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ON THE AMPHIBIAN *CRASSIGYRINUS SCOTICUS* WATSON FROM THE CARBONIFEROUS OF SCOTLAND

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CONTENTS

The holotype of *Crassigyrinus scoticus* Watson from the Viséan (Lower Carboniferous) of Edinburgh shows the side of the skull of a very primitive amphibian with fish-like proportions, an osteolepiform fish configuration of bones round the nostril and a preopercular bone on the cheek. '*Macromerium scoticum*' Lydekker from the same locality and horizon proves to be a *Crassigyrinus* mandibular ramus. This is corroborated by discovery of a skull and anterior skeleton of *Crassigyrinus* from the Namurian (basal Upper Carboniferous) of Cowdenbeath, Fife.

The skull of *Crassigyrinus* is also shown to have a loosely articulated basioccipital which did not form a finished occipital condyle and a mandible with coronoid teeth. However, it shares a number of derived (synapomorph) characters with the anthracosauroid amphibia of the Carboniferous and early Permian, notably the characteristic tabular horn, the probable absence of posttemporal fossae, the nature of the dermal ornament, the histology of the teeth and a true basipterygoid articulation. The last character may also indicate relations to loxommatid and seymouriamorph amphibia and amniotes. The pattern of bones of the *Crassigyrinus* skull table, however, is the primitive tetrapod ('temnospondyl') one.

The postcranial skeleton is both primitive and degenerate. The vertebrae each have a single crescent-shaped centrum ('intercentrum') and neural arches as poorly ossified, unfused bilateral halves. Prezygapophyses are unbuttressed facets and postzygapophyses totally lacking. There is room for a virtually unconstricted notochord. The diameter of the centra increases posteriorly from the small (partly reconstructed) atlas–axis complex. Ribs are long, well-ossified and cylindrical, but lack well-ossified rib-heads. The fore-limb is minute, with a typical primitive tetrapod humerus, which, however, retains some foramina otherwise seen only in *Ichthyostega* and fishes. The elongate ventral scales are unlike those of any 'labyrinthodont' amphibia.

It is suggested that the apparent 'otic notches' of *Crassigyrinus* may mark the position of persistent spiracles, while the stapes, not preserved in any specimen, may have been like that known in the Coal Measure anthracosaurs and in the primitive temnospondyl *Greererpeton*. Combined with an air-filled spiracular cleft the stapes could have been tuned to underwater rather than aerial hearing. *Crassigyrinus* appears to have been a large *Amphiuma*-like underwater predator.

A case is made for the 'sister-group' relation of *Crassigyrinus* to the anthracosauroids and a cladogram presented of the subgroups involved. It is, however, difficult to make a case for the close relationship of *Crassigyrinus* and the Seymouriamorpha and the closeness of relationship of the latter to anthracosauroids is questioned. *Crassigyrinus* shares several primitive characters with *Ichthyostega*, but they are only distantly related, so that the loss of those characters in all other tetrapods must have been polyphyletic. There are other characters in which one or the other is clearly the more primitive, but the polarity of a number of alternative character states in the two genera is equivocal. The cladistic use of out-group comparison is impotent to solve the problem because rival sister-groups for the Tetrapoda have been proposed using, *inter alia*, the disputed characters.

INTRODUCTION

Until recently the only known specimen of *Crassigyrinus scoticus* Watson (1929) was the holotype. This consists of the right side of the skull of a large amphibian exposed in external view on a massive block of ironstone. Only the cheek region and the side of the snout are present: the skull table, the middle pre-orbital region and the left side are completely missing and nothing was known of the braincase or palate. In 1973 I redescribed the holotype, after complete cleaning of the external surface by 'airbrasive' treatment, and was able to show its remarkably primitive nature. The configuration of the dermal bones of the side of the skull is intermediate between that of a crossopterygian fish such as *Eusthenopteron* and that of *Ichthyostega* (representing one of the earliest amphibia in which the skull roof is known). Similarly the lateral line system of the side of the skull, while appearing is open grooves, or sulci, as in other early amphibia, has a course corresponding to that of crossopterygian fish. In addition a large pre-opercular bone is retained. Furthermore the external nostril of *Crassigyrinus* appeared to have been enclosed by two dermal bones, the anterior tectal and lateral rostral, as described by Jarvik (1952) in *Ichthyostega* but lost, at least external as ossifications, in later amphibia.

However, despite its primitive nature, the holotype of *Crassigyrinus* is relatively late. Watson attributed the inadequately labelled specimen to the Gilmerton Ironstone (Upper Viséan, late Lower Carboniferous) of the Edinburgh area on the character of the matrix. That horizon has now been corroborated by spore analysis undertaken by Dr A. H. V. Smith (Panchen 1973).

One of the most important discoveries of Carboniferous amphibia in recent years was made by Mr S. P. Wood, not far from Edinburgh, at Cowdenbeath, Fife (Andrews *et al.* 1977). It consisted of specimens from a rich bone-bearing bed at the Dora opencast coal site, southeast of Cowdenbeath in Namurian (basal Upper Carboniferous) strata. Among the many fossil amphibia found at Cowdenbeath is the skeleton, discovered by Mr Wood, of a large amphibian. Complete development of the skull demonstrated that it was a second specimen of *Crassigyrinus* and also that the skull table, while like that of anthracosaur amphibia in form with characteristic tabular horns, had a temnospondyl and thus primitive configuration of the dermal bones (Panchen 1980).

The Dora bone bed at Cowdenbeath was first discovered as a vertical section cut by the contractors for the National Coal Board. Later, however, a large area of the bed was exposed by removal of the overburden. The exposed area was found to be divided into three horizontal platforms of increasing height towards the southwest, separated by faults roughly at right angles to the artificial cliff at which the bed was first exposed. The *Crassigyrinus* skeleton was recovered at the edge of the middle platform and it is probable that the posterior part of the specimen was lost when the original cut was made. The exposed bed was gridded in 0.33 m squares before collection by Mr Wood. These were numbered parallel to the edge and lettered at right angles to it, so that each square is uniquely designated by a letter and a number. The skeleton was found at the edge, at the level of numbers 59–60 (map in Smithson 1984). The isolated quadrate and posterior jaw specimens (R.S.M. 1975.48.50–51: see below) were found on the upper platform of the three, separated from the skeleton by a fault. Unfortunately they are not further localized by the grid system. The isolated interclavicle listed below (University of Newcastle 1978.3.15D2) was found at square A30 on the lower platform.

Apart from their topographical position another important point must be made about the discovery of the Cowdenbeath specimens (see Mode of life, below). The Dora bone bed is vertically divisible into three layers of different lithology (Smithson 1983). The basal layer is of a hard, black, unbedded siltstone, the middle layer is a characteristic clayband ironstone, with siderite nodules or aggregates in some areas, and the upper layer is of soft dark grey unbedded siltstone with rootlets prominent, giving the characteristic seatrock lithology. The skeleton was discovered in the basal layer, encroaching to some extent into the middle one, whereas the other specimens (and the vast majority or all the Cowdenbeath vertebrates) were found in the upper layers.

In his original account of the holotype of *Crassigyrinus* and other Scottish Carboniferous amphibia Watson (1929) very tentatively suggested an association between an incomplete right jaw ramus and the holotype of *Crassigyrinus*. This other specimen, also from the Gilmerton Ironstone, was the holotype of '*Macromerium*' *scoticum* Lydekker (1890). The association was supported by Romer (1947) and Panchen (1970). However, in my more recent redescription of both the *Crassigyrinus* holotype and '*Macromerium*' (Panchen 1973) I rejected any connection between the two. Development of the Cowdenbeath skull has made it clear that the '*Macromerium*' jaw is in fact a specimen of *Crassigyrinus* and as a result two other undescribed museum jaw specimens have been similarly identified.

It is now possible, therefore, to give a fairly complete and detailed account of the skull and some of the skeleton of *Crassigyrinus scoticus*. The anthracosaurs from the associated Cowdenbeath amphibian fauna are described by Dr Timothy Smithson (1983, 1984), who has already produced a preliminary account of the whole fauna (Smithson 1980*a*) and described from it a new temnospondyl amphibian (Smithson 1980*b*).

MATERIALS AND METHODS

The specimens attributed to *Crassigyrinus scoticus* Watson are listed below.

(i) Royal Scottish Museum, Department of Geology: 1859.33.104 (originally number 272), Hugh Miller Collection. Right side of skull on ironstone, exposed in external view. Holotype Watson (1929), also figured Panchen (1973). Labelled 'Carboniferous limestone', probably Gilmerton Ironstone (= Rough Parrot Coal), Lower Limestone Group of the Lothian Basin (P_2 Goniotites zone), Upper Viséan, Lower Carboniferous; possibly Venturefair pit, Gilmerton, near Edinburgh, Lothian Region, Scotland.

(ii) British Museum (Natural History), Department of Palaeontology: R310. A right jaw ramus, lacking the articular region, on ironstone, exposed in lateral, external view. Holotype of '*Macromerium*' *scoticum* Lydekker (1890) (for *Macromerion* Fritsch 1889 *in errore*). Watson (1929), Panchen (1970, 1973). Gilmerton Ironstone, Gilmerton.

(iii) Institute of Geological Sciences, Edinburgh, Palaeontological Department: G.S.E. 4722. A complete but damaged left jaw ramus on ironstone, exposed in internal view. Gilmerton Ironstone, Gilmerton.

(iv) Institute of Geological Sciences, Edinburgh, Palaeontological Department (unregistered). Anterior 12 cm of a right jaw ramus on ironstone, exposed in lateral, external view. Probably Gilmerton Ironstone.

(v) British Museum (Natural History), Department of Palaeontology: R 10000. Articulated skull and partial skeleton on shale, exposed in ventral view. Collected by Mr S. P. Wood. Figured Andrews *et al.* (1977) and (in part) Panchen (1980). 'Dora Bonebed': seatrock (rooty muddy siltstone or shale) below coal seam sequence under Lochgelly Blackband Ironstone, Limestone Coal Group (Lower Namurian A: E_1 stage), basal Upper Carboniferous. Dora opencast site (National Coal Board) near Cowdenbeath, Fife, Scotland.

(vi) Royal Scottish Museum, Department of Geology: 1975.48.50. Posterior 8 cm of a left jaw ramus, including crushed but otherwise well-preserved articular region. Collected by Mr S. P. Wood (SPW 1005). Dora bonebed, Cowdenbeath, as (v) above.

(vii) Royal Scottish Museum, Department of Geology: 1975.48.51. Fragment including left quadrate condyle, can be articulated with and probably from same individual as R.S.M. 1975.48.50 (vi above). Collected by Mr S. P. Wood (SPW 1113). Dora bonebed, Cowdenbeath.

(viii) B.M. (N.H.), Department of Palaeontology: R 30532. Poorly preserved anterior palate in ventral view on massive ironstone block. Labelled 'Portion of Palate, ? *Anthracosaurus russelli*?, L. Carboniferous [D.M.S.W.]' (*sic*) '? Airdrie Ironstone, ? Burdiehouse (Lydekker) Purchased 1856' (and in pencil) '? Gilmerton'. Probably Gilmerton Ironstone on the character of the matrix.

(ix) (? *Crassigyrinus*) University of Newcastle, Department of Zoology: 1978.3.15DZ. An isolated incomplete interclavicle, free of matrix. Collected by Mr S. P. Wood, prepared by Dr T. R. Smithson. Dora bonebed, Cowdenbeath.

The holotype specimens of *Crassigyrinus* and '*Macromerium*' had had their exposed surfaces completely cleaned using an S.S. White industrial airbrasive unit with calcium dolomite powder for previous studies (Panchen 1970, 1973) and no further cleaning was necessary. The exposed surfaces of the two rediscovered jaw specimens have been similarly freed of the last traces of matrix, but using sodium bicarbonate airbrasive powder (dolomite being no longer obtainable).

The Cowdenbeath skeleton (figure 1) was exposed in ventral view by Mr Wood, by completely manual preparation. He also largely completed the cleaning of the ventral surface of the skull and of the exposed elements of the postcranial skeleton including large numbers of ventral scales. After registration in the Department of Palaeontology, British Museum (Natural History) a latex mould of the exposed surface of the whole specimen was prepared by Mrs P. P. Hamilton-Waters followed by a fibreglass cast painted in natural colours for exhibition.

The dorsal surface of the skull specimen has now been completely cleaned by me after detaching the whole from the rest of the skeleton. Preliminary cleaning was by dental mallet and mounted needles followed by airbrasive development. A simple two-dimensional model of the skull roof was made by fixing a tracing of its outline and sutures on to a sheet of dental wax, with a drawing of the holotype and its mirror image for the sides of the skull and one of the Cowdenbeath skull for the skull table and more anterior medial region. It was found that the two specimens represented individuals of such closely similar size that little or no adjustment for scale was necessary. The wax sheet was then softened and moulded into a three-dimensional model by using the apparent width of the Cowdenbeath palate as a control. Photographs of the final model were used as an aid to reconstruction.

The postcranial skeleton presented intractable problems of development and description. The specimen, exposed in ventral view, was meticulously cleaned by Mr Wood but much of the axial and appendicular skeleton was obscured by the hundreds of small elongate scales. My original intention was to remove each of these scales individually and to preserve a record of the position and interrelationships of each by putting it into position in the museum's plaster mould. However, this philosophy of perfection had to be compromised to complete the work in reasonable time.

A map of the whole of the preserved postcranial skeleton, including every scale (figure 17), was prepared from photographs by using the casts and specimens for reference. Then selected bones were removed from the matrix and prepared as far as possible with the inevitable loss of some scales. However, the pattern of the latter is preserved in the map and the Museum's casts and moulds.

The palatine tusk from the Gilmerton palatal specimen (B.M.N.H., R 30532) was sectioned by Mr Brian Richardson of the Department of Geology, University of Newcastle upon Tyne. Photomicrographs of the resulting thin sections were taken by the author on a Leitz Orthoplan photomicroscope in the Zoology Department using Kodak Pan X film. The negatives were printed on high contrast (grade 4) paper.

SKULL

The extent and condition of preservation of the holotype skull and the '*Macromerium*' mandible have already been described and illustrated (Panchen 1973) as has the dorsal surface of the skull table of the Cowdenbeath skull (Panchen 1980). The Cowdenbeath skull, together with both jaw rami, is almost complete, but has been subjected to considerable distortion and disruption and is thus rather difficult to interpret (figures 2–5, plates 2 and 3). The skull table was originally attached to the first postcranial block but was removed, completely cleaned, and mended into the skull. The basioccipital bone was similarly developed out as a separate specimen.

The Cowdenbeath skull has been subjected to post-mortem compression which has distorted it asymmetrically. The left side of the skull and the lateral surface of the left jaw ramus appear in dorsal view, with the disrupted midline bones in front of the skull table to their right, while the lower part of the right side, plus the right mandible, appear in ventral view. The latter thus obscure much of the palate, which is further covered posteriorly by the irremovable interclavicle. However, the nature of the compression and distortion suggests that the overall width of the skull is still preserved, more or less throughout its length, by the separation of the jaw rami.

Because of the extreme depth of the *Crassigyrinus* skull (despite its generic name!) disruption of the skull roof has been particularly severe and is exacerbated by the fact that the skull table and most of the post-nasal midline dermal bones, plus, to a lesser extent, the braincase, have been pushed back until the posterior edge of the skull table is at the level of the back of the suspensorium. Part of the left side of the braincase and the underlying parasphenoid appear in dorsal view, as does the mesial surface of the right epipterygoid including the conical recess for the basal articulation. The quadrate rami of both pterygoids also appear in dorsal view, with the left obscuring the dorsal part of the cheek region behind the disrupted preopercular.

All superficial bone surfaces have been completely cleaned and the preservation of those surfaces in the skull is very good, as it is throughout the specimen. The condition of the newly described jaw ramus and other cranial specimens is noted as appropriate in the following description.

Dermal skull roof

The skull roof of *Crassigyrinus scoticus* differs from that of other large Palaeozoic amphibia in (i) the great postorbital length, reflecting the enormously long suspensorium; (ii) the great depth of the side of the skull, which, if my restoration is correct (figures 7, 9, 11) was almost vertical; and (iii) the large quadrangular orbits with a very narrow interorbital region. All these features except the narrow interorbital region could be seen and were described in the holotype (Panchen 1973). The skull table of the Cowdenbeath specimen with its 'temnospondyl' (that is, primitive) pattern, anthracosaur-like tabular horns and large rounded otic 'notches' has already been described (Panchen 1980). The present complete study allows a reconstruction of the whole skull roof and corroborates details of the side of the skull originally derived from the holotype.

As noted in the original description of the holotype the pattern of dermal bones of the right 'cheek region' behind the anterior margin of the orbit is quite certain and will be clear from the lateral reconstruction of the whole skull (figure 9). The most notable features are a large preopercular bone, an almost perpendicular jugal–lacrimal suture well behind the anterior margin of the orbit and a narrow maxillary bone which overlaps the large quadratojugal ventrally, thus excluding the jugal from the jaw margin. In the Cowdenbeath skull the corresponding region is partly preserved, from a level a little below the orbital margin on the left, but adds nothing new. The quadratojugal–jugal suture is visible, as is a rather disrupted fragment of the preopercular.

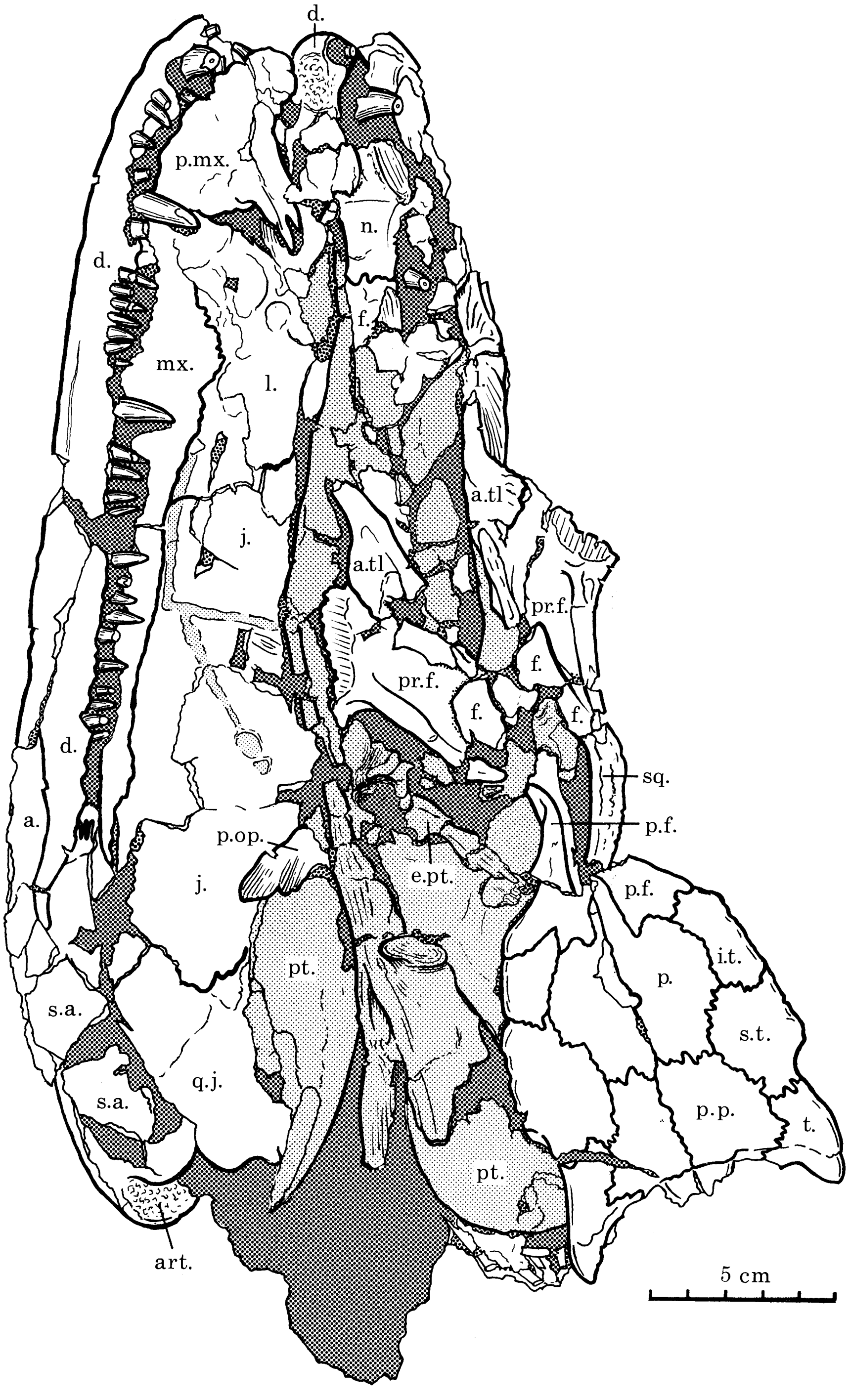


FIGURE 3. The Cowdenbeath skull, dorsal view. Half natural size. Heavy stipple-matrix, light stipple-braincase and palatal bones. a., Angular; art., articular; a.tl., anterior tectal; d., dentary; e.pt., epipterygoid; f., frontal; i.t., intertemporal; j., jugal; l., lacrimal; mx., maxillary; n., nasal; p., parietal; p.f., postfrontal; p.mx., premaxillary; p.op., preopercular; p.p., postparietal; pr.f., prefrontal; pt., pterygoid; q.j., quadratojugal; s.a. surangular; sq., squamosal; s.t., supratemporal; t., tabular. (For braincase see figure 10.)

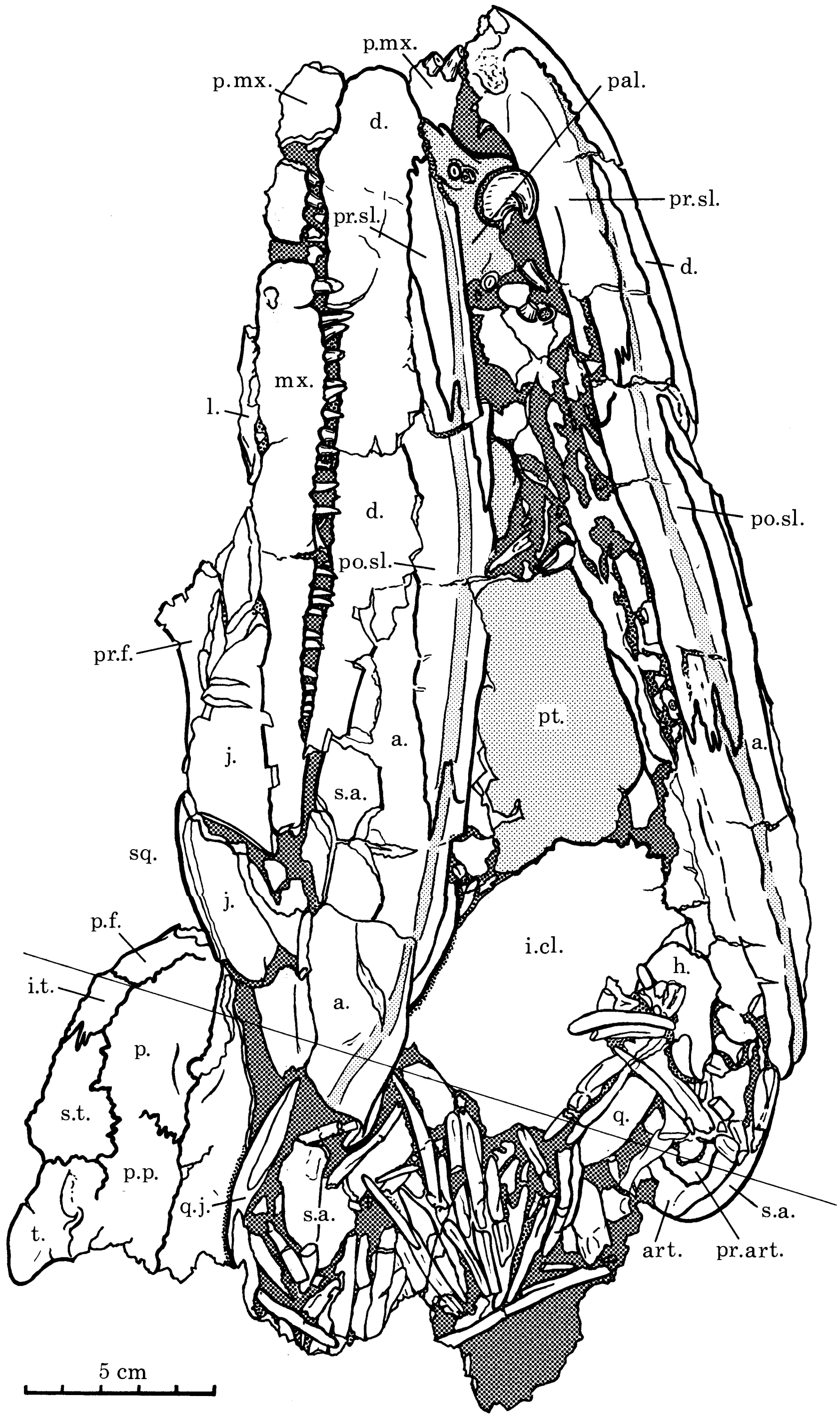


FIGURE 4. The Cowdenbeath skull, ventral view. Half natural size. h., Humerus; i.cl., interclavicle; pal., palatine; pr.art., prearticular; po.sl., postsplenial; pr.sl., presplenial; q., quadrate; other abbreviations and conventions as in figure 3. (Line indicates limit of figure 16.)

Figure 1. *Crassigyrinus scoticus* Watson, the Cowdenbeath specimen, ventral view.

FIGURE 2. *Crassigyrinus scoticus* Watson, skull from Cowdenbeath skeleton, dorsal view.

FIGURE 5. *Crassigyrinus scoticus* Watson, skull from Cowdenbeath skeleton, ventral view.

FIGURE 6. *Crassigyrinus scoticus* Watson (B.M.N.H., R 30532) palate, probably from Gilmerton Ironstone.

The interpretation of the snout region of the holotype was much less certain. The corresponding region is preserved in the Cowdenbeath skull, and detailed comment is therefore necessary. The sloping anterior margin of the orbit is formed by a large prefrontal bone which extends round the antero-ventral corner of the orbit and can be seen in the holotype to contact the jugal, thus narrowly excluding the lacrimal from the orbital margin. The orbital border of the prefrontal is massively thickened but in front of this thickening the bone is deeply concave. Both prefrontals are present in the Cowdenbeath skull and, despite the disruption in that region, are instantly recognizable. Similarly the right lacrimal is complete in the holotype, while most of the left is visible in the Cowdenbeath specimen together with a fragment of the right. Like the prefrontal the lacrimal has marked concavities in its surface that were commented on in describing the holotype but are equally visible in the newer specimen. The anterior margin of the lacrimal, visible in both, is convex and extends somewhat in front of the vertical maxillary–premaxillary suture immediately below it. It is the region anterior to these boundaries that is difficult to interpret.

The first difficulty is that in the holotype three sites had been proposed for the position of the right external naris (fenestra exonarina). First, the maxillary–premaxillary suture terminates dorsally in a deep concavity immediately below the lacrimal which could conceivably be interpreted as a nostril. However, I rejected that interpretation in 1963 and do so now. Unfortunately in the Cowdenbeath skull the corresponding region is obscured by a large dentary tooth on the left and disrupted on the right. The second interpretation was Watson's (1929). In the holotype a stout process extends dorsally from the massive premaxillary to contact the nasal. That process is parallel by a second mesial to it and thus below the dermal surface. The groove between the processes, then matrix-filled, was interpreted by Watson as the naris. Cleaning of the groove (Panchen 1973) revealed a line of junction which might have been a compressed nostril. However, Watson's interpretation depended on the assertion that the premaxillary of the holotype is missing and that the bone here identified as premaxillary is merely the anterior end of the maxillary. That assertion, never very convincing, may be rejected with confidence in the light of the Cowdenbeath skull. In the latter the left premaxillary is preserved complete with its external dorsal process and terminates antero-mesially in the midline. The deep process is not, however, visible.

The third site for the external naris in the holotype is situated immediately in front of the lacrimal. As preserved it is floored with bone which is continuous with a small ventrally pointed superficial ossification. The whole thus forms the ventral border of the nostril as well as its floor. By analogy with *Eusthenopteron* (Jarvik 1942) and *Ichthyostega* (Jarvik 1952) I have interpreted this bone as the lateral rostral, homologue of the tetrapod septomaxillary (Panchen 1967*b*). Thus the part occluding the nostril would be Jarvik's processus dermintermedius while the ventral, superficial part is the pars facialis. In the holotype there appears to be a small rectangular bone bordering the naris posterodorsally, but the principal bone above the nostril, seen in the holotype, corresponds to the anterior tectal of *Eusthenopteron* and *Ichthyostega*. It contacts the prefrontal posteriorly and just in front of that contact has a short suture with the lacrimal behind the small supernumerary bone.

In the Cowdenbeath skull the posterior border of the left premaxillary is well preserved and separated by a correctly shaped matrix gap from the anterior border of the lacrimal. However, the lateral rostral and supernumery bone (if any) are not preserved *in situ*, if at all. It is nevertheless very important to note that both anterior tectals are present and almost complete.

They retain their attachment to the respective prefrontals and thus, because of the longitudinal disruption of the specimen, have been shifted back some 8 cm in relation to the premaxillary. However, their identity is not in doubt and the snout can only be reconstructed satisfactorily if they are restored to exactly the position represented in the holotype, so that the tapering anterior process of each fits between the naris and the premaxillary process. Thus *Crassigyrinus* has a very primitive configuration of the snout which is essentially similar to that of an osteolepiform fish such as *Eusthenopteron*. I was rather reluctant to draw this inference, first because of its important phylogenetic implications (see The primitive characters of *Crassigyrinus*, below) and secondly because I had wrongly restored a similar configuration in the snout of the anthracosaur *Palaeoherpeton* (Panchen 1964). (Watson (1926) was correct in asserting that the premaxillary of the *Palaeoherpeton* ('*Palaeogyrinus*') holotype is lost: the configuration of the snout should be restored to closely resemble that of *Eogyrinus* (Panchen 1972*a*).) However, I find my conclusion about *Crassigyrinus* inescapable.

In the original description of the Cowdenbeath *Crassigyrinus* skull table it was noted that there appeared to be a persistent lateral kinetism comprising a potentially movable articulation on each side between at least the supratemporal and the 'cheek region' (squamosal and ? postorbital), that the ornament was of the anthracosaur type, with a system of large irregular shallow pits and ridges, and that the tabulars extended back as the characteristic anthracosaur tabular horns, strongly resembling those of the (possibly gephyrostegid) anthracosaur *Eoherpeton watsoni* (Panchen 1975, 1980). However the configuration of the dermal bones is undoubtedly 'temnospondyl', as noted above, with a large supratemporal on each side having a long suture with its respective postparietal. This represents the primitive condition for tetrapods, in contrast to the derived anthracosaur condition in which a tabular–parietal suture is achieved by the relative migration backwards of the parietal–postparietal suture (Panchen 1975). The pattern of dermal bones is absolutely certain, being represented by clear sutures on both sides of the table and corroborated in ventral view. It should also be noted that a large intertemporal bone is retained, a primitive feature shared with all anthracosaurs in contrast to its reduction or loss in most 'temnospondyls'.

Other features of the skull table region may also be noted. The pineal foramen, situated between the parietals, is of anthracosaur form and size, being circular, raised on a slight eminence and having a diameter of just under 5 mm. Below the posterior rim of the table both postparietals and tabulars have a preserved occipital exposure, terminating laterally in a concave inner face on the tabular horn on each side. The horns resemble those of *Eoherpeton* in having a proximal heavily ornamented region in continuity with the table dorsally, succeeded by a rounded unornamented cone whose upper surface is below table level. They are not, however, biramous like those of *Anthracosaurus russelli* and some other embolomerous anthracosaurs (Panchen 1977*b*).

The supposed otic notches take the form of deep embayments on each side in dorsal view centred at the transverse level of the supratemporal–tabular suture. A strong rectangular process of the supratemporal extends laterally in front of each 'notch' forming its anterior margin.

In ventral view the skull table (figure 8) appears very similar to that of embolomerous anthracosaurs, for example, *Palaeoherpeton* ('*Palaeogyrinus*': Panchen 1964; figure 3), but the long supratemporal-postparietal suture, representing the primitive condition, is clearly visible on both sides. The pineal foramen is situated, as seen from below, at the bottom of a deep pit some

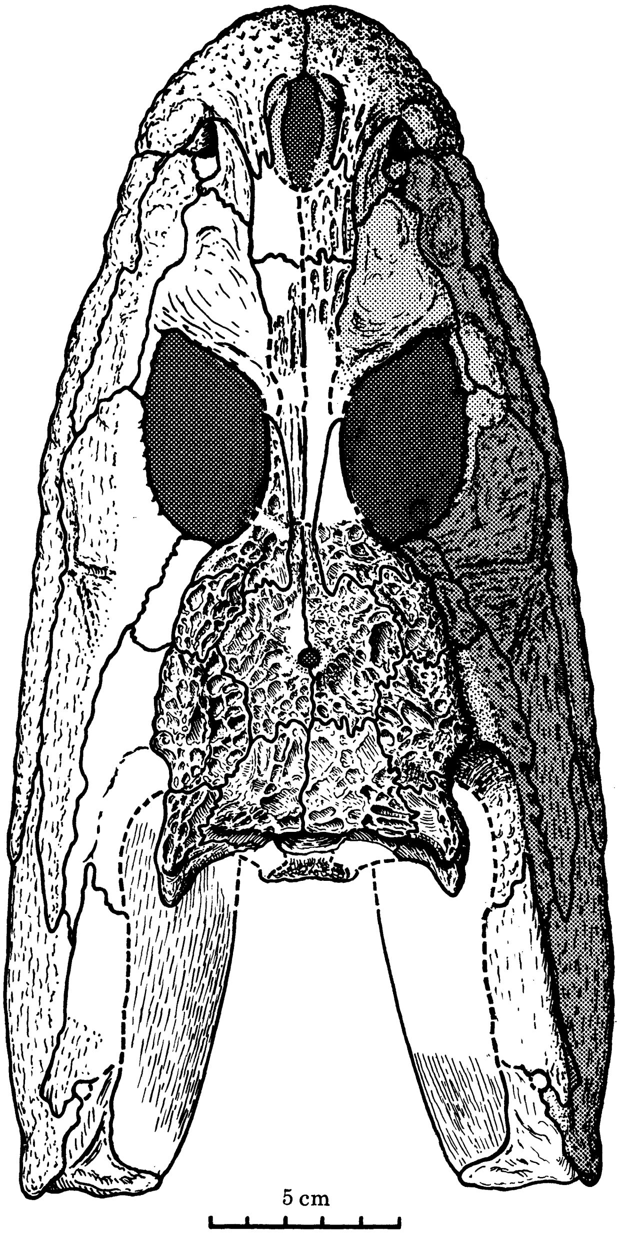


FIGURE 7. *Crassigyrinus scoticus* Watson, composite restoration of the skull, dorsal view. Half natural size.

2 cm in diameter which no doubt roofed a pineal fontanelle in the braincase of the type seen in *Palaeoherpeton*. The pit, formed at the junction of the two parietals, can be seen to extend forwards mesially on the right parietal: the corresponding region on the left is little preserved. The margin of the pit is defined by a sharp ridge. Laterally on each side lie two parallel ridges, the outer of which defines the margin of a convex central area of the parietal.

The right supratemporal bone shows a well-defined contact area for articulation with the cheek region, represented by the squamosal. This area takes the form of a roughened, faintly concave surface which tapers anteriorly. It corresponds to, but is much narrower than the concave articular area for the squamosal seen in embolomerous anthracosaurs (Watson 1926;

Panchen 1964). Immediately behind it is the somewhat rugose lateral projection of the supratemporal which forms the anterior boundary of the otic notch.

The form of the squamosal contact does not suggest that there was much mobility between table and cheek region. However, the contact surface continues forward on to the intertemporal (for the postorbital) and, although well preserved and completely cleaned, shows little or no sign of sutural interdigitations. There is, nevertheless, a spike of the supratemporal extending forward under the margin of the intertemporal which bears faint sutural ridges. Overall, however, it seems probable that the 'lateral kinetism' extended forward to the intertemporal as in *Eoherpeton* (Panchen 1975). At the front of the intertemporal a lateral projection marks the beginning of the dorsal margin of the orbit, which continues forward as the thickened edge of the postfrontal.

Posteriorly the edge of the skull table between the tabular horns is closely similar to that of isolated anthracosaur tables. There is a medial backward projection formed by the postparietals which is convex and rounded in dorsal view but has a strongly concave dorsal surface and a convex ventral one. It is inclined downward and like its much steeper flanking areas represents the occipital exposure of the table. The occipital tabular is formed by the posterior buttress which, in contacting the opisthotic, formed the dorsal end of the paroccipital process as in all 'labyrinthodonts'. In occipital view the tabular is closely similar to that of anthracosaurs (for example, *Palaeoherpeton*, Panchen 1964, figure 2). Mesial to it is the shallower occipital surface of the postparietals, sharply separated into lateral regions and the medial projection.

Despite my previous assertion (Panchen 1980, p. 339) it is rather difficult to tell whether posttemporal fossae were present in *Crassigyrinus*. Their absence is an important feature ('autapomorphy') of the Embolomeri. The posteroventral edges of the postparietals in the *Crassigyrinus* table have been freed of every trace of matrix but are still equivocal. If fossae were present the edges flanking the median process would have formed their upper margin. On the right most of the true edge is preserved and is tapered to a blunt blade with no sign of sutural interdigitations although its under-surface is somewhat rugose (figure 8): on the left the true edge is present only mesially but is rounded and shows what may be sutural ridges.

Another line of evidence is possible. Beaumont (1977) figures and comments on the impression of the posttemporal fossae on the underside of the skull table of *Loxomma acutirhinus* and other loxommatids, in which the deep forward pocketing of the fossae leaves a smooth concave impression under each postparietal with a mesial as well as lateral opisthotic facet on each side. The skull table of *Crassigyrinus* is totally different: there is no fossa impression and the posterior part of each flanking postparietal, where the proximal fossa roof would be, is rugose and possibly sutural. Therefore, although there is no certainty it seems highly probable that posttemporal fossae were absent in *Crassigyrinus* as in embolomeres.

Most other features of the occiput of *Crassigyrinus* are unknown. The basioccipital is described below but it is not known whether the supraoccipital was present as a distinct occipital ossification (see discussion of this ossification in Heaton (1980)). There is therefore insufficient evidence to reconstruct an informative occipital view of the skull.

The dermal ornament of the *Crassigyrinus* skull roof is faithfully reproduced in the reconstructed figures and was commented on in the description of the holotype (Panchen 1973) and of the skull table of the Cowdenbeath skull (Panchen 1980). In general terms it is like that of embolomeres and unlike the sharply-defined honeycomb pattern of loxommatids. This coarse

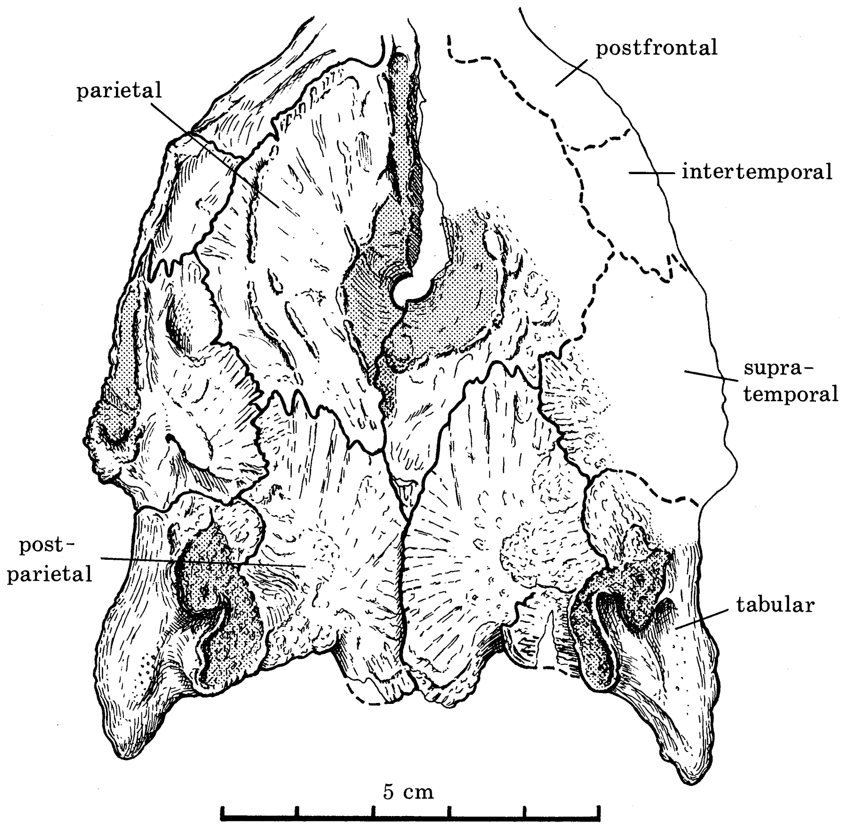


FIGURE 8. *Crassigyrinus scoticus* Watson, Cowdenbeath specimen, skull table from below. Natural size.

irregular ornament is particularly marked on the skull table, the squamosal and postorbital, and in the pitting of the premaxillary. The anterior part of the jugal, with the lacrimal and prefrontal, has a pattern of large shallow concavities and the maxillary is notably rugose anteriorly.

Parasphenoid and braincase

Data on the braincase of *Crassigyrinus* are confined to those features visible in the Cowdenbeath skull (figure 10). Only the left side is visible, but the underlying parasphenoid can be reconstructed in ventral as well as lateral view. Preservation of the parasphenoid extends from the posterior boundary of the parasphenoid body, which underlies the otic region and is approximately 60 mm in length, forward to the processus cultriformis, underlying the sphenethmoid, which extends the total length to about 150 mm. In ventral view the parasphenoid body is divided into bilateral arms ornamented with longitudinal ridges, which must have clasped the basioccipital (figure 11). These join at about 24 mm but a little way in front of their junction there is a deep median concavity which extends forward to the level of the basicranial articulation. The posterior forking and the concavity appear as an exaggeration of the condition seen in embolomeres (Panchen 1964, 1972*a*, 1977*b*).

In lateral view (figure 10*a*) the parasphenoid body extends far dorsally with a maximum height of 20 mm behind the basipterygoid process of the basisphenoid. However, there is no line of junction apparent between parasphenoid and basisphenoid behind or on the basipterygoid

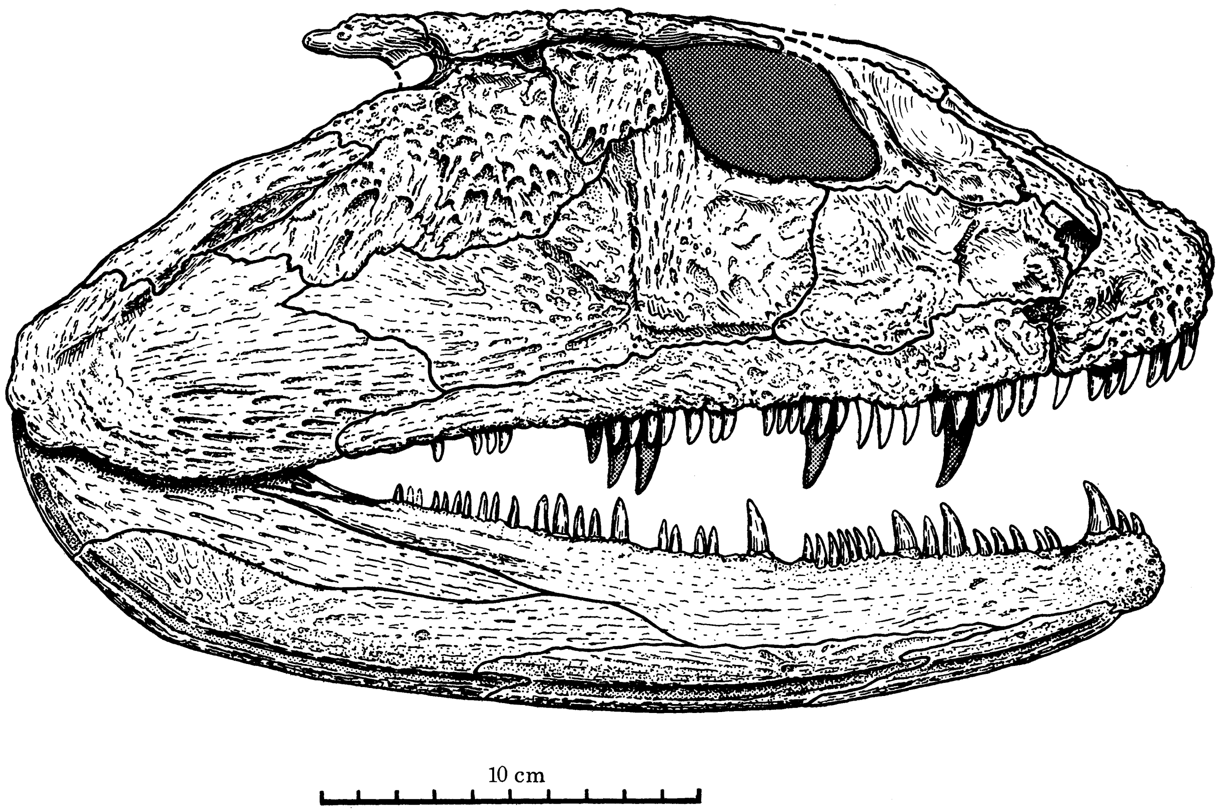


FIGURE 9. *Crassigyrinus scoticus* Watson, composite restoration of the skull, lateral view. Half natural size.

process. In front of the process the parasphenoid extends forward as the processus cultriformis which is clearly demarcated from the braincase. Immediately in front the p. cultriformis reaches a height of 10 mm but after about 20 cm is sharply reduced to a shallow slender process underlying the sphenethmoid region. When reconstructed in the whole skull, the processus cultriformis extends to within 80 mm of the tip of the snout, corroborating the suggestion that it was visible ventrally between palatal rami of the pterygoids as in eogyrinid embolomeres (Panchen 1964, 1972*a*) rather than being restricted by the junction of the pterygoids to form a palatal plate as in *Anthracosaurus russelli* (Panchen 1977*b*). *Eoherpeton* (Panchen 1980; Smithson 1984, and personal communication) and *Seymouria* (White 1939). Only part of the ventral edge of the sphenethmoid is visible above the processus cultriformis in the *Crassigyrinus* skull.

The basipterygoid process, although incomplete, is very distinctive. Like that of anthracosaurs and other primitive 'labyrinthodonts' the cartilage-finished articular surface faces anteriorly. In *Crassigyrinus* it is inclined back at about 30° to the transverse plane. As in loxommatids (Beaumont 1977) the articular surface is divisible into two areas. Ventrally it is strongly convex and when complete was probably almost hemispherical. The narrower dorsal area appears to have been concave, but with a thickened rim. The whole terminates a massive buttress whose axis is at about 45° to the sagittal plane and which is closely similar to that of embolomeres. There is no sutural line separating the basipterygoid process of the basisphenoid from the investing body of the parasphenoid, but the parasphenoid is ornamented by fine longitudinal ridges around the base of the buttress which gives way to the smooth surface of the buttress itself. Just as in *Palaeoherpeton* and *Eogyrinus* the circumference of the buttress is strongly concave ventrally, marking the course of the carotid artery and there is also a (very small) carotid foramen in this carotid groove vertically below the articular surface.

At this point, although it pertains to the palate, it is convenient to describe the basal region of the epipterygoid, which bears the conical recess into which the basipterygoid process fits. The mesial surface of part of the *right* epipterygoid is exposed in the Cowdenbeath skull. As noted in the introductory section distortion of the specimen has separated the conical recess of the epipterygoid by about 50 mm longitudinally from the level of the basipterygoid process with which it would have articulated.

The epipterygoid of primitive tetrapods, an endochondral ossification of the palatoquadrate, consists of three regions; first, a palatal ramus in front of the conical recess, which lies above the palatal ramus of the pterygoid and is thus concealed by the latter in palatal view; secondly the columella cranii with the conical recess at its base, and thirdly the quadrate ramus which is applied to the lateral surface of the quadrate ramus of the pterygoid and thus concealed by the latter in mesial or palatal view. In the *Crassigyrinus* skull a small part of the right palatal ramus, the conical recess and the columella cranii are exposed to view. Part of the left quadrate ramus is also exposed (see section on palate, below).

The conical recess forms the posterior termination of an epipterygoid buttress somewhat similar to that of the basipterygoid process, as in embolomeres. However, in the Cowdenbeath specimen only the ventral part of the buttress is present so that it rises to the full height of the conical recess only posteriorly at the recess: anteriorly it continues forward as the somewhat ornamented palatal ramus, of which only 10 mm is visible in front of the buttress. It is uncertain, because of poor preservation, whether the buttress was only a ventral core when complete. The conical recess is shaped to fit the basipterygoid process closely with a hemispherical pit ventrally and the poorly preserved remnants of a dorsal articular surface corresponding to the concave dorsal part of the basipterygoid process.

It is very important to note that the basal articulation of *Crassigyrinus* is a true articulation with some mobility, as in embolomeres and loxommatids, denoting intracranial kinetism. In the primitive colosteid temnospondyl *Greererpeton* (Smithson 1982 and personal communication) the 'articulation' appears to have been immobile, and in later temnospondyls, such as *Eryops* (Sawin 1941) and Watson's 'capitosaur series' (Watson 1919, 1951) the junction is strengthened by a pterygoid–parasphenoid suture.

The columella cranii of *Crassigyrinus* is poorly preserved. It extends posterodorsally from the conical recess at an angle of 30° to the vertical. At its base, where it forms the dorsal rim of the conical recess, it is 15 mm wide (anteroposteriorly), but a posterior concavity diminishes it to 7 mm immediately above this. It then widens dorsally and appears to be in continuity with a broad, roughly triangular, area of bone with a foliose edge at its dorsal end (figure 10*a*). Its overall measurable height along its axis, from the dorsal edge of the recess, is 40 mm. Indentations in the foliose edge of the bone may represent the two dorsal incisions originally described by Watson in *Palaeoherpeton* as for the maxillary and mandibular branches of the fifth cranial nerve (Watson 1926; Panchen 1964).

The triangular area in the specimen, bounded by the columella cranii anteriorly the skull table dorsally and the body of the parasphenoid ventrally, is largely occupied by smooth, mainly featureless bone, which may in part be otic capsule. However, some or all may pertain to the right pterygoid, or epipterygoid. None is certainly identifiable as braincase, although a roughly

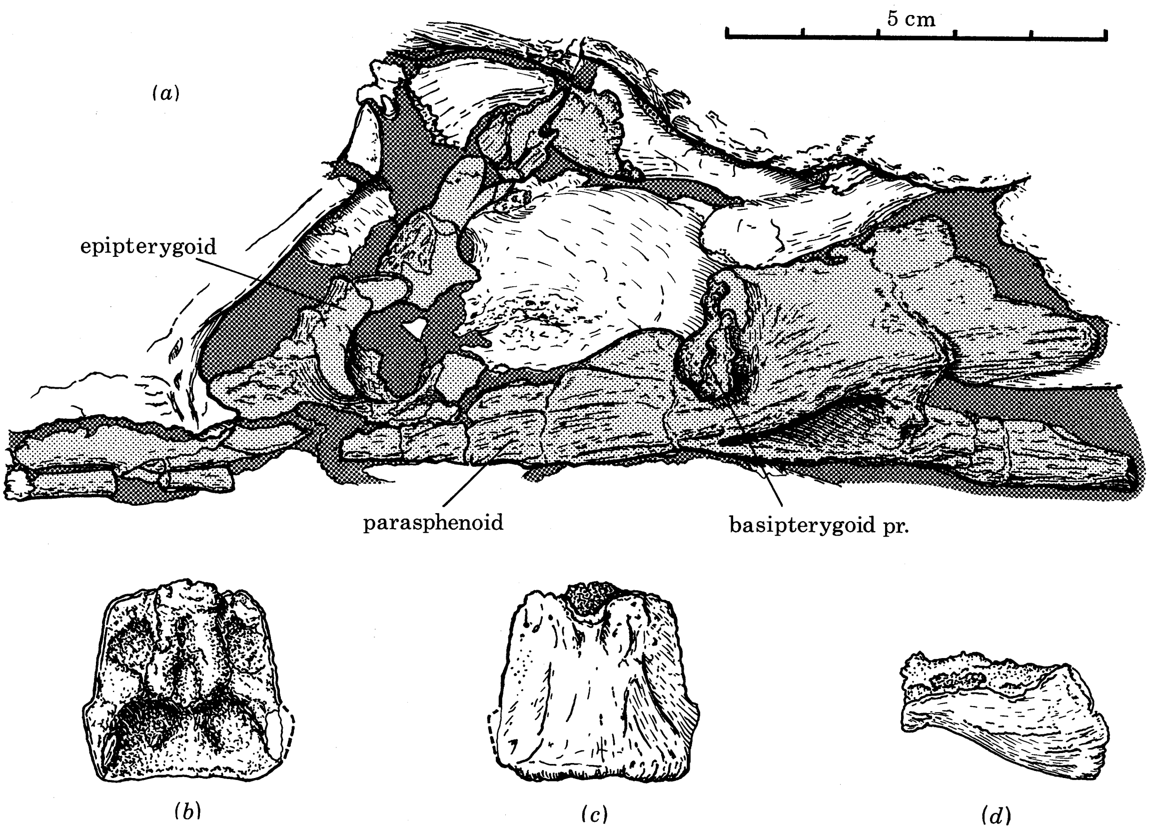


Figure 10. *Crassigyrinus scoticus* Watson, neurocranium of Cowdenbeath specimen. Natural size. (*a*) Braincase as exposed in dorsal view (light stipple-basisphenoid, parasphenoid and epipterygoid); (*b*)–(*d*), basioccipital in dorsal, ventral and left lateral view.

hemicylindrical area above the parasphenoid body may represent the otic capsule. However, and very unfortunately, no trace of the fenestra ovalis is identifiable.

The only remaining part of the braincase preserved is the basioccipital. This was present in the Cowdenbeath specimen as an isolated bone some 60 mm behind the skull table (figures 10*b–d* and 16). Although its dorsal, posterior and anterior surfaces are all of unfinished bone its bilateral symmetry leads me to believe that it is virtually complete, and hardly distorted. It has been completely removed and freed from matrix. A neural arch and two scales were impacted into the dorsal surface posteriorly and have now been removed. Ventrally and laterally it is finished with smooth periosteal bone marked with minute pits and grooves. More importantly there are well-marked bilateral ridges which converge anteriorly and presumably separate a ventral exposed area from lateral ones, which were overlapped by the posterior arms of the parasphenoid. the lateral overlap areas are not distinguishable in texture from the exposed ventral one.

Posteriorly the basioccipital has a rim that is straight but inclined somewhat forward in side view. It is somewhat broken away on the right but when complete would have been semi-circular in posterior view. The rim marks the margin of the basioccipital contribution to the occipital condyle. Extending forward and slightly down from it on each side of the upper surface is a clearly marked cartilage-finished surface for the junction of each exoccipital. However, and importantly, the whole condyle, to judge from the basioccipital, must have been deeply concave to a depth of over 12 mm compared to its horizontal diameter of 28 mm. Smithson (1982) notes that the condyle of *Greererpeton* is also deeply concave, but in *Crassigyrinus* it is lined with unfinished, cartilage-surfaced bone. Unless completely filled with a plug of cartilage it must have housed an appreciable anterior projection of the notochord, representing an intermediate condition between that of *Ichthyostega*, in which the notochord extends forward to the basicranial region, and the embolomeres and other primitive tetrapods with a single, concave, but finished condyle.

Anterior to the hollow region, the unfinished upper surface has a raised median area with a central axial groove, which may have housed a further extension of the notochord. Flanking this area are concave areas on each side which are probably for the extended junction of their respective exoccipitals.

Palate

The exposed part of the basal epipterygoid of *Crassigyrinus* has been described above from the Cowdenbeath skull (see section on parasphenoid and braincase). Information on other palatal ossifications comes from that skull, from an isolated quadrate from Cowdenbeath (R.S.M. 1975.48.51) and from an enigmatic British Museum specimen (R30532), which may, like the holotype, be from the Gilmerton Ironstone.

In the Cowdenbeath skull the whole right side of the palate is concealed by the right mandible in ventral view and the interclavicle conceals most of the quadrate ramus of the left pterygoid. However, the extreme posterior end is visible, together with part of the quadrate. The dorsomesial surfaces of both quadrate rami are exposed in dorsal view and the right also shows the somewhat eroded quadrate surface. There is a small part of the quadrate ramus of the epipterygoid exposed on the left. More anteriorly a large area of the left pterygoid is visible in ventral view and in front of that a part of the palatine. The latter bears a long palatal tusk near its anterior end as well as several smaller teeth. A second more posterior palatine tusk is visible in the holotype and partly concealed in the Cowdenbeath skull. Nothing is visible of the ectopterygoids in either specimen and only a trace of the left vomer is seen in contact with the palatine in the Cowdenbeath palate.

The isolated quadrate from Cowdenbeath is identifiable as *Crassigyrinus* because of its perfect fit with the rear end of a left jaw ramus (R.S.M. 1975.48.50) which is quite diagnostic. In some respects the quadrate condyle is similarly shaped to that of *Eogyrinus* (Panchen 1972*a*) and *Anthracosaurus* (Panchen 1977*b*). Thus it is convex from front to back along its whole mesial–lateral length, but strongly concave along that length with its strongest curvature laterally. Also its posterior rim is strongly defined as in *Eogyrinus*, with a shallow groove, visible in dorsal view beyond the rim. The anterior boundary, however, terminates in the ventral surface of the quadrate rather than standing clear of it. In this respect it is more like the simpler condyle of *Anthracosaurus*. It resembles both in being curved backwards rather than being directly transverse.

In articulation with the articular of the jaw ramus two other noteworthy features become clear. Firstly, the lateral half of the condylar surface is constricted from behind, against the backward curvature of the whole but 'rolls round' further dorsally at the back at the constriction. This configuration corresponds to a sharp upwardly directed crest at the back of the articular glenoid which is a continuation of a median keel to the jaw ramus. Secondly, in articulation, although the fit of quadrate and articular is close, about 15 mm of the glenoid anteromesially is unoccupied and it is clear that the epipterygoid, for which there is a well-preserved vertical contact surface on the quadrate, must have taken part in the formation of the condyle. The action of the jaw joint is further discussed below (see section on lower jaw).

Other contact surfaces are well preserved on the isolated quadrate. The bone is flanked by the vertical epipterygoid contact mesially and by that for the quadratojugal, also vertical, laterally. The overlap area for the quadrate ramus of the pterygoid is on the dorsomesial surface and takes the form of a well-defined surface with raised edges and strong longitudinal sutural ridges covering the whole area. The specimen is broken anteriorly, so it is not certain how long the whole was.

In the Cowdenbeath skull the ventral surface of the pterygoid, from the level of the occipital condyle to the level of the basal articulation is seen to be covered with a uniform shagreen of fine denticles as in embolomeres. A small area further forward, separated from the main area in the specimen by a patch of scales, is similarly ornamented. This is in contrast to the exposed dorsomesial surface of the quadrate ramus, seen in dorsal view, which is smooth and lacks denticles. In the intact skull the two surfaces would be in continuity with one another as each quadrate ramus rotates through more than a right angle from its contact with the quadrate to the ventromesial orientation of the palatal ramus with its denticles. Parts of both quadrate rami are visible in dorsal view. On the right, only the most posterior 45 mm, together with the quadrate, are visible, but on the left exposure extends forwards for 100 mm. The whole dorsolateral edge of the quadrate ramus, which contacts with cheek region, is thus exposed on the left and is of some complexity. The posterior 50 mm of the exposed edge appears to have contacted the mesial edge of the preopercular. Within that length the posterior 40 mm, which is convex upwards, has a slightly hollowed sutural edge between 3 and 5 mm wide, but the anterior 20 mm broadens out to nearly 10 mm and is double, having a deep cavity in the middle. The two rims of the cavity meet at the front of the preopercular contact. Anterior to the latter the pterygoid presumably contacted the squamosal, the two surfaces forming the floor of the otic notch. This region of the exposed quadrate ramus is flared laterally with a single edge until it disappears under the displaced end of the preopercular in the specimen. In the specimen about 25 mm of the edge of the quadrate ramus of the epipterygoid is seen protruding from below the pterygoid.

Little can be said about the anterior bones of the palate. The exposed area of the left palatine, which bears the tusk, also includes the mesial wall of the choana, which is steeply inclined into the choanal fenestra, forming a nearly vertical wall rather than a mere horizontal margin. Posteromesial to the choana and just in front of the tusk there is a closely set pair of teeth apparently sharing the same socket. Just behind them is a further tooth (see section on dentition, below).

Posterior to this an area of palatine bearing a second large tusk has been disrupted so that the tusk is deflected sideways and part of its exposed root may be seen between the bone and the lower jaw ramus under which the crown is concealed. This area of palatine is partly covered by a bone fragment bearing a similar pair of small teeth to those near the choana.

The massive palatal specimen (R30532) referred to above (in materials and methods and introduction to this section) was purchased by the British Museum (Natural History) in 1856 and has defied convincing identification ever since. It comprises the anterior part of the palate (agreed to be amphibian) exposed on a massive block of ironstone which is strikingly similar to

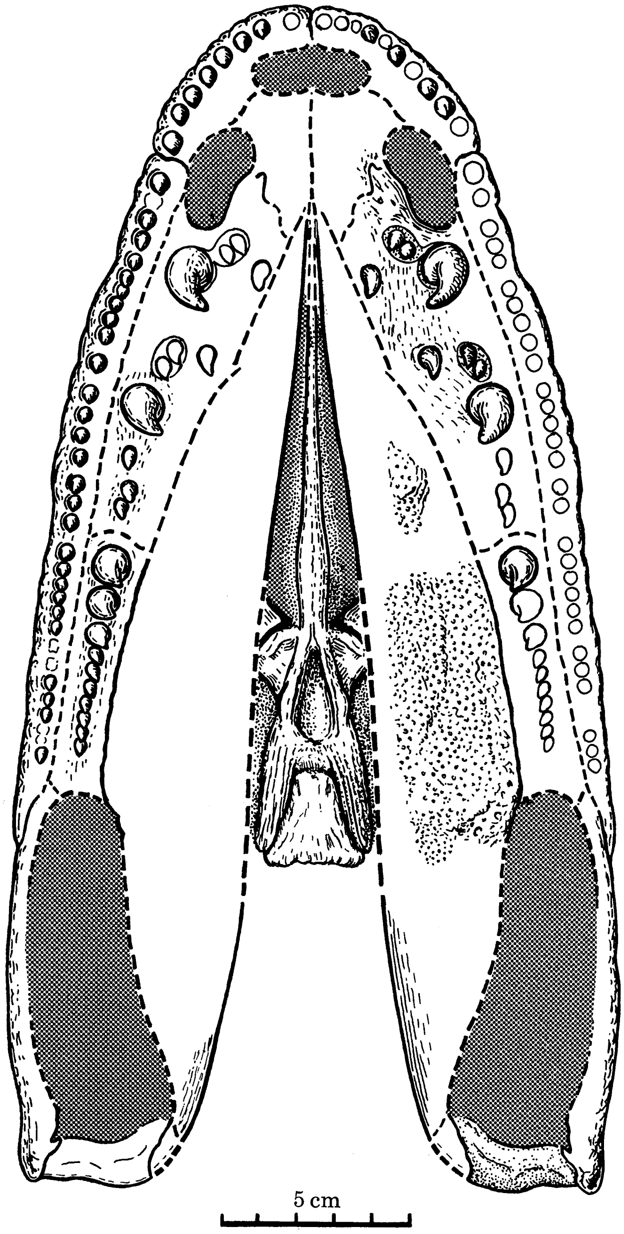


FIGURE 11. *Crassigyrinus scoticus* Watson, composite restoration of the skull, palatal view. Half natural size.

that on which the holotype of *Crassigyrinus* is preserved. The preservation of the British Museum palate is very poor and much of its state is almost certainly attributable to the crude preparation of the last century when confronted with what must have been an intractable specimen. Preservation extends almost from the tip of the snout to what was probably the occipital level, where the whole block is broken off obliquely (figure 6, plate 4).

Reasons for its attribution to *Crassigyrinus* are several. First, judging from the matrix, the horizon, and possibly the locality, may be the same as those of the holotype. Secondly, it represents a skull only slightly larger than the holotype and the Cowdenbeath specimen. Third is the nature of the dentition. The badly eroded stumps of marginal teeth are visible on the morphological right of the specimen and probably represent the whole extent of the premaxillary and maxillary dentition of *Crassigyrinus*, except that the mesial premaxillary dentition is lost with the transected tip of the snout. Preservation is too poor to allow a tooth count, but the size and spacing of the teeth is consistent. The length of the tooth row estimated from the midline and measured round the curve of the upper jaw margin is approximately 260 mm compared with approximately 225 mm in both the holotype and in the Cowdenbeath skull. The maximum width of the palatal specimen, apparently at the level of the basal articulation (which is also the most posterior level at which the whole width is preserved) is 170 mm. The reconstructed palatal width (figure 11) at that level is 150 mm. The palatal specimen and the reconstruction, drawn mainly from the Cowdenbeath specimen (if correct), therefore represent palates of closely similar proportions.

The most striking feature of the palatal specimen is the palatal dentition discussed below, which not only corroborates its identification but then yields more important data on *Crassigyrinus scoticus*. Unfortunately the bones of the palate are very poorly preserved and it is for this reason that the specimen has resisted identification for so long. In front of the most anterior palatal tusk there is a matrix-lined concavity on the morphological left corresponding in position to the choana, but only eroded bone (probably the underside of the skull roof) at the corresponding level on the right. More posteriorly the braincase is visible in horizontal section, with the eroded mass of the basisphenoid posteriorly, a hollow area corresponding to the otic region and a solid but disrupted sphenethmoid region. Apart from the places where teeth are implanted it is difficult to tell whether the rest of the eroded bone pertains to the palate or to the skull roof.

Lower jaw

The several specimens now available allow a virtually complete reconstruction of the lower jaw. The holotype of '*Macromerium scoticum*' previously described (Panchen 1973) yields information on the lateral surface of a jaw ramus from the anterior end to a level just in front of the adductor fossa. Both jaw rami are present in the Cowdenbeath skull and thus allow corroboration or correction of data from '*Macromerium*'. The separate articular region of a left ramus from Cowdenbeath has already been noted (see section on palate, above): although laterally crushed it is complete, with excellent bone preservation, forward to the middle of the adductor fossa, where it is broken off transversely. Finally, there are two specimens from the Gilmerton Ironstone: the more important (I.G.S. Edinburgh: G.S.E. 4722) a left jaw ramus, although somewhat damaged, gives fairly complete data on the jaw in mesial view except in that area between the adductor fossa and the jaw angle. The second I.G.S. specimen (unregistered) consists merely of 120 mm from the front of a right ramus, exposed in lateral view, but shows a good dentition. All the specimens represent skulls of closely similar size.

In lateral (external) view the jaw ramus is typical of those of early 'labyrinthodonts'. Its resemblance (as '*Macromerium*') to that of loxommatids has already been noted (Panchen 1973) and Beaumont's (1977) account of the jaw of *Megalocephalus* as well as mine of that of *Eogyrinus* (Panchen 1970, 1972*a*) may be used as standards of comparison. The shape and external pattern of dermal bones are similar to those of *Megalocephalus* (figure 12) and the *Crassigyrinus* jaw lacks the deep adductor region and high surangular crest characteristic of embolomeres. The pattern of bones, similar in all three genera, needs little comment, except to note that the posterior end of the tooth-bearing dentary, as seen in both rami of the Cowdenbeath skull, terminates in a slender spike below the level of the shallow surangular crest. Above this spike the surangular–posterior coronoid suture is visible in external view, and is then reconstructed as running longitudinally back in the plane of the crest so that in effect a blade of the posterior coronoid forms most of the inner surface at the top of the outer wall of the adductor fossa. This is seen in the I.G.S. jaw.

As in loxommatids and embolomeres there is a strongly defined mandibular sulcus of the lateral line system paralleling the ventral margin of the ramus from just below the articular to the front of the presplenial ('splenial'), but no oral sulcus of the type seen in *Eogyrinus*. The dermal ornament, as with the skull roof, is of embolomere rather than loxommatid type. Elongated pit and ridge ornament, unlike the loxommatid honeycomb pattern, is most strongly developed ventrally near the sulcus. The symphysial region of the dentary is pitted like the premaxillary, as in *Eogyrinus*. The dentition of the dentary is considered in the next section.

In mesial view the jaw ramus is remarkably primitive and again lacks the specialized features of the jaw of *Eogyrinus* and other embolomeres. Notably the two enormous mandibular fenestrae and the deeply depressed and angled inner margin of the adductor fossa of embolomeres are not developed. The symphysial contact area is seen in the Cowdenbeath skull as well as in the I.G.S. jaw: its form, with the posterior extension embraced by the presplenial and anterior coronoid, will be clear from the figure. The surface itself is cartilage finished and somewhat concave. This and its limited area makes it seem probable that there was some degree of movement possible between the two rami, as in *Eogyrinus*. The area of the dentary in front of the symphysis is recessed and rugose for attachment of a symphysial ligament as in *Megalocephalus*.

The pattern of dermal bones is again that of a primitive tetrapod and, while somewhat more irregular, is closely similar to that of *Megalocephalus*, being without the complications produced by the fenestrae in *Eogyrinus*. There are the usual two splenials (pre- and postsplenial) and three coronoids, which, as in both other forms, are denticulate. However, in *Crassigyrinus* the coronoid denticles are borne on restricted rugose areas as in *Eogyrinus* and other embolomeres, rather than being uniformly distributed as in *Megalocephalus*: on the anterior coronoid of *Crassigyrinus* the rugose area bears fine pits rather than denticles. Significantly more primitive than either of the Coal Measure genera is the presence of large teeth on the coronoids of *Crassigyrinus* in addition to the denticles; however, teeth also occur on the posterior coronoid of *Anthracosaurus russelli* (Panchen 1981). Of the two teeth on the anterior coronoid the anterior one, at the level of back of the symphysis, is complete and *in situ* on the left ramus of the Cowdenbeath skull and represented by its eroded root in the I.G.S. ramus. The posterior one is represented by its root in the I.G.S. ramus and probably by a detached crown beside the correct location on the Cowdenbeath ramus. Two teeth are also present on the middle coronoid (coronoid 2) and are *in situ* on the I.G.S. ramus, the first with a highly eroded crown, the second only as its root. It is possible that teeth were also present on the posterior coronoid (coronoid 3) as in *A. russelli* but, apart from the region of the fossa, only its anterior end is preserved.

A significant feature, seen in the I.G.S. ramus, is the presence of a series of pits on the dentary below and mesial to the tooth row. They are six in number: their position will be clear from the figure. The most anterior one is a replacement pit for the parasymphysial tusk, but three of the others are smooth-walled excavations whose apparent function it was to receive the tips of the palatal tusks when the jaws were closed. Their position was useful in reconstructing the palatal dentition.

While there are no mandibular fenestra there are several small foramina ventrally on the mesial surface of the jaw, as is usual in 'labyrinthodonts'. Four are seen in postsplenial of the I.G.S. jaw, although they may have been obscured in the intact jaw by overlap of the prearticular. Two larger ones, certainly exposed, are incised in the boundary between angular and prearticular.

The region of the back of the adductor fossa and the articular behind it is seen most clearly in the separate articular region from Cowdenbeath, with some details corroborated from the I.G.S. ramus and from the left ramus from the Cowdenbeath skull. The relation of the surangular to the articular is shown particularly clearly in the Cowdenbeath articular specimen. The jaw ramus is characterized by a median keel, already referred to, which reaches its apex as a pointed projection at the back of the articular glenoid surface. The apex of this projection is formed posteriorly by the surangular. A suture marking the mesial boundary of the surangular is clearly visible on the posterior surface. This suture is median to the ramus at its apex but soon moves mesially so that there is a modest wrap-around of the surangular on to the mesial surface of the jaw ramus to contact the prearticular. Lateral to the apex of the projection the edge of the bone at the back of the articulation is broken away and the surangular can be seen in section to form an outer shell covering the articular. Laterally the surangular actually forms part of the articular glenoid, encroaching by a maximum of 7 mm onto that surface. However, the surangular part of the glenoid is ornamented and pitted like dermal bone whereas the articular surface is cartilage-finished. The boundary between the two is sharply defined. Anteriorly the surangular also appears to form the posterior wall of the adductor fossa, extending right round to contact the prearticular mesially. Thus the surangular covers the posterior surface of the articular only as far as the midline but covers the complete anterior surface.

In the Cowdenbeath articular specimen the mesial surface of the articular is exposed and post-mortem disruption has caused it to overlap the prearticular anteroventrally so that the latter is broken off posterodorsally and forced inside the articular. However the exposed surface of the articular is roughened for bony contact and the investing prearticular is preserved posterodorsally and also posteriorly where it forms the median suture with the surangular. It is almost certain, therefore, that the whole surface of the articular was covered by the prearticular mesially as it was by the surangular laterally and anteriorly. In an intact ramus only the glenoid surface of the articular would have been exposed to view.

The shape of that glenoid surface closely mirrors that of the condyle on the quadrate specimen so that the fit between the two is very accurate. However the glenoid extends mesially by more than 15 mm beyond the quadrate, leading to the conclusion that part of the condyle must have been formed by the epipterygoid (see section on the palate, above).

The shape of the glenoid fossa is similar to that described in detail in *Eogyrinus* (Panchen 1972*a*, p. 308 and figure 12). Like that of *Eogyrinus* it differs from a simple hemicylindrical roller hinge in three ways: (i) it is saddle-shaped, being concave from front to back, but slightly convex from side to side; (ii) although exaggerated by compression and a vertical break, the axis was not a transverse straight line, but was curved, being convex backwards; (iii) because of the median projection, which is near the lateral end of the glenoid, the latter is 'screw-shaped', like the scapula glenoid of primitive tetrapods, and faces dorsally at its mesial end but somewhat anteriorly laterally. None of these departures from a simple roller hinge is as marked as in *Eogyrinus*, nor does the glenoid extend laterally or mesially beyond the adjacent sides of the

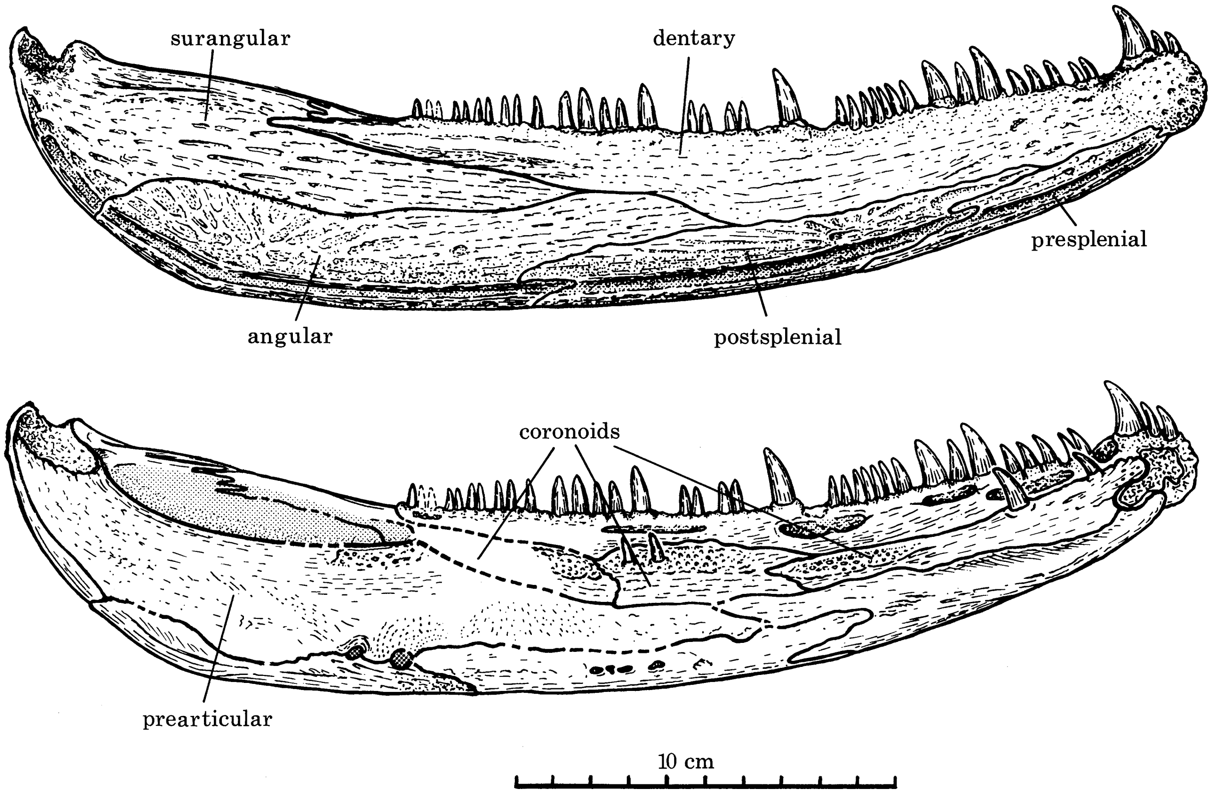


FIGURE 12. *Crassigyrinus scoticus* Watson, composite restoration of the lower jaw in the plane of each ramus. Half natural size. (*a*) Right ramus, lateral; (*b*) left ramus, mesial.

ramus, as does that of the *Eogyrinus*. Nevertheless the functional effects of its shape must have been to some extent similar.

In describing the *Eogyrinus* jaw articulation I suggested that as the mouth opened the glenoids moved laterally along their respective quadrate condyles (effected by the screw-shaped glenoid), but that instead of this resulting in a net divergence between the two rami it resulted in each ramus rotating about its long axis (as a result of the saddle shape), while the backward curvature of the glenoids, representing arcs of a circle centred at the symphysis, allowed a smooth divergence of the articulars around the circumference. The suggested functional reasons for this complex jaw motion were (i) that torsion in the rami or stress in an elastic symphysis, or both, would accumulate energy as the jaws opened: this would assist in closure; (ii) as the dentitions of lower and upper jaw approached during closure the rotation about a longitudinal axis of the dentary dentition would minimize the chance of tip to tip collision with the maxillary dentition, which would jam the jaws, preventing complete closure.

In *Crassigyrinus* the same system seems to have prevailed but with a more modest degree of longitudinal rotation. There is, however, another factor. The median projection, whose apex forms part of the back of the glenoid, appears to have acted, with the corresponding indentation in the quadrate condyle, as a lock to prevent excessive opening of the jaws and thus dislocation of the joint. This may have been more necessary in *Crassigyrinus* with its very deep skull and comparatively slender jaws, than with the deep, heavily muscled jaws of *Eogyrinus*.

Dentition

Information on the dentition of *Crassigyrinus* comes from a number of specimens. That of the holotype, comprising an incomplete premaxillary and maxillary dentition with one visible palatal tusk, has already been described, as has that of the '*Macromerium*' lower jaw (Panchen 1973). Upper marginal dentitions are also visible in the Cowdenbeath skull (premaxillary on the left and the right, maxillary on the right: figures 2–4) and in the palatal specimen presumed to be from Gilmerton. Dentary dentitions are visible in '*Macromerium*', the two I.G.S. jaw specimens and mainly on the left in the Cowdenbeath skull. The complete I.G.S. jaw ramus also shows at least part of the coronoid dentition as noted above. Reconstruction of the palatal dentition depends mainly on the Cowdenbeath skull and the Gilmerton palate.

Six poorly preserved and widely spaced premaxillary teeth are represented in the holotype, four on the left in the Cowdenbeath skull and six on the right, mostly as roots or stumps. Data from all three suggests a count of eight teeth on each premaxillary. Twenty-five maxillary teeth are visible on the type but their spacing originally suggested a total count of about 40. Twenty-three are clearly visible on the right in the Cowdenbeath skull but certainly do not reach to the posterior end of the tooth row. A total maxillary count of 35 tooth sites (with teeth or replacement pits) now seems more probable. The upper marginal teeth are of distinctive shape, being bullet-shaped and slightly recurved. They are striated from base to tip of the crown but lack any anterior or posterior keel. The maxillary teeth are remarkably small and uniform, being slightly smaller at the posterior end of the series but lacking any 'canine peak' in size. The largest (in the holotype) has a basal diameter of 4 mm and a crown length of 10 mm. The shortest (also in the holotype, at the back) has a diameter of 2.5 mm and a length of about 5 mm. Those in the Cowdenbeath skull, although most have the tip of the crown missing, do not appear to exceed 3 mm and 7 mm respectively. The largest premaxillary tooth, near the front of the series in the holotype, measures 5 mm and an estimated 10 mm. The premaxillary teeth are also stouter in the Cowdenbeath skull but were probably not significantly longer.

The dentary dentition is very different from the upper marginal one, resembling that of loxommatids, or at least *Megalocephalus* (Beaumont 1977), in having larger tusk-like teeth alternating with series of small teeth like those of the maxillary. The total tooth count, estimated from '*Macromerium*', the Cowdenbeath skull and the I.G.S. ramus, is about 45, close to the total upper jaw marginal count. However, while the small teeth are of comparable length to the maxillary teeth, though usually stouter, the dentary tusks are very considerably larger. All four jaw specimens show a massive parasymphysial tusk with a crown length between 15 and 18 mm (incomplete in the Cowdenbeath jaw) and a basal diameter of 8 or 9 mm. In each specimen the tusk is preceded by a single tooth, but it is possible to see the extreme anterior dentition of the right dentary as well as the left in the Cowdenbeath skull and here there appear to have been two tooth sites. On the left the tusk is succeeded by a large replacement pit. The next tusk posteriorly lies at between 30 and 40 mm behind the parasymphysial one in all the jaw specimens with six or seven tooth sites between.

This next tusk is the first of a group of three large teeth in the Cowdenbeath skull. The last of these is separated by 35 mm from the next, solitary, tusk. The latter, however was probably the middle one of a group of three. Beyond that the distinction between tusks and teeth is less clear cut. The pattern in the restoration is taken from the Cowdenbeath left ramus.

One important feature of the dentary tusks should be noted. Distally they bear anterior and posterior keels of the type that Beaumont describes as characteristic of loxommatids. These are most sharply defined in the '*Macromerium*' tusks and those of the I.G.S. anterior jaw specimen. This, together with the distribution of the tusks, was the principal reason for attributing '*Macromerium*' to the Lower Carboniferous loxommatid *Loxomma allmanni* (Panchen 1973). The coronoid dentition, comprising two teeth on the anterior coronoid and two on the middle coronoid, is described in the previous section (on the lower jaw).

The palatal dentition of *Crassigyrinus* is reconstructed from the holotype, the Cowdenbeath skull, the Gilmerton palate and, by inference, from the I.G.S. jaw ramus. It is not known whether there were any vomerine teeth in *Crassigyrinus*. Virtually none of the vomer is visible in the Cowdenbeath skull and no trace of teeth can be found on the disrupted bone in the vomerine region of the palatal specimen. Preservation however is too poor to be able to assert their absence. This is unfortunate as toothless vomers are a diagnostic character of embolomerous anthracosaurs (Panchen 1975). However, the considerable dentition of the other paired lateral bones of the palate, the palatines and the ectopterygoids, can be reconstructed in some detail, although possibly not completely.

The dentition of the palatines consists on each side of two large tusks and a number of smaller teeth. The anterior tusk, lying just behind the choana, is present on the morphological left of the Cowdenbeath skull and is complete and in its proper orientation. It has a basal diameter of 10 mm buccolingually and 9 mm anteroposteriorly. The crown height is 25 mm but the tusk appears longer as the surrounding bone socket projects beyond the general level of the palatine so that the tusk (as seen from below) is raised on an eminence. The socket is also somewhat eroded around the root and posteromesially is separated from the root so that overall another apparent 10 mm is added to the crown height. The crown is fairly uniformly tapered towards the tip and is quite strongly recurved so that the tip points posteromesially. The tusk is not lanceolate like the dentary tusks and has a circular or subcircular section throughout.

The second tusk, also presumed to be on the palatine for reasons given below, is visible and almost complete in the holotype, but only in side view projecting below the maxillary. It is also present *in situ* on the left in the Cowdenbeath skull but is compressed sideways and largely concealed so that only part of the root is visible (see section on the palate, above). It is also covered by a fragment of bone bearing two small teeth as noted in the description of the palate. Both tusks are present on both sides, although severely eroded, on the Gilmerton palate. There is no sign in any specimen of a second tusk, or replacement pit accompanying any of the palatine tusks, as it does in many labyrinthodonts including the loxommatids and anthracosaurs.

The distribution of small teeth on the palatine is more difficult to reconstruct. It has already been noted that a pair of small teeth (each diameter *ca.* 4 mm and height *ca.* 9 mm) is situated anteromesially to the anterior palatine tusk and close to the choanal margin. The similar pair covering the site of the second tusk may have been similarly related to it. However there is also a solitary tooth *in situ* between the tusks but mesial to them in the same specimen. Several palatine teeth are visible on the Gilmerton palate. On the left a solitary tooth is present *in situ* directly mesial to the anterior tusk and within 2 cm of the midline. On the same side a pair of teeth correspond in position to the solitary one between but mesial to the tusks in the Cowdenbeath skull. On the right of the Gilmerton palate there is one tooth in each case apparently occupying the corresponding sites to the ones on the left. However, the specimen has suffered gross distortion such that the originally transverse planes connecting each of the tusks of a bilateral pair are no longer perpendicular to the midline; those tusks on the left being further back than their opposite numbers. Finally, on the right, there are three palatine teeth, spaced as shown in the restoration, following the posterior palatine tusk.

The ectopterygoid dentition is visible only on the Gilmerton palate. On the left the first tusk is almost complete and is flattened so that it now points backwards. Part of the eroded second tusk is visible mesial to it. Behind these, however, no more ectopterygoid is preserved, but the complete dentition, although badly eroded, is preserved on the right. It consists of three large teeth, the first two of which are comparable to the palatine tusks in size and the third a little smaller, followed by at least seven teeth similar in size to the maxillary ones they parallel. This arrangement is similar to that found in embolomeres (unlike the palatine dentition) and represents an apparently more primitive condition than the isolated 'tusk pair' (tooth and replacement pit) found in loxommatids. It thus seems fairly certain that the palatine–ectopterygoid suture was situated immediately in front of the first tusk.

However, the occlusion of upper and lower dentitions in *Crassigyrinus* is more reminiscent of that of the loxommatids in which there are peaks in the lower dentition represented by the dentary tusks. Also in the upper dentition there are three peaks, represented in *Megalocephalus* by one vomerine, one palatine and one ectopterygoid tusk, and in *Crassigyrinus* by two palatine tusks and the ectopterygoid group. However, in *Crassigyrinus* there is not the clear occlusal alternation of upper and lower tusks described by Beaumont in the loxommatid.

It has already been pointed out that a series of fossae, situated in the dentary mesial to the tooth row, received the tips of the palatal tusks when the jaw was closed. Apart from the parasymphysial tusk replacing pit, there were five of these, whose position is seen in the mesial restoration of the lower jaw. The first corresponds in position to the choana and may have allowed a freer circulation of inspired air when the jaw was closed. The second is correctly placed to receive the anterior palatine tusk, the third the posterior one. The fourth long fossa receives the three ectopterygoid tusks, whose presence was predicted from the fossa before they were recognized in the Gilmerton palate, a conclusion corroborating its identity. It is improbable that the very small fifth fossa, seen near the adductor chamber in the I.G.S. jaw, received a tooth or tusk.

The internal histological structure of the teeth of early amphibia appears to be of considerable significance. Schultze (1969, 1970) was able to show a morphocline in tooth structure from the condition seen in some osteolepiform fish ('polyplocodont') through to that seen in advanced temnospondyl amphibians ('labyrinthodont' s.s.). The significant features are best seen in large palatal tusks sectioned transversely at or near the junction of root and crown. Among osteolepiforms with polyplocodont teeth the primitive condition is represented by *Eusthenopteron* and *Strepsodus*. In these genera the characteristic folding of dentine into the open pulp cavity is very irregular and at root level the surrounding 'bone of attachment' extends inward radially to the ends of the folds and their branches. A second, more advanced, group is represented by the fish *Panderichthys* in which the axis of each fold is represented by primary dentine and there is little or no incursion of bone radially into the root.

However, in *Panderichthys* the primary radial infoldings are of zigzag form at alveolar level and most of the angles bear short side branches. The condition of *Ichthyostega* is almost identical and short side branches are retained in the tusks of the loxommatid *Megalocephalus* (figure 13*b*). (All the loxommatid teeth located by Schultze were *Megalocephalus*, not *Megalocephalus* and *Loxomma*, but Beaumont (1977) reports similar teeth in the other genera of the Loxommatidae.)

All these teeth are characterized by Schultze as polyplocont. Later temnospondyls (edopoids,

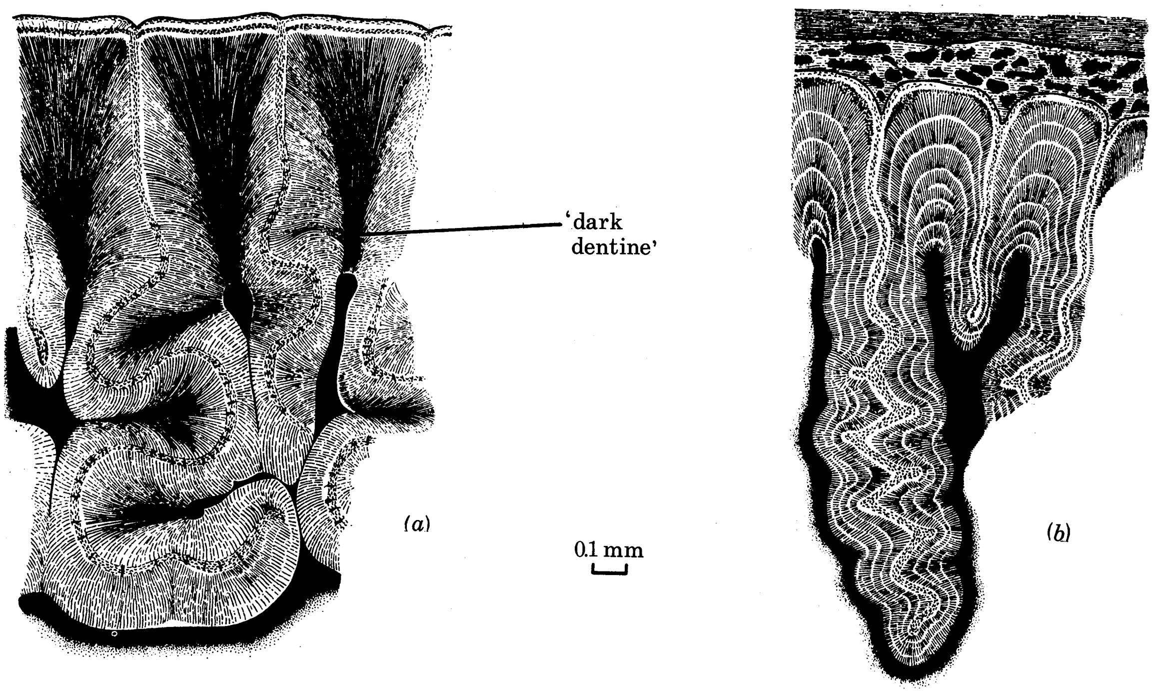


Figure 13. Tusks in transverse section to show infolded primary and secondary dentine. From Schultze 1969. (*a*) *Eogyrinus attheyi* Watson (note 'dark dentine') (after Atthey 1876). (*b*) *Megalocephalus pachycephalus* (Barkas) (after Embleton & Atthey 1874).

trimerorhachoids, eryopoids) represent stages towards the labyrinthodont (s.s.) condition with loss of the side branches. *Kotlassia* and *Seymouria* also appear to be at an intermediate stage. The fully labyrinthodont stage, with total loss of side branches, is reached in most capitosaurs (*Benthosuchus*, Bystrow 1938) and those trematosaurs studied. It is seen at its most advanced in the tusks of *Mastodonsaurus*, in which almost all the pulp cavity is occluded by branch-free but intricately folded dentine with its surrounding secondary dentine (Schultze 1969, figure 17).

It is a notable and surprising fact that this advanced labyrinthodont condition has also been reached in the Embolomeri. It was first illustrated in *Eogyrinus* by Atthey (1876, plate XI, as '*Anthracosaurus russelli*') in contrast to *Megalocephalus* (Embleton & Atthey 1874, plate VII, as '*Loxomma allmanni*'): both excellent sets of drawings were executed by William Dinning. The condition in *Anthracosaurus russelli* (Panchen 1977*b*) and in *Pholiderpeton scutigerum* is similar to that in *Eogyrinus* and rather poor sections (of maxillary teeth only) of *Archeria* available to me suggest but do not confirm that this is also the case within the third family of embolomeres.

The teeth of *Eogyrinus* are without side branches of the primary dentine and have a primary dentine pattern almost as meandering as in *Mastodonsaurus* although the occlusion of the pulp cavity is not so extreme (figure 13*a*). However, another feature is characteristic of, but not unique to the teeth of embolomeres: it was first noted and described by Atthey. Between each successive pair of radial infoldings of primary dentine ('zentrale globuläre Schicht' of Bystrow, 'Globulärzone' of Schultze) there is a wedge-shaped zone of 'dark dentine' with densely packed tubules oriented radially. This is clearly separated from the secondary dentine surrounding the primary folds ('light dentine') with sparser tubules directed towards the primary dentine of the fold. In *Anthracosaurus russelli* the same pattern is evident, but no doubt because of the mode of preservation, the colour pattern is reversed (Panchen 1977*b*) with the 'dark dentine' appearing light orange and the 'light dentine' dark brown. In both species the distinction is clearly visible in broken teeth with the naked eye, but in similarly preserved *Megalocephalus* teeth it is not apparent.

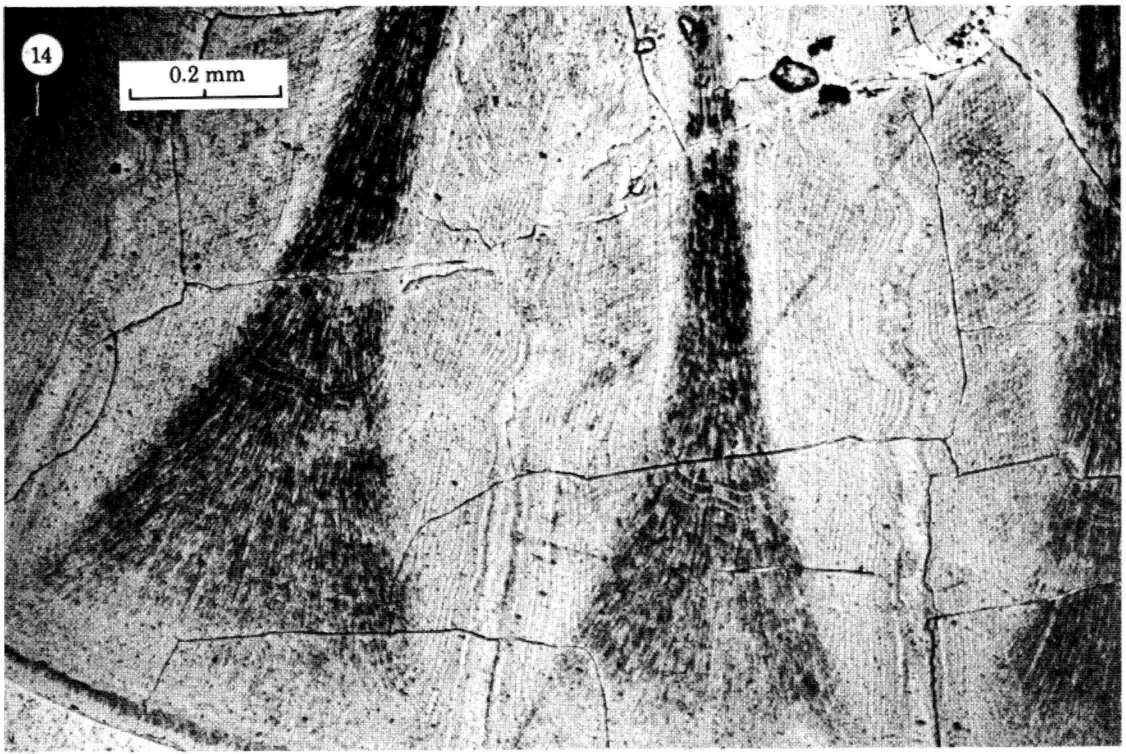
In *Crassigyrinus* the left anterior palatine tusk of the Cowdenbeath skull was cleanly broken at several levels and clearly showed the embolomere condition. It was not, however, possible to section it at alveolar level without damaging the adjacent mandible. It was possible to section the left posterior palatine tusk of the Gilmerton palate. To the naked eye its histology appears identical to that of the Cowdenbeath tusk (figures 14 and 15, plate 5) (thus further corroborating its identity) and closely similar to that of *Eogyrinus*. The best section is taken just above the root–crown junction. None of the folds of primary dentine shows a side branch although the folding is less tortuous than that of the *tusks* of *Eogyrinus*. However, the 'dark dentine' area between each fold is as conspicuously developed as in *Eogyrinus* (with the colours reversed as in *Anthracosaurus* in reflected light, but not in transmitted light), and under a high power microscope the pattern of tubules is seen to be identical. It is also noteworthy that the growth-lines in the secondary dentine, representing layers added as the tooth matures (Bystrow 1938), are much less conspicuous in *Crassigyrinus* and *Eogyrinus* than in *Megalocephalus*. This distinction is accurately represented in Dinning's drawings (figure 13). So strong is the resemblance between the tusks of *Crassigyrinus* and those of *Eogyrinus* and *Anthracosaurus* that given sections of the former alone, I would have unhesitatingly identified them as those of an embolomere. It seems therefore that the state of the tooth histology is a shared derived character uniting Palaeostegalia (*Crassigyrinus*) and embolomerous anthracosaurs.

However, its distribution in other anthracosaurs, notably *Eoherpeton*, *Proterogyrinus*, *Gephyrostegus* and seymouriamorphs (other than *Kotlassia* and *Seymouria*) is not known. A further note of warning must be sounded: great care must be exercised in comparing the tooth histology of one 'labyrinthodont' species with another. In a single tooth the pattern seen in transverse section varies strikingly from the tip of the crown to the root (for example, Atthey 1876; Schultze 1969) and the side branches characteristic of polyplocont teeth only appear near or in the root in most teeth and tusks. Then there is a difference, apparently related only to size, between the complexity of the tusks and the relative simplicity of marginal teeth. Very small teeth often show no labyrinthodont (s.l.) pattern at all: hence the non-labyrinthodont status of most, but not all microsaurs (Vaughn 1972). Furthermore individual teeth obviously varied with their individual age as secondary dentine was laid down in successive layers (Bystrow 1938).

POSTCRANIAL SKELETON

Axial skeleton

The only known specimens of the vertebrae and ribs of *Crassigyrinus* are those preserved in the Cowdenbeath skeleton. Because the postcranial skeleton is exposed from below, only the centra of the vertebrae together with a number of ribs were apparent after Mr Wood's initial development. A total of 31 centra were exposed, mostly in ventral view with a few appearing in end view. They were preserved more or less in linear order from a point very little behind the skull right to the back of the specimen. Most of the ribs were also preserved near the vertebral axis so that post-mortem disruption of the axial skeleton had not been too severe. Approximately



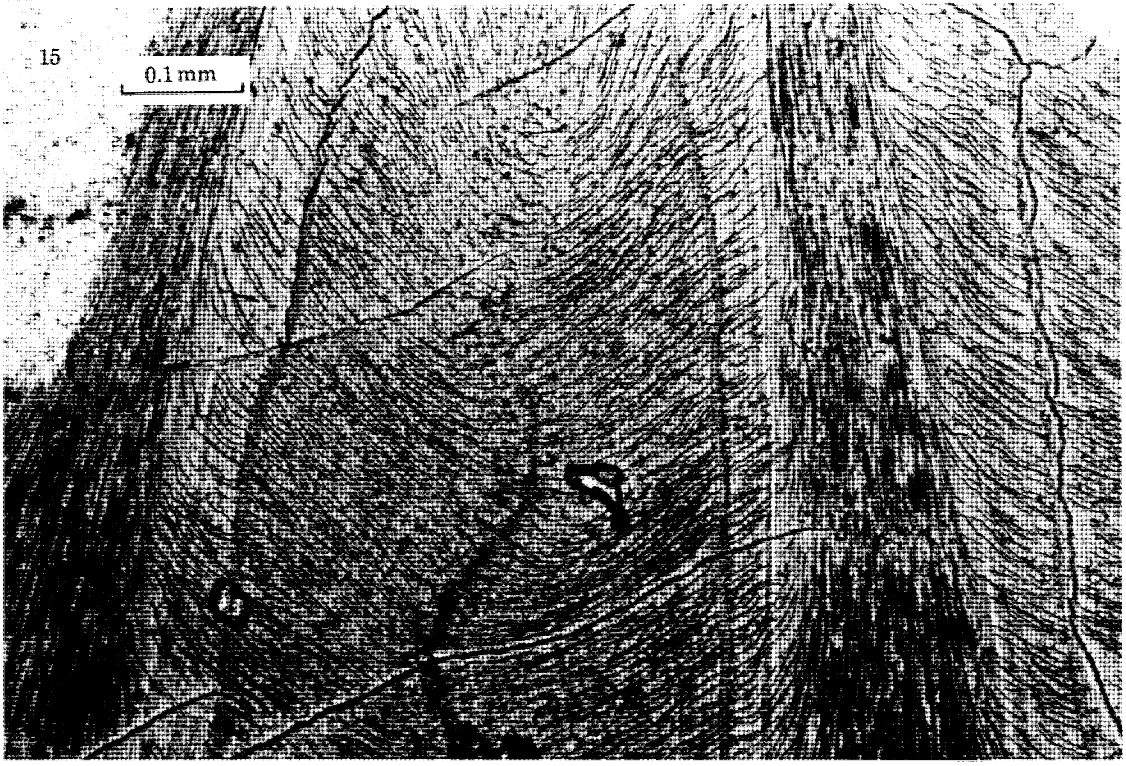


FIGURE 14. *Crassigyrinus scoticus* Watson, T.S. at base of palatine tusk of B.M.N.H., R 30532, to show infolded primary with secondary dentine separated by 'dark dentine'. Magn. × 100.

FIGURE 15. *Crassigyrinus scoticus* Watson, T.S. palatine tusk as above (figure 14), to show dentine tubules. Magn. × 160.

35 ribs were apparent when allowance was made for incompletely exposed, broken or fragmentary specimens (figure 16).

Because the numbers of individual centra and ribs were similar it was suggested by Dr Smithson (in Panchen 1980) that the vertebrae were diplospondylous; that is, that the number of segments represented was half the number of centra or ribs and thus between 15 and 18. The suggestion appeared to be corroborated by my removal of two adjacent centra (numbers 15 and 16). The difference between them was rather small, but I tentatively suggested that one was an intercentrum and the other a pleurocentrum and thus that they represented the anterior and posterior central elements respectively of a single vertebra.

Several more centra have now been removed (figure 17*a*–*b*) and all are of the same general type. Also in the process of their removal parts of other ribs have been encountered: for this and other reasons noted below I no longer accept my original interpretation of the *Crassigyrinus* vertebra as diplospondylous.

Apart from their inherent interest another reason for removing more centra was to uncover specimens of the neural arches of *Crassigyrinus*. None of the latter was originally recognized although at least three were in fact exposed but not completely cleaned during Mr Wood's initial development. Other specimens are now developed out and cleaned.

All the recognized centra of *Crassigyrinus* are of similar shape, but, within the single skeleton, they differ quite remarkably in size. All are half-hoops in anterior or posterior view and more or less wedge-shaped in lateral view with the apex of the wedge directed dorsally and the greatest antero-posterior length ventrally. Unless there was a considerable quantity of internal cartilage, it is clear that the notochord of *Crassigyrinus* was very little constricted by the centra, which are mere hollow shells that extended only about half way around the circumference of the notochord. The external surface of each is concave from front to back and finished with periosteal bone round the whole circumference, while the internal surface, which is continuous with the anterior and posterior surface, is cartilage-finished. All the developed specimens show what are presumably small neural arch facets, as more or less well defined either anteriorly or posteriorly facing hollows on each side of the apex.

The difference described between centrum 15 ('intercentrum') and centrum 16 ('pleurocentrum') was that in the former the apex in side view is half way between the back and front, while the latter has a vertical 'posterior' rim right up to the apex, while the 'anterior' rim with the facets on each side slopes back to meet it. However, the other specimens now developed out show intermediate conditions. This is more emphatically the case because of the remarkable irregularity of the centra. Reasonably well-preserved specimens are bilaterally asymmetrical with respect to length and shape and are generally much more like the centra of 'crossopterygian' fish than the more substantial and more regular centra of tetrapods. Similarly the periosteal surface is variable between the two sides of a single centrum as it is between centra, in terms of ridges, hollows and patterns of nutrient foramina.

Regional variation is strongly marked in two particulars, size and degree of co-ossification of bilateral halves. The most anterior specimen lay 45 mm behind a line joining the two jaw angles of the skull and approximately the same distance obliquely in front of the preserved position of the detached basioccipital (figure 16). It is not improbable that it is the atlas centrum (figure 17*a*). It is quite remarkably small and is both well preserved and undistorted. Because this is so it is clear that it occupied considerably less than half the circumference of the notochord. The centrum has a height of less than 12 mm but represents an arc of a circle of approximately 26 mm diameter. The length of the centrum reaches a maximum of 8 mm. Both in ventral and end view there is a marked constriction in the ventral midline suggesting the recent ossification of bilateral halves. In this, as in its overall shape, it strikingly resembles the anterior intercentra of the osteolepiform fish *Eusthenopteron* and *Osteolepis* (Andrews & Westoll 1970*a*, *b*). It is somewhat less wide than the corresponding condylar region of the basioccipital, but the latter may be slightly flattened and the two could well have articulated together.

Subsequent centra increase fairly regularly in length, height and, where visible in extension round the notochordal circumference, towards the back of the specimen. The overall circumference itself also increases backwards (figure 18). Three relatively enormous centra are preserved in close articulation near the back of the specimen (numbers 25–27: figure 17*d*). Each has an overall length a little over twice that of number 1 and a diameter of approximately 35 mm. Thus the whole axial diameter increased steadily as far as the skeleton is preserved, as in fish such as osteolepiforms and also notably in the extant coelacanth *Latimeria* (Andrews 1977). There is also no suggestion of division into bilateral halves in the posterior centra.

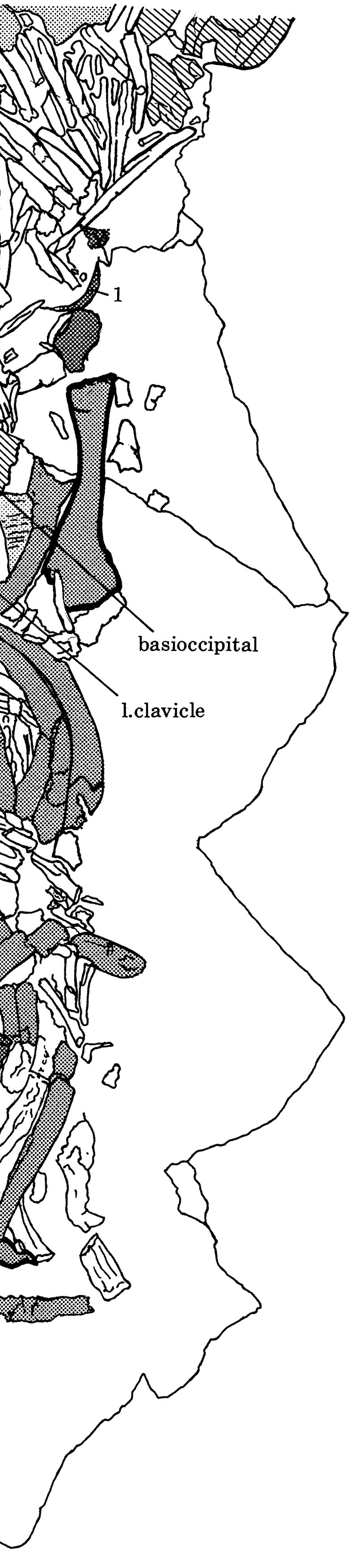
After number 1 the next centra to be removed and completely cleaned form a sequence including the two first removed (numbers 14–17). All four have well-developed 'neural arch' facets as elongate elliptical hollows about 10 mm in length facing upwards and outwards as well as along the axis. Numbers 14 and 17 are strongly constricted in the midline in ventral view (figure 17*b*, *c*), the other two less so, but all four are indented on the inner surface along the midline, again suggesting late co-ossification of two halves. Unlike number 16, originally identified as a pleurocentrum, the other three all correspond in lateral view to the form considered to be that of an intercentrum, with both anterior and posterior edges converging to an apex. However, number 14 approximates more to the 'pleurocentrum' shape and it could be claimed that they constitute a series of alternating pleurocentra and intercentra with their assigned numbers representing the correct sequence. However, the asymmetry of the individual specimens and the variation between them makes this rather unconvincing.

The neural arches of *Crassigyrinus* are remarkable for their primitive or degenerate condition. All those visible occur as separate bilateral halves with no sign of suture or fusion in the middle. They lack clear zygapophyses of tetrapod type and they are very small for the size of the animal. None has been found in natural articulation with a centrum and in the absence of clearly defined matching articular facets on each it is not clear precisely what their mutual orientation was.

Three incompletely preserved ossifications closely associated with the first centrum may represent the arches of the atlas–axis complex. The first and most complete is a half neural arch, apparently from the left (figure 17*e*). Like the other preserved neural arches it is a thin, leaf-like structure finished in smooth periosteal bone externally but cartilage-finished on its mesial, internal, surface. Ventrally there is an inclined and somewhat laterally facing facet which may correspond to the transverse process. Anteriorly (?) the periosteal bone extends round to face forwards for the upper two thirds of the arch. Immediately below this finished surface there is an anteriorly facing facet which, if the specimen is correctly identified, presumably articulated with a pro-atlas. Posteriorly the arch extends back as a rounded projection in side view which presumably overlapped the axis arch as in the primitive anthracosaur *Proterogyrinus* (Holmes 1984) and later tetrapods (figure 18*a*). Two small but much more massive bones may be interpreted as the halves of the axis arch and at least appear to form a bilateral pair: the more complete is illustrated in figure 17*f*. It has an inturned rim of finished bone presumably forming the anterior surface of the neural spine, an unfinished

FIGURE 16. *Crassigyrinus scoticus* Watson, plan of Cowdenbeath skeleton as origi
stipple-appendicular skeleton; medium stipple-ribs; dark stipple-centra an
figured ribs in heavy outline. Rectangle indicates patch of scales in figure

on as originally exposed in ventral view (for rest of skull see figure 4). Oblique hatching-skull bones; light centra and neural arches; solid black-individual scales in figure 20 (other scales blank); centra numbered; in figure 20. n.a., Separated neural arch in figure 17.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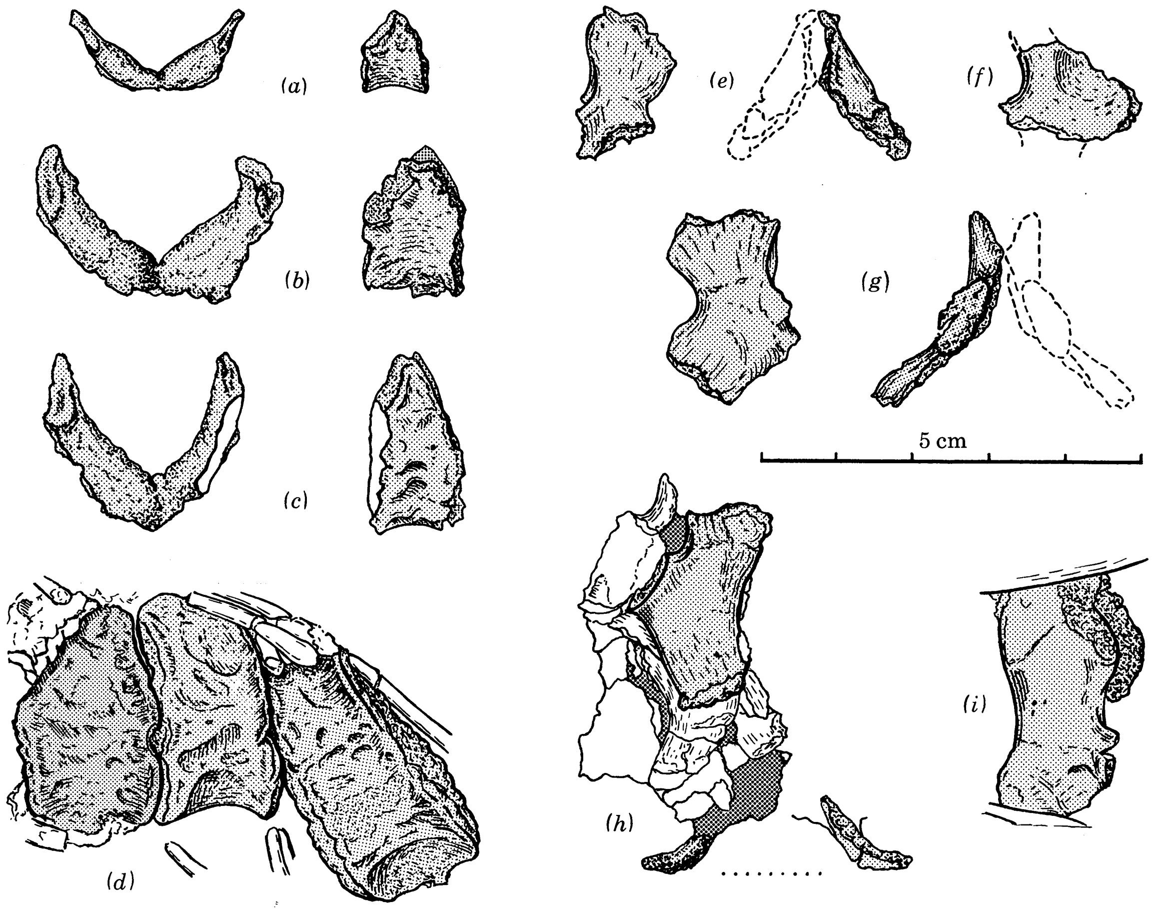

FIGURE 17. *Crassigyrinus scoticus* Watson, trunk vertebrae. Natural size. (*a*)–(*c*) Centra in (?) posterior and (?) right lateral view: (*a*), number 1 (? atlas); (*b*) number 14; (*c*) number 17; (*d*) centra numbers 25–27, ventral view as preserved; (*e*)–(*i*) neural arches; (*e*) (?) atlas arch, left lateral and anterior; (*f*) (?) axis arch, left lateral; (*g*) number 14, right lateral and anterior; (*h*) neural arches associated with centrum 17 (stipple: best exposed arch) and (?) pleurocentrum from obverse; (*i*) separated neural arch, right lateral (see figure 16).

mesial surface and a massive, (?) backwardly projecting process apparently corresponding to those of the presumed atlas arch, but its identity and orientation are both very doubtful. If my interpretation of all these supposed neural arch elements is correct they are remarkable, as is the first centrum, for their small size. The cranio-cervical joint of *Crassigyrinus* could only have been immobile as in most fish, with a large notochordal contribution and critical bracing by the dermal pectoral girdle and its associated musculature.

Several neural arch halves are associated with the extracted sequence of centra, numbers 14–17. Both sides of a neural arch, one very incomplete, are associated with number 14, and a complex of several neural arch halves are compressed together with number 17. The more complete half arch from number 14 (figure 17*g*) is somewhat similar to the (?) atlas arch, being a thin, leaf-like piece of bone, cartilage-finished on its mesial surface. Its dorsoventral orientation is not quite certain. The one I favour is that the ramus, having an inturned anterior edge of finished bone near its apex, is the neural spine as in the atlas arch and the other, a thin, somewhat backwardly directed, transverse process. The specimen is thus a right half arch.

The dorsal and ventral rami meet at a point that is the apex of an anteriorly directed process representing the prezygapophysis. Above the apex, between it and the inturned anterior edge, is a somewhat damaged region of the edge, which appears to represent a cartilage-finished zygapophysial facet facing anterodorsally. However, this is unlike the stoutly buttressed facet of a typical tetrapod vertebra and there is no sign of a postzygapophysis at all. The configuration is essentially that seen in the neural arches of *Osteolepis* (Andrews & Westoll 1970*b*). There is a curved embayment of the posterior edge of the arch corresponding to the prezygapophysial process. The antero-posterior length of the arch at any vertical level is approximately the same as the overall length of the corresponding centrum, again suggesting that the vertebrae of *Crassigyrinus* were monospondylous.

It is not clear whether there was a bone-to-bone contact between neural arch and centrum. It is possible to fit the antero-ventral corner of the transverse process into the backwardly facing centrum facet so that the inner surface of the neural spine reaches the midline, but this leaves the ventral half of the facet unoccupied. It seems more probable that the correct orientation is that shown by Andrews & Westoll (1970*a*, text-figure 20) for the mid-trunk vertebrae of *Eusthenopteron*, with the antero-ventral corner of the transverse process situated postero-ventral to, and slightly separated from, the apex of the centrum (figure 18).

The half arches associated with centrum 17 form a tangled and impacted mass which cannot be separated without destroying the individual specimens (figure 17*h*). Dorsally, however, the external surfaces of a right and a left half arches are exposed and virtually complete. Another left arch, with its mesial, cartilage-finished surface exposed, is impacted between them. Below these three is an inextricable mass of apparent arch fragments. The only point of interest here is a small banana-shaped piece of bone with a periosteal finish round its outside curve. It is probably a fragment of the apex of a centrum, but it could just possibly be a pleurocentrum to the intercentrum represented by all the recognized centra, so that *Crassigyrinus* would then have rhachitomous vertebrae.

The exposed left half arch from this whole specimen is in general similar to the right arch with number 14. However, it is of interest in that the prezygapophysis is much better preserved. Its outer rim and the outer half of the articular facet itself are visible, showing that the facet is elliptical with a strongly defined laterally projecting rim. There is still no sign of a correspondingly postzygapophysial facet.

The external surface of four neural arch specimens are exposed near one another on the skeletal block. They are situated a little way from centra 19–22 (figure 16). The most complete half arch (figure 17*i*) has a shorter prezygapophysis than the best number 17 arch but a relatively long neural spine with a convex dorsal edge, which is not completely exposed.

Thus in their level of organization, degree of ossification and general appearance the vertebrae of *Crassigyrinus* are like those of osteolepiform fish rather than those of primitive tetrapods. It now seems certain that there is a single crescentic centrum to each vertebra. This is the intercentrum of Andrews & Westoll (1970*a*, *b*: 'ventral vertebral arch' of Jarvik 1952, 1980). Apart from the doubtful fragment noted above no pleurocentrum ('interdorsal') of the type seen in *Eusthenopteron* has been detected let alone the large inverted wedges of *Osteolepis* and early temnospondyls. Similarly the neural arches of *Crassigyrinus* are small, fragile and poorly ossified and as far as is known always present as bilateral halves. Postzygapophyses, formerly thought of (with prezygapophyses) as an autapomorphous feature of tetrapods, appear to be absent. However, while the vertebrae of *Crassigyrinus* are osteolepiform-like the ribs are not.

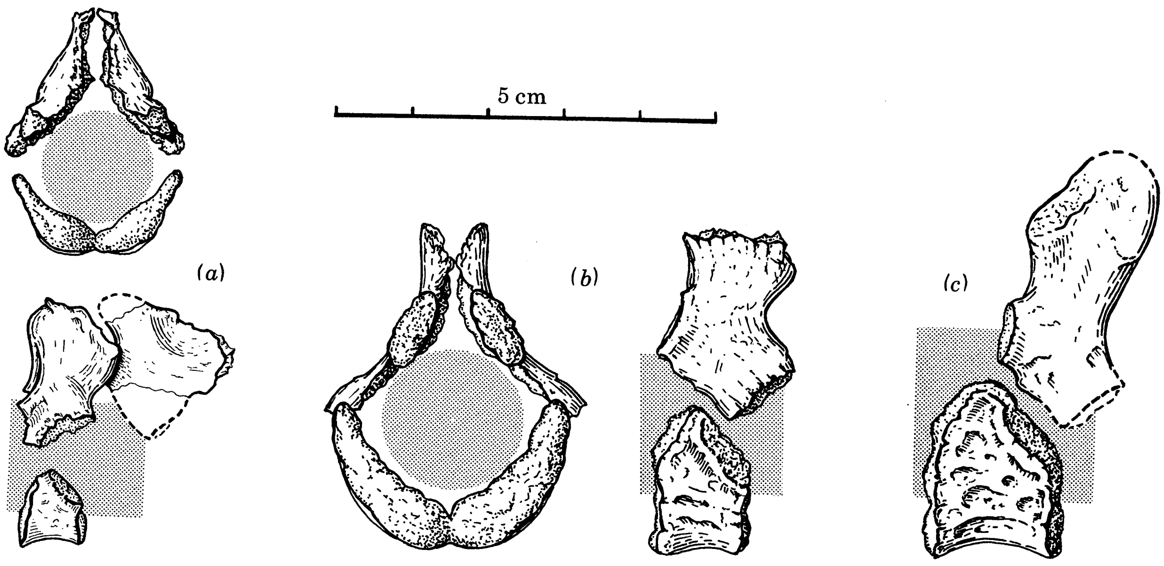

FIGURE 18. *Crassigyrinus scoticus* Watson, vertebrae reconstructed from Cowdenbeath specimen. Natural size. (*a*) Atlas, anterior and left lateral with axis arch; (*b*) number 14, anterior and left lateral; (*c*) posterior trunk, based on centra numbers 25–27 and separated neural arch (figure 17*i*). Stipple-minimum notochordal diameter.

The majority of trunk ribs exposed conform to a single pattern (figure 19). They are well-ossified hoops of compact bone whose curvature must have followed that of the body. The shaft is circular or elliptical in cross section with, occasionally, a longitudinal groove giving a C-shaped section. Typically they are ornamented with longitudinal striations. In all these respects they are closely similar to the ribs of anthracosaurs such as *Eogyrinus* (Panchen 1966), *Pteroplax* (Boyd 1980), and *Eoherpeton* (Smithson 1980*a*, 1984). This anthracosaur type of rib contrasts with that seen in many early temnospondyls such as *Eryops* (Moulton 1974), *Pholidogaster* (Romer 1964), *Greererpeton* (Smithson 1984) and *Neldasaurus* (Chase 1965). In all these forms the rib shaft has at least a narrow backwardly directed blade, which may be developed as a strong uncinate process (*Eryops*). An extreme condition is shown by *Ichthyostega* (Jarvik 1980) in which there is very considerable overlap between successive rib blades. Bladed ribs also occur in the early but aberrent adelogyrinids (Brough & Brough 1967).

I have suggested (Panchen 1966, 1967*a*) that the temnospondyl type of rib, particularly in large terrestrial forms such as *Eryops*, might contribute to axial support in compensation for the inherent weakness of the rhachitomous vertebra. Anthracosaurs (and early reptiles) on the other hand had an axis, with stout pleurocentra firmly sutured or fused to the neural arches, in which vertebrae contributed much more to the girder function.

However, in *Crassigyrinus* where the rib heads are visible, they are relatively feeble. The proximal end of the rib is expanded in one plane into the head but the head region is very thin and not clearly differentiated into capitulum and tuberculum. This is correlated with the thin, poorly ossified transverse processes of the neural arches and the lack of any apparent capitular facet on the centra.

Because most of the specimens are fragmented, little can be said about regional differentiation in the ribs. Three apparently complete ribs in the region of centra 18–24 each, have an overall length of approximately 11 cm measured round the curve of the shaft. Assuming a body diameter of about 15 cm, which is consistent with the size of the skull and the restored width

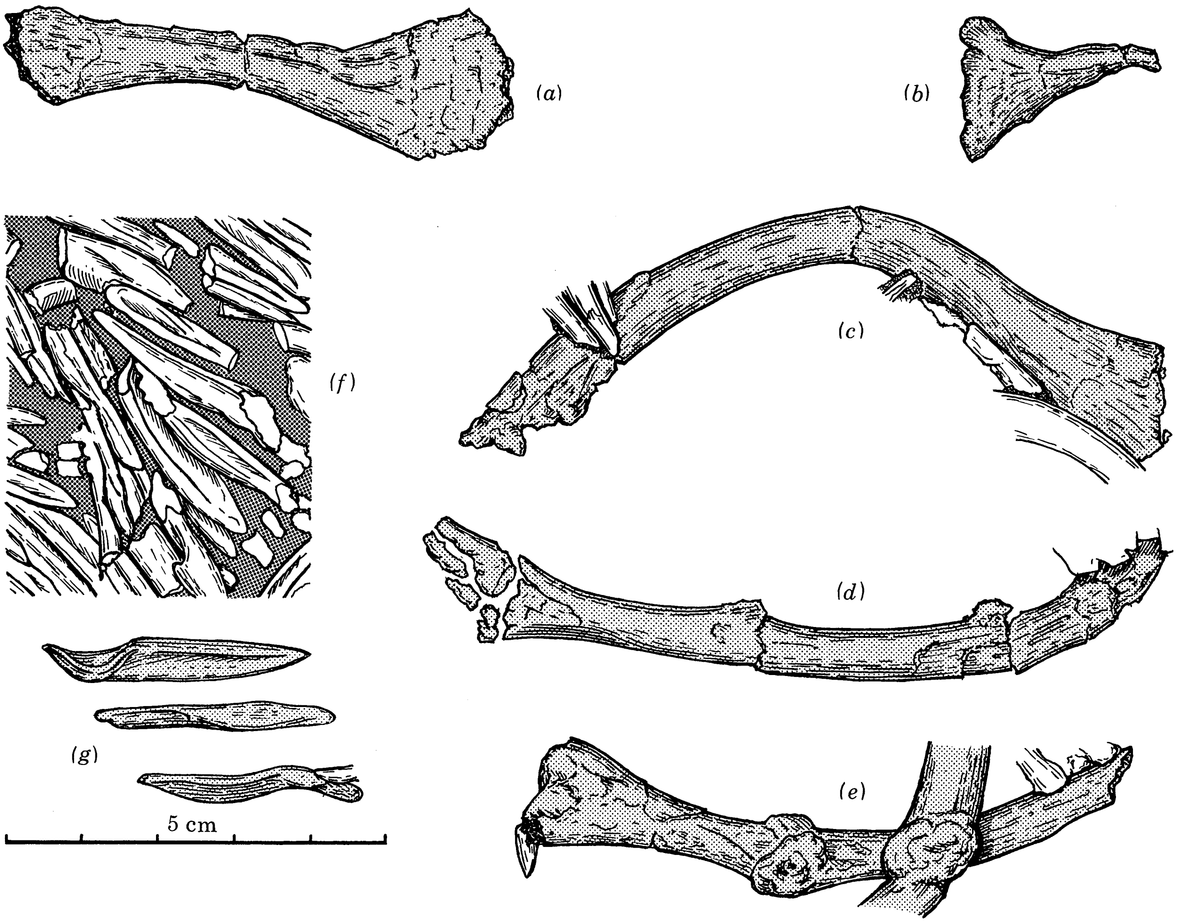

FIGURE 19. *Crassigyrinus scoticus* Watson, ribs and scales. Natural size. (*a*)–(*e*) Ribs as exposed on Cowdenbeath specimen (see figure 16): (*a*) 'thoracic'; (*b*) (?) immediately presacral; (*c*), (*d*) posterior trunk; (*e*) anterior trunk with healed fracture and detail of another; (*f*), (*g*) ventral scales as exposed (see figure 16): (*f*) patch from anterior trunk region; (*g*) individual scales.

of the pectoral girdle (see below), such ribs must have extended round the flanks well beyond the midpoint dorsoventrally. They would thus have been part of an exceptionally extensive ribcage.

Most of the other trunk ribs exposed to view appear to have been of similar size and shape to these three. It is worth noting, however, that three ribs lying between centra 9 and 11, and another adjacent to centrum 18, appear to have been fractured and subsequently healed during the life of the animal. They thus show a mass of swollen ankylosed bone at the site of the fracture in the middle of the shaft (figure 19*e*).

Only two apparent rib specimens deviate markedly from the standard pattern. One very small rib (figure 19*b*) was preserved posteriorly overlapping the ischium (figure 16). Its overall length is only 27 mm and the shaft tapers rapidly to a point from the typical wide but thin head. It is presumably an immediately presacral rib, by analogy with those of anthracosaurs. The other specimen (figure 19*a*), was preserved overlying the left clavicle and immediately adjacent to a normal rib. It is 85 mm long with a shaft that is straight in anterior view and slightly sigmoid in lateral view. The presumed head is similar to that of other ribs but distally the shaft expands into a spoon-shaped area convex on one side (? anteriorly) and concave, following the sigmoid curvature of the shaft, on the other. The specimen is almost certainly a rib, but it is just possible that it is an element of the hyobranchial skeleton. It somewhat resembles such an element figured but not described by Carroll (1980) below a skull of *Greererpeton*. If a rib it is certainly one of the modified type that underlie the pectoral girdle as seen in the axis of anthracosaurs.

The presence of the ischium (see below) associated with an apparently immediately presacral rib suggests that the whole of the trunk is represented in the Cowdenbeath specimen. Accepting that it was monospondylous it seems that only a little over 30 segments are represented. This is significantly less than the 40 or more of the embolomere *Archeria* but it is probable that a long tail was present in *Crassigyrinus*.

Appendicular skeleton

As with the axial skeleton, the appendicular remains are certainly known only from the Cowdenbeath skeleton. The interclavicle is preserved obliquely between the jaw rami of the skull, covering the posterior palatal area (figure 5). Since the completion of figures 4 and 21 (left) the remaining traces of matrix together with a few scales have been removed, so that its ventral, external surface is almost completely exposed. Both clavicles are preserved almost completely a short distance behind the skull. In each case the ventral external surface of the main body of the bone has been completely cleaned and in the case of the right clavicle the long ascending process, which dips steeply into the matrix, has been cleared to its apex. The right cleithrum is also preserved and lay adjacent to the right clavicle. There is no trace of either scapulocoracoid.

The major part of a left forelimb is associated with the Cowdenbeath skull and lay immediately to the right of the interclavicle, as seen in ventral view, situated between the bone and the back of the left jaw ramus. It consists of an almost perfect humerus, at least one epipodial and what appear to be scattered bones of the carpus and manus (figure 21). If it is indeed that of *Crassigyrinus* it is the most extraordinary feature of that bizarre animal. The humerus has been completely developed out with the airbrasive machine and is now a separate specimen, matrix-free and apparently uncrushed. Apart from the limb specimen another presumed epipodial was preserved as an isolated specimen some 7 cm behind the clavicles: it is complete and has been detached and cleaned.

The only pelvic element preserved in the Cowdenbeath skeleton is the single right ischium preserved near the back of the specimen (figure 16) adjacent to centrum number 31 as well as the presacral rib described above.

The interclavicle is of the general type characteristic of early 'labyrinthodont' amphibia. It is of rhomboidal shape as seen from below (figure 20) with lateral wings marking the back of the overlap area for the clavicle on each side. Posteriorly it tapers to a blunt spatulate termination ('parasternal process': Brough & Brough 1967). Anteriorly it is surprisingly broad, and is truncated to give a rectangular anterior end. This is somewhat asymmetrical despite apparent complete preservation with a more extensive anterior development of the clavicular overlap area on the morphological left.

The surface of the bone is irregular and swollen but not strongly ornamented, but this lack of ornament does not seem attributable to *post mortem* erosion when the flanking jaw rami have such sharply incised ornament. Nor is it attributable to careless preparation. Such ornament as there is appears to be of the anthracosaur type.

This fact, together with the shape of the interclavicle, further reinforces the apparent affinity of *Crassigyrinus* with the embolomeres, the spatulate parasternal process being particularly characteristic. The overall shape of the bone falls well within the range of variation seen in the various anthracosaur interclavicles already described (for example, Holmes 1980, figure 3).

A second interclavicle from Cowdenbeath (Newcastle Zoology Department number 1978.3.15 DZ) may conceivably also be *Crassigyrinus*, although its appearance is somewhat different from that of the first (figure 20*b*, *c*). The surface of the bone is much more regular and the whole ventral surface is rather flat. The dermal ornament is clear, relatively small, but sharply incised. It is also clearly of the anthracosaur type and comparable to that seen on the cheek region of the Cowdenbeath *Crassigyrinus* skull. Posteriorly the shape is similar to that of the first interclavicle although the parasternal process is more pointed, forming the apex of a rather more regular triangle. The width across the lateral wings is almost identical as is the length posterior to them. An area is missing anteriorly in our Newcastle specimen but it may reasonably be restored to an identical overall length. However, the anterior apex is again more pointed and lacks the rectangular overlap areas of the associated interclavicle.

The Newcastle specimen is isolated and has been completely cleaned on both surfaces by Dr Smithson. The inner, dorsal, surface is generally smooth but both anterior and posterior processes are marked by indistinct striations, with the addition of irregular longitudinal grooves at the back. The lateral wings have a markedly convex surface resulting from a transverse thickening of the bone, and the parasternal process is similarly strengthened along the midline.

This specimen may seem very different from the associated interclavicle. However, Dr Smithson assures me that there is no other Cowdenbeath amphibian to which it might belong. I suggest tentatively that it might be *Crassigyrinus*, if one assumes that the Cowdenbeath skeleton represents a mature, even elderly, individual while it represents an adolescent.

The clavicles are in general of characteristic 'labyrinthodont' shape, although the ventral ornamented body of each is relatively longer and narrower than that of other Carboniferous species. Particularly this shape stands in strong contrast to that of short expanded form of the clavicle of the primitive Mississippian anthracosaur *Proterogyrinus* (Holmes 1980). The external ornament in the *Crassigyrinus* clavicle takes the form of irregular ridges and grooves parallel to the long axis of the bone. Very characteristic is a broad, sharply defined sulcus with a more or less smooth floor paralleling the leading anterolateral edge of the body of the bone. A similar recessed area occupies the posteromesial corner and extends forward a short distance as a less distinct groove.

The dorsal surface of the clavicular body can be seen in part only on the right bone. Only the anterior end is exposed and is smooth but marked by a few parallel longitudinal grooves towards the apex.

The ascending process of the clavicle, which in the complete girdle would have buttressed the anterior edge of the scapula, is remarkably long and slender. Measured along its axis from the point of junction with the body of the bone it is some 6 cm compared with 9 cm for the length of the body from the same point. Although some breakage and distortion have occurred between the two parts of the right clavicle, the ascending process seems to have been oriented at a relatively shallow angle, about 60° to the horizontal as restored in figure 20. Like the clavicular body it is marked by a broad longitudinal groove as well as striations along the anterolateral surface, although the groove is more ill-defined.

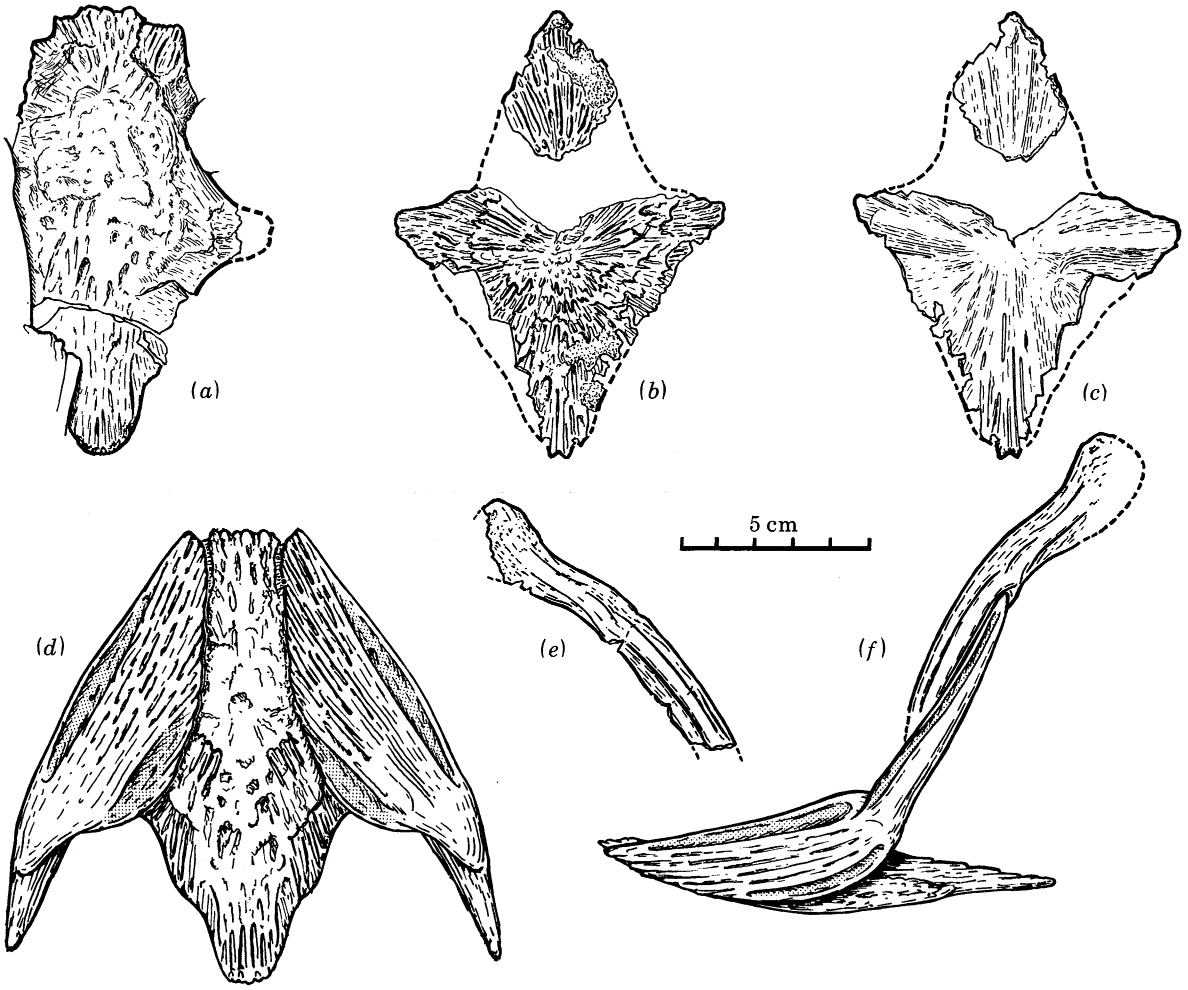

FIGURE 20. *Crassigyrinus scoticus* Watson, pectoral girdle. Half natural size. (*a*) Interclavicle of Cowdenbeath specimen as preserved, ventral; (*b*), (*c*) (? *Crassigyrinus*) University of Newcastle: 1978.3.15 DZ: interclavicle in ventral and dorsal view; (*d*) interclavicle and clavicles in articulation; (*e*) cleithrum; (*f*) whole dermal girdle restored in left lateral view.

The single right cleithrum (figure 20*e*) is closely similar to those of *Archeria* (Romer 1957) and *Proterogyrinus* (Holmes 1980). The shaft was broken with the two resulting fragments at an angle as preserved. However, after removal from the matrix and complete cleaning the two were mended and very little bone was found to be missing from the junction. The ventral tip of the shaft is missing and what was probably a small area of the dorsal plate is also lost, but otherwise the specimen is almost complete.

The shaft comprises the major part of the cleithrum. As in *Archeria* and *Proterogyrinus* it is massive, bowed forward in lateral view and is virtually straight in anterior view. In section it is elliptical with the anterior and posterior edges terminating in vertical ridges. Externally the shaft is dominated by a thick rounded ridge extending the elliptical section to a subtriangular shape, as referred to by both Romer and Holmes. The ridge arises dorsally on the lower part of the dorsal plate and extends ventrally as far as the specimen is preserved. It is not quite parallel to the whole of the shaft, being bowed forward less. Thus the well-defined pre-ridge area is wider dorsally than ventrally while the opposite is true of the postridge area. Ventrally, the postridge area, while flat, is considerably inset from the ridge with a well-marked groove at their junction. In this ventral region the area was overlapped by the clavicular spine. Mesially there is also a hollowing corresponding to the external postridge area but the rest of the shaft is smoothly rounded and faintly ornamented with longitudinal striations.

The dorsal plate, which as far as preserved is relatively much smaller than that of *Archeria* or even *Proterogyrinus*, arises smoothly by thinning of the shaft. Its convex anterior border is preserved and this intact edge extends round dorsally to the summit of the bone. Posteriorly, however, the edge is broken, although it is improbable that the intact bone extended much further in this direction. The whole dorsal plate is somewhat spoon-shaped with the concavity of its outer surface emphasized by the beginning of the external ridge.

As in *Archeria* and *Proterogyrinus* the dorsal plate almost certainly covered the exposed anterior edge of a cartilaginous dorsal extension of the scapula blade, so that the dorsal edges of both coincided. Because of the degenerate nature of the forelimb (see below) it is probable that an even larger proportion of the missing scapulocoracoid was cartilaginous than in the two anthracosaurs.

The length of the external overlap area behind the cleithral ridge suggests that clavicle and cleithrum overlapped extensively. This is shown in the attempted restoration of the whole dermal girdle (figure 20*d*, *f*). In the restoration, clavicles and interclavicle may be restored into their natural interrelations without fear of serious error, with the clavicular body extending somewhat behind the lateral wing of the interclavicle. In lateral view (figure 20*f*) the cleithrum has been added (reversed from the left). The width of the interclavicle plus clavicles, thus restored, is somewhat less than that of the skull (13 cm compared with 16 cm) to which a little should be added for the cleithra. The overall height (cleithra included) is just under 13 cm. Oriented with the restored skull this brings the top of the cleithrum to about 4 cm above the level of the jaw articulation.

The left forelimb was a wholly unexpected discovery. A group of small bones near the angle of the left jaw of the Cowdenbeath skull were thought before development to be elements of the hyobranchial skeleton (figures 4 and 21). Notably, a stapes was identified and before separation and cleaning it seemed similar to the stapes of *Greererpeton* (Smithson 1982; Smithson & Thomson 1982), *Pholiderpeton* and *Palaeoherpeton* (Clack 1983), in scale as well as form. Development however, showed it to be a beautifully preserved but minute left humerus, accompanied by the radius. Because they represent such a small limb (the overall length of the humerus is 36 mm, that of the radius 26 mm) their association with *Crassigyrinus* may well be questioned. Did this animal really have a vestigial limb of which the humerus was approximately half the length of the longer diagonal of the orbit? On balance I favour its attribution to *Crassigyrinus* for the following reasons.

(i) The humerus, described below, is much more primitive than that of any known tetrapod (apart from *Ichthyostega*) yet described.

(ii) The humeri of primitive Mississippian temnospondyls (*Greererpeton*, Holmes 1980) and anthracosaurs (*Proterogyrinus*, Holmes 1980; *Eoherpeton*, Smithson 1984; *Brukterpeton*, Boy & Bandel 1973) are now well known, but the present specimen cannot easily be assigned to either of these taxa.

(iii) There is no other amphibian in the Cowdenbeath fauna to which it can convincingly be assigned.

(iv) The poor ossification suggests an immature or degenerate humerus.

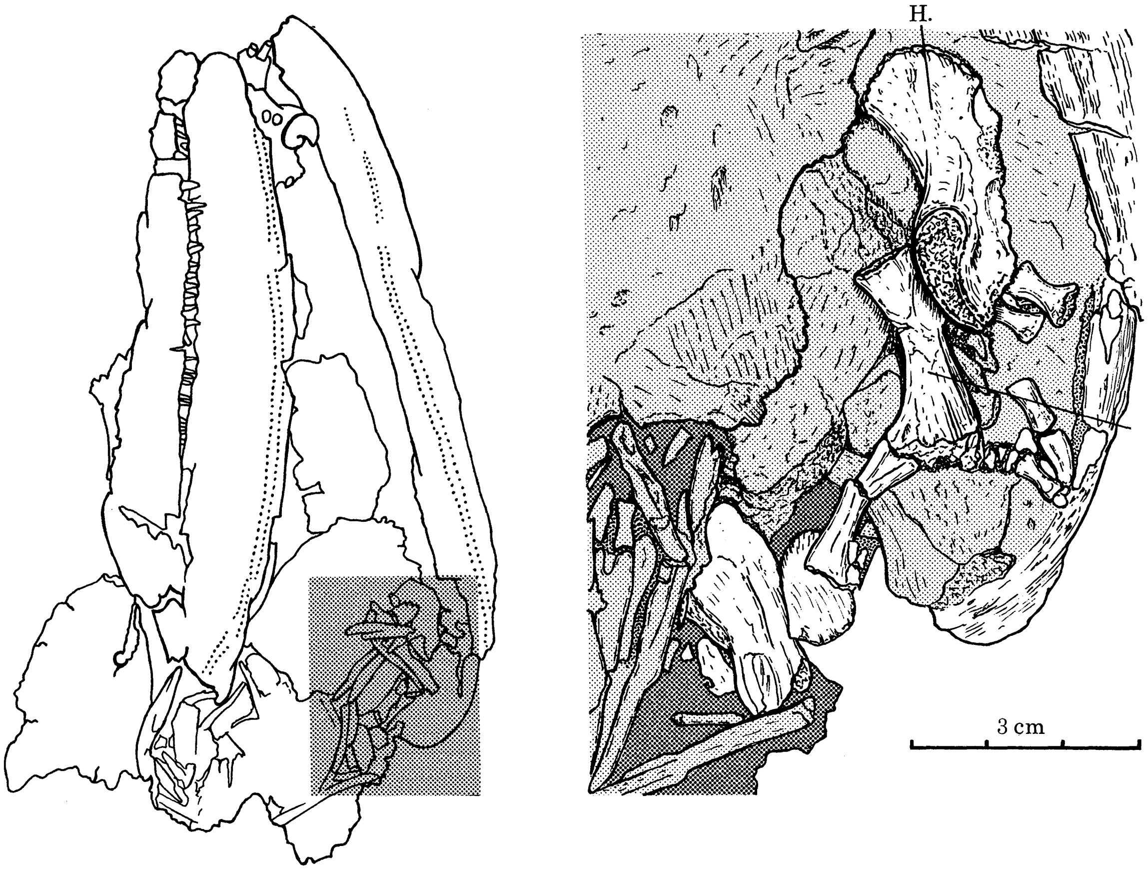

FIGURE 21. *Crassigyrinus scoticus* Watson, Cowdenbeath specimen to show preservation of fore limb. Left, skull in ventral view (before development). Stippled area figured in detail in right. Right figure: natural size (see text). H., humerus; R., radius.

The overall shape of the humerus is similar to that of *Greererpeton* and an immature *Proterogyrinus* (Holmes 1980, figure 7) and is shown in figure 22 in the six standard views introduced by Romer and used in his account of the humerus of *Archeria* (Romer 1957). It differs in dorsal and ventral view from those of *Greererpeton* and *Proterogyrinus* in that the angle that the proximal edge of the entepicondyle makes with the posterior edge proximal to it is much greater (*ca.* 140°) than in the other two (*ca.* 90°). In dorsal view in the distal plane (figure 22*e*) the ectepicondyle is well defined and very prominent and is quadrangular in section, reaching a height of 5 mm at its distal end. Its upper margin is concave in profile so that it rises proximally as well as distally, terminating proximally is a well-defined process for the latissimus dorsi at 5 mm from the caput humeri. The process has its apex broken off in the specimen.

The articular surface of the head of the humerus is, as is often the case, cartilage-finished and deeply concave between the dorsal and ventral periosteal bone on either side of it. This concave cartilage-finished surface is in continuity with one forming the anterior edge of the bone and further continuing round past the end of the ectepicondyle and the distal end of the bone. The surface then turns to face posterodistally and terminate at the proximal edge of the entepicondyle. This lack of ossification along the whole proximal, anterior, distal and posterior edge of the bone suggests its degenerate nature.

The proximal 15 mm of the unfinished anterior edge is quite thick, reaching about 7 mm.

It is then sharply constricted. The area immediately proximal to this constriction represents the deltopectoral crest. On the ventral surface immediately adjacent to the crest is a rectangular eroded area which probably represents a low but extensive tuberosity. It seems probable that this was for the brachialis muscle. The tuberosity also marks the origin of a low ridge which passes posterodistally but then curves round towards the anterior border to end below the anterior face of the ectepicondyle. This ridge has been homologized with the ventral diagonal ridge of the rhipidistian humerus (Holmes 1980).

Other areas of muscle origin and insertion may be reconstructed after Romer's account of the humerus of *Archeria* and Holmes' of that of *Proterogyrinus* (figure 23). On the proximal dorsal surface there is a strongly marked concavity anteroproximal to the latissimus dorsi insertion for the scapulohumeralis muscle. Posterior to this and separated from it by a ridge extending proximally from that insertion is another concavity, which is not however markedly rugose, for the subcoracoscapularis. On the proximal ventral surface, a large triangular posterior concavity is for the insertion of the coracobrachialis brevis musculature while anterior to it a narrow but marked sulcus above the brachialis tuber presumably marks the insertion of the supracoracoideus. A rather ill-defined tuber below the head on the posterior edge at the level of the latissimus dorsi insertion probably corresponds to Romer's subscapularis insertion.

Of the articular regions the unfinished nature of the caput humeri has already been noted. However, it should be noted that, as in *Archeria*, there is little sign of the 'screw-shaped' form corresponding to that of the scapular glenoid seen in terrestrial primitive tetrapods. The articulations for radius and ulna are not clearly defined because of the unfinished distal end. It is, however, clear that the radial articulation was not a markedly ventrally directed process as in *Proterogyrinus*, let alone a very proximal ventrally directed facet as figured by Jarvik (1980) in *Ichthyostega*. In *Crassigyrinus* it is presumably marked by the wide and deeply concave unfinished distal surface immediately below the end of the ectepicondyle. However, while the margins of this area face anterodistally they also have a slight ventral inclination and are well proximal to the distal point of the bone. The ulna articulation must have been situated between the two.

As in all early tetrapod humeri (possibly excepting *Ichthyostega*) there is some 'torsion' between the planes of the proximal and distal ends. This may be measured as the angle between the long axis of the proximal articular surface and the plane of the entepicondyle and is approximately 40°. This may be compared with 37° in *Proterogyrinus*, 30° in *Archeria* and 88° for *Eryops* (Holmes 1980).

As described so far the tiny humerus attributed to *Crassigyrinus* follows the pattern of other known primitive aquatic labyrinthodonts, such as *Greererpeton*, *Proterogyrinus* and *Archeria*. The anterior unfinished edge is attributable to its apparent status as a degenerate and vestigial bone. Like the humerus of *Greererpeton*, anthracosaurs and early reptiles it has a well-developed entepicondylar foramen which passes from the posterior dorsal surface, near the proximal end of the entepicondyle, in a ventrodistal direction to emerge rather more anteriorly in the ventral surface. Both dorsal and ventral foramina terminate grooves for the nerves and blood vessels that passed through them. Dorsally an indistinct groove lies proximal to the foramen between the planes of the posterior edge of the head and the edge of the entepicondyle. Ventrally there is a better-defined groove, running distally to the edge of the bone.

However, apart from the entepicondylar foramen ('canal b' in *Ichthyostega*: Jarvik 1980, figure 166) there are other foramina present in the *Crassigyrinus* humerus which are otherwise

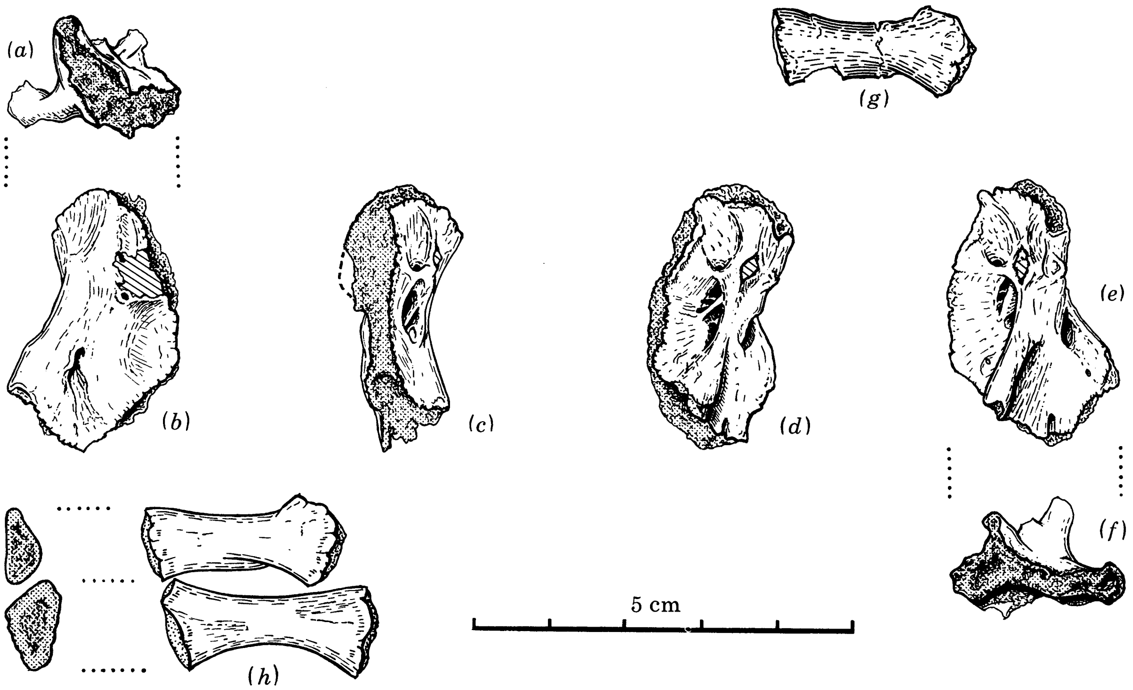

FIGURE 22. *Crassigyrinus scoticus* Watson, Cowdenbeath specimen, fore limb. Natural size. (*a*)–(*f*) Left humerus: (*a*) proximal; (*b*) in plane of distal ventral surface; (*c*) anterior; (*d*) in plane of proximal dorsal surface; (*e*) in plane of distal dorsal surface; (*f*) distal; (*g*) left ulna, extensor view; (*h*) left radius and ulna in articulation, proximal and extensor views.

represented only in *Ichthyostega* among tetrapods, but may be homologized with those in the humerus of *Eusthenopteron* (Andrews & Westoll 1970*a*). Most notable is a small foramen immediately anterior to the latissimus dorsi process in the dorsal surface. It lies at the distal end of the concavity for the scapulohumeralis muscle. Immediately distal to this foramen, and separated from it by a short bony bridge, is a large and complex foramen. This consists of an elongate concavity in front of the base of the ectepicondyle separated into two foramina by a high narrow oblique bridge of bone. The anteroproximal of the two foramina so defined has a series of ridges in its proximal wall. It also has a perforation in its proximal wall which communicates with the first foramen. The channel so formed may be homologized with the ectepicondylar foramen of *Eusthenopteron* (Andrews & Westoll 1970*a*). It corresponds to 'canal a' in *Ichthyostega*. The lower foramen in the concavity may correspond to the small foramen anterior to the distal opening of the ectepicondylar foramen of *Eusthenopteron* and rather more certainly to 'canal e' in *Ichthyostega*. It is subdivided into a series of pits and foramina some or all of which may perforate the bony surface.

On the ventral surface of the *Crassigyrinus* humerus at the anterodistal corner of the eroded brachialis tuber is a small foramen. A less certainly defined foramen is present at the anteroproximal corner. It is possible that these correspond to distal and proximal openings of Jarvik's 'canal d' in *Ichthyostega* and to a proximal pair of the series of foramina through the ventral ridge in *Eusthenopteron*. Thus only Jarvik's 'canal c' appears not to be represented. The dorsal opening of canal c in *Ichthyostega* is figured as lying just distal to the entepicondylar foramen. In the *Crassigyrinus* humerus there is a well-marked notch in the dorsal surface at the distal apex of the bone which might conceivably correspond if the distal ossification is assumed to be very incomplete.

Thus the (?) *Crassigyrinus* humerus is comparable to that of *Ichthyostega* and *Eusthenopteron* in the primitive distribution of foramina. However, in his brief description of the *Ichthyostega* humerus, Jarvik (1980, pp. 231–232) remarks on the difficulty of comparing that humerus to those of *Eusthenopteron* and *Eryops*. He thus perpetuates the curious tradition (Andrews & Westoll 1970*a*; Rackoff 1980) of using the humerus of *Eryops*, an advanced and aberrant Permian temnospondyl, to represent the primitive tetrapod condition. The humerus of *Ichthyostega* is in fact closely comparable to that of *Archeria* as was noticed in the description of the latter by Romer (1957). The comparison was elaborated by the late Professor Romer (personal communication) and it is now clear from our knowledge of *Greererpeton*, *Proterogyrinus*, the present humerus and those of other species from Cowdenbeath, that *Archeria* was close to the primitive condition seen in *Ichthyostega*. Once the misidentification of the anterior keel as 'ectepicondyle' and ectepicondyle as 'dorsal ridge' in the latter have been corrected and the loss of the primitive canals accepted the resemblance is very close. It seemed worthwhile, therefore, to interpret the comparative anatomy and musculature of the *Ichthyostega* humerus as well as the Cowdenbeath specimen in terms of the Romer–Holmes reconstruction (figure 23).

As figured by Jarvik only one feature of the *Ichthyostega* humerus is unique and anomalous. The articular surface of the radius is shown to be an ellipse on the ventral surface, entirely detached from the distal end of the bone and with its proximal end at the level of the entepicondylar foramen. It also appears to be a flat surface rather than a condyle. The ulna articulation is then restored in the position of the radial articulation of *Archeria* and *Proterogyrinus*. Thus articulated the forearm of *Ichthyostega* would have been totally immobilized relative to the humerus. It is certainly true that in many more advanced early tetrapods, notably *Eryops* and *Diadectes* (for example, Andrews & Westoll 1970*a*; text-figure 12) the radial condyle has moved onto the distal ventral surface, but its morphological position is clearly homologous with that of *Archeria*; it is a condyle, thus forming a ball-and-socket joint, and it retains its proximity to the ulna articulation. It is to be hoped that the evidence on which the reconstruction of the *Ichthyostega* humerus is based will eventually be published.

The left radius was preserved adjacent to the humerus under the Cowdenbeath *Crassigyrinus* skull and more or less in natural relation to it (figure 21). Removal from the underlying jaw region has not been attempted. Comparison with those of *Archeria* (Romer 1957, figure 4) and *Proterogyrinus* (Holmes 1980, figure 7) suggests that the dorsal (extensor) surface is uppermost in palatal view, but mesial, lateral and distal surfaces are visible in part; and, with removal of the humerus the proximal articular surface is completely exposed. The latter is triangular in outline with the apex of the triangle directed mesially, away from the position of the ulna (figure 22*h*). The proximal surface is concave and cartilage-finished, while the distal articular surface appears to have been convex, as in *Proterogyrinus*. The extensor surface bears longitudinal ridges distally and at its distal end is convex on its mesial side and somewhat concave laterally. The characteristic ridge separating the extensor and flexor muscle groups, seen in *Archeria* and *Proterogyrinus*, is present running down the lateral edge, but is not prominently developed.

The overall length of the radius is 26 mm. With a humerus length of 36 mm, the (?) *Crassigyrinus* radius is relatively much larger than that of *Archeria* (for example, 33 mm compared with 63 mm) or *Proterogyrinus* (for example 36 mm compared with 62 mm).

Posterior to the radius under the Cowdenbeath skull is a much more slender bone of similar

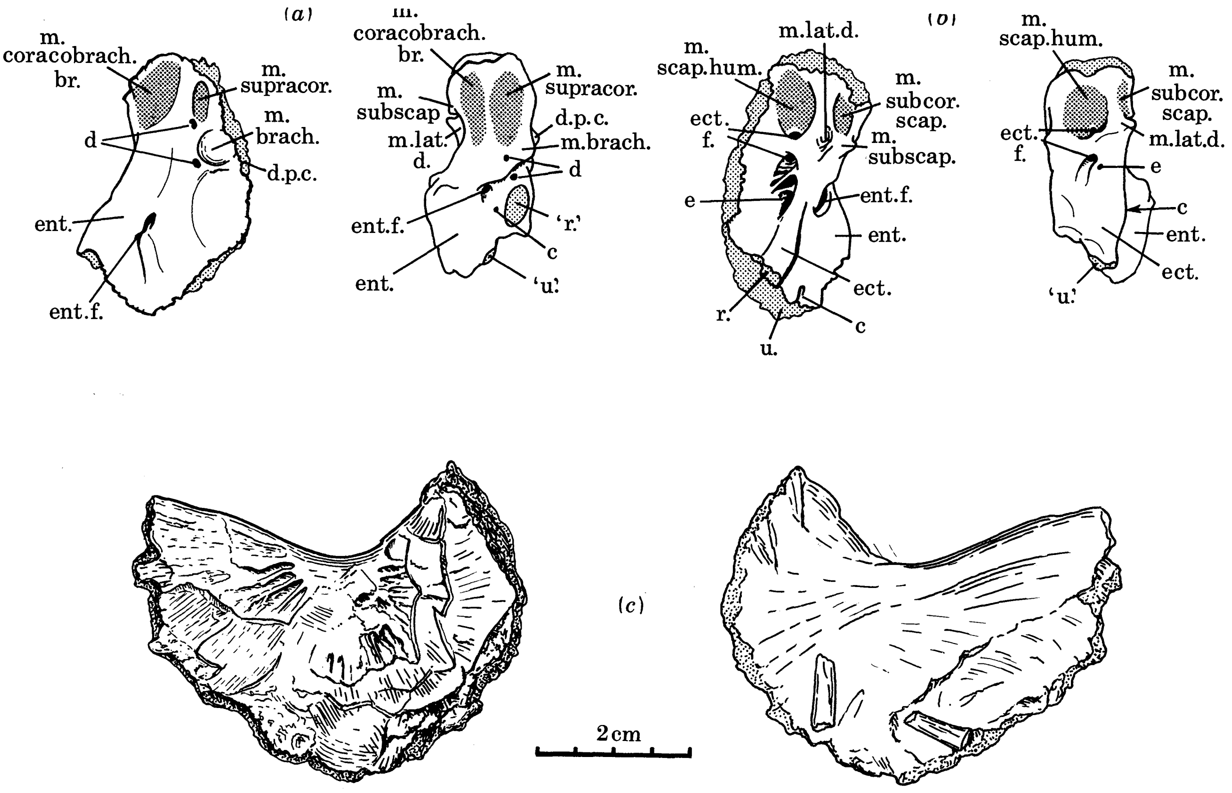

Figure 23. (*a*), (*b*) Restored humeri of *Crassigyrinus* and *Ichthyostega* respectively (*Ichthyostega* after Jarvik 1980). Not to scale. (*a*) Ventral view; (*b*) dorsal, in plane of proximal surface. Areas of unfinished bone: light stipple; reconstructed areas of muscle origin and insertion: medium stipple. Muscle origins and insertions: d.p.c., deltopectoral crest; m.brach., brachialis; m. coracobr. br., coracobrachialis brevis; m. lat. d., latissimus dorsi; m. scap. hum., scapulo-humeralis; m. subcor. scap., subcoracoscapularis; m. subscap., subscapularis; m. supracor., supracoracoideus. ect., ectepicondyle; ect. f., ectepicondylar foramen (Jarvik's 'canal a'); ent., entepicondyle; ent. f., entepicondylar foramen (Jarvik's 'canal b'); c, d, e: Jarvik's canals c, d and e, respectively; r., radial condyle; u., ulnar condyle. (*c*) Right ischium in lateral and medial view. Natural size.

length (figure 21). It is just possible that this is a degenerate ulna – not unexpected with such a reduced limb. However, it is more probably part of the hyobranchial skeleton and the small isolated bone referred to above is a more likely candidate. The latter is less stout than the radius and is remarkable in being hemicylindrical in shape, one surface presumably the ventral (flexor) one being almost completely flat (figure 22*g*, *h*). In dorsal view both ends of the bone are expanded; one terminates in a flat articular surface inclined very slightly dorsally, and strongly oblique to the axis, the other in two facets set at about 60° to one another and more or less symmetrical to the axis. Comparison with *Proterogyrinus* suggests that the latter end is distal, but if so there is even less ossification of the olacrenon than in that anthracosaur. However, when humerus, radius and (?) ulna are placed in articulation, their relative positions, particularly those of the distal ends of the epipodials, are very similar to those of *Proterogyrinus*. If the reconstructed orientation is correct then the problematic bone is a left ulna and its rounded cylindrical surface is the dorsal one.

Little can be made of the scattered small cylindrical bones situated to the left of the humerus and radius in palatal view (figure 21). It is improbable that many carpals are ossified: few are known in either *Archeria* or *Proterogyrinus*. However, small fragments of bone adjoining the distal end of the radius may be carpals. The scattered short cylindrical bones figured are presumably metacarpals and phalanges.

The ischium of *Crassigyrinus* (figure 23*c*) is roughly kidney-shaped in lateral view with a V-shaped curvature to its thickened posterodorsal edge. There are thus defined a short anterior ramus, which expands further towards the region of the acetabulum, and a longer posterior ramus which would have formed the posterior part of the puboischiadic plate. The specimen appears to be complete but there must have been a considerable extension of the whole rounded anteroventral edge in cartilage. That edge is of irregular unfinished bone, somewhat compressed in the specimen, and there is little or no sign of a symphysial surface mesially for junction with the ischium of the other side. Similarly there is little suggestion of an acetabular surface anterodorsally on the lateral side. A curious feature of the bone is an analogue of dermal ornament on the lateral surface, radiating from the apparent centre of ossification. At one stage this suggested interpretation as a dermal bone.

The shape of the ischium is, owing partly to its poor ossification, very different from that of other primitive amphibia. This is strongly the case for *Archeria* (Romer 1957) and *Ichthyostega* (Jarvik 1980). However, less well ossified specimens of the ischium of the primitive anthracosaur *Proterogyrinus* (Holmes 1984, figure 34) are a much closer match.

Scales

Scales of *Crassigyrinus* have been recognized exclusively in the Cowdenbeath skeleton, in which they are present in vast numbers from the back of the skull to the end of the specimen. Ironically, as they obscure so much of the detail of the underlying postcranial skeleton, they nowhere occur as a considerable area in articulation. All the preserved scales appear to be ventral scales (gastralia) and if this is so there is no evidence of dorsal squamation. The total pattern of preservation is illustrated in figure 16 and individual scales in figure 19.

All the scales appear to be composed of compact bone seen as rings of concentric laminae in transverse section. The scales are elongate and spindle-shaped with a longitudinal, and probably ventral, rounded ridge along their axis. Well-preserved specimens may show a spoon-shaped external (ventral) termination at one end while the other is pointed or may possibly bear an internal (dorsal) spoon-shaped hollow. Small groups of articulated scales show that these depressions are for mutual articulation. It is probable that the total pattern was *en chevron* as in embolomeres (Cope & Matthew 1915; see Panchen 1970; Panchen 1972*a*) and other 'labyrinthodonts' (for example, Colbert 1955; Carroll 1980, figure 2).

The general uniformity of scale shape does not apply to a group of scales situated between the interclavicles and particularly a series of three adjacent to centrum number 3 (figure 16). One of these is illustrated as the first of the individual scales in figure 20. It is relatively short (34 mm) and very wide as exposed, probably on its side, reaching over 5 mm at its widest point adjacent to the 'spoon-shaped' termination. It then tapers to a point at its other end. The spoon shape is seen in profile as a deep triangular depression. The other two scales lie parallel to it and the three appear to be in articulation. The reason for their uncharacteristic shape is not known.

The characteristic shape of *Crassigyrinus* scales is unlike that of either labyrinthodonts or microsaurs (Carroll & Gaskill 1978). The scales of Nectridea are described as somewhat more elongate (Milner 1980), but the closest resemblance is to those of Aïstopoda. Wellstead (1982) describes 'spindle-shaped' scales from the Lower Carboniferous form *Lethiscus*, while those of *Ophiderpeton* are much finer and needle-shaped (Boyd 1982).

Discussion

Mode of life

Description of the anatomy of *Crassigyrinus* contributes to current discussion of the functional morphology of early tetrapods in a number of ways. Particularly this is the case for discussion of intracranial kinetism, the middle ear region, jaw mechanics, the craniocervical joint and the axial skeleton.

It was noted in describing the braincase of the Cowdenbeath skull that the basipterygoid process of the basisphenoid forms a true articulation with the conical recess, as in embolomeres (Panchen 1964, 1970, 1972*a*), loxommatids (Beaumont 1977), and early reptiles (Heaton 1979). In these groups, and probably in the seymouriamorphs and cotylosaurs (Heaton 1980), a true synovial joint was almost certainly present, allowing some degree of rotation or sliding movement of the palatal bones on each side relative to the braincase. This contrasts with the temnospondyl condition in which the basal 'articulation' consists of a probably immobile peg-and-socket arrangement (Smithson 1982).

In embolomeres and other anthracosauroids (*sensu* Smithson 1984) the basal articulation is correlated with the apparent retention from osteolepiform-like ancestors of a skull table–cheek kinetism. The pattern is closely similar in *Crassigyrinus*. The braincase is very firmly attached to the skull table posteriorly, notably by broad facets on the tabular which contact the paroccipital processes of the opisthotics. However, the lateral borders of the skull table, particularly represented by the supratemporal, are not firmly sutured to the dorsomesial edge of the cheek region, particularly the squamosal. This apparently mobile junction may be continued forward to that between the intertemporal and the postorbital, or the latter may be more firmly conjoined.

The whole arrangement may be contrasted with the temnospondyl condition in which the basal articulation is immobile and the skull table and cheeks firmly sutured. The primitive temnospondyl condition, represented by *Greererpeton* (Smithson 1982), appears to have involved relatively feeble connections between the back of the braincase and the skull table. The paroccipital processes were largely cartilaginous and the principal mesial contact was a very limited one between the exoccipitals, representing the occipital arch, and the postparietals. This contact is a derived feature of temnospondyls (see below). In *Greererpeton*, as demonstrated by Carroll (1980) and Smithson it is correlated with a unique bracing function of the stapes.

It is difficult to understand the adaptive significance of the *Greererpeton* condition. In osteolepiform and other 'rhipidistian' fish the contact between the otic braincase and the skull table is a very firm one. In later temnospondyls such as *Eryops* (Sawin 1941) a firm connection is re-established via both exoccipitals and paroccipital processes, yet in *Greererpeton* the stapes, homologue of the fish hyomandibular, becomes involved in a suspensory role which is almost the direct opposite of that of the latter (Smithson & Thomson 1982).

The loxommatids are anomalous in having a firmly attached braincase and mobile basal articulation as in anthracosaurs, with no exoccipital-skull table contact, but a firmly sutured connection between skull table and cheek. Beaumont has suggested a unique but plausible kinetic mechanism for these amphibia which involves slight movement between the pterygoids and the lateral palatal bones and flexing of the suspensorium.

Nothing has advanced our knowledge of the adaptive significance of the anthracosauroid kinetism since my early account (Panchen 1964), but discovery of the stapes in the Coal Measure embolomere *Pholiderpeton* and its recognition in the closely related *Palaeoherpeton* (Clack 1983) as well as in *Greererpeton* has revolutionized ideas in the middle ear of early tetrapods.

Clack concludes, I now believe correctly, that a tympanum-bearing otic notch was absent in embolomeres and it is similarly unlikely that it was present in other anthracosauroids, such as *Eoherpeton* and *Gephyrostegus* (Smithson 1984). Nevertheless *Crassigyrinus*, a primitive relation of the anthracosaurs (see below), has a strong curved embayment on each side of the skull table and the level of the tabular–supratemporal suture. The orthodox interpretation of this would be as an otic notch, but it is perhaps improbable that the very primitive, very aquatic *Crassigyrinus* should have a tympanum when its closest amphibian relatives appear to lack one. It is also clear (Clack 1983) that the embolomere stapes is not well adapted as a transducer of airborne sound in an impedance matching middle ear. It is even more improbable that *Crassigyrinus* possessed such a transducing stapes. I wish to suggest therefore that the 'otic notch' of *Crassigyrinus* marked the opening of a persistent spiracle.

The persistence of the spiracle in 'labyrinthodonts' was suggested by Dr R. L. Carroll at a meeting of the Society of Vertebrate Paleontology in 1980. Significantly he gave this as an explanation of the 'otic notch' in loxommatids. It is hinted at by Clack for embolomeres. Carroll's suggestion was that the spiracles were inhalant foramina for aerial respiration when the head was partly submerged and the mouth and nostrils under water. This accords with my suggestion (Panchen 1967*b*) that an air-filled buccal cavity was characteristic of early tetrapods. It also relates to middle ear function in early tetrapods.

Clack rightly draws attention to the resemblance between the stapes of *Greererpeton* and that of *Pholiderpeton* and there is little doubt in my mind that the stapes of *Crassigyrinus* was similar. This allows one to conclude that the plesiomorph condition of the tetrapod stapes was to have a large somewhat quadrangular footplate, a stapedial foramen and stapedial groove and a distal region consisting of a somewhat flared plate of bone whose posterior and distal edges are cartilage finished (Clack 1983, figures 4 and 5). However, unlike that of *Greererpeton*, the embolomere stapes seems to have had no bracing or suspensory function. Clack concentrates less on the morphological differences between the two types of stapes. That of embolomeres has a much less massive distal plate. I suggest that in this case the distal plate was embedded in the wall of the air-filled spiracular cleft. This would represent the primitive tetrapod condition, which might well have also occurred in *Crassigyrinus*, *Ichthyostega* and loxommatids. In colosteids such as *Greererpeton*, the otic notch, and thus the spiracular opening, was lost when the stapes assumed its unique bracing function.

Thus early tetrapods, including *Crassigyrinus*, would have had a middle ear adapted for underwater hearing. It would have been comparable to the arrangement in herrings and other clupeomorph fishes and in the Ostariophysi. In both these teleost groups the swim-bladder is involved in the hearing mechanism (Bone & Marshall 1982). In the Ostariophysi the swim-bladder is linked to the inner ear by the Weberian mechanism, but a closer parallel is provided by clupeids (Allen *et al.* 1976; Denton & Blaxter 1976). In the herring the swim-bladder is connected by fine tubes to paired auditory bullae partly filled with utricular perilymph which is separated from the swim-bladder gas by a stiff elastic membrane (the prootic membrane).

The gas in the bullae is acoustically isolated from that in the bladder except at very low frequencies, so that the paired bullae would be comparable to the suggested spiracular clefts of *Crassigyrinus* and others. Transmission in the two cases would, however, be different; by means of the prootic membrane in one case and the stapes via the fenestra ovalis in another. Other teleosts have analogous systems: anabantids have an air-filled respiratory chamber above the gills connected to the inner ear by a thin-walled window and mormyrids have isolated gas bladders closely associated with each inner ear sacculus. The latter are derived in ontogeny from the swim-bladder. Underwater hearing in fish with a swim-bladder–ear connection extends to a surprisingly high frequency, reaching 7 kHz (von Frisch 1936) compared with *ca.* 400 Hz for those without (Bone & Marshall 1982). Thus I am suggesting that in *Crassigyrinus*, embolomeres and possibly loxommatids, there was a highly adapted underwater ear rather than the 'amphibious' ear suggested by Clack. Nevertheless, the reception of airborne sound, at least of low frequency, was probably also possible.

Later temnospondyls with a rod-like stapes directed toward an otic notch almost certainly had a tympanum as the first stage of an impedance-matching aerial middle ear. As Clack notes, a similar adaptation appears to have occurred convergently in seymouriamorphs, unless the latter are to be derived from temnospondyls rather than anthracosauroids (see below). It is almost certainly the case that the tympanum of amniotes was separately derived from that of any amphibian group (Lombard & Bolt 1979; Clack 1983).

The mechanics of the jaw articulation of *Crassigyrinus* are discussed above where I conclude that the adaptation is similar to that of *Eogyrinus* (Panchen 1972*a*) and other embolomeres producing a system which, in opening, stores energy to help in closure. The unique feature among amphibians of *Crassigyrinus*, particularly when compared with the embolomeres, is the great depth of the skull in comparison with the relatively shallow mandible. Two teleost analogies suggest themselves. First, the shallow jaw but wide gape of bathypelagic 'gulpers' (for example, Bone & Marshall 1982) and, secondly, the tropical reef-living Moray eels (Muraenidae). In the first case one could point to the convergent reduction in the postcranial skeleton, particularly the paired appendage and also to the enormous orbits of *Crassigyrinus* (as an indication of life in dim light).

However, a coal swamp environment is not like that of the deep sea and the main conclusion to be reached from the large orbits is that *Crassigyrinus* was a persistently underwater form. The eyes of fish and subaquatic tetrapods do not have the size constraints of aerial eyes imposed by the necessity of the latter being spherical. Thus with no corneal refraction and an almost spherical lens, fish eyes can be relatively very large, enhancing visual acuity, without encroaching inwards into other cranial structures (Walls 1963). A striking parallel among reptiles is the truly enormous orbits of fossil marine ichthyosaurs.

Crassigyrinus appears to have a very primitive, or possibly degenerate craniocervical joint. The basioccipital is not formed into the principal part of an occipital condyle, as in embolomeres and as paralleled in teleost fishes. It also seems probable that the notochord extended at least a little way into it. Furthermore, the basioccipital appears to have been loosely articulated with the parasphenoid and thence with the rest of the braincase. The atlas–axis complex, if correctly identified, was also relatively unspecialized and it seems likely that there was very limited mobility of the head about the vertebral column. Thus the well-ossified dermal pectoral girdle would have been more involved with a similar bracing function to that of bony fish, and as an origin of cranial and axial muscles, than with forelimb action.

In respect of its minute fore limbs *Crassigyrinus* is remarkably like the extant urodeles *Amphiuma* and *Siren*. Both are aquatic eel-like salamanders and in the case of *Siren* adept at burrowing through entangled vegetation as well as in the substratum (Noble 1931). The poorly ossified vertebrae and feeble rib-articulations of *Crassigyrinus*, whether primitive or degenerate, also point to a permanently aquatic form, as dependent on the notochord and axial muscle as on the skeleton for axial support.

The picture that emerges of *Crassigyrinus* is of a sluggish eel-like amphibian living in large bodies of water within the coal swamps of the Viséan and Namurian. Like the embolomeres it was clearly a major predator, but possibly of relatively smaller prey, by analogy with the Moray eels noted above. The latter are adapted, albeit in a marine environment, for preying on a variety of fish and invertebrates in rock crevices.

At Gilmerton the holotype of *Crassigyrinus scoticus* is associated with *Loxomma allmanni* (Beaumont 1977), *Pholidogaster pisciformis*, both large apparently aquatic predators, and the apparently more terrestrial *Eoherpeton watsoni* (Panchen 1975; Smithson 1984). The association with *Eoherpeton* appears to continue at Cowdenbeath. The Cowdenbeath amphibian fauna has been summarized by Smithson (1980*a*). There is also a considerable fish fauna, with the spines of *Gyracanthus* excessively common, as they are at many Coal Measure sites (Andrews *et al.* 1977). However, one point is of considerable interest. The Dora bone bed at Cowdenbeath is divisible into three layers (Smithson 1983 and above). The *Crassigyrinus* skeleton and two poor but intact specimens of the palaeoniscid fish *Pseudogonatodus* were the only finds in the hard basal siltstone layer. Nothing was found in the middle layer of clayband ironstone, while all the remaining specimens, fish and amphibia, were found in the soft, rooty siltstone of the upper layer. Most of these specimens were well preserved and thus not reworked, but were totally disarticulated. It is therefore reasonable to assume an environmental change, perhaps from a stable, thermally stratified lake, as at some Coal Measure sites (Panchen 1970), to considerable but more transient water bodies. Thus *Crassigyrinus* and *Eoherpeton* at Cowdenbeath may not have been part of the same ecological community.

Crassigyrinus and the Anthracosauria

Crassigyrinus scoticus Watson is a uniquely primitive and aberrant amphibian. After description of the holotype (Panchen 1973) I proposed the order Palaeostegalia for the reception of *Crassigyrinus* in the monotypic family Crassigyrinidae. However, the characters suggested as diagnostic of the Palaeostegalia (fish-like skull proportions, presence of a preopercular and possible course of the infraorbital lateral line sulcus on the jugal, together with an osteolepiform configuration of bones round the nostril) are all primitive. I accept the cladistic precept that because of this they alone cannot characterize a taxon. Fortunately, however, *Crassigyrinus scoticus* is now known to have several unique character states. There are the enormous quadrangular orbits, the extreme constriction of the interorbital region, particularly the frontals and parietals, and the great depth of the cheek region, notably the depth of the jugal and lacrimal bones below the orbit. The shallowness of the mandible relative to the rest of the skull might also be cited, but the proportions in this respect are not very different from those of *Eusthenopteron* and other osteolepiform fish (Jarvik 1980). This, however, is not the case with the extreme depth of the cheek. It also seems probable that the bizarre reduction of the forelimb, characterized by the minute but relatively well-formed humerus, must be regarded as an autapomorphy. It is highly improbable that it denotes close relationship to any other early amphibian taxon, such as the Aïstopoda or Lysorophia, with strongly reduced or absent limbs.

By pursuing cladist methodology one may then propose a 'sister-group' relation between *C. scoticus* and the anthracosaur amphibia of the Carboniferous. The characters of *Crassigyrinus* proposed as synapomorphies uniting the two are as follows.

(i) *The dermal ornament on the skull roof and dermal pectoral girdle*

This contrasts with the characteristic dermal ornament of temnospondyl 'labyrinthodonts' and of loxommatids, whatever the relationships of the latter. Temnospondyl ornament consists of a raised honeycomb pattern which becomes extended in zones of intensive growth (Bystrow 1935). That of the anthracosaurs is less regular than the temnospondyl type and characteristically consists of rounded pits more widely separated by less sharp ridges. Most diagnostic, however, is the fact that the pits are all open in one direction on some areas of the skull, with the height of their walls diminishing towards the opening like deeply indented ripple marks. This type of ornament is clearly shown on the holotype squamosal of *Crassigyrinus*. Among the anthracosaurs themselves the characteristic ornament has been described or noted in *Palaeoherpeton* (*'Palaeogyrinus'*, Panchen 1964), *Pholiderpeton* (*'Eogyrinus'*, Panchen 1964), *Eogyrinus* (Panchen 1972*a*) and in a reduced state in *Anthracosaurus* (Panchen 1977*b*). All these are British Coal Measure embolomerous anthracosaurs. However, similar ornament also occurs in the North American Pennsylvanian embolomere *Eobaphetes* (Panchen 1977*b*), in the Permian *Archeria* (J. A. Clack, personal communication) and in the pre-Coal Measure Scottish Anthracosaur *Eoherpeton* (Panchen 1975).

That the anthracosaur type of ornament is derived, compared with the temnospondyl pattern, is suggested by the presence of the latter in primitive temnospondyls such as *Pholidogaster* (Panchen 1975) and *Greererpeton* (Smithson 1982), in the loxommatids (Beaumont 1977 and below), which are only doubtfully temnospondyl (Panchen 1980; Smithson 1982, and below). Ornament similar to that of the temnospondyls also occurs in the microsaur *Pantylus* (Romer 1969) and in the nectrideans *Scincosaurus* (Milner 1980) *Diceratosaurus* and *Diplocaulus* (Bystrow 1935). Significantly, it also occurs in the seymouriamorph *Kotlassia* (Bystrow 1944). The condition in *Seymouria* is not adequately characterized but is described by White (1939) as 'the reticulate sculpture characteristic of the contemporaneous Amphibia'.

Anthracosaur ornament is difficult to describe adequately in words, but it is worth noting that those experienced in handling Carboniferous amphibia can separate anthracosaur dermal bone material from that of loxommatids and temnospondyls with ease. It is also worth nothing that when the Cowdenbeath *Crassigyrinus* was first discovered it was immediately identified by Mr Wood and the author as an anthracosaur. Such intuitive judgements carry no weight in a cladist parsimony argument, but are of some force among practical palaeontologists (Panchen 1982).

(ii) *The tabular horns*

Many Palaeozoic and early Mesozoic amphibia have tabulars that project backwards beyond the general posterior margin of the skull table. Therefore the nature of the anthracosaur horn must be defined with some care. It consists in part of an extension posteriorly, and sometimes somewhat laterally, of the ornamented external surface of the tabular bone. This ornamented superficial surface of the horn terminates sharply in a rounded posterior margin, but below it the horn continues backwards as a deeper unornamented process. This is a rounded cone in *Crassigyrinus* and *Eoherpeton*. In embolomeres there appears to have been a morphocline from the primitive condition as in these two genera, through a blade-like unornamented region in *Palaeoherpeton* and probably other members of the subfamily Eogyrininae to the development of a biramous horn, foreshadowed in *Eobaphetes* and fully developed in *Anthracosaurus* (Panchen 1977*b*).

In loxommatids (Beaumont 1977) a small conical process, comparable to the unornamented part of the horn of *Eoherpeton*, but relatively smaller, projects backwards from the occipital surface of the tabular. However, it is not situated under the outer corner of the tabular as in anthracosaurs and the small quadrangular ornamented part of the tabular does not project back to form the ornamented part of the horn. In the aberrent loxommatid, *Spathicephalus* the ornamented tabular does project backward at its posterolateral corner but this projection is quite separate from the conical process or 'tabular button'. A small tabular button also occurs in some temnospondyls, such as *Greererpeton* and *Edops* (Smithson 1982).

In the keraterpetontid nectrideans there is a spectacular development of the tabular to give the distinctive arrowhead-shaped skulls of the Carboniferous forms and the bizarre boomerang shape of the skulls of the Permian *Diploceraspis* and *Diplocaulus* (Milner 1980). However, the nectridean horns, formed throughout of ornamented bone are not comparable to anthracosaur horns.

The anthracosaur tabular horn may not seem a very compelling character, but like the nature of the dermal ornament it is quite characteristic to those used to handling the actual specimens. Taken in combination with the next character, however, as part of the architecture of the occipital region, the whole is quite unique.

(iii) *The lack of posttemporal fossae*

The posttemporal fossae of Palaeozoic amphibia are the homologues of the fossae Bridgei of fishes (for example, Panchen 1972*b*) and the relationships of the fossae are particularly well shown in Jarvik's (for example, 1980) reconstructions of *Eusthenopteron* (see also Panchen 1972*b*, figure 5). The fossae are entirely absent in all known Embolomeri, in all of which the back of the skull table is emarginated to form a deep embayment in dorsal view. This is bordered on each side by the tabular horns. Presumably the embayment is correlated with the elimination of the fossae. The occipital region of *Crassigyrinus*, if my hypothesis of a fossa-less occiput is correct, is closely similar to that of embolomeres even to the detail of a small spoon-shaped backward projection of the conjoined postparietals in the midline just below the back of the skull table. Furthermore it is now known (Smithson 1984) that *Eoherpeton* lacked posttemporal fossae, contrary to my original account (Panchen 1975). This conclusion is based on new material, also from the Cowdenbeath collection (Smithson 1984).

Once again *Kottlassia* does not show the anthracosaur condition. As figured by Bystrow the occiput is remarkably temnospondyl-like with fully developed fossae and no tabular horn or button. The condition of *Seymouria* is difficult to interpret. White notes that an occipital downgrowth of the tabular 'reduces the posttemporal fenestra', that is, that there is a normal 'labyrinthodont' pair of fossae, each of which is partly occluded by downgrowth of its respective occipital tabular. After inspection of a well-preserved *Seymouria* occiput in the Museum of Comparative Zoology, Harvard University (M.C.Z. 1086), I agree with this interpretation. However, Holmes (personal communication and 1984) interprets both the fossae of *Seymouria* and their absence in anthracosaurs differently.

(iv) *The histology of the teeth*

This has been fully discussed in describing the dentition. The tusks of *Crassigyrinus*, just as in the embolomeres, are of advanced labyrinthodont (s.s.) grade (Schultze 1969), but have the special anthracosaur feature of Atthey's 'dark dentine'.

These four characters, taken together, strongly suggest a 'sister-group' relationship between *Crassigyrinus* and the anthracosaurs and I know of no evidence for any rival hypothesis of the relationships of *Crassigyrinus*. In referring to the anthracosaurs I have not so far in this discussion given them any formal taxonomic name. In my most recent discussion of their relationships (Panchen 1980) I presented a scheme for the phylogeny of the taxon Anthracosauria within which a primary dichotomy was suggested between the Embolomeri plus 'Herpetospondyli' on one hand and Gephyrostegoidea (including *Eoherpeton*) plus Seymouriamorpha on the other. Unfortunately, however, it has since been shown (Smithson 1984) that the braincase characters used to unite *Eoherpeton* and the Seymouriamorpha are either spurious or non-diagnostic. This is partly because of the inadequacy of preservation of the otic region in the type of *Eoherpeton*. Thus it is not the case that *Eoherpeton* has posttemporal fossae, a periotic tube, or basal tuberae of the parasphenoid. Other shared characters of the braincase, which Heaton (1980) regarded as unique to Cotylosauria (seymouriamorphs and diadectomorphs) plus reptiles and I regarded as uniting *Eoherpeton* and seymouriamorphs, are probably primitive tetrapod features. Thus, as Smithson (1984) points out, *Greererpeton* (Smithson 1982), as well as *Proterogyrinus* (Holmes 1984) and *Eoherpeton*, have an unossified laterosphenoid region: lack of ossification in the synotic region is also probably a primitive or degenerate feature. I conclude therefore, in agreement with Smithson (1984), that *Eoherpeton* is related to the *Embolomeri* rather than the Seymouriamorpha. It was included in the Gephyrostegoidea because of the strong resemblance to *Gephyrostegus* in the shape of the skull and the features of the dermal skull roof, but the material of *Gephyrostegus* is not such as to give unequivocal information on the critical regions of braincase and occiput (Carroll 1970; Panchen 1980). However, I think it probable that *Gephyrostegus* is to be included with the anthracosaurs rather than the Seymouriamorpha.

Thus I propose that *Crassigyrinus* is the sister-group of a taxon comprising the Embolomeri (families Eogyrinidae, Archeriidae and Anthracosauridae), *Proterogyrinus scheelei*, *Eoherpeton watsoni* and probably the family Gephyrostegidae Romer. Holmes (1984) has concluded that *Proterogyrinus* should be included within the Embolomeri as a fourth family, the Proterogyrinidae Romer, and I concur with this. The term 'Herpetospondyli' (Panchen 1975, 1980) then lapses.

The whole anthracosaur taxon is referred to by Smithson (1984) as Anthracosauroideae, a revival of Watson's (1929) term for the Embolomeri, extended to include *Eoherpeton* and the Gephyrostegidae. He further concludes that the Anthracosauroideae are the sister-group of the Seymouriamorpha, together making up the Anthracosauria (s.l., see Panchen 1980). However, study of *Crassigyrinus* poses problems about the integrity of both the Anthracosauroideae and the Anthracosauria.

The Embolomeri (including *Proterogyrinus*) are well characterized by the deep mandibular ramus with two large Meckelian fenestrae in the mesial surface (confluent in *Anthracosaurus russelli*). Other early tetrapods have a single large Meckelian fenestra, for example *Greererpeton* (Smithson 1982) and the Diadectomorpha (for example, Heaton 1980). However, the double fenestra is characteristic and Smithson (1983) notes what may be a unique embolomere feature in that the anterior coronoid forms part of the border of the anterior fenestra, thus separating the prearticular and presplenial bones. This latter condition is described in *Anthracosaurus*, *Eogyrinus*, and probably occurs in *Archeria* (Stovall 1948). No embolomere is known to lack it but Dr Clack tells me that she doubts its presence in *Pholiderpeton*. Loss of vomerine tusks may also be an embolomere autapomorphy, but the condition of *Proterogyrinus* is not known and other anthracosauroids, particularly *Eoherpeton*, may well be tuskless.

If *Proterogyrinus* is to be included within the Embolomeri then the eponymous vertebrae are not characteristic. Typical embolomerous vertebrae, with massive cylindrical pleurocentrum and disc-shaped intercentrum are known from the families Archeriidae (Panchen 1970) and Eogyrinidae, but I now doubt their presence in *Anthracosaurus*. The vertebrae attributed by Huxley (1863) are more probably eogyrinid (Panchen 1977*b*; J. A. Clack, personal communication). In *Proterogyrinus* the intercentra are the crescentic wedges characteristic of most 'labyrinthodonts' and the pleurocentra, while of embolomere type, are rather less well ossified. However it appears almost certain (Panchen 1977*a*; Holmes 1984) that in the living animal the intercentrum was chondrified to an embolomerous disc.

I wish to suggest that this was true of all Anthracosauroideae and represents both an autapomorph feature and an important adaptation of the whole group. I can discern no other apomorph feature that excludes *Crassigyrinus*: the only autapomorphy cited by Smithson (1984) is emargination of the skull table with consequent loss of the posttemporal fossa, which does not do so.

In all anthracosauroids the pleurocentrum is a well-ossified constricted cylinder with paired, anterodorsally facing, facets for the close adhesion of the neural arch. Occasionally the two are fused. The pleurocentra are always amphicoelous, with a variable degree of constriction of the notochord. In typical embolomeres the intercentrum can be seen to form the 'ball' of ball-and-socket joints between successive pleurocentra (Panchen 1966, 1967*a*). There is evidence that this was also the case in other anthracosauroids. In *Eoherpeton* (Smithson 1984) the intercentra are massive and horseshoe-shaped and in some instances contact anterior facets on the neural arch, while others are less ossified dorsally. Some degree of ball-and-socket movement probably occurred but this must have been somewhat constrained. In *Gephyrostegus* Carroll (1970) suggests that the small crescentic intercentra were chondrified dorsally. It is of note that a specimen of *Geophyrostegus* in the Narodni Museum, Prague (N.M.P.: M.398) has embolomerous tail vertebrae (A. C. Milner and A. R. Milner, personal communication) and that the tail vertebrae of *Proterogyrinus* tend towards an embolomerous condition.

Thus the vertebrae of anthracosauroids are unique among early tetrapods in this functional diplospondyly (except perhaps for the 'embolomerous microsaur' *Acherontiscus*: Carroll 1969*b*). All temnospondyls, even those with well-developed pleurocentra (*Doleserpeton*, *Tersomius*, *Greererpeton*, *Neldasaurus* and others, see Panchen (1977*a*)) have oblique rather than transverse intercentrum–pleurocentrum–intercentrum articulations. Gastrocentrous early amphibia, with massive cylindrical pleurocentra and reduced crescentic intercentra, such as some microsaurs, seymouriamorphs, diadectomorphs (and early reptiles) do not appear to be functionally diplospondylous. It may be significant that all these latter groups develop 'swollen' neural arches with more or less horizontal zygapophyses in some or all of their members.

Thus it is possible to characterize the Anthracosauroideae (*sensu* Smithson), but if that taxon is the sister-group of *Crassigyrinus* the relationship of anthracosauroids and seymouriamorphs is immediately called into question. None of the synapomorphies proposed to unite the former groups is present in any seymouriamorph. In the latter the dermal ornament is not of anthracosaur type, tabular horns are absent, posttemporal fossae are present, and the teeth do not show 'dark dentine'.

Traditionally (Säve-Söderbergh 1935; Romer 1947, 1966) the pattern of the skull table has been used to divide the 'Labyrinthodontia' into two groups. The Temnospondyli normally lack a tabular–parietal contact and were regarded by many as related to at least some extant Amphibia (Bolt 1969), while the anthracosauria (s.l.), with that contact were considered to be in some way related to reptiles (Carroll 1969*a*, 1970; but see Panchen 1972*b*). I pointed out long ago (Panchen 1964) that the temnospondyl condition, with tabular–parietal contact excluded by supratemporal–postparietal contact, was primitive. Thus unless some other autapomorphy of the Temnospondyli can be found, the group may well be polyphyletic. This is emphasized by the fact that *Crassigyrinus* shares that primitive state. Therefore, if the synapomorphies uniting *Crassigyrinus* and anthracosauroids are valid, the tabular–parietal contact uniting anthracosauroids and seymouriamorphs must be a case of parallelism or homoplasy.

Other early amphibian groups, the Aïstopoda, the Nectridea, intasuchid temnospondyls (Konjukova 1953) and diadectomorphs, as well as early reptiles, have a tabular–parietal contact. However, this is absent in the earliest aïstopod *Lethiscus* (Wellstead 1982) and may well have developed within the group, thus weakening the proposal of sister-group relationship to the Nectridea ('Holospondyli', Bossy 1976) as Smithson (1984) points out. In at least keraterpetontid Nectridea the tabular–parietal contact is undoubtedly related to the enormous growth of the tabular, as it may well be in anthracosauroids. This appears not to be the case in seymouriamorphs and it should be noted that Parrington (1956) in exploring patterns of dermal bone growth was able to reproduce that of the *Seymouria* skull table assuming 'circular growth' of both parietal and tabular, whereas, as I have suggested (Panchen 1980), that of the anthracosauroid (and nectridean) tabular is almost certainly elliptical.

The tabular–parietal contact of proterothyrids ('romerian captorhinomorph' reptiles) is of a very different nature. The skull table is dominated by the paired parietals, which have expanded laterally with the loss of the intertemporals and contraction backwards of the supratemporals to flank the tabulars. Because of the reduction of these bones, together with the postparietals, the posterior border of the parietals in proterothyrids is almost a straight line corresponding to the transverse kinetic line of the skull roof of osteolepiform fish such as *Eusthenopteron* (figure 24*d*, *e*). Thus it would be possible to postulate the origin of the early reptile configuration from the fish one without any intermediate 'labyrinthodont' stage.

This is perhaps improbable, but even if origin of the reptile configuration via the temnospondyl one is assumed, it is not necessary to postulate an intermediate anthracosaur condition (Panchen 1975). Two hypothetical phylogenetic routes are possible from primitive temnospondyl to primitive reptile: one, assuming loss of the intertemporals before establishment of the tabular–parietal contact, does not pass through the anthracosaur condition, the other (in which the sequence is reversed) does (figure 24*a*–*d*). A similar argument applies, with perhaps less force, to the origin of the skull table pattern of diadectomorphs, which also lack an intertemporal (figures in Heaton 1980).

Whatever the nature of tabular growth, circular or elliptical, in anthracosauroids and seymouriamorphs, the tabular–parietal contact undoubtedly arose by backward migration of the parietal–postparietal suture relative to the supratemporal–tabular one, in a skull table

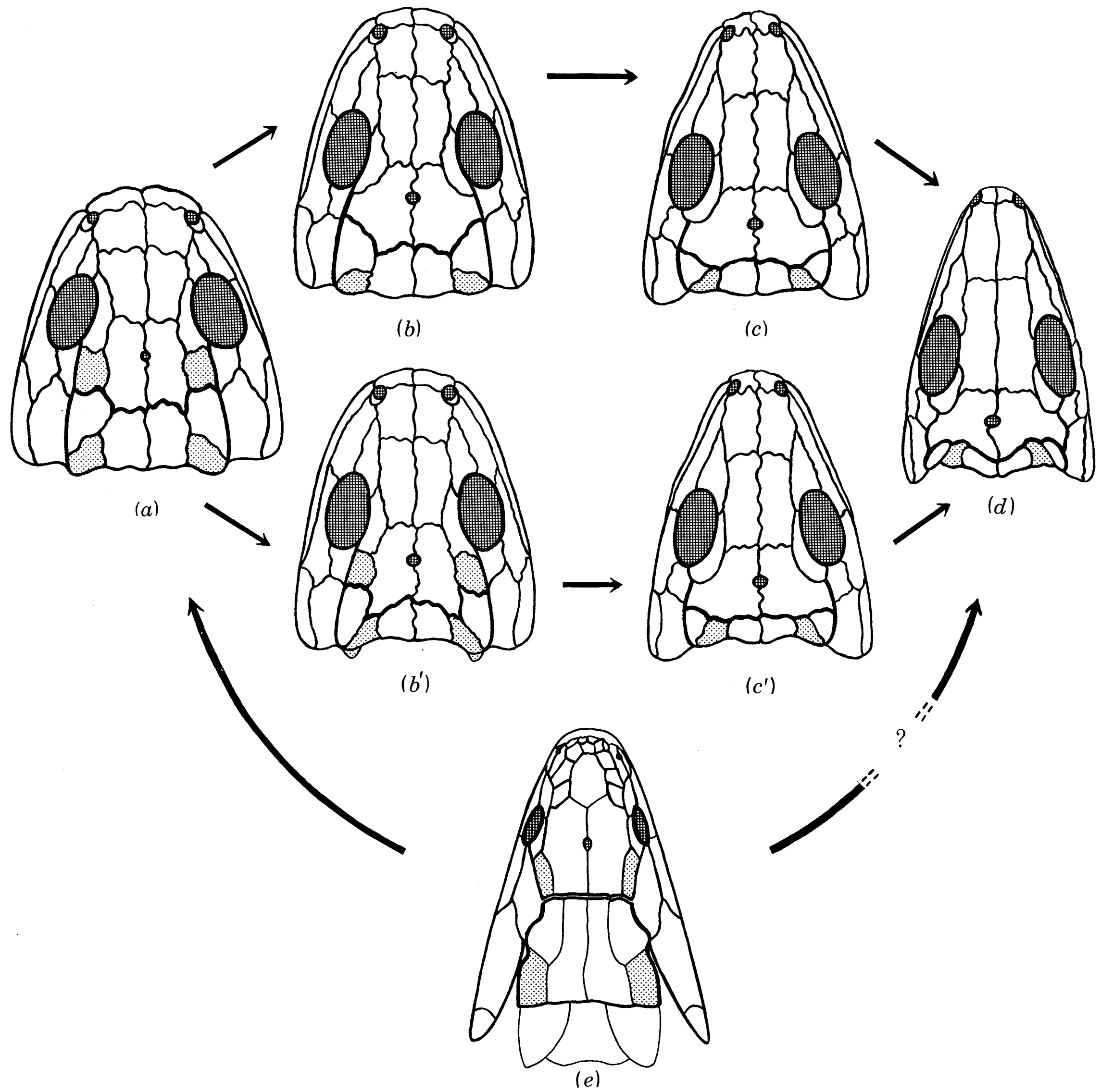

FIGURE 24. Possible modes of origin of the primitive reptile skull roof (*Anthracodromeus*) from a primitive tetrapod condition. (*a*), (*b*), (*c*), (*d*), With loss of intertemporal before tabular–parietal contact: no anthracosaur stage; (*a*), (*b′*), (*c′*), (*d*), tabular–parietal contact before loss of intertemporal: (*b′*), anthracosaur stage. (*e*), *Eusthenopteron*, representing ancestral fish condition, to show origin of primitive tetrapod configuration of skull table and possible direct derivation of reptile from fish condition. Tabular and intertemporal, light stipple; transverse kinetic line double in (*e*), heavy line in (*a*)–(*d*). Modified after Panchen (1975); *Anthracodromeus*, after Carroll & Baird (1972), *Eusthenopteron*, after Jarvik (1980).

retaining all these ossifications plus the intertemporal. It is thus reasonable to confine a hypothesis of synapomorphy of tabular–parietal contacts to taxa in which that contact occurs on a 'complete' skull table (Smithson 1984). This confines the apparent synapomorphy to anthracosauroids and seymouriamorphs.

However, I can see no other characters linking the two as sister-groups. In seymouriamorphs there is a unique squamosal–intertemporal suture, a true autapomorphy (Smithson 1984), consequent in part on the loss of the lateral kinetism between skull table and cheek. The kinetism is retained in anthracosauroids. The otic notch in seymouriamorphs is an embayment of the squamosal, which forms the upper border of the notch and sutures with the skull table. It almost certainly housed a tympanum and is correlated with a short, dorsally directed, and no doubt sound-conducting stapes. On the other hand the 'otic notch' of anthracosauroids, when present, is unlikely to have housed a tympanum and the stapes, where known, is an improbable component for an impedance-matching middle ear (previous section and Clack (1983)). This removes my principal objection to close anthracosauroid–reptile relationship (Panchen 1972*b*) but I know of no positive reasons for asserting it.

Gastrocentrous vertebrae cannot be cited as a seymouriamorph–anthracosauroid synapomorphy. There are too many parallels in other groups, mostly with the characteristic dome-shaped neural arches which are lacking in anthracosaurs. Other shared characters, such as five-fingered manus (Romer 1957), postcervical ribs lacking uncinate processes and the atlas–axis complex (Holmes 1984) are probably plesiomorph features. Therefore the possibility cannot be dismissed that the tabular–parietal contact in each group was independently derived from different ancestors with the temnospondyl configuration. This is supported by the condition of *Crassigyrinus* and the very temnospondyl-like skull of *Kotlassia* as described and figured by Bystrow (1944). Thus the Anthracosauria (s.l.), as defined by Romer (1947, see also Olson (1971); Panchen (1980); Smithson (1984)), is probably a polyphyletic group. This conclusion was reached by Heaton (1980) but for reasons that seem to me to be invalid (see above).

In reconstructing the phylogeny of the 'Anthracosauria' (Panchen 1980) I suggested, very tentatively, that they might bear sister-group relationship to the Loxommatoidea as 'Neostegalia', with the Palaeostegalia (*Crassigyrinus*) as plesiomorph sister-group to the latter. This suggestion was made on the (probably invalid) ground of similarity in the vertebrae. The vertebrae of *Crassigyrinus* were then thought to be diplospondylous with closely similar crescentic intercentra and pleurocentra. The loxommatid *Megalocephalus* is known to have small crescentic intercentra (Baird 1957; Beaumont 1977; figure 16) and unassociated more complete crescents in the Hancock Museum were identified as possible *Megalocephalus* pleurocentra. This may yet prove correct, giving *Megalocephalus* somewhat *Proterogyrinus*-like vertebrae, but it can no longer be maintained that they resemble those of *Crassigyrinus*. Apart from the vertebrae it was merely suggested that nothing debarred loxommatids from descent from a generalized 'palaeostegalian' ancestor.

However, Smithson (1982) has given several significant reasons for suggesting that loxommatids are not temnospondyls. A common feature of all temnospondyls is the junction of the exoccipital bones with the skull roof. This is undoubtedly a derived condition of some importance as it represents a contact between the occipital arch and the skull table, which is absent in anthracosauroids, diadectomorphs and reptiles, as well as in *Eusthenopteron* and other 'rhipidistian' fishes. It is present in microsaurs, with the exception of *Pantylus*, and may represent a temnospondyl–microsaur synapomorphy. The contact is also shown by Bystrow in *Kotlassia*, but Smithson is not the only one to suspect that Bystrow's account may be a conflation of at least two very different amphibia: Watson's (1954) description of *Karpinskiosaurus*, according to Bystrow a synonym of *Kotlassia*, represents a very different animal.

Loxommatids do not have the exoccipital–skull table contact, but they do have a type of mobile basipterygoid articulation not found in temnospondyls or microsaurs, but present in anthracosauroids (plus *Crassigyrinus*) and early reptiles (Beaumont 1977; Heaton 1979). The basal articulation also seems to have been mobile in seymouriamorphs whereas in temnospondyls and microsaurs a simple peg-and-socket junction was probably always immobile (Smithson 1982) and, as Watson (1919) originally showed, is reinforced by a parasphenoid–pterygoid suture in *Eryops* and more advanced temnospondyls. Last, I suggested (Panchen 1980) that an apomorph feature of all temnospondyls is the presence of interpterygoid vacuities, whereas the loxommatids have the pterygoids conjoined anterior to a short exposure of the parasphenoid, thus forming a palatal plate. This character is also opposed to the apparent plesiomorph condition in which the pterygoids flank the processus cultriformis of the parasphenoid throughout their length in front of the basal articulation, as seen in *Eusthenopteron* and eogyrinid embolomeres. However, the palatal plate hardly defines a monophyletic group: it occurs in *Ichthyostega*, *Anthracosaurus* (but with unique features), *Eoherpeton*, *Seymouria* (but not *Kotlassia*!) and *Keraterpeton inter alia*. Loxommatids also parallel embolomeres (not including *Proterogyrinus*) in their heavily ossified unitary braincase, a character which they may also share with *Crassigyrinus* and could therefore be seen as potential in all anthracosauroids.

Thus in summary, it may be suggested that loxommatids belong to a 'reptiliomorph' ramus of early tetrapods also including *Crassigyrinus*, anthracosauroids, seymouriamorphs, probably diadectomorphs, and reptiles, distinguished by a true basal articulation. Furthermore they are excluded from the temnospondyls by the nature of their occipit and palate. Dr Smithson has urged a closer relationship between loxommatids and *Crassigyrinus* based on the striking similarity of their dentary dentition. This similarity originally caused me (Panchen 1973) to identify the holotype of '*Macromerium scoticum*' as *Loxomma*, but it is not reflected in similarities in the maxillary or palatal dentition and is therefore, I believe, not adequate evidence of sister-group relationship between the two.

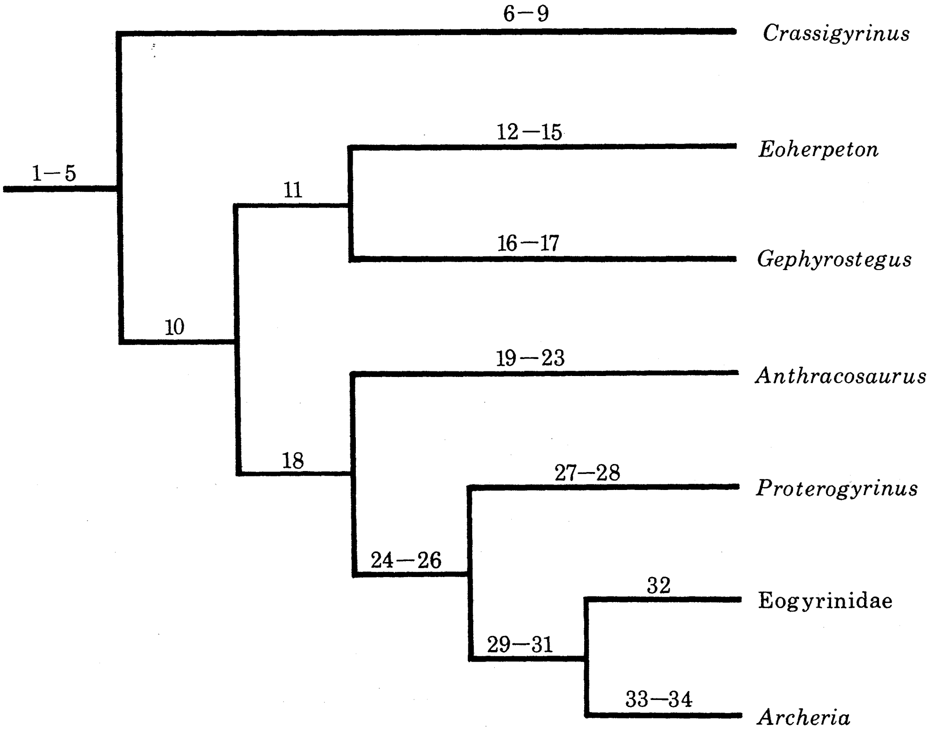

Figure 25. Cladogram representing an hypothesis of relation of *Crassigyrinus* and taxa within anthracosauroids (see text, numbers refer to apomorph characters in table 1).

I present as figure 25 and table 1 a cladogram to represent the relation between *Crassigyrinus* and the several groups of anthracosauroids. The characters used, and to some extent the arrangement, are taken from Panchen (1980 and previous publications); Smithson (1984); Holmes (1984) and those cited above. I make no attempt to place the overall clade within a larger reptiliomorph grouping, nor (with great restraint!) do I suggest yet another amendment of the nomenclature of the groups involved.

The primitive characters of Crassigyrinus

> 'I suggest that we might make progress with the problem of tetrapods by taking that [cladogram construction is basic to taxonomy] to heart, and going back to the problem that Owen and Bischoff argued about – what are the characters of tetrapods? With a comprehensive answer to that question we could make better use of the fossil record, looking in it not for ancestors, but for the sequence in which those tetrapod characters arose.'
>
> Patterson 1980, p. 172

Most of the characters of *Crassigyrinus* discussed in the last section were apomorph, either autapomorphies (unique to *Crassigyrinus* or to the higher taxa, Crassigyrinidae, Palaeostegalia, of which it is the sole known representative), or synapomorphies suggesting its uniquely close relationship to the anthracosauroids. However, for the traditional palaeontologist the interest of *Crassigyrinus* is more likely to be its strikingly primitive features. These features are presumed

TABLE 1. APOMORPH CHARACTERS OF *CRASSIGYRINUS* AND ANTHRACOSAURS

(See figure 25.)

(1) ? consolidated braincase (also loxommatids)†
(2) characteristic dermal ornament
(3) tabular horn with superficial and deep component (see text)
(4) 'dark dentine'
(5) posttemporal fossae absent
(6) large quadrangular orbits
(7) constricted parietals and frontals in interorbital region
(8) deep cheek below orbit
(9) minute fore limb
(10) functionally embolomerous vertebrae, with ventrally ossified pleurocentra
(11) ? spiracular embayment ('otic notch') lost‡
(12) accessory rib articulations on transverse processes
(13) relatively large and massive postcranial skeleton
(14) massive horseshoe-shaped intercentra
(15) ? braincase ossification reduced†
(16) frontals included in orbital margin
(17) ? tabular horn lost
(18) two enlarged Meckelian fenestrae (? ant. coronoid bordering anterior one)
(19) confluent Meckelian fenestrae
(20) palate consolidated and reinforced
(21) loss of lateral kinetism
(22) biramous tabular horn
(23) massive dentition, only two premaxillary teeth
(24) surangular crest
(25) descending pterygoid flange
(26) oblique glenoid on scapulocoracoid
(27) ? braincase ossification reduced†
(28) 32 presacral vertebrae§
(29) lacrimal excluded from orbit by long prefrontal–jugal suture
(30) trunk vertebrae fully embolomerous
(31) *ca.* 40 trunk vertebrae§
(32) three to four premaxillary teeth (primitively five plus)
(33) long spatulate snout
(34) maxillary teeth numerous (*ca.* 60) uniform, closely set, peg-like with recurved tips

† Assumes that a consolidated braincase is primitive for *Crassigyrinus* and anthracosauroids and possibly indicates sister-group relationship of the whole with loxommatids: implies parallel reduction of ossification in *Eoherpeton* (? + *Gephyrostegus*) and *Proterogyrinus*.

‡ Assumes that the 'otic notch' of *Gephyrostegus* is not the homologue of the spiracular embayment of *Crassigyrinus* and embolomeres: if incorrect *Eoherpeton*, *Gephyrostegus* and embolomeres constitute an unresolved trichotomy as Smithson (1984) concludes (see section on mode of life).

§ *Gephyrostegus* has 24 presacral vertebrae which may represent the primitive 'labyrinthodont' number. It is unlikely that *Anthracosaurus* had the anguilliform shape of the other embolomeres.

to be shared with its immediate fish ancestors and as such are plesiomorph as far as its tetrapod relationships are concerned. They are thus discarded in the construction of a cladogram representing those relationships. Traditionally they were used in the construction of phylogenetic 'trees' purporting to show ancestor–descendent sequences. This activity is scorned by cladists (Forey 1982), but the plesiomorph characters of *Crassigyrinus*, like those of *Ichthyostega*, do constitute data of taxonomic importance. Furthermore some of them, together with some from *Ichthyostega*, can also be used to cast doubt on the validity of aspects of cladist methodology.

Patterson in the passage quoted at the head of this section and again in Rosen *et al.* (1981) rightly emphasizes the importance of characterizing tetrapods by a series of agreed autapomorphies. The primitive characters of *Crassigyrinus* and *Ichthyostega* demonstrate that a number of features, formerly thought to be autapomorphies of the Tetrapoda, are in fact confined to a group or groups of lower rank. This would not be known without the fossil record. To me this is one of the most important functions of palaeontological data and refutes the claim of some cladists that fossil evidence is useless for the classification of living organisms.

Gaffney (1979) uses the primitive characters of *Ichthyostega* in this way. He first attempts to demonstrate that tetrapods constitute a monophyletic group. He then seeks to show that there is a monophyletic group of lower rank ('Neotetrapoda'), comprising all known tetrapods except *Ichthyostega*, and that *Ichthyostega* is its plesiomorph sister-group. Rosen *et al.* (1981) accept Gaffney's reasoning. They also accept that all his characters are either present in all tetrapods in the first case, or distinguish 'neotetrapods' in the second (with one exception discussed below). However, they object on theoretical grounds to the use of Gaffney's term 'Neotetrapoda' (see below), and, even more importantly, assert that four of Gaffney's supposed tetrapod autapomorphies are in fact valid synapomorphies uniting tetrapods and lungfish (Dipnoi).

Gaffney's tetrapod characters, somewhat abridged, are as follows (those claimed by Rosen *et al.* to be lungfish synapomorphies are marked thus †).

(i)† Ethmosphenoid and otico-occipital moieties of braincase united or separated only by suture; 'rhipidistian' transverse kinetic hinge on dermal skull roof absent.

(ii) Otico-occipital region of skull compact in comparison with that of rhipidistians.

(iii) Otic notch.

(iv) Single pair of nasal bones, with or without internasal.

(v) Stapes.

(vi) Fenestra ovalis.

(vii) Carpus, tarsus and dactyly.

(viii)† Pectoral girdle free from skull; posttemporal, supracleithrum and anocleithrum absent; scapulocoracoid relatively larger than dermal pectoral elements.

(ix) Iliac blade of pelvis extending dorsally to level of vertebral column and attached to column by sacral rib or ribs.

(x)† Well-developed ischiac (*sic*) ramus of pelvis, well-developed pubic symphysis, both as part of large pubo-ischiadic plate.

(xi)† Ribs well developed and directed ventrally.

Some of Gaffney's characters may be questioned in the light of recent work, despite their acceptance by Rosen *et al.* (1981). Gaffney does not define 'otic notch' in terms of a restored tympanum, but without doing so it is almost impossible to decide on any criterion whether a notch was present or not in any particular case. If on the other hand an otic notch is defined as a tympanum-bearing structure, recent work makes it impossible to retain it as a tetrapod autapomorphy (Lombard & Bolt 1979; Carroll 1980; Smithson & Thomson 1982; Smithson 1982, 1984; Clack 1983, and section on Mode of life, above).

The definition of a stapes is similarly difficult. If it is defined in part as one of the components of an impedance-matching middle ear for airborne sound, then a stapes is not a tetrapod autapomorphy. Gaffney distinguishes the stapes from its homologue the fish hyomandibular as follows: having (i) an expanded proximal footplate intimately associated with the fenestra ovalis; (ii) no contact with an ossified operculum; (iii) the distal portion small or unossified; (iv) overall small size in relation to the skull. Of these characters (iii) and (iv) are not really diagnostic and one might think that the stapes of, for example, captorhinomorph reptiles and sphenacodont pelycosaurs do not conform to them. With (ii) one might question whether the stapes should be defined by its lack of contact with a non-existent entity, the tetrapod operculum. The remaining character (i) is valid but, on its own, inadequate. Smithson & Thomson (1982) gives an alternative definition based on the apparent takeover by the tetrapod stapes of what was some of the territory of the otic capsule. It is diagnostic in practical terms ('operational') in that compared with the fish hyomandibular the canal considered to be for the truncus hyoideomandibularis nerve is missing and a new canal, considered to be for the orbital (stapedial) artery, is present. Defined in this way the stapes appears to be a tetrapod autapomorphy, but of course the stapes of *Ichthyostega* and *Crassigyrinus* are unknown. Similarly the fenestra ovalis of both is unknown. The remainder of Gaffney's tetrapod autapomorphies, apart from those described as lungfish synapomorphies by Rosen *et al.* (1981) appear to be valid.

The supposed synapomorphies are all multiple characters (and so would wreak havoc in any parsimony argument!). This also results in the assertion of similarity to lungfish being, at best, only partly true in each case.

Thus, in (i), the braincase of most tetrapods is united without suture across the otico-occipital–ethmosphenoid junction as in lungfish (or derivable from that condition), but a suture persists in ichthyostegids (Säve-Söderbergh 1932; Jarvik 1980), which if truly plesiomorph invalidates the lungfish synapomorphy. On the other hand, no tetrapod (and not all 'rhipidistia') has the dermal transverse hinge. In the case of (viii) the claim of synapomorphy by Rosen *et al.* (1981, p. 164) is demonstrated by them to be almost totally untrue on their pages 217–220 (figures 39–40): the primitive lungfish *Chirodipterus* has a girdle attached to the skull and including posttemporal, supracleithrum and anocleithrum. A trivial difference in relative size of its scapulocoracoid compared with that of *Eusthenopteron* does not approach the fish-tetrapod difference and overall Gaffney's autapomorphy stands. For Gaffney's (x) the only evidence offered by Rosen *et al.* is the entirely cartilaginous pelvic girdle of the extant lungfish *Neoceratodus*, which does not (indeed cannot) show a bony symphysis between paired pubes and certainly bears no resemblance to the massive paired pubo-ischiadic plates of early tetrapods (for example, *Ichthyostega* (Jarvik 1980); *Archeria* (Romer 1957)). Number (xi) is more difficult: most workers interpret the ribs of tetrapods as dorsal ribs that are curved ventrally to form a rib cage, while those of Dipnoi are ventral or pleural ribs. However Rosen *et al.* question this. Nevertheless, they accept bicipital ribs as a 'synapomorphy' (*sic*, that is, autapomorphy) of tetrapods (see below). The views of Rosen *et al.* are to be further discussed in a review in preparation by Dr Smithson and myself, meanwhile it may be noted that a more restricted list of tetrapod autapomorphies can be extracted from these supposed tetrapod–lungfish synapomorphies. These are (i) braincase moieties united by close suture or fused; (ii) the whole of Gaffney's number (viii); the whole of his number (x) if the bony pelvic girdle is referred to.

Having satisfied himself, undoubtedly correctly, that tetrapods are monophyletic, Gaffney goes on to define his taxon 'Neotetrapoda' by reference to the (then) unique features of *Ichthyostega* (and sometimes *Acanthostega* (Jarvik 1980)), as reported by Jarvik. Thus the following are *not* autapomorphies of the Tetrapoda, but are given as autapomorphies of the 'Neotetrapoda' (Gaffney's numbers):

(xii) notochord excluded from otico-occipital region in adult;

(xiii) preopercular and subopercular absent;

(xiv) median bony fin supports with lepidotrichia absent;

(xv) lateral line system in sulci not closed canals on skull roof or absent;

(xvi) ethmosphenoid and otico-occipital moieties of braincase fused in adult, not separated by suture.

The plesiomorph states of all these characters are those reported in *Ichthyostega*. It was noted above that Rosen *et al.* (1981) declined to accept that the braincase of *Ichthyostega* was divided by transverse suture (Gaffney's characters (i) and (xvi)). However, Säve-Söderbergh's and Jarvik's assertion is strongly supported by the condition, described by both of them, of a parasphenoid confined to the ethmoid moiety in ichthyostegids. Rosen *et al.* (1981, p. 230) are 'uncertain' about this feature!

Crassigyrinus, like *Ichthyostega*, shows a series of plesiomorph tetrapod characters. Those where the state is also known in *Ichthyostega* can be divided into four categories.

(*a*) Character states (within tetrapods) uniquely shared by *Ichthyostega* and *Crassigyrinus*:
  (i) occipital condyle not developed;
  (ii) preopercular bone on cheek (also *Acanthostega*);
  (iii) anterior tectal present.

(*b*) Characters in which *Ichthyostega* is clearly more primitive:
  (iv) enclosed lateral line canals (also *Acanthostega*);
  (v) notochordal tunnel under otico-occipital region of braincase.

(*c*) Characters in which *Crassigyrinus* is clearly more primitive:
  (vi) larger preopercular;
  (vii) no clear postzygapophyses;
  (viii) ? ribs not properly bicipital (possibly a degenerate feature).

The characters in category (*c*), particularly the lack of postzygapophyses, demonstrate that their respective apomorph features, that is, small or absent preopercular, postzygapophyses, and ribs with distinct and well-developed tubercular and capitular heads, cannot be accepted as tetrapod autopomorphies. This was not known before the description of *Crassigyrinus.* The characters in category (*b*) have already been interpreted in this way by Gaffney and many previous authors. This is also the case with category (*a*) but these characters allow a further insight.

Ichthyostega and *Crassigyrinus* do not appear to be united by any valid synapomorphy within the Tetrapoda. Indeed the apomorph features of *Ichthyostega* (consolidated skull roof without skull table–cheek kinetism, loss of intertemporal) suggest temnospondyl rather than anthracosaur affinities. *Crassigyrinus*, on the other hand, if the argument in the last section is accepted, is the sister-taxon to the anthracosauroids, and is, one may assert, an anthracosaur. Thus the common ancestor of anthracosaurs and (at least) *Ichthyostega* had a cheek region with a large preopercular bone, a snout region with an anterior tectal and lacked a well-formed occipital condyle (but see below for the last). Thus unless temnospondyls (and loxommatids) and all other tetrapods are derived from anthracosaur stock, the apomorph states of these characters, loss of preopercular and anterior tectal and origin of the occipital condyle must have arisen polyphyletically within tetrapods. They do not therefore constitute autapomorphies characterizing a taxon within tetrapods such as Gaffney's 'Neotetrapoda'. With the discovery of more Devonian and early Carboniferous tetrapods, more, or all, of Gaffney's 'neotetrapod' autapomorphies might well disappear. For this reason I can see the force of the objection of Rosen *et al.* to the creation of named taxa ('Neotetrapoda') including extant organisms 'formulated for, or because of, the cladistic position of a fossil'. Patterson & Rosen (1977) suggest a convention, use of the term *plesion* for the plesiomorph fossil sister group, for coping with this difficulty. It also copes with the objection that a single fossil species (or even specimen) may be the sole representative of a nested series of monotypic taxa, when its large sister group is assigned a high rank. However, I have not followed this convention with *Crassigyrinus scoticus* (Crassigyrinidae, Palaeostegalia) because I believe that the relation of the anthracosauroids to any living taxon is as yet unresolved.

(*d*) The fourth category of *Ichthyostega–Crassigyrinus* characters is perhaps the most interesting one because it throws a new light on the validity of cladistic practice. These are characters in which the states of *Ichthyostega* and *Crassigyrinus* differ and there has been controversy about the polarity of those character states. They are set out as table 2.

TABLE 2. CONTRASTING CHARACTERS OF *ICHTHYOSTEGA* AND *CRASSIGYRINUS* OF CONTROVERSIAL POLARITY

((D), plesiomorph assuming Dipnoi to be the sister-group of tetrapods; (O), plesiomorph assuming Osteolepiformes to be the sister-group of tetrapods.)

	Ichthyostega		*Crassigyrinus*	
(ix)	braincase divided by suture	(O)	braincase consolidated	(D)
(x)	parasphenoid underlying ethmoid region only	(O)	parasphenoid underlying whole braincase	(D)
(xi)	course of infraorbital lateral line canal *c.f.* dipnoans	(D)	course of infraorbital canal *c.f.* osteolepiforms (Panchen 1973)	(O)
(xii)	external nostril marginal	(D)	external nostril not near jaw margin	(O)
(xiii)	pars facialis of lateral rostral reduced	(D)	pars facialis not reduced	(O)
(xiv)	'fused' postparietals	(D)	separate postparietals	(O)

To assign polarity to one or other of each of these pairs of contrasting characters the standard cladistic technique is that of 'out-group comparison' (for example, Eldredge & Cracraft 1980; Wiley 1981). Thus the plesiomorph state of a character within tetrapods is ascertained by its occurrence in a group of higher rank of which the Tetrapoda is a subgroup. This poses, with two exceptions, no difficulty in the case of the characters in categories (*a*)–(*c*). In each case the primitive character state listed is of general occurrence in a larger group (usually bony fish) of which the Tetrapoda is a cladistic subgroup. The two exceptions are (*a*) (i) and (*b*) (v). Neither *Crassigyrinus* nor *Ichthyostega* has a fully formed occipital condyle, while *Ichthyostega*, uniquely among early tetrapods, is reported to have a notochordal tunnel extending forwards to the trabecular region of the braincase. Both characters may be paedomorphic rather than primitive within the Gnathostomata, as well-formed occipital condyles appear in many Chondrichthyes and most Osteichthyes, but not, however, in osteolepiforms. Both the degree of ossification of the condyle and the loss of the notochordal tunnel are associated with degree of ossification (or chondrification in sharks) of the vertebral column and thus inversely correlated with persistence of the notochord. However, the primitive nature of the notochordal tunnel of *Ichthyostega* seems to be universally accepted, even by Rosen *et al.* (following Gaffney), and is usually cited as demonstrating relationship to osteolepiforms or 'Rhipidistia'. Nevertheless, a similar condition can also occur in early Dipnoi (*Chirodipterus* (Miles 1977); *Dipnorhynchus* (Thomson & Campbell 1971); *Dipterus* (E. I. White 1965)). The primitive feature of *Ichthyostega* and *Crassigyrinus* is best regarded not as the imperfect condyle and associated notochordal tunnel, but the lack of the characteristic mobile cranio-cervical joint of tetrapods, for which a well-formed condyle is essential.

In the case of the characters set out in table 2 (category *d*) there is an actual dispute about polarity. In each case the appeal is to a limited 'outgroup', that is, the sister-group of the Tetrapoda, and the polarity of each pair of character states depends on the identification of that sister group. The rival claimants are the Osteolepiformes and the Dipnoi. Traditionally the osteolepiforms have been regarded as tetrapod ancestors (see Patterson (1980) and historical survey in Rosen *et al.* (1981, pp. 166–178). However, cladists claim that ancestral groups cannot be recognized in the fossil record and are also paraphyletic, having no unique apomorph characters. Rosen *et al.* (1981) further make the more specific claim that, whatever its status with respect to tetrapods, Osteolepiformes cannot be characterized by autapomorphies. Ironically they also neglect to cite the autapomorphies of Dipnoi, while clearly regarding them as a monophyletic group.

Both osteolepiforms and dipnoans can be characterized and Dr Smithson and I discuss their status at length in our forthcoming review. Meanwhile to give them respectability I will cite autapomorphies for each. That of the Osteolepiformes is illustrated by Rosen *et al.* (their figure 43). The cheek plate of the skull of both osteolepiforms and primitive tetrapods consists of seven dermal bones: maxillary, lacrimal, jugal, postorbital, squamosal, quadratojugal and preopercular. However the configuration of these differs consistently between the two groups. In osteolepiforms, the squamosal contacts the maxillary, precluding any contact between jugal and quadratojugal: in tetrapods the converse occurs, with a jugal–quadratojugal contact. We believe both these conditions to be derived from the plesiomorph condition represented by porolepiforms (also Rosen *et al.*, figure 43) in which the critical area is occupied by two supernumary ossifications. Dipnoi may be characterized by the histology of the tooth plates or marginal denticles, or both (Smith 1979), and the course of the mandibular adductor muscles, which extend over the top of the neurocranium to originate either on the walls of the 'medial temporalis fossa' (Jarvik 1980) or postcranially (T. R. Smithson, personal communication).

In table 2 each character state of a pair may be regarded as primitive, depending on whether Osteolepiformes or Dipnoi is the sister-group of tetrapods, and this is indicated in the table. However, the problem posed by these rival primitive characters may be stood on its head, so that each character state may be used as a synapomorphy uniting tetrapods and the tetrapod sister-group that the state favours. The vicious circle is thus closed: a character state is 'proved' primitive because of its occurrence in the 'outgroup', that is, the sister-group of tetrapods; but that same character state is used as evidence, that is, a synapomorphy, to establish the same sister-group relationship. There seems to me to be no escape from this circularity of reasoning. Like the use of parsimony (Panchen 1982), and in fact closely related to it, this aspect of cladist methodology breaks down when there is a genuine taxonomic controversy to be resolved.

This study would have been impossible without the loan of all known material of *Crassigyrinus* from three institutions, the Royal Scottish Museum, the British Museum (Natural History) and the Institute of Geological Sciences, Edinburgh. The most important specimen in advancing our knowledge of *Crassigyrinus* was the Cowdenbeath skeleton collected with the rest of the tetrapod and fish material from that site by Mr Stanley Wood. As with other studies his unique talent as a collector has done much to further the cause of British vertebrate palaeontology. During part of the period of the work on *Crassigyrinus* Mr Wood was employed as a technician by the University of Newcastle upon Tyne on a N.E.R.C. grant (GR3/2983) awarded to the author.

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REFERENCES

Allen, J. M., Blaxter, J. H. S. & Denton, E. J. 1976 The functional anatomy and development of the swimbladder–inner ear–lateral line system in herring and sprat. *J. mar. biol. Ass. U.K.* **56**, 471–486.

Andrews, S. M. 1977 The axial skeleton of the coelacanth, *Latimeria*. In *Problems in vertebrate evolution* (ed. S. M. Andrews, R. S. Miles and A. D. Walker), pp. 271–288. London: Academic Press.

Andrews, S. M., Browne, M. A. E., Panchen, A. L. & Wood, S. P. 1977 Discovery of amphibians in the Namurian (Upper Carboniferous) of Fife. *Nature, Lond.* **265**, 529–532.

Andrews, S. M. & Westoll, T. S. 1970*a* The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Trans. R. Soc. Edinb.* **68**, 207–329.

Andrews, S. M. & Westoll, T. S. 1970*b* The postcranial skeleton of rhipidistians excluding *Eusthenopteron*. *Trans. R. Soc. Edinb.* **68**, 391–489.

Atthey, T. 1876 On *Anthracosaurus russelli*, Huxley. *Ann. Mag. nat. Hist.* **18**, 146–167.

Baird, D. 1957 Rhachitomous vertebrae in the loxommid amphibian *Megalocephalus*. *Bull. geol. Soc. Am.* **68**, 1698.

Beaumont, E. H. 1977 Cranial morphology of the Loxommatidae (Amphibia: Labyrinthodontia). *Phil. Trans. R. Soc. Lond.* B **280**, 29–101.

Bolt, J. R. 1969 Lissamphibian origins: possible protolissamphibian from the Lower Permian of Oklahoma. *Science, Wash.* **166**, 888–891.

Bone, Q. & Marshall, N. B. 1982 *Biology of the fishes*. Glasgow & London: Blackie.

Bossy, K. V. H. 1976 Morphology, paleoecology and evolutionary relationships of the Pennsylvanian urocordylid nectrideans (Subclass Lepospondyli, Class Amphibia). Ph.D. thesis, Yale University.

Boy, J. A. & Bandel, K. 1973 *Brukterer peton fiebigi* n.gen. n.sp. (Amphibia: Gephyrostegida) der erste Tetrapode aus dem rheinischwestfälischen Karbon (Namur B; W-Deutschland). *Palaeontographica* (A) **145**, 39–77.

Boyd, M. J. 1980 The axial skeleton of the Carboniferous amphibian *Pteroplax cornutus*. *Palaeontology* **23**, 273–285.

Boyd, M. J. 1982 Morphology and relationships of the Upper Carboniferous aïstopod amphibian *Ophiderpeten nanum*. *Palaeontology* **25**, 209–214.

Brough, M. C. & Brough, J. 1967 Studies on early tetrapods. I. The Lower Carboniferous microsaurs. II. *Microbrachis*, the type microsaur. III. The genus *Gephyrostegus*. *Phil. Trans. R. Soc. Lond.* B **252**, 107–165.

Bystrow, A. P. 1935 Morphologische Untersuchungen der Deckknochen des Schädels der Wirbeltiere. I. Schädel der Stegocephalen. *Acta zool., Stockh.* **16**, 65–141.

Bystrow, A. P. 1938 Zahnstructur der Labyrinthodonten. *Acta zool., Stockh.* **19**, 387–425.

Bystrow, A. P. 1944 *Kotlassia prima* Amalitzky. *Bull. geol. Soc. Am.* **55**, 379–416.

Carroll, R. L. 1969*a* Problems of the origin of reptiles. *Biol. Rev.* **44**, 393–432.

Carroll, R. L. 1969*b* A new family of Carboniferous amphibians. *Palaeontology* **12**, 537–548.

Carroll, R. L. 1970 The ancestry of reptiles. *Phil. Trans. R. Soc. Lond.* B **257**, 267–308.

Carroll, R. L. 1980 The hyomandibular as a supporting element in the skull of primitive tetrapods. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 293–317. London: Academic Press.

Carroll, R. L. & Baird, D. 1972 Carboniferous stem-reptiles of the family Romeriidae. *Bull. Mus. comp. Zool. Harv.* **143**, 321–363.

Carroll, R. L. & Gaskill, P. 1978 The order Microsauria. *Mem. Am. phil. Soc.* **126**, 1–211.

Chase, J. N. 1965 *Neldasaurus wrightae*, a new rhachitomous labyrinthodont from the Texas Lower Permian. *Bull. Mus. comp. Zool. Harv.* **133**, 153–225.

Clack, J. A. 1983 The stapes of the Coal Measure embolomere *Pholiderpeton scutigerum* Huxley (Amphibia: Anthracosauria) and otic evolution in early tetrapods. *Zool. J. Linn. Soc.* **79**, 121–148.

Colbert, E. H. 1955 Scales in the Permian Amphibian *Trimerorhachis*. *Amer. Mus. Novit.* no. 1740, 1–17.

Cope, E. D. & Matthew, W. D. 1915 Hitherto unpublished plates of Tertiary Mammalia and Vertebra. *Am. Mus. nat. Hist. Monograph Ser.* No. 2, plates 1–154.

Denton, E. J. & Blaxter, J. H. S. 1976 The mechanical relationships between the clupeid swimbladder, inner ear and lateral line. *J. mar. biol. Ass. U.K.* **56**, 787–807.

Eldredge, N. & Cracraft, J. 1980 *Phylogenetic patterns and the evolutionary process: method and theory in comparative biology*. New York: Columbia University Press.

Embleton, D. & Atthey, T. 1874 On the skull and some other bones of *Loxomma allmanni*. *Ann. Mag. nat. Hist.* **14**, 38–63.

Forey, P. L. 1982 Neontological analysis versus palaeontological stories. In *Problems of phylogenetic reconstruction* (ed. K. A. Joysey and A. E. Friday), pp. 119–157. London: Academic Press.

Frisch, J. von 1936 Über den Gehörsinn der Fische. *Biol. Rev.* **11**, 210–246.

Fritsch, A. 1889 *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens*, Band II (1885–1889). Prague.

Gaffney, E. S. 1979 Tetrapod monophyly: a phylogenetic analysis. *Bull. Carneg. Mus.* no. 13, 92–105.

Heaton, M. J. 1979 Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian Oklahoma and Texas. *Bull. Oklahoma Geol. Surv.* no. 127, 1–84.

Heaton, M. J. 1980 The Cotylosauria: a reconsideration of a group of archaic tetrapods. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 497–551. London: Academic Press.

Holmes, R. B. 1980 *Proterogyrinus scheelei* and the early evolution of the labyrinthodont pectoral limb. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 351–376. London: Academic Press.

Holmes, R. B. 1984 The Carboniferous amphibian *Proterogyrinus scheelei* Romer and the early evolution of tetrapods. *Phil. Trans. R. Soc. Lond.* B **306**, 431–524.

Huxley, T. H. 1863 Description of *Anthracosaurus russelli*, a new labyrinthodont from the Lanarkshire coal field. *Q. Jl geol. Soc. Lond.* **19**, 56–68.

Jarvik, E. 1942 On the structure of the snout of crossopterygians and lower gnathostomes in general. *Zool. Bidr. Upps.* **21**, 235–675.

Jarvik, E. 1952 On the fish-like tail in the ichthyostegid stegocephalians. *Meddr Grønland* **114**, no. 12, 1–90.

Jarvik, E. 1980 *Basic structure and evolution of vertebrates* (2 vols). London: Academic Press.

Konjukova, E. D. 1953 Terrestrial vertebrate fauna of the Lower Permian of the northern pre-Urals (River Inta basin). *Dokl. Acad. Nauk SSSR* **89**, 723–726. (In Russian.)

Lombard, R. E. & Bolt, J. R. 1979 Evolution of the tetrapod middle ear: an analysis and reinterpretation. *Biol. J. Linn. Soc.* **11**, 19–76.

Lydekker, R. 1890 On two new species of labyrinthodonts. *Q. Jl geol. Soc. Lond.* **46**, 289–294.

Miles, R. S. 1977 Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *Zool. J. Linn. Soc.* **61**, 1–328.

Milner, A. C. 1980 A review of the Nectridea (Amphibia). In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 377–405. London: Academic Press.

Moulton, J. M. 1974 A description of the vertebral column of *Eryops* based on the notes and drawings of A. S. Romer. *Breviora* no. 428, 1–44.

Noble, G. K. 1931 *The Biology of the Amphibia*. New York: McGraw-Hill.

Olson, E. C. 1971 *Vertebrate paleozoology*. New York: Wiley-Interscience.

Panchen, A. L. 1964 The cranial anatomy of two Coal Measure anthracosaurs. *Phil. Trans. R. Soc. Lond.* B **247**, 593–637.

Panchen, A. L. 1966 The axial skeleton of the labyrinthodont *Eogyrinus attheyi*. *J. Zool., Lond.* **150**, 199–222.

Panchen, A. L. 1967*a* The homologies of the labyrinthodont centrum. *Evolution* **21**, 24–33.

Panchen, A. L. 1967*b* The nostrils of choanate fishes and early tetrapods. *Biol. Rev.* **42**, 374–420.

Panchen, A. L. 1970 *Handbuch der Paläoherpetologie*. Teil 5a. Anthracosauria. Stuttgart: Fischer.

Panchen, A. L. 1972*a* The skull and skeleton of *Eogyrinus attheyi* Watson (Amphibia: Labyrinthodontia). *Phil. Trans. R. Soc. Lond.* B **263**, 279–326.

Panchen, A. L. 1972*b* The interrelationships of the earliest tetrapods. In *Studies in vertebrates evolution – essays presented to Dr F. R. Parrington F.R.S.* (ed. K. A. Joysey and T. S. Kemp), pp. 65–87. Edinburgh: Oliver & Boyd.

Panchen, A. L. 1973 On *Crassigyrinus scoticus* Watson, a primitive amphibian from the Lower Carboniferous of Scotland. *Palaeontology* **16**, 179–193.

Panchen, A. L. 1975 A new genus and species of anthracosaur amphibian from the Lower Carboniferous of Scotland and the status of *Pholidogaster pisciformis* Huxley. *Phil. Trans. R. Soc. Lond.* B **269**, 581–640.

Panchen, A. L. 1977*a* The origin and early evolution of tetrapod vertebrae. In *Problems in vertebrate evolution* (ed. S. M. Andrews, R. S. Miles and A. D. Walker), pp. 289–318. London: Academic Press.

Panchen, A. L. 1977*b* On *Anthracosaurus russelli* Huxley (Amphibia: Labyrinthodontia) and the family Anthracosauridae. *Phil. Trans. R. Soc. Lond.* B **279**, 447–512.

Panchen, A. L. 1980 The origin and relationships of the anthracosaur amphibia from the Late Palaeozoic. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 319–350. London: Academic Press.

Panchen, A. L. 1981 A jaw ramus of *Anthracosaurus russelli* Huxley (Amphibia: 'Labyrinthodontia') from the Northumberland Coal Measures. *Palaeontology* **24**, 85–92.

Panchen, A. L. 1982 The use of parsimony in testing phylogenetic hypotheses. *Zool. J. Linn. Soc.* **74**, 305–328.

Parrington, F. R. 1956 The patterns of dermal bones in primitive vertebrates. *Proc. zool. Soc. Lond.* **127**, 389–411.

Patterson, C. 1980 Origin of tetrapods: historical introduction to the problem. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 159–175. London: Academic Press.

Patterson, C. & Rosen, D. E. 1977 Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bull. Am. Mus. nat. Hist.* **158**, 81–172.

Rackoff, J. S. 1980 The origin of the tetrapod limb and the ancestry of tetrapods. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 255–292. London: Academic Press.

Romer, A. S. 1947 Review of the Labyrinthodontia. *Bull. Mus. comp. Zool. Harv.* **99**, 1–368.

Romer, A. S. 1957 The appendicular skeleton of the Permian embolomerous amphibian *Archeria*. *Contr. Mus. Geol. Univ. Mich.* **13**, 103–159.

Romer, A. S. 1964 The skeleton of the Lower Carboniferous labyrinthodont *Pholidogaster pisciformis*. *Bull. Mus. comp. Zool. Harv.* **131**, 129–159.

Romer, A. S. 1966 *Vertebrate paleontology* (3rd edn.). Chicago: University Press.

Romer, A. S. 1969 The cranial anatomy of the Permian amphibian *Pantylus*. *Breviora*, no. 314, pp. 1–37.

Rosen, D. E., Forey, P. L., Gardiner, B. G. & Patterson, C. 1981 Lungfishes, tetrapods, paleontology and plesiomorphy. *Bull. Am. Mus. nat. hist.* **167**, 159–276.

Säve-Söderbergh, G. 1932 Preliminary note on Devonian stegocephalians from East Greenland. *Meddr Grønland* **94**, no. 7, 1–107.

Säve-Söderbergh, G. 1935 On the dermal bones of the head in labyrinthodont stegocephalians and primitive Reptilia. *Meddr Grønland* **98**, no. 3, 1–211.

Sawin, H. J. 1941 The cranial anatomy of *Eryops megacephalus*. *Bull. Mus. comp. Zool. Harv.* **88**, 407–463.

Schultze, H.-P. 1969 Die Faltenzähne der rhipidistiiden Crossopterygier, der Tetrapoden und der Actinopterygier-Gattung *Lepisosteus*. *Palaeontogr. ital.* **65** (*N.S.* **35**), 59–137.

Schultze, H.-P. 1970 Folded teeth and the monophyletic origin of tetrapods. *Amer. Mus. Novit.* no. 2408, 1–10.

Smith, M. M. 1979 Structure and histogenesis of tooth plates in *Sagenodus inaequalis* Owen considered in relation to the phylogeny of post-Devonian dipnoans. *Proc. R. Soc. Lond.* B **204**, 15–39.

Smithson, T. R. 1980*a* An early tetrapod fauna from the Namurian of Scotland. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 407–438. London: Academic Press.

Smithson, T. R. 1980*b* A new labyrinthodont amphibian from the Carboniferous of Scotland. *Palaeontology* **23**, 915–923.

Smithson, T. R. 1982 The cranial morphology of *Greererpeton burkemorani* Romer (Amphibia: Temnospondyli). *Zool. J. Linn. Soc.* **76**, 29–90.

Smithson, T. R. 1983 The anthracosaur amphibia from the Namurian of Scotland. Ph.D. thesis, University of Newcastle upon Tyne.

Smithson, T. R. 1984 The morphology and relationships of the Carboniferous amphibian *Eoherpeton watsoni* Panchen. *Zool. J. Linn. Soc.* (In the press.)

Smithson, T. R. & Thomson, K. S. 1982 The hyomandibular of *Eusthenopteron foordi* Whiteaves (Pisces: Crossopterygii) and the early evolution of the tetrapod stapes. *Zool. J. Linn. Soc.* **74**, 93–103.

Stovall, J. W. 1948 A new species of embolomerous amphibian from the Permian of Oklahoma. *J. Geol.* **56**, 75–79.

Thomson, K. S. & Campbell, K. S. W. 1971 The structure and relationships of the primitive Devonian lungfish – *Dipnorhynchus sussmilchi* (Etheridge). *Bull. Peabody Mus.* no. 38, 1–109.

Vaughn, P. P. 1972 More vertebrates including a new microsaur, from the Upper Pennsylvanian of Central Colorado. *Contr. Sci.* no. 223, 1–30.

Walls, G. L. 1963 *The vertebrate eye and its adaptive radiation*. New York: Hafner.

Watson, D. M. S. 1919 The structure, evolution and origin of the Amphibia – the 'Orders' Rachitomi and Stereospondyli. *Phil. Trans. R. Soc. Lond.* B **209**, 1–73.

Watson, D. M. S. 1926 Croonian Lecture – the evolution and origin of the Amphibia. *Phil. Trans. R. Soc. Lond.* B **214**, 189–257.

Watson, D. M. S. 1929 The Carboniferous Amphibia of Scotland. *Palaeont. hung.* **1**, 219–252.

Watson, D. M. S. 1951 *Paleontology and modern biology*. New Haven: Yale University Press.

Watson, D. M. S. 1954 On *Bolosaurus* and the origin and classification of reptiles. *Bull. Mus. comp. Zool. Harv.* **111**, 297–450.

Wellstead, C. F. 1982 A Lower Carboniferous aïstopod amphibian from Scotland. *Palaeontology* **25**, 193–208.

White, E. I. 1965 The head of *Dipterus valenciennesi* Sedgwick & Murchison. *Bull. Br. Mus. nat. Hist.* (*Geol.*) **11**, 1–45.

White, T. E. 1939 Osteology of *Seymouria baylorensis* Broili. *Bull. Mus. comp. Zool. Harv.* **85**, 325–409.

Wiley, E. O. 1981 *Phylogenetics: the theory and practice of phylogenetic systematics*. New York: Wiley-Interscience.

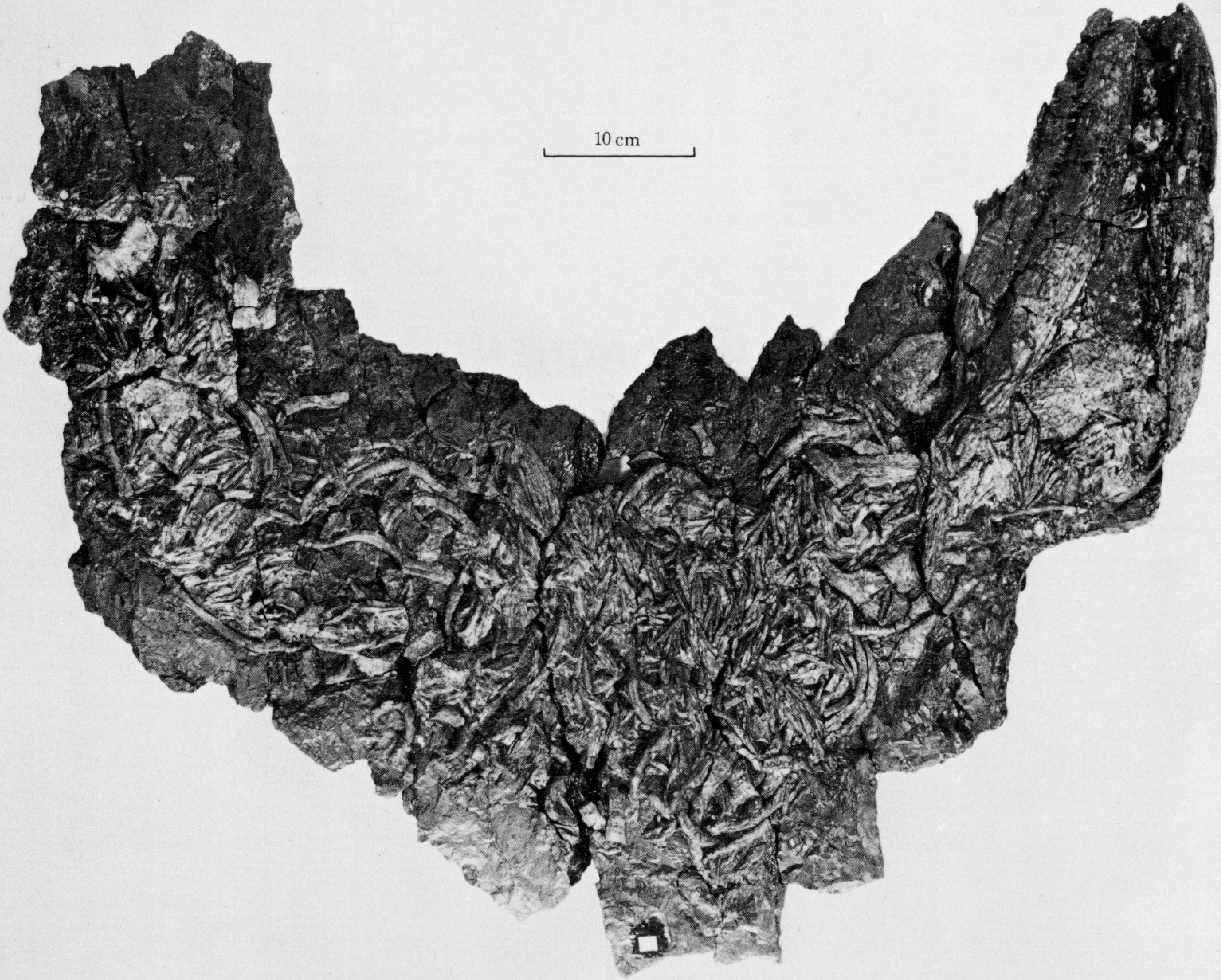


FIGURE 1. *Crassigyrinus scoticus* Watson, the Cowdenbeath specimen, ventral view.

FIGURE 2. *Crassigyrinus scoticus* Watson, skull from Cowdenbeath skeleton, dorsal view.

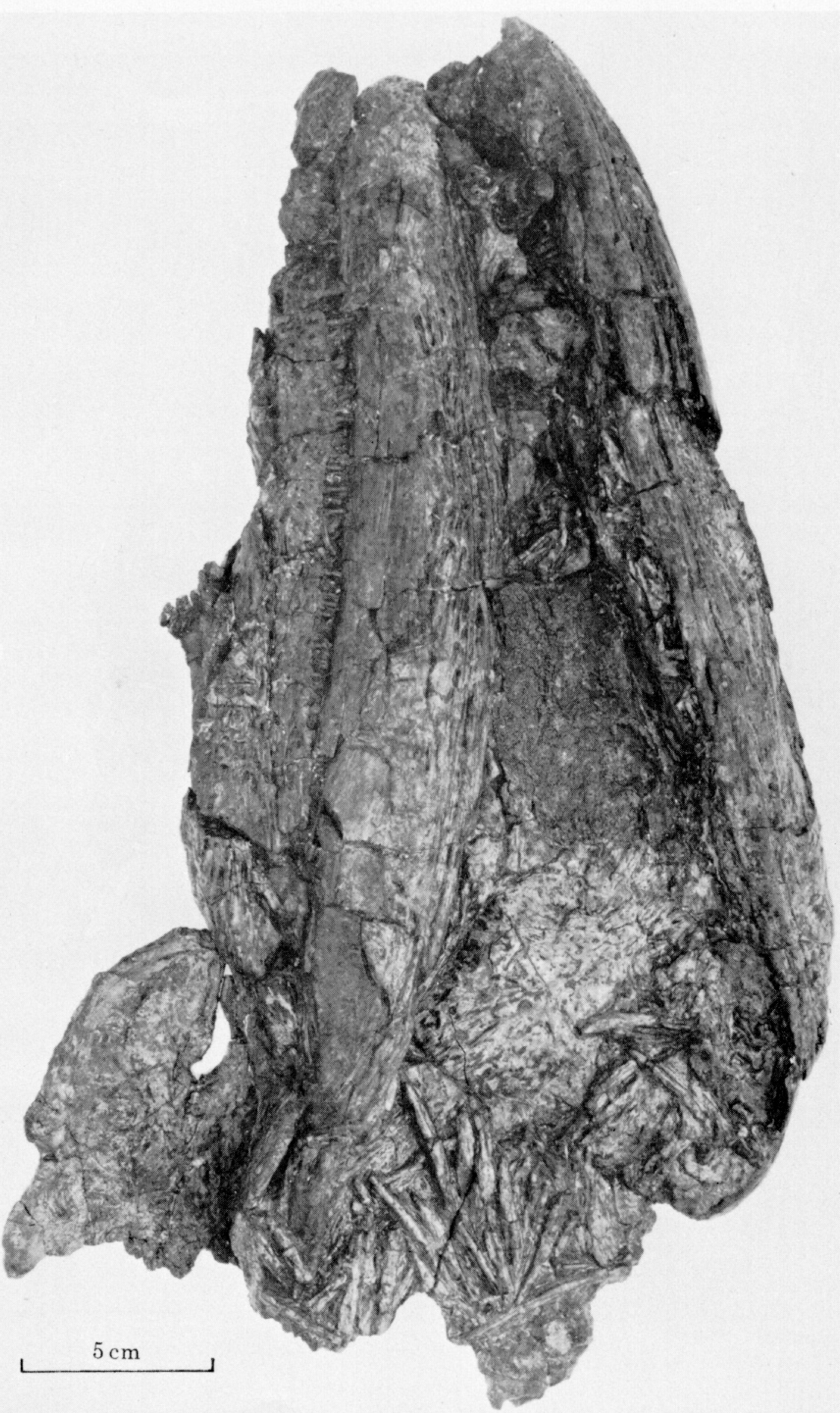
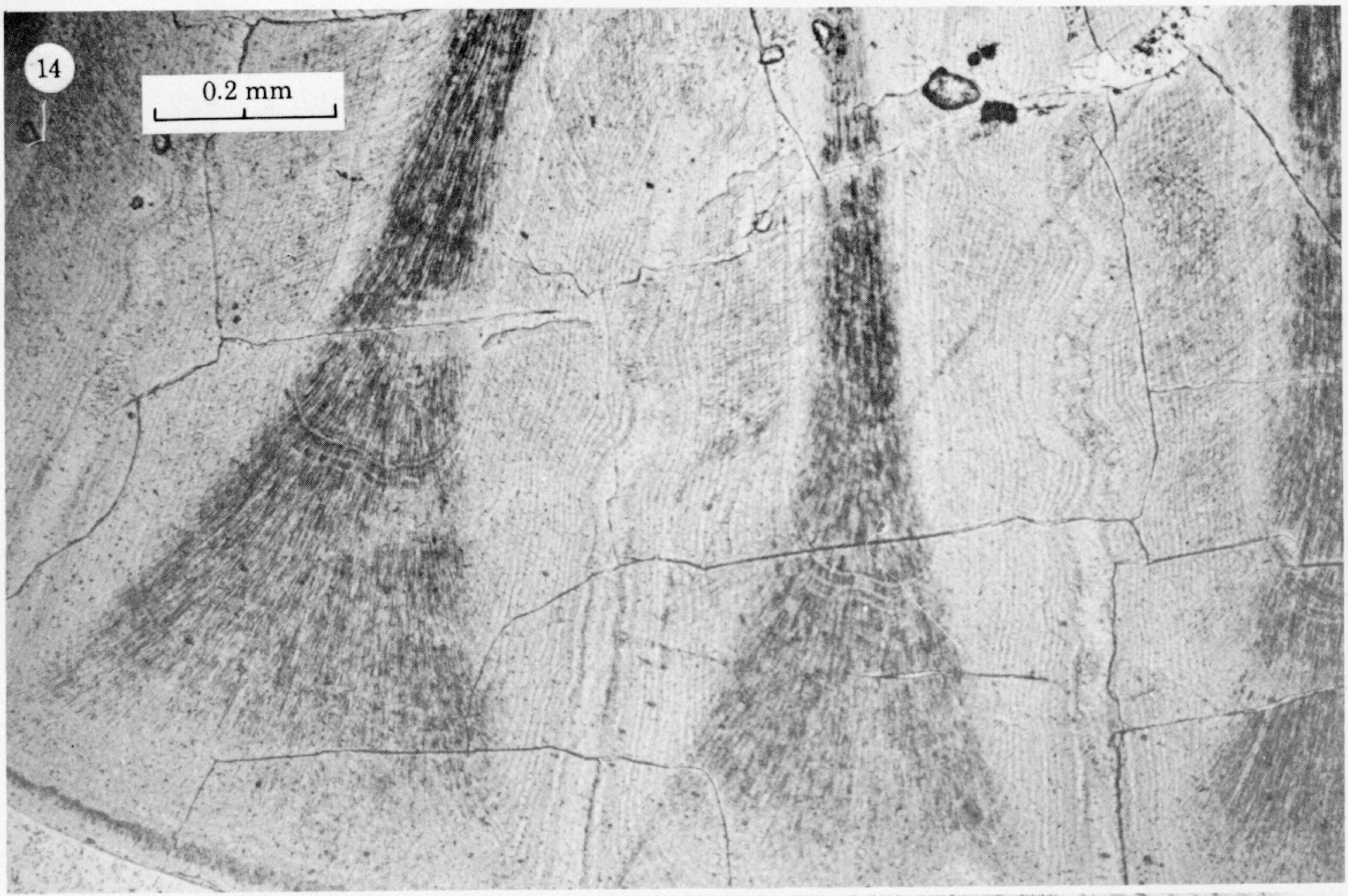


FIGURE 5. *Crassigyrinus scoticus* Watson, skull from Cowdenbeath skeleton, ventral view.

FIGURE 6. *Crassigyrinus scoticus* Watson (B.M.N.H., R 30532) palate, probably from Gilmerton Ironstone.



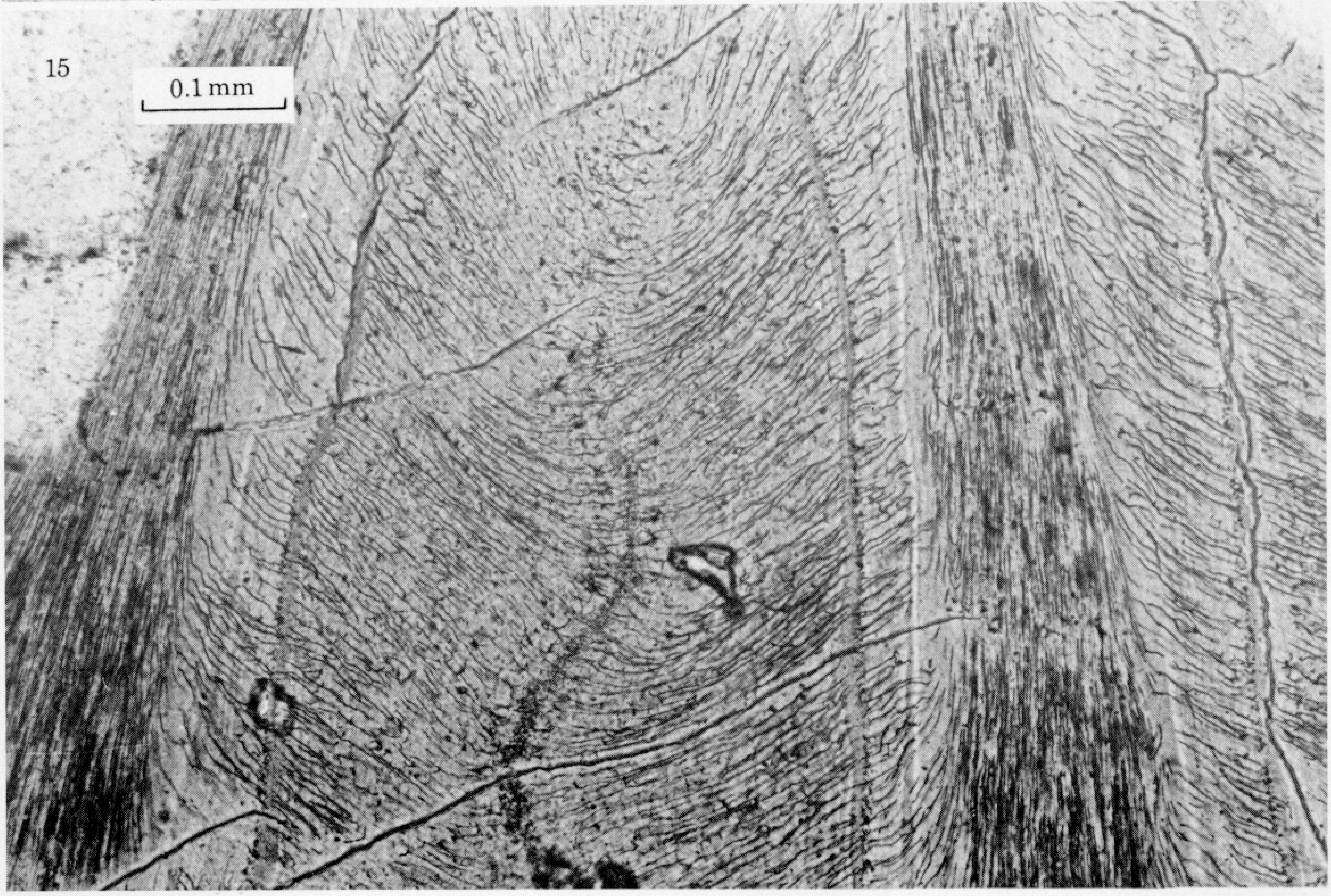


FIGURE 14. *Crassigyrinus scoticus* Watson, T.S. at base of palatine tusk of B.M.N.H., R 30532, to show infolded primary with secondary dentine separated by 'dark dentine'. Magn. ×100.

FIGURE 15. *Crassigyrinus scoticus* Watson, T.S. palatine tusk as above (figure 14), to show dentine tubules. Magn. ×160.

FIGURE 16. *Crassigyrinus scoticus* Watson, plan of Cowdenbeath skeleton as originally exposed in ventral view (for rest of skull see figure 4). Oblique hatching-skull bones; light stipple-appendicular skeleton; medium stipple-ribs; dark stipple-centra and neural arches; solid black-individual scales in figure 20 (other scales blank); centra numbered; figured ribs in heavy outline. Rectangle indicates patch of scales in figure 20. n.a., Separated neural arch in figure 17.

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