

TWO NEW SPECIMENS OF *ANTHRACOSAURUS* (AMPHIBIA: ANTHRACOSAURIA) FROM THE NORTHUMBERLAND COAL MEASURES

by J. A. CLACK

ABSTRACT. Two specimens from the Low Main Seam at Newsham, Northumberland are attributed to the genus *Anthracosaurus*. The first is a skull table (Hancock Museum specimen G 13.78) previously attributed to '*Eogyrinus*' (= *Pholiderpeton*, Clack 1987). This skull table was used in the past to demonstrate the presence of a 'kinetic line' between the embolomere skull table and cheek. The holotype of *A. russelli* lacks such a kinetic line, but the apparent paradox can be resolved if the 'kinetic line' was not mobile in the later embolomere families Eogyrinidae and Anthracosauridae, but acted as a butt joint to resist vertical forces.

The second specimen (Hancock Museum specimen G 24.39) is an isolated right jugal. It shows an unusually excavated orbital margin, which leaves the bone very narrow below it. This unique character is confirmed as present in the holotype of *A. russelli*. Incorporation of this jugal into new reconstructions shows the skull to be higher and narrower than formerly appreciated, and without any conspicuous 'lateral flare' in the suspensorial region.

Characters of the skull table including dermal ornament are used to construct a cladogram of the embolomeres, including the isolated skull table pertaining to *Pteroplax*.

ANTHRACOSAURUS was a large carnivorous anthracosaur related to the embolomereous Eogyrinidae, found in the British Coal Measures of Westphalian A and B (Upper Carboniferous) age. It is now known from several specimens. The holotype of *A. russelli* Huxley (1863) consists of an almost complete skull lacking the lower jaw, from the Airdrie or Mushet's Blackband Ironstone. After Huxley's brief description, that of D. M. S. Watson in 1929 gave a fuller account of the specimen in his review of Scottish Coal Measures Amphibia. The specimen was thoroughly prepared and redescribed by Panchen (1977). A second partial skull consisting of the snout and well-preserved anterior palate derives from the Top Busty seam of the Durham Coalfield, Lower Coal Measures (*communis* zone, Westphalian A) (Panchen 1977), and a partial lower jaw was discovered in the Hancock Museum, probably from the Low Main Seam at Newsham (Westphalian B). This was described by Panchen in 1981. The skull is thus known in some detail.

The postcranial skeleton of *Anthracosaurus* remains a mystery. Until recently some vertebrae and an interclavicle were attributed to the genus (Panchen 1977), but these must now be discounted. The dorsal vertebrae ((BGS)GS 56580, GS 56581) from Airdrie are undiagnostic and may equally well pertain to *Pholiderpeton* (= '*Eogyrinus*', Clack 1987) which also occurs at this locality. The attribution of embolomereous vertebrae made by Panchen was based on the presence of occluded notochordal pits in the centra. However, this character has been discovered in both *Pholiderpeton* and *Archeria* (Clack 1987), and cannot be used as a taxonomically significant character because of its wide distribution and sporadic occurrence. The interclavicle (RSM 1971.11.4) which probably derives from Airdrie is clearly that of the eogyrinid *Pholiderpeton*, whose interclavicle is now known from the holotype of *P. scutigerrum* (Clack 1987). Thus there is no certain evidence that *Anthracosaurus* was either fully embolomereous or long-bodied.

The genus is characterized by a number of features unique among anthracosaurs (autapomorphies) which distinguish it from the contemporary eogyrinids and result in its being placed in a separate family. These features are associated with its evident carnivorous adaptations and include consolidation of the palate with elimination of the mid-line suture, extension of the pterygoids laterally to

cover the palatines, massive dentition with reduced tooth count especially on the premaxilla, and a lateral shelf on the surangular suggesting elaboration of the adductor musculature. Also unique is the single large Meckelian fenestra, presumed to be derived from confluence of the two fenestrae found in the eogyrinids. Two other characters are relevant to the present discussion. The holotype specimen appears to lack the skull table–cheek kinetism seen in other embolomeres, having the supratemporal and squamosal firmly sutured, and in dorsal view the suspensorium of the holotype appears laterally flared.

The skull table now referred to *Anthracosaurus* (specimen (HM)G 13.78 in the Hancock Museum) was first mentioned by Hancock and Atthey (1868) and later the underside was figured by Atthey (1877) as *Pteroplax cornuta*. In the same paper, he also described a smaller skull table and included it in the same species. The underside of (HM)G 13.78 was described in detail but the upper side was mentioned only briefly. In 1926 Watson separated this skull table from the smaller one described by the two earlier authors, and assigned it (as DMSW 35) to *Eogyrinus attheyi*, though noting that the determination was ‘not quite certain’. He described the dorsal surface as ‘so much eroded that the sculpture is completely destroyed’ and, like Atthey, described in detail and figured the underside.

The specimen is notable for being one of two skull tables, the other being the holotype of ‘*Palaeogyrinus*’ (= *Palaeoherpeton*, Panchen 1970), which showed ‘a shallow groove . . . (on the underside of the supratemporal) . . . which received the squamosal, that bone not being attached to any bone of the table’. Thus Watson concluded that the skull table was kinetically articulated with the cheek, a primitive condition deriving from the osteolepiform kinetism, and characteristic of embolomeres. Romer (1963) chose the smaller of Hancock and Atthey’s two skull tables as the lectotype of *Pteroplax cornuta* but did not distinguish between the genera *Pteroplax* and *Eogyrinus*. In 1964, Panchen began his series of papers redescribing the British and American embolomeres with a paper on ‘*Palaeogyrinus*’ and in it he accepted Watson’s separation of Hancock and Atthey’s two skull tables, assigning the larger again to *Eogyrinus*. The smaller skull table constitutes the only certain cranial material to pertain to *Pteroplax*, though Boyd (1980) has attributed postcranial material. The upper surface of (HM)G 13.78 has not been described in any detail, having always been dismissed as badly preserved or eroded. Conversely, the underside of other embolomere skull tables have either been unavailable or not considered as having taxonomic value. My recent study of *Pholiderpeton* (Clack 1987) has shown several taxonomically significant features of the underside of the skull table. A description of the underside of the skull table of *Pteroplax* which the author prepared was included in the analysis. Specimen (HM)G 13.78 has been re-examined in the light of these.

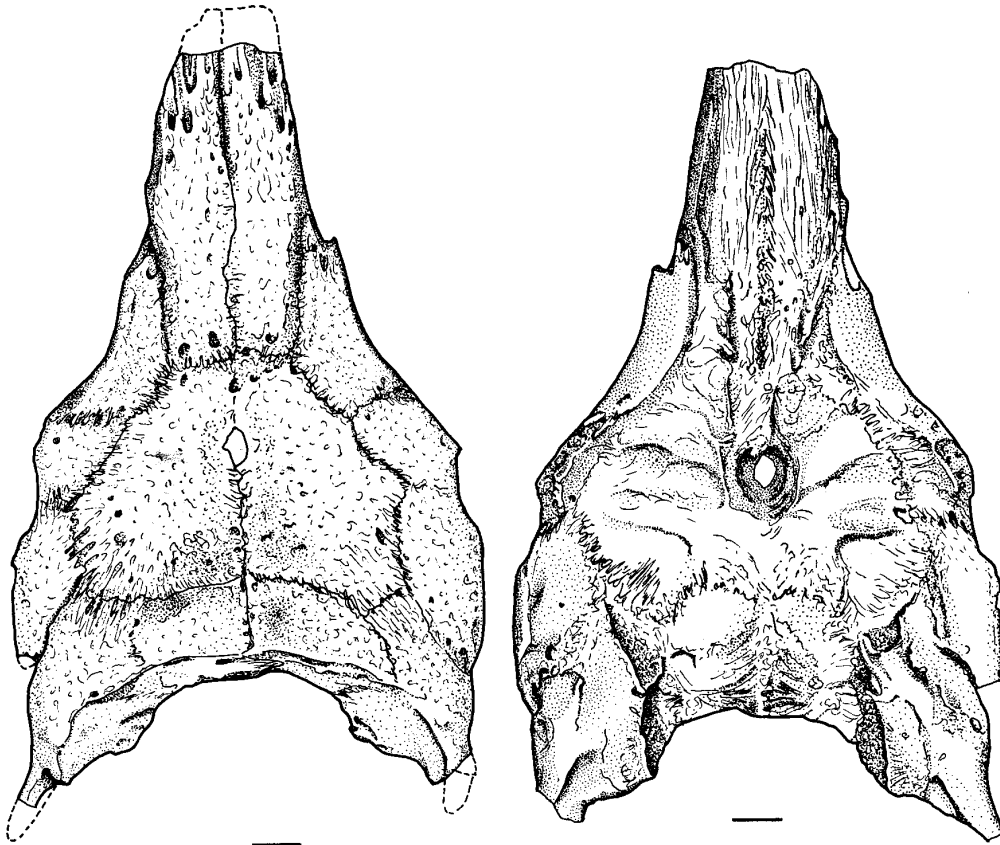
The second specimen to be referred to *Anthracosaurus* is (HM)G 24.39, an isolated jugal which has not been described before, but which has been catalogued as this genus by the Hancock Museum on my advice (Boyd and Turner 1980). Like the skull table, it originated from the Low Main Seam at Newsham, Northumberland and is therefore also Westphalian B in age.

Abbreviations used for specimens: (HM)G, Hancock Museum, Newcastle upon Tyne; RSM, Royal Scottish Museum, Edinburgh; (BGS)GS, British Geological Survey, Nottingham; (BMNH)R, British Museum (Natural History).

SYSTEMATIC DESCRIPTION

Skull table

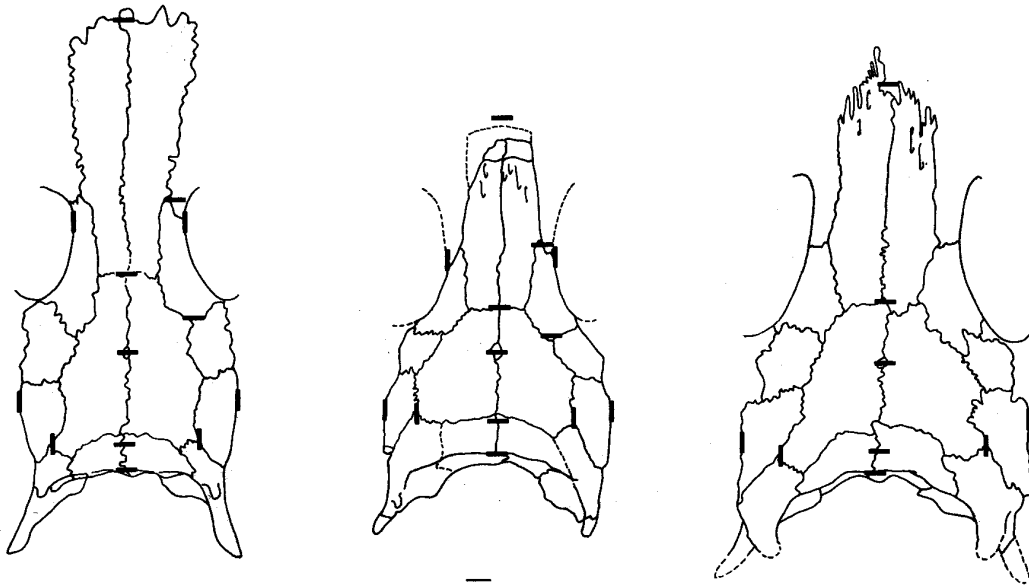
Specimen (HM)G 13.78 consists of an isolated skull table completely free of matrix. The bone is in good condition and is robust and paler in colour than the majority of amphibian dermal bone deriving from the Low Main Seam. The skull table has separated from the snout bones along the prefrontal–postfrontal and frontal–nasal sutures, and from the cheek along the line usually described as the lateral kinetism in embolomeres, that is along the lateral margins of the intertemporal, supratemporal, and tabular bones. The dermal ornament is poorly developed by comparison with



TEXT-FIG. 1 (left). Skull table, (HM)G 13.78, in dorsal view. Low Main Seam, Newsham, Northumberland. Dotted lines indicate extent of frontals and tabular horns in Dinning's figure (Atthey, 1877). Scale bar: 10 mm.

TEXT-FIG. 2 (right). Skull table, (HM)G 13.78, in ventral view. Low Main Seam, Newsham, Northumberland. Scale bar: 10 mm.

the skull tables of eogyrinid embolomeres. In particular the comparison with '*Eogyrinus*' (= *Pholiderpeton*, Clack 1987) forces the description of this ornament as 'eroded'. However, the ornament of the holotype of *A. russelli* is described by Panchen (1977, p. 454) as 'very little developed' and 'reduced'. Direct comparison of the two specimens shows them to be extremely similar. The 'eroded' appearance of (HM)G 13.78 is entirely consistent with a specimen pertaining to *Anthracosaurus* and does not require the surface to be regarded as damaged, as attribution to *Pholiderpeton* has demanded. Ornament type varies between embolomere families more strongly than was previously recognized (Clack 1987). For example, comparison of ornament on the parietals alone reveals the following: in *Pteroplax*, the well-defined pits are discrete and approximately uniform in size, elongated even near the parietal foramen; in both *Archeria* and *Proterogyrinus* the pits are discrete but elongated only towards the bone margins; in eogyrinids, however, the pits vary in size and coalesce with one another in an irregular manner, though they are well defined. They are elongated only towards the lateral margins of the parietals. In



TEXT-FIG. 3. Comparison of three embolomere skull tables showing positions at which measurements in Table 1 were taken. *Left*, *Pholiderpeton attheyi* (holotype); *centre*, (HM)G 13.78; *right*, *Anthracosaurus russelli* (holotype).

Anthracosaurus the pits are poorly developed and of low profile, such that no definable pattern is evident. This is one of the features used here to support attribution of (HM)G 13.78 to *Anthracosaurus*.

The type of ornament is the most immediately compelling character supporting attribution of (HM)G 13.78 to *Anthracosaurus*, but on examination a number of other similarities become apparent, particularly with respect to skull table proportions.

The frontals of (HM)G 13.78 are parallel-sided as far as they are preserved, a condition seen in *A. russelli*, but not in *Pholiderpeton*, where the lateral margins diverge anteriorly. The anterior margin of the frontals in (HM)G 13.78 exhibit marked longitudinal grooves consistent with a surface for the deeply fimbriated suture between nasals and frontals seen in *A. russelli*.

Atthey (1877, p. 373) described the frontals as 'worn' anteriorly. Comparison of his figure with the skull table in its present state shows that about 7 mm have been lost from the frontals since that date. However, even allowing for this and adding a further 3 mm for post-mortem damage, a comparison of the length of the frontals with the parietal foramen-postparietal length and also with the width of the skull table shows both *A. russelli* and (HM)G 13.78 to be similar to each other. They differ from *P. attheyi* in having relatively short frontals (Table 1 and text-fig. 3).

A. russelli possesses remarkably short postfrontals when compared with *P. attheyi*, whether the comparison is made in terms of postparietal-parietal foramen length or in terms of maximum skull table width. (HM)G 13.78 also shows short postfrontals, closer in proportion to those of *A. russelli* than to *P. attheyi* (Table 1 and text-fig. 3). Consequent upon the shortness of the postfrontals, the prefrontal forms a substantial portion of the dorsal margin of the orbit. In *Pholiderpeton*, this bone contributes dorsally only to the anterior corner of the orbit margin.

Clack (1987) used parietal proportions (length (f): width (g)) to distinguish between certain embolomere skull tables, for example those of eogyrinids, archeriids, and *Pteroplax*. In these terms, skull table (HM)G 13.78 again falls closer to the holotype of *A. russelli* than to *Pholiderpeton*

(Table 1 and text-fig. 3). The parietals of (HM)G 13.78 are noticeably broader than long, giving a characteristically short skull table. In 1977 Panchen noted that the long suspensorium of *A. russelli* was a consequence of the length behind the skull table and that the orbit-quadrates distance was not very different from that of '*Eogyrinus*'. This must be in part a result of the shortness of the skull table itself in *Anthracosaurus*. Another consequence of the short skull table in both *A. russelli* and (HM)G 13.78 is the relative position of the parietal foramen. In both these specimens, it is situated only a little behind the posterior margin of the orbits, whereas in *Pholiderpeton* it lies some way behind the orbit margin (text-fig. 3).

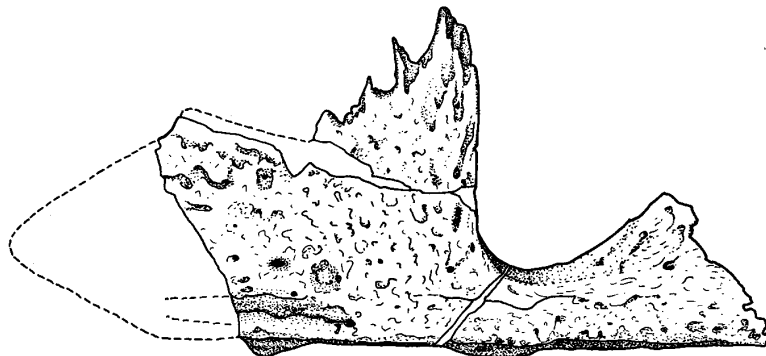
The lateral margins of (HM)G 13.78 show a rough emargination at the region of the supratemporal-intertemporal suture. In the holotype of *A. russelli* a similar irregularity appears in the skull table margin and is occupied by a dorsal growth of the postorbital. This is one of the pieces of evidence which Panchen (1977) used to support the suggestion that the 'lateral kinetism' of embolomeres was no longer present in *Anthracosaurus*, but was sealed by an interdigitating suture. The lateral margins of the intertemporal in (HM)G 13.78 show pits and sculpture on the underside, also consistent with a conventional suture having existed between this bone and the postorbital in the intact skull.

The postparietals and posterior parts of the parietals of (HM)G 13.78 show distinct depressions about the mid-line. Less regular depressions occur in a similar place in the skull table of the holotype of *A. russelli*. As these features occur over the thickest bone of the skull table it seems unlikely that they have resulted from post-mortem compression. In *Pteroplax* and *Proterogyrinus* (Holmes 1984) the parietal foramen appears on a mid-line ridge bounded by longitudinal furrows and such irregularities of the dorsal surface of the table have been used as taxonomic characters in these two genera (Holmes 1984; Clack 1987). It is probable that the depressions seen in the skull table of *Anthracosaurus* are also characteristic.

Both tabular horns are now incomplete in (HM)G 13.78, though Atthey (1877) figured the left as complete and the right as almost complete. The reader is referred to Dinning's excellent plate in Atthey's paper. However, the specimen has been refigured here as Atthey misinterpreted some of its features (e.g. left tabular buttress interpreted as the quadrate), with consequent inaccuracies in the figure. Atthey showed the horns to possess a lower blade similar to those of other embolomeres, bearing faint longitudinal striations as in *Pholiderpeton scutigerum*, *Pteroplax cornuta*, and *Palaeoherpeton decorum*. They are, however, less expanded posteriorly than in those genera. The lower blades in the holotype of *A. russelli* are both incomplete, but as far as preserved resemble those of other embolomeres. Panchen (1977) restored them in the oblique ventrolateral orientation which they possess in the preserved specimen, which is rather different from the almost horizontal orientation restored in *Pholiderpeton* by the present author. A characteristic of embolomere tabular horns is that they are actually or incipiently biramous (Holmes 1984; Clack 1987), with an upper component consisting of a boss or process separated from a lower component by a pit or notch. In anthracosaurids, eogyrinids, and archeriids, the lower component is blade-like (Clack 1987). In *A. russelli* the upper process has a substantial base and has been restored by Panchen (1977) as a process orientated ventromesially. Specimen (HM)G 13.78 exhibits only a small boss at this point, which though separated from the lower blade base by a pit, shows no evidence that it was ever the substantial process seen in *A. russelli* and for this reason (HM)G 13.78 is referred only to *Anthracosaurus* sp.

The underside of the skull table shows two characters by which it may be distinguished from that of an eogyrinid. In all the eogyrinids examined the ventral surface of the parietals shows smooth bone bearing conspicuous ridges radiating away from the region of the parietal foramen to give this region of the skull table a fluted appearance (Clack 1987). (HM)G 13.78 shows this feature in only a poorly developed form and the bone surface is roughened. Strong development of the fluting has been considered by Clack as a character distinguishing eogyrinids and it is found in *Pholiderpeton*, *Palaeoherpeton*, and *Neopteroiplax*.

In eogyrinids the tabular exhibits a pair of mesially directed facets for attachment of the opisthotics. These lie at the ends of well-developed buttresses separated by a deep groove. In (HM)G 13.78,



TEXT-FIG. 4. Isolated right jugal, (HM)G 24.39, in external view. Low Main Seam, Newsham, Northumberland. Scale bar: 10 mm.

although the tabular bears facets in a similar position to those of eogyrinids, they are not readily distinguishable as two separate facets, nor are they separated by a noticeable groove as they are in eogyrinids. This could be interpreted as a result of poor preservation, but in *Archeria* for example, the form of the facets is consistent throughout a number of skull tables, despite differential preservation (Clack 1987).

Jugal

The isolated jugal (HM)G 24.39 is complete anteriorly but has part of its posterior border missing. Part of the posterodorsal border has also been damaged, though probably little is missing. It is completely exposed over the external surface, though some of the internal surface is still embedded in matrix.

The dermal ornament is of the same 'eroded' nature seen in the skull table referred to *Anthracosaurus* above and that seen in the holotype of *A. russelli*. The jugal is characterized by a deeply excavated orbital margin, rendering the jugal very narrow below it. As with the skull table, direct comparison of the isolated example with the holotype skull reveals an identical shape in the two jugals, though (HM)G 24.39 is from a slightly smaller individual. The unusual shape of the jugal does not emerge from Panchen's reconstruction, because of the foreshortening effect on the sloping cheek of both dorsal and lateral views. However, the characteristic shape can be seen in the photograph (Panchen 1977, fig. 1).

The jugal (HM)G 24.39 is damaged along its posterior border at the point where the 'temporal fenestra' occurs in *A. russelli*. In the holotype the bone here is extremely thin, so such damage in the isolated specimen is not surprising and is consistent with the presence of a fenestra.

The only segment of lateral line canal to be found in *A. russelli* occurs along the posteroventral border of the jugal, parallel with the lower margin. It is shallow but clearly defined. What may be the anterior end of a lateral line canal is present in (HM)G 24.39 in the corresponding position. In *A. russelli* the jugal does not form any part of the jaw margin. The holotype of *Pholiderpeton scutigera* shows that this was also the case in this genus, and a broad flat surface for suture with the maxilla can be seen along the ventral margin of the bone. In (HM)G 24.39 the ventral margin is likewise broad and flat, suggesting that this jugal formed no part of the jaw margin, even allowing for the loss of the posterior part of the bone.

TABLE 1. Comparison of measurements of three embolomere skull tables, (HM)G 13.78, *Anthracosaurus russelli* (holotype), and *Pholiderpeton attheyi* (lectotype).

Measurements in mm	Specimens		
	G 13.78	<i>A. russelli</i>	<i>P. attheyi</i>
fr	76	96	106
pp-parfor	43	46	48
sktw	97	120	90
pofr	38	40	52
io	42	62	44
f	50	62	72
g	69	88	62
Ratios			
fr : pp-parfor	1.76	2.08	2.21
fr : sktw	0.78	0.80	1.17
pofr : sktw	0.39	0.33	0.58
pofr : pp-parfor	0.88	1.04	1.08
io : pp-parfor	0.97	1.35	0.92
io : sktw	0.43	0.52	0.48
sktw : pp-parfor	0.44	0.38	0.53
f/g %	72	70	116

Key: fr, frontal length; pp-parfor, postparietal-parietal foramen length; pofr, postfrontal length; sktw, maximum skull table width; io, minimum interorbital width; f, parietal length; g, parietal width.

DISCUSSION

The characters on which skull table (HM)G 13.78 may be confidently attributed to *Anthracosaurus* can be summarized as follows:

1. Ornament poorly developed—'eroded' in appearance.
2. Short frontals with deeply fimbriated suture for nasals; parallel-sided (diverging anteriorly in eogyrinids).
3. Short postfrontals.
4. Parietals noticeably broader than long.
5. The two latter characters contribute to a short skull table with parietal foramen only just behind the level of posterior orbit margin; also prefrontal contributing about 50 % to dorsal orbit margin.

The following characters exclude (HM)G 13.78 from the Eogyrinidae:

1. Fluting on underside of parietals poorly developed.
2. Tabular facets almost confluent, not conspicuously double nor separated by a deep groove.

Text-fig. 3 shows outline drawings of the three skull tables under consideration, (HM)G 13.78, the holotype of *A. russelli*, and the lectotype of *P. attheyi*, and shows positions at which measurements were taken. Table 1 sets out the measurements and proportions derived from these. In all the proportions examined, except that of the relative interorbital width, (HM)G 13.78 is seen to fall closer to *A. russelli* than to *Pholiderpeton*. The differences which exist between (HM)G 13.78 and *Pholiderpeton* may reflect individual variation within one species, and the similarities to *A. russelli* no more than coincidence. However, a study of eleven skull tables of *Archeria crassidisca* (Clack

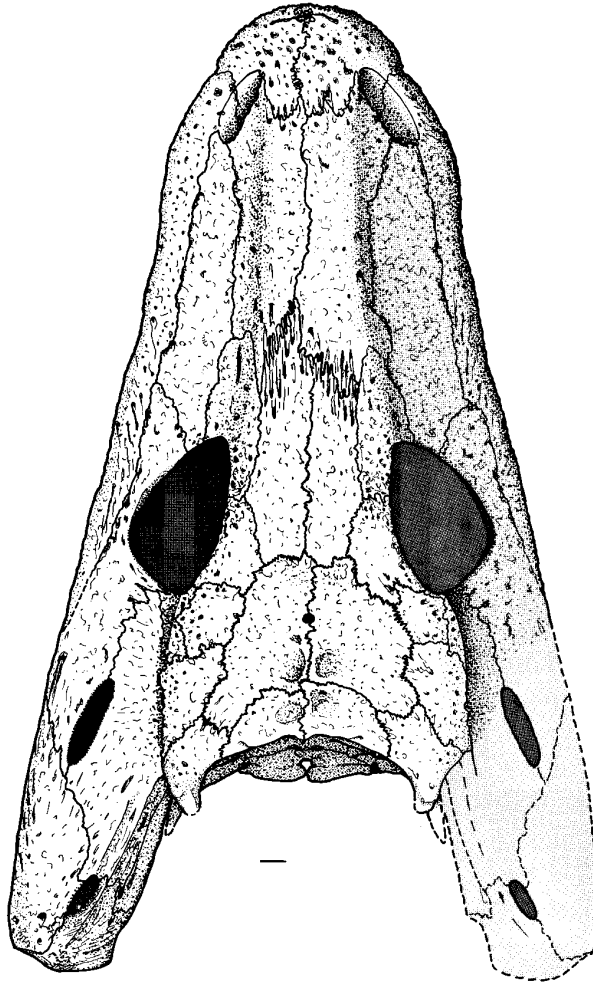
1987) shows a remarkable consistency within the members of one species of embolomere. The resemblances between (HM)G 13.78 and *Anthracosaurus russelli* are therefore inferred to be significant. The differences which do exist, for example in relative interorbital width, could be accounted for by the fact that (HM)G 13.78 derives from a smaller (?younger) individual.

Reference of skull table (HM)G 13.78 to *Anthracosaurus* has interesting consequences. This is one of the two skull tables which Watson (1926) used to establish the presence of a 'lateral kinetism' in embolomeres. The under-surface of the supratemporal is smooth throughout and concave except for the extreme lateral edge which is slightly curled under. Watson interpreted this to mean that the supratemporal was not securely sutured to the squamosal but that the squamosal facet sat beneath the supratemporal concavity, with the gap filled by connective tissue. He interpreted '*Palaeogyrinus*' (= *Palaeoherpeton*, Panchen 1970) in the same way, and embolomeres have been regarded as 'kinetic' by most authorities ever since. The kinetism has been perceived as a remnant of the rhipidistian kinetic mechanism.

If (HM)G 13.78 is correctly assigned to *Anthracosaurus*, a paradox results in that in the holotype of *A. russelli* the kinetism has apparently been eliminated by suturing. The paradox may be resolved by consideration of the form and possible function of the junction in eogyrinids and anthracosaurids. In my recent study of *Pholiderpeton* (Clack 1987) it was shown that the lateral supratemporal-tabular margin in this genus was, contrary to previous assessments, convex and pitted, exactly matching the shape of the squamosal facet. The condition is seen in the holotype of *P. scutigerum*, *P. attheyi* (specimen (BMNH)R 8426), and *Palaeoherpeton*. In these specimens at least, there could have been no cartilaginous padding present between the skull table and cheek. In all these genera it is evident that the suture between intertemporal and postorbital was a conventional suture, effectively immobilizing the skull table-cheek junction. The form of the supratemporal-squamosal junction with its broad pitted contact resembles that seen between lachrymal and maxilla; both occur in areas of stress, and appear designed to resist and disperse vertical forces. In these families the 'kinetic line' appears to have been modified to become a strengthened butt joint. In both *A. russelli* and apparently also in *Neopteroptax* (Romer 1963), the junction was securely sutured such that the 'kinetic line' was completely eliminated. The degree to which this consolidation occurred may have varied with age or between species, thus no pitting is seen in (HM)G 13.78 at the lateral supratemporal margin, but the intertemporal-postorbital suture was sealed. This condition is presumably derived from that seen in *Proterogyrinus* (Holmes, 1984), *Pteroptax*, and *Archeria* in which pitting on the supratemporal margin is also absent. In these non-eogyrinids the intertemporal-postorbital suture is not sealed (*Archeria*, Holmes, pers. comm.), perhaps allowing some remnant movement. Panchen (1977, p. 455) suggests that the sealed 'kinetic line' in *Anthracosaurus russelli* was possibly a factor related to age and of no taxonomic significance, and in this context it is relevant that specimen (HM)G 13.78 is from a smaller individual than the holotype specimen.

Examination of the jugal (HM)G 24.39 shows it to be notably tall posterior to the orbit. It is thereby made clear that the posterodorsal border of the jugal of the holotype of *A. russelli* has been damaged or pushed under the postorbital and postfrontal bones. It is also apparent that rather more crushing has occurred along the lachrymal-nasal suture than was allowed for by Panchen (1977). Another striking feature to emerge from the new restoration of the jugal is the deeply triangular orbits which *Anthracosaurus* must have possessed. This represents an additional autapomorphy, not obviously an adaptation to carnivory, by which to characterize the genus *Anthracosaurus*. Non-circular orbits are found in a number of Palaeozoic tetrapods, for example, *Pholiderpeton* (Clack 1987), *Carbonoherpeton* (Klembara 1986), *Eoherpeton* (Panchen 1975); loxommatids (Beaumont 1977), *Crassigyrynus* (Panchen 1985), and also apparently in one of the ichthyostegids (*Ichthyostega kochi*, Säve-Söderbergh 1932). No single explanation may be applicable to them all and there have been several suggestions (position of a salt gland, muscle insertion, muscle-bulging space) as to the function of the loxommatid 'keyhole' (see Beaumont 1977). Most recently, Bjerring (1987, in press) suggested that the asymmetrical orbits of these forms also housed an electric organ by which to locate or stun prey.

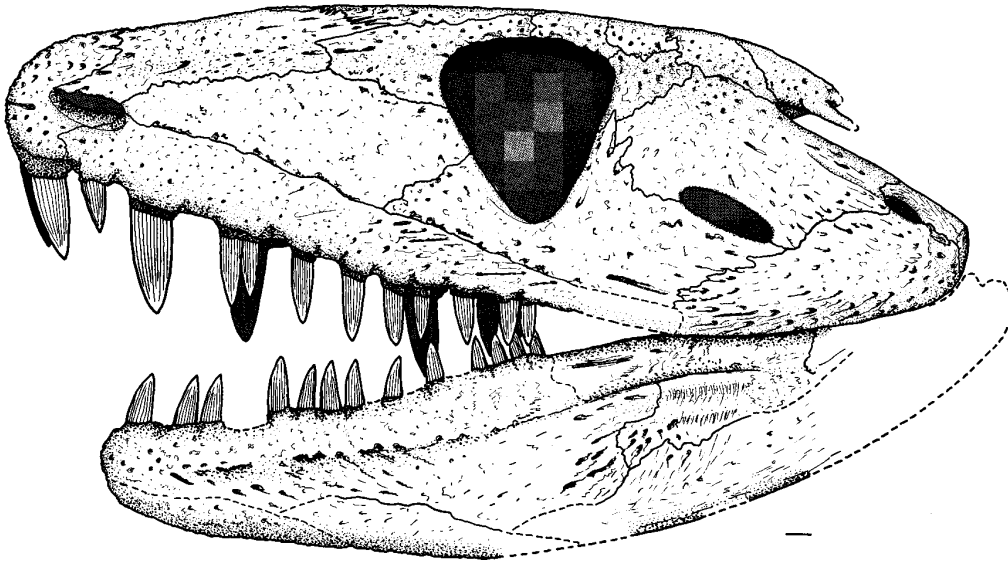
The completeness of the palate indicates that the width of the skull is essentially undistorted and



TEXT-FIG. 5. New reconstruction of skull of *Anthracosaurus russelli* in dorsal view, from holotype and (HM)G 24.39. Scale bar: 10 mm.

in dorsal view the anterior part of the skull would have been very little different from Panchen's restoration. However, it is now evident that the side of the face was rather deeper than he restored it. In consequence of a deeper orbital region, the suspensorium must be restored as deeper and as this region is almost undamaged in the holotype, the skull must also be made narrower at this point. Thus the 'lateral flare' must be reduced as a result. I have attempted new reconstructions incorporating these features (text-figs. 5 and 6). One further difference between the new reconstructions and those of Panchen (1977) lies in the interpretation of the quadrate region. Now that this region is more completely known in the genus *Pholiderpeton* (Clack 1983, 1987), that of *Anthracosaurus* is seen to be essentially similar to that of the former genus.

This study shows that it is possible to characterize isolated embolomere skull tables more precisely than in the past. Future discoveries may be identifiable at least as far as family or may, like *Pteroplax*, be excluded from any currently defined family. Using characters of the skull table alone, with the remaining anthracosaur families as the outgroup, it is possible to draw up a

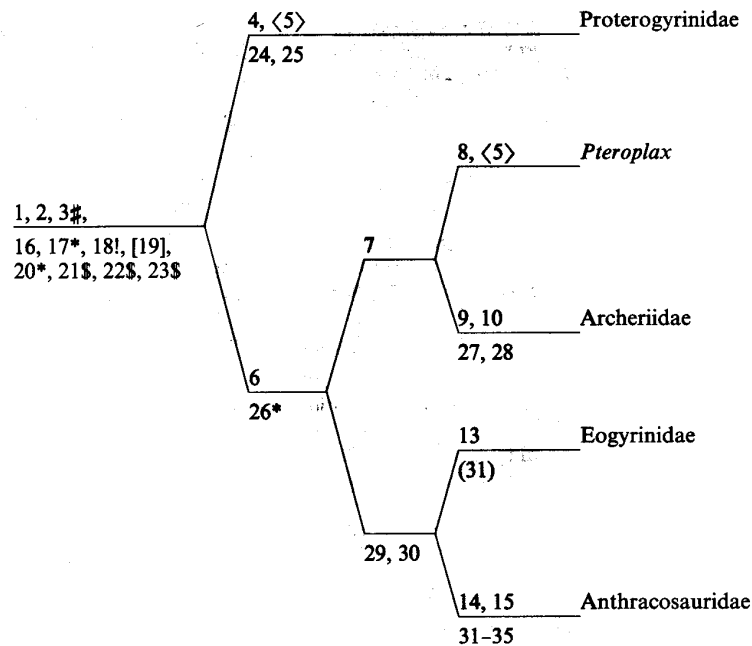


TEXT-FIG. 6. New reconstruction of skull of *Anthracosaurus russelli* in lateral view, from holotype and (HM)G 24.39. Lower jaw redrawn from Panchen (1981). Scale bar: 10 mm.

cladogram of the embolomeres, and to include the little-known genus *Pteroplax*. The characters are as follows:

1. Parietal ornament regular, pits discrete and elongated, especially towards the margins.
2. Tabular horn biramous, differentiated into upper and lower components separated by a notch or pit.
- 3#. Tabular bearing double facets for reception of opisthotic.
4. Tabular horn with lower component short, distinctively narrow and finger-like.
- <5. Parietal foramen on midline ridge bounded by grooves.>
6. Lower component of tabular horn blade-like.
7. Pits on underside of parietal and postparietal for reception of columella cranii and ?opisthotic.
8. Skull table and especially parietals markedly elongate.
- <5. Parietal foramen on mid-line ridge bounded by grooves.>
9. Parietals form distinctive arrow-shape.
10. Loss of anterior tabular facet.
11. Intertemporal-postorbital suture.
12. Parietal ornament irregular, pits vary in size, coalescing to form a groove and ridge system.
13. Marked fluting on underside of parietal.
14. Parietal ornament reduced to give 'eroded' appearance.
15. Parietals broader than long.

This character distribution supports the scheme of relationships proposed by Clack (1987) and may be added to the cladogram presented there. The additional characters cited by Clack (1987) are listed below, and the cladogram presented in text-fig. 7.



TEXT-FIG. 7. Cladogram of the embolomere families.

- 16. Two large Meckelian fenestrae, or a derivation thereof.
- 17*. Surangular crest usually developed.
- 18!. Opisthotic with free lateral processes.
- [19. Vomers tuskless.]
- 20*. Processus alaris of jugal contacts pterygoid.
- 21\$. Pleurocentra ossified as rings.
- 22\$. Oblique glenoid of scapulocoracoid.
- 23\$. Humerus with low degree of twist, condyle only slightly helical.
- 24. Expanded cleithrum.
- 25. Nasals excluded from naris by premaxillary-lachrymal suture.
- 26*. Lachrymal excluded from orbit by long prefrontal-jugal suture.
- 27. Skull elongate in snout region.
- 28. Numerous marginal teeth, about sixty.
- 29. Digitiform process of opisthotic.
- 30. Medially directed flange of exoccipital.
- 31. Massive dentition, reduced in number; two premaxillary teeth.
- 32. Single large Meckelian fenestra, produced from confluence of two.
- 33. Palate reinforced; pterygoids fused in mid-line; pterygoids cover palatines; pterygoids lacking denticles.
- 34. Enlarged orbit with ventrally excavated jugal.
- 35. Lateral shelf on surangular.

Key:

- * Implied reversal in *Anthracosaurus*.
- # Implied reversal in *Archeria*; also present in *Crassigyrinus*.
- ! Character unknown in *Archeria*.
- < > Character developed in parallel within embolomeres?
- [] Character distribution uncertain.
- \$ Unknown in *Anthracosaurus*.

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