

A new baphetid (stem tetrapod) from the Upper Carboniferous of Tyne and Wear, U.K., and the evolution of the tetrapod occiput

J.A. Clack

Abstract: A new genus and species of baphetid, *Kyrinion martilli*, is described from the Westphalian A (Upper Carboniferous) of Tyne and Wear, England. The skull, braincase, and partial lower jaws are preserved in a nodule of iron-rich seat-earth, in an almost uncrushed state. The occiput and both stapes are in place. The palate and braincase are united by a continuous sheet of denticulated pterygoid and parasphenoid eliminating the interpterygoid vacuities completely, and the parasphenoid bounds deep parasphenoidal tubera; the marginal palatal bones, pterygoid, and dentary are united by interdigitated sutures, rendering the whole skull akinetic. The orbits are approximately triangular, without the “pinching in” that defines an antorbital embayment in other baphetids. The maxilla has a very narrow exposure beneath and posterior to the orbit, and though it and the lacrimal lack lateral line grooves, there is a short stretch on the quadratojugal. Unlike *Megalocephalus*, the lower jaw symphysis is relatively simple and does not bear a “brassicata” structure and the parasymphysial plate lacks teeth. The stapes is broad and flat distally, with its distal end lying against the palatal bones as in other early tetrapods, but it is difficult to envisage a structural role for this element as suggested by recent hypotheses. The basi- and exoccipitals co-ossified as in some specimens of *Greererpeton* and *Acanthostega*, but unlike the latter, the condyle is almost fully ossified. The exoccipitals do not contact the skull roof as they do in temnospondyls, but fully ossified paroccipital processes suture with the tabulars, a feature suggested as synapomorphic for baphetids plus temnospondyls. The specimen also preserves a rib, possibly but not certainly cervical, and an atlas arch. The proatlantes of *Loxomma* are described and figured.

Résumé : Un nouveau genre et une nouvelle espèce de baphetidé, *Kyrinion martilli*, est décrit à partir du Westphalien A (Carbonifère supérieur) de Tyne et Wear, en Angleterre. Le crâne, la boîte crânienne et des parties de mâchoires inférieures sont préservés à l'intérieur d'un nodule d'un paléosol (“seat-earth”) riche en fer, dans un état pratiquement non écrasé. L'occipital et les deux stapes sont en place. Le palais et la boîte crânienne sont réunis par un ptérygoïde denticulé et un parasphénoïde en feuillet continu, éliminant complètement les vacuités de l'interptérygoïde et le parasphénoïde limite les tubérosités parasphénoïdales profondes; les os marginaux du palais, le ptérygoïde et le dentaire sont unis par des sutures interdigitées, ce qui rend le crâne entièrement akinétique. Les orbites sont approximativement triangulaires, ne présentant pas le « ‘pincement’ » qui définit l'enfoncement antorbital chez les autres baphetidés. Le maxille a une exposition très étroite sous-jacente et postérieure à l'orbite et, malgré l'absence de sillons latéraux sur le maxille et le lacrimale, il y a une courte extension sur le quadratojugal. Contrairement au *Megalocephalus*, la symphyse mandibulaire inférieure est relativement simple et ne porte pas de structure « en forme de choux-fleur » et la plaque parasymphysiale n'a pas de dent. Le stapes est large et à partie distale plate, avec son extrémité distale posée contre les os du palais comme chez les autres tétrapodes précoces, mais il est difficile d'envisager un rôle structural pour cet élément comme le suggèrent de récentes hypothèses. Les basi- et exoccipitaux sont co-ossifiés comme chez quelques spécimens de *Greererpeton* et *Acanthostega*, mais contrairement à ce dernier le condyle est presque totalement ossifié. Les exoccipitaux ne touchent pas le plafond du crâne comme ils le font chez les temnospondyles, mais la suture du processus paroccipital est complètement ossifiée avec les tabulaires, un caractère suggéré comme synapomorphe pour les baphetidés et les temnospondyles. Le spécimen montre aussi une côte, probablement mais pas certainement cervicale, et un arc de l'atlas. Les pro-atlantes de *Loxomma* sont décrites et représentées.

[Traduit par la Rédaction]

Introduction

The baphetids are a group of primitive stem tetrapods whose position in early tetrapod phylogeny remains unclear. Among the first Carboniferous tetrapods to be recognised (e.g., Dawson 1863), they have influenced ideas about early tetrapod evolution ever since. Placed by Romer among the “Labyrinthodontia,” they were allied with temnospondyls on the basis of what are now considered to be primitive characters: their similar skull shape and comparable pattern of skull roof bones and dermal ornament. Opinion has changed several

Received 6 February 2002. Accepted 25 July 2002. Published on the NRC Research Press Web site at <http://cjcs.nrc.ca> on 29 April 2003.

Paper handled by Associate Editor B. Chatterton.

J.A. Clack. University Museum of Zoology, Downing St., Cambridge, CB2 2EJ, U.K. (e-mail: j.a.clack@zoo.cam.ac.uk).

times over the past twenty years, and they have been placed variously as related to “anthracosaurs” (Panchen 1980; Panchen and Smithson 1988; Clack 1998a), as a stem plesion near the base of the tetrapod tree (Ahlberg and Milner 1994; Carroll 1995; Laurin and Reisz 1997), or back with temnospondyls, (Clack 2001a, 2002).

Four genera were initially recognised: *Baphetes*, *Loxomma*, *Megalocephalus* and *Spathicephalus*. More recently, the genus *Eucritta* has been added, though with reservations (Clack 1998a, 2001a). *Baphetes* (four species), *Loxomma* (two or three species) and *Megalocephalus* (one or two species) were last fully reviewed in 1977 by Beaumont, whereas *Spathicephalus* has received greater attention more recently (Beaumont and Smithson 1998). Long known from little but cranial material, postcranial material of *Baphetes* was described for the first time the same year (Milner and Lindsay 1998). A preliminary analysis of baphetid relationships was attempted in 1997 (Milner 1997), and a full review is in progress (A.C. Milner personal communication, 2000).

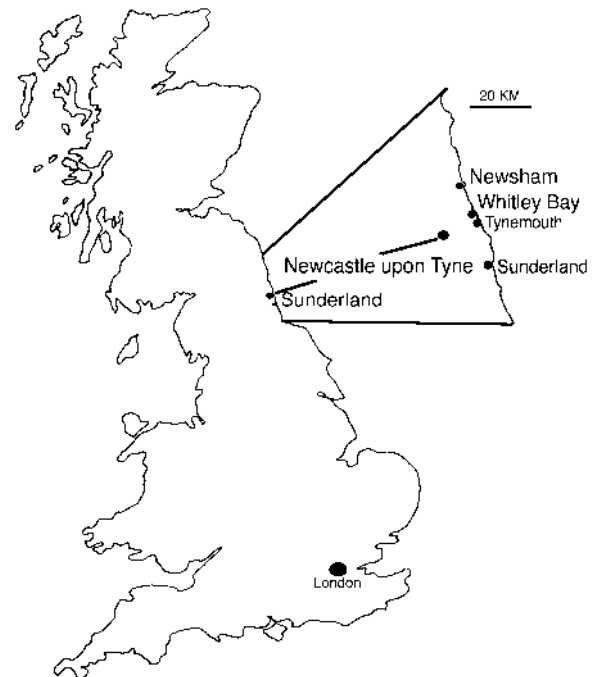
All except for *Eucritta* share a striking feature of the orbit, which is enlarged by the presence of an antorbital embayment that gives the vacuity a “key-hole” shape. *Eucritta* shows what may be the beginnings of this, having rather small antorbital expansions. The function of this strange feature has inspired several explanations, from accommodation for a salt gland (Romer 1947), a space for a bulging pterygoideus muscle (Beaumont 1977), to housing for an electrosensory organ (Bjerring 1986), but none is satisfactory or easily testable. *Spathicephalus* is the most specialized of the genera, with a broad, spatulate, and extremely flattened skull, in which the orbits are very close together. The teeth are also specialized and remarkable for their large number and uniform appearance. They may be adapted for filter feeding (Beaumont and Smithson 1998).

This paper describes a new genus and species of baphetid from a specimen found in 1993 on the coast near Whitley Bay, Tyne and Wear, U.K. (Figs 1, 2, 3a). As well as the skull and partial lower jaws, the specimen preserves a rib, a possible ceratohyal and a probable atlas arch. The new specimen shares at least one feature with each of the existing genera, except *Eucritta*, that is not known to occur in any of the others. It also shows differences from each and has apomorphies of its own. Erection of a new genus is, therefore, considered to be justified.

Baphetids are only known from the mid–Late Carboniferous. *Eucritta* is marginally the earliest, appearing with *Loxomma allmani* in the Viséan. The latter is the only tetrapod genus known to cross the boundary from the Lower to the Upper Carboniferous (Smithson 1985). *Spathicephalus* is the next earliest, from the early Namurian, while *Megalocephalus* ranges from Westphalian A–C and *Baphetes* ranges from Westphalian C–D. *Loxomma* has been considered the most primitive genus (Beaumont 1977), though relationships remain to be fully explored. Dated as Westphalian A, in terms of time-range the new specimen is unremarkable.

The major importance of the specimen described here lies in the excellent preservation of its occipital region, complete with both stapes lying in life position. The occiput is a key region in the early evolution of tetrapods as it changes from a rather inflexible, notochordal structure to one that is responsible for supporting muscles that move the head, and

Fig. 1. Map showing location of Whitley Bay: map of Great Britain with enlargement of section of coastline to the right. Newcastle upon Tyne is the location of the Hancock Museum. Newsham is the location of the mine that yielded fossils from the Low Main Seam.



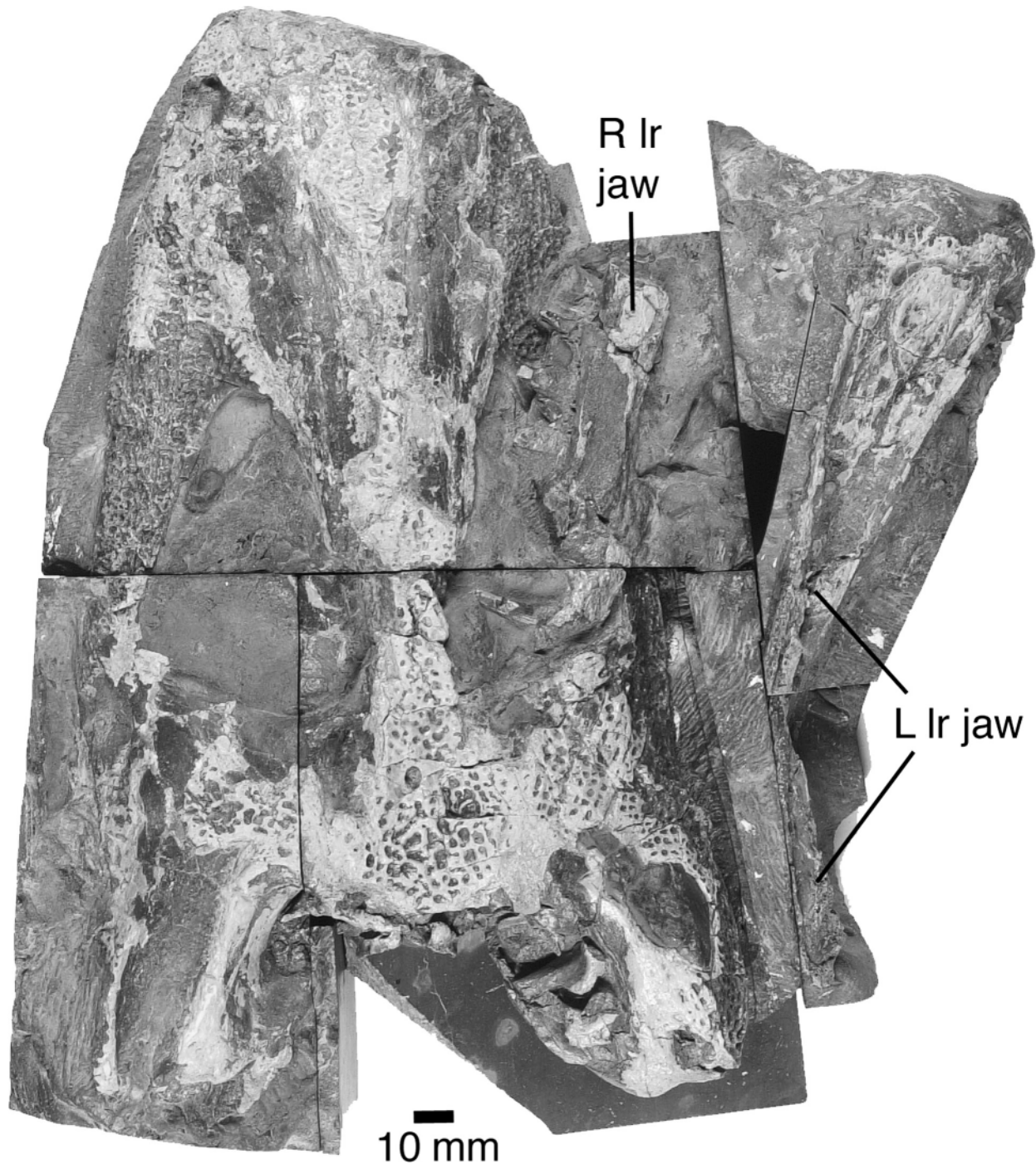
maintaining its horizontal position in a terrestrial environment. The occiput of *Baphetes* was described by Beaumont (1977) from rather flattened and incomplete material, and the present specimen shows significant differences from her interpretation. Since her description, the occiputs of several other early tetrapods have been discovered including that of the Devonian *Acanthostega*. The occiput of baphetids deserves renewed attention in the light of these findings as well as more recent ideas about occipital evolution (e.g., Smithson 1982; Clack 1998c) and tetrapod phylogeny. It will also be of use in outgroup comparison and in establishing character polarity in studies of the evolution of amniote occiput. For example that by Berman (2000) used *Acanthostega* rather than a Carboniferous tetrapod, whereas slightly less primitive tetrapods might in some circumstances be more useful as outgroups.

The new baphetid specimen preserves both stapes close to life position. Baphetid stapes are not well known. Prior to that described here, only two had been reported (Watson 1929; Beaumont and Smithson 1998). As primitive tetrapods long allied with temnospondyls, baphetid stapes are of interest from the point of view of the evolution of the otic region and the acquisition of an aurally adapted ear. Temnospondyls may have been the first group to have evolved such a mechanism (Clack 1992). The new specimen also gives details of the skull construction. Robust and heavily sutured, the skull was akinetic, and this throws light on hypotheses of skull kinesis in baphetids and possibly other early tetrapod groups.

Geological setting

The specimen was an isolated find discovered on the

Fig. 2. *Kyrinion martilli* NEWHM: 2000.H845, dorsal view of specimen. Photograph of specimen in dorsal view. L, left; lr, lower; R, right.



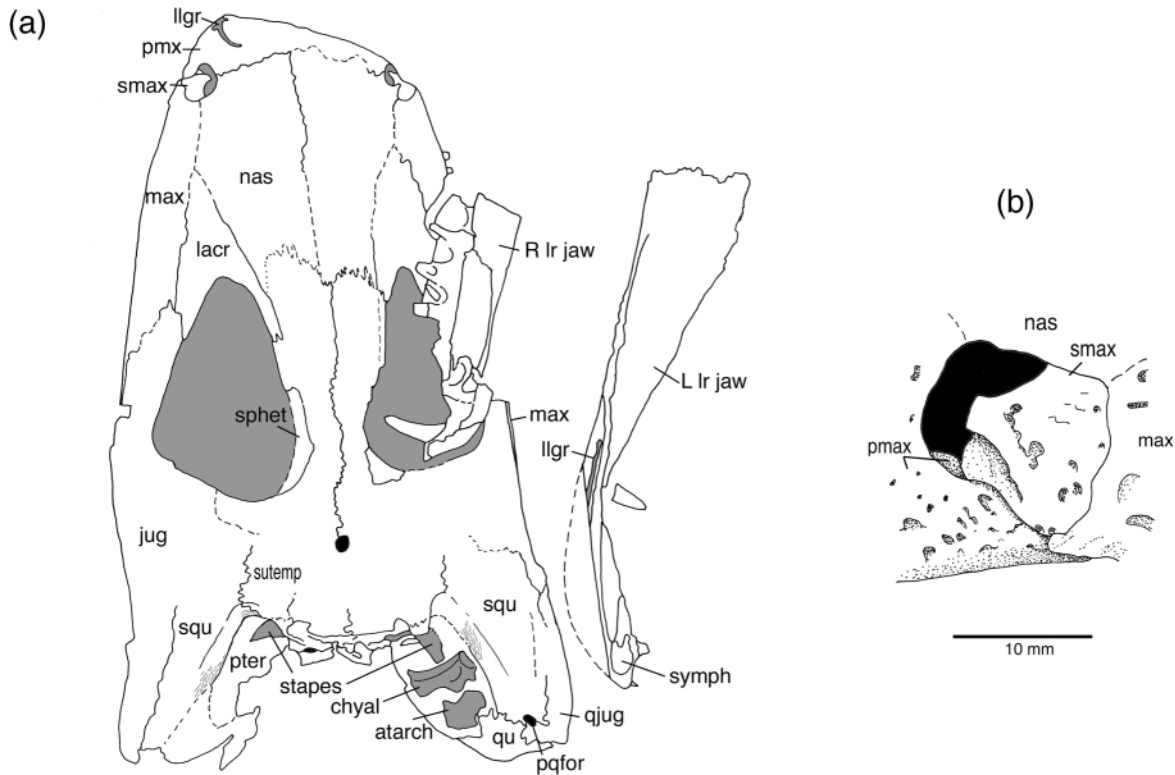
beach at Whitley Bay (Fig. 1) at the base of the Pleistocene boulder clay that lies above the Carboniferous deposits in the area. Presumably the specimen had been transported in the ice sheet that deposited the boulder clay, but its source is unclear.

Spore analysis was carried out by Dr J.E.A. Marshall of Southampton Oceanographic Centre, Southampton, U.K., who provided the following information. The sample analysed contained a very large number of spores and pollen, though these were mostly poorly preserved because of damage to and thinning of the exine. The dominant element is

Lycospora, particularly *L. pellucida*. Other abundant identifiable elements include the saccate pollen *Florinites*, possibly *F. pumicosus*. Densospore taxa include *Cingulizonates bialatus*, *Cristatisporites solaris*, *Densosporites annulatus* and *Radiizonites aligerens*. The latter has a range restricted to the RA spore zone, which is late Westphalian A. Other identifiable elements included *Lophotriteles vulgaris*, *Secarisporites remotus*, and *Crassispora kosankei*. The sample contained no significant elements indicating an age younger than late Westphalian A.

Outcropping in and around the area where the specimen

Fig. 3. *Kyrinion martilli* NEWHM: 2000.H845. (a) Interpretive diagram of specimen in dorsal view, orbits, hyobranchial, and axial elements shaded grey. (b) Enlargement of septomaxilla, atarch, atlas arch; chyal, ceratohyal; jug, jugal; L, left; lacr, lacrimal; llgr, lateral line groove; lr, lower; max, maxilla; nas, nasal; pter, pterygoid; pmx, premaxillary; pqfor, paraquadrate foramen; qjug, quadratojugal; qu, quadrate; R, right; smax, septomaxillary; sphet, sphenethmoid; squ, squamosal; sutemp, supratemporal; symph, symphysis.



was discovered are several coal seams including the well-known Low Main Seam from which large numbers of tetrapod specimens have derived in the past. However, the Low Main Seam is dated as Westphalian B, ruling it out as a source for the specimen. Furthermore, the specimen is preserved in an iron-rich seat-earth containing many plant macro-fragments. More usually, tetrapod specimens are found in the shales above coal-seams, including those from the Low Main Seam. In the area of Whitley Bay, several of these seat-earth facies outcrop, and to the north of St. Mary's Island there is at least one whose lithology greatly resembles that of the specimen to be described (personal observation). However, though lower in the sequence than the Low Main Seam, these horizons appear to be early Westphalian B (Jones 1967).

Material and methods

The specimen was discovered in 1993 by Dr. David Martill and acquired by the Hancock Museum. The skull is only slightly compressed, with its right side more distorted than the left, especially in the region of the skull table. The tip of the snout has been eroded away. The snout seems to have preserved its natural profile, as does the left suspensorium (Figs. 2, 4). Much of the surface of the skull roof has been eroded during its passage through the boulder clay, but in some places this has left a good natural mould of the inner surface. In other places, the bone is broken through. The palate has been bowed upwards into the skull cavity, and the ptery-

goids and parasphenoid cultiform process are somewhat fractured. The left lower jaw is more complete than the right, but it has been rotated to expose its inner surface on the right hand side of the specimen. Only a short length of the right lower jaw is present, from the symphysis to the posterior end of the anterior coronoid, and lies in the right orbit.

The specimen, which is extremely heavy, was prepared by first reducing the size and weight of the specimen using a diamond wire saw with a wire of 0.3 mm diameter. Other cuts were made to facilitate preparation of areas otherwise awkward or impossible to reach, and these also allowed examination of sections through the skull. Mechanical preparation by pneumatic pen, dental mallet, and mounted needle was then undertaken. Weathered bone is creamy in colour, whereas that exposed by preparation is coffee coloured. Photographs were taken using a Nikon D1 digital camera and processed using Adobe Photoshop 6.

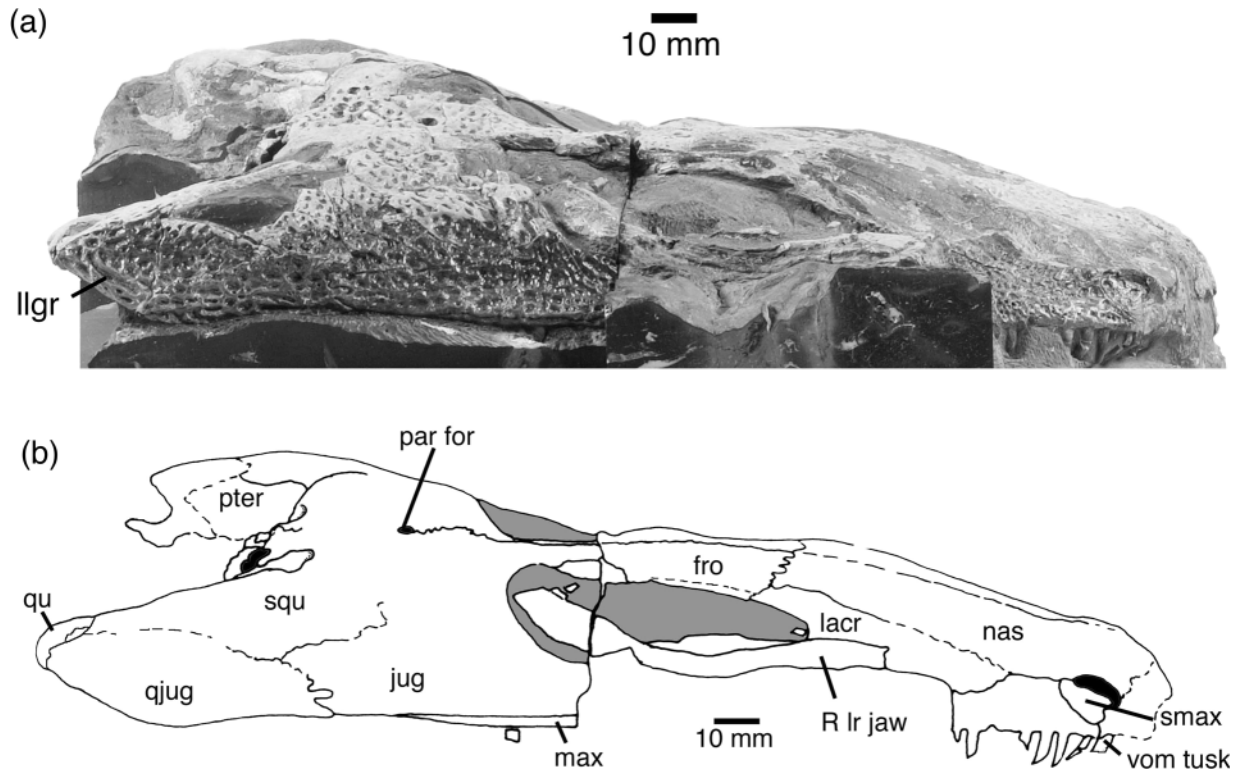
Systematic palaeontology

Kyrinion martilli gen. et sp. nov. (Figs. 2–9)

HOLOTYPE AND ONLY KNOWN SPECIES: Hancock Museum, Tyne and Wear, U.K., NEWHM: 2000.H845 A single skull about 270 mm long, both lower jaws present in part, preserved almost uncrushed in an ironstone nodule.

ETYMOLOGY: *Kyrinion*: *Kyreo*, Greek, light upon, find, meet; and *inion* Greek, occiput; *martilli*, after its discoverer, Dr.

Fig. 4. *Kyrinion martilli* NEWHM: 2000.H845, lateral view of specimen. (a) Specimen in right lateral view, (b) Interpretive diagram (orbits shaded grey). fro, frontal; jug, jugal; L, left; lacr, lacrimal; lr, lower; max, maxilla; nas, nasal; par for, parietal foramen; qjug, quadratojugal; qu, quadrate; R, right; smax, septomaxillary; squ, squamosal; vom, vomerine.



David Martill. Reference to the chance finding by Dr. Martill of this specimen with a particularly fine occiput.

HORIZON AND LOCALITY: Eroded from the boulder clay of Whitley Bay, Tyne and Wear, U.K., the specimen derives from a seat-earth facies, dated as late Westphalian A (late Langsettian) on spore analysis.

DIAGNOSIS:

Apomorphies: Baphetid with approximately triangular orbits, lacking constriction at jugal–postorbital and probably postfrontal–prefrontal junctions; very narrow maxillary exposure posterior to orbit; parasphenoid and pterygoids almost completely covered by shagreen of very fine denticulation, coarser denticulation on cultriform process; deep parasphenoid pockets (tubera parasphenoidales) for hypaxial muscles; shagreen of very fine denticulation on at least coronoid one (*Loxomma* shows what may be a more primitive condition with scattered coarse shagreen on coronoid three); parasymphysial (“adsymphysial”) plate lacks teeth; no lateral line grooves on the lacrimal or maxilla, but with a short stretch on the quadratojugal.

Other characters: lacrimal does not reach the naris (shared with *Megalocephalus*); pterygoid and parasphenoid co-ossified eliminating the interpterygoid vacuities (shared with *Spathicephalus*); 10 premaxillary teeth (shared with *Baphetes*); large dentary fangs (shared with *Megalocephalus*)

Description

Skull roof

About 270 mm long and 180 mm wide, the skull is of a

conventional size and shape for a baphetid, and where preserved, the dermal ornament is of a standard pattern (in the following description, the genus *Eucritta* is excluded from the term “baphetid” for convenience, since it either lacks the features under discussion, or they are unknown for that genus). The orbits have an anterior extension as in most baphetids, but unlike the others, there appears to be no constriction at the posterior boundary around the jugal–postorbital suture that in others marks the orbit proper from the antorbital embayment. This margin is well preserved either in bone or as a natural mould, so the phenomenon seems to be real. Above the orbit, the prefrontals and postfrontals are badly damaged or missing at the point where they would normally produce the corresponding constriction in the orbit margin. However, again judging from the natural mould of the bones preserved on the left side, the constriction seems to be absent. Thus, the orbit has a more triangular shape than in other baphetids, though like them, it is deep posteriorly with the anterior extension tapering to a point (Figs. 2–4).

The broad snout is like *Baphetes* in shape, but more posteriorly it is nearly parallel sided, more like *Megalocephalus*. Although in some places the sutures are obvious, in other places, especially on the skull table, they have been completely obliterated and can be seen neither on the surface nor in section where this is available. Occasionally, the natural mould of the internal surface provides a clue, but because of bone overlaps, the internal and external positions do not necessarily coincide.

Despite erosion of the snout, part of the left premaxilla is preserved, and shows a short length of lateral line groove as

in other baphetids (Fig. 3). At least 10 teeth are present, as in *Baphetes*; *Megalocephalus* and *Loxomma* have only eight premaxillary teeth. A higher number may be a primitive character. The bones of the snout are for the most part badly preserved and sutures are difficult to make out, one result of which is that the presence of internasals (median rostrals), expected in baphetids, cannot be confirmed. Indeed, on balance, the appearance of the specimen suggests their absence.

Both septomaxillae are present, and show a similar pattern to other baphetids, except that an internal prong can be seen projecting anteriorly into the naris, leaving only a small crescentic opening for the naris itself. The suture between the septomaxilla and the maxilla is a smooth curve. Beneath it, only a narrow process of the maxilla reaches the premaxilla (Fig. 3b).

The rest of the snout is unremarkable apart from two features. The lacrimal does not reach the orbit, so in this respect the new animal resembles *Megalocephalus* rather than other baphetids. The lacrimal forms a greater proportion of the dorsal antorbital embayment margin than in other forms, including *Megalocephalus*. Secondly, lateral line grooves are absent on the lacrimal and maxillae. Apart from *Spathicephalus*, which has no lateral line grooves on the skull roof, other genera have a section of groove running from the narial area, along the maxilla, and upwards onto the lacrimal, where in some cases it branches. In the case of the specimen described by Milner and Lindsay (1998), multiple branches are present here.

The dorsal boundary of the maxilla is hard to make out just posterior to the naris, where it shares a common suture with the nasal, but more posteriorly it can be easily traced, and the bone becomes extremely narrow quite suddenly below the orbit and posterior to it. This can be seen not only on the surface but in section. Maxillary teeth are relatively small, but without further extensive preparation, it is not possible to count them. The maxilla does not contact the quadratojugal, though this seems to be a variable feature in baphetids (Fig. 4).

Apart from the suspensorium, other parts of the skull roof are difficult to interpret. For example, though there appears to be space for an intertemporal on each side, the sutures cannot be made out with certainty. The intertemporal is present in *Loxomma* and *Baphetes*, but absent in *Megalocephalus* and *Spathicephalus*. The tabulars and posterior parts of the postparietals have been sheared off, so the proportions of the skull table cannot be firmly ascertained; as it is, it appears to have the short form seen in *Megalocephalus*, but this may be an artefact of preservation.

The structure of the suspensorium is quite clear. The squamosal and the quadrate ramus of the pterygoid are closely sutured along the rear margin of the cheek, with the quadrate exposed dorsoventrally. There is no evidence of the "stapedial groove" described by Beaumont (1977) in *Baphetes*, though in the better represented right side, the presumed atlas arch obscures some of the region that the groove might occupy. The paraquadrate foramen is exposed on the right side, bounded between the squamosal and the quadratojugal. The squamosal bears some striations that may be muscle-scarring above and along its suture with the pterygoid, continuing into the temporal notch. The squamosal contributes a tapering process under the supratemporal at the apex of the temporal

notch, but does not appear to underlie the skull table as it does in some specimens of *Loxomma* (Beaumont 1977).

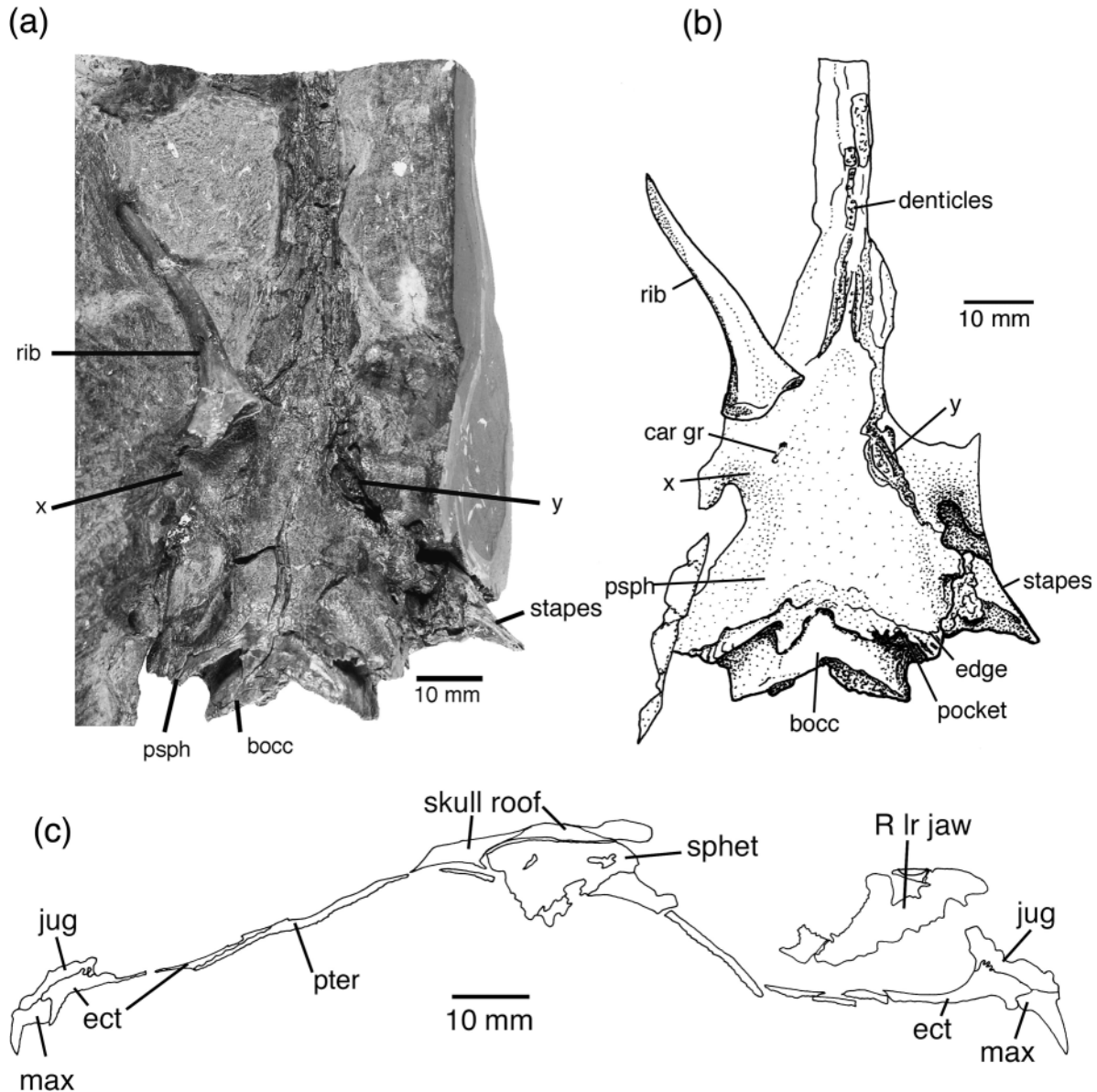
Palate, occiput, and braincase

Only part of the palate around the braincase and parasphenoid has been prepared (Fig. 5), though some of its structure can be inferred from sections (Fig. 5c). One large vomerine tusk can be seen where the right premaxilla has been sliced through (Fig. 4), confirming the presence of such teeth as in other baphetids. A transverse section through the entire skull at about the mid-point of the orbit shows the palate to have the primitive closed construction of other baphetids. This section also shows that the ectopterygoid and pterygoid were denticulated, but no other teeth are evident on the ectopterygoid. This is consistent with an ectopterygoid that bears only large tusks anteriorly but no row of small teeth, such as those seen in anthracosaurs and more primitive early tetrapods. The section also shows that the pterygoid and ectopterygoid overlapped broadly in a ridged suture and that the ectopterygoid was strongly sutured to the maxilla and jugal (Fig. 5c). The section also shows the sphenethmoid, whose approximately triangular cross-section encloses paired foramina for the olfactory nerve, but otherwise the section is uninformative. The cultriform process is crushed so as to obscure its shape (Fig. 5).

One of the most surprising features of the palate is that the pterygoid and parasphenoid were co-ossified to form a continuous sheet across the basal articulation and, probably but not certainly, along the length of the cultriform process (Fig. 5). Interpterygoid vacuities were entirely absent. A comparable morphology is only seen elsewhere in the aberrant *Spathicephalus* and is very unusual among early tetrapods. The dermal bone sheet has been fractured on the left to reveal the position of the basal articulation, but on the right it is intact and shows a foramen that might have housed the internal carotid, though it is rather small for such an interpretation. The cultriform process is crushed to quite a large extent, but a small patch of coarse denticles is present anteriorly. Otherwise, the parasphenoid and pterygoid are covered in a dense shagreen of very fine denticles that proved very difficult to prepare. The posterior margin of this shagreen field is sharply defined, leaving only a narrow undenticulated strip along the posterior margin of the parasphenoid. This is in contrast to *Megalocephalus*, in which only the central part of the parasphenoid bears shagreen; *Baphetes*, in which the body of the parasphenoid bears none at all; and *Loxomma*, in which it varies from absent to a small central patch.

The lateral wings of the parasphenoid are expanded ventrally into extensive pockets, the parasphenoidal tubera, to either side of the midline. They are ridged and furrowed internally, where hypaxial musculature presumably inserted (Figs. 5–7). The pockets are much more capacious than those shown by Beaumont for other baphetids, and this could be accounted for by compression undergone by most of the specimens she examined. However, where other genera have paired, undenticulated depressions either side of the midline in the ventral surface of the parasphenoid, that area in *Kyrinion* is entirely denticulated. In *Kyrinion*, all of the muscle insertion would have been housed within the pocket, whereas in other genera, presumably at least some of the muscle was inserted externally. The parasphenoidal pockets of *Kyrinion* most

Fig. 5. *Kyrinion martilli* NEWHM: 2000.H845, palate and ventral view of braincase. (a) Photograph. (b) Interpretive specimen drawing: x, continuous sheet of denticulated bone across pterygoid–parasphenoid junction; y, breakage at basiptyergoid junction. (c) Diagram of section through entire skull. bocc, basioccipital; car gr, carotid groove; ect, ectopterygoid; edge, edge of parasphenoid; jug, jugal; lr, lower; max, maxilla; pocket, parasphenoidal tuber; psph, parasphenoid; pter, pterygoid; ptf, posttemporal fossa; R, right.



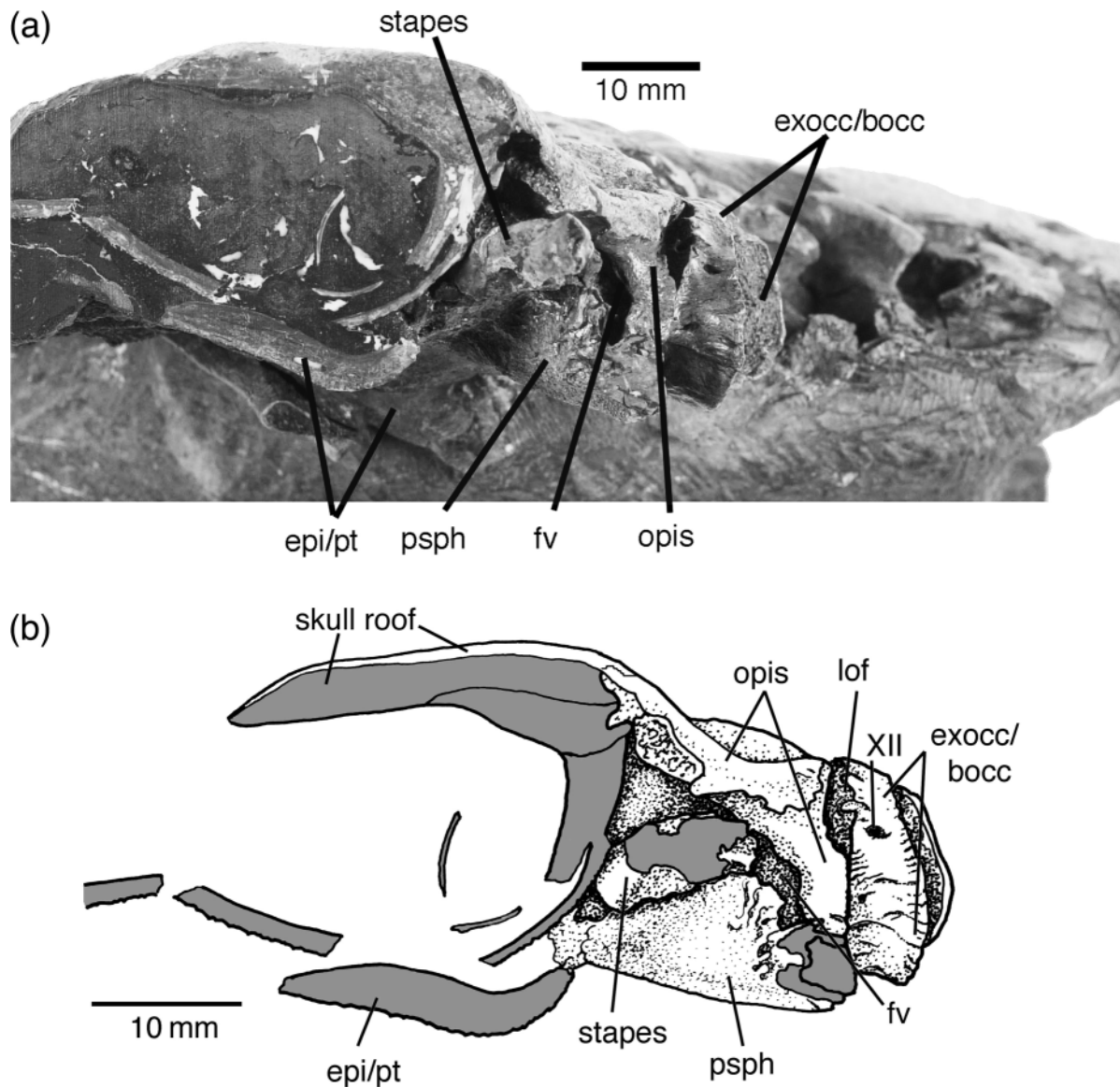
closely resemble those of *Greererpeton* in extent, though in the latter, they are positioned much more anteriorly, and the parasphenoid is relatively shorter, exposing more of the basioccipital. In *Kyrinion*, the centralmost part of the parasphenoid margin between the pockets is sutured to the basioccipital. Lateral to the pockets, the wings of the parasphenoid rise up at the sides of braincase, making contact with the ventral edge of the stapes, and possibly with the opisthotic. At this level, they lack shagreen.

The basioccipital and exoccipital cannot be distinguished and appear co-ossified (Figs. 6, 7). This configuration is probably primitive as it occurs in *Eusthenopteron* (Jarvik 1980) and also in the Devonian *Acanthostega* (Clack 1998c) and in some specimens of *Greererpeton* (Smithson 1982; Godfrey 1989). However, in other specimens of *Greererpeton*

(eg. KU 87695, personal observation), the exoccipitals are separate elements (Figs. 8a, 8b). This may reflect changes during ontogeny, although KU 87695 is not a small specimen of *Greererpeton*. The occipital condyle of *Kyrinion* is oval with a notochordal pit at its midpoint and the foramen magnum above it.

The form of the basi-exoccipital in *Kyrinion* bears closest resemblance to those of *Acanthostega* and *Greererpeton*. In lateral view, the resemblance to *Acanthostega* is particularly striking, but where the latter is fully notochordal, *Kyrinion* has a well-developed occipital condyle. In lateral view, the basi-exoccipital is narrow, sheathed by a sheet of periosteal bone with fluted edges (Fig. 6). There is a foramen, presumed to be for cranial nerve XII, just above mid-height and a second smaller one lower down. The exoccipital

Fig. 6. *Kyrinion martilli* NEWHM: 2000.H845, lateral view of braincase from the left. (a) Photograph. (b) Interpretive specimen drawing. Sectioned bone shaded grey. bocc, basioccipital; epi/pt, epipterygoid–pterygoid complex; exocc, exoccipital; fv, fenestra vestibuli; lof, lateral otic fissure; opis, opisthotic; psph, parasphenoid; XII, cranial nerve XII.



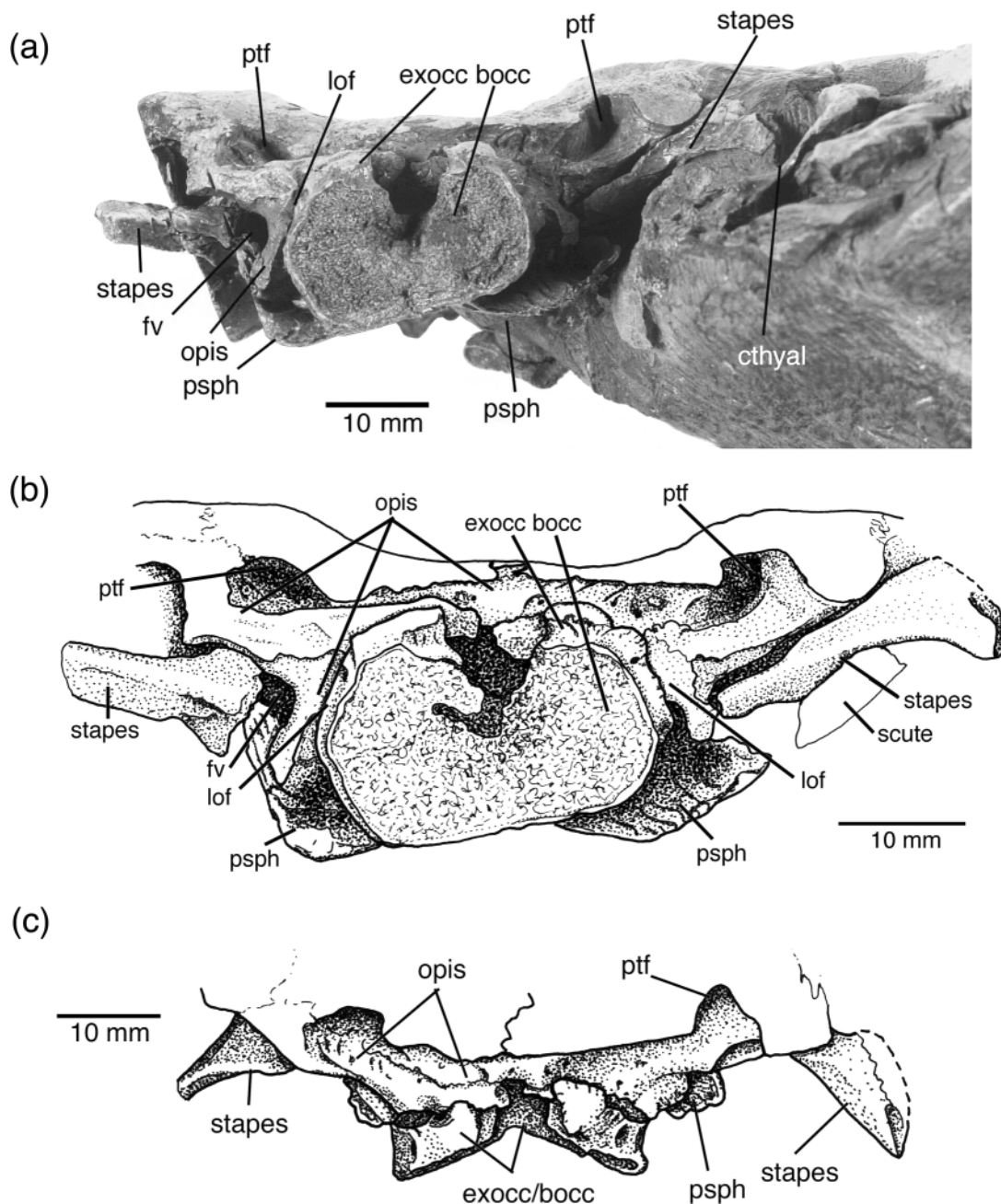
component forms a short stout pillar dorsally that contacts the opisthotic, though facets for the contact cannot be seen. The lateral otic fissure is unsealed, and where it has been somewhat opened up, on the left side, a facet for the basioccipital can be seen on the internal face of the opisthotic. This lower facet appears to be the equivalent of the lower of two “exoccipital” facets noted by Beaumont (1977) in *Loxomma*, *Megalocephalus*, and *Baphetes*. Because of this, the occipital region appears less deep dorsoventrally than as restored by Beaumont.

The opisthotic forms a continuous structure across the dorsal midline with no sutures to delimit paired ossifications or to mark a supraoccipital component (Fig. 7). It is slightly peaked at the midline, as shown for *Megalocephalus* by Beaumont (1977). It becomes excavated laterally for the posttemporal fossae. The form closely resembles that of *Acanthostega*, and the resemblance is amplified by the fact

that the tabulars have been eroded away to a great extent, leaving the most posterior part of the posttemporal fossae exposed dorsally. These embayments look like the tabular embayments in *Acanthostega*, though they are in fact artefacts of preservation. Resemblance to *Acanthostega* is continued in the presence of several tiny foramina around the midline in the posterior face of the opisthotic. In *Acanthostega*, one of these is assumed to be for the occipital artery, but in *Kyrinion* the three or four small openings look rather small for this.

In *Acanthostega*, the paroccipital processes are mostly unossified, and there are no specialized facets on the tabular to receive them. In *Kyrinion*, however, the paroccipital processes are fully ossified and suture strongly with the tabulars, as seen in temnospondyls. Below the paroccipital processes, the opisthotic sends down a robust process that forms the posterior component of the otic capsule and whose smoothly profiled

Fig. 7. *Kyrinion martilli* NEWHM: 2000.H845. (a) Photograph of occiput in posterior view. (b) Specimen drawings of posterior. (c) Dorsal views of occiput. bocc, basioccipital; chyal, ceratohyal; exocc, exoccipital; fv, fenestra vestibuli; lof, lateral otic fissure; opis, opisthotic; psph, parasphenoid; ptf, posttemporal fossa.



anterior wall forms the posterior margin of the large fenestra vestibuli. It is much more fully ossified than the equivalent structures in *Acanthostega* or *Greererpeton* and probably contacted the parasphenoid.

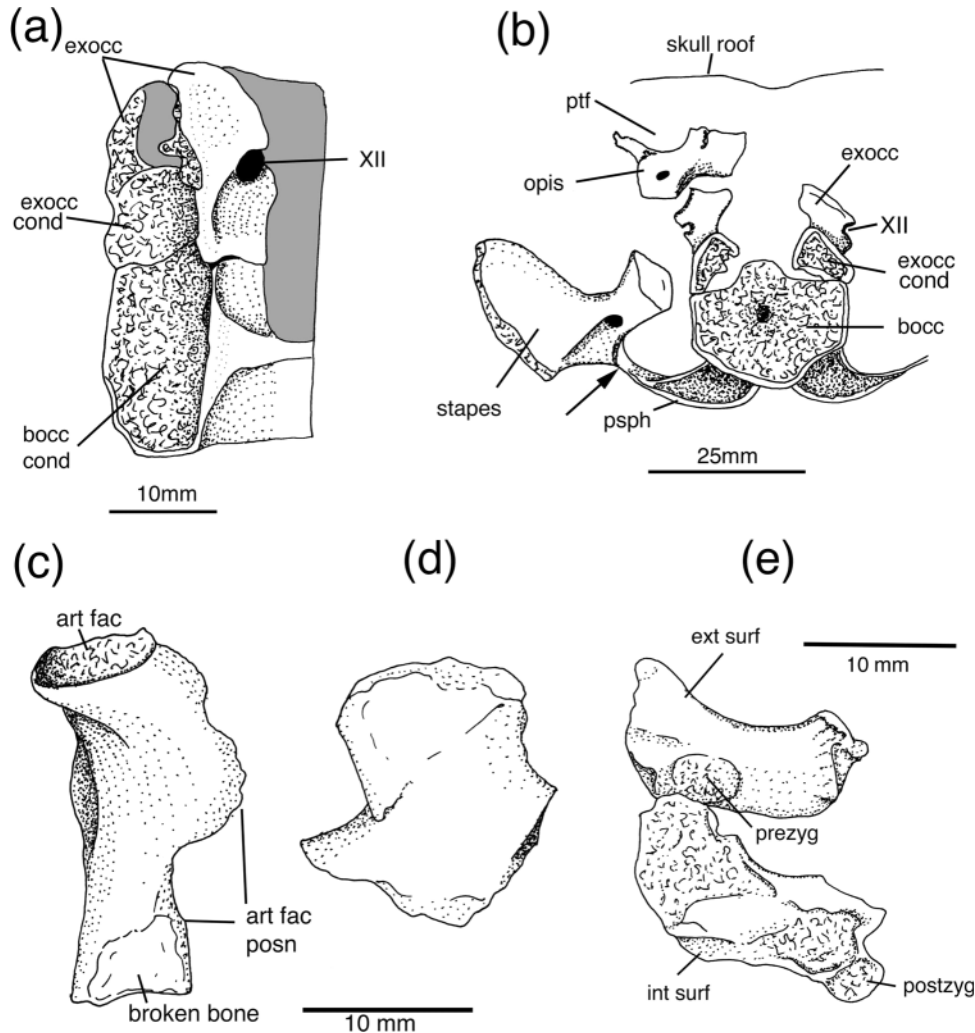
No part of the proötic or basisphenoid is available for description.

Hyobranchial skeleton — stapes and ceratohyal

Kyrinion preserves the stapes on both sides of the skull, though neither is complete. The left lacks its distal region but has its proximal part well exposed, if somewhat crushed. The right has part of its distal region preserved, where it

shows the expanded plate-like form now known from a range of other early tetrapods (Figs. 3a, 5, 7). This is triangular in shape, though it lacks some of its distal margin. The proximal region is crushed almost flat. There is no good evidence of a stapedia foramen that would be expected in an early tetrapod, though some later temnospondyls also lack this feature. On the left, the proximal region bearing the footplate is seated within the fenestra vestibuli and appears to contact and possibly suture with the lateral wing of the parasphenoid. Sutural contact between the stapes and parasphenoid is a well-known phenomenon among temnospondyls, though it is usually associated with more derived forms, such as large

Fig. 8. Drawings of occipital regions of the *Greererpeton*-like colosteid KU 87695. (a) Camera lucida drawing of oblique view of right side of occipital arch. (b) Sketch of posterior view of occiput. Arrow shows contact between footplate of stapes and parasphenoid. (c, d) *Kyrinion martilli* NEWHM: 2000.H845 (c) Ceratohyal viewed from the midline. (d) Probable atlas arch. (e) Atlas arches—proatlantes of holotype of *Loxomma rankini*. art fac posn, position of articular facet; bocc, basioccipital; cond, condyle; exocc, exoccipital; ext surf, external surface; int surf, internal surface; opis, opisthotic; psph, parasphenoid; ptf, posttemporal fossa; postzyg, postzygapophysis; prezyg, prezygapophysis, XII, cranial nerve XII.



capitosaurs (Schoch and Milner 2000). However, one colosteid specimen also shows this contact (Fig. 8b)

An element at first taken to be a displaced stapes lies against the palatoquadrate ossification on the right side, just posterior to the actual stapes (Figs. 2, 3a, 8c). It has a robust proximal end bearing an articular facet, narrows a little to form a shaft, and then expands again into a distal plate. It carries an oval-shaped articular facet at its extreme distal end, and another around the mid-point on the almost hidden undersurface. The exposed surface of the distal plate is concave, with the posterior margin a smooth rounded buttress. The identity of this element remains uncertain, though it may be a ceratohyal (A.C. Milner, personal communication, 2000). However, nothing like the strongly marked articular facets exist on the ceratohyal of *Acanthostega*, one of the few other early tetrapods in which this element is known (Coates and Clack 1991). The ceratohyal of *Acanthostega* is a relatively longer but much less robust element, which is associated

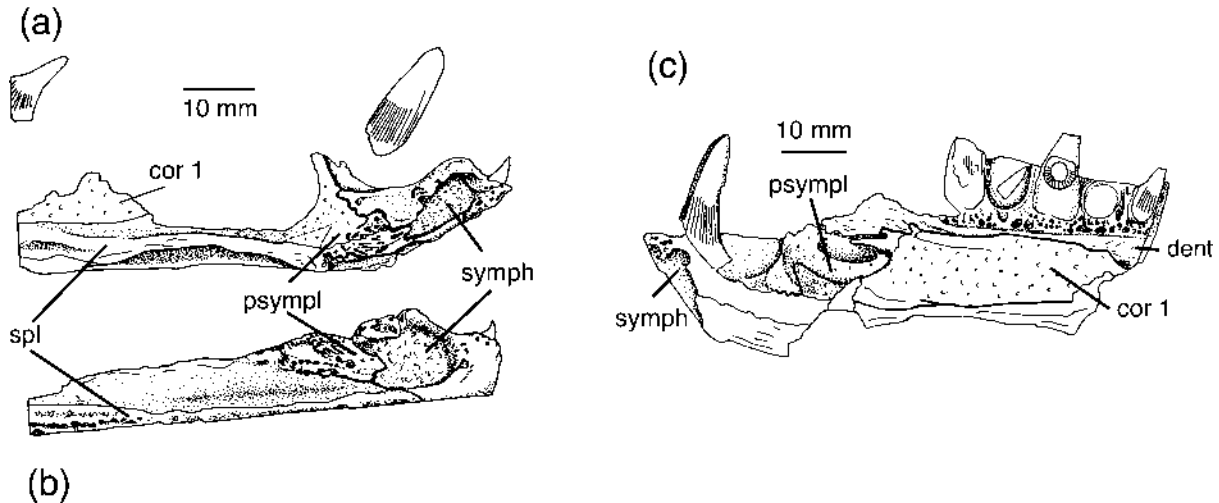
with a system of grooved branchial arches interpreted as part of a functional internal gill apparatus. The ceratohyal of *Dvinosaurus* is short and robust like the element in *Kyrinion*, but whereas the proximal and distal ends are unfinished, the bone bears no obvious articular facets (Bystrow 1938). I am not entirely convinced that this element in *Kyrinion* is a ceratohyal, but for the present can produce no better explanation.

Lower jaw and dentition

Baphetid lower jaws, apart from those of *Megalocephalus* (Beaumont 1977; Ahlberg and Clack 1998), are not well known. *Loxomma* is known only from one lower jaw preserving the posterior third, and only the external surface is known for *Baphetes*. *Spathicephalus* is probably the best known, including the inner face of the anterior portion of the ramus (Beaumont and Smithson 1998). The two partial jaws of *Kyrinion* show differences from all three genera (Fig. 9).

There are at least two large dentary teeth and a corre-

Fig. 9. *Kyrinion martilli* NEWHM: 2000.H845, specimen drawings of right and left lower jaw portions. (a) Dorsal view of symphyseal and anterior coronoid region of left ramus. (b) Ventral view of the same. (c) Symphyseal and anterior coronoid region of right ramus. cor, coronoid; dent, dentary; psympl, parasymphysial plate; spl, splenial; symph, symphysis.



spondingly large replacement pit at the anterior end of the jaw that contrast markedly in size with the maxillary teeth, a feature shared with *Megalocephalus*. This size-discrepancy is not present in *Baphetes* or *Loxomma* as far as can be ascertained. However, *Kyrinion* differs from *Megalocephalus* in other ways. Although it appears to have a parasymphysial plate (whose boundaries are not entirely clear) this is toothless and does not bear the “brassicata” structure seen at the symphysis in *Megalocephalus pachycephalus* (Ahlberg and Clack 1998). The anterior coronoid (the only one available) in *Kyrinion* bears a shagreen of very fine denticles that match those of the palate. A few are also present on the parasymphysial plate. *Megalocephalus* has fine sculpturing but lacks any shagreen on the coronoids; and though *Loxomma* does show shagreen on coronoid three, the denticles are rather sparse. *Spathicephalus* likewise lacks coronoid shagreen, whereas the parasymphysial plate bears a row of nearly 30 small teeth (Beaumont and Smithson 1998). The symphyseal surface in *Kyrinion* is plain and flat, and there is an open groove for the mandibular lateral line on the splenial (Fig. 9).

The tooth-crowns of *Kyrinion* conform to the baphetid pattern and are lanceolate, flattened at the apex, and bear characteristic keels antero-posteriorly, with labyrinthine infolding at the base.

Axial skeleton

Two elements of the axial skeleton are preserved in *Kyrinion*, a rib and a possible atlas arch (Figs. 2, 3a, 5, 8d). The rib is double-headed, with the shaft more or less round in section, curving gently and tapering gradually towards the distal end. It has no distal expansions or uncinat processes, and to that extent is unlike the only other known baphetid ribs. A possible anterior trunk rib is present in the specimen described as cf. *Baphetes* by Milner and Lindsay (1998), which has a triangular distal expansion most closely resembling those of whatcheeriids (Lombard and Bolt 1995; Clack 2002). This may mean that the rib associated with *Kyrinion* is more anterior, possibly a

first cervical. Cervical ribs are also often flanged or expanded distally in early tetrapods, so even as a cervical rib, this one would be unusual, and another possibility is that it is a displaced presacral rib.

The possible atlas arch is a small element preserved posterior to the ceratohyal, and consists of a more or less rectangular neural spine, and small processes front and rear (Fig. 8d). The posterior one bears a facet expected in a zygapophysis. The element most closely resembles the posterior part of the atlas arch of *Proterogyrinus*. Its anterior part appears to have been broken off.

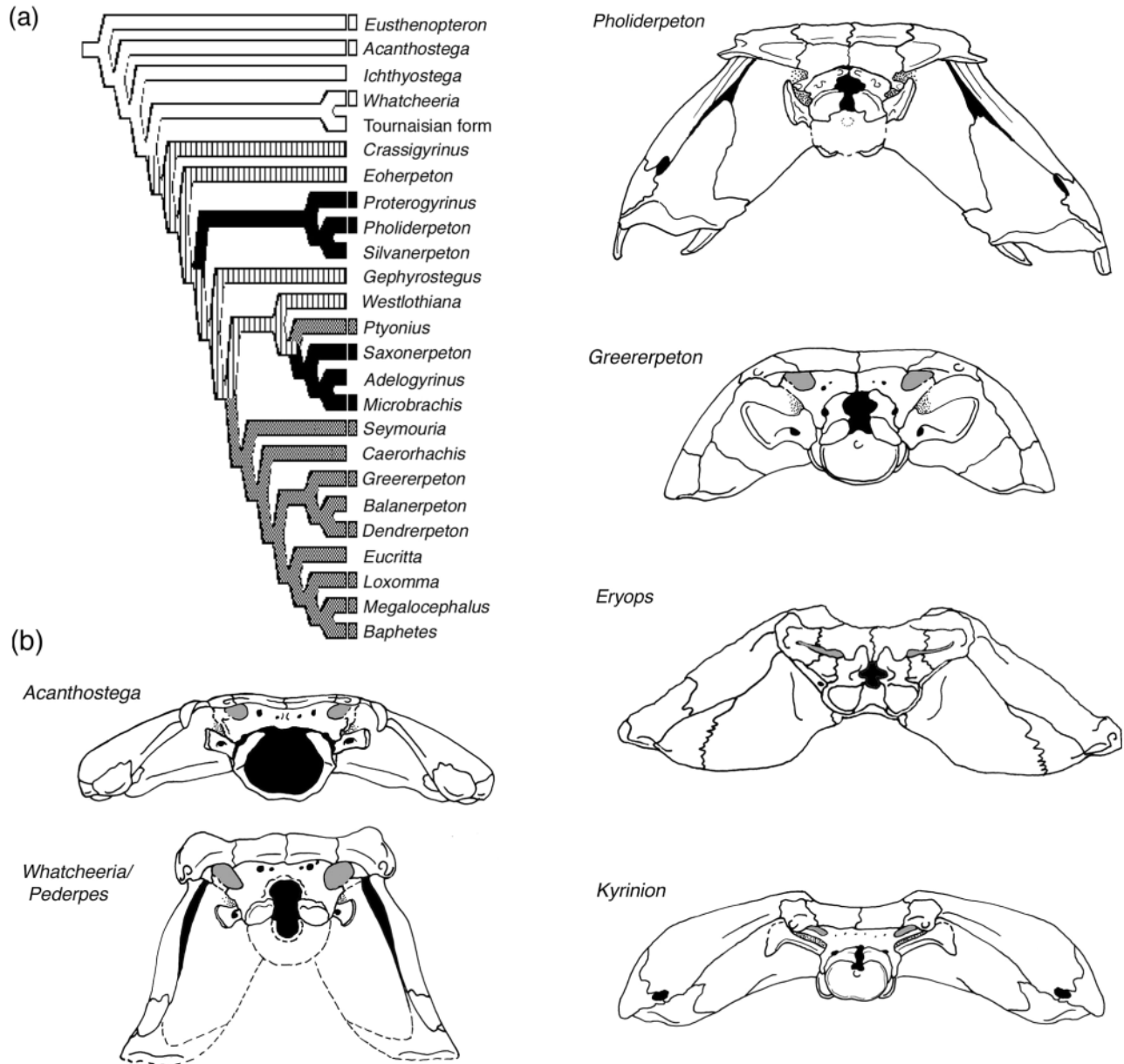
A pair of possible atlas arches have recently been prepared from the holotype specimen of *Loxomma rankini* (GLAHMS V2023), though as they are relatively smaller than that in *Kyrinion*, they may be proatlantes. These are illustrated and recorded here for comparison with the element in *Kyrinion* (Fig. 8e). They have shorter neural spines and smaller zygapophyseal facets than the atlas arch of the embolomere *Pholidropteron* (Clack 1987), though are otherwise comparable.

Discussion

Aspects of the skull of *Kyrinion* that are of particular interest are the occipital region, the stapes, and the new information it gives on skull construction. Its mosaic of characters shared with other baphetid genera will be of significance when a fuller review of baphetid systematics is undertaken in the future. At present, *Kyrinion* does not seem to be any more closely related to one of the original genera than to the others. For the following discussion, baphetids are treated as members of a clade containing temnospondyls and colosteids, a grouping recovered by the author following a cladistic analysis of early tetrapods, including *Pederpes finneyae*, a new Tournaisian form similar to *Whatcheeria* (Clack 2002). In that study, “anthracosaurs” appeared as a paraphyletic stem tetrapod lineage, though the embolomeres remained monophyletic. However, the systematics of “anthracosaurs” are in need of revision, a project which will be undertaken in the near future with M. Ruta.

Early tetrapod occiputs are represented by very few

Fig. 10. (a) Cladogram of early tetrapods showing distribution of paroccipital process (POP) character-states. (a) Open branches, unossified POP; hatched branches, ambiguous or unknown state; black branches, POP absent; shaded branches, ossified POP contacts tabular. (b) Occipital reconstructions of six early tetrapods: *Acanthostega*, a primitive Devonian tetrapod; *Whatcheeria-Pederpes* (based on GLAHMS 100815, FMPRI801, and Lombard and Bolt 1995); *Pholiderpeton*, a Westphalian embolomere (from Clack 1987); *Greererpeton*, a colosteid (based on KU 87695 and Smithson 1982); *Eryops*, a Permian temnospondyls (based on Sawin 1941); *Kyrinion*. Posttemporal fossae shaded in grey, paroccipital processes shown by broken lines where not ossified (skulls not to scale).



well-preserved specimens and even fewer retaining three-dimensional structure. The Late Devonian *Acanthostega* is the earliest, represented by good material (Clack 1998c) (Fig. 10), followed by the mid-Carboniferous *Greererpeton*, represented by a size range of skulls showing ontogenetic changes (Smithson 1982; Godfrey 1989). The baphetid occiput was described by Beaumont (1977), but her material was dorsoventrally compressed and the basioccipital is only known in *Megaloccephalus*. Neither *Acanthostega* nor *Greererpeton* were known from braincase material in 1977, and her reconstructions were made in the light of the occiputs of later temnospondyls, such as *Edops* and *Eryops*.

“Anthracosaurs” (i.e., embolomeres plus *Eoherpeton* and *Gephyrostegus*) usually have poorly preserved occiputs and often lack the basioccipital, though *Anthracosaurus russelli* (Panchen 1977), *Pholiderpeton scutigerum* (Clack 1987), and *Archeria crassidisca* (Clack and Holmes 1988) are probably representative. Again, most of these have been described since 1977. As part of the current investigation, I also reexamined specimens of *Greererpeton* and an unnamed colosteid probably congeneric (though not apparently conspecific) with *Greererpeton* (KU 87695) (Bolt and Lombard 2001) and found some differences from the reconstructions given by Smithson (1982) that are relevant in this

context. I have also examined specimens of *Whatcheeria deltae*, and combining information from this species with that of *Pederpes*, have produced a reconstruction of the whatcheeriid occiput. My interpretation differs somewhat from that of Lombard and Bolt (1995).

With respect to *Greererpeton*, apart from the separation of the basi- and exoccipital components noted earlier in the text, the main difference that I found from Smithson's (1982) interpretation was that a small opisthotic element intervenes between the exoccipital and skull roof. This bears a facet, against which the exoccipital articulated (Fig. 8). One possibility is that in the specimens available to Smithson, the skulls had been dorsoventrally crushed to disrupt this association and bring the exoccipitals up against the postparietals, making the whole occipital exposure less deep than it should be. My reconstruction shows this realignment. It also removes the postparietal-exoccipital contact, a major character that Smithson used to unite colosteids with temnospondyls. Instead this colosteid has the more primitive arrangement found in "anthracosaurs," *Acanthostega* and *Eusthenopteron* (Fig. 10). Another small difference lies in our interpretations of foramina. A large foramen is partially enclosed by the exoccipital, which I interpret as for cranial nerve XII, whereas at this position in his reconstruction, Smithson (1982, fig. 15) suggests nerve X. That nerve would undoubtedly have exited somewhere along the lateral otic fissure, but it is not clear where. The opisthotic of KU 87695 shows a foramen that probably also served for the occipital artery.

In the case of *Whatcheeria*, I have reinterpreted the openings on the occipital face of the opisthotic seen in FMPR 1809, in the light of similarities to *Acanthostega*. Lombard and Bolt (1995, text-Fig. 2, FMPR 1809) suggested that the round openings beneath the postparietals were the posttemporal fossae. Compared with *Acanthostega*, these appear to me to be openings for the occipital arteries, and the posttemporal fossae themselves lie further laterally (Fig. 10). Their dorsal margins can be seen as smooth, curving embayments under the opisthotics. The opisthotics bear unfinished processes that match facets on the undersides of the tabulars, suggesting to me that the paroccipital processes were only partially ossified but contacted the tabulars via cartilaginous continuations, as suggested in *Acanthostega* and *Greererpeton*.

Differences between the occiput of *Kyrinion* and the baphetid occiput as reconstructed by Beaumont (1977) lie mainly in the relation of the basi-exoccipital to the opisthotics. Where she has suggested a double contact between the opisthotic and exoccipital, *Kyrinion* suggests that, as described earlier in the text, the lower of the two opisthotic facets in fact contacted the basioccipital part of the basi-exoccipital. The result is a rather shallower occipital region than she suggested (Fig. 10). The other main difference is seen in lateral view. The opisthotic sends down a robust process to contact the parasphenoid and bound the posterior wall of the fenestra vestibuli, but it is narrower than shown by Beaumont. The posterior wall of the fenestra vestibuli is formed by a smoothly rounded buttress, and the margin of the fenestra vestibuli is of greater diameter than Beaumont suggested (Fig. 6). The size of the fenestra vestibuli is thus more in keeping with the size of the proximal end of the stapes, and of that now known in early tetrapods generally.

During the early evolution of tetrapods, stabilization of the occiput must have been important to animals that increasingly engaged in activities on land. Here, the head had to be maintained in a stable position against the pull of gravity. At the same time, reduction in the importance of the branchial skeleton in breathing and loss of associated musculature may have allowed increasing flexibility of the neck joint (Smithson 1982; Janis and Keller 2001). Smithson (1982) noted a contrast in the way the occipital arch attaches to the rest of the braincase between temnospondyls (and microsaurs) and anthracosaurs. In the latter, a primitive condition is maintained, wherein the exoccipitals articulate with the otic capsule at the opisthotic. In the former, the exoccipitals increase in size and importance, contacting the skull roof and eventually replacing the opisthotic as the main surface for attachment of expaxial muscles. He noted that the condition in anthracosaurs was in effect similar to that of osteolepiforms, such as *Eusthenopteron*, in which the lateral otic fissure remained unsealed even in the adult.

Now that several more early tetrapod occiputs have been described, more details can be added to this observation. Considered in the light of the phylogeny of early tetrapods, as discussed in Clack (2001a, 2002), a consistent picture is emerging (Fig. 10).

Co-ossification of the basi- and exoccipitals is a primitive feature seen in the tetrapodomorph fish *Eusthenopteron*, *Acanthostega*, and some specimens of *Greererpeton*. In *Acanthostega*, the form is particularly similar to that of *Eusthenopteron*. In *Whatcheeria*, the basi-exoccipital contacts the opisthotic at oval facets, though it is not clear whether the basioccipital is a separate ossification from the exoccipitals, nor whether the construction was notochordal (J. R. Bolt, personal communication). In all of these forms, the lateral otic fissure remains open even in the adult, with facets on the opisthotic for articulation with the basi-exoccipital.

In *Eusthenopteron*, the otic capsule was ossified laterally into paroccipital processes that contacted, though did not suture with, the skull table under the tabular bones along their lateral margins. However, in *Acanthostega*, *Whatcheeria*, and *Greererpeton*, these processes remained unossified (Fig. 10). Unfinished bone along the lateral margins of the opisthotics suggest continuation in cartilage, and in *Whatcheeria* and *Greererpeton*, this is matched by unfinished facets under the tabulars. In *Acanthostega*, as in *Eusthenopteron*, the undersurface of the tabular was covered in unfinished bone. For tetrapods, then, the primitive condition seems to have been to have unossified paroccipital processes, a feature in keeping with the generally poorly ossified state of the internal surfaces of the otic capsule.

In embolomeres, paroccipital processes are absent, and this was one of the features formerly defining "anthracosaurs" as a group (Panchen 1964, 1970, 1980). In these animals, the tabular produces complex facets to receive the opisthotic near its suture with the postparietals, and its posterior exposure is increased by a deep occipital flange (Fig. 10). The "anthracosaur" *Eoherpeton* appears to show such a condition, though some recent analyses have placed this animal as a stem plesion basal to embolomeres (Clack 2002). The occiput of *Eoherpeton* is not well known and may deserve reexamination in the light of *Acanthostega*, *Whatcheeria*, and *Kyrinion*, along with reexamination of "anthracosaur"

relationships generally. The occiput of the other non-embolomeres "anthracosaur," *Gephyrostegus*, is also known only from poorly preserved and flattened material. However, loss of the paraoccipital processes may be a shared derived character uniting embolomeres, as suggested by Panchen, but only further work will confirm whether or not it also unites them with other "anthracosaurs."

By contrast, from a condition such as that in *Greererpeton*, baphetids and temnospondyls have both developed fully ossified paroccipital processes, firmly sutured to the tabulars laterally, to enclose posttemporal fenestrae in a similar position to those of *Eusthenopteron* (Fig. 10). The cladistic analysis suggests that this is a shared derived character uniting baphetids and temnospondyls to the exclusion of "anthracosaurs," and is not the primitive condition (cf. Berman 2000). The structure is different from that in amniotes, whose paroccipital processes and posttemporal fossae may not be strictly homologous with those of temnospondyls or baphetids. Smithson's suggestion (1982) of a contrast in structure in the occiput between temnospondyls and "anthracosaurs" may extend to the structure of the opisthotic and its attachment to the skull roof. He suggested that "anthracosaurs" and "loxommatids" (ie. baphetids) retained a more or less primitive occipital structure in having the otic capsules form most of the contact between the braincase and the skull roof. However, it now appears that both groups are derived in different respects: "anthracosaurs" in having lost the paroccipital process, and baphetids and temnospondyls having ossified it fully and sutured it to the tabular.

While the structure of *Kyrinion* lends support to Smithson's ideas on occipital construction, it may refute another by Clack (2001b). In a study of the embryonic components that make up the occipital region and extending it to fossil forms such as *Eusthenopteron*, *Acanthostega*, and *Greererpeton*, Clack suggested that the occipital condyle, as distinct from the basioccipital that bears it, may have been formed from addition of a further embryonic segment to the occipital arch component. From the similarities of the occipital arch seen in *Kyrinion*, *Greererpeton*, and *Acanthostega*, it is clear that they must all have been formed from the same number of embryonic segments. They are closely comparable in size, morphology, and number of hypoglossal foramina. Ossification of the condylar region must have resulted from some other process.

Stapes of early tetrapods are now quite well known, including those from the Devonian *Acanthostega*, *Pederpes* (Clack 2002), the colosteid *Greererpeton*, and the embolomeres *Pholiderpeton* and *Palaeoherpston*. They show a common pattern of a large footplate region, a robust but short shaft, and an expanded distal plate. They usually have a large stapedial foramen. Baphetid stapes have now been reported from three specimens. The first was recorded by Watson (1929), in *Baphetes kirkbyi* (NEWHM G15.91), where it was described as "short, presumably articulating with the otic region mesially and having its outer end terminating on the level of the outer surface of the skull. It is extremely massive, its antero-posterior breadth being nearly two centimetres and its thickness half a centimetre, despite the crushing which it has undergone" (Watson 1929, p. 239). Unfortunately, as noted by Beaumont (1977), the bone is now missing from this skull, and all that remains is the

space from which it has disappeared. A latex peel made from the space showed a bulbous bilobed proximal end and an expanded distal end, but was otherwise rather amorphous. Watson's description is consistent with what is now known of baphetid stapes and those of early tetrapods generally, though formerly it might have been considered unlikely. The second baphetid stapes to be described was that of *Spathicephalus* (Beaumont and Smithson 1998), though again this is very flattened, and there is no evidence for a stapedial foramen. It too appears to have had a robust shaft and expanded distal plate as in other early tetrapods.

All three baphetid stapes are flattened, and in the case of *Kyrinion*, this is surprising given the rest of the skull and braincase preservation. It could be that baphetid stapes were in reality flattened, or possibly rather poorly ossified internally. Lack of a stapedial foramen might also be a real phenomenon. Whether or not the distal plate lay against the palatoquadrate ossifications, as suggested by Beaumont and Smithson (1998), is debatable. There is a depth of matrix of at least 5 mm between the right stapes and the palatoquadrate bones in *Kyrinion*, though less on the left.

Carroll (1980), Smithson (1982), and Clack (1983, 1989, 1992, 1994) have suggested that primitively, the tetrapod stapes was involved in structural support for the braincase in skulls that were not fully autostylic, and in which the contacts between the braincase and palate were either kinetic or poorly ossified. The stapes was viewed as helping to stabilize the braincase with respect to the palate, and the large, plate-like distal portion rested against the palatoquadrate in forms such as *Greererpeton*, *Pholiderpeton*, and *Acanthostega*. In *Kyrinion*, and also in *Spathicephalus*, the stapes retains a similar form to that seen in these more primitive taxa, indeed it is more extensive than in *Acanthostega* and *Pederpes*, but the skull is constructed in such a manner as to eliminate any sign of kinetism. It was clearly fully autostylic. This may mean either that hypotheses for the early function of the stapes are incorrect, or that *Kyrinion* retained the primitive form of stapes but that its function had changed. Temnospondyls, if correctly interpreted as the sister-group to baphetids, reduced the distal portion of the stapes to a bar, as in the primitive temnospondyl *Dendrerpeton* (Clack 1983). In more derived temnospondyls, the stapes sometimes failed to ossify distally, or was a relatively narrow rod, and is generally considered to have functioned as a hearing ossicle. It is not obvious that the stapes of *Kyrinion* was any more likely to have functioned as a hearing ossicle than those of the more primitive taxa, however. Clack (1992) suggested that temnospondyls were the earliest group to modify the stapes into a hearing ossicle as a result of consolidation of the skull and elimination of mobility at the basal articulation. Ossification of the paraoccipital processes in the baphetid-temnospondyl clade might have been the first step along this road.

One feature that the stapes of *Kyrinion* shares with more derived temnospondyls (Schoch and Milner 2000) (and also with the *Greererpeton*-like specimen KU 87695) is its connection to the parasphenoid, which presumably limited its ability to vibrate as a hearing ossicle is usually required to do, though not necessarily in the case of low frequency ground-borne sound reception.

Kinetism of one form or another has frequently been suggested as possible in the skulls of several early tetrapod

groups. Embolomeres and other “anthracosaurs,” for example, are thought to have had some form of mobility between the skull table and the cheek, and at the basal articulation (Panchen 1964, 1972). Colosteids were originally considered to have a “kinetic line” between the skull table and the cheek (Romer 1969), though a restudy by Smithson (1982) considered the line to be an artefact of preservation. He considered neither the skull roof nor the basal articulation to be mobile. In baphetids, Beaumont (1977) envisaged a different form of kinetism, between the marginal palatal bones and the pterygoid, and at the back of the suspensorium between the cheek and palatoquadrate ossifications. This she viewed as compensatory movement for that at the basal articulation, in the absence of a kinetic cheek. Clack (1994) suggested similar regions of mobility in the skull and palate of *Acanthostega* that necessitated the strut-like function of the stapes.

The solidly constructed skull of *Kyrinion* shows no kinetic potential, with its interdigitating sutures tying the cheek to the skull roof via the palatal margins and up the suspensorium. In this animal, like *Spathicephalus*, there was no movement possible at the basal articulation. It remains to be seen whether this emerges as a synapomorphy between these taxa or a convergent development, but in either case, Beaumont’s (1977) suggestion does not apply to them.

Most recently, Bolt and Lombard (2001) have described new material of colosteid lower jaws and linked a complex “brassicate” structure at the symphysis with possible kinetism in the skull roof. In their new material, a kinetic line between the skull table and the cheek does seem to have been present, as Romer suggested (Romer 1969). Bolt and Lombard proposed that movement along that line was accommodated by corresponding movement at the symphysis, and furthermore, that since a similar brassicate structure is found in *Megalocephalus*, it too should show a kinetic line. Having examined the material, I can find no evidence for a kinetic skull table, but possibly Beaumont’s suggestion of kinetism between the palate and skull roof does apply to *Megalocephalus* and correlates with movement at the symphysis. *Kyrinion* shows neither a kinetic skull nor a brassicate symphyseal structure. The potential for kinetism in early tetrapod skulls might be a suitable subject for study by Finite Element Analysis.

Acknowledgments

In dedicating this paper to Bob Carroll, I acknowledge his broad and deep influence on early tetrapod palaeontology and on my own input and perspectives on the subject. The work could not have been completed without the contributions of many people, but particularly that of my preparator Sarah Finney. This specimen she found especially frustrating to work on, but has done wonders with it. I thank Steve McLean of the Hancock Museum for sanctioning any preparation that we wished to undertake, Dave Martill for his perspicacity in recognising that the specimen was “something interesting,” and John Marshall for his palynological report. John Bolt kindly allowed access to specimens of *Whatcheeria* and colosteids that he and Eric Lombard are currently working on, and I thank them both for hospitality and good co-operation over the years. I thank the referees, Stuart

Sumida and Dave Berman and the Associate Editor for their help in improving the manuscript, and Mary Atkins and Henry Disney for advice on ancient Greek. The work was carried out under Natural Environment Research Council grant GR3/09333 to the author.

References

- Ahlberg, P.E., and Clack, J.A. 1998. Lower jaws, lower tetrapods — a review based on the Devonian genus *Acanthostega*. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **89**: 11–46.
- Ahlberg, P.E., and Milner, A.R. 1994. The origin and early diversification of tetrapods. *Nature (London)*, **368**: 507–514.
- Beaumont, E.I. 1977. Cranial morphology of the Loxomatidae (Amphibia: Labyrinthodontia). *Philosophical Transactions of the Royal Society of London, Series B*. **280**: 29–101.
- Beaumont, E.I., and Smithson, T.R. 1998. The cranial morphology and relationships of the aberrant Carboniferous amphibian *Spathicephalus mirus* Watson. *Zoological Journal of the Linnean Society*, **122**: 187–209.
- Berman, D.S. 2000. Origin and early evolution of the amniote occiput. *Journal of Paleontology*, **74**: 938–956.
- Bjerring, H.-C. 1986. Electric tetrapods? *In Studies in Herpetology. Edited by Z. Roček*. Charles University, Prague, pp. 29–36.
- Bolt, J.R., and Lombard, R.E. 2001. The mandible of the primitive tetrapod *Greerpeton*, and the early evolution of the tetrapod lower jaw. *Journal of Paleontology*, **75**: 1016–1042.
- Bystrow, A.P. 1938. *Dvinosaurus* als neotenische form der stegocephalan. *Acta Zoologica*, **19**: 209–295.
- Carroll, R.L. 1980. The hyomandibula as a supporting element in the skull of primitive tetrapods. *In The terrestrial environment and the origin of land vertebrates. Edited by A.L. Panchen*. Academic Press, London and New York, pp. 293–317.
- Carroll, R.L. 1995. Problems of the phylogenetic analysis of Paleozoic choanates. *In Studies on early vertebrates. Edited by M. Arsenault, H. Lelièvre, and P. Janvier*. Miguasha, Quebec. *Bulletin du Muséum national d’histoire naturelle, Paris*, **17**: 389–445.
- Clack, J.A. 1983. The stapes of the Coal Measures embolomere *Pholiderpeton scutigerum* Huxley (Amphibia: Anthracosauria) and otic evolution in early tetrapods. *Zoological Journal of the Linnean Society*, **79**: 121–148.
- Clack, J.A. 1987. *Pholiderpeton scutigerum* Huxley, an amphibian from the Yorkshire Coal Measures. *Philosophical Transactions of the Royal Society of London, Series B* **318**: 1–107.
- Clack, J.A. 1989. Discovery of the earliest-known tetrapod stapes. *Nature (London)*, **342**: 425–427.
- Clack, J.A. 1992. The stapes of *Acanthostega gunnari* and the role of the stapes in early tetrapods. *In Evolutionary biology of hearing. Edited by D. Webster, R. Fay and A.N. Popper*. Springer-Verlag, New York, pp. 405–420.
- Clack, J.A. 1994. Earliest known tetrapod braincase and the evolution of the stapes and fenestra ovalis. *Nature (London)*, **369**: 392–394.
- Clack, J.A. 1998a. A new Lower Carboniferous tetrapod with a mélange of crown group characters. *Nature (London)*, **394**: 66–69.
- Clack, J.A. 1998b. The Scottish Carboniferous tetrapod *Crassigyrinus scoticus* (Lydekker) — cranial anatomy and relationships. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **88**: 127–142.
- Clack, J.A. 1998c. The neurocranium of *Acanthostega gunnari* and the evolution of the otic region in tetrapods. *Zoological Journal of the Linnean Society*, **122**: 61–97.
- Clack, J.A. 2001a. *Eucritta melanolimnetes* from the Early Carboniferous of Scotland, a stem tetrapod showing a mosaic of

- characteristics. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **92**: 72–95.
- Clack, J.A. 2001b. The otoccipital region — origin, ontogeny and the fish-tetrapod transition. *In* Major events in early vertebrate evolution. *Edited by* P.E. Ahlberg. Systematics Association Symposium, Vol. 61, London, pp. 392–505.
- Clack, J.A. 2002. An early tetrapod from Romer's Gap. *Nature (London)*, **417**: 72–76.
- Clack, J.A., and Holmes, R. 1988. The braincase of the anthracosaur *Archeria crassidisca* with comments on the interrelationships of primitive tetrapods. *Palaeontology*, **31**: 85–107.
- Coates, M.I., and Clack, J.A. 1991. Fish-like gills and breathing in the earliest known tetrapod. *Nature (London)*, **352**: 234–236.
- Dawson, J.W. 1863. Air breathers of the coal period. Dawson Brothers, Montréal, Que.
- Godfrey, S.J. 1989. Ontogenetic changes in the skull of the Carboniferous tetrapod *Greererepton burkemorani* Romer, 1969. *Philosophical Transactions of the Royal Society of London, Series B*, **323**: 135–153.
- Janis, C., and Keller, J. 2001. Modes of ventilation in early tetrapods: costal aspiration as a key feature of amniotes. *Acta Palaeontologica Polonica*, **46**: 137–170.
- Jones, J.M. 1967. Geology of the coast section from Tynemouth to Seaton Sluice. *Transactions of the Natural History Society of Northumberland*, **16**(3): 153–192.
- Laurin, M., and Reisz, R. 1997. A new perspective on tetrapod phylogeny. *In* Amniote origins — completing the transition to land. *Edited by* S. Sumida, and K. Martin. Academic Press, London, pp. 9–59.
- Lombard, R.E., and Bolt, J.R. 1995. A new primitive tetrapod, *Whatcheeria deltae*, from the Lower Carboniferous of Iowa. *Palaeontology*, **38**: 471–494.
- Milner, A.C. 1997. A new specimen of *Baphetes* from Nýřany, Czech Republic and the intrinsic relationship of the Baphetidae. *Journal of Vertebrate Paleontology*, **17A**: 65A.
- Milner, A.C., and Lindsay, W. 1998. Postcranial remains of *Baphetes* and their bearing on the relationships of the Baphetidae (= Loxommatidae). *Zoological Journal of the Linnean Society*, **122**: 211–235.
- Panchen, A.L. 1964. The cranial anatomy of two Coal Measure anthracosaurs. *Philosophical Transactions of the Royal Society of London, Series B*, **242**: 207–281.
- Panchen, A.L. 1970. Anthracosauria. *Handbuch der Palaeoherpetologie*. Teil 5A. Fischer, Stuttgart, Germany.
- Panchen, A.L. 1972. The skull and skeleton of *Eogyrinus attheyi* Watson (Amphibia: Labyrinthodontia). *Philosophical Transactions of the Royal Society of London, Series B*, **263**: 279–326.
- Panchen, A.L. 1977. On *Anthracosaurus russelli* Huxley (Amphibia: Labyrinthodontia) and the family Anthracosauridae. *Philosophical Transactions of the Royal Society of London, Series 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. *Edited by* A.L. Panchen. Academic Press, London and New York, pp. 319–350.
- Panchen, A.L., and Smithson, T.R. 1988. The relationships of the earliest tetrapods. *In* The phylogeny and classification of the tetrapods. *Edited by* M.J. Benton. Clarendon Press, Oxford, Vol. 1, pp. 1–32.
- Romer, A.S. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology, Harvard*, **99**: 3–366.
- Romer, A.S. 1969. A temnospondylous labyrinthodont from the Lower Carboniferous. *Kirtlandia*, **1969**: 1–20.
- Sawin, H.J. 1941. The cranial anatomy of *Eryops megacephalus*. *Bulletin of the Museum of Comparative Zoology, Harvard*, **88**: 407–463.
- Schoch, R.R., and Milner, A.R. 2000. Stereospondyli. *Handbuch der Paläoherpetologie*, Tiel 3B, Verlag Dr Friedrich Pfeil, München, Germany.
- Smithson, T.R. 1982. The cranial morphology of *Greererepton burkemorani* (Amphibia: Temnospondyli). *Zoological Journal of the Linnean Society of London*, **76**: 29–90.
- Smithson, T.R. 1985. The morphology and relationships of the Carboniferous amphibian *Eoherpeton watsoni* Panchen. *Zoological Journal of the Linnean Society of London*, **85**: 317–410.
- Watson, D.M.S. 1929. The Carboniferous Amphibia of Scotland. *Palaontologica Hungarica*, **1**: 219–252.