Durham specimen is well preserved and has been cleaned with the Airbrasive machine.

The palate of *Anthracosaurus russelli* shows the general features to be expected in the palate of an anthracosaur. Thus it is 'closed' with little or no development of interpterygoid vacuities, a primitive labyrinthodont condition common to all batrachosaurs. More specifically, the vomers are narrow and toothless between large choanae; there is an enormous 'tusk-pair' on each side in the palatine region, and in the ectopterygoid region there is a further series of palatal tusks or pits marking their sites.

The holotype shows that the basal articulation was still mobile. The epipterygoids themselves are not visible but the prominent basipterygoid processes with which they articulated are: they are described below as part of the braincase.

In all these general features the palate of *Anthracosaurus* corresponds to that of *Eogyrinus*, but significant differences, in addition to the very different shapes of the skull in palatal view, may be seen by comparison of both *Anthracosaurus* specimens with the lectotype of *Eogyrinus*. They will be noted in the detailed description which follows.

The choanae of *Anthracosaurus* are very much larger than those of *Eogyrinus*, so that the paired vomers of the former are confined to the form of a thick bar between them rather than forming a plate of bone.

The detailed form of the vomer is restored from the County Durham specimen (figure 3) and can be seen from the palatal reconstruction (figure 6). In the specimen the right vomer is incomplete at the point of junction with the well-developed median posterior process of the premaxillaries and along its median border, so that the line of suture with the other vomer is not preserved. However, its laterally facing posterior junction surface to suture with the palatine and pterygoid is preserved, so that the suture, although disrupted, can be restored with confidence, except near the midline.

The most notable feature seen in the right vomer is the presence of a large pit which is best interpreted as for Jacobson's organ. This pit is an elongate concavity over 25 mm in longitudinal length with beautifully preserved bone over its whole surface and bearing within it a small elongate pit, 4 mm in length, postero-mesially.

Watson (1929) described evidence of the presence of Jacobson's organ in a specimen of *Eogyrinus* from Airdrie, attributed by him to *Pholiderpeton*, but the specimen is poorly preserved in the vomerine region and I was unable to convince myself of the presence of that evidence (Panchen 1972*a*). In this specimen of *Anthracosaurus*, however, there can be no doubt of the presence of the pit, whatever its interpretation.

The vomers are seen in transverse section in the holotype and are restored in the anterior section. They separate paired cavities which presumably housed cartilaginous olfactory capsules. Dorsally the conjoined vomers appear to form two parallel longitudinal channels, probably for the paired superficial ophthalmic nerves, but the evidence is not very clear.

Behind the vomerine region the palate of *Anthracosaurus* was uniquely adapted to the mechanical demands of its powerful dentition. In this region the structure of the palate may be reconstructed from the well preserved surface of the County Durham specimen together with data from the exposed sections in both specimens.

In the area immediately behind the palatine tusks the surface of the palate appears to be of smooth unbroken bone from one maxillary contact to the other. Similarly the area between the posterior palatine tusks shows no suture defining the mesial borders of the palatines. In this general area the midline suture between the pterygoids, if present, is obscured by a longitudinal break in the specimen. However, more posteriorly, where the break leaves the midline no interpterygoid suture could be traced.

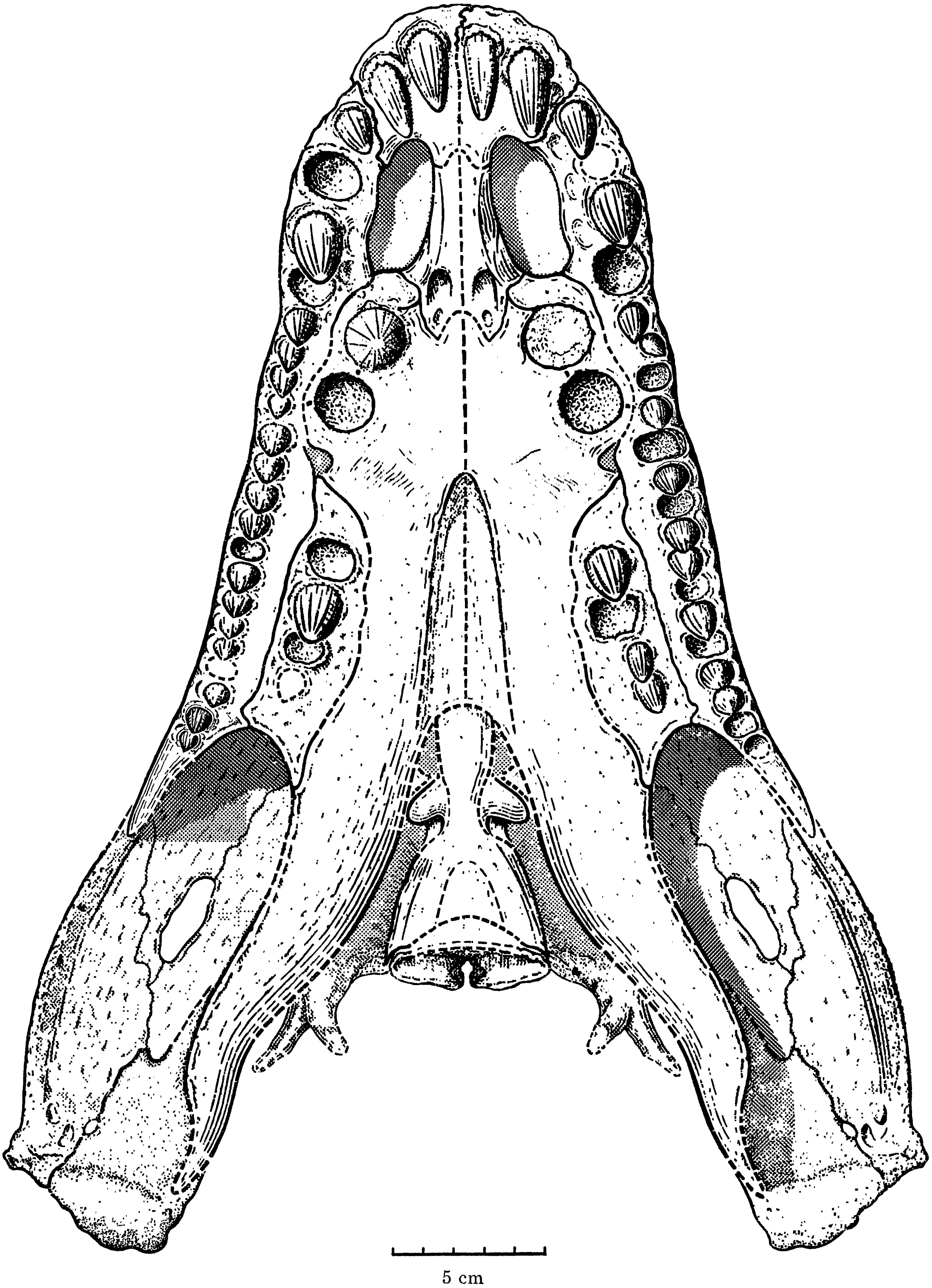

Figure 6. *Anthracosaurus russelli* Huxley, composite restoration of the skull, palatal view. Half natural size.

Thus behind the transverse break in the County Durham specimen there is no apparent palatal exposure of the palatine bones, the whole palatal surface in front of and between the ectopterygoids being formed by unornamented pterygoids, possibly fused together in the midline. The palatal surface of the holotype is not well enough preserved to confirm or refute this interpretation.

Inspection of the transverse breaks in both specimens makes it clear, however, that the palatines were neither missing nor fused to the pterygoids.

In the County Durham skull both posterior palatine tusks are present, but the anterior ones are represented only by disrupted replacement pits. The right posterior tusk is present as a stump broken post-mortem at the base of the crown, while the left has been split by the transverse break.

The section shows that the left tusk is implanted in a massive palatine bone situated internally (dorsally) to the pterygoid. The pterygoid, however, surrounds and sheaths the base of the tusk, at least dorsally and mesially.

The massive palatines may also be seen in section in the second break in the holotype, where their extensive sutures with maxillary and lacrimal can be traced in section. The relationship of the palatines to the underlying pterygoids is not, however, clear in the type, as much of the latter appear to have been chiselled away.

The holotype does show, however, that paired processes extended upwards on either side of the braincase from the dermal surface of the palate. These are preserved complete but disrupted and detached in the County Durham skull, but probably arose from the pterygoids rather than the palatines which are sharply truncated mesially well short of the midline. The restored structure of these areas of the palatine will be clear from the second reconstructed section (figure 8*b*).

More anteriorly there appears to have been a palatal exposure of the palatines, preserved on both sides in the County Durham skull. There has been considerable post-mortem disruption in the region of the anterior palatine replacement pits, but a pterygoid-palatine suture can be traced on the left, running from an antero-mesial point on the rim of the replacement pit obliquely forwards and inwards towards the region of the vomerine suture.

On the right where the vomer is well preserved the palatine-vomer suture is present but somewhat opened up. The right palatine-pterygoid suture is disrupted, with the front of the pterygoid forced post-mortem under (dorsal to) the palatine.

Thus the palatine is exposed mesially only in front of the anterior tusks (or pits). Its exposure can be seen to extend some way round the lateral side of the left pit. It has been restored in the palatal reconstruction flanking both anterior and posterior tusk sites, but disruption and breakage has obscured this area in the specimen.

The County Durham skull shows a curious minor feature situated about half a centimetre behind the level of the back of the posterior palatine tusk and thus immediately in front of the ectopterygoid. At this point the lateral border of the pterygoid, adjacent to the maxillary, is deeply embayed to produce a triangular fenestra a little less than a centimetre across. This is clearly marked with a border of rounded finished bone on the right and is clear although closed by compression on the left.

Unfortunately the flanking maxillary is missing on both sides so that it is impossible to say whether the embayment was an open fenestra, as restored, or closed by a tongue of bone.

Behind this point the ectopterygoid bones, unlike the palatines, had a normal palatal exposure, extending back on each side to the anterior border of the subtemporal fossa. The left ectopterygoid is incompletely preserved in palatal view in the County Durham skull and shows about a centimetre of its true mesial border. In the holotype the maxillary-ectopterygoid suture is completely traceable on the left, while the pterygoid-ectopteryoid suture was traced at the front of the ectopterygoid, extending back from the maxillary border for about 2.5 cm, and at the back for about 2 cm to where it terminates at the fossa. There is no sign of a processus alaris of the jugal which extended inwards along the anterior border of the fossa in *Eogyrinus*, thus separating the ectopterygoid from the fossa. In *Anthracosaurus* the ectopterygoid appears to form a major part of that anterior border.

While the palatal exposure of the ectopterygoids in *Anthracosaurus* appears normal, it is also clear that, like the palatines, they had an extensive mesial overlap with the pterygoids, thus contributing to the striking massiveness of the palate.

This overlap region of the ectopterygoid is visible in oblique section on the right of the County Durham specimen. Anteriorly and laterally, adjacent to the triangular embayment› the ectopterygoid is nearly 15 mm thick, allowing the implantation of the massive anterior tusk, which is not however preserved on the right. The ectopterygoid at this point is underlain by a pterygoid less then 2 mm thick. In the oblique section the ectopterygoid tapers postero-mesially, and is only 3 mm thick immediately lateral to its true mesial edge where it tapers to a rounded point in section. The mesial edge is seen in section at the back of the specimen butting against the medial concavity of the pterygoids described below.

Because the exposed section of the ectopterygoid is oblique it is uncertain from the County Durham specimen whether the reduction in thickness of the hidden region of the ectopterygoid is primarily from lateral (where the tusks are implanted in the exposed area of the bone) to mesial, or anterior to posterior. However, the third transverse section exposed in the holotype shows a sudden diminution in thickness of the ectopterygoid at the lateral edge of the overlap area, so that that area is thin throughout. The holotype section also shows a sharp ventral step in the ectopterygoid at the edge of the overlap area to accommodate the lateral edge of the underlying pterygoid. However, the corresponding edge of the pterygoid is missing at the level of the section.

The restored relationship of all the palatal bones in this plane will be clear from the reconstructed section.

The whole structure of the pterygoids will now be reviewed and compared with that of *Eogyrinus*.

The pterygoids of *Eogyrinus* have an ornamented palatal surface throughout their length. The quadrate ramus of the pterygoid in *Eogyrinus* (and *Palaeoherpeton*) is covered with minute denticles. This covering extends forward to the approximate level of the palatine-ectopterygoid suture. Anterior to it the pterygoids in *Eogyrinus* are marked with a series of deep longitudinal grooves and ridges and some sparse and irregular ornament.

In *Anthracosaurus*, on the other hand, as has already been noted, this anterior region of the pterygoids forms a flat smooth plate. In the County Durham specimen preservation of the pterygoids extends back beyond this anterior region for about 60 mm and again all the exposed pterygoid surface is smooth.

Parts of the true surface of the quadrate ramus of the pterygoid appear to be preserved in the holotype, although this is less than certain, but once again there is no sign of denticles.

In *Eogyrinus*, while the palate is 'closed', with no great development of interpterygoid vacuities, the pterygoids are narrowly separated in front of the basal articulation. The processus cultriformis of the parasphenoid, underlying the braincase, lies between them and they diverge posteriorly towards the articulation. It is uncertain whether they were in contact anteriorly.

Anteriorly they were also broadly separated from the maxillaries by the normal palatal exposure of the palatines in contrast to the condition in *Anthracosaurus* reconstructed above.

In *Anthracosaurus* the midline region of the palate between the ectopterygoids is marked by a large bullet-shaped concavity of which about 55 mm is preserved to the back of the County Durham specimen. The apex is directed forward and the concavity reaches a width of nearly 30 mm and a depth of nearly a centimetre posteriorly. Anteriorly it is a little deeper.

The whole is floored by a continuous well-preserved bony surface. This bony floor is little more than 1 mm thick as revealed in section at the back of the specimen. There appears to have been some irregular breakage and overriding of adjacent parts of the floor, but there is no trace of any separation or even suture between the pterygoids in the midline.

Thus the pterygoids of *Anthracosaurus* were firmly united medially at least to a level more than half-way along the length of the ectopterygoids. They must therefore have concealed the processus cultriformis of the parasphenoid from palatal view except immediately in front of the basal articulation.

Part of the processes cultriformis is preserved in the holotype. It can be seen on either side of the ventral edge of the sphenethmoid braincase in the section. It is also visible in longitudinal section along the break in the County Durham specimen.

The complete closure of the anterior palate in *Anthracosaurus* is paralleled in *Seymouria* (White 1939), but not in the more neotenous seymouriamorphs *Kotlassia* (Bystrow 1944) and *Discosauriscus* (Špinar 1952).

In *Eogyrinus* and *Palaeoherpeton* the quadrate ramus of the pterygoid, forming the mesial border of the subtemporal fossa on each side, is a deep plate of bone. In lateral view it extends down with a strongly convex profile between the back of the tooth row and the quadrate condyle. It reaches well below the level of either and well below the convex border of the cheek region.

In *Anthracosaurus* the quadrate ramus, well preserved on the left in the holotype, is relatively narrow and tapers strongly posteriorly, so that its distal end is a finger-like process lying along the mesial edge of the quadrate. It is very unlikely that the ramus projected below the level of the deepest part of the cheek region, or even significantly below the level of the tooth row.

Correlated with the wide lateral flare of the cheek region, the subtemporal fossae of *Anthracosaurus* are considerably wider than those of *Eogyrinus* and are not constricted anteriorly by the quadrate ramus. They are also considerably larger, measuring some 175 mm from front to back (including the quadrate condyle) compared to about 145 mm in *Eogyrinus*.

The left quadrate of the holotype is well preserved ventrally. Its lateral suture with the quadratojugal was traced forwards to the point where both meet the squamosal: anteriorly to that point the quadrate is sharply constricted laterally and its lateral suture becomes difficult to trace. It is probable however that the ossification of the primary palatoquadrate was continued forward from the massive quadrate as a well ossified epipterygoid of the type described in *Palaeoherpeton* (Panchen 1964).

The left quadrate condyle is well preserved. It is somewhat smaller than that of *Eogyrinus* and also simpler in structure.

The quadrate condyle of *Eogyrinus*, together with the articular glenoid in which it moved, had a complex structure which would have resulted each jaw ramus turning about its own longitudinal axis as the jaws opened. This rotation resulted in the ventral edges of the rami converging, while the dorsal tooth-bearing margins diverged as the jaw was lowered (Panchen 1972).

The features of the quadrate condyle of *Eogyrinus*, of which the glenoid forms an accurate natural mould, are (i) a toroidal (*sensu* Panchen 1972) or saddle-shaped surface, i.e. convex from front to back but concave from lateral to mesial, at least in its central region, (ii) both condyles with an axis which was not transverse but lay on the circumference of a circle, centred approximately at the jaw symphysis, (iii) the glenoid, and thus the condyle rotating in it, being 'screw-shaped' like that of the scapulo-coracoid of primitive tetrapods: thus the plane connecting anterior and posterior edges of the glenoid rotates anteriad from the mesial to the lateral side.

This last feature caused each glenoid to move laterally along its condyle as the jaw opened and the saddle-shaped surface turned their mutual divergence into a twisting of the rami rather than a separation.

In *Anthracosaurus* the 'screw-shaped' feature of the condyle is absent, but without a preserved articular it cannot be asserted that it was absent in the glenoid and thus that the characteristic twisting of the jaw did not occur.

The other features of the *Eogyrinus* condyle are present but to a lesser degree. The articular surface of the *Anthracosaurus* condyle is gently and uniformly concave from side to side and convex from front to back. Its axis also forms an arc, but the flattening of the whole cheek region makes it uncertain where the centre of the circle would lie.

The curved axis makes it seem probable that a screw-shaped glenoid was present in *Anthracosaurus*, but probably not to such a marked degree. Without it the form of the condyle would have limited the extent to which the jaw could be lowered. Also the fact that its axis was apparently not transverse would have tended to separate the jaw rami at the symphasis.

However, in the absence of the screw-shape, both these effects might be seen, with an elastic connection of the rami at the symphysis, as aids to jaw closure.

A similar series of pits and foramina to those in *Eogyrinus* is seen in the quadrate region. The paraquadrate foramen, present in *Eogyrinus*, is represented by a conspicuous kidney-shaped pit in the ventral surface of the quadratojugal alongside the quadrate suture. It appears, however, to be imperforate. A second pit about 5 mm antero-laterally to it probably corresponds to a similar pit in *Eogyrinus*.

Finally in *Eogyrinus* there appeared to be a pit or foramen perforating the quadrate itself near or through the suture with the quadratojugal. In *Anthracosaurus* there is a gap in that suture extending forward from a point some 15 mm from its posterior end for 12 mm. It may represent lack of ossification or erosion, but its borders, at least mesially, appear to be in part of finished bone and it has therefore been restored as a quadrate foramen.

Little need be said about the restoration of the whole palate (figure 6). It is a composite with data from the holotype and from the County Durham specimen. For that reason, bilateral symmetry has been assumed and data transferred from one side to the other. This contrasts with the dorsal restoration, which was drawn from the holotype alone.

A number of the unique features of the *Anthracosaurus* palate and its relationship to the skull roof may be related to the functional morphology of the jaw mechanism.

The paired dorsal processes of the pterygoids, seen in the second reconstructed section, probably provided on their lateral surfaces an area of origin for part of the pterygoideus muscle. The processes also define two lateral cavities in which that muscle presumably ran on each side.

If this assumption is correct the pterygoideus must have been unusually large and extended very far forward, thus contributing a strong kinetic-inertial element to a powerful adductor musculature (Olson 1961; Panchen 1970).

The very large subtemporal fossa also suggests that that main adductor mass extended well forward in both origin and insertion and thus added a greater degree of occlusal pressure than was possible in *Eogyrinus*. This, and the great bulk of muscle suggested by the size of the fossa, correlates well with the exceptional dentition.

Occiput and braincase

The general features of the occiput of *Anthracosaurus* were described and figured by Watson (1929, fig. 4). Some additional surface cleaning has allowed the tracing of most of the sutures.

The occipital condyle is exceptionally large with a maximum width, perhaps slightly exaggerated by compression, of over 50 mm. Ventrally its border is incomplete because a large section of the basioccipital has been sheared off along an oblique plane at about 15° to the horizontal, as seen from behind. The height of the intact condyle may be estimated at nearly 45 mm.

Although rounded the condyle is roughly pentagonal in shape in posterior view, with the apex directed dorsally. It is deeply concave, with a well-marked central pit corresponding in position to the notochordal perforation of an embolomerous vertebra. The condyle is so large, relative to the depth of the occiput, that it encloses the foramen magnum. The dorso-lateral walls of the foramen are formed by processes of the exoccipitals which also form the centre of the dorsal rim of the condyle, but do not quite meet in the midline.

As in other primitive labyrinthodonts the single condyle is formed from three bones, a massive basioccipital ventrally and paired exoccipitals dorso-laterally. Despite surface damage the suture separating basioccipital and exoccipitals is easily seen for most of its length, as it has become opened and matrix-filled.

In palatal view the basioccipital can be seen in section where the base of the condyle is broken off. It is flanked by the parasphenoid which sheathed the whole otic region of the braincase and reached, ventro-laterally at least, right to the rim of the condyle.

The exoccipitals extend antero-dorsally from the rim of the condyle to terminate in a transverse suture on each side. Laterally in the plane of this suture a well-marked vagus foramen is visible on each side, as noted by Watson. The true boundary of the exoccipital cannot be traced with confidence beyond either foramen.

The exoccipital suture is with an area of bone which separates the bones and the foramen magnum from the occipital exposure of postparietals and tabulars. The area of bone must therefore represent the occipital exposure of a median supraoccipital and flanking opisthotics, the latter forming massive paroccipital processes between tabulars and exoccipitals.

However, no sutures defining the supraoccipital could be traced and despite a rather poor bone surface it seems probable that supraoccipital and opisthotics were fused into a single massive ossification.

In other respects the area of the occiput above the foramen magnum and condyle is similar to that described in *Palaeoherpeton* (Panchen 1964, fig. 2; 1970, fig. 1*c*). Post-temporal fossae are totally absent although there are paired shallow concavities immediately dorsal to the exoccipitals.

A notable minor feature in which *Anthracosaurus* resembles *Palaeoherpeton* is the presence of a lateral finger-like process of the opisthotic, best seen on the right, which interlocks with a similar descending process of the tabular.

The occipital exposures of the tabulars and postparietals are closely similar to those of *Palaeoherpeton*. Each tabular forms a massive buttress to its paroccipital process, having a wide diagonal suture with the opisthotic region. Ventro-laterally the tabular reaches a level well below the top of the condyle: dorso-mesially it is on a level with the ventral edge of the postparietals. The complex form of the tabular horn has been described with the skull roof.

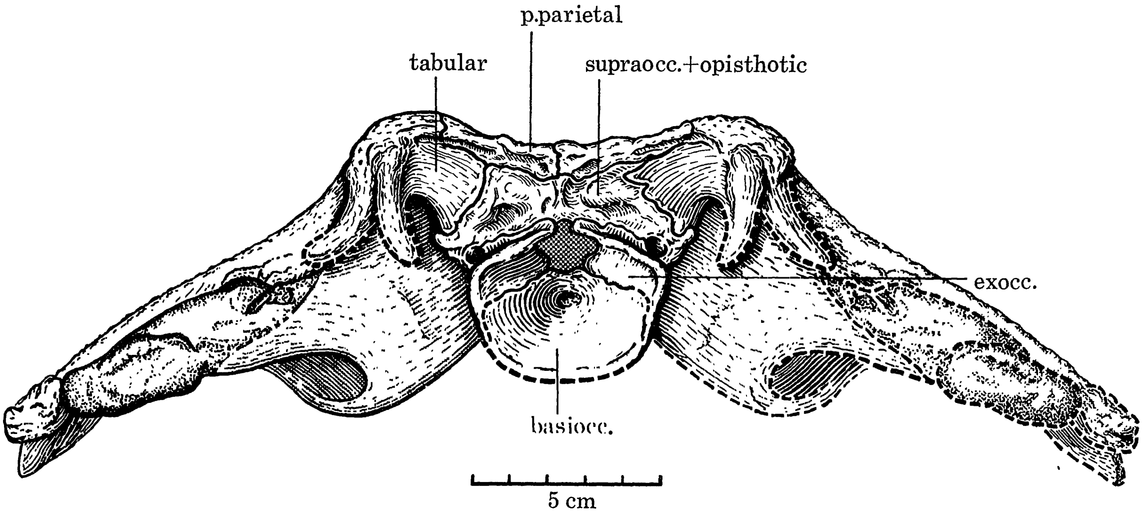

FIGURE 7. *Anthracosaurus russelli* Huxley, restoration of the skull from the holotype, occipital view. Half natural size.

The median suture between the postparietals was easily traced onto the occipital surface.

One more occipital feature may be noted: a narrow but quite deep furrow runs from the lateral part of each postparietal laterally onto the tabular, reaching almost to the level of the tabular horn. This furrow thus gives a well defined rim to the back of the skull table on each side.

Information on the more anterior structure of the braincase comes from two sources. The braincase is exposed but damaged in palatal view in the holotype, and is visible in the transverse breaks in both skull specimens.

In the holotype the braincase, with its sheathing parasphenoid, is visible from the occipital condyle forward to the approximate level of the posterior palatine tusk. However, from the condyle to a point about 2 cm in front of the basal articulation the ventral surface has been stripped off along the same plane as the base of the condyle, conceivably by a misplaced stroke of the chisel. In front of this region the sphenethmoid region of the braincase is visible in palatal view first as the damaged ventral edge of a thick interorbital septum and then as disrupted streaks of bone between the pterygoids.

The general appearance of the otic region of the braincase, behind the basal articulation, corresponds to that of *Eogyrinus* (Panchen 1972*a*, fig. 10*b*) and *Palaeoherpeton* (Panchen 1964, fig. 8), but virtually no detail can be elucidated.

It has already been noted that the parasphenoid on each side can be seen to extend back to the rim of the condyle. The cut edge of the parasphenoid can be seen laterally in palatal view and is separable from the basisphenoid by its more compact texture in section. On the right, part of the dorsal border of the parasphenoid is visible and a depression in its margin may indicate the rim of the fenestra ovalis, but this is by no means certain.

Both basipterygoid processes of the basisphenoid are preserved as noted in the description of the palate. The articular surface of the right process is in part preserved. The surface faces obliquely forward at about 30° to the transverse plane and has a slight downward inclination. In the intact skull it would have extended below the level of the midline parasphenoid. Probably half the articular surface was below that level, as in *Eogyrinus* and *Palaeoherpeton*, but its lower part is removed by the oblique cut. The same damage has reduced the left process to general palatal level so that it is visible only as a horizontal section.

However, the section exposed in the vicinity of the left process shows that the parasphenoid clasped the base of the process very tightly. Thus the carotid groove, which runs round the base of the process posteriorly and ventrally, was probably formed in parasphenoid rather than basisphenoid, in contrast to the condition in *Eogyrinus*. The groove is preserved and visible in part as finished bone on the right, but the junction between parasphenoid and basisphenoid round the circumference of the process cannot be clearly distinguished.

The paired carotid foramina, present ventra-laterally in front of the processes on *Eogyrinus* and *Palaeoherpeton* cannot be distinguished in the damaged bone surface of *Anthracosaurus*.

As in these other two anthracosaurs the parasphenoid expands immediately anterior to the basipterygoid processes and then tapers gradually for the rest of its extension forward as the processus cultriformis. However, no useful information on parasphenoid or braincase is obtainable from the palatal view of the holotype concerning the sphenethmoid region.

The braincase is visible in vertical section in the longitudinal break in the County Durham skull and in transverse section in the same specimen and in the most posterior break in the holotype.

The longitudinal section in the County Durham skull passes obliquely forward through the left otic capsule and reaches the midline where the break meets the transverse break. The skull roof is also present and includes a section through the tabular-opisthotic buttress which appears to be very similar to that described in detail in *Palaeoherpeton*.

The otic capsule itself appears in section as a small lumen of about 9 mm average diameter surrounded by massive walls almost 10 mm thick, but with a narrow channel leading forward out of the capsule. In fact the 'lumen' of the capsule is probably the fenestra ovalis seen from within and the apparent massive walls merely the lateral walls of the capsule seen in parasagittal section. The channel then marks the course of the prootic-basisphenoid suture immediately anterior to the fenestra. Antero-dorsal to the fenestra is a series of ill-defined cavities apparently closed by compression which probably contained the semi-circular canals. The whole structure suggests very strongly the interior view of the left otic capsule seen in *Eogyrinus* (Panchen 1972*a*, fig. 9*a*).

Immediately anterior to the otic capsule the section shows that the braincase had a continuous bony roof some 6 mm thick underlying the parietals and surrounding a fenestra below the pineal foramen. The structure at this point again appears to be just as restored in *Eogyrinus* and *Palaeoherpeton*. Ventrally at the same transverse level the section passes through the basisphenoid floor of the braincase at a point which must have been just anterior to the basipterygoid processes.

The remainder of the section passes forward in a vertical plane through the massive interorbital septum formed by the sphenethmoid, but yields little structural information. It is, however, possible to trace the processus cultriformis forward to the level of the transverse break in the specimen, as a band of compact bone underlying the sphenethmoid. The processus is thus known to have reached forward at least to the level of the posterior palatine tusks and may well have contacted the vomers.

The section of the braincase shown in the posterior reconstructed section is drawn from the type specimen with very little necessity for restoration. The structure of the sphenethmoid at this level is very similar to that of other anthracosaurs, being strongly tropibasic. Thus there is a massive interorbital septum below the wide dorsal region of the sphenethmoid which is channelled or tunnelled to convey cranial nerves forward to the snout region.

Paired tunnels through the bone probably conveyed vomeronasal nerves (by analogy with the reconstruction in *Eryops* (Sawin 1941) and *Palaeoherpeton*), but a lateral pair of channels for the olfactory tracts also appear to be present, as in those forms. The lateral channels in *Anthracosaurus* are defined by dermal roofing bones dorso-laterally, (i.e. the frontals and prefrontals) and by small lateral processes of the sphenethmoid ventro-mesially.

Ventrally the interorbital septum can be seen to be clasped by the processus cultriformis which extends quite considerably up the side of the septum on either side. It is in situ but incomplete in the specimen.

It is of interest to note that this section is in an approximately corresponding plane to the foremost of three which I reconstructed in *Palaeoherpeton* (Panchen 1964, fig. 9*a*). The form of the sections is similar in general but in *Palaeoherpeton* the olfactory channels were roofed by lateral extensions of the sphenethmoid rather than by dermal bone.

In *Palaeoherpeton* the second reconstructed section is at a level about two-thirds back in the orbit. At this level the olfactory channels have a lateral sphenethmoid wall and again the sphenethmoid extends to the full width of the frontal bones dorsally in the Derbyshire specimen on which the reconstruction was based.

A section is in part exposed at a similar level in the County Durham specimen of *Anthracosaurus* and this shows a wide process extending laterally at the top of the sphenethmoid to underlie the frontal completely. It also appears from this section that the sphenethmoid may have contained a single very thick-walled cavity at this level rather than the four discrete canals of *Palaeoherpeton*. This would be a continuation forward of the single cavity which appears in the third, posterior section in *Palaeoherpeton* at pineal level.

In *Palaeoherpeton* I considered that the lateral wall of the olfactory canals and possibly that of the vomeronasal canals inside them, were formed by a downgrowth contacting the interorbital septum, so that the division between the two could still be traced. There is no unequivocal evidence of this in *Anthracosaurus*.

The anterior section of the braincase is exposed in the transverse break in the County Durham skull and is thus in the transverse plane of the posterior palatine tusks. Data from that section has, however, been transferred to the second reconstructed section at the level of the anterior tusks. There is no sign of the sphenethmoid at this latter level in the holotype, so conceivably it terminates at a point between the two planes.

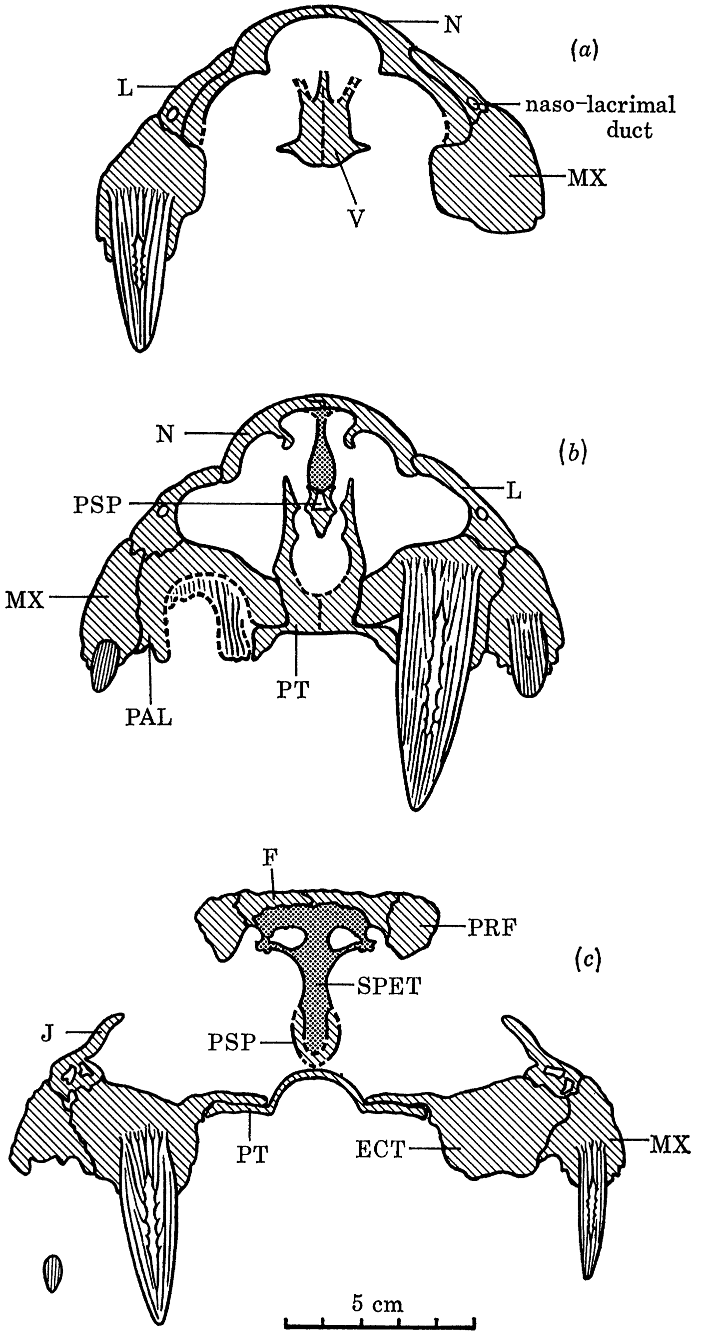

FIGURE 8. *Anthracosaurus russelli* Huxley, reconstructed transverse sections of skull. Half natural size. Dermal bone hatched, braincase stippled. ECT, ectopterygoid; F, frontal; J, jugal; L, lacrimal; MX, maxillary; N, nasal; PAL, palatine; PRF, prefrontal; PSP, parasphenoid; PT, pterygoid; SPET, sphenethmoid; V, vomer (see text and figure 9).

This extreme anterior end of the sphenethmoid appears in section merely as a solid drop-shaped mass of bone in the midline. It is still underlain by the sphenethmoid and attached to the dermal roof. The sphenethmoid, however, is slightly more complex, being rhombic in outline with its apex truncated by the sphenethmoid contact. The upper half of its area contains a cavity, which probably received the unossified lower edge of the sphenethmoid, present in life as cartilage.

In front of this level there is no further sign of an ossified braincase. The olfactory capsules were presumably present in cartilage, as was probably the case in all labyrinthodonts in contrast to the ossified capsules of their fish ancestors (e.g. *Eusthenopteron*: Jarvik 1942, 1954). I have already noted the presence of paired cavities, formed by the vomers and the skull roof of the snout, to house the capsules. They are shown in the anterior restored section.

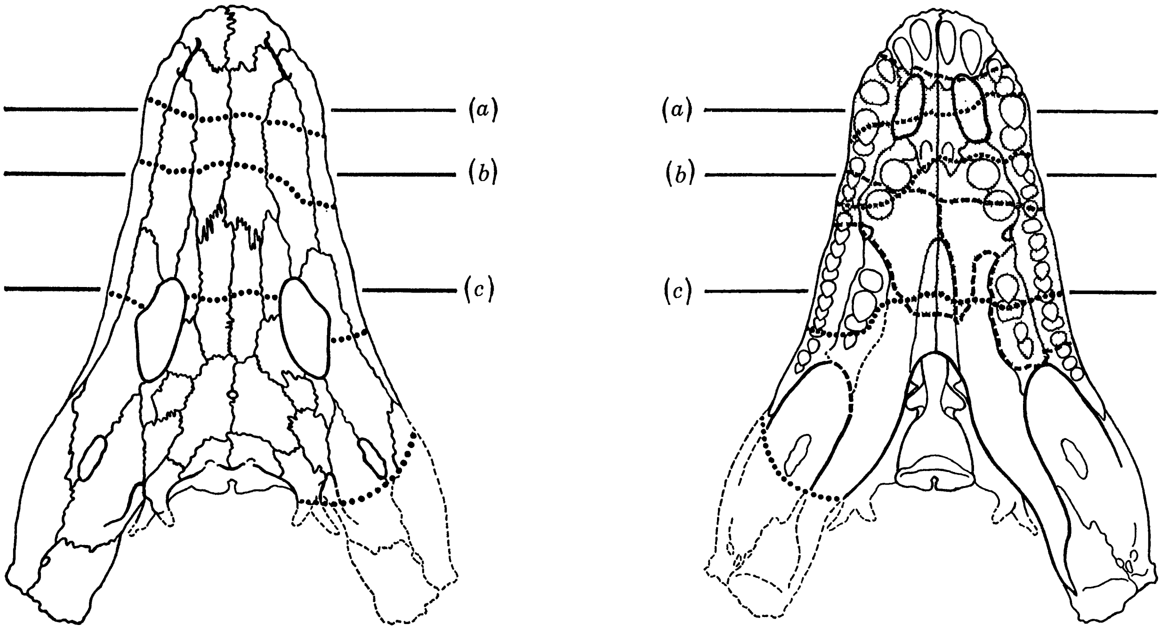

FIGURE 9. *A. russelli*, dorsal and palatal views of skull to show preservation and planes of reconstructed sections (*a*)–(*c*) in figure 8. Area of Usworth Colliery specimen stippled; heavy dotted line, breaks in holotype; heavy broken line, breaks in Usworth specimen; light broken line, restored.

Lower jaw

Both known specimens of the lower jaw of *Anthracosaurus russelli* represent the anterior region of a left jaw ramus exposed in mesial view and account for approximately one half of the reconstructed total length of the jaw. They are attributable to *Anthracosaurus* on locality, horizon and morphology.

The British Museum specimen (figure 10) shows a large meckelian fenestra of the type characteristic of embolomerous anthracosaurus and seen particularly in *Eogyrinus* (Panchen 1970, 1972*a*). Several features distinguish both specimens from the jaw of *Eogyrinus*. These include the profile of the ramus, which while tapered does not reach the extremely small symphysial depth of *Eogyrinus*, the size and form of the dentary teeth (see below), as well as their internal anatomy. This latter is seen in the most posterior tooth preserved in the British Museum specimen, which is represented by a stump exposing a transverse section, and by most of the teeth of the Kelvingrove specimen which are eroded to show longitudinal or oblique sections.

The preservation of the British Museum specimen is moderately good but crushing in front of the fenestra has resulted in rupture of the presplenial parallel to the lower edge of the ramus and collapse of its dorsal area into the meckelian cavity. The ventral part of the bone is also thrust forward slightly relative to the rest of the ramus. Most of the sutures figured were fairly easily traced, but there is some doubt about those surrounding the middle coronoid, as the bone surface is not well preserved in this region.

The Kelvingrove specimen has been eroded down so that it presents a longitudinal section in the plane of the ramus and gives no additional information about the relationship of the bones which comprise it. It does, however, exhibit a well-preserved dentition. Description of the jaw will be confined largely to the British Museum specimen.

Judging from the length of the preserved dentary tooth row the whole region of the jaw in front of the adductor fossa is preserved. Thus when the jaw is restored in articulation with the holotype skull the complete tooth row of the latter extends for only about a centimetre behind the last tooth preserved in the jaw ramus. Also below that tooth the bone is eroded, but comparison with *Eogyrinus* suggests that the eroded posterior border of the posterior coronoid may represent the true termination of that bone and thus the anterior border of the fossa.

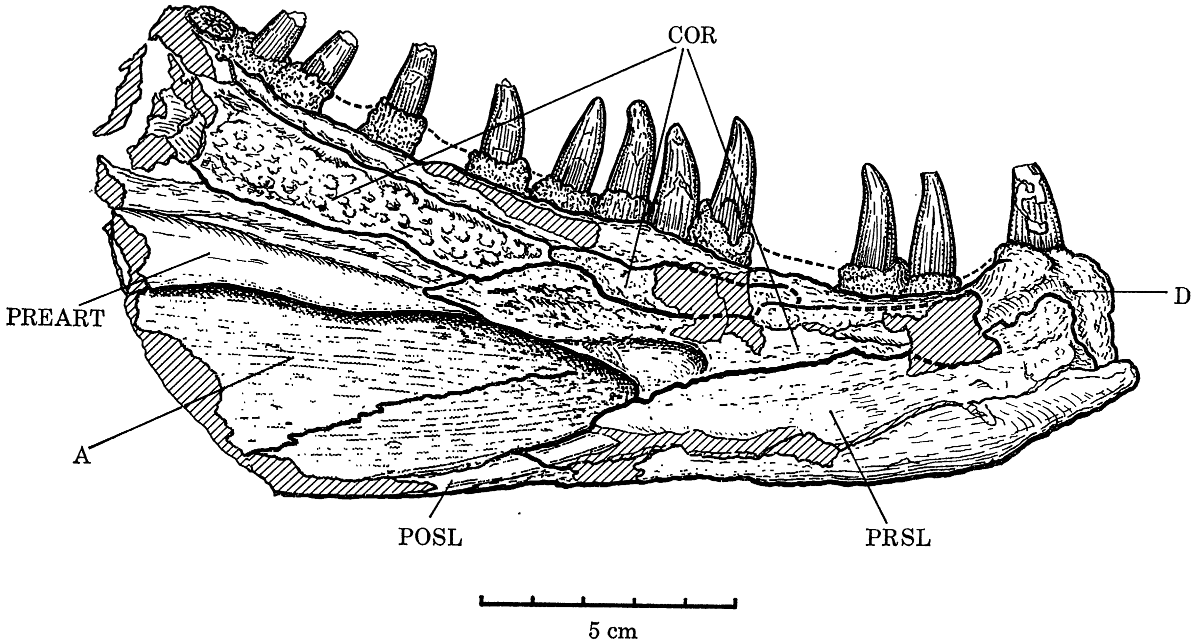

FIGURE 10. *Anthracosaurus russelli* Huxley, left jaw ramus: BM(NH) R4822, mesial view. Two-thirds natural size. A, angular; COR, coronoids; D, dentary; POSL, postsplenial; PREART, prearticular; PRSL, presplenial.

If this is the case it is evidence for what would be the most characteristic feature of the jaw of *Anthracosaurus*. As far as preserved, only one large meckelian fenestra, whose boundaries are beautifully preserved in the specimen, occupied the region characterized by two fenestrae in the jaw of *Eogyrinus*.

This feature appears to be unique to *Anthracosaurus russelli* amongst anthracosaurs. In every adequately preserved and described embolomerous anthracosaur jaw there are two fenestrae in each ramus (Panchen 1970). These include jaws from the eogyrinids *Eogyrinus*, *Neopteroplax* (Romer 1963), the archeriids *A. crassidisca* (Case 1915), *A. victori* (Stovall 1948) and also the disputed *Eobaphetes* (see below).

The upper border of the fenestra is formed for approximately the posterior two-thirds of its preserved length by the prearticular. This prearticular border shows a shallow projection ventrally into the fenestra which corresponds in position to the bar separating the two fenestrae in *Eogyrinus*. The region of the prearticular also corresponds to the condition in *Eogyrinus* in having an area of very smooth bone directly above the fenestra, which is defined dorsally by a well-marked horizontal ridge. The smooth bone presumably marks an area of muscle origin.

Antero-dorsally the border of the fenestra is formed by a bone here interpreted as the anterior coronoid. It has already been noted that the pattern of coronoids is not absolutely certain because of lack of certainty in tracing the boundaries of the middle coronoid. However, the border of the anterior fenestra of *Eogyrinus* is formed in an exactly similar way. A hollow area for muscle insertion is well preserved just in front of the fenestra.

The pattern of dermal bones is in general similar to that of the corresponding region in the *Eogyrinus* jaw. However, the pattern of the coronoids, if correctly traced, is somewhat different. The principal differences concern the relatively smaller size of the middle coronoid and the greater extent of the anterior coronoid. The anterior coronoid underlies the whole of the small middle coronoid and has a broad oblique suture with the long posterior coronoid. This contact is not nearly attained in *Eogyrinus*.

The surface of all three coronoids is rather poorly preserved in *Anthracosaurus*, but the whole of the posterior and middle coronoid appear to have been covered with denticles as in other anthracosaurs. This denticulate area, as in *Eogyrinus*, appears to have been continued forward on the dorsal part of the anterior coronoid including its posterior region, in contrast to the condition in *Neopteroplax*.

Above the posterior and middle coronoids the dentary projects mesially as a well-defined shelf, but anteriorly this shelf appears to have been formed by the anterior coronoid itself. Above the coronoids the dentary teeth appear to sit on the shelf, but each tooth is surrounded at its base by a sheath of spongey bone some 6 mm high formed from the dentary. It is probable that the outer surface of the dentary, not visible in the specimen, reached to the top of these 'sheaths' as in *Eogyrinus* and it has been so restored.

In the symphysial region the dentary rises as a massive bone well above the level immediately behind that region. The symphysial dentary is crowned by a single tooth, slightly stouter than average, in the British Museum jaw, but in the Kelvingrove jaw there are three large closely crowded teeth in the symphysial region. The latter specimen also shows that the dentary had an average thickness of well over a centimetre, forming the roof of the meckelian cavity, and that this depth was fully occupied by the roots of the teeth.

There is no clearly defined symphysial surface on the British Museum jaw. The area below the symphysial tooth has its exposed surface largely formed from the presplenial. However, the dentary does extend down in front of the presplenial anteriorly, to the level of the ventral displaced part of that bone, and symphysis may have been confined to this rather poorly preserved dentary surface. This would then exactly correspond to the condition in *Eogyrinus*.

As in *Eogyrinus* the presplenial accounts for over half of the depth of the ramus for most of the region in front of the fenestra. The oblique suture separating pre- and postsplenial was traced in the ventral border of the fenestra. The lateral wall of the fenstra is formed by the inner surface of the bones of the lateral surface of the jaw and is well preserved in the British Museum specimen. It is thus possible to trace most of the exposed part of the postsplenial-angular suture in the fenestra.

This suture is the only available evidence on the pattern of dermal bones on the lateral surface of the jaw. Thus, although there was undoubtedly some degree of overlap in the suture, its course may be transferred to a restoration of the lateral surface.

Such a restoration has been included in the overall reconstruction of the skull in lateral view. It has been assumed, without direct evidence, that as in other anthracosaurs the dermal ornament on the jaw mirrors that on the snout. The outline of the anterior part of the jaw is from the B.M. specimen, as is the dentition. Posteriorly there is no direct evidence, but, as noted above, a modest retroarticular process, like that of *Eoherpeton* (Panchen 1975), has been restored to allow the insertion of almost horizontal depressor mandibulae muscles. It should also be repeated that the shallowness of the cheek region of the skull roof makes it improbable that there was a high surangular crest to the jaw of the type seen in *Eogyrinus*.

Dentition

The unique nature of the dentition of *Anthracosaurus russelli* has already been emphasized. The dental formula (Chase 1963; Panchen 1970) is 0–2–2 (2); pmx 2, mx 20 in contrast to 0–2–2 (7); pmx 3 or 4, mx 45 for *Eogyrinus attheyi*. The difference in the count of marginal teeth, with a similar length of tooth row in the two type skulls, is a measure of the difference in tooth size between the two species. The difference in form of the teeth between *Anthracosaurus* and *Eogyrinus* was described in my anthracosaur monograph (Panchen 1970). Briefly the teeth and tusks of *Anthracosaurus* are massive rounded cones in shape, while the much smaller marginal teeth of *Eogyrinus* are nearly cylindrical for about two-thirds of the crown length. Also the axis of *Anthracosaurus* teeth is not so recurved as that of *Eogyrinus* teeth. In the latter the apex in a perpendicular tooth often lies behind the posterior edge of the base.

The dentition is remarkably well preserved in the holotype skull of *Anthracosaurus* and this is used exclusively in the reconstruction of the upper dentition.

The two premaxillary teeth are present in each premaxillary bone in the specimen, those on the right by broken stumps but those on the left by nearly complete teeth. The bases of the right teeth are elliptical in section with the long axis of the ellipse running antero-posteriorly. Both are of a similar size with the axes of the ellipse 15 mm × 12 mm.

The two left premaxillary teeth are very different in size from one another, the outer one being considerably larger. Only the short axis of their elliptical bases is measurable: that of the mesial tooth is 12 mm, that of the lateral tooth 14 mm. Both teeth have been bent back horizontally by compression of the snout, but it is probable that in life they were inclined backwards. The mesial tooth has been broken by the post-mortem compression, but is complete and has a crown length of 40 mm. The lateral tooth, of which the apex is missing, may have been somewhat longer. The distal half of the mesial tooth has a strongly developed ridge running longitudinally on its mesial and distal side, giving the tooth a lanceolate appearance like those of loxommatids. All the premaxillary teeth are typical of *Anthracosaurus* in having a pattern of longitudinal ridges and depressions giving them a fluted appearance. This fluting reflects the internal structure but may have been exaggerated by post-mortem shrinkage of the tooth.

On the right premaxillary the lateral tooth is very close to the premaxillary-maxillary suture, but the left lateral tooth is separated from the suture by about a centimetre. It is possible that an additional small tooth, missing in the specimen, occupied the intervening space, which is obscured by the lateral tooth and matrix.

The first maxillary tooth, represented on each side by a stump of the crown, is similar but somewhat smaller than the smallest premaxillary tooth. The long axis of the elliptical section at the base is directed postero-mesially and measures 12 mm in the right tooth and 14 mm on the left. The next three tooth sites in the series constitute the canine peak and bear teeth which rival the palatal tusks in size. On both sides of the holotype their representation is the same, consisting of a replacement pit (obscured by matrix and a fracture on the left), a tooth, broken off at the base with the rest of the crown missing, and another pit.

The right anterior and left posterior pit both show partially resorbed roots in their cavities. The teeth are more nearly circular in section than the more anterior teeth, with a basal diameter of nearly 17 mm.

The remaining maxillary teeth are all of similar diameter to one another, the variation between them being due mainly to their age after eruption. However, the terminal tooth or pit on each side is small. The elliptical section of the base of all the teeth is somewhat quadrangular, with the long axis of the ellipse in a transverse plane. Long axis diameters vary between 8.5 and 11 mm, with the exception of the right terminal tooth whose diameter is only about 5 mm.

The arrangement of teeth and replacement pits on either side will be clear from the palatal restoration of the skull. There are 20 tooth sites on the left, but there may be 21 on the right: a gap between the 17th tooth and the one following it, obscured again by matrix and a fracture, probably represents a replacement pit. It would then be the 18th and is followed by three teeth.

All the maxillary teeth on the left of the skull are preserved merely as stumps. On the right, however, numbers 6–16 (with a pit at number 13) are complete or almost complete. Compression of the specimen has crushed the crowns inwards, so that they lie in a horizontal transverse plane and point towards the midline. Most have broken at the base but their relative position has hardly been disturbed.

Like the premaxillary teeth they are fluted, at least near the base, and lanceolate near the apex with the defining longitudinal ridges anteriorly and posteriorly. They are, however, relatively more slender than the premaxillary teeth.

They vary in length in a way that is not reflected in the basal diameter of the teeth opposite on the left and is probably not attributable just to individual age. Numbers 9, 10, 11 and 12 are the longest (approximately 30, 25, 31 and 28 mm respectively). Behind these four, as far as can be judged, the teeth diminish in length posteriorly, while numbers 6, 7 and 8 are smaller teeth after a somewhat more massive stump at five.

Thus from mx 6 to the end of the series at mx 20 or 21 the length of the teeth, with individual variation, increases to a peak spanning mx 9–12 and then decreases towards the end of the series.

In the County Durham skull the sites of the first six maxillary teeth are represented in unbroken sequence on the right, while most of the series commencing with mx 2 is present on the left. On the left the transverse fracture has eliminated perhaps two teeth and the end of the series is obscured by poor preservation but comparison with the holotype suggests that the tooth count was about the same.

The size distribution of teeth at the front of the maxillary series was similar but not identical to that of the holotype. On the right the first tooth, represented by a pit, was apparently larger than that in the holotype. The second, represented by the stump of a tooth (apparently in the process of shedding) on the left and a pit on the right, was relatively small (*ca.* 13 mm diameter). The third tooth (a pit on both sides) was very large, as in the holotype, with a pit diameter of 16 or 17 mm. The fourth tooth in the County Durham specimen (a stump on both sides) is, in contrast to that of the holotype, a relatively small tooth with a basal diameter of 11 mm and is followed by smaller teeth of the general series.

Thus the 'canine' peak of the Durham skull is formed by mx 1 and mx 3 with a small mx 2, while that of the holotype extends from mx 1 to mx 4, with mx 2 and mx 3 the largest teeth.

Anthracosaurus has the usual tusk pair on each palatine bone. In the holotype only the right anterior site has an implanted tusk which is broken off near the base of the crown. It is roughly circular in section and very large, with a basal diameter of just over 17 mm, which is marginally larger than mx 3.

The left anterior tusk appears to have been recently shed. The pit is occupied by an incomplete ring of root material at an early stage of resorption.

Both posterior palatine tusks are represented by their replacement pits, which Huxley mistakenly identified as choanae. The right pit has a considerably eroded margin probably to be attributed to the original development, while the left was further excavated by Watson, who confirmed that it was indeed a tusk pit and not a choana.

In the County Durham specimen the stumps of both posterior palatine tusks are preserved, although a break passes through the left, exposing it in section, with a loss of much of its substance. Its root is over 30 mm deep and its estimated diameter 15 mm. It is probable therefore that the more massive palatine tusk of the holotype was even more deeply rooted. The right tusk also has a diameter of 15 mm.

Both the replacement pits for the anterior palatine tusks in the County Durham skull have had their margins disrupted by a degree of antero-posterior compression, as noted in the description of the palate.

The dentition of the ectopterygoids consists of a tusk pair and two additional teeth on each side. The tusk pair is preserved on both sides in the holotype but the additional teeth are represented only by a pit on the right, the site of the second tooth having been excavated to expose the orbit in the original development. Both teeth are, however, present on the left and the dentition of the left ectopterygoid is present in the County Durham specimen.

The ectopterygoid tusks in the holotype are represented by tusks followed by a pit on the left and the opposite arrangement on the right. The right tusk (basal diameter 15 mm) is present as a stump, but the left is complete although the crown is broken and lies horizontally. Its overall crown length is nearly 45 mm, but its depth from the plane of the palate is enhanced by the fact that a conical bone, descending from the palatal surface for some 8 mm, surrounds the root immediately above the crown. This is true of many of the teeth both marginal and palatal in the holotype and particularly of the large palatine tusk.

In the County Durham specimen the left anterior ectopterygoid tusk is present as a stump. The specimen was originally exposed in the roof of a colliery workings and the tusk and some of the maxillary teeth have been ground smooth to expose a smooth section, possibly by mechanical pit props.

Following the tusk pair in the holotype, the ectopterygoid teeth are of similar size. The anterior tooth is complete and has a basal diameter of 8 mm and a crown length of 25 mm.

The dentition of the British Museum lower jaw is shown in figure 10, and in the lateral reconstruction of the skull (figure 5). Most of the teeth forming the dentary dentition in this specimen are completely preserved. Those in the Kelvingrove jaw are also preserved to their apexes, either as longitudinal sections or sharp impressions.

The form, size and number of the teeth alone would be sufficient to distinguish the two *Anthracosaurus* jaws from that of *Eogyrinus.* In external form the dentary teeth are similar to those from the middle of the maxillary series, but are proportionately somewhat shorter and, in the British Museum jaw, slightly constricted below the apex to give a hooked appearance.

The dentary teeth are fairly uniform in size, except that the posterior two or three teeth in both jaw specimens diminish towards the end of the series.

In the British Museum jaw the teeth have a basal diameter of approximately 8 mm throughout, with the exception of the symphysial tooth which is somewhat stouter at 10 mm. The crown height of the complete teeth, which do not include the symphysial tooth or the last four of the series, varies between 16 and 22 mm.

It has already been suggested in the description of the jaw that the complete length of the tooth row is present in the British Museum specimen. The inclusive distance between the first (symphysial) and the last tooth is 175 mm. Twelve teeth are represented. Together with spaces representing replacement pits the total dentition was probably eighteen, compared to a dentary dentition in *Eogyrinus* of over 40.

The inclusive length of the tooth row in the Kelvingrove jaw is 168 mm with 18 tooth sites, so that in this case the complete dentition is probably also represented. The range of tooth size between the symphysial teeth and the posterior three teeth is similar to that in the British Museum jaw. However, the last three teeth are complete as impressions to their apex and have a crown height of 14, 14 and 12 mm.

The most important difference between the two jaws is that anteriorly the teeth in the Kelvingrove specimen occur as an unbroken series in contrast to the isolated symphysial tooth of the B.M. jaw. The fourth tooth of the Kelvingrove jaw corresponds in position to the second B.M. tooth. Thus the first three teeth in the former specimen may be regarded as the symphysial series.

All three are very large teeth, the second being both longest (by 2 or 3 mm) and stoutest, with a crown height of approximately 30 mm and a basal diameter of 12 mm.

The internal structure of all the teeth and tusks of *Anthracosaurus russelli* is closely similar to that of *Eogyrinus* as noted by Schultze (1969) and Panchen (1970). As in all labyrinthodont teeth the labyrinthine structure is seen at its most complex near the base of the crown. The teeth of both genera are of advanced labyrinthodont type in which the infoldings of primary dentine (Globulärzone: Schultze) appear in section as single, very tortuous radial lines. In primitive temnospondyls, such as loxommatids, there are short side branches at each angle in the course of the infolded dentine. These are absent in anthracosaurs.

One feature of the teeth of both anthracosaurs, again seen in transverse section, is highly characteristic. It was first described and figured in *Eogyrinus* ('*Anthracosaurus*' in error) by Atthey (1876).

In all labyrinthodont teeth the infolded primary dentine is surrounded by concentrically zoned orthodentine with tubules running from the primary infolding out to the inlets of the pulp cavity between the folds. At the lateral extremity of these inlets of the pulp cavity there are, however, dentine tubules which run straight to the periphery of the tooth, fanning out as they go.

The dentine through which they pass thus lies between successive labyrinthine infoldings and, in *Eogyrinus*, is characteristically darker than the infolded dentine. It was described by Atthey (1876: Plate XI) as dark dentine.

A similar differentiation of the dentine is seen in the holotype of *Anthracosaurus*. In this case, however, in all those teeth and tusks whose broken crown reveals a transverse section, the colouring is reversed.

Atthey's 'dark dentine' is of a light orange-brown colour, while the petal-like regions of infolded dentine are stained almost black so that together they give the impression of a black composite flower with a white centre, represented by the mineral-filled pulp cavity. The lighter meandering line of the primary dentine can easily be seen with a hand lens running radially along the axis of each petal.

This very strongly contrasted differential staining of the teeth appears to be characteristic of specimens from the Airdrie Blackband Ironstone, including the holotype and both lower jaw specimens. The colour difference is also present, however, in the County Durham skull where the two types of dentine appear as different tones of greyish brown. Once again the light-coloured infoldings of primary dentine are easily seen.

Postcranial skeleton

None of the postcranial remains from Airdrie which have been associated with *Anthracosaurus russelli* can be attributed to that species with certainty. With the exception of the interclavicle all are certainly from Airdrie and all, including the interclavicle, appear to be from the Blackband Ironstone on the character of the matrix. However, *Eogyrinus attheyi* occurs at Airdrie and also in Lanarkshire at Newarthill (Panchen 1972*a*). The Newarthill horizon is very close to that of the Blackband Ironstone and the Airdrie *Eogyrinus* skull is attributed to the slightly higher Palace Craig only on the character of the matrix.

The type horizon for *Eogyrinus attheyi* (the Low Main Seam, Newsham, Northumberland) is, like the Palace Craig, Lower Similis–Pulchra zone. However, it lies between the horizon of the Palace Craig and that of the Airdrie Blackband and is thus little higher than the latter (Panchen 1970, Table 3). Thus specimens of *Anthracosaurus* and *Eogyrinus* are separable neither on horizon nor locality.

One slab, containing vertebrae and ribs, was attributed to *Anthracosaurus* by Huxley. It was sent to him by the same Mr Russell who forwarded the holotype skull, but not at the same time. The specimen consists of a block of Blackband Ironstone some 3 cm thick, but with the upper surface of carbonaceous shale. Four ribs are preserved, but the shafts of two of them are represented for much of their length by impressions. There is also a fragmentary impression of a fifth rib (figure 11).

The vertebral remains are in most respects of typical embolomerous vertebrae closely similar to those of *Eogyrinus* (Panchen 1966) and the ribs are indistinguishable from those of the latter. A pleurocentrum, with its neural arch in articulation, is exposed in posterior view. Most of the left side of the arch is missing as is the neural spine above zygapophysial level. Only the right postzygapophysis is preserved and visible, but it is displaced and distorted. However, the right transverse process is well preserved.

An incomplete intercentrum is slightly overlapped by the pleurocentrum and thus probably pertains to the same vertebra.

The highly placed and large transverse process of the neural arch, together with the relatively high position of the parapophyses on the intercentrum, suggest that this is an anterior trunk or 'thoracic' vertebra (Panchen 1966, p. 205) and this suggestion is corroborated by the nature of the associated ribs. The latter have the form of rib-head and length of shaft (although all are incomplete) characteristic of thoracic ribs in *Eogyrinus*.

A second complete but highly compressed intercentrum is also present.

One important feature distinguishes the three centra from those described in *Eogyrinus*. In all three the notochordal canal no longer perforates the centrum. In the pleurocentrum its position is marked by a slight irregular depression in the concave posterior face. In the intercentra the depression is clearer, having a circular rim of about 5 mm diameter. Within this is a slightly convex plug of bone which gives the impression of secondary growth. There can be no doubt about the structure as each exposed vertebral face has been completely cleared of matrix with the Airbrasive machine.

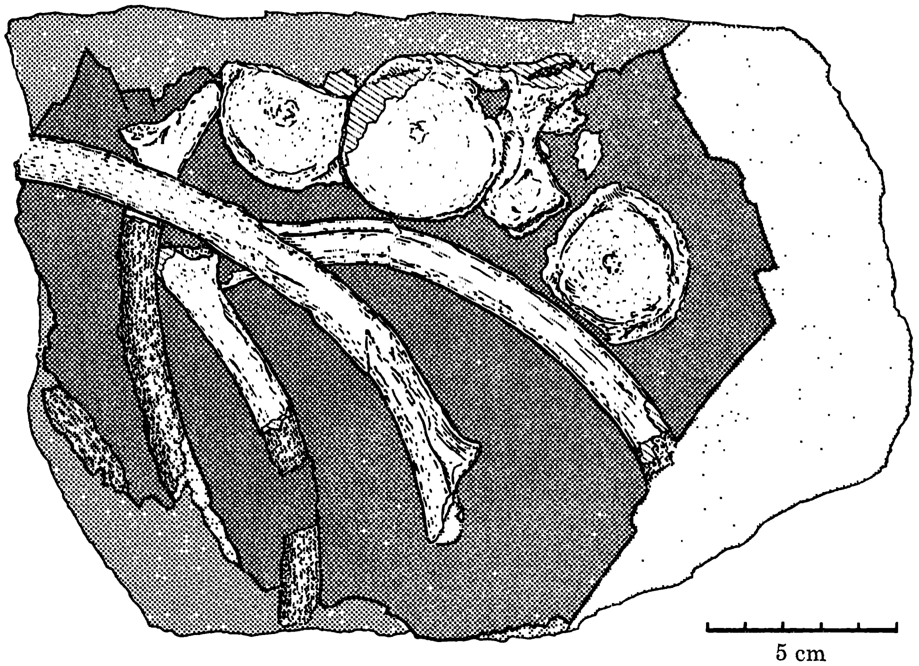

FIGURE 11. *?Anthracosaurus russelli* Huxley, vertebrae and ribs as preserved: B.M.(N.H.) 37324. Half natural size. Matrix stippled.

It is difficult to assess the significance of this character. Complete closure of the notochordal canal has never before been recorded in an embolomerous vertebra (but is seen in *Eobaphetes* – see below). It could be merely an age character and thus the present vertebrae could not be distinguished from those of *Eogyrinus*. On the other hand it may be characteristic of *Anthracosaurus russelli*, so that the present slab is attributable to that species. Further evidence permits one to argue either way.

The principal argument against attribution to *Anthracosaurus* is that while this is the first record of embolomerous vertebrae with an occluded notochordal canal, the occlusion is paralleled in *Eobaphetes* and was only revealed by freeing the articular surface of the centrum by Airbrasive treatment. Apart from the topotype material of *Eogyrinus* in the Hancock Museum, there are many isolated embolomerous centra in collections throughout Britain and the U.S.A., most of which are not developed to show the notochordal perforation. Only development of all of these would establish the significance of the condition attributed to *Anthracosaurus*.

Secondly the occlusion might be seen as an age character, occurring only in large mature specimens. Fortunately this can be in part refuted by two other specimens from Airdrie. These are two isolated pleurocentra (G.S. 54119–20) which, being in the same collection as the holotype, are probably of the 'number of vertebral bodies' sent by Mr Russell to Huxley (1863, p. 62) but not further described. One of these is of approximately the same size as the pleurocentrum on the slab, with an average diameter of the posterior face of 42 mm. This is somewhat less than that of the holotype pleurocentra of *Eogyrinus* (48 mm) but is closely comparable to that of the pleurocentra of the articulated *Eogyrinus* column from Newsham. The second isolated Airdrie pleurocentrum (G.S. 54120) is somewhat smaller (35 mm).

Both these pleurocentra have been completely freed of matrix and both show occlusion of the notochordal canal. In both cases it is more like that of the intercentra in Huxley's specimen, with a clearly marked depression. However, occlusion is rather more complete, with less strongly marked depressions both anteriorly and posteriorly in the smaller centrum than in G.S. 54119.

G.S. 54120 is thus either from a smaller individual than either G.S. 54119 or the vertebrae on the slab, or conceivably is from a fairly posterior caudal vertebra of a similarly sized individual. However, in that case, by analogy with all other labyrinthodont caudal vertebrae, it would be expected to be less well ossified than those of the trunk. In either case, therefore, if notochordal occlusion were merely a growth character it would be surprising to find it in this specimen unless the vertebra represents an elderly but dwarf individual.

The matrix of the two pleurocentra strongly suggests the Blackband Ironstone as does that of the Huxley slab. Thus negative evidence supports the uniqueness of these specimens from the Airdrie Blackband and attribution to *Anthracosaurus*. Furthermore, the slab vertebrae and G.S. 54119 are both nearly of a size to match that of the holotype skull. The occipital condyle of the latter, presumably closely comparable in area to at least the anterior trunk vertebrae, has a minimum width of 50 mm, a height of 40 mm (as restored) and an average diameter of about 45 mm. This is larger than the 42 mm of Huxley's figured pleurocentrum on the slab and of G.S. 54119. They should not therefore be attributed to the holotype but all the dimensions noted are well within the range of variation seen in specimens of *Eogyrinus* vertebrae from Newsham.

Thus on balance I favour the attribution of the occluded vertebrae to *Anthracosaurus*. I make no apology for labouring the evidence for this attribution at some length as it is of prime importance both taxonomically and functionally to establish that *Anthracosaurus* was embolomerous.

Two other vertebral specimens are possibly to be attributed to *Anthracosaurus*. In both the matrix is ironstone and, as both are registered from Airdrie, it is probably Blackband. They both take the unusual form of being natural moulds from which all trace of bone has disappeared (figure 12).

The better specimen (G.S. 56581) yielded a good latex cast of three articulated vertebrae in left lateral view. The anterior one lacks its intercentrum but the posterior one is succeeded by the next posterior intercentrum. Parts of the preceding and succeeding neural arches are also present.

As preserved the vertebrae appear typically embolomerous, with large rectangular neural spines, and are not distinguishable from those of *Eogyrinus*. Comparison with *Eogyrinus* suggests that they are posterior trunk vertebrae: the transverse processes are situated relatively ventrally and bear a restricted articular facet for the tuberculum of the rib. On the other hand there is no sign of haemal arches on the intercentra and they are thus distinguished from early caudals. Some rotted bone, perhaps representing a vertebra, is present in the antero-dorsal corner of the block.

The latex cast taken from the second specimen (G.S. 56580) is much less clear. It shows three articulated neural arches with the characteristic rectangular neural spines in right lateral view. The prezygapophyses of the next posterior arch are also represented. Centra are not certainly present.

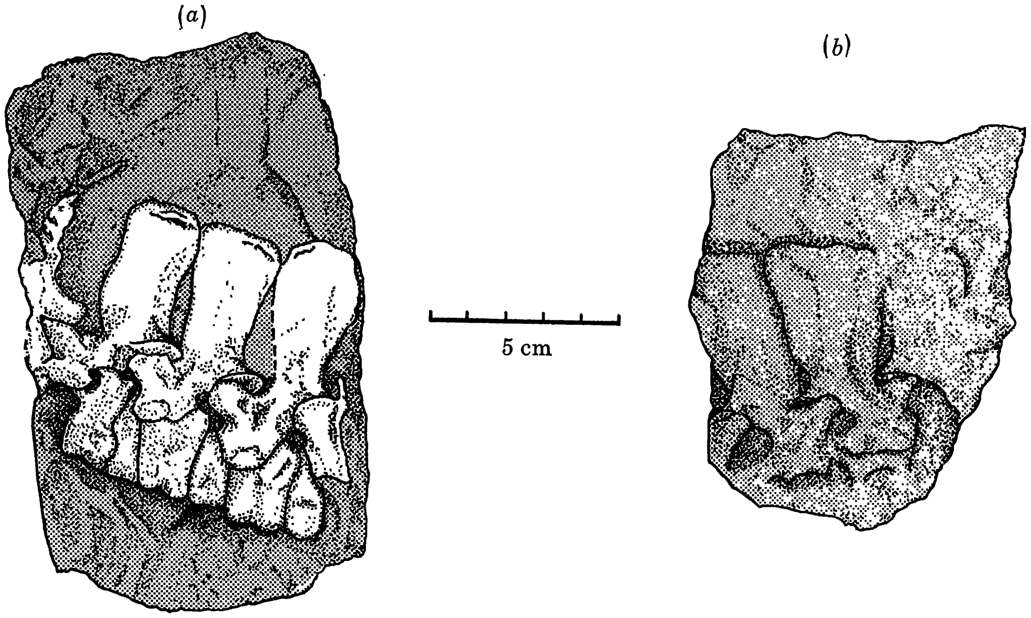

FIGURE 12. ?*Anthracosaurus russelli* Huxley, dorsal vertebrae in lateral view, from latex casts of natural moulds. Half natural size. (*a*), G.S. 56581, left lateral view; (*b*), G.S. 56580, right lateral view.

The form of the neural spines and the possible presence of two rib articulations, one below the other, suggests that the vertebrae may be immediately post-sacral. Thus in *Eogyrinus* at least the first four caudal vertebrae bear distinctive caudal ribs, whose tuberculum articulates with the neural arch, but whose capitulum is borne on a process of the pleurocentrum immediately below it.

The interclavicle collected by William Grossart has not been figured or described before. It is attributed to *Anthracosaurus* largely because of the features which contrast it with the specimen from Newsham attributed to *Eogyrinus* (Panchen 1972*a*, fig. 13). Some of these features were noted in the description of the Newsham interclavicle. The specimen is not certainly from Airdrie but the probability of it being so seems high (see above – Materials and methods, p. 450).

Like the Newsham specimen the Grossart interclavicle is preserved on a block of matrix with its ventral, external surface exposed. It is broken off posteriorly, so that the parasternal process characteristic of anthracosaurs, if originally present, is no longer preserved. Some of the thin edge of the bone is broken away laterally on both sides but the true outline appears to be preserved in part on the morphological left as impression on the matrix. Anteriorly preservation is almost complete (figure 13*a*).

The preservation of the surface is very good and shows the distinctive dermal ornament well. No cleaning of the external surface was necessary.

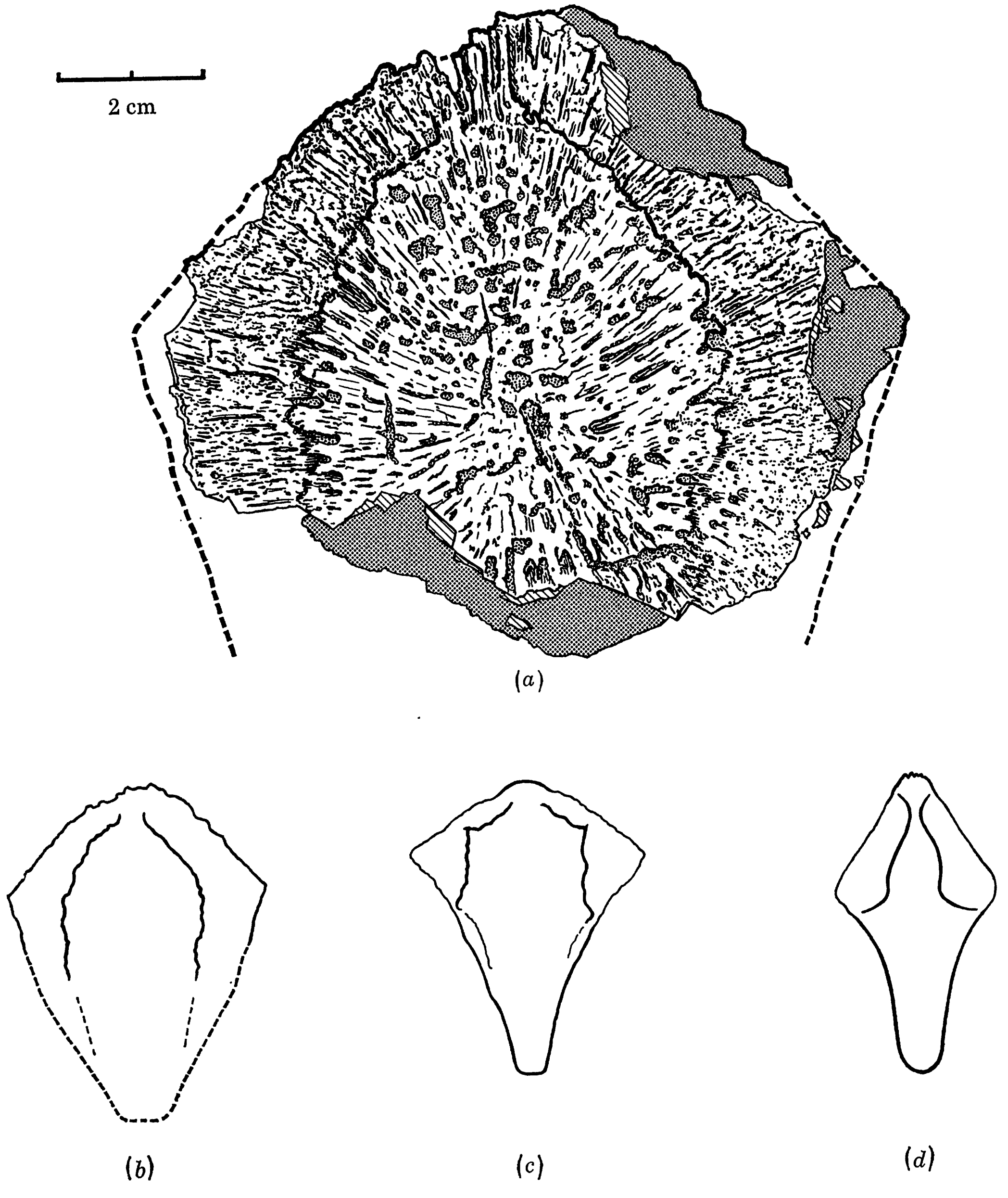

FIGURE 13. Anthracosaur interclavicles in ventral (external) view. (*a*), *?A. russelli*, RSM 1971.11.4. Natural size. (*b*)–(*d*), from 3 anthracosaur families. One third natural size. (*b*), *?A. russelli*: (*c*), *?Eogyrinus attheyi*; (*d*), *Archeria* sp. (*c*) and (*d*) after Panchen 1972*a*; (*d*) from Romer.

The outline of the preserved region is in general similar to that of the Newsham specimen. Both reach their maximum width in the region that was clearly overlapped on each side by the clavicles. In the Newsham specimen, however, the clavicular overlap area extends laterally as a more acutely triangular process, with its laterally directed apex forming rather less than a right angle. In the Grossart specimen, on the other hand, the corresponding angle is about 120° and is thus even greater than that in the interclavicle of *Archeria* (figure 13*b*–*d*).

As in the Newsham specimen the inner margin of each overlap is clearly marked both by a change in level and in ornament. Also similar is the fact that the overlap areas appear to extend round the anterior end of the specimen and almost meet in the midline. The central area between them is in general similar to that in the Newsham specimen but is less clearly quadrangular and relatively slightly smaller. In both these respects it inclines somewhat towards the condition in *Archeria.*

In absolute size it is somewhat greater in area than the corresponding region of the Newsham specimen, although the maximum width of both the central area and of the whole specimen are little different. The difference is largely due to the broad extension backwards of the overlap area on each side from its lateral apex. The overlap areas are incomplete, but their shape suggests that the overlapping clavicles were significantly longer antero-posteriorly in the region of overlap. In this the specimen again inclines towards the condition in *Archeria.*

The dermal ornament is distinctly different from that of the Newsham specimen. In the central area of the latter it is sparse and irregular but in relatively high relief. It consists of a series of deep, widely spaced rounded pits in a convex, somewhat swollen surface. In the Grossart interclavicle the central area is flat or even somewhat concave. This may be due to post-mortem compression, but the section visible at the back of the specimen shows the central area to have been of almost uniform thickness.

The ornament is less sparse and irregular but is in very low relief. It consists of a generally radial arrangement of small, flat-bottomed and very shallow pits, each having a shallow groove or grooves extending radially from it. The ornament on the overlap areas is essentially similar but on a much smaller scale as well as being more closely packed.

The difference in ornament between the two interclavicles corresponds well with the difference in ornament in the two holotype skulls to which they are respectively attributed. It seems not unreasonable, therefore, to associate the present Grossart interclavicle with *Anthracosaurus russelli* and the Newsham one with *Eogyrinus attheyi*, as I suggested when describing the latter bone.

If both these attributions are correct we now have representative interclavicles from all three families of embolomerous anthracosaurs, the Anthracosauridae, the Eogyrinidae and the Archeriidae (figure 13*b*–*d*). It is to be hoped that further discoveries will reveal the extent to which each is typical of its own family.

THE FAMILY ANTHRACOSAURIDAE

The provenance of Eobaphetes kansensis *Moodie*

The original material of *Eobaphetes kansensis* consists of two specimens registered in the U.S. National Museum as numbers 6699 and 6680. The first was designated the holotype of *Erpetosuchus kansensis* Moodie (1911) and the second may be regarded as a paratype. However the generic name *Erpetosuchus* was preoccupied (Newton 1894) and Moodie (1916) renamed the genus *Eobaphetes.*

The holotype consists of the median and left suspensorial region of the skull exposed in ventral view together with three vertebral centra (the latter interpreted by Moodie as two rib fragments). This is overlain by the middle region of the right mandible (interpreted by

Moodie and by Romer (1930, 1963) as maxilla). The paratype consists of an almost complete left mandible. Both specimens were collected by the late Gustav Hambach and purchased by the Museum. The specimens were drawn to Moodie's attention and subsequently loaned to him by a Mr C. W. Gilmore of that institution.

There is, however, a third specimen of *Eobaphetes* unknown to Moodie. It is accompanied by a pencilled note addressed to Gilmore by the head curator R. S. Bassler: 'Hambach sends this to me as a part of his collection. I imagine the horizon and locality is the same as the specimens Moodie described. Please give the tooth to Gidley with our best compliments. R.S.B.'

To Dr Donald Baird belongs the credit for rediscovery of the 'Bassler Block', for pointing out the true nature of the holotype and for demonstrating that all three specimens are parts of the same skull (see below).

The two original specimens were said by Moodie (1911) to be from the Coal Measures of Washington County, Kansas, and he notes that 'on a slip of paper accompanying the specimens was written in pencil, evidently by Mr Hambach, "Coal Measures, Washington Co., Kansas"'.

That slip of paper has presumably been lost.

Moodie then goes on to note that no coal-measure deposits were indicated in Washington County in a recently published geological map of Kansas (Geol. Surv. Kans. 1908) but that they outcropped in the adjacent Marshall County.

In 1925 Romer reviewed the then known Palaeozoic tetrapod localities in Kansas. He suggested that the horizon of *Eobaphetes* was the same as that of a series of plants described by White (1912) from near the town of Washington, Washington County, Kansas. These were attributed by White, on the suggestion of Dr J. W. Beede, to an upper Wolfcampian (Chase group) horizon. Subsequently, however, Beede (1922) suggested that the plant horizon was Pennsylvanian on the evidence of White's flora. Romer suggested that it might be at the level of the Cottonwood Limestone, then thought by some to be Pennsylvanian.

Romer (1930), while attributing *Eobaphetes* to the Linton genus *Leptophractus*, does not comment on its horizon. In 1935, however, in a review of the early Texas 'red-bed' fauna and that of nearby states, he again gives an horizon near that of the Cottonwood which he correlates with the Coleman Junction limestone of the Putnam formation, Wichita group, of North Central Texas. More recent work (Dunbar *et al.* 1960) corroborates this correlation, with the upper Council Grove group (below the Chase) of Kansas, in which the Cottonwood Limestone is situated, equivalent to the Putnam. However, the whole of the Wichita is now generally regarded as Lower Permian (Romer 1958*a*; Dunbar *et al.* 1960; Smith 1964).

Thus until comparatively recently *Eobaphetes* was agreed to come from an unknown seam of coal, probably of Lower Permian age, from Washington County, Kansas.

However, in 1963 Romer, at the suggestion of Dr Nicholas Hotton III and Dr G. A. Cooper of the U.S. National Museum, published an entirely new interpretation.

Hambach's collection, purchased by that Museum in 1909, consisted mainly of echinoderms, in which he was principally interested, but contained other plant and animal fossils including *Eobaphetes*. Hambach was said not to have worked in Washington County, Kansas, but he had collected and described echinoderms from the Brentwood limestone of Washington County, Arkansas (Hambach 1908). Immediately above this limestone is situated the Baldwin coal which was worked at the beginning of the century. Hotton and Cooper therefore suggested that Moodie had misread Hambach's original label, substituting 'Kansas' for 'Arkansas'.

The Baldwin coal lies in the Woolsey member, Bloyd formation, Morrow series and is thus very early Pennsylvanian (Moore *et al.* 1944). In European terms the Bloyd formation is equivalent to an horizon lying somewhere near the Westphalian–Namurian boundary of the Upper Carboniferous and thus might well predate the British Coal Measures. Recent work by Quinn (1963) suggests that this is indeed the case, as was pointed out to Romer (1963) by Dr Baird. Quinn equates the Hale formation, immediately underlying the Bloyd, with the H and R_1 zones, Namurian A and B on the basis of goniatites (correlation chart in Panchen 1970).

Thus the joint hypothesis of Hotton, Cooper, Romer and Baird turns *Eobaphetes* from a Permian relict of the large embolomeres of the Coal Measures to probably the earliest known skull of an embolomerous anthracosaur, as Romer (1963) pointed out.

It is highly probable, however, that Hambach did collect in Kansas and quite likely that he did so in Washington County. As recalled by the late Dr Raymond C. Moore to Dr Frank C. Foley of the Kansas Geological Survey (to whom I am indebted for this information), Hambach had been technical assistant to G. C. Swallow. The latter was Director of the Second Kansas Geological Survey in 1865. Swallow worked in northwestern Missouri in 1853 and then continued field studies in northeastern Kansas (where Washington Co., Kansas, lies). It is likely that Hambach accompanied him.

Dr Foley also notes that it was Swallow, together with a civil engineer, Frederick Hawn, who in 1858 announced for the first time the recognition of Permian rocks in North America. If Hambach had been working in Kansas before their recognition of Permian fossils, he would have regarded all the Palaeozoic strata of eastern Washington County and adjoining counties as 'Coal Measures'.

Eobaphetes is preserved in a poor humic coal. This is unusual for a Carboniferous labyrinthodont, most of which occur in shales with different degrees of organic content, or in ironstone nodules. Soon after suggesting the hypothesis to Romer, Dr Hotton sent a sample of this coal matrix to Dr James M. Schopf of the U.S. Geological Survey for analysis. Dr Schopf has kindly sent me the results.

The coal was first subjected to chemical and calorific analysis by Dr Forrest E. Walker of the U.S. Bureau of Mines (Sample No. CGL-173). The results of this analysis may be compared with those of 13 samples of the Baldwin coal, all from Washington Co., Arkansas, quoted by Croneis (1930) (table 2). It may be seen that the statistical probability that the *Eobaphetes* matrix represents a sample of the Baldwin coal is very small. The critical values of fixed carbon content and volatile matter, expressed as the carbon ratio, show it to be a coal of much lower rank. This is echoed by the calorific content which was 13590 B.T.U. for the Baldwin coal and 10890 B.T.U. for the *Eobaphetes* matrix. Furthermore, the latter value would have been much increased by nearly 55 years of evaporation of the contained moisture in the Museum before analysis.

Dr Schopf has told me that a coal closely comparable in rank and composition is the Nodaway coal from Page County, Iowa, which has, when fresh, about 12% moisture and a calorific value of 9390 B.T.U. Loss of moisture of the type suffered by the *Eobaphetes* matrix would increase this to something over 10000 B.T.U., a value closely comparable to that of the latter.

The Nodaway coal of Iowa, Missouri and Kansas lies in the Howard Limestone formation (Zeller 1968), which is placed in the lower part of the Wabaunsee group in Iowa, Kansas and

Missouri (Moore 1948, 1949). The Howard Limestone is agreed to be at the same horizon throughout and is Virgilian and thus uppermost Pennsylvanian (Moore *et al.* 1944). This is equivalent to the European Upper Stephanian.

Thus, unless the coal surrounding the *Eobaphetes* specimens is very uncharacteristic of the seam from which they were derived (as suggested to me by Dr Baird) it is in the highest degree improbable that *Eobaphetes* came from the Baldwin coal. The latter is the only coal seam recorded from Washington County, Arkansas.

TABLE 2. COMPARISON OF BALDWIN COAL AND *EOBAPHETES* MATRIX

(Baldwin coal, Washington Co., Ark. after Croneis (1930, p. 362: samples no. 7 and 8 not tabulated); *Eobaphetes* matrix – U.S. Bureau of Mines report, sample no. CGL-173: 7 Feb. 1963.)

Baldwin Coal	moisture	vol. mat.	fixed carbon	ash	carbon ratio
1	0.54	30.04	61.09	8.33	67.03
2	0.61	26.89	61.57	10.93	69.60
3	3.35	29.14	61.24	6.27	67.75
4	0.59	30.79	61.92	6.70	66.80
5	0.20	25.91	55.73	18.16	68.26
6	7.40	25.98	58.30	8.32	69.17
9	1.20	27.18	66.50	5.12	70.98
10	4.79	22.96	66.35	5.90	74.29
11	0.35	18.17	69.13	12.35	79.20
12	3.07	24.15	65.72	7.06	73.13
13	1.80	23.25	61.82	13.13	72.67
14	6.44	23.58	58.51	11.47	71.27
15	0.59	26.91	61.58	10.92	69.59
mean	2.38	25.77	62.27	9.59	70.75
s.d.	2.46	3.40	3.76	3.69	3.46
Eobaphetes matrix	3.40	37.70	48.80	10.10	56.40
deviation from mean	1.02	11.93	13.48	0.51	14.35
t	0.41	3.51	3.58	0.14	4.14
P	> 0.1	$\leqslant 0.01$	$\leqslant 0.01$	> 0.1	$\leqslant 0.01$

As well as sending the *Eobaphetes* matrix for chemical analysis Dr Schopf himself conducted a spore analysis. The coal macerated well, unlike the expectation for a high rank coal such as the Baldwin coal, but according to Schopf the results of the investigation favoured Pennsylvanian rather than an early Permian horizon.

I quote from his letter (1 May 1972):...'The abundant forms include auriculate megaspores and a very common type of *Endosporites* which Chaloner (1953, 1958) has shown belong with a form he called *Lepidostrobus zea* and subsequently identified with *Polysporia mirabilis* of Newberry. Newberry's old material was associated with the Sharon coal, lower Pottsville Series, Ohio, which is regarded as the same age as the coal-bearing shale of Washington County, Arkansas [i.e. bearing the Baldwin coal]. *Lepidostrobus zea* comes from the lower Similis–Pulchra zone of Yorkshire and Ayrshire. I have no doubt that all of these fossils represent one rather distinctive group of arborescent lycopsids. Their range is pretty much restricted to the Pennsylvanian so far as known, but they certainly do get into at least the Middle Upper Pennsylvanian and might go higher....'

He then lists other associated spores, of which *Calymospora* and *Laevigatosporites* cf. *vulgaris* were common.

Thus a Pennsylvanian date was indicated by this analysis, which, however, did not certainly rule out a horizon as early as that of the Baldwin coal. Dr Schopf regarded the latter as more probably equivalent to the *Sphenopteris hoeninghausi* zone of Europe, i.e. Westphalian A (Crookall 1955), rather than Namurian. Nor did it rule out a Stephanian horizon although this seemed even less probable, but a Permian horizon for *Eobaphetes* was excluded.

Another line of evidence led me independently to suspect the combination of locality and horizon attributed to *Eobaphetes* by Romer (1963). In monographing the embolomerous anthracosaurs I plotted the known localities for these amphibia on a 'pre-drift' map of Europe and North America in relation to the palaeoequator (Panchen 1970, fig. 18). The distribution of known sites in space and time suggested a geographical radiation of the embolomeres from an area defined by the Appalachian region in the west and Great Britain in the east. By the end of the Carboniferous they had reached as far west as Texas and as far east as Prague, but no other anthracosaur is known to have reached as far as Arkansas in the early Pennsylvanian. In this respect the reputed provenance of *Eobaphetes* was the only anomaly.

Thus on the published evidence an impasse appeared to have been reached. Moodie's original attribution was excluded by the lack of any 'Coal Measure' strata from Washington County, Kansas, Romer's (1925, 1935) hypothesis of a Permian horizon by Schopf's spore analysis (and the absence of any recorded coal of any sort from that County), while the Baldwin coal hypothesis (Romer 1963) was rendered unacceptable by the coal analysis, corroborated by the evidence of embolomere distribution.

In an attempt to resolve the impasse a large sample of the *Eobaphetes* matrix was sent to Dr A. H. V. Smith of the National Coal Board who had generously agreed to conduct a second spore analysis. His conclusions are sufficiently important to be quoted at length (in litt. 18 May 1976):...'The maceration residue from pieces from each of the six small lumps of coal yielded a well preserved assemblage of spores from which about 30 species were identified. The assemblage was dominated by *Endosporites globiformis*. Other relatively common forms belonged to the genera *Laevigatosporites*, *Calamospora* and several genera containing small monolete forms.

Of particular stratigraphical significance are the occurrence of *Cadiospora sphaera*, *Microreticulatisporites sulcatus* and *Raistrickia aculeata*. These species indicate that the coal is of Westphalian D or Stephanian age. The presence of the various small monolete forms supports this conclusion.

An unusual feature of the assemblage was the absence of species of *Lycospora*. This is usually the dominant spore in most assemblages from bright coal in the Coal Measures. Since the matrix material was derived from a coal layer having at least a thickness of 1.5–2.0 cm the absence of *Lycospora* spp is more likely to be for stratigraphical reasons than to the occurrence of an unusual facies.

In the U.S.A. *Lycospora* becomes very scarce in the upper part of the McLeansboro Group or in strata of equivalent age (Clendening 1962; Peppers 1964). In Europe the same is true of strata of uppermost Stephanian age. The observed species of the genera *Endosporites*, *Calamospora* and *Laevigatosporites* have all been recorded from the Upper McLeansboro group and other species figured by Peppers were also recognized.

This evidence suggests that the fossil is of Westphalian D–Stephanian age with a strong probability of it being uppermost Stephanian....'

Thus while Dr Smith reaches a different conclusion from Dr Schopf on the spore evidence, the latter's evidence based on coal analysis is in accord with a late Pennsylvanian horizon.

This horizon very strongly reinforces the conclusions reached below on the relationships of *Eobaphetes*, where it is discussed in that context.

Finally it seems probable to me that the reported 'Washington County, Kansas' (? 'Washington Co.') is more probably a misreading of 'Washington Coal' (as suggested to me by Mrs Angela Milner) or 'Washington Creek' rather than 'Washington County, Arkansas' (usually abbreviated 'Ark'). However, even with Dr Foley's help, I have been unable to localize either.

Eobaphetes kansensis: *description*

The major part of the dermal skull roof of *Eobaphetes* is preserved in the holotype and the Bassler block (figure 14). The skull table, comprising easily traced postparietals, parietals, tabulars, supratemporals and intertemporals, is complete and intact. Preservation also extends forward to include both postfrontals with their orbital margins, a fragment of the left postorbital, the major part of the frontals, the right prefrontal and some roofing bone flanking it.

The left cheek region and suspensorium, extending forward to the front of the jugal and adjacent lacrimal and thus to the side of the snout, is preserved on the Bassler block. Proximally the posterior cheek region, comprising a dorso-mesial part of the squamosal, is preserved in its natural relation to the skull table on the holotype block.

Despite their long separation the holotype and Bassler blocks fit together, bone to bone, for a length of just over 2 cm within the squamosal which spans them. The fit is so precise that there can be no doubt whatsoever that a single skull is represented. Further, but unnecessary, corroboration is given by the outline of the coal matrix for adjacent areas of the blocks and by the continuation of the right mandible as natural mould on the Bassler block.

Furthermore, the dorsal edge of the paratype left mandible is preserved as natural mould almost in articulation with the left suspensorium on the Bassler block. Thus there is no doubt that all three specimens represent a single skull, as was first realized by Dr Baird.

The skull table of *Eobaphetes* is in all respects similar to that seen in other embolomerous anthracosaurs. Its proportions lie between those of *Anthracosaurus* and *Eogyrinus* in relative width although this is somewhat exaggerated by post-mortem compression. A measure of this width is the ratio of maximum table width divided by pineal-postparietal length. This is 2.53 for *Anthracosaurus* (but exaggerated by the concave contour of the back of the table) and 1.67 for the *Eogyrinus* holotype (from table 1). The dimensions for *Eobaphetes* are table width *ca.* 85 mm, pineal-PP length 37 mm, giving a ratio of 2.03 with a less concave border to the table.

In *Eobaphetes* the table increases steadily in width posteriorly, forming a truncated triangle, while that of *Anthracosaurus* is rectangular and that of *Eogyrinus* elliptical, at least in its lateral contours.

Importantly, however, the skull of *Eobaphetes* has retained the kinetism between table and flanking cheeks characteristic of eogyrinids and primitive for tetrapods, in contrast to the condition in *Anthracosaurus*.

The tabular horn is virtually complete on both sides of the *Eobaphetes* skull and is extremely long, extending a little further behind the level of the centre back of the skull table (*ca.* 42 mm) than the pineal-PP length.

While nearly complete, the horns are flattened and probably somewhat eroded. Once again, however, they appear to be intermediate in structure between those of *Anthracosaurus* and the Eogyrinidae. They appear to be biramous, as in *Anthracosaurus*, but the axes of the two rami are almost in the same vertical plane so that they do not diverge in dorsal view. In the specimen the rami are separated only by a thin layer of matrix posteriorly in the right horn and are compressed together on the left.

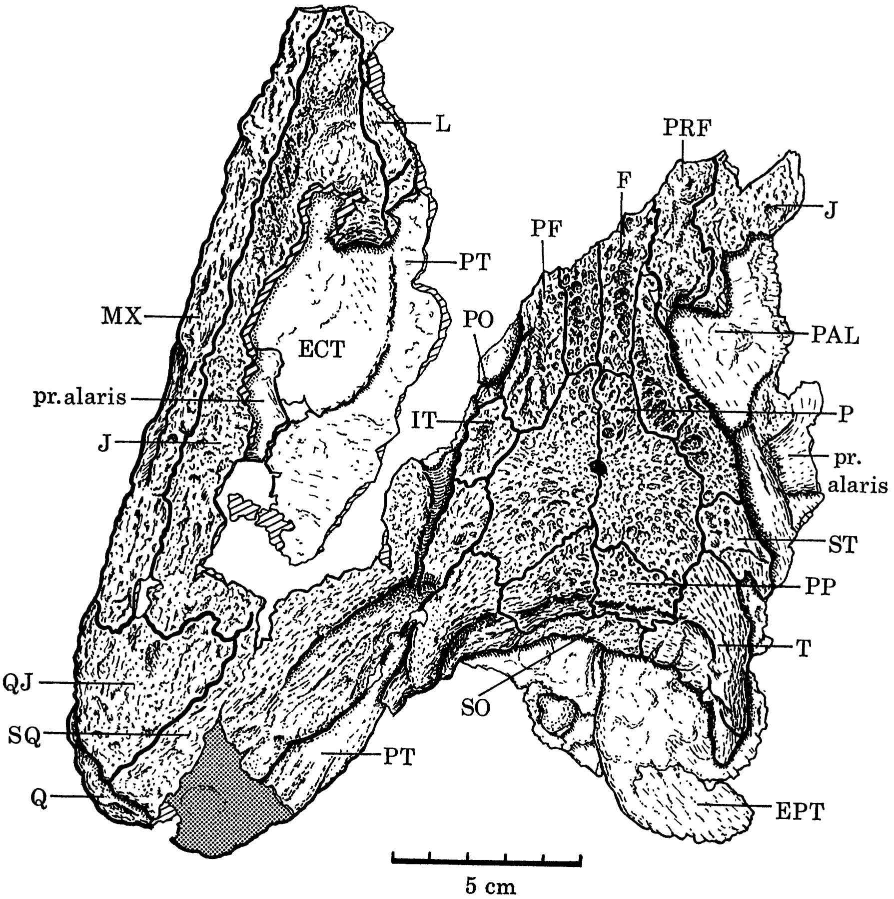

Figure 14. *Eobaphetes kansensis* Moodie, skull as preserved (holotype and 'Bassler block') dorsal view. Half natural size. EPT, epipterygoid; IT, intertemporal; P, parietal; PF, postfrontal; PO, postorbital; PP, postparietal; Q, quadrate; QJ, quadratojugal; SO, supraoccipital; SQ, squamosal; ST, supratemporal; T, tabular; Other abbreviations as in figure 8.

The distal end of the lower ramus, which extends some 8 mm beyond the upper on both sides, does, however, turn laterally at its end on the left, somewhat in the manner of *Anthracosaurus*.

Thus it is easy to reconstruct a series in the development of the tabular horns of embolomeres, with the primitive condition probably represented by *Eogyrinus*. In the *Eogyrinus* horn the upper ramus is represented by an ornamented extension of the tabular and the lower ramus is a mere further extension at a less superficial level. In *Palaeoherpeton* and *Pteroplax*, however, the lower ramus was blade-like with a deep ovoid transverse section. This may also have been the case in *Eogyrinus* and thus characteristic of the British Eogyrinidae (Panchen 1964, 1972*a*).

In *Eobaphetes* and *Anthracosaurus* on the other hand there is an increasing divergence of the two horns, the upper acquiring a free extension beyond its junction with the lower.

More anteriorly the pattern of the frontals and postfrontals is closely similar to that of *Eogyrinus*, as is their relationship with the front of the parietals. A fragment of the left postorbital sutures with the postfrontal, just excluding the intertemporal from the orbit.

The interorbital width may again be compared with that of *Anthracosaurus* and *Eogyrinus* by division by the pineal-PP length. The ratio for *Anthracosaurus* is 1.38, for *Eogyrinus* 0.83. The minimum interorbital width of *Eobaphetes* is *ca.* 37 mm giving a ratio of 1.0, again between those of the other two skulls.

A considerable area of the right prefrontal is preserved in *Eobaphetes*, showing its suture with the postfrontal and about 17 mm of that with the frontal. Its flanking suture is also easily traced. Laterally to that suture there is a further area of the skull roof preserved and the identity of the bone or bones comprising it is critical.

In *Eogyrinus* large rectangular prefrontals have a long lateral suture each with its respective jugal, thus excluding the lacrimal from the orbit, in contrast to the condition in *Anthracosaurus*. The evidence is reasonably good that the *Eogyrinus* condition is present in *Eobaphetes*. On the right, while somewhat meso-laterally compressed post-mortem, the prefrontal is of a similar shape to that of *Eogyrinus*. Also the presumed jugal to the right of it curves round to form the anterior end of the lateral orbital margin, just as in *Eogyrinus*, although the orbit is compressed in width in *Eobaphetes*.

Furthermore, part of the antero-lateral margin of the orbit is preserved on the left (in the Bassler block). Mesial to the preserved border the presumed jugal-prefrontal suture extends forward until a small length of transverse suture can be traced running mesially. This must represent the prefrontal-lacrimal suture and thus the posterior boundary of the lacrimal. The lacrimal-jugal suture then extends forward to the front of the specimen.

The pattern of sutures on the cheek region differs from those of both *Anthracosaurus* and *Eogyrinus*, although in the latter case the sutures of the posterior cheek are to some extent reconstructed (Panchen 1972*a*; fig. 6).

The maxillary of *Eobaphetes* appears as a lateral strip of bone uniformly just over 1 cm wide extending from the front of the Bassler block back to a transverse suture marking the anterior edge of the quadratojugal. Thus, as in *Anthracosaurus*, but not apparently in the eogyrinids (see below), the jugal is excluded from the jaw margin. While the sutures of the jugal with prefrontal, lacrimal, maxillary and quadratojugal, together with the posterior 5 mm of its suture with the squamosal, are all preserved; much of the body of the bone is broken away to expose the dorsal surface of the palate.

A major part of the left squamosal is preserved spanning both blocks. The whole cheek region has been compressed into the horizontal plane of the skull table, thus disarticulating the kinetic squamosal-skull table joint.

The articular surface of the squamosal is thus exposed at the level of the anterior half of the supratemporal and just beyond that of the intertemporal-supratemporal suture.

It is strikingly like that similarly exposed in the specimen of *Pholiderpeton* from Swanwick in the English Coal Measures ('*Eogyrinus*': Panchen 1964, fig. 15), a specimen of closely similar size. As in *Pholiderpeton* a flange of the squamosal extends mesially to the inner edge of the superficial surface of the squamosal, so that the surface of the flange is roughly a hemicylindrical concave one. In eogyrinids this surface articulates with a similar, but ventrally facing, hemicylindrical concave area on the ventral surface of the skull table, so that considerable connective tissue packing must have been present between the two. There seems little doubt that a precisely similar articulation occurred in *Eobaphetes* although the ventral surface of the skull table is not accessible.

In *Eobaphetes* the squamosal is almost completely preserved posterior to the kinetic articulation. Mesially its suture with the quadrate ramus of the pterygoid is exposed, together with a broad strip of that ramus, in dorsal view. Lateral to the suture an area about 2 cm wide is defined laterally by a low ridge as well as by its longitudinally striated surface texture. This area represents the occipital area of the squamosal and terminates anteriorly in the otic notch. The boundary of the notch is well defined by a sharpening of its boundary ridge on the squamosal. Its dorso-mesial border is formed in the normal way by the tabular horn and the postero-lateral corner of the supratemporal just enters its margin.

Posteriorly the squamosal extends back to its suture with the quadrate, preserved as bone on the Bassler block and as a natural mould of the dorsal surface on the adjoining holotype. As preserved the dorsal exposure of the quadrate has an antero-posterior width of less than 5 mm, in striking contrast to the condition in *Anthracosaurus*.

Also in contrast to *Anthracosaurus* is the dermal ornament covering the whole preserved skull roof. That of *Eobaphetes* is closely similar to the ornament of eogyrinids although somewhat finer in scale. It is clearly and sharply developed over the whole medial skull region, including the skull table, preserved in the holotype block. As in eogyrinids the ornament is rather less regularly developed on the cheek region, but maxillary and jugal are quite strongly ornamented in a coarse irregular pattern.

Signs of the lateral line system are somewhat doubtfully present in *Eobaphetes*. A coarsening of the ornament on the intertemporal, postfrontal and frontal, seen more clearly on the better preserved right side, suggests the forward course of the supraorbital sulcus. If correctly identified the sulcus follows exactly the same course as in *Palaeoherpeton* (Panchen 1964, 1970) and has a visible extension backward greater than that of *Eogyrinus*, where it is not visible behind the orbit.

On the cheek region traces of the infraorbital sulcus appear on the jugal, extending from orbital level forward to the front of the specimen just mesial to the maxillary suture, again as in *Palaeoherpeton* (and *Eogyrinus*).

The dorsal part of the occipital surface of *Eobaphetes* is preserved in situ behind the skull table and is of typical embolomere type. No post-temporal fossae are present. The sutures bounding the occipital exposure of tabulars and postparietals were also traced and although not quite certain throughout their length they establish unequivocally the presence of an exposed ossification mesial to the tabulars and ventral to the postparietals. Thus the supraoccipital area is ossified, but, as in *Anthracosaurus*, no clear separation between supraoccipital and opisthotics could be found. It is not clear in the case of *Eobaphetes*, however, that any part of the paroccipital process of the opisthotic is preserved in its natural position on either side.

The area of bone exposed in dorsal view immediately behind this occipital surface is difficult to interpret, despite the fact that it has been completely cleared of matrix. On the right, the right quadrate rami of the pterygoid and epipterygoid appear to have been reflected round from their original position as a vertical blade between the basal articulation and the quadrate. Their ventro-mesial surface thus appears in dorsal view with the ventro-lateral edge of each now almost in the midline.

This establishes that the quadrate ramus of the pterygoid was a deep blade like that of eogyrinids and not a mere thickened border to the subtemporal fossa, as in *Anthracosaurus*. It also appears to have had a roughened surface, seen also in ventral view on the left ramus, although not so clearly denticulate as that of *Eogyrinus* and *Palaeoherpeton*.

However, the surface of the right ramus is much eroded and posteriorly is in part missing thus exposing the surface of the epipterygoid. There also seems to have been some degree of fusion between the rami. Nevertheless it is established that a distinct epipterygoid ramus of the type described in *Palaeoherpeton* (Panchen 1964, fig. 5) was also present in *Eobaphetes*.

To the left of this area, rotted bone behind the occiput appears to pertain to the braincase and a rounded bony boss situated on top of this may represent the condylar region of the right exoccipital.

More of the palate is exposed in dorsal view to the right of the skull table and orbital region and also on the left where much of the jugal is missing on the Bassler block.

Anteriorly on the latter a long suture, convex mesially, separates a lateral and mesial palatal bone. The lateral bone is the ectopterygoid and its irregular surface laterally marks the position of the hidden palatal dentition. Mesial to the suture is the pterygoid. The dorsal exposure of the ectopterygoid is relatively very much wider than the ventral exposure of that bone in any described anthracosaur and suggests a broad overlap of the pterygoid as seen in section in *Anthracosaurus*.

Posterior to the ectopterygoid–pterygoid suture the pterygoid extends laterally to meet a massive buttress, which projects towards it as a flattened and truncated cone. This latter is the processus alaris of the jugal, which in eogyrinids joins with the pterygoid to exclude the ectopterygoid from the subtemporal fossa (Panchen 1964, figs 13, 16; 1972*a*, fig. 7), but is absent in *Anthracosaurus*. It is thus an important feature uniting *Eobaphetes* and the eogyrinids.

Behind this junction of palatal jugal and pterygoid the subtemporal fossa is well defined anteriorly, but a strip of rotted bone spans the fossa 1 cm behind its anterior border.

The processus alaris is also visible in dorsal view on the right, but it has moved forward, relative to the pterygoid, and lies in the curve of the pterygoid–ectopterygoid suture. The ectopterygoid itself is missing except as remnants of rotted bone. However, a little of the surface of the pterygoid overlapped by the ectopterygoid is preserved.

Anteriorly, at the point where the right ectopterygoid suture begins its lateral curve into the transverse plane the pterygoid is overlapped by another sheet of bone, which extends forward from that point. This, if it does not represent mere disruption of the pterygoid, must be the palatine, which thus has an even greater mesial overlap with the pterygoid than does the ectopterygoid.

Two low projections, one visible in the dorsal surface of the palatine itself, the other causing the postero-lateral corner of the prefrontal to protrude, presumably mark the sites of the palatine tusks. The outline of the corresponding sockets may be dimly discerned in the palatine on the poorly preserved bone of the ventral surface, but none of the right palatal dentition is preserved.

The only palatal tusk exposed is represented as a natural mould on the Bassler block just below the anterior end of the lacrimal (see below).

In ventral view most of the palatal surface on the holotype block is obscured by the large portion of right mandible which lies across it (figure 15). Anterior to the mandible the bone, representing the ventral surface of the palatine and of the prefrontal and its flanking roofing bones, is mostly badly rotted and yields no further significant information.

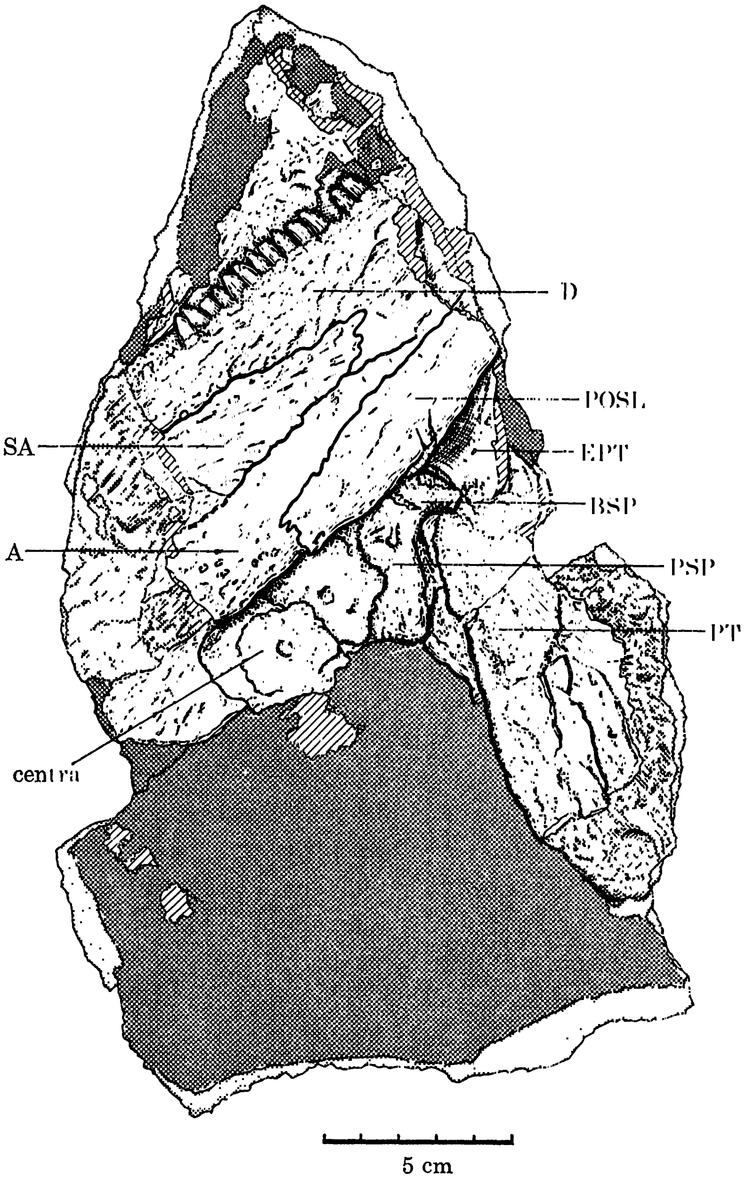

FIGURE 15. *Eobaphetes kansensis* Moodie, holotype block before development. Half natural size. Matrix (incl. natural mould) stippled. BSP, basisphenoid; EPT, epipterygoid; SA, surangular. Other abbreviations as in figures 8 and 10.

Posterior to the mandible the ventral surface of the left suspensorial region is exposed on the right of the specimen. The quadrate ramus of the pterygoid and the under surface of the squamosal are preserved as bone and originally lay over a natural mould of the dorsal surface of the squamosal and quadrate. Unfortunately the ventro-lateral free edge of the quadrate ramus is broken away so that its depth cannot be checked. However, the dorsal edge of the ramus is preserved and visible in ventral view. Comparison of the position of this dorsal edge with the position of the squamosal-pterygoid contact seen in dorsal view shows that the two bones had a mutual overlap of more than a centimetre.

There is no clear sign of a discrete left quadrate ramus of the epipterygoid. However, the left epipterygoid certainly appears on the right of the specimen immediately behind the mandible. This is at the level of the basal articulation. In the eroded area behind the articulation, while ornamented pterygoid appears mesially, it may be eroded away to reveal epipterygoid laterally, as on the right in dorsal view.

The left basal articulation is complete and exposed to view. Its structure appears exactly as in eogyrinids. The epipterygoid buttress is particularly well preserved and retains its connection to a wedge-shaped broken piece of the body of the epipterygoid whose broken edge just posterior to the buttress shows it to have reached a thickness of at least 6 mm.

The articulate surface at the postero-mesial end of the buttress retains its articular connection to the basipterygoid process of the basisphenoid. Mesial to the process the underlying parasphenoid is well preserved and extends back to its true posterior edge. Mesial to the basal articulation the parasphenoid bears well marked rugosities, presumably for muscle origin.

Part of the lateral wall of the braincase is visible dorso-lateral to the parasphenoid body and posterior to the basal articulation. This is formed by the basisphenoid and posteriorly shows what may be the antero-ventral border of the fenestra ovalis. It is not clear, however, that any of the otic capsule is preserved in situ, and bone surface behind this border appears to pertain to the tabular.

The morphological right side of the parasphenoid body is obscured by one of three overlapping vertebral centra. Only the dorso-lateral surface of the right quadrate ramus of the epipterygoid (see above) is exposed beyond them and behind the mandible.

The three centra are considerably .compressed and eroded but that on the right of the specimen appears to be a pleurocentrum while the middle one which overlaps it is an intercentrum. The third, on the left, appears to be a pleurocentrum but is largely obscured by the latter. They appear to have been normal embolomerous centra, with a diameter of just over 2 cm, but with the notable feature that the notochordal perforation is seen in the first two to be occluded, just as in the centra of *Anthracosaurus.*

The (paratype) left jaw ramus of *Eobaphetes* is almost completely preserved and is now completely free of matrix. As figured by Moodie it is complete in one piece, but as now preserved (and as received by me) it is in two parts separated by a gap, so that in lateral, external view parts of the angular and surangular are missing, and in internal view parts of these bones and also of the prearticular and the extreme posterior end of the postsplenial are also lacking.

Apart from meso-lateral compression, which has also forced the ramus into a single vertical plane, there is very little distortion. Fortunately the larger, anterior piece of the specimen fits very accurately into its mould on the Bassler block. The latter also preserves the true outline of the dorsal edge of the articular and surangular. Thus the three preserved parts (paratype pieces and Bassler mould) can be restored into their natural orientation with complete confidence (figure 16).

The pattern of sutures on the middle region of the lateral surface of the left ramus is completely corroborated by the easily traced sutures of the right ramus on the holotype block. This was particularly valuable in the region where the anterior ends of the surangular and angular meet the dentary and where sutures and post-mortem cracks in the left ramus could be confused. Otherwise the sutures are relatively easy to trace on both sides of the latter.

In general features the lower jaw in *Eobaphetes* is closely comparable to that of *Eogyrinus*, which has been described in considerable detail and may thus be used as a standard of comparison (Panchen 1970, 1972*a*).

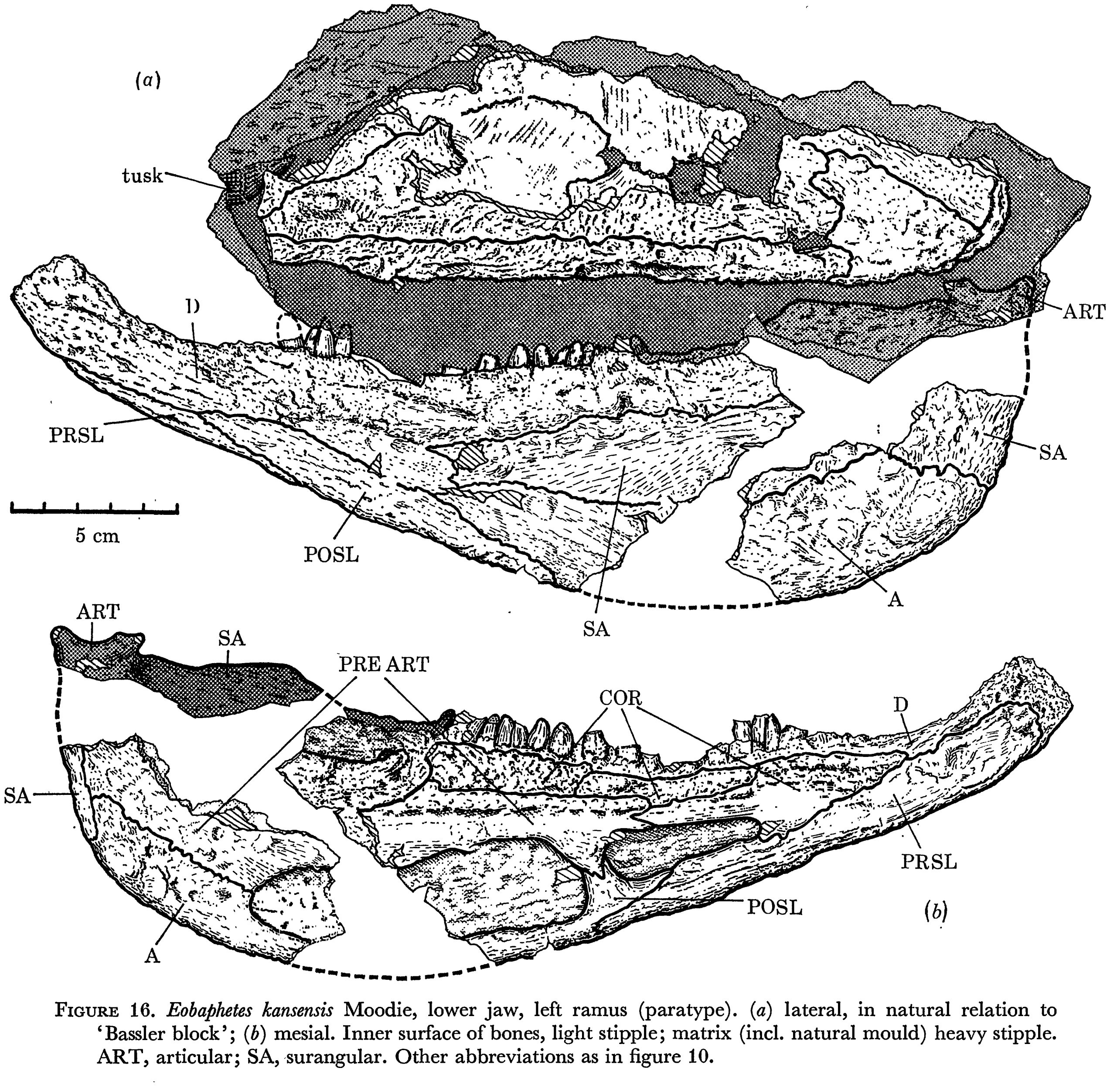

FIGURE 16. *Eobaphetes kansensis* Moodie, lower jaw, left ramus (paratype). (*a*) lateral, in natural relation to 'Bassler block'; (*b*) mesial. Inner surface of bones, light stipple; matrix (incl. natural mould) heavy stipple. ART, articular; SA, surangular. Other abbreviations as in figure 10.

The shape of the *Eobaphetes* ramus is closely comparable to that of *Eogyrinus*, very deep posteriorly, particularly at the level of the adductor fossa, but shallow anteriorly with a very narrow symphysis. In *Eobaphetes* this shallowness is exaggerated by loss of the teeth and erosion of the top of the dentary just behind the symphysis.

As in *Eogyrinus* and other embolomeres, but in contrast to *Anthracosaurus*, there are two meckelian fenestrae in the mesial face of the ramus whose relationships to the surrounding dermal bones and to the adductor fossa are, in general terms, similar to those of *Eogyrinus*.

There is no unequivocal sign of the lateral line system on the external surface of either left or right ramus, but the surface of the former is somewhat worn and there is some disruption of the postsplenial in the latter where the mandibular sulcus would be expected to run.

The ramus also differs slightly in shape from that of *Eogyrinus*. Two features may be of importance. Firstly the whole ramus has a marked upward curvature, so that the dentary tooth row was apparently concave dorsad. This is exaggerated by the dentary erosion referred to, and possibly by the flattening of the ramus, but was probably a feature of the intact jaw. Secondly the surangular crest immediately in front of the articular glenoid, which forms the high lateral wall to the adductor fossa, is flat-topped as preserved in natural mould.

In *Eogyrinus* the surangular crest is very high and convexly rounded in lateral view: in *Eobaphetes* it extends well above the tooth row anteriorly but appears to lack the thin blade above the ridge seen in mesial view in *Eogyrinus*. The difference may be of taxonomic significance.

Differences in sutural pattern between the two may also be noted. Laterally the surangular extends further forward above the angular in *Eobaphetes*. Thus, whereas in *Eogyrinus* the dentary-angular suture lies entirely in front of the dentary-surangular one and is smoothly continuous with it, in *Eobaphetes* there is a marked irregular step up in the dentary outline behind a very limited contact with the angular to accommodate the contact with surangular process, which reaches further forward than the angular dorsally.

On the mesial surface of the ramus the surangular wraps round the back of the ramus to appear in mesial view and suture with the prearticular and angular, as in *Eogyrinus*. Also as in *Eogyrinus* the insertion of the depressor mandibulae appears on the angular just below its surangular suture. In *Eobaphetes* it is represented by a low elongate boss rather than a rugose area.

Other minor features include a greater extension of the prearticular down the bar separating the fenestrae, so that its suture with the postsplenial is at a mid-point along the bar rather than near the top, and a greater backward extension of the presplenial.

The pattern of the three coronoids is similar to that in *Eogyrinus*, with a prearticular-middle coronoid suture and no contact between anterior and posterior coronoids, in contrast to the *Anthracosaurus* condition (see above).

The coronoids of *Eobaphetes* were figured as denticulate by Moodie as are those of *Eogyrinus*. Romer (1963) contrasted this with the condition in *Neopteroplax* in which the region of the anterior coronoid is described as lacking denticles.

All three coronoids in *Eobaphetes* are highly rugose but distinct denticles having the structure of teeth can only be seen, sparsely distributed, on the posterior coronoid. This sparseness of distribution is a sign of some erosion of the coronoid surface, but unfortunately a denticulate anterior coronoid cannot therefore be used as a taxonomic feature in *Eobaphetes*.

Apart from the coronoid denticles and the single tusk impression only the dentary dentition is visible in *Eobaphetes*. All past references to the maxillary dentition refer to the misidentified right mandible.

Moodie figured 26 dentary teeth on the left mandible from actual teeth, impressions and roots, with none in the symphysial region and two replacement gaps at posterior presplenial level.

In the present state of the specimen an impression of a tooth on the Bassler block is the most posterior dentary tooth preserved and, as it coincides with the front of the adductor fossa, is probably the genuine last member of the series. It is preceded by a curious dorsal bony process (probably displaced, but see below) and then nine preserved teeth with insufficient gaps for any more between them. This group is preceded by three sites marked by two bony tooth bases seen in mesial view and one actual stump. Then comes a group of four preserved teeth, the foremost of which is the most anterior tooth with any of the crown preserved.

Anterior to the 17 tooth sites so far noted bases apparently become more difficult to estimate. Two bony tooth bases apparently precede the anterior tooth. Between them and the symphysial region is the eroded region of the dentary.

In the symphysial region, however, there are the remains of the roots of at least two teeth. Anterior to the plane of the front of the presplenial is a massive root, now laterally compressed, with an anterior fragment which may pertain to the same tooth or represent an anterior smaller tooth. Immediately behind the massive root is another, now posterior to the level of the presplenial suture. Once again it is difficult to tell whether the compressed root represents one tooth or two. If one it is even larger than the preceding one.

An estimate of the total dentary tooth count for one ramus may be made from the distance spanned by the posterior ten teeth, assuming a similar average size throughout. This allows for large tusk-like teeth anteriorly to be succeeded by small teeth in the eroded gap corresponding to the small teeth in a similar position in *Eogyrinus*. This gives approximately a dozen teeth to be added to the 17 noted above and a total count of 29 or 30.

A series of 13 teeth is preserved on the section of right mandible, most of them complete. The hindmost is situated at about 1 cm anterior to the plane of the posterior termination of the postsplenial. It thus appears to correspond to the penultimate tooth in the left ramus. A poorly preserved stump may be present in the right ramus centred 1 cm behind the last tooth. If so it would correspond in position to the last tooth on the left, with, significantly, a gap corresponding to the bony process.

The remaining teeth on the right ramus are remarkably well preserved and are tightly crowded with only one unfilled site, the third from the front, to bring the total to 15 sites with the doubtful hindmost stump. The fifteenth site from the back coincides with only the twelfth on the left ramus, again illustrating a lack of correspondence between left and right of the type noted in Lower Carboniferous anthracosaurs (Panchen 1975).

The shape of the teeth in *Eobaphetes* is characteristic and significant. The single palatal tusk preserved as a natural mould on the Bassler block appears to represent a complete crown but was flattened and disrupted before leaving its impression. It is uncertain whether it is from the palatine or ectopterygoid, but its present position relative to the orbit suggests the latter.

It is strikingly similar to the ectopterygoid tusk in the *Leptophractus* syntype from the American museum, but at 25 mm is 25 % longer and appears to have been proportionately wider at the base. The tusks of both specimens differ from the preserved ectopterygoid tusk of *Anthracosaurus* in having sharp anterior and posterior ridges distally which meet at the point of the crown and in being more recurved. They thus resemble the mid-maxillary teeth of *Anthracosaurus* in the former feature.

The dentary teeth of *Eobaphetes* are distinguishable from those of *Leptophractus* only by size. Those of both species are similarly closely packed and resemble one another in the shape

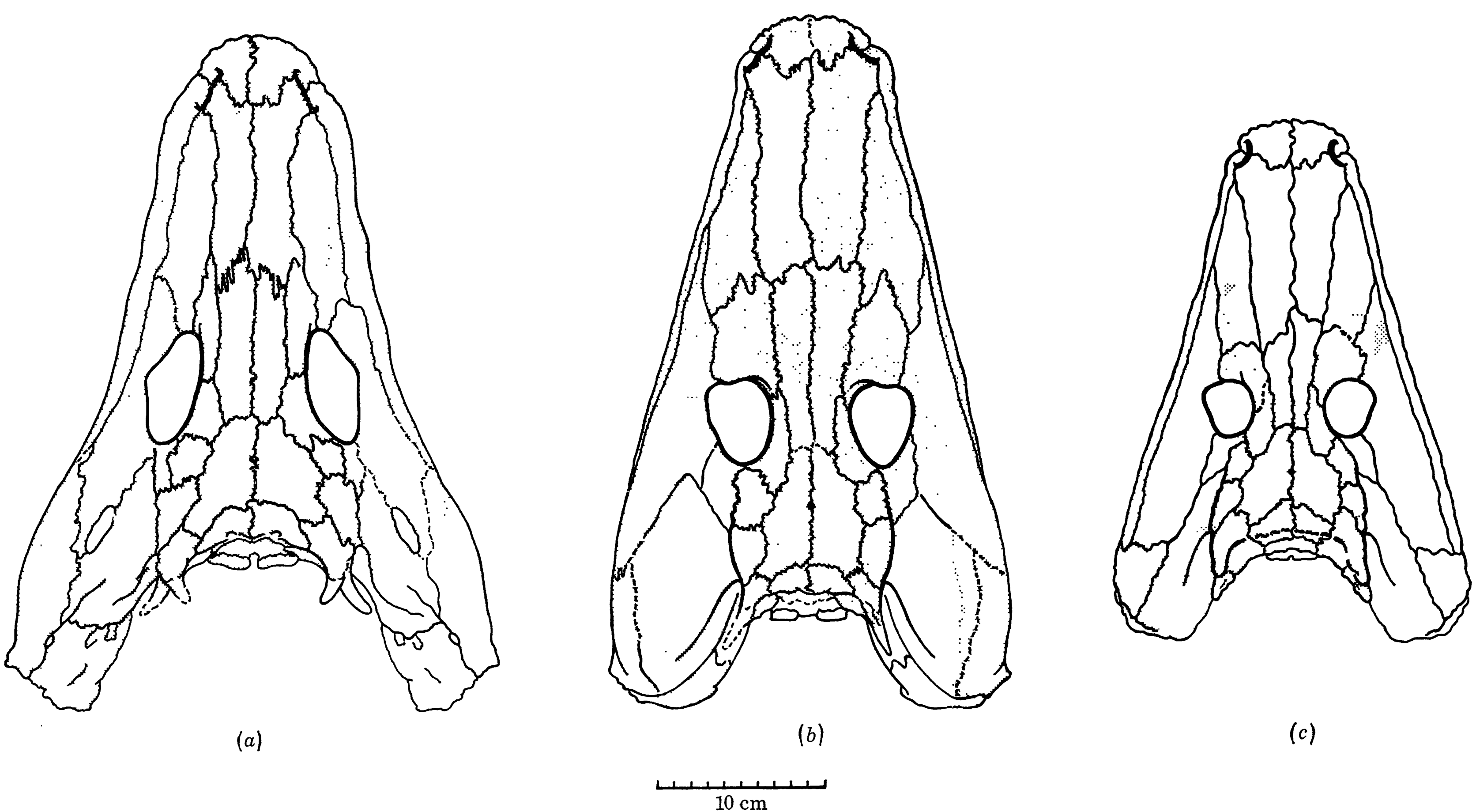

FIGURE 17. Reconstructed anthracosaur skulls in dorsal view. One quarter natural size. (*a*), *Anthracosaurus russelli*; (*b*), *Eogyrinus attheyi* (composite); (*c*), *Eobaphetes kansensis*. Preserved areas, light stipple. Reconstructed sutures and boundaries, broken line only in preserved areas.

and proportions of their crowns. The complete teeth from the right ramus in *Eobaphetes* have a crown height of 7–8 mm and a basal diameter of 4–5 mm: the corresponding dimensions for *Leptophractus* are 5–6 mm and 3–4 mm respectively.

In both specimens the teeth are short, stout and blunt, tapered mostly near the tip and recurved to a degree that brings the tip of the crown nearly to the transverse level of the back of the base. In these respects, together with their close packing, they are sufficiently distinctive to suggest a close relationship between *Eobaphetes* and *Leptophractus.*

All the data available make it possible to essay an outline reconstruction of the skull roof of *Eobaphetes* for comparison with those of *Anthracosaurus* and *Eogyrinus.* The three are presented together as figure 17. There is insufficient evidence for the reconstruction of informative palatal or occipital views of *Eobaphetes* and with no maxillary dentition known a lateral view would add little to that from dorsal aspect or to the figures of the specimen as preserved.

The overall length (Q length) of the skull may be estimated with a reasonable expectation of accuracy from that of the mandibular ramus. The divergence of the two rami posteriorly in the intact skull was an approximate function of the width of the skull table, the width of the cheek regions at the level of the back of the skull table in the plane of their dermal bones and the slope and curvature of the cheek regions at that level.

In *Eogyrinus* a close approximation to the median length of the lower jaw with the rami in their natural relationship is based on a divergence of twice the width of the skull table. Thus in *Eobaphetes* the median length has been estimated as the height of an isosceles triangle of side equal to the length of a ramus (310 mm) and base twice the width of the skull table (2 × 82 mm with allowance for flattening). This gives a median length of the lower jaw of 299 mm and with an increase of about 1 cm for the skull length (as in *Eogyrinus*) a quadrate length of *ca.* 310 mm. The estimate is corroborated by the fact that in *Eogyrinus* the length of a single jaw ramus is closely similar to the quadrate length (408 mm and 410 mm respectively).

The form of the skull and the unknown details of the anterior snout region of the *Eobaphetes* reconstruction have been restored in frankly *Eogyrinus* fashion. There is some evidence of overall skull shape in the preserved long straight maxillary and the form of the suspensorial region in dorsal view. Both these suggest a very *Eogyrinus*-like shape in contrast to that of *Anthracosaurus.* This is supported by the skull shape of the much larger *Neopteroplax,* to which *Eobaphetes* appears to be closely related.

The overall width at the level of the back of the skull table is reconstructed from the flattened specimen by restoring a curvature of the cheek downwards similar to that of *Eogyrinus,* again suggested by the similarity in shape in the respective flattened type specimens.

Anthracosaurus lancifer (*Newberry*) *and* Leptophractus obsoletus *Cope*

The large embolomerous anthracosaurs from Linton, Ohio have been most recently treated by Romer (1963) and Panchen (1970). In 1970 I also reviewed their taxonomic history.

The three principal skull specimens, each of which consists of the natural mould of the snout region of a large labyrinthodont seen in lateral view, were all referred to *Leptophractus obsoletus* by Cope (1873, 1875). The two original specimens, representing somewhat smaller individuals than the third, may be regarded as syntypes of *L. obsoletus* Cope (1873) but were not figured in the original description. All three are figured by Cope in 1875 and the larger specimens consisting of part and counterpart were figured by Romer after etching and casting of both blocks by Dr Baird.

Romer regarded all three specimens as embolomeres on the nature of the ornament, the external form of the teeth, the apparent lack of vomerine tusks and the fact that all three had suffered compression from side to side, suggesting a deeper skull than that of the contemporary loxommatids. There is little doubt that he was correct.

In 1963 Romer separated the larger specimen from the original two as *Anthracosaurus lancifer*, but had presumably reversed his decision by 1966 when he gave *Leptophractus* as a synonym of *Anthracosaurus* (together with *Eobaphetes* and *Erpetosuchus*). Three problems thus remain:

(1) is the larger specimen distinct from *Leptophractus obsoletus*?

(2) if that separation is valid is *Anthracosaurus lancifer* (Newberry) available as a name for that specimen?

(3) may any of the Linton specimens be referred to the family Anthracosauridae?

The second problem is best considered first. The name *Rhizodus lancifer* Newberry (1856) was assigned to a single tooth from Linton considered by Newberry to be from a crossopterygian fish of that genus. The specimen appears to be a lanceolate tooth lacking any root in a canneloid matrix. Inspection, however, shows the crown to be covered not with enamel but a shiny layer of iron pyrites. Proximally this is broken away but no internal structure is seen as the substance of the 'tooth' is also of canneloid shale. Thus the specimen consists of a natural cast within a natural mould. This is often the case with Linton specimens in which the original bone or tooth is partially or completely rotted away.

The 'tooth' was associated with the larger embolomere by Romer mainly on the negative evidence of the absence of any identifiable crossopterygian remains from Linton. It is probable that the original tooth was that of a labyrinthodont and the size and form are not inconsistent with its attribution to the larger embolomere. However, the loxommatid *Megalocephalus* also occurs at Linton (Baird 1957) and '*Rhizodus lancifer*' is not certainly distinguishable from the teeth of specimens of that genus. Watson (1929) in fact attributed it to '*Orthosaurus*' (*Megalocephalus*) *pachycephalus*, the British species. It is closely comparable, for example, to the largest tooth on a *Megalocephalus* dentary G24.34 (DMSW 17) in the Hancock Museum.

Thus, without any evidence of internal structure, the specific name of '*Rhizodus*' *lancifer* must be regarded as a 'nomen vanum' to be confined to the holotype. It is not therefore available to designate the larger embolomere.

The intrinsic evidence for or against attribution of the large specimen to *Anthracosaurus* is meagre. There is little to add descriptively to Romer's account.

It is important that, as Romer notes, a naso-labial groove runs from the external nostril to the jaw margin. This is an eogyrinid feature hardly developed in *A. russelli.*

Undoubtedly the principal reason for Romer's (1963) attribution of the specimen to the genus *Anthracosaurus* was the size of the marginal and palatal teeth. Of the maxillary teeth the fifth is the largest, with a basal diameter of 13 mm and a crown length estimated by Romer at *ca.* 35 mm. By the anterior ectopterygoid level crown length had diminished to *ca.* 25 mm and diameter 8–10 mm.

The largest maxillary tooth of *A. russelli* has a basal diameter of 17 mm but unknown length. The maxillary teeth at ectopterygoid level are of comparable diameter to those of '*A. lancifer*' but reach a somewhat greater length.

The anterior dentary teeth in the latter are again comparable to those of *A. russelli* in diameter but are considerably shorter, extending only 12–13 mm above the outer rim of the dentary compared to 16–22 mm in *A. russelli*. This is correlated with a significant difference in shape. In lateral view the dentary teeth of *A. russelli* are roughly conical but taper principally near the tip of the crown so that the sides of the tooth are more nearly parallel lower down. They are variably recurved but again the backward curvature occurs, if at all, near the tip.

In '*A. lancifer*' the relatively shorter dentary teeth are more uniformly tapered and recurved. In this respect they are very closely comparable to the more posterior teeth preserved in the mandible of *Eobaphetes*.

The palatine tusk of '*A. lancifer*' is even larger than that of *A. russelli*: Romer records a basal diameter of 25 mm(!) but at 45 mm it is relatively short, being comparable in length to the much more slender ectopterygoid tusk of *A. russelli* (diameter 15 mm). The ectopterygoid tusk of the American form is similarly short and stout.

The original skull of '*A. lancifer*' was very large: Romer gives a tentative but reasonable estimate of its PP length as 355 mm (*A. russelli*: 295 mm; *Eogyrinus*: 340 mm; *Neopteroplax*: 336 mm; *Eobaphetes*: *ca.* 245 mm, from figure 17). Thus comparison of tooth size with that of *A. russelli* is reasonable.

Romer also gives estimates of the marginal tooth count of '*A. lancifer*' of pmx 3, mx 25, dentary 27 compared to pmx 2, mx 20–21, d *ca.* 18 for *A. russelli*.

On balance, and without consideration of extrinsic evidence, I would be inclined to reject '*A. lancifer*' from the genus *Anthracosaurus* on grounds of the presence of a naso-labial groove and the form and estimated number of the teeth. Thus the binomen *Anthracosaurus lancifer* is not an available name to describe the specimen.

Rejection from the genus *Anthracosaurus* is supported by comparison with other American Pennsylvanian embolomeres. Apart from the syntypes of *Leptophractus obsoletus* the most important forms for comparison are *Eobaphetes* and *Neopteroplax conemaughensis* Romer (1963).

Enough is known of the cranial anatomy of the last species to be certain that it is an eogyrinid (Romer 1963; Panchen 1970). This is important because it shows that a member of that family can develop the massive anterior marginal and palatal dentition seen in '*A. lancifer*'. As in the latter, there are three large premaxillary teeth in *Neopteroplax* and the largest maxillary tooth reaches a basal diameter of 15 mm, larger than that of the Linton form, in the region of the canine peak.

Similarly *Neopteroplax* has a palatine tusk of the same diameter as that of '*A. lancifer*' (25 mm) and an anterior ectopterygoid tusk of similar diameter (17–18 mm) to that of the Linton form.

However, in *Neopteroplax*, unlike *Anthracosaurus russelli*, the maxillary canine peak is followed by a large number of relatively small teeth of only about 6 mm diameter giving a total maxillary count of some 35 teeth. Thus the massive anterior dentition of '*A. lancifer*' is inadequate for its assignment to the genus *Anthracosaurus* or even the family Anthracosauridae.

Comparison with the dentary dentition of *Eobaphetes* emphasizes this point. The stumps of very large teeth are preserved anteriorly above the jaw symphysis, but posteriorly the dentary teeth of *Eobaphetes* are small and closely packed, giving an estimated dentary total of 29 or 30 teeth, closely comparable to Romer's estimate for '*A. lancifer*'.

Finally it must be asked if the distinction can be maintained between '*A. lancifer*' and *Leptophractus obsoletus*. A certain amount of confusion has surrounded the specific name *L. obsoletus* (Panchen 1970) but it correctly refers to the two syntype skull specimens. Of these I have unfortunately only seen the American Museum specimen, figured by Cope (1875, pl. XXXIX, fig. 1) and subsequently etched and recast by Dr Baird. Apart from part of the maxillary and dentary dentition and the complete crown of a palatine tusk it shows part of the surface of a denticulate pterygoid. This feature both suggests its eogyrinid (as distinct from anthracosaurid) nature and suggests (by analogy with *Eogyrinus*) that the tusk near the front of the specimen is ectopterygoid rather than palatine.

The marginal teeth are very small, with those of both the maxillary and dentary having a basal diameter of about 4 mm and a crown height of 7–8 mm. The tusk has a basal diameter of *ca.* 10 mm and a crown height of *ca.* 18 cm. Both teeth and tusks are of the distinctive '*A. lancifer*' – *Eobaphetes* shape.

As I pointed out in 1970 there is, on the limited evidence available, nothing inconsistent about attributing *Leptophractus* to *Neopteroplax*, or more correctly *Neopteroplax* to *Leptophractus*, with the Linton specimens as immature individuals of Romer's newer species. This suggestion, however, was made on the assumption of the distinctness of '*A. lancifer*'. It is perhaps inherently improbable that three similar and very incomplete skull specimens of embolomeres from Linton should represent two different species, and once again there is nothing inconsistent with regarding the American Museum specimen of *Leptophractus* as a growth stage of '*A. lancifer*'. Further the form of the teeth and the presumed eogyrinid nature of both skulls are significant common features.

Thus, provisionally, the large Linton embolomere may be referred to *L. obsoletus*. One further possibility, which does not conflict with this conclusion, may be noted.

In describing *Eogyrinus attheyi* I noted that the lectotype skull is much more heavily built than the anterior skull specimen from Airdrie (Panchen 1972*a*, pl. 24). This applies particularly to the marginal teeth which are both larger and less uniform in size in the lectotype with apparently similarly sized skulls.

I then suggested sexual dimorphism as an explanation and this might well apply to the apparently smaller and lighter syntypes contrasted with the more massive specimen of *Leptophractus obsoletus*.

Diagnosis of the families Anthracosauridae and Eogyrinidae

The term Anthracosauridae Cope (1875) was used by Romer (1945*b*) to characterize a family of Embolomeri distinct from eogyrinids. In 1947 he gave a brief diagnosis: 'Cheek region expanded. Jaw articulation far behind level of occipital condyle'. On this basis his family Anthracosauridae comprised *Crassigyrinus scoticus* together with the type genus *Anthracosaurus*, then including only *A. russelli*.

Crassigyrinus was also included, with expressed doubt, by Romer (1966) but is now known not to be an anthracosaur (Panchen 1970, 1973).

In 1963 Romer included the large *Leptophractus* specimen of Cope in the genus *Anthracosaurus* as '*A. lancifer*', citing the dentition of the latter, with massive tusks and anterior teeth and the estimated maxillary tooth count of 25. He also noted the resemblance of *Eobaphetes* to '*A. lancifer*', but distinguished the latter generically from the *Leptophractus obsoletus* syntypes. These he associated with the eogyrinids and *Archeria* without assigning them to a family.

In 1966, however, apparently influenced by Dr Baird, Romer reduced the genera *Eobaphetes* and *Leptophractus* to synonomy with *Anthracosaurus* within the family Anthracosauridae and ranged all other embolomerous anthracosaurs in the family Cricotidae.

In my review of the Anthracosauria (*s.s.* Embolomeri) in 1970, I divided the group into three families: Anthracosauridae, Eogyrinidae and Archeriidae, the latter containing the genus *Archeria* together with two genera named only from postcranial remains (*Cricotus* and *Spondylerpeton*) whose position remains uncertain. The three families were diagnosed principally on skull shape and on the number and character of the teeth.

However, with my redescription of all the material of *Eogyrinus attheyi* (Panchen 1972*a*) and the present redescription of *Anthracosaurus russelli* it is possible to give more comprehensive diagnoses of their respective nominate families.

Apart from the dentition and the shape of the cheek region the following features of *A. russelli* seem to me to be taxonomically significant:

(1) the relatively high and mesially situated external nares;
(2) the lack of a naso-labial groove to each naris;
(3) the widely separated and laterally-facing orbits;
(4) the biramous tabular horns;
(5) the enormous dorsal exposure of the quadrate;
(6) the lack of any table-cheek kinetism;
(7) the orbital lacrimal;
(8) the maxillary-quadratojugal contact;
(9) the absence of a processus alaris of the jugal;
(10) the reduced dermal ornament and lateral line pattern;
(11) the total form of the pterygoids, (*a*) extending laterally to the palatine tusks, (*b*) meeting in a median suture from the vomers to almost the level of the basal articulation, (*c*) lacking a descending flange of the quadrate ramus, (*d*) apparently lacking any denticulate ornament;
(12) the single 'fused' mandibular fenestra in each jaw ramus;
(13) ?the lack of a high surangular crest;
(14) ?the occluded vertebral centra;
(15) ?the form of the interclavicle.

In all these characters *Anthracosaurus* may be contrasted with *Eogyrinus attheyi*. Apart from numbers 7 and 8, which must be regarded as primitive, most or all of these features enhance the opinion suggested by the skull form and the dentition, that *Anthracosaurus* was a much more formidable and much more terrestrial carnivore than the piscivorous *Eogyrinus*.

Thus an extensive diagnosis may be given in each case distinguishing the family Anthracosauridae, represented by *A. russelli*, from the Eogyrinidae, represented by *E. attheyi* and the other British species. Before discussing the family placement of the Pennsylvanian forms from the U.S.A. It is necessary to consider their interrelationships a little further.

I think that there is good evidence for the close interrelationship of *Neopteroplax*, *Leptophractus* and *Eobaphetes*. The first and the last are the best known and are united by the following characters (Romer 1963 and above):

(1) skull shape (as restored in *Eobaphetes*, but particularly based on that of the quadrate region and the straight maxillary);
(2) the form of the tabular horn (Romer 1963, fig. 1);
(3) a kinetic skull table;
(4) a prefrontal-jugal suture excluding the lacrimal from the orbit;
(5) eogyrinid ornament;

(6) ?denticulate pterygoids;
(7) a low flat-topped surangular crest;
(8) depressor mandibulae insertion on angular a rounded boss.

There may also be a common feature in the form of the orbits. Romer notes that those of *Neopteroplax* are more circular than those of *Eogyrinus*. In restoring the orbits of *Eobaphetes* the constraints imposed by the preserved orbital margins also suggested relatively small orbits, of probably circular shape, with a comparable relative interorbital width.

Of these common characters, all but numbers 2, 7 and 8 are common to eogyrinids and there is little doubt that *Neopteroplax* at least should be assigned to the Eogyrinidae. However, consideration of the dentition of *Neopteroplax* clarifies the use of this feature in embolomere taxonomy.

As noted above the anterior marginal and also palatal teeth of *Neopteroplax* are as massive as those of *Anthracosaurus russelli*. Thus the distinctive feature of the *Anthracosaurus* dentition is not so much the massiveness of the anterior teeth and palatal tusks, but the large size of the marginal teeth as a whole and the low marginal and ectopteryoid count.

On the other hand the distinctive features of the dentition of the American forms is the massiveness of the anterior dentition combined with a relatively high marginal count and, except anteriorly, small uniform maxillary and dentary teeth. This is seen in *Neopteroplax*: the massive anterior dentition may be seen and the high marginal count inferred in '*A. lancifer*', the reverse observation and inference is the case in *Leptophractus* and *Eobaphetes*. This type of dentition, together with the distinctive shape of the teeth in *Eobaphetes* and *Leptophractus* (incl. '*A. lancifer*') (tooth shape is unknown in *Neopteroplax*) distinguishes the American genera from British eogyrinids as well as from *Anthracosaurus*.

Furthermore, if a Westphalian D or Stephanian dating for *Eobaphetes* is accepted (as I accept it) on the basis of the coal analysis reported by Dr Schopf, the spore analysis of Dr Smith and the palaeogeographical evidence (see above), then the three American genera are united stratigraphically as well as geographically.

Leptophractus is from the Upper Allegheny series (Westphalian D) of eastern Ohio, *Neopteroplax* from the Upper Conemaugh, the succeeding series, of the same area (of middle Stephanian time) and both occur within the time span from within which *Eobaphetes* is thought to have occurred.

The possibility should also be noted that the original material of *Cricotus heteroclitus* is to be referred to the same assemblage. Until the distinction was resolved by Romer (1945*a*) *Cricotus* was confused with the Permian genus *Archeria* and is still usually placed in the family Archeriidae (Panchen 1970). However, in discussing the horizon of *Eobaphetes* Dr Smith (above) notes the importance of the McLeansboro group as a possible lower horizon for *Eobaphetes*. This is the horizon from which *Cricotus* comes.

The material is confined largely to vertebrae as is that of another form from Illinois, *Spondylerpeton spinatum* Moodie from the Allegheny series of that state. If both these are referred to the Eogyrinidae, *Archeria* would be the sole representative of an exclusively Permian family.

In most characters other than the distinctive ones noted above *Leptophractus*, *Eobaphetes* and *Neopteroplax* are certainly eogyrinid and I propose to give them subfamily status within the Eogyrinidae. *Neopteroplax* with a somewhat higher marginal tooth count (mx *ca.* 35 compared to 25–30 in *Eobaphetes* and *Leptophractus*) is perhaps more doubtfully placed in this assemblage. I have retained the generic distinction between *Eobaphetes* and *Leptophractus*, rather than synonomizing them as urged by Dr Baird, largely because the latter senior genus is so ill known.

Thus the family Anthracosauridae comprises only the genus and species *Anthracosaurus russelli* with an extensive suite of characters distinguishing it from the Eogyrinidae (and Archeriidae).

Anthracosaurus russelli is almost certainly a member of the infraorder Embolomeri, so the diagnosis of that group must be modified to admit the occurrence in that species of the following characters:

(1) otic notch bordered by a process of the supratemporal (also *Eobaphetes*);
(2) loss of skull table – cheek kinetism (also within suborder Anthracosauria);
(3) reduction of dermal ornament;
(4) orbital lacrimal;
(5) fusion of two large meckelian fenestrae.

The family Anthracosauridae may then be placed with the divided family Eogyrinidae within the framework of my recent revised classification of the order Batrachosauria (Panchen 1975). Complete diagnosis of the Archeriidae must await detailed description of the skull of *Archeria*.

In the diagnoses characters of doubtful validity and/or significance have been cited within brackets.

class: **AMPHIBIA**
subclass: LABYRINTHODONTIA
order: **Batrachosauria**
suborder: Anthracosauria
infraorder: Embolomeri

(1) family: Anthracosauridae Cope

Large anthracosaurs with massive skull, quadrate ramus of the pterygoid long, correspondingly long suspensorial region behind skull table, cheek region flared outwards and shallow, [small 'temporal vacuity' in squamosal-jugal suture on each side]; firm suture between temporal bones of skull table and squamosal. Fenestrae exonarinae relatively dorsally placed, lacking a clear naso-labial groove, orbits widely separated facing laterally. Tabular horns biramous with diverging rami. Dermal ornament reduced.

Lacrimal enters orbital margin, wide dorsal exposure of quadrate behind truncated squamosal, no processus alaris of the jugal; pterygoids smooth, united by suture anterior to basal articulation, extending laterally to level of palatine tusks, and lacking a descending flange of the quadrate ramus. Meckelian fenestrae of jaw ramus confluent, no surangular crest.

Dentition of large fluted teeth and tusks, somewhat recurved, palatal tusks conical, marginal teeth lanceolate at tip of crown. Two tusks and two teeth on ectopterygoid, usually two premaxillary teeth, *ca.* 20 teeth each on maxillary and dentary.

[Exposed ventral area of interclavicle ovoid.] [Vertebral centra with occluded notochordal canal.]

Type and only known genus: *Anthracosaurus* –

Genotype and only known species: *A. russelli* Huxley.

(2) family: Eogyrinidae Watson

Small to large anthracosaurs with elongate triangular skull less massive than that of

Anthracosauridae, quadrate ramus of pterygoid and suspensorium relatively shorter, cheek region deep without lateral flare; skull table–cheek kinetism retained. Fenestrae exonarinae near jaw margin with marked naso-labial groove, orbits facing dorso-laterally. Tabular horn with one principal ramus. Dermal ornament well-developed and characteristic.

Lacrimal excluded from orbit by prefrontal-jugal suture, dorsal exposure of quadrate reduced – squamosal not truncate reaching posteriorly to same level as quadratojugal, processus alaris of jugal excludes ectopterygoid from margin of subtemporal fossa; pterygoids denticulate with free internal margin for at least most of their extension from basal articulation to vomers, not extending laterally to palatine tusks, and bearing a deep descending flange of the quadrate ramus. Two meckelian fenestrae of jaw ramus separated by prearticular-postsplenial bar.

Dentition variable: more than two teeth following ectopterygoid tusk pair, at least three premaxillary teeth, at about 25 teeth each on maxillary and dentary.

[Exposed ventral area of interclavicle quadrangular.] Vertebral centra sometimes with occluded notochordal canal.

Type genus: *Eogyrinus* – Genotype and only known species: *E. attheyi* Watson.

(*a*) subfamily Eogyrininae *nov.*

Mainly European Westphalian and ?Stephanian embolomeres.

Orbits somewhat heart – or kidney-shaped, tabular horn single – an ovoid blade or finger-like process extending beyond a thickened proximal region, supratemporal usually excluded from margin of otic notch. Jaw ramus with high rounded surangular crest, strongly convex dorsally. [Depressor mandibulae insertion a rugose area on the angular], [anterior coronoid denticulate].

Dentition of slender cylindrical tusks and teeth, tapered and recurved near the tip of the crown, with or without a 'canine peak'. Ectopterygoid tusk pair succeeded by *ca.* 6 small teeth, maxillary dentition of 30–50 similar teeth, 'canine' teeth if present markedly smaller than tusks.

[Vertebral centra with persistent notochordal perforations.]

Eogyrinus attheyi Watson
Pteroplax cornutus Hancock & Atthey
Palaeoherpeton decorum (Watson)
Pholiderpeton scutigerum Huxley
?*Pholiderpeton bretonense* Romer
?*Calligenethlon watsoni* Steen
?*Diplovertebron punctatum* Fritsch (? = *Nummulosaurus kolbii* Fritsch)

(*b*) subfamily Leptophractinae *nov.*

American Late Pennsylvanian (Des Moines-Virgilian) embolomeres.

Orbits sub-circular in outline; tabular horn massive, [incipiently biramous with proximal region extending over and diverging from spatulate main ramus]; supratemporal extending as a narrow process into margin of otic notch. Jaw ramus with straight-edged surangular crest, [depressor mandibulae insertion a rounded boss on angular], [anterior coronoid lacking denticles].

Dentition of short conical fluted teeth, uniformly recurved and with lanceolate tips. Tusks exceptionally massive, premaxillary and anterior maxillary teeth large with marked canine peak but remaining maxillary and all but anterior dentary teeth small, uniform and closely packed. Ectopterygoid dentition a graded series of *ca.* 6 tusks diminishing posteriorly. Maxillary dentition *ca.* 25–35.

[Vertebral centra may have occluded notochordal canals.]

Leptophractus obsoletus Cope (incl. '*Anthracosaurus lancifer*')
Eobaphetes kansensis Moodie
Neopteroplax conemaughensis Romer
?*Neopteroplax relictus* Romer
?*Spondylerpeton spinatum* Moodie
?*Cricotus heteroclitus* Cope

No mention has been made in the diagnoses above of one very important feature: in *Anthracosaurus* and *Eobaphetes* it is certain that the maxillary contacts the quadratojugal, thus excluding the jugal from the external jaw margin. This is undoubtedly a primitive character, not only for Embolomeri, but for anthracosaurs as a whole. It occurs in the Lower Carboniferous anthracosaur *Eoherpeton* (Panchen 1975) and was certainly primitive for tetrapods as a whole (Panchen 1973).

The condition in eogyrinids is uncertain and equivocal. Of the members of the Eogyrinidae listed above, apart from *Eobaphetes*, only *Eogyrinus*, *Palaeoherpeton* and *Neopteroplax* yield any evidence. In *Eogyrinus* the total length of the maxillary is reasonably certain on both sides but restoration of the anterior boundary of the quadratojugal is less so being dependent on some 2 cm of its anterior suture, traced on the left side and dorsal surface only (figure 17*b*).

The pattern in *Palaeoherpeton* is closely similar, as restored, to the pattern in *Eogyrinus* (Panchen 1964 – '*Palaeogyrinus*') and here the evidence is much stronger with clear natural moulds of all the disarticulated constituent bones. Thus the lack of maxillary-quadratojugal contact may be a derived feature characteristic of the subfamily Eogyrininae in contrast to the condition in *Eobaphetes*.

However, Romer restores *Neopteroplax* with a pattern similar to that of *Eogyrinus* and *Palaeoherpeton*. If correct this could either mean that it should be grouped with the two latter forms, rather than *Eobaphetes*, or, alternatively, that the derived condition is not confined to the subfamily Eogyrininae and is thus of no taxonomic value at the subfamily level. It should be noted, however, that the pattern in *Neopteroplax* is by no means certain. Romer notes that part of the jugal-quadratojugal suture is missing on the left (the only side on which the cheek is preserved) and that the sutures throughout are difficult to trace. There is perhaps a close analogy with the preservation in *Eogyrinus*.

One final point may be made. Of the two subfamilies into which the family Eogyrinidae has been divided all the Leptophractinae are North American while the certain members of the Eogyrininae are European. However, two species of doubtful status ?*Pholiderpeton bretonense* Romer (1958*b*, 1963) and *Calligenethlon watsoni* Steen, while North American, have been tentatively referred to the latter subfamily. It is interesting to note that both are from Nova Scotia, which lay to the northeast of the Caledonian/Appalachian orogen which formed a faunal barrier in Palaeozoic times (Milner & Panchen 1973). Thus, from a European point of view, while trans-Atlantic they are cis-Appalachian.

I am glad to be able to acknowledge the help of many institutions and individuals in making this study possible. The holotype of *Anthracosaurus russelli* was borrowed from the Institute of Geological Sciences and that of *Eobaphetes kansensis* from the U.S. National Museum. Other material was on loan from the British Museum (Natural History), the Hunterian Museum of Glasgow University, the Glasgow City Museum, the Royal Scottish Museum and the Sunderland Museum. In addition Dr Bobb Schaeffer of the American Museum of Natural History and Dr Stig Bergstrom of Ohio State University arranged for the preparation of latex casts of important specimens for me and I was able to use the facilities of the Hancock Museum as well as these other institutions for critical comparisons.

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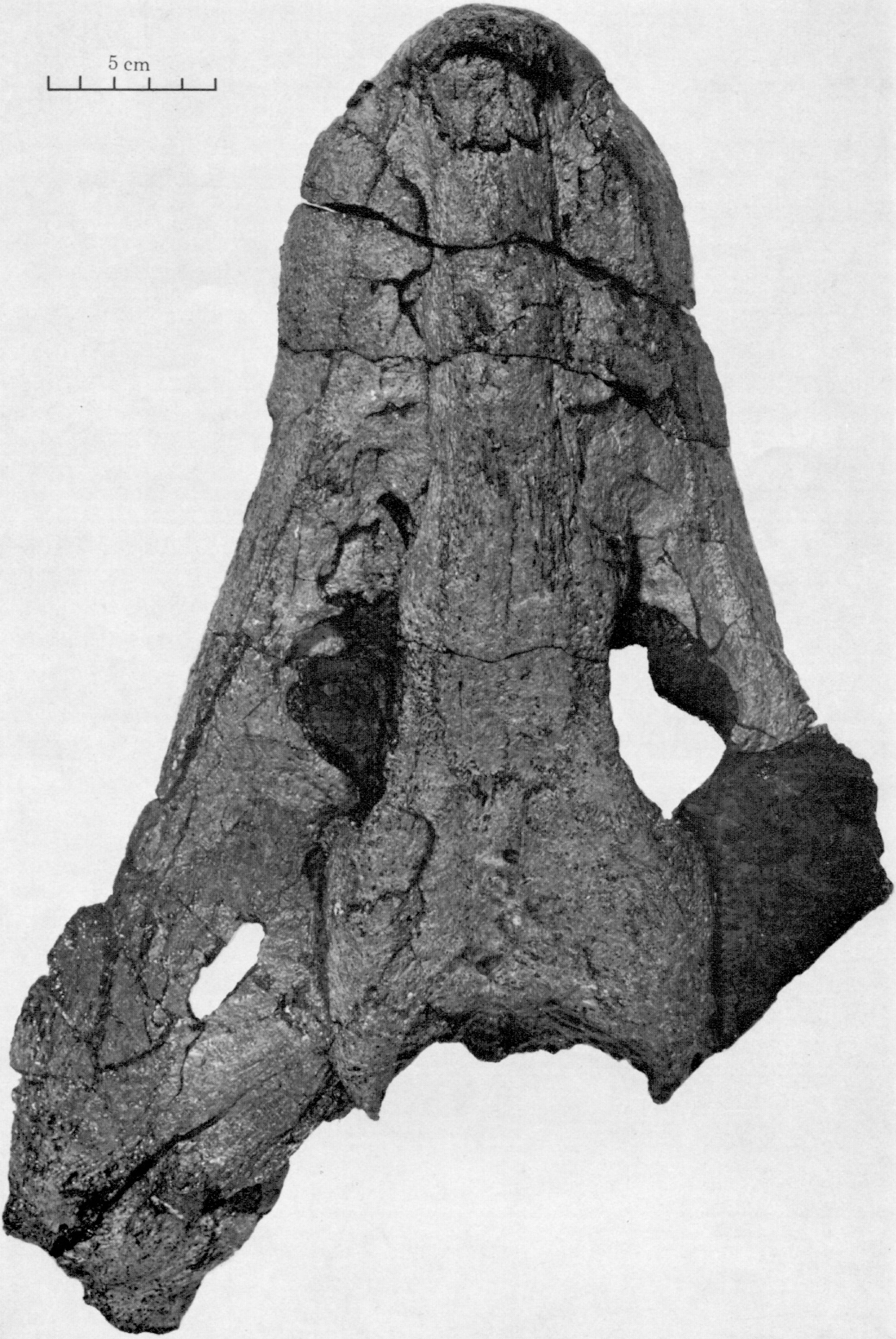
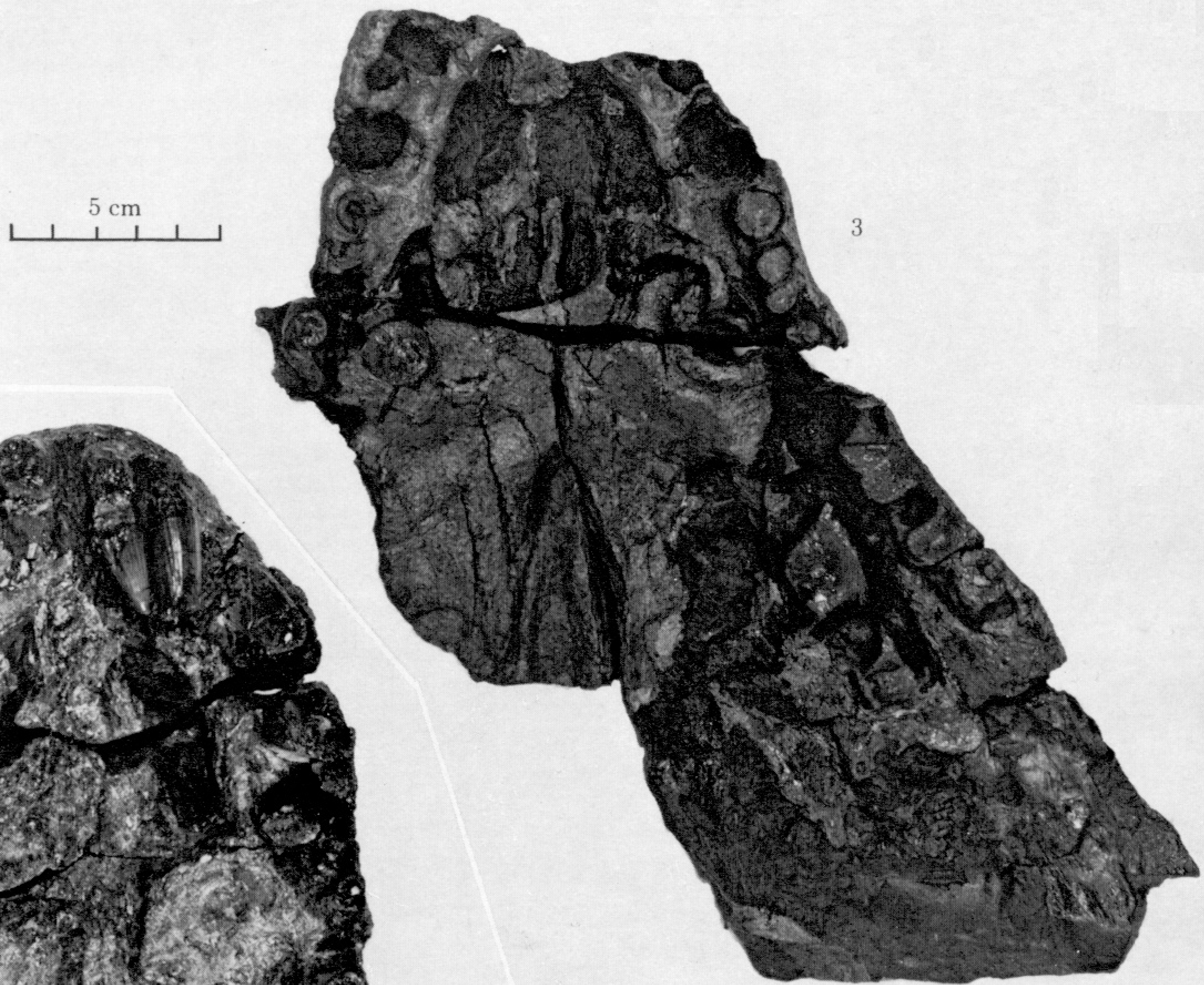


FIGURE 1. *Anthracosaurus russelli* Huxley, holotype skull in dorsal view. Half natural size.



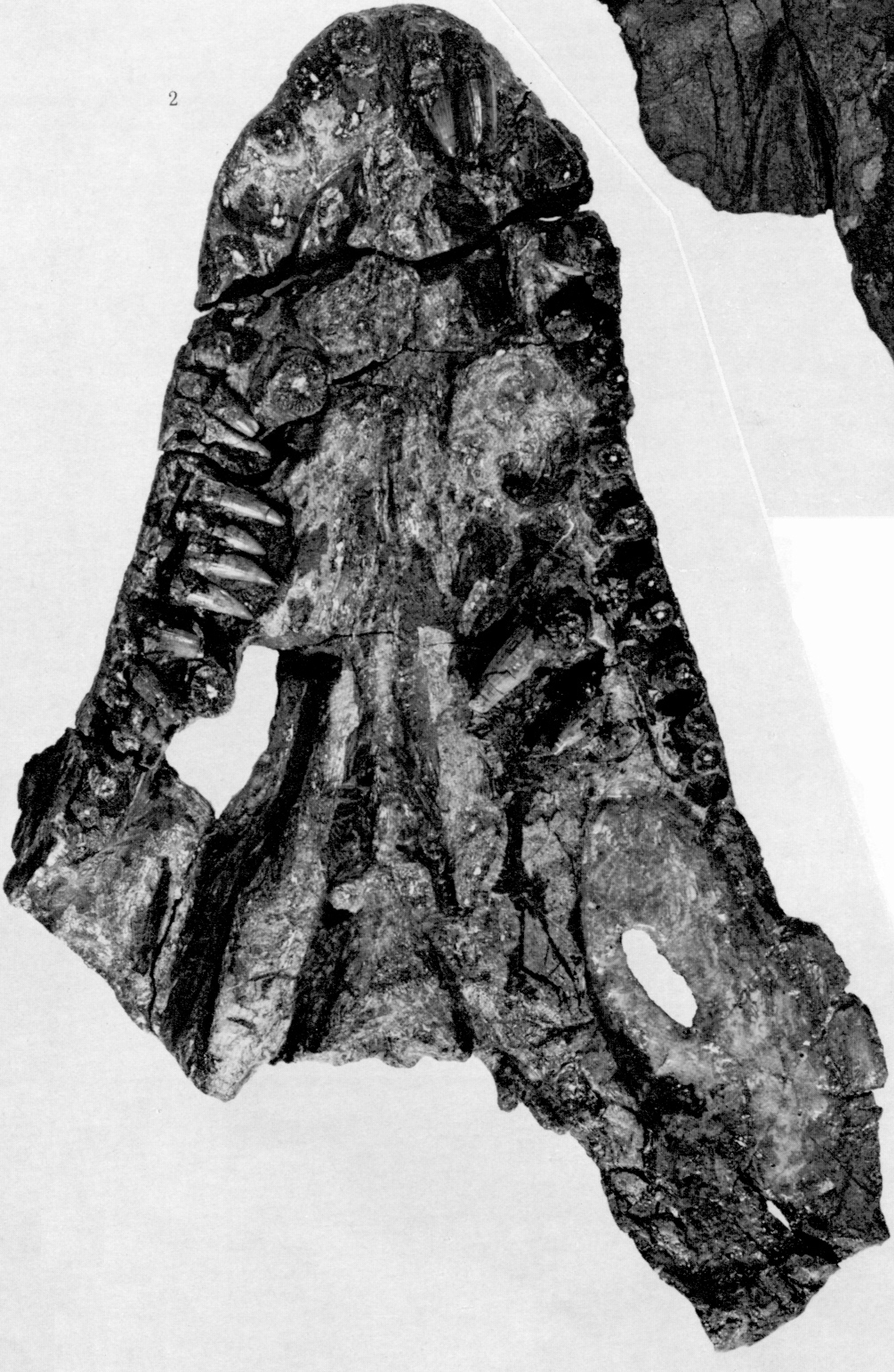


FIGURE 2. *Anthracosaurus russelli* Huxley, holotype skull in ventral view.

FIGURE 3. *Anthracosaurus russelli* Huxley, Usworth Colliery specimen in ventral view.