A JAW RAMUS OF THE COAL MEASURE AMPHIBIAN *ANTHRACOSAURUS* FROM NORTHUMBERLAND

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ABSTRACT. The partial left jaw ramus of a large amphibian, from the Low Main Seam (Middle Coal Measures) of Newsham, Northumberland, is described for the first time. It is attributed to *Anthracosaurus russelli* Huxley and represents a previously unknown region of the jaw. The surangular crest is unlike that of other embolomerous anthracosaurs, the articular is widely exposed and the surangular restricted anteriorly by the depth of the adjacent dentary. The long posterior coronoid bears teeth of characteristic form and structure. A new restoration of the whole jaw of *Anthracosaurus* is presented. Anatomical differences from that of other embolomeres can be correlated with the massive dentition and long shallow suspensorium of *Anthracosaurus*.

THE holotype of *Anthracosaurus russelli* Huxley (1863) consists of a massive, almost complete skull lacking the lower jaw, from the Airdrie or Mushet's Black Band Ironstone. It was discovered by workmen of the Monkland Iron and Steel Company, near Airdrie (then Lanarkshire, now Strathclyde Region), about twelve miles east of Glasgow in 1861. 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 and Walker 1961; Panchen 1970). After Huxley's brief description of the exposed palate, the skull was further described by Watson (1929) who cleared the occipital surface.

Until relatively recently the holotype was the only specimen of *A. russelli* described, apart from some doubtfully attributed vertebrae and ribs noted by Huxley. In 1966 a second partial skull, consisting only of the snout with a well-preserved anterior palate, was discovered at Usworth Colliery, near Washington, then in County Durham (now in the County of Tyne and Wear) (Panchen, Tilley, and Steel 1967). The horizon was a sandstone roofing the Top Busty seam of the Durham coalfield and is thus of Lower Coal Measure age (Communis zone: Westphalian A).

In 1977, after completing the cleaning of the holotype, I published a revised account of *A. russelli* and attributed to that species several other specimens from Airdrie, including two incomplete left jaw rami, a snout fragment, an isolated tusk, a few vertebrae and ribs, and (more doubtfully) an interclavicle. It was concluded in that review that *A. russelli* was the only known member of the family Anthracosauridae Cope (1875), which together with the Coal Measure Eogyrinidae and the Lower Permian Archeriidae comprise the infraorder Embolomeri (Panchen 1970). The embolomeres were large aquatic predatory amphibians known, at least in the case of *Archeria*, to have been long-bodied and anguilliform (Romer 1947), although *Anthracosaurus* may have been more terrestrial in habit. They are the characteristic group within the suborder Anthracosauria, order Batrachosauria. The systematics and phylogeny of batrachosaurs has recently been reassessed (Panchen 1980).

The present specimen is registered in the Hancock Museum, Newcastle upon Tyne, as G24.35 and has not before been described, although a small label in the late Professor D. M. S. Watson's handwriting is enclosed with the specimen: 'Part of lower jaw of a labyrinthodont *New* (D.M.S.W.).' A small rectangular label of much earlier date was attached to the specimen and in handwriting like that of Thomas Atthey was inscribed 'No. 1'. The recent registration label attributes the specimen to the Low Main Seam, Newsham (Northumberland), and to the Atthey collection.

The Low Main Seam, worked out at Newsham near the end of the last century, was characterized by a roofing of black (or canneloid) shale from which comes the fish and amphibian fauna. It is of some interest that the coal seam at Newsham itself was expanded into a thick 'swelly' which extended for some 8 km almost due south from Newsham and was between about 120 and 185 m wide. Its northern end is within the area of the Newsham black shale and its direction in line with that of contemporary depositional currents (Land 1974). It is pointed out by Land that it is not sufficiently sinuous to be a river channel and strata above and below are unaffected, so that its association with the fossiliferous shale is something of a mystery.

The horizon of the (Northumberland) Low Main Seam has been revised (Land 1974). It is still Westphalian B and (British) Middle Coal Measures, but lying below the Northumberland Bensham seam is now established as Modiolaris Zone, *not* Similis-pulchra Zone as recorded in Panchen (1970, 1972) and in Panchen and Walker (1961, from Hopkins in Trueman 1954). This brings the Northumberland Low Main very close indeed to the horizon of Airdrie Blackband Ironstone from which the type of *A. russelli* came.

DESCRIPTION

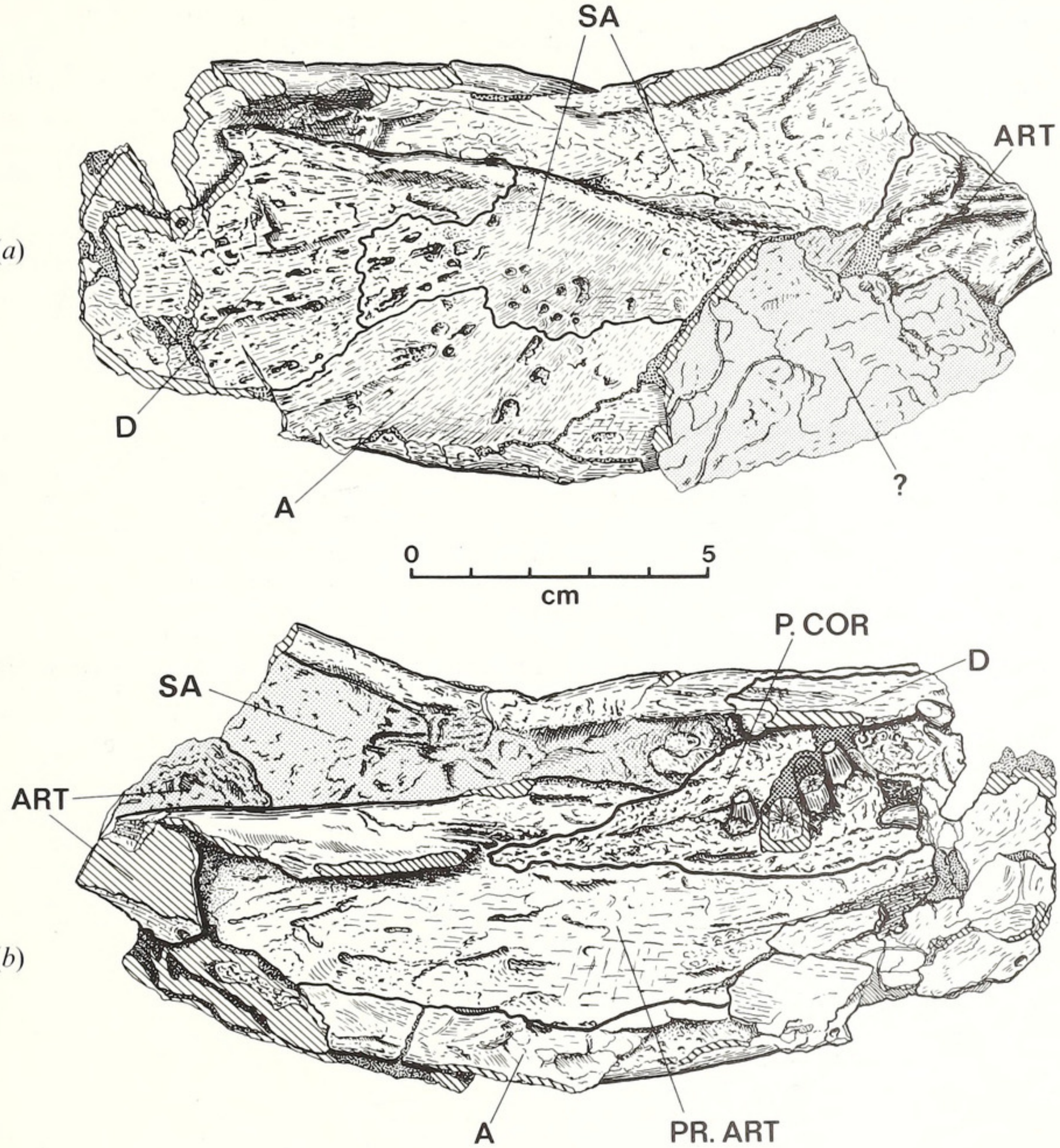
The specimen consists of the incomplete posterior part of a left mandible, probably comprising rather less than half of the total length of the original ramus (text-fig. 1). It had been largely cleared of the black-shale matrix before the present study. Virtually all the matrix has now been removed from all visible surfaces by means of an S.S. White Industrial Airbrasive Unit using sodium bicarbonate powder. Lateral and mesial surfaces of the ramus are thus completely exposed to view except that a piece of extraneous bone, of double thickness and probably pertaining to the palate, has been left in place. It is situated postero-ventrally on the lateral surface and would be difficult to remove without irreparable damage.

Preservation extends, as seen in lateral view, from the back of the dentary and includes most of the surangular and the angular. Part of the articular is also included, but not the articular glenoid fossa. In mesial view the posterior part of what must have been a very long posterior coronoid is preserved, as is much of the prearticular, including the mesial border of the adductor fossa. The sutures on the lateral surface were traced with ease. On the mesial surface the presence of a long posterior spur to the posterior coronoid is not absolutely certain (see below).

The preservation of the bone surface is very good over most of the ramus. However, the specimen has suffered considerable compression latero-mesially and almost certainly some distortion, such that the ossifications of the mesial surface (particularly the prearticular and posterior coronoid), appear to have been forced posteriorly relative to the lateral surface of the ramus and the articular. The latter bone may also have moved forward somewhat relative to the lateral bones in front of it as well as the mesial ones. When compared to the jaw ramus of *Eogyrinus attheyi* Watson (Panchen 1972), reconstructed principally from the excellent lectotype also from the Low Main Seam at Newsham, the present specimen seems remarkably shallow dorso-ventrally, and also to have dorsal and ventral margins which closely parallel one another. The shallowness is somewhat exaggerated, however, by erosion of the ventral edge of the specimen (i.e. the angular bone) and also by the fact, visible on the lateral surface, that the ventral part of the angular has been disrupted and forced up to overlap the more dorsal part of the same bone.

A very striking feature of the lateral surface of the bone is a massive horizontal shelf extending from just in front of the articular, through the surangular and the dentary, to the front of the specimen. Above this shelf, the surangular crest is perfectly in a vertical plane but is inset by the width of the shelf, which reaches nearly a centimetre about half-way along the surangular bone. Anteriorly the part of the dentary above the shelf has been forced down *post mortem* inside the ventral part, again diminishing the apparent height of the ramus.

The shelf seems to have marked the jaw margin. Thus it would presumably have occluded with the ventral, quadratojugal, margin of the back of the upper jaw when the mouth was closed in the intact skull. (Some thickening in the shelf region is present in the jaw ramus of *Eogyrinus*, but the dramatic inset of the surangular crest does not occur.) Thus in occlusion the surangular crest must have lain relatively mesially within the subtemporal fossa of the skull, suggesting that some of the adductor musculature must have inserted on the lateral surface of the surangular crest. This suggestion is corroborated by a markedly rugose area on that lateral surface above the shelf, and on the shelf itself. Furthermore, while the surangular crest of *Eogyrinus* has normal dermal ornament on its lateral surface and terminates as a blade dorsally, the present surangular has the muscle insertions noted laterally and a thickened dorsal rim with a concave dorsal surface, again suggesting muscle insertion. This thickened edge reaches a transverse width of a centimetre some 3 cm from the back of the preserved surangular then tapers slightly anteriorly before again widening out to nearly 2 cm in the region of the surangular-dentary suture. However, in this latter region it is convex.



TEXT-FIG. 1. *Anthracosaurus russelli* Huxley, partial left jaw ramus H.M.: G24.35 as preserved ($\times \frac{3}{4}$); (*a*), Lateral view; (*b*), mesial view. A, angular; ART, articular; D, dentary; P.COR, posterior coronoid; PR.ART, prearticular; SA, surangular; '?', unidentified (? palatal) bone.

The pattern of dermal bones in lateral view will be clear from text-fig. 1*a*. The dentary was clearly an exceptionally deep bone dorso-ventrally compared to that of *Eogyrinus* and other eogyrinids (e.g. *Eobaphetes*: Panchen 1977; *Neopteroplax*: Romer 1963) and to that of *Archeria* (Stovall 1948). The dentary is relatively deep anteriorly in *Neopteroplax*, as figured by Romer, but in the present specimen the deep region extends well behind the back of the dentary tooth row, so that the lateral exposure of the surangular bone behind it is relatively very short. On the assumption that the specimen is *Anthracosaurus*, this accords well with the Kelvingrove Museum jaw ramus (Panchen 1977) in which the exceptionally deep roots of the dentary teeth may be seen. In the Newsham specimen the well-preserved lateral surface of the back of the dentary is ornamented with a series of longitudinal pits in a rugose surface. This type of ornament is also present on the anterior process of the surangular, but elsewhere on the surangular and angular the bone surface is generally smooth or marked with very fine antero-ventrally directed striations and only scattered shallow pits (except for the muscle scars on the surangular, which have already been noted). Nowhere on the specimen is there any sign of lateral line sulci.

Some of the features of the surangular have already been described. In lateral view the surangular crest rises from a point well behind the back of the tooth row at an angle of about 30° to the point where the bone is broken off posteriorly. Its upper edge is straight or somewhat concave. In *Eogyrinus*, on the other hand, the crest commences immediately behind the tooth row and has a high curved and convex profile. The angular bone is obscured posteriorly by the extraneous bone already referred to. It presents no remarkable features laterally apart from the ornament and lack of any sign of the mandibular lateral line sulcus. Its mesial exposure is considered below.

The articular appears to have had a wide lateral exposure, again in contrast to *Eogyrinus* (but see below: 'Discussion'). It is marked by a prominent ridge inclined upwards from the horizontal from the level of the surangular shelf at the front of the articular. This ridge is seen to be a massive thickening of the bone from the section exposed in posterior view. It is possible that the area below the ridge was covered by the angular in the intact jaw.

In mesial view (text-fig. 1*b*) most of the exposed surface of the specimen is made up of the surangular, forming the lateral wall of the adductor fossa, and the prearticular, forming the mesial wall of that fossa below the surangular exposure. Below the prearticular is the very narrow mesial exposure of the angular, somewhat disrupted in the specimen, the two bones meeting in a straight horizontal suture. The upper edge of the prearticular is greatly thickened as in *Eogyrinus*, but in striking contrast is more or less straight and horizontal in mesial view, rather than deeply concave and angled. This thickening, which reaches its maximum about half-way along its length, produces a considerable overhang above the body of the bone, no doubt exaggerated by compression. Anteriorly rugose horizontal ridges suggest muscle insertion. The body of the bone is unremarkable, being flat and lightly ornamented with striations and sparse longitudinal pits. It does, however, have a considerably larger surface area than in *Eogyrinus* because of the smaller meckelian fenestra.

In the British Museum jaw ramus BM(NH) R.4822 it was shown that a single meckelian fenestra in *A. russelli* replaced the two large fenestra present in *Eogyrinus* and other embolomeres. A slight constriction in the width of the fenestra produced by thickening of the prearticular above appeared to represent a vestige of the bony bar separating the two typical embolomere fenestrae. In the present specimen part of the postero-dorsal rim of the fenestra, formed by the prearticular, is visible anteriorly, but most of the rim, and the back of the fenestra itself, is obscured by overlying displaced bone, possibly pertaining to the angular. No more posterior fenestra appears to be present. More displaced bone is present in front of the preserved part of the prearticular. Above this latter extraneous bone is a block of bone bearing part of the root of a massive tooth. It presumably pertains to the dentary but may not be *in situ*.

Dorsally the dentary-surangular suture is visible extending longitudinally for 25 mm until its course moves obliquely down in mesial view to reach the anterior limit of the adductor fossa. Thus in the complete jaw at least the last 4 cm of the dentary must have lacked teeth. A single small tooth crown, probably the last dentary tooth, is embedded at the front of the specimen.

Immediately below the dentary in mesial view is situated the most posterior of the three coronoids typically present in the anthracosaur jaw. This posterior coronoid is perhaps the most remarkable bone preserved in the jaw specimen. As in *Eogyrinus*, it is a ruguse bone bearing small denticles and forming the anterior margin of the adductor fossa. However, although the sutures traced are less than absolutely certain, a long spur of the posterior coronoid appears to extend back under the fossa and below the thickened prearticular rim; so that the posterior coronoid is spliced into the prearticular. In describing the British Museum jaw ramus of *A. russelli* (R.4822) I suggest that the back of the specimen, which terminated before the adductor fossa, marked the back of the posterior coronoid. The Newsham specimen shows it to have been an even longer and more extensive bone.

Most remarkable of all, however, and in striking contrast to *Eogyrinus*, is the presence of a short series of massive coronoid teeth. Five of these are preserved as a linear series. The first is somewhat displaced, but the others are *in situ*. The first and second have almost complete crowns, with estimated heights of 20 and 23 mm respectively. The third tooth is slightly larger than the second but is broken off about half-way down the crown, exposing a clear and characteristic transverse section, while the fourth, apparently the largest of the series, has been cut out with a rectangle of surrounding bone by some previous worker, presumably for sectioning. However, an oblique section through the root mesially and crown laterally is thus exposed. This fourth tooth has a diameter at the alveolus of 6·5 mm compared to 5·0–5·5 mm for the second, third, and incomplete fifth tooth.

The teeth are highly characteristic of *A. russelli* and closely similar to the marginal and palatal teeth of the holotype. The coronoid teeth are massive cones with strongly marked longitudinal grooves and, to judge from the first, blunt rounded apexes to the crown. They are quite unlike the more slender cylindrical marginal teeth with strongly backwardly recurved apexes seen in eogyrinids (Panchen 1970, fig. 4*b*).

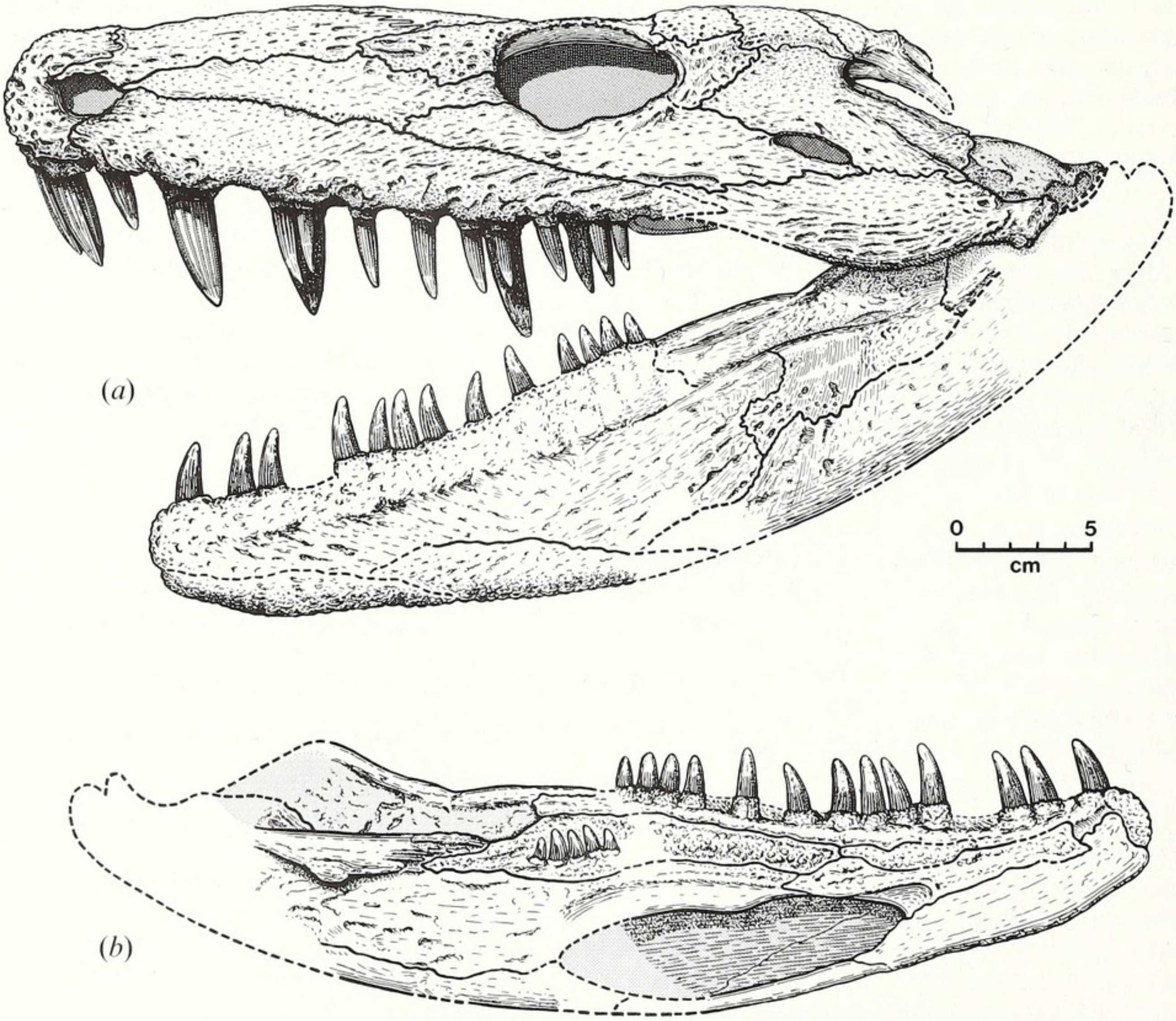
Apparently diagnostic, also, is the appearance of *Anthracosaurus* teeth in transverse section, and it was this appearance that first suggested that the present specimen might be referred to *A. russelli*. Firstly the teeth are characteristically anthracosaur as first described by Atthey (1876) in *Eogyrinus* ('*Anthracosaurus russelli*' in errore) in that near the base of the tooth the primary dentine has labyrinthodont infoldings which are highly tortuous but lack the short side branches seen in the contemporary loxommatids and other temnospondyls (Schultze 1969; Panchen 1970). Secondly, however, the appearance of the orthodentine surrounding the infolded primary dentine is highly characteristic. This was divided by Atthey into two types: firstly his 'dark dentine', appearing as peripheral wedges between successive labyrinthine infoldings and with tubules directed to the periphery of the tooth, and secondly 'light dentine', surrounding each fold of primary dentine and with tubules directed towards it (Atthey 1876, pl. XI). In the holotype of *A. russelli* the colouring of the two types of dentine is transposed as seen in reflected light (Panchen 1977). Atthey's 'light dentine' in *Anthracosaurus* is stained very dark brown and its periphery is sharply defined, whereas his 'dark dentine' in the holotype is of a light orange-yellow colour. The tooth section, with its white mineral-filled pulp cavity thus gives the appearance of a nearly black daisy-like flower with a white centre on an orange background. In the Usworth *Anthracosaurus* skull the colour difference is maintained but with shades of greyish-brown. In the present specimen the staining of the coronoid teeth is like that of the holotype. It is obvious, however, that this character must be due to the nature of the matrix and the mode of preservation as well as the histology of the tooth. Differential staining of the *Anthracosaurus* type also occurs in the ectopterygoid teeth of the eogyrinid specimen (A2) from Swanwick Colliery, Derbyshire, first attributed to *Eogyrinus* (Panchen 1964) and later to *Pholiderpeton* (Panchen 1970, 1972). It also appears to occur in the holotype of *Pholiderpeton scutigerum* now being redescribed by Miss J. A. Agnew. However, in both *Pholiderpeton* specimens the boundary between 'light' and 'dark' dentine is not so clearly defined. I have inspected all of Atthey's tooth sections of *Eogyrinus* ('*Anthracosaurus*') from Newsham and from Fenton, Staffordshire, preserved in the Hancock Museum. In every case the staining is just as he described it. None of his thin sections appears to correspond with the coronoid tooth crown removed from the Newsham *Anthracosaurus*.

DISCUSSION

The jaw ramus from Newsham is certainly that of an anthracosaur and equally certainly not that of *Eogyrinus*. It also seems very improbable that it belongs to *Pteroplax*, the only other anthracosaur certainly known from the Low Main Seam at Newsham. The specimen is radically different from that of any known eogyrinid in its structure, and ornament, and in the lack of lateral line sulci. All these features are consistent with its attribution to *A. russelli* and the form and histology of the coronoid teeth, while they cannot now be regarded as totally diagnostic, supply strong corroborating evidence. If the identification is accepted, the specimen can be used, together with the two jaw rami already known from the type locality at Airdrie (British Museum (NH): R.4822 and Glasgow City Museum, Kelvingrove: G73-87QA) to give an almost complete reconstruction of the lower jaw. It is a fortunate coincidence that the Newsham specimen supplies information about the posterior end of the ramus missing from the other two. It appears, however, to be from a slightly smaller specimen than the British Museum jaw, although how much smaller is difficult to judge because of the vertical compression of the Newsham specimen. In reconstruction the latter has been slightly enlarged to match the size of the British Museum jaw and the holotype skull.

In lateral view (text-fig. 2*a*) the anterior part of the jaw ramus is based on the British Museum specimen as in Panchen (1977). The only suture for which there is any evidence is that between the postsplenial and dentary, visible only in mesial view. This has been transferred to the lateral reconstruction, but, as the width of bone overlap in the suture is not known, its position is obviously subject to error. In the post-dentary region the reconstruction is based on the new specimen. It is assumed (see above) that the angular did enclose the articular below the ridge on the latter bone. There is, however, a problem concerning the lateral exposure of the articular above this reconstructed extension of the angular. The surangular-articular suture is easily visible both laterally and mesially in the Newsham specimen and there is virtually no overlap. An extensive mesial exposure of the articular, behind the suture, would not be surprising, but an equal lateral exposure would. If it were assumed that the Newsham specimen represents a much smaller jaw than the British Museum specimen, which matches the holotype skull, then the preserved part of the articular would be considerably nearer to the articular glenoid fossa, missing in the specimen, than has been restored. This assumption, however, would involve a greater degree of 'scaling up' in reconstruction of the smaller specimen and would make the surangular crest both too high and too near the glenoid to fit in the subtemporal fossa of a skull of the size and shape of the restored holotype (text-fig. 2*a*). An alternative interpretation is that the apparent surangular-articular suture is not a suture at all, but that the broken postero-ventral edge of the surangular has been impacted against the front of the lateral surface of the articular. On this latter interpretation, which I cannot dismiss, the surangular would have extended back above the articular ridge parallel to and possibly contacting the angular, so that the articular was visible laterally only in the immediate region of the glenoid.

The mesial restoration (text-fig. 2*b*) calls for little comment. As restored from both specimens, the posterior coronoid is exceptionally long, and the middle coronoid is very short as traced in the British Museum specimen. However, the topographical relations of all three coronoids are similar to those in *Eogyrinus* (Panchen 1972: fig. 11). The most significant difference from the jaw of *Eogyrinus* is the single, rather than two, meckelian fenestra in *Anthracosaurus*. It might have been expected that a further fenestra or foramen would be present behind the single but constricted one in *Anthracosaurus*, however, the Newsham specimen almost certainly rules out this expectation.



TEXT-FIG. 2. *Anthracosaurus russelli* Huxley ($\times \frac{1}{3}$); (*a*), restoration of the skull and lower jaw in left lateral view, skull from the holotype, jaw from BM(NH) R.4822 and H.M.: G24.35; (*b*), lower jaw in mesial view from the same latter two specimens.

The difference in form between the jaw ramus of *Anthracosaurus*, as restored, and that of *Eogyrinus* and other embolomeres, is very striking. The massive anterior region with its large but few teeth matches the snout and its dentition. More posteriorly, as restored from the Newsham specimen, the jaw lacks the great depth of the eogyrinid jaw, but this is again reflected in the relatively shallow elongate suspensorial region of the skull. Similarly, the broad exposure of the articular, if correctly restored, is echoed in the similar exposure of the quadrate.

As in the original reconstruction of the jaw (Panchen 1977), a small retroarticular process has been restored to provide a suitable orientated insertion for the depressor mandibulae muscles originating on the occiput and tabular horns. The insertion of the adductor mandibulae muscles was mainly, as in all primitive tetrapods, in the adductor fossa which is, however (because of the shape of the jaw), much shallower than that of *Eogyrinus*. This insertion was supplemented by insertion on the summit and on both sides of the surangular crest and the lateral shelf below it. In addition there appears to have been a strong insertion at the front of the thickened mesial border of the fossa.

The restored jaw ramus has the anterior boundary of the adductor fossa at a distance of 16 cm from the posterior rim of the articular glenoid, and this agrees accurately with the quadrate condyle/subtemporal fossa length in the preserved skull. The former distance, ignoring the retroarticular process, comprises approximately 42% of the jaw length. The corresponding figure in *Eogyrinus attheyi* is approximately 34%. Thus in *Anthracosaurus*, apart from extending the length over which the adductores mandibulae inserted, the long fossa moves the mid-point of insertion and line of action of the muscles away from the jaw articulation and towards the tooth row, compared with *Eogyrinus*. This both increases the static pressure exerted on food items when the jaw is near closure and reduces compression forces on the jaw articulation, which would have enabled *Anthracosaurus* to use its massive dentition to cope with larger prey than the similarly sized *Eogyrinus*. An exactly similar phenomenon was first pointed out by Parrington (1934) in the evolution of mammal-like reptiles, in which primitive forms are like *Eogyrinus* with a longer tooth row and adductor muscles whose action may be resolved as a force near the articulation, while the more advanced (therapsid) forms transfer the compression stress more onto the tooth row.

Acknowledgements. I am grateful to Mr. A. M. Tynan, Curator of the Hancock Museum, for the opportunity to study the jaw specimen from Newsham. It was brought to my attention by Mr. Michael Boyd, while he was temporarily employed in the Museum. The manuscript was typed by Mrs. E. B. Kinghorn.

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Typescript received 17 December 1979