A new specimen of *Baphetes* from Nýřany, Czech Republic and the intrinsic relationships of the Baphetidae

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Abstract

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'*Loxomma*' *bohemicum* from the Upper Carboniferous assemblage from Nýřany, Czech Republic, is a nomen dubium restricted to the type and only specimen. The new binomen *Baphetes orientalis* is created for a skull referred to *Baphetes bohemicus* by later authors. A previously undescribed baphetid specimen from Nýřany is referred to *B. orientalis* despite differences in skull proportions. It comprises a skull in dorsal aspect, mandibles and some associated postcranial elements. The skull possesses sclerotic ring elements within the orbital region of the dorsal fenestration of the skull, confirming the eye location. The elongate gastralia are arranged perpendicular to the interclavicle edge in contrast to the condition in temnospondyls and colosteids. Cladistic analysis of 24 characters of 11 baphetoids was carried out using *Acanthostega* and *Crassigyrinus* as outgroups. *Eucritta* was the most primitive baphetoid, with *Spathicephalus* being the sister-taxon to the remaining taxa, justifying a monotypic Spathicephalidae as a sister-taxon to the Baphetidae. The Baphetidae are divided into a subfamily Baphetinae nom.nov. containing two *Baphetes* species; and a subfamily Loxommatinae with *Loxomma* as a paraphyletic grade leading to a *Megalocephalus* + *Kyrinion* clade. The Linton taxon '*Baphetes*' *lintonensis* is transferred to the genus *Loxomma* to give the new combination *Loxomma lintonensis*.

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Introduction

The Baphetidae (= Loxommatidae) are one of the predominant groups of large tetrapods in the continental vertebrate assemblages of the Carboniferous. They are known largely from cranial material and only two specimens with associated postcranial elements have previously been reported (Baird 1957; Milner and Lindsay 1998). Most baphetid specimens are from the British Isles with a few from Nova Scotia, Ohio and the Czech Republic. In Beaumont's revision (Beaumont 1977), three genera were assigned to the family, namely *Loxomma*, *Baphetes* and *Megalocephalus*. Clack (2003a) subsequently described a fourth baphetid, the genus *Kyrinion*, from the north of England. A further genus, *Spathicephalus*, was described by Watson (1929) but was not redescribed in Beaumont (1977). It was placed without explanation, in the monotypic family Spathicephalidae by Beaumont (1977) within the Loxommatoidea (now Baphetoidea). Beaumont

and Smithson (1998) later redescribed *Spathicephalus* and provided a justification for the family Spathicephalidae as a sister-taxon to the Baphetidae, but their reasoning was typological rather than cladistic. Finally, Clack (1998a, 2001) described the tetrapod *Eucritta melanolimnetes* from East Kirkton as a plausible basal baphetid which might be the sister-taxon to the remaining genera. Clack (2002a, 2003a) undertook cladistic analyses in which *Loxomma*, *Baphetes* and *Megalocephalus* were represented by single operational taxonomic units (OTU) and found weak evidence that *Baphetes* and *Megalocephalus* were more closely related to each other than to *Loxomma*. This pattern was also found by Ruta and Bolt (2006) and Ruta and Clack (2006).

Until now, the Upper Carboniferous vertebrate assemblage from Nýřany, Czech Republic, has been a minor source of baphetid material, having produced two doubtful specimens and one informative one. The first two specimens from Nýřany to be attributed to the family were reported and
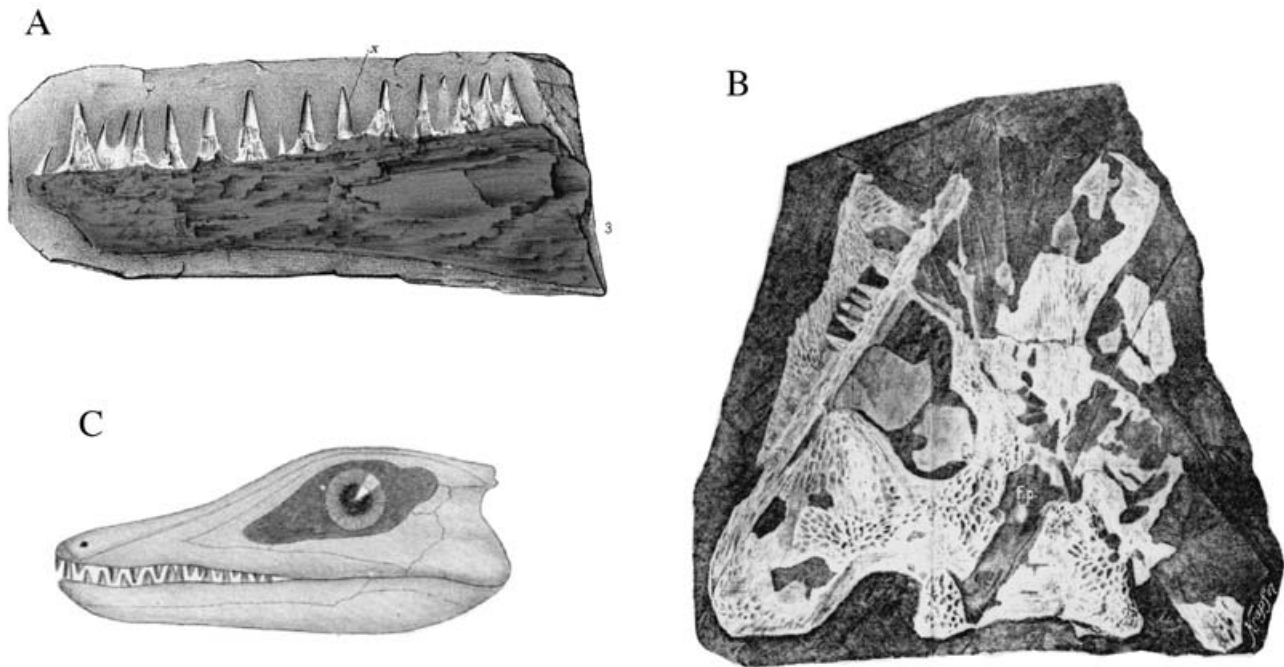
Fig. 1—**A**. *Loxomma bohemicum* Fritsch. nomen dubium. Nýřany, Czech Republic. The holotype mandible as figured by Fritsch (1885), pl. 58, fig. 3. —**B**. *Baphetes orientalis* sp. nov. Nýřany, Czech Republic. Lost counterpart of holotype as figured by Broili (1908). —**C**. Reconstruction of '*Loxomma*' skull with eyeball in place, after Webster-Smith (1926).

described by Fritsch (1885; pl. 58, figs 3–9). Both were fragments of large mandibles, which Fritsch named *Loxomma bohemicum*. The holotype specimen figured by Fritsch (Fig. 1A), was housed in the collection of the German Charles-Ferdinand University in Prague and a second (unfigured) specimen was held in the collection of Herr Bayer of Plzeň. The fate of these specimens is unknown. This means that the holotype is lost but not necessarily destroyed and a neotype cannot be created. It is doubtful if these specimens are determinate although later authors have assigned other material to this species.

The first undoubted Nýřany baphetid specimen, comprising a good skull on counterpart slabs, appears to have been collected in the late 19th or early 20th century, too late for Fritsch to incorporate it in his studies. The two counterparts were given or sold to two separate institutions, one passing to the Národní Museum, Prague and the other going to the Alte Akademie collections at Munich. The latter counterpart was described and figured by Broili (1908; pl. 1, fig. 2 reproduced here as Fig. 1B) as a specimen of the temnospondyl *Sclerocephalus credneri*, although its identity is clear from Broili's figure. The Munich specimen was destroyed in an air-raid in 1944 and Broili's figure is all that remains of it. The Prague counterpart was described by Steen (1938) and assigned to Fritsch's *L. bohemicum*. It is clear, from Broili's figure, that most of the bone had been preserved on the Munich counterpart and the Prague specimen was acid-etched, probably by

Steen, to give a clean mould of the skull roof. This specimen was described in more detail by Beaumont (1977; fig. 25) and reassigned to the genus *Baphetes*. The problem of the identity of the type specimen was noted but not resolved.

In 1983, the authors located an undescribed specimen of Nýřany baphetid in the collections of the Naturhistorisches Museum in Vienna. The specimen was represented by a single counterpart and comprised much damaged bone on the surface of a slab of coal. Most of the bone was acid-etched away by A.C.M. to reveal a small skull and some postcranial elements. The pterygoid exposure in the orbit, and the gastralia were cleanly preserved as bone so were not acid-etched, and are still represented by the original material. The specimen was mentioned as *Megalocephalus* by Milner (1987; p. 506) and Sequeira and Milner (1993; p. 679), but has proved not to belong to that genus, being correctly reported as a *Baphetes* specimen by Milner and Milner (1997; p. 65A). The published situation is that the Nýřany assemblage includes two skulls of a baphetid for which the current name is *Baphetes bohemicus*, although the original material including the holotype is probably indeterminate (see below).

The purpose of this work is twofold. First, to describe and figure the undescribed specimen, which reveals some new anatomical information about the baphetids; and second to undertake a phylogenetic analysis to attempt to determine the internal relationships of the group. The material assigned to the families Baphetidae and Spathicephalidae has not

been subjected to a full cladistic analysis and it was not self-evident that all the present families and genera are monophyletic. The nomenclature used in the systematic section and the description below assumes two conclusions from the analysis and discussion (i) that the new specimen is a juvenile of the same taxon as the previously described skull from Nýřany and (ii) that the small skull from Linton, described as the basis of the taxon *Baphetes lintonensis*, should be referred to the genus *Loxomma*.

Institutional abbreviations for the catalogue numbers of specimens studied in this work are as follows: AMNH: American Museum of Natural History, New York, USA; BMNH: Department of Palaeontology, The Natural History Museum, London, UK; BSP: Bayerische Staatsammlung für Geologie und Paläontologie, Munich, Germany; NMP: Národní Museum, Prague, Czech Republic; NMW: Naturhistorisches Museum, Vienna, Austria.

The status of Loxomma bohemicum *Fritsch (1885)*

As noted in the Introduction, Fritsch (1885: p. 16) named *Loxomma bohemicum* on the sole basis of two mandibular fragments, the holotype (Fritsch 1885; pl. 58, figs 3–9) in the German University at Prague and another (unfigured) in the private collection of Herr Cajetan Bayer of Plzeň. To our knowledge, these specimens have not been located since that time and all that is available are plaster casts and Fritsch's figures, all of the holotype. There is, however, no positive evidence that the specimens have been destroyed, they are simply lost. Plaster casts were made and one, NMP M535, survives in the collections of the Národní Museum. The figured holotype (Fig. 1A) was clearly an anterior fragment of the mandible of a large primitive tetrapod with a skull at least 400 mm long. It is too large and robust to belong to most known Nýřany tetrapods, but is likely to belong to the temnospondyl *Capetus palustris*, redescribed by Sequeira and Milner (1993). Sequeira and Milner (1993; text-fig. 8B) depict a fragment of a large *Capetus* mandible comparable in scale and appearance to that of '*L. bohemicum*'. This is the only known Nýřany taxon that attained a size compatible with the '*L. bohemicum*' mandible figured by Fritsch, the largest certain Nýřany baphetid specimen having a skull 180 mm long.

Steen (1938) noted the holotype to be generically and specifically indeterminate, but then assigned an informative baphetid skull to *L. bohemicum* to provide the taxon with a determinate baphetid specimen. This was not and is not a valid taxonomic procedure. Beaumont (1977) followed Steen's taxonomy without comment, treating the referred Prague skull as a 'topotype'. This is not a category of type specimen regulated by the International Committee for Zoological Nomenclature (ICZN 1999, p. 120).

To summarize, it appears that the binomina *L. bohemicum* and *B. bohemicus* are nomina dubia that must be restricted to the lost holotype mandible, which might equally belong to

the temnospondyl *C. palustris*. For this reason, the unequivocal baphetid taxon from Nýřany requires a new specific name. Only if the lost holotype should be rediscovered and prove to be determinately baphetid, might a further revision then be necessary.

Systematics

TETRAPODA Goodrich (1930)
Superfamily BAPHETOIDEA (Cope 1875 as –idae)
 (Included taxa: Baphetidae, Spathicephalidae, *Eucritta*)
Family BAPHETIDAE Cope (1875)
(LOXOMMATIDAE Lydekker 1889; LOXOMMIDAE Watson 1917)
BAPHETES Owen (1854)
 Type species. *Baphetes planiceps* Owen (1854) from the Middle Pennsylvanian of Stellarton, Nova Scotia.
 Baphetes orientalis sp.nov.
 Figures 1B–5

Synonymy

Sclerocephalus credneri Fritsch; Broili 1908 p. 49, pl. 1, fig. 2 *non* Fritsch (1901)
Loxomma bohemicum Fritsch; Steen 1938 p. 237 text-figs 23, 24, pl. V fig 2 *non* Fritsch (1885)
Loxomma bohemicum Fritsch; Romer 1947 p. 96, fig. 17 *non* Fritsch (1885)
Baphetes bohemicus (Fritsch) Beaumont 1977 p. 89 fig. 25 *non* Fritsch (1885)
Baphetes bohemicus (Fritsch); Milner 1980 p. 453 *non* Fritsch (1885)
Baphetes bohemicus (Fritsch); Milner 1987 p. 506 *non* Fritsch (1885)
Megalocephalus sp.; Milner 1987 p. 506
Baphetes bohemicus (Fritsch); Milner and Milner 1997 p. 65A *non* Fritsch (1885)
Baphetes bohemicus (Fritsch); Milner *et al.* 2007 p. 69 *non* Fritsch (1885)

Holotype NMP M.1388 (previously ČGH 3509), a skull with detached maxillae, preserved as an acid-etched mould of the dorsal surface (Steen 1938; text-fig. 23, pl. V fig. 2; Beaumont 1977; fig. 25). The counterpart, BSP catalogue number unknown [Schadel II, Broili 1908, taf. 1 fig. 2 reproduced here as Fig. 1(B) was destroyed in Munich in 1944].

Nomenclature Species name derived from *oriens -entis* = eastern, referring to the easternmost record of a baphetid.

Diagnosis Species of *Baphetes* in which:
i) the anterior jugal and lacrimal are unusually wide in a 180-mm skull, producing a wide muzzle;
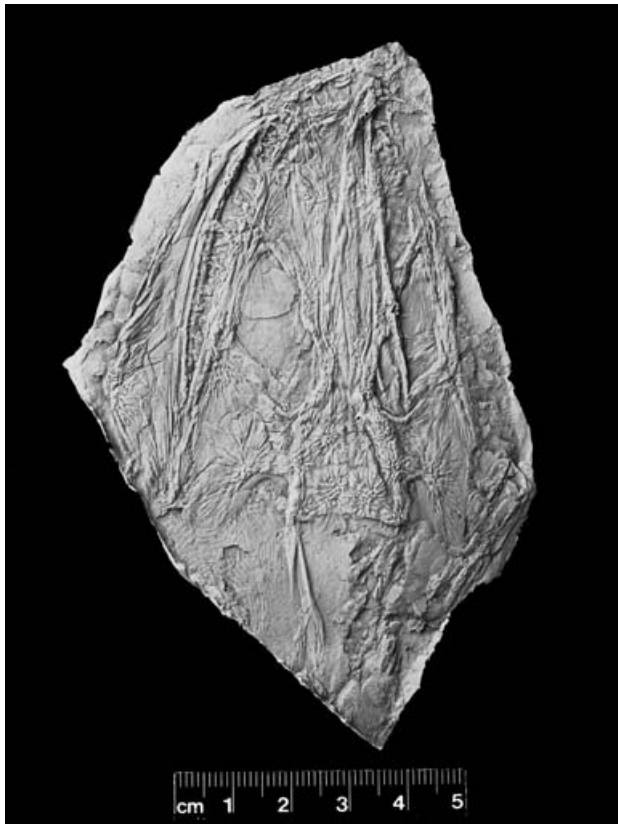ii) the posteromedial ramus of the jugal bulges to produce all of the lateral constriction between the orbit and the

Fig. 2—*Baphetes orientalis* sp. nov. Nýřany, Czech Republic. Photograph of latex cast of NMW 1898.X.42.

antorbital fenestra, and in doing so excludes the lateral 'finger' of the postorbital from the orbit margin.

Beaumont (1977; p. 89) also defined the Nýřany baphetid by the presence of prominent lateral line sulci in the cheek region *contra B. kirkbyi*. However, these also occur in the small *Loxomma* ('*Baphetes*') *lintonensis* skull from Linton and may well be a characteristic of juvenile baphetid skulls, as discussed later.

Locality and horizon Gaskohle, Nýřany Series, Asturian (= Westphalian D), Upper Carboniferous; Nýřany, Czech Republic.

Referred specimen NMW 1898.X.42, a small skull, pectoral girdle and gastralia, from the type locality (Figs 2–4). Now preserved largely as an acid-etched mould, but with no counterpart known.

Description

The holotype of *B. orientalis* was described by Beaumont (1977; pp. 89–92) as a topotype of *B. bohemicus* and that description is not repeated here. A reconstruction of the skull roof based on that of Beaumont is reproduced in Fig. 5(B). Specific features are discussed comparatively with the new specimen described below.

Description of the new specimen

General features NMW 1898.X.42 (Figs 2–4) comprises a specimen on a single slab of coal, without a counterpart. It was acid-etched, except for the left orbit and the posterior region of the interclavicle and the gastralia, which were left intact. It is therefore described from a latex cast of the acid-etched impression, except for the above-mentioned regions. The major component of the specimen is a skull with a midline length of 71 mm, visible in dorsal aspect. This is significantly smaller than the holotype skull described by Steen (1938) and Beaumont (1977), which is about 180 mm long. In NMW 1898.X.42, the left cheek is spread out laterally, while the right cheek is compressed and partly folded under the skull roof. Very little of the palate is visible except such elements as are seen within the orbits and antorbital fenestrae. The left mandible is spread out next to the left cheek and is fully visible in lateral aspect. The right mandible is crushed under the middle region of the skull and is largely visible as a pair of raised ridges running anteriorly under the snout. The symphyseal region of the right mandible protrudes anterior to the skull and is visible in symphyseal aspect, the adductor fossa region is exposed through the right orbit. Postcranial elements extend backwards behind the left cheek and tympanic embayment and comprise the posterior region of an interclavicle in dorsal aspect, the stem of the right clavicle pushed backwards (the blade being obscured by the left tabular), the almost fully visible right cleithrum also pushed backwards and with the head partly off the slab, and finally several rows of gastralia. No axial or limb elements are visible.

Skull roof The skull roof is, in most respects, like those of other specimens assigned to *Baphetes* and this description concentrates on features that are believed to be novel or of systematic significance. Most bones are described from the uncrushed left side of the skull. Most dermal roofing elements bear striate–radiate ornament with only a few reticulate pits in the centre of each bone. On the slower-growing skull table, the pitted areas occupy most of the surface of the bones, whereas over the snout and cheeks, where considerably more allometric growth can be anticipated, the pitted areas are small. By virtue of its size and the poor development of pitting, this individual can reasonably be assumed to have been a juvenile when it died. In this respect it bears a close resemblance to AMNH 6944, the small (75 mm) skull roof from Linton described by Beaumont (1977; fig. 24) as the holotype of *B. lintonensis* and here referred to *Loxomma*. In that specimen the skull table elements are covered in reticulate pitting but the other elements retain
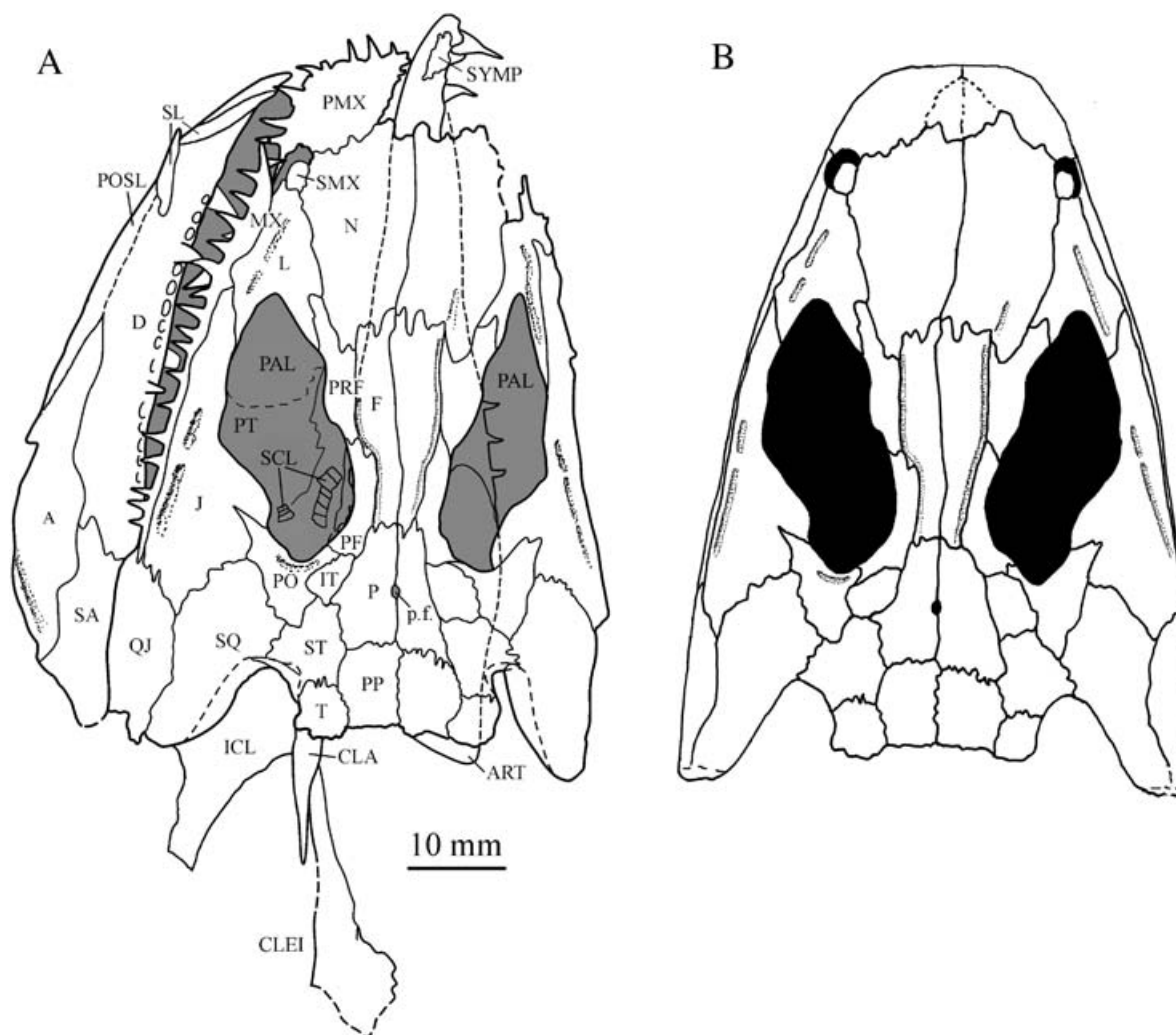
Fig. 3—*Baphetes orientalis* sp. nov. Nýřany, Czech Republic. —**A**. Interpretive drawing of NMW 1898.X.42. —**B**. Reconstruction of skull roof of NMW 1898.X.42. Abbreviations for this figure and Fig. 4: A, angular; ART, articular; CLA, clavicle; CLEI, cleithrum; D, dentary; F, frontal; GAST, gastralia; ICL, interclavicle; IT, intertemporal; J, jugal; L, lacrimal; MX, maxilla; N, nasal; P, parietal; PAL, palatine; PF, postfrontal; p.f., pineal foramen; PMX, premaxilla; PO, postorbital; POSL, postsplenial; PP, postparietal; PRF, prefrontal; PSP?, possible parasphenoid cultriform; PT, pterygoid; QJ, quadratojugal; SA, surangular; SCL, sclerotic plates; SL, splenial; SMX, septomaxilla; SQ, squamosal; ST, supratemporal; SYMP, mandibular symphysis; T, tabular.

striate–radiate ornament with just a few central pits. These two juvenile specimens are significantly smaller than any other baphetid skull and cannot be assumed to have the same proportions as adults of the same species.

The premaxilla is a massive element, typical of baphetids, with no trace of an alary process extending over the nasal. The symphyseal region of the right mandible has been crushed through the snout-tip in front of the nasals and it is not possible to determine whether or not internasal elements were present as in many other baphetids. The external naris is small and situated close to the jaw margin. It is capped by a small rectangular septomaxilla bearing dermal ornament and apparently not attached to the bones surrounding the

naris. The mediolateral margins of the naris are formed by the nasals and by the lacrimals. In this specimen, the lacrimal extends up to the naris and there is no maxillary–nasal contact anterior to the lacrimal as in the longer-snouted *Megalocephalus* and *Kyrinion*. The most significant difference between this specimen and the holotype is the shape of the snout, in particular the lacrimal contribution. In NMW 1898.X.42, the lacrimals are comparatively slender 'arrowhead'-shaped bones, whereas in the holotype they are about twice as large, relatively, and result in the snout of this specimen being broader than in any other *Baphetes*. That condition is unique to the holotype whereas the condition in NMW 1898.X.42 is the generalized condition found in *Loxomma* species and
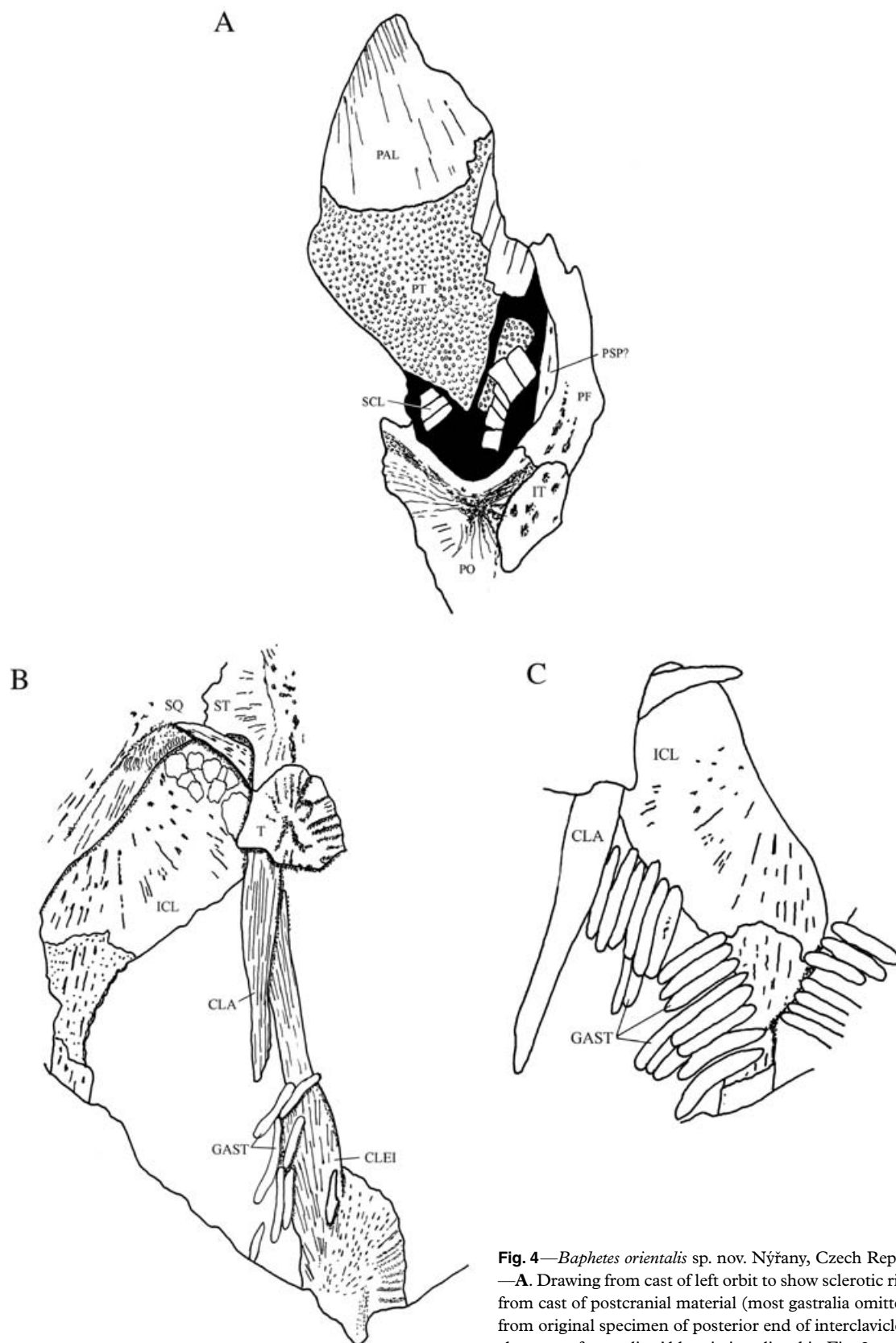
Fig. 4—*Baphetes orientalis* sp. nov. Nýřany, Czech Republic.
—**A**. Drawing from cast of left orbit to show sclerotic ring. —**B**. Drawing from cast of postcranial material (most gastralia omitted) —**C**. Drawing from original specimen of posterior end of interclavicle and associated chevrons of gastralia. Abbreviations listed in Fig. 3.
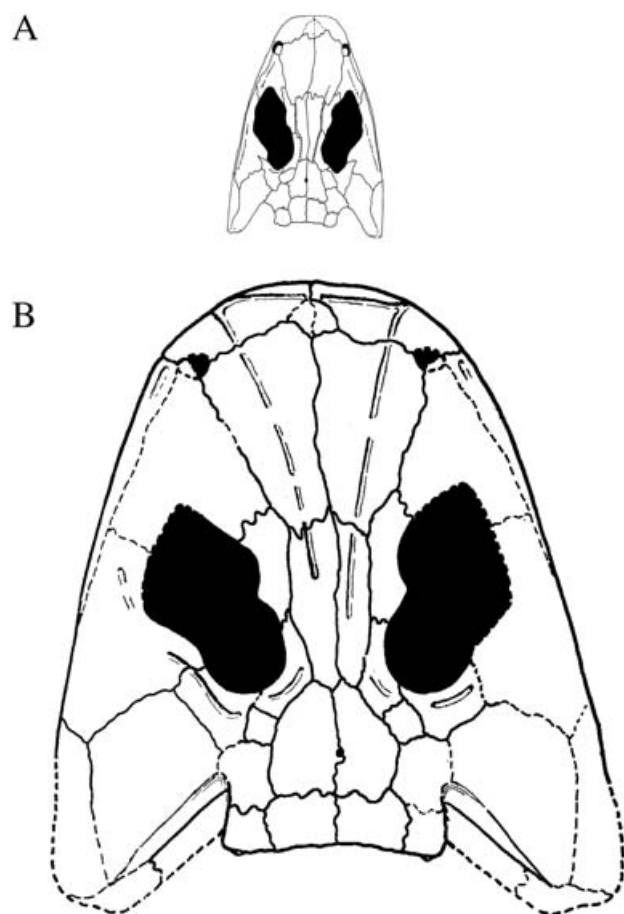
Fig. 5—*Baphetes orientalis* sp. nov. Reconstructions of dorsal skull roofs to scale —**A**. NMW 1898.X.42; —**B**. NMP M1388 (after Beaumont 1977; fig. 25b). The jugal–quadratojugal suture is modified from Beaumont's original reconstruction based on first-hand observation by ARM.

edge of the antorbital fenestra. This indentation is followed by a large gently curved convexity, which not only demarcates the anterodistal margin of the orbit but also excludes the distal end of the postorbital from the orbit margin. This is an unusual configuration but is seen on the left side of the larger skull from Nýřany figured by Beaumont (1977; fig. 25a).

The jugal extends to the level of the anterior edge of the antorbital fenestra, further forward than in any other baphetid (the condition in the larger holotype is unknown). It broadens posteriorly, its posterior width being about three times its anterior width. It is excluded from the jaw margin by the long slender maxilla, which reaches back to the level of the posterior orbit margin and contacts the quadratojugal. The quadratojugal is a massive rhomboidal bone. The quadrate is not visible and may have not yet ossified. The large squamosal forms much of the dorsomedial region of the cheek and sutures broadly with the supratemporal behind the temporal ('otic') notch. As in other baphetids and unlike temnospondyls, the squamosal forms only the lateral region of the notch margin, the supratemporal playing a major role in the dorsomedial notch margin. The term 'squamosal embayment' sometimes used to describe this region in early tetrapods, is certainly not appropriate in the context of the Baphetidae. In NMW 1898.X.42, the supratemporal–squamosal suture contacts the otic notch at its anteriormost level, but in many baphetids the supratemporal extends around this point and occupies the entire anterior region of the notch. This may be a size-linked relationship because it appears to be most pronounced in the largest baphetid skulls and does not occur in the 70- to 75-mm NMW 1898.X.42 and AMNH 6944.

The skull table is slightly wider than long, being 40 mm wide from one posterolateral corner of the tabular to the other, and 35 mm long from the same corners to the posteriormost margin of the orbit. This is shared with the holotype, which also possesses an unusually wide skull table for a baphetid. The postorbital extends fingers of bone on both sides. The medial finger of bone borders the anterior edge of the intertemporal and makes a narrow contact with the postfrontal. The lateral finger extends within the border of the jugal and is excluded from the orbit margin. A less pronounced version of this relationship also occurs on the left side of the larger type specimen (and probably on the right side although it does not appear in Beaumont's reconstruction) and does not appear to be found in any other described baphetid. It is the only autapomorphy of the species. The intertemporal is present as in *Loxomma* and *Baphetes*, and is a small element about one-third as large as the supratemporal. A typical parietal is present and the parietals border a distinct pineal foramen, which lacks any thickening of bone around it. The most unusual feature of the skull table is the anteroposterior elongation of the postparietals, which are almost as large as the parietals. Again this is matched in the small skull from Linton, AMNH 6944. The stepped border

other *Baphetes* species. This will be discussed below as a possible ontogenetic shape change. The nasals are large, roughly rhomboidal elements expanding slightly anteriorly. The frontals, prefrontals and postfrontals are all slender elements forming a narrow interorbital region.

The orbit with its associated antorbital fenestra is one of the most characteristic features of baphetids and varies in shape and configuration within the group. In NMW 1898.X.42, the antorbital fenestra is about 1.5 times the area of the orbit, giving a relationship very similar to that in *B. kirkbyi*. As in most baphetoids (except *Spathicephalus* and *Kyrinion*), the orbit and antorbital fenestra form a 'waisted' opening, the constriction in NMW 1898.X.42 being produced by local expansion of the prefrontal and the jugal. The prefrontal bears a convex thickening in its posterior half, this thickening being followed by a sharp indentation posteriorly marking the anteromedial orbit margin. The jugal has an angular indentation halfway along its length marking the posterodistal

of the postparietals and tabulars against the bones anterior to them characterizes these two small specimens, and as with several structures, presents us with the problem of whether this is a juvenile characteristic or a taxonomically significant feature.

Palate The only palate elements that are visible are those exposed in the space of the antorbital fenestra and orbit. In both antorbital fenestrae, parts of the dorsal surface of the palatines are visible and broad sheets of bone with striate markings radiating from a point anterior to the exposure of the bone (Fig. 4A). In the posterior region of the left antorbital fenestra, the palate has not been acid-etched and the original bone of the anterior ramus of the left pterygoid is visible in ventral aspect and its covering shagreen of tiny denticles is preserved. In all visible features, the palate corresponds to that of *B. kirkbyi* described and figured by Beaumont (1977).

Mandible The left mandible is completely visible in labial aspect, although the curved anterior region is crushed and the splenial has been displaced and broken. In general configuration, it closely resembles that of *Megalocephalus* as figured by Beaumont (1977; fig. 14). The dentary extends for about three-quarters of the length of the mandible and bears no ornament except for anteroposterior striations. The splenial approaches to with 2–3 mm of the symphysis and extends back as a striate bone about one-quarter of the length of the mandible. Its posterior half has snapped off and is displaced to one side leaving a slot on the ventral jaw margin. The postsplenial is a longer element that extends almost to the angle of the jaw. The angular bears a central patch of ornament on the jaw angle with weak striations extending anteriorly and stronger striations extending posterodorsally. The surangular is another large striated element but the articular is hidden by the quadratojugal.

A few features of the lingual face of the mandible are visible. The right mandible has the symphyseal region exposed anterior to the skull and the adductor region exposed in the right orbit. The left mandible has the coronoids crushed up behind the mandibular tooth row. The anterior of the right mandible bears a large boss with the roughened symphyseal surface on it. It is the same shape as the symphysis figured by Ahlberg and Clack (1998; fig. 18c) for *Megalocephalus*, but it cannot be determined whether a parasymphyseal plate is involved or not. The medial lamina of the splenial appears to extend forward and terminate immediately ventral to the symphyseal surface. On the left mandible, the denticle-covered surface of middle and posterior coronoids had been pushed up behind the marginal dentition. The sutures cannot be determined but it is clear that denticle-bearing coronoids extended alongside the posterior two-thirds of the marginal dentition. Inside the right orbit, a portion of the lingual face of the mandible can be seen including the posterior end of the dentary with a few small teeth, followed

by part of the adductor fossa in which the inner face of the surangular is visible.

Lateral line sulci Because much of the surface ornament is striate–radiate, lateral-line sulci are poorly developed but a few can be seen (Fig. 3A). Both supraorbital sulci are visible, close together on the posterior region of the frontals, diverging anteriorly and running along the anterolateral edges of the frontals. There is only a faint suggestion of the canals further forward just behind the centre of ossification of the right nasal. Parts of an infraorbital sulcus are visible on the left postfrontal and at the posterolateral edge of the left jugal. As in the holotype, no sulci are visible on the squamosals or the skull table. On the mandible, the mandibular canal forms a clear groove along the posterior edge of the angular but is not determinable anterior to this because of the crushing along the mandible edge.

Dentition The marginal dentition is visible on the left side of the specimen. All marginal teeth are large conical spikes, those on the maxilla and dentary being slightly recurved. The left premaxilla has space for about 12 teeth, six of which are visible. This corresponds to the condition in *Baphetes* (10–11 teeth + spaces) reported by Beaumont, compared with eight premaxillary teeth + spaces in *Loxomma* and *Megalocephalus*. The maxillary tooth + space count is about 35 comprising 19 teeth and 16 spaces. The teeth are slightly larger next to the centre of ossification of the maxilla and reduce gradually in size posteriorly. There is no evidence of pseudocanine 'peaking' along the maxilla or dentary. The mandibular marginal dentition is damaged and a tooth-count is not possible but it appears that there are fewer, larger marginal teeth on the dentary. In the right orbit it can be seen that the tiny posteriormost dentary teeth overlap the level of the anterior end of the adductor fossa opening. No palatal fangs are visible.

Sclerotic ring NMW 1898.X.42 is noteworthy as the first baphetid specimen to have sclerotic ring elements *in situ*. The presence of sclerotic plates in all early tetrapod groups can reasonably be assumed but in some families such as the Colosteidae and Diplocaulidae, they have never been observed (A.R.M., personal observation). They were unknown in baphetids until they were reported as isolated plates in the disarticulated specimen of *Baphetes* found near Wigan by Milner and Lindsay (1998; p. 218). In NMW 1898.X.42, about nine plates are arranged in two sections at the back of the left orbit (Fig. 4A). It may be noted that this confirms that the eye was situated in the space generally accepted as the orbit and that the antorbital fenestra was indeed antorbital. This has generally been assumed by most workers, but for much of the middle of the 20th century, the most copied and reproduced reconstruction of a baphetid skull was that first used in the popular work by Webster-Smith (1926; pl. 48 fig. 1) in which the eye was placed in the antorbital space (Fig. 1C).

Appendicular skeleton Unless one assigns *Eucritta* to the Baphetidae, NMW 1898.X.42 is the first baphetid specimen to have a significant amount of articulated postcranium associated with it. Baphetids were notorious for much of the 20th century for the absence of postcranial elements that could be securely associated with the skull material. Baird (1957) was the first to recognize a specimen of *Megalocephalus lineolatus* from Linton with several neural arches and an intercentrum and this specimen was figured by Beaumont (1977; fig. 16b). The major advance in our knowledge of the baphetid postcranium came when Milner and Lindsay (1998) described and figured a specimen of *Baphetes* (BMNH R.9663) in an incomplete concretion, in which several post-cranial elements were present in a dissociated state, including clavicle, humerus, radius, ilium, ischium, tibia and fibula.

In NMW 1898.X.42, part of the pectoral girdle is present in association behind the left cheek. The interclavicle (Fig. 4B,C) is partly exposed in dorsal (interior) view behind the left otic notch. It appears to have been 'kite-shaped', i.e. rhomboidal with a posterior extension. The visible region is similar in shape to the interclavicle of *Eucritta* (Clack 2001; figs 1c and 5b) and to the interclavicle from Newsham attributed to *Megalocephalus* by Tilley (1971; unpublished thesis). The right clavicle is wedged in the left otic notch. Part of its blade is visible within the notch and its stem extends backwards behind the left tabular (Fig. 4B). The stem appears to have been a flat strip of striated bone narrowing slightly towards its dorsal end. Alongside the stem of the right clavicle is the right cleithrum. The strap-like cleithrum stem is the same width as the wider section of the clavicle stem, resembling the condition in the larger *Baphetes* described by Milner and Lindsay (1998; p. 223). Above the clavicle stem, it expands slightly into an ovoid flange, possibly a post-branchial lamina (noted also by Milner and Lindsay in their material) and 10 mm dorsally it expands further into the cleithrum head (Fig. 4B). This is a larger ovoid with its axis in line with the cleithrum stem, but with the expansion entirely to one side of the stem line. The centre of ossification, indicated by the striate–radiate bone surface, is in line with the stem. The distal end of the cleithrum is off the slab. The specimen has been crushed flat but there is no evidence that the cleithrum head is recurved backwards or forwards in relation to the stem.

Gastralia Gastralia are present as partly dispersed chevrons seen as impressions in dorsal (internal) aspect where acid-etched but still preserved as intact elements visible in ventral (external) view where not etched (Fig. 4B,C). Each is a flat oval structure, typically about six times as long as wide, with no sculpture visible on the dermal surface. They are parallel-sided along the long axis and do not have posterior expansions as seen in the larger *Baphetes* specimen from Wigan (Milner and Lindsay 1998; p. 231). The chevrons of gastralia in the vicinity of the shoulder girdle exhibit one remarkable feature in contrast to those of temnospondyls as

recently reviewed by Witzmann (2007). Over much of the ventral trunk of temnospondyls, the chevrons of gastralia are anteriorly directed but at a point a short distance behind the pectoral girdle, the pattern reverses and the chevrons are posteriorly directed. This results in the presence of a nodal point where the anteriorly and posteriorly directed chevrons meet. It also means that the gastralia that lie alongside the posterolateral edges of the interclavicle have their long axes parallel with the edge of the interclavicle. Witzmann noted that in *Archegosaurus (*op.cit., fig. 2c), *Sclerocephalus* and *Branchierpeton*, the nodal point was behind the interclavicle whereas in *Cheliderpeton* (Fritsch 1885; pl. 56 fig. 2), it coincided with the posterior end of the interclavicle. This also occurs in the colosteid *Greererpeton* (Godfrey 1989, fig. 3a). In NMW 1898.X.42 however, the anteriorly directed chevrons run all the way forwards along the sides of the interclavicle and, as a result, the elongate gastralia are perpendicular to the interclavicle edge rather than parallel to it (Fig. 4c). We know of no precedent for this condition, although the scalation of early tetrapods is still poorly known. Similar elongate gastralia are found in *Acanthostega* (Coates 1996) and *Crassigyrinus* (Panchen 1985) but in neither taxon can the arrangement of gastralia around the interclavicle be seen. In *Eucritta*, the anterior gastralia are partly dispersed. It is clear that the anteriorly directed chevrons reach the end of the interclavicle (Clack 2001 fig. 2) but the arrangement lateral to the interclavicle is unclear. It is possible that the arrangement of gastralia in NMW 1898.X.42 represents the primitive tetrapod condition, which is then modified in colosteids and temnospondyls.

Unity of the Nýřany baphetid material

NMP M1388 and NMW 1898.X.42 are the only two determinate baphetid specimens from Nýřany but they differ significantly in size and proportions (Fig. 5) and unity cannot be assumed. However, we consider that they represent different ontogenetic stages of a single taxon and place NMW 1898.X.42 in the hypodigm of *B. orientalis.* One character that does seem to be derived and unique to the two specimens is the relationship of the jugal to the postorbital. The bulge separating the lateral region of the antorbital fenestra from the orbit is composed of the jugal growing outside the postorbital and excluding its distal ramus from the orbit margin. This is very pronounced in NMW 1898.X.42 and less pronounced but still visible in the larger NMP M1388. This feature has not been reported in any other baphetid. Both specimens primitively retain the inter-temporal (compared with *Megalocephalus* and *Spathicephalus*) and in both, the lacrimal primitively separates the maxilla from the naris (compared with *Megalocephalus* and *Kyrinion*). Associated characters of uncertain polarity are the broad snout and a premaxillary tooth-count of 10–11, which Beaumont used as defining features of *Baphetes*. NMP M1388 has the broad snout but the premaxillary tooth-count is

unknown, although scaling the visible premaxillary teeth against the hypothetical extent of the premaxillary suggests a count of 10–11. The much smaller NMW 1898.X.42 has a less broad snout but does have up to 12 premaxillary teeth. The combination of one synapomorphy with the series of shared *Baphetes* characters of uncertain polarity or primitive state in the only two baphetids from this locality leads us to conclude that they belong to the same taxon and the following systematic analysis supports this.

Systematic analysis

External relationships The external relationships of the Baphetidae are problematic and they have variously been suggested to be temnospondyls (e.g. Romer 1947), stem-amniotes (Panchen 1980), either stem-tetrapods or stem-temnospondyls (Carroll 1995), stem-tetrapods (Laurin and Reisz 1997; Ahlberg and Clack 1998; Ruta *et al.* 2003; Ruta and Coates 2007), or stem-temnospondyls (Clack 2002a, 2003a). It was clear to us that our new material offered few data that would have a bearing on this problem, although we note that the gastralia are like those of the stem-tetrapods *Acanthostega* and *Crassigyrinus* and their configuration in relation to the interclavicle is suggestive of a more primitive state than that shared by colosteids and temnospondyls.

Internal relationships We hoped that we might be able to clarify the internal relationships of the Baphetidae and on their relationship to *Eucritta* and *Spathicephalus*, in particular the following.

i) Does *Eucritta* fall inside or outside a clade Baphetoidea including the Baphetidae and *Spathicephalus*?

ii) Is *Spathicephalus* the sister-taxon to the Baphetidae or does it fall within the clade?

iii) Are the genera *Loxomma*, *Megalocephalus* and *Baphetes* monophyletic and what is their relationship to each other and to the monotypic *Kyrinion*?

Included taxa The analysis was carried out using 13 taxa including two outgroup taxa (Appendix 1). The outgroups selected were *Acanthostega* and *Crassigyrinus*, both stem-tetrapods with skulls approaching the size of, or of similar size to, those of baphetids and both recently thoroughly redescribed. *Eucritta melanolimnetes* was included as an ingroup taxon as it has appeared as a primitive relative of baphetids in some recent analyses. Most described baphetid taxa were included, including some represented by single incomplete skulls such as *Loxomma allmanni* and *Kyrinion martilli*. The two baphetid taxa from Linton, Ohio were included on the basis of the species nomenclature and content given by Beaumont (1977). Hook and Baird (1986) proposed a taxonomic revision of this material in which the *Megalocephalus* species would have become *M. enchodus* through addition of a specimen with senior synonymy, while the type of *M. lineolatus* would be transferred to *Baphetes* to

give the binomen *B. lineolatus* incorporating '*B*'. *lintonensis* as a junior synonym. Regrettably, these changes were presented as unsupported assertions and the reasoning and supporting data were never published. We have chosen to retain Beaumont's species-level taxonomy (but not generic identities) and specimen content until a reasoned alternative is presented. The two Nýřany specimens were scored individually in the data matrix to determine if the analysis would treat them as immediate relatives.

Excluded taxa Some taxa were omitted in the later preparatory analyses. *Baphetes planiceps* Owen (1854) and *Spathicephalus pereger* Baird (1962) from Nova Scotia were excluded because in preliminary analyses, their character-state distributions proved to be redundant with respect to *B. kirkbyi* and *S. mirus*, respectively. *Loxomma rankini* Beaumont (1977) was eventually omitted as it was represented by one skull fragment bearing only 10 characters out of the 24 used and it was very unstable in position in the resulting cladograms.

Characters and protocol Because only external cranial characters and mandibular characters were present in significant numbers for distributions to be meaningful, only 24 characters could be identified as useful (Appendices 2 and 3). Several other characters were eliminated as uninformative because they were compromised by missing data or because they defined only one terminal taxon. Some characters were taken from Clack (2001) and these are indicated with the numbers assigned to them in that analysis. Analysis was performed using PAUP Version 4.0b10 (Swofford 2002) and MACCLADE Version 3.04 (Maddison and Maddison 1992). All characters were treated as unordered and as of equal weight. The analysis was performed under a heuristic search with tree-bisection reconnection.

Results

Sixteen trees were obtained with the following characteristics: tree length 65 steps; Consistency Index 0.54; Retention Index 0.53; Homoplasy Index 0.46; Rescaled Consistency Index 0.29. A preferred topology from these 16 is depicted in Fig. 6(A) and a 50% majority rule consensus tree, including clade robustness percentages, is depicted in Fig. 6(B). The agreement subtree, in which all 16 shortest trees agree upon mutual relationships, included eight of the 13 taxa considered in this analysis. All three outgroups are removed from it, as well as two of the 10 baphetoid operational taxonomic units, namely *Spathicephalus* and *Loxomma acutirostris*. The preferred tree is one of the closest to the consensus tree, differing only in the positions of *Eucritta* and of *B. kirkbyi*. The following discussion is based largely on these two trees.

Eucritta melanolimnetes This taxon always fell outside the rest of the ingroup but its precise position was an unresolved trichotomy in the consensus tree. In some analyses it was the
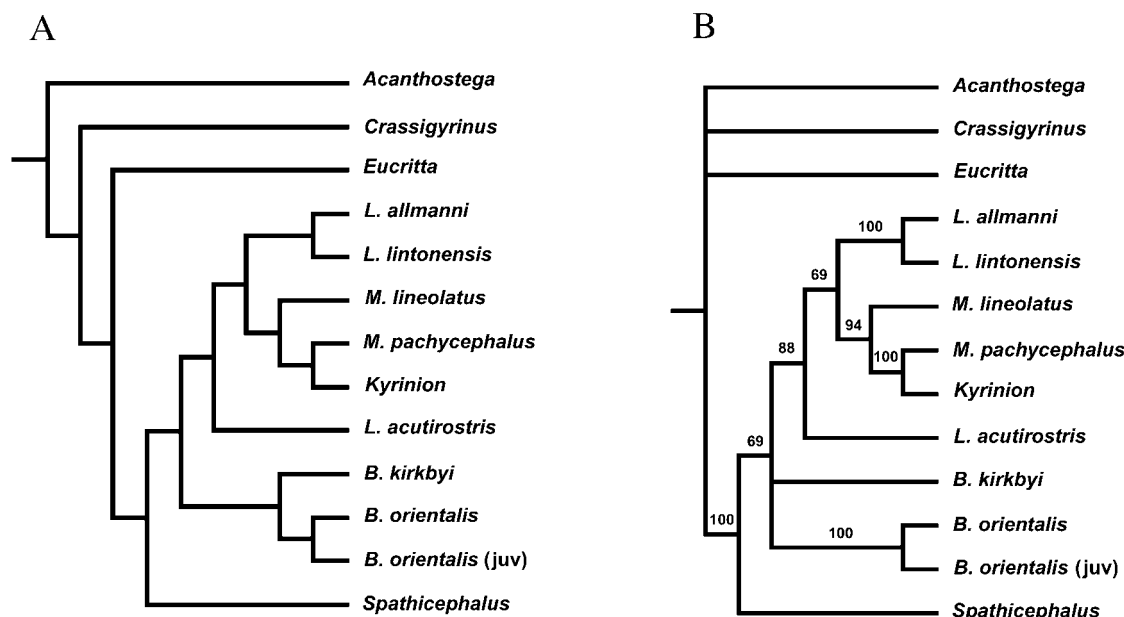
A

B

Fig. 6—**A**. Selected cladogram from 16 obtained. —**B**. Fifty per cent majority rule consensus cladogram from 16 obtained. Figures at nodes indicate percentages of trees in which clades appear.

sister-taxon of the rest of the ingroup, in others it was the sister-taxon of *Crassigyrinus*. We do not regard the latter result as significant or valid. In the much more extensive analyses of primitive tetrapods by Clack (2001) and Ruta and Coates (2007), *Eucritta* never occurs in proximity to *Crassigyrinus*. Our analysis is restricted to cranial characters that vary within the Baphetoidea and our two positions of *Eucritta* depend on single conflicting cranial characters. Clack (2001) and Ruta *et al.* (2003) both place *Eucritta* outside the other baphetoids. In Clack's analysis and some of Ruta and Coates' analyses, *Eucritta* is always the sister-taxon to the other baphetoids; in other analyses of Ruta and Coates (2007), *Eucritta* is the sister-taxon to the Temnospondyli. We did not include a temnospondyl in this analysis so cannot resolve this. Ruta *et al.* (2003; p. 277) observed that the node that incorporated *Eucritta* with temnospondyls was defined by 'several homoplastic features some of which relate to optimizations of missing character scores'. Clack (2001; p. 89) noted that most of the characters uniting *Eucritta* with baphetids were found elsewhere. We note that one possible unique feature shared by *Eucritta* and *Baphetes* (but un-described for other baphetids) is the anterior process on the clavicle described in *Baphetes* by Milner and Lindsay (1998; p. 223, figs 4,5) and apparently present as a damaged structure in *Eucritta* (Clack 2001; p. 83, figs 1C,2C). We suggest that this may more clearly relate *Eucritta* to baphetids than any number of homoplasies. In conclusion, we agree with Clack (2001) that *Eucritta* is a primitive relative of the baphetids but as a result of our upgrading of the group to

superfamily status, we place *Eucritta* without family attribution in a superfamily Baphetoidea outside the Baphetidae and Spathicephalidae.

Family Spathicephalidae Spathicephalus mirus appeared as the sister-taxon to the Baphetidae in 10 of the trees and in the consensus tree, confirming the view of Beaumont and Smithson (1998) that it merits a separate family. In this analysis, it is defined by states of the snout-shape (character 2: 1 > 2), intertemporal absence (12: 0 > 1), small pineal (13: 0 > 1), square supratemporal (14: 2 > 1), tabular shape (17: 1 > 2) and high premaxillary tooth count (22: 1 > 2), but there are many other autapomorphous features (see Beaumont and Smithson 1998) which were excluded to simplify the analysis. *Spathicephalus pereger* Baird (1962) also belongs here, being excluded from the analysis only because its character-set was redundant with respect to that of *S. mirus*. With the content restricted to *Spathicephalus*, it can be argued that Spathicephalidae is a redundant taxon, but we take the view that it is a sufficiently distinctive form, that to include it in an enlarged Baphetidae would make that family unacceptably morphologically diverse. We also note that there are two contemporaneous mandible-based taxa, currently considered as Tetrapoda *incertae sedis*, which might well prove to be relatives of *Spathicephalus* and might ultimately give this family a multigeneric content. These are *Doragnathus woodi* (Smithson 1980) and *Sigournea multidentata* (Bolt & Lombard 2006), both of which are clearly distinct from *Spathicephalus* but which are plausible immediate relatives.

Family Baphetidae The Baphetidae *sensu* Beaumont (1977) appears as a monophyletic family defined in this analysis by the jugal configuration (7: 0 > 2) and subdivided into two clades, one poorly supported clade comprising two species of *Baphetes*, and the other well-supported clade comprising *Loxomma*, *Megalocephalus*, *Kyrinion* and one species previously assigned to *Baphetes*, here renamed *Loxomma lintonensis*.

Subfamily Baphetinae This is an admittedly weakly supported grouping found in nine out of 16 trees. In the other seven trees, it is paraphyletic with respect to the remaining baphetids with *B. kirkbyi* closer to them. It is defined by the postorbital involvement in the jugal process (8: 0 > 1), comprises *B. kirkbyi* and *B. orientalis*, and effectively also includes the type species *B. planiceps*, which was omitted from the analysis only because it was redundant with respect to *B. kirkbyi* in such characters as it possesses (which do not include the defining character 8). As noted by Beaumont (1977; p. 76), *B. planiceps* cannot be separately diagnosed from the better-represented *B. kirkbyi* and they may represent the same taxon. With the inclusion of the type species, this clade can be designated as the Subfamily Baphetinae. The two Nýřany specimens appear as sister terminal taxa in all 16 trees, which is what one would expect if they were ontogenetically different members of a single species. This reinforces our view that NMW 1898.X.42 belongs in *B. orientalis* with the holotype. This subfamily therefore includes three of the four *Baphetes* species recognized by Beaumont. The chronological and phylogenetic implications of this grouping are discussed below.

Subfamily Loxommatinae This clade is found in the consensus tree and most of the 16 component trees. It has *Loxomma acutirostris* as its most primitive member, followed by *L. allmanni* (+ *L. lintonensis* see below), the *Loxomma* species forming a paraphyletic series with respect to a long-snouted clade made up of *Megalocephalus* and *Kyrinion*. The post-*acutirostris* clade and the *Megalocephalus* + *Kyrinion* clades were two of the most robust, appearing in 15 of the 16 alternative trees. *Megalocephalus lineolatus* appears as the sister-taxon to *M. pachycephalus* + *Kyrinion* and the phylogeny can be summarized as *Loxomma* and *Megalocephalus* being successive grades approaching *Kyrinion* as the most derived terminal taxon. The family level name Loxommatinae (first used by Lydekker 1889 as Loxomatinae) is the senior name applicable for this taxon. Despite the conclusion that *Loxomma* and *Megalocephalus* are paraphyletic grades, the overall results are not particularly robust, and we feel it is premature to create new genera for *L. acutirostris* and *M. lineolatus* to ensure monophyly of all taxa.

The position of Beaumont's *B. lintonensis*, based on the single juvenile specimen AMNH 6944, was the only anomalous result of this analysis. Instead of clustering with the other *Baphetes* species, it appears as the sister-taxon to *L. allmanni* in all 16 trees and can only logically be

transferred to the genus *Loxomma*. However, consideration of the critical features distinguishing *Loxomma* from *Baphetes* as listed by Beaumont (1977 pp. 32,76) suggests that this is less problematic than it first appears. *Loxomma* was distinguished by having a high triangular skull, orbit and antorbital vacuities equal in length, a premaxilla with space for eight teeth, and jugal excluded from the jaw margin. *Baphetes* was distinguished by a broad flat snout of parabolic outline, antorbital vacuity larger than orbit, premaxilla with space for 10–11 teeth and jugal in or out of jaw margin. Other characteristics given for these genera by Beaumont served to distinguish them from *Megalocephalus* and are not relevant. In AMNH 6944, the snout is broad but allowing for ontogenetic change, it is consistent with what one might expect in a juvenile *Loxomma* and, in fact, the only *Loxomma* with a snout is the type of *L. acutirostris*, the snout in other species being unknown. The antorbital vacuities of AMNH 6944 are *Loxomma*-like, no bigger than the orbits, and not *Baphetes*-like. The premaxillae are not preserved and the tooth count is unknown. The jugal is excluded from the jaw margin as in *L. acutirostris* and not included as in *B. kirkbyi* or *B. orientalis*. In conclusion, the characteristics of this specimen place it more readily in the grade *Loxomma* than in *Baphetes* and we propose transferring it to *Loxomma* as *L. lintonensis* nov. comb.

Loxomma rankini was not included in the analysis, but from the limited number of characters it possesses it could belong to the Loxommatinae and occupy a position at the base of the *Megalocephalus–Kyrinion* clade as in some respects (fine sculpture, square skull table) it resembles a *Megalocephalus* that has retained an intertemporal. We suggest a provisional position within the Loxommatinae.

Discussion

In 1977, Beaumont revised the three genera *Loxomma*, *Baphetes* and *Megalocephalus* in a precladistic framework. Characters were not considered as primitive or derived and several of the alternative states used by Beaumont to define genera and species include one alternative that is primitive and non-defining (e.g. intertemporal present, lacrimal in contact with external naris). The stratigraphical range of specimens was also implicitly used in considering their identity (Beaumont 1977; p. 90 for *B. bohemicus*). Beaumont did not attempt a phylogeny or discuss the relationships of the three genera, but did note that *Loxomma* was the earliest and seemingly the most primitive genus, and from occasional comments in Beaumont's descriptions, it does appear to be used as the primitive standard of comparison for characteristics of *Megalocephalus* and *Baphetes*. There is the implication that both *Megalocephalus* and *Baphetes* are defined by unique features not found in *Loxomma*, but not that they share any character-states that would relate them to the exclusion of *Loxomma*. By using outgroup comparison for polarity, at least one of *Loxomma*'s features, the premaxillary tooth count

of eight, switches from primitive to derived. As a result, one of Beaumont's defining characters for *Baphetes* – 10–11 premaxillary teeth – becomes primitive, while the reduced premaxillary count in *Loxomma* and *Megalocephalus* becomes a shared derived feature.

The only cladistic analyses to incorporate *Loxomma*, *Baphetes* and *Megalocephalus*, all based on single species, are those of Clack (1998a,b, 2001), Ruta and Bolt (2006) and Ruta and Clack (2006). Clack found an immediate relationship between *Baphetes* and *Megalocephalus* to the exclusion of *Loxomma* as did Ruta and Bolt (2006) and Ruta and Clack (2006), in contrast to the immediate relationship between *Megalocephalus and Loxomma* to the exclusion of *Baphetes* found in this work. Clack (2001) found both alternative topologies in her five most parsimonious trees. We feel that by using more baphetids, albeit with fewer characters, we may have resolved this issue.

The systematic results of this work are summarized here.
Superfamily: BAPHETOIDEA (Cope) Milner and Lindsay (1998)
Eucritta melanolimnetes Clack (1998a) [Viséan]
Family SPATHICEPHALIDAE Beaumont (1977)
Spathicephalus Watson (1929) [Namurian]
Spathicephalus mirus Watson (1929)
Spathicephalus pereger Baird (1962)
Family Baphetidae Cope (1875)
Subfamily BAPHETINAE (Cope) new rank
Baphetes Owen (1854) [Langsettian – Asturian]
Baphetes planiceps Owen (1854)
Baphetes kirkbyi Watson (1929)
***Baphetes orientalis* sp. nov.**
Subfamily LOXOMMATINAE Lydekker (1889) (as Loxomatinae)
Loxomma Huxley (1862) [Viséan-Asturian]
Loxomma acutirostris Watson (1929)
Loxomma allmanni Huxley (1862)
***Loxomma lintonensis* (Beaumont) nov. comb.**
Loxomma rankini Beaumont (1977)
Megalocephalus Barkas (1873) [Langsettian-Asturian]
Megalocephalus lineolatus (Cope) Baird (1957)
Megalocephalus pachycephalus (Barkas) Lehman (1955)
Kyrinion Clack (2003a) [Langsettian/Duckmantian]
Kyrinion martilli Clack (2003a)

Phylogeny and ghost lineages

As with many cladistic analyses, the resultant set of relationships raises interesting issues of phylogeny and ghost lineages. It is clear that the group was present and diversifying in the late Viséan, at which time *Eucritta* and *L. allmanni* were tangibly present. Previous workers have generally tacitly accepted that Spathicephalidae, as a sister-taxon to Baphetidae, were present as a Viséan ghost-lineage as well. A new conclusion from our analysis is that Baphetinae (as sister-group to Loxommatinae, not descendants of *L. allmanni*)

were already present in the Viséan, and that within Loxommatinae, the *L. acutirostris* lineage and the stem of the *Megalocephalus–Kyrinion* clade were already present as well as *L. allmanni*. Our first conclusion is therefore that the adaptive radiation of the group was substantially under way in the Viséan, despite the first appearance in the Westphalian of some constituent groups.

After a pre-Westphalian ghost history, the Baphetinae are represented by the early Westphalian *B. planiceps* and *B. kirkbyi* which may be identical, and the late Westphalian *B. orientalis* which has evolved a broader muzzle and a more exaggerated jugal expansion into the orbit margin.

Autapomorphies of individual species notwithstanding, the Loxommatinae can be seen as a broad evolutionary sequence from *L. acutirostris* as the most primitive form via *L. allmanni* + *lintonensis*, *L. rankini*, *M. lineolatus* and *M. pachycephalus* to *Kyrinion martilli* as the most derived form. This ranking from the cladogram is not reflected in the stratigraphical relationship of all of these species, with *L. acutirostris*, *L. lintonensis* and *M. lineolatus* all 'appearing late' with implied ghost-lineages. In particular, the late Westphalian *L. lintonensis* represents a late range extension for the genus from Westphalian B to Westphalian D. It appears as the sister-taxon to *L. allmanni*, but could equally be a descendant form. *Megalocephalus* occurs throughout the Westphalian and *Kyrinion* is an early Westphalian specimen and our analysis implies that the diversification of this clade had probably happened by the earliest Westphalian. A general conclusion then is that, although much of the diversity of the Baphetoidea is represented by Westphalian taxa, the pattern of relationships suggests that much of the diversification took place in the Viséan, and the diversification within the Loxommatinae had taken place in the Namurian at latest. In Beaumont's systematic framework, *Loxomma*, *Baphetes* and *Megalocephalus* coexisted at least in the early Westphalian; in ours, the recognition of *L. lintonensis* means that they coexisted throughout the Westphalian.

Ontogeny of the baphetid skull

Previously, the only purported example of a baphetid species represented by adult and juvenile material was *M. pachycephalus* as described by Beaumont. As well as the abundant large material, she reported a 40-mm juvenile skull from Jarrow, Ireland (Beaumont 1977; pp. 47,75). Later restudy showed this to be a large skull of the aïstopod *Ophiderpeton brownriggi* (Milner 1994; fig. 4). Consequently, *B. orientalis* is the only baphetid represented by two skulls of very different sizes. Ontogenetic series of stem-tetrapods or basal crown-tetrapods are barely known and cannot be assumed to be identical to those of temnospondyls. As baphetids are a clade with unique morphological characteristics, it is possible that their ontogeny also has unique features. For that reason, we itemize several features that appear to be correlated with absolute size in this small sample of specimens.

At a 71-mm skull length, NMW 1898.X.42 is about two-fifths of the linear dimensions of the 180-mm holotype of *B. orientalis* (Fig. 5), the only comparably small baphetid skull being AMNH 6944, the 75-mm holotype of *L. lintonensis* from Linton, Ohio. Comparison of these two skulls in the 70–80 mm range with baphetid skulls of 150 mm or more reveals the following differences.

Dermal ornament Large baphetids have fully reticulate 'honeycomb' ornament on all dermal bones of the skull roof with little trace of any radiating pattern associated with bone growth. The two small specimens show that reticulate ornament developed first on the skull table which is fully reticulate in AMNH 6944 (Beaumont 1977; fig. 24a) and partly developed in NMW 1898.X.42 (Fig. 2). This is in significant contrast to the rest of the skull where the dermal bones have only a few central pits and the rest of each bone is covered by radiating striations. This differentiation is more extreme than the situation in temnospondyl ontogenies and it appears that the skull table reached an approximation of its adult shape early in baphetid development whereas the snout and cheeks continued to undergo rapid allometric shape change.

Lateral-line sulci Large baphetid skulls (250 mm or more in length) either possess a concentration of lateral-line sulci around the snout (*Megalocephalus* Beaumont 1977; fig. 8; *B. kirkbyi* Beaumont 1977; fig. 21) or the situation is unknown (*Loxomma* Beaumont 1977; fig. 2c). Both *B. orientalis* skulls and the *L. lintonensis* skull retain a more extensive series of such sulci on the postorbital and jugal [Beaumont (op.cit., fig. 24a) also figures them on the squamosals of *L. lintonensis* but these are not convincing on the casts available to us]. These three specimens are the smallest three baphetid skulls and the retention of the posterior lateral-line sulci could be a purely ontogenetic phenomenon relating to the smaller size of the skulls. Beaumont (1977; p. 92) suggested that it could be an ontogenetic-phylogenetic phenomenon representing a clade of late *Baphetes* which were more paedomorphic than their earlier relatives, but we consider this less likely, having concluded that the Linton specimen belongs to *Loxomma* and is not an immediate relative of *B. orientalis*.

Snout shape If our conclusion is correct that the two Nýřany specimens are representatives of a single species, then the ontogeny of the snout is of interest. The snout of the smaller specimen has narrow 'arrowhead'-shaped lacrimals and is similar in shape to those of the larger *B. kirkbyi* and *L. acutirostris* – presumably the primitive baphetid condition. In the larger specimen the lateral ramus of the lacrimal and the corresponding anterior ramus of the jugal are much wider, giving a broader muzzle in the large specimen and implying a unique ontogeny within the Baphetidae. This implies a change in snout shape between a 71-mm and a 180-mm

skull, which as a general phenomenon is unremarkable and the normal situation in long-snouted temnospondyls. However, whereas the growth series of 'crocodile-like' temnospondyls tends to show snout elongation in ontogeny, here the snout does not lengthen proportionally but widens with ontogeny by widening of the lacrimals and jugals. The presence of the antorbital fenestrae apparently constrains the pattern of snout enlargement in baphetids and it is possible that the unique skull roof configuration is associated with a comparably unique pattern of ontogenetic change. A second implication is that the snout in the 75-mm *L. lintonensis* skull may not have the same shape as the snout of the adult of that species.

Otic notch margin The Baphetidae are noteworthy for the character that the otic notch is not only bordered medially by the supratemporal but that this element extends anterolaterally to form much of the anterior border of the notch as well, in contrast to the situation in temnospondyls where the squamosal forms the anterior margin of the otic notch. This is not the situation in the small *B. orientalis* and *L. lintonensis*, in which the supratemporal–squamosal suture runs forwards from the anteriormost point of the otic notch and the supratemporal does not 'dominate' the otic notch margin. Given the phylogenetic separation of these two specimens it appears that this is the juvenile condition and that the extension of the supratemporal around the otic notch is an adult feature that develops in skulls of 100 mm or more.

Postparietals In primitive tetrapods (e.g. *Acanthostega*, *Crassigyrinus*, *Greererpeton*), the postparietals are generally significantly anteroposteriorly longer than the tabulars giving a stepped suture across ahead of the tabular-postparietal series. This phenomenon is significantly less pronounced in most baphetids but elongate postparietals appear as state-reversals of character 15 in the two small specimens. They are the only two baphetids to have elongate postparietals and this appears to be a primitive feature retained in juveniles and lost by allometric growth in ontogeny.

In conclusion, ontogeny in baphetids may incorporate unique patterns of developing dermal ornament over the skull, loss of lateral-line sulci on the postorbital and jugal, unique patterns of bone growth around the antorbital fenestra, progressive lateral outgrowth of the supratemporal behind the otic notch, and broadening and shortening of the postparietals.

Conclusion

The new specimen of *B. orientalis* described in this work is a useful addition to the available material in that it adds several pieces of information to our understanding of the morphology and ontogeny of the Baphetoidea. Unfortunately our knowledge of baphetoids is still relatively patchy, and despite using as many characters as we could find that might provide

information about relationships within the group, the results are not robust and more data are needed. For this reason, we avoided providing new generic names for some taxa, restricting ourselves to reassigning '*Baphetes*' *lintonensis* to *Loxomma*, on relatively strong evidence.

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Appendix 1 Taxa and sources used in analysis.

Outgroups:	
Acanthostega gunnari	Clack (1994, 2002b, 2003b), Ahlberg and Clack (1998)
Crassigyrinus scoticus	Panchen (1985), Clack (1998a), Ahlberg and Clack (1998)
Ingroups:	
Baphetes kirkbyi	Beaumont (1977)
Baphetes orientalis	Beaumont (1977)
Baphetes orientalis (juvenile)	This work
Eucritta melanolimnetes	Clack (2001)
Kyrinion martilli	Clack (2003a)
Loxomma acutirhinus	Beaumont (1977)
Loxomma allmanni	Beaumont (1977)
Loxomma ('*Baphetes*') *lintonensis**	Beaumont (1977) and first hand
*Megalocephalus lineolatus**	Beaumont (1977)
Megalocephalus pachycephalus	Beaumont (1977), Ahlberg and Clack (1998b)
Spathicephalus mirus	Beaumont and Smithson (1998)
Excluded taxa:	
Baphetes planiceps	Redundant taxon in relation to *B. kirkbyi*
Spathicephalus pereger	Redundant taxon in relation to *S. mirus*
Loxomma rankini	Limited data and destabilizing effect.

*Taxonomic note. The nomenclature and character-state distribution for the Linton baphetids follows Beaumont (1977) see text.

Appendix 2 Characters and states

1. In large skulls, skull table ornament fine like rest of dermal surface of skull (0); skull table ornament coarse like rest of dermal surface of skull (1); in large skulls, skull table with finer ornament than rest of skull (2) (Original – taxa represented by skulls less than 100 mm long treated as unknown.).

2. Preorbital snout less than 50% of total skull length (0); approximately 50% of total skull length (1); preorbital snout at least 65% of skull length (2) (Orig.).

3. Orbit shape round or oval (0); orbit with angle at anterolateral corner (1); emarginated margin including prefrontal, lacrimal and jugal forming antorbital fenestra (2).

4. Antorbital vacuities absent or rudimentary (0); similar in size to orbit or not more than 20% larger (1); more than 20% larger than orbit (2) (Orig.).

5. Premaxilla anteroposterior depth < 40% maximum width (0); anteroposterior depth > 40% maximum width (1) (Orig.).

6. Naris posterior margin formed by lacrimal, and maxilla excluded (0); naris posterior margin formed by maxilla, which contacts nasal and excludes lacrimal from narial margin (1) (Clack C14part & C20).

7. Medial process of jugal demarcating anterolateral edge of orbit: absent (0); anterior (1); posterior (2).

8. Medial process of jugal incorporates postorbital: no (0); yes (1).

9. Jugal excludes distal ramus of postorbital from orbit margin; no (0); yes (1).

10. Maxilla contacts quadratojugal (0) does not contact quadratojugal (1) (Clack C17).

11. In largest individuals, skull table 1onger than wider than long (0); square (1) (modified from Clack C87).

12. Intertemporal present (0); intertemporal absent (1). (Clack C8).

13. Pineal foramen large on a raised boss (0); pineal foramen small and flush with skull table surface (1) (Orig.).

14. Supratemporal arrowhead-shaped (0); skull table portion of supratemporal square (1); supratemporal elongate (2) (Orig.).

15. Postparietal longer than wide (0); wider than long (1); equant (2) (Orig.).

16. Tabular with no posterior boss (0); tabular with posterior boss (1); tabular with blade (2) (Clack 40).

17. Tabular longer than wide (0); equant (1); wider than long (2) (Orig.).

18. Squamosal posterodorsal margin shape; convex (0); sigmoidal (1); concave (2) (Clack C35).

19. Jaw suspensorium behind occiput (0); jaw suspensorium level with occiput (1) (Orig.).

20. Anterior palatal fenestra/depression: double (0); single (1); absent (2) (Clack C77).

21. Jugal: no alary process on palate (0); alary process on palate (1) (Clack C12).

22. Premaxillary tooth number: 8 (0), 10–14 (1); 15–30 (2) (Orig.).

23. Ectopterygoid: row of three or more smaller teeth present (0); absent (1) (Clack C58).

24. Dentary teeth uniform (0); dentary teeth showing 'peaking' (1) (Orig.).

Appendix 3 Data matrix

	0 0 0 0 0 1 2 3 4 5	0 0 0 0 1 6 7 8 9 0	1 1 1 1 1 1 2 3 4 5	1 1 1 1 2 6 7 8 9 0	2 2 2 2 1 2 3 4
Acanthostega	0 0 0 0 0	1 0 0 0 0	0 1 1 0 0	1 0 0 0 0	0 1 0 0
Crassigyrinus	2 0 0 0 1	0 0 0 0 0	1 0 1 1 0	1 1 0 0 0	0 2 0 1
Baphetes kirkbyi	1 1 2 1 0	0 2 1 0 1	0 0 0 2 1	1 0 1 0 2	0 1 1 ?
Baphetes orientalis	1 1 2 1 0	0 2 1 1 ?	0 0 1 2 1	1 1 2 ? ?	? ? 1 ?
Baphetes orientalis (juv)	? 1 2 1 1	0 2 1 1 0	0 0 1 2 0	0 1 2 1 ?	? 1 1 0
Eucritta melanolimnetes	? 0 1 0 0	0 0 0 0 ?	0 0 0 2 0	0 1 2 0 ?	? ? 0 0
Kyrinion martilli	1 2 2 2 1	1 0 0 0 1	1 ? 0 ? ?	? ? 2 0 ?	? ? 1 1
Loxomma acutirhinus	1 1 2 1 0	0 1 0 0 ?	1 0 0 2 2	1 2 0 0 2	0 0 1 ?
Loxomma allmanni	? ? 2 1 ?	? 2 1 0 ?	1 0 ? 2 2	0 1 ? 0 ?	? ? ? ?
Loxomma lintonensis	? 1 2 1 ?	0 2 1 0 0	1 ? 0 2 0	0 0 0 0 ?	1 ? 1 0
Megalocephalus lineolatus	1 2 2 2 ?	? ? ? ? 0	1 1 ? 1 2	? ? ? 1 ?	? ? ? 0
Megalocephalus pachycephalus	2 2 2 2 1	1 2 0 0 0	0 1 1 2 2	1 1 0 0 1	1 0 1 1
Spathicephalus mirus	? 2 2 1 0	0 0 0 0 0	0 1 1 1 1	1 2 1 0 2	? 2 1 0