New information on *Lethiscus stocki* (Tetrapoda: Lepospondyli: Aistopoda) from high-resolution computed tomography and a phylogenetic analysis of Aistopoda

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Abstract: High-resolution computed tomography provides an alternative to serial sectioning and other destructive techniques of studying fossils (data available at http://www.DigiMorph.org). This technology was used to study the oldest aistopod *Lethiscus stocki*. The fossil is found to have approximately 30 closely spaced teeth on its maxilla and dentary, a short vomer, a palatine running nearly the entire length of the maxilla that is toothed at least posteriorly, and a choana that is located at the premaxilla–maxilla suture. It has a lower jaw with a high articlular facet for the quadrate condyle; a lateral fossa for the adductor musculature, superficially similar to the mammalian masseteric fossa; and a sutural pattern that closely resembles that of *Oestocephalus*. Previously reported pectoral elements are not evident in the scans and may be best interpreted as fractures on the surface of the nodule associated with sedimentary inclusions. Relationships among all relatively complete aistopods were analyzed using parsimony. Two most parsimonious trees were found, differing in the arrangement of the outgroup taxa. *Phlegethontia* and *Pseudophlegethontia* are found to be sister taxa to *Coloraderpeton* and *Oestocephalus*, with *Ophiderpeton* and *Lethiscus* placed as successively more distant taxa. This topology renders Ophiderpetontidae, as previously conceived, paraphyletic. *Lethiscus* is confirmed to be the most basal aistopod. A new classification of Aistopoda is presented. This study shows that the palatoquadrate of higher aistopods is derived in-group, which is consistent with the trends in aistopods of peramorphosis in the endochondral skeleton and paedomorphosis in the dermal skeleton.

Résumé : La tomographie informatisée à haute résolution fournit une alternative aux séries de coupes et aux autres techniques destructives d'étude des fossiles (http://www.DigiMorph.org). Cette technologie a été utilisée pour étudier le plus vieil aistopode *Lethiscus stocki*. On a découvert qu'il avait environ 30 dents rapprochées sur le maxillaire et le dentaire, un vomer court, un palatin qui fait presque toute la longueur du maxillaire, lequel a des dents au moins dans la partie postérieure, et une choane qui est située à la suture du prémaxillaire et du maxillaire. Sa mâchoire inférieure a une haute fossette articulaire pour le condyle de l'os carré, une fosse latérale pour le muscle adducteur qui est superficiellement similaire à la fosse du masseter et un patron de sutures qui ressemble beaucoup à celui de *Oestocephalus*. Des éléments pectoraux rapportés antérieurement ne sont pas évidents dans les balayages et peuvent être mieux interprétés comme des fractures à la surface du nodule, associées aux inclusions sédimentaires. Les relations entre tous les aistopodes relativement complets ont été analysées en utilisant la parcimonie. Deux arbres à grande parcimonie ont été trouvés, ils diffèrent selon l'arrangement des taxons hors-groupes. On a trouvé que *Phlegethontia* et *Pseudophlegethontia* étaient des taxons-frères de *Coloraderpeton* et *Oestocephalus*; *Ophiderpeton* et *Lethiscus* sont placés en tant que taxons successivement plus distants. Cette topologie rend les Ophiderpetontidae paraphylétiques, tel que conçu auparavant. *Lethiscus* est confirmé en tant que l'aistopode le plus basal. On présente une nouvelle classification des Aistopoda. Cette étude montre que le palato-carré des aistopodes supérieurs est dérivé à même le groupe, ce qui concorde avec les tendances chez les aistopodes de péramorphose dans le squelette endochondral et de pédomorphose dans le squelette dermique.

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Introduction

In a recent series of papers, Milner (1994), Carroll (1998*a*, 1998*b*), and Anderson (2002, 2003*a*, 2003*b*) have reconsidered a group of elongate, limbless Paleozoic tetrapods, known as aistopods, in the light of newly available specimens from Nýřany, Czech Republic, and Mazon Creek, Illinois. Aistopods have highly fenestrate skulls, approximately 60–65 precaudal

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vertebrae, and up to 230–250 vertebrae total. Their vertebrae are distinct in having a single, spool-shaped centrum fused indistinguishably with a single neural arch at extremely small size and a spinal nerve foramen just posterior to the transverse process (except for the atlas of *Oestocephalus*). Aistopods are part of a larger monophyletic assemblage of tetrapods named Lepospondyli that shares characters such as simple, spool-shaped centra, absence of the intertemporal, no squamosal notch, no atlas intercentrum, an absence of labyrinthodont in-folding of the dentine, and an odontoid process on the atlas (Anderson 2001).

Traditionally, aistopods have been divided into two families, Ophiderpetontidae and Phlegethontiidae (Baird 1964; McGinnis 1967). “Ophiderpetontids” in this sense (*Ophiderpeton* and *Oestocephalus*) have blunt snouts, orbits placed well anterior to the mid length of the skull, ventrally open temporal fenestra, and thick dermal scalation with tightly packed ventral gastralia and trapezoidal to circular dorsal osteoderms (Baird 1964; Milner 1994; Carroll 1998*a*, 1998*b*; Anderson 2003*b*). Dorsal osteoderms also cover the temporal fenestra of “ophiderpetontids.” “Ophiderpetontids” have the jaw articulation posterior to the occiput. *Oestocephalus*, one “ophiderpetontid,” has “k-shaped” ribs, with the main rib shaft, a “tuberculum,” and anterior (or costal) and posterior processes forming the arms of the “k” on all rib-bearing vertebrae. Phlegethontiids are characterized by narrow snouts, large orbits just anterior to the mid length of the skull, retention of a lower temporal arch, quadrate condyles anterior to the occiput, and thin gastralia, but no dorsal osteoderms (Gregory 1948; Baird 1964; McGinnis 1967; Lund 1978; Anderson 2002). Phlegethontiids have distinct “k-shaped” ribs until the 6th or 7th rib, at which point the posterior process becomes reduced to a small projection. Both “ophiderpetontids” and phlegethontiids have sickle-shaped remnants of the pectoral girdle, possibly the cleithrum (Carroll 1998*b*) or fused clavicle and cleithrum (Anderson 2002, 2003*b*), located in the region of vertebrae 3–5.

Closer examination has found that aistopod diversity is greater than portrayed by this two morphotype division. Wellstead (1982) named the genus *Lethiscus* and established the family Lethiscidae for the single specimen previously thought to be of *Ophiderpeton* (Baird 1964). *Lethiscus* is from the Viséan Wardie Shales of Scotland and predates the deposits of Jarrow, Ireland, and East Kirkton, Scotland (Wellstead 1982; Milner 1994), making it the oldest known lepospondyl. Anderson (2003*a*) described a new genus of aistopod, *Pseudophlegethontia*, which shows morphology intermediate between the “ophiderpetontid” and phlegethontiid conditions. In common with phlegethontiids, *Pseudophlegethontia* has a pointed snout, orbits just anterior to the middle of the skull, quadrate condyles anterior to the occiput, thin gastralia and no dorsal osteoderms, despite being larger than the size at which they are known to thickly cover “ophiderpetontids” (Anderson 2003*b*). However, it has no lower temporal arch, a skull table with separate, sutured elements, and large posterior processes of the rib at least to the 57th vertebra, which are characters present in “ophiderpetontids.” Anderson (2003*a*) placed *Pseudophlegethontia* into a new, monotypic family. Anderson also rediagnosed Phlegethontiidae (Anderson 2002) and Ophiderpetontidae (Anderson 2003*b*), and erected a new family, Oestocephalidae, to reflect the separation of *Oestocephalus* and *Coloraderpeton* from *Ophiderpeton* found in a preliminary phylogenetic analysis (Anderson 2003*b*).

A thorough phylogenetic analysis of Aistopoda requires reconsideration of the oldest aistopod *Lethiscus stocki*. *Lethiscus* is important to restudy since it is the most basal representative of Aistopoda and it could potentially have combinations of plesiomorphic and apomorphic characters crucial to linking aistopods with one of the many morphologically different lepospondyl or “labyrinthodont” clades. The specimen was known for a hundred years before Wellstead’s description, but was not studied because of the intractable nature of its matrix (Baird 1964). It is preserved in a long, cylindrical, siderite concretion that is split into many fragments throughout the preserved column of 78 vertebrae. Since it is a unique specimen, etching away the bones and casting the resulting natural molds (Baird 1955) is undesirable. Etching would also destroy important histological information (Wellstead 1982). New technologies now exist that may improve our knowledge of this aistopod.

High-resolution computed tomography (HRCT) has been increasingly employed by paleontologists to examine internal structures or morphology at risk of destruction from conventional preparation (Rowe et al. 1995, 1997, 1999; Cifelli et al. 1999; Brochu 2000; Ketcham and Carlson 2001). HRCT has wide applications, having recently been used to study subjects as diverse as fossils in amber (Grimaldi et al. 2000), squamate palpebral ossifications (Maisano et al. 2002), elasmobranch cranial anatomy (Maisey 2001*a*, 2001*b*, 2001*c*), mammalian inner ear morphology and patterns of evolutionary changes (Rowe 1993, 1996*a*, 1996*b*), and the origin of marsupial tooth replacement (Cifelli et al. 1996) and was instrumental in documenting the *Archaeoraptor* forgery (Rowe et al. 2001). The type, and only, specimen of *Lethiscus* was brought to the HRCT Facility at the University of Texas at Austin in November 1998, for examination. This scanner uses higher energy levels than conventional medical CT scanners, making it possible to resolve extremely fine details (tens of microns in size). This paper presents the results of the CT scans, and incorporates this new information into a phylogenetic analysis of Aistopoda. It further discusses the possible heterochronic origin of the aistopod skull in the light of a developmental series of *Phlegethontia* and presents a new phylogeny.

Materials and methods

The specimen (MCZ 2185) was scanned at the High-Resolution X-ray Computed Tomography Facility at The University of Texas at Austin (Ketcham and Carlson 2001) by Richard Ketcham on November 25–27, 1998. Each portion of the specimen was suspended in florist’s foam to keep its position stable. All of the skull except for a dorsal fragment preserving a mold of the internal skull roof were scanned, as were the vertebral sections No. 2 (containing vertebrae 5–7 and the putative pectoral elements), No. 22 (with vertebrae no. 53–55), and No. 24 (vertebrae 59–61; see Wellstead 1982 for the numbering scheme). Part and counterpart of the vertebral sections were held together with elastic bands.

The scanner settings were as follows for all four pieces. X-ray energies were set to 180 kV and 0.133 mA. X-rays were pre-filtered to reduce beam hardening artifacts using one brass plate of 1/16 inch in thickness. The specimen was scanned in an offset mode of 160% to increase the resolution within subvolumes of the specimen by selective reconstruction of the raw absorption data. Control over the translational positioning of the specimen ensured that the maximum magnification (hence, maximum resolution) was achieved. Source–object distance was 81 mm, yielding a slice thickness of 0.190 mm and inter-slice spacing of 0.144 mm. Each slice was acquired using 1200 views (angular orientations), with two samples per view. The image fields of reconstruction were: 39 mm for the major skull fragment, 33 mm for the left rostrum fragment, 25 mm for vertebral pieces Nos. 2 and 22, and 34 mm for piece No. 24. The reconstruction scale was 22 and reconstruction offset was 500.

The raw CT data (available at http://www.DigiMorph.org) were prepared for processing using Adobe Photoshop 5 and Corel Photo-Paint 8. Reslicing, analysis, and production of images was done using a MacIntosh PowerPC, using NIH Image software from the National Institutes of Health, the United States of America (http://rsb.info.nih.gov/nih-image/about.html).

All characters relevant to aistopod systematics discovered through the course of this and other recent studies (McGinnis 1967; Milner 1994; Carroll 1998*a*; Anderson 2002, 2003*a*, 2003*b*) were used to examine the in-group relationships. The matrix includes twenty-seven characters (16 cranial, 11 postcranial) and seven aistopod taxa. All relatively complete taxa were included, including *Lethiscus stocki*, *Ophiderpeton* (a composite of *O. brownriggi* and *O. kirktonense*), *Oestocephalus amphiuminum* (*O. nanum* was not included because it is redundant with *O. amphiuminum*, except for a possible reduction in the amount of dorsal osteoderms), *Coloraderpeton brilli*, *Phlegethontia longissima*, *P. linearis*, and *Pseudophlegethontia turnbullorum*. *Sillerpeton permianum* and *Phlegethontia* "*phanerhapha*" were not included in the analysis because they are primarily known from skull fragments. All characters are binary, except 25 and 26 (see Appendix A), which were unordered, permitting direct transformations between any two states. Missing data were indicated by a question mark and inapplicable characters by a dash.

Determining which taxon is the closest outgroup to aistopods is not entirely straightforward. Carroll (1995) and Laurin and Reisz (1997) found adelospondylids to be the lepospondyl group closest to aistopods; however, neither of these studies accounted for the large suite of characters correlated with limblessness (Carroll 1995), so this grouping might be an artifact of the elongate limbless morphytype. Anderson (2001), who did consider the problem of characters correlated with limb loss, found aistopods had their closest relationship with lysorophians, which suggests that effects of elongation and limb loss might not have been fully compensated in Anderson's matrix. This clade was placed within the base of the nectrideans. A close relationship between aistopods and nectrideans is consistent with some previous hypotheses (Thompson and Bossy 1970; Smithson 1985). Also controlling for correlates of limblessness, Carroll and Chorn (1995) found a sister group relationship between aistopods and nectrideans in an analysis of only vertebral characteristics. Given the uncertainty of the closest sister group to aistopods, we chose four separate lepospondyl taxa to serve as outgroups, based upon their relative completeness, basal position within their respective clades (following Anderson 2001), and previous hypotheses of close relationships with aistopods: the adelospondylid *Adelogyrinus* (Andrews and Carroll 1991; Carroll and Andrews 1998), the microsaur *Asaphestera* (Carroll and Gaskill 1978), the lysorophian *Brachydectes* (Wellstead 1991, 1998), and the nectridean *Scincosaurus* (Milner 1980; Bossy and Milner 1998).

The phylogenetic analysis was performed on the same PowerPC. Data were manipulated using MacClade (Maddison and Maddison 1992) upgraded to release 3.07 via the internet (http://ag.arizona.edu/ENTO/macclade/maclade.html; Maddison and Maddison 1997). The matrix was analyzed using PAUP* 4.0b4a (Swofford 1998), using the branch-and-bound algorithm. Bootstrap values were calculated over 1000 branch-and-bound replicates. All tree statistics were calculated using MacClade.

Abbreviations

Institutional

AMNH, American Museum of Natural History, New York, N.Y., U.S.A.; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvannia, U.S.A.; FMNH, Field Museum of Natural History, Chicago, Illinois, U.S.A.; MCP, Mazon Creek Paleontological Collection, Northeastern Illinois University, U.S.A. Chicago, Illinois, U.S.A.; MCZ, Museum of Comparative Zoology, Cambridge, Mass., U.S.A.; NMW, Naturhistorisches Museum Wien, Vienna, Austria; USNM, National Museum of Natural History, Washington, D.C., U.S.A.

Anatomical

a, angular; alv, alveolus for a tooth; ap, anterior (costal) process of the rib; art, articular; bp, basipterygoid process; c, choana; ca, foramen for the carotid artery; cen, centrum; cp, cultriform process; d, dentary; ep, epipterygoid; f, frontal; gas, gastralia; gl, glenoid of the articular; j, jugal; lr, longitudinal ridge; ls, lateral spine; m, maxilla; mf, "masseteric fossa"; nc, neural canal; ns, neural spine; ot, olfactory tract; p, palatine; parf, parietal foramen; pc, palpebral cup; pe, posterior element of the jaw; pf, postfrontal; pm, premaxilla; pp, parapophysis; pq, palatoquadrate–pterygoid; prf, prefrontal; ps, parasphenoid; qc, quadrate condyle; sa, surangular; sp, splenial; s, squamosal; st, supratemporal; stp, stapes; t, tabular; tp, transverse process; tr, transverse ridge of the stapes; tub, tuberculum; v, vomer; vf, ventral frontal sulcus; vsn, ventral notch for the sqamosal; V, foramen for the trigeminal nerve; zy, zygapophysis; II, foramen for the optic nerve.

Results

Computed tomography scans

Bone and matrix are of sufficiently different density that they read fairly distinctly. A thin layer of pyrite that coats the bone surface often aids this discrimination. Unfortunately, the bone is obscured by two factors. First, the nodule's matrix at the air interface has the same pixel value as bone produced by refraction, which impedes the use of some aspects of the processing software. In effect, this thin layer of similarly coloured matrix in the scan creates a shell around the objects of interest. Additional irregularities throughout the matrix also have the same density as bone, which makes removing the nodule's margin ineffectual, as a "cloud" of obscuring pixels remains. Second, and more serious, the crystalline calcite that frequently infills cavities within the specimen has the same density as bone. This is especially problematic in the braincase area, which encloses a large crystal of calcite, creating a large, featureless mass obscuring all morphology.

Despite these difficulties, we have discovered significant new information using HRCT. The left mandible is folded under the skull (Fig. 1), but it is more medially placed than portrayed by Wellstead (but this might be due to different perspectives between his X-ray images and ours). In a series of horizontal reslices, the full lateral jaw morphology is shown (Figs. 1, 2). *Lethiscus* has a similar articulation with the quadrate as *Oestocephalus* (Carroll 1998*a*; Fig. 2). The articular facet is placed high above the tooth row on the posterior terminus of the jaw, with no retroarticular process. There is a fossa on the lateral surface of the jaw for attachment of adductor musculature, as in *Oestocephalus*, but unlike any other aistopod (Milner 1994; Carroll 1998*a*; Anderson 2002, 2003*a*, 2003*b*). The surangular is the deepest bone on the posterolateral surface, and it reaches anteriorly one-third of the length of the tooth row (Fig. 1). The angular is restricted to the ventral portion of the lateral jaw, but it has an anterior extent of almost half the length of the mandible. The dentary covers three-quarters of the total length of the jaw, as in *Oestocephalus* and *Coloraderpeton*. The splenial seems to have rotated laterally to slightly overlap the dentary, so it is unclear whether the splenial had a lateral exposure in the undistorted jaw.

Teeth are uniform in size and are tightly packed together, as in *Oestocephalus*. At least 30 teeth were present on the maxilla and dentary (Figs. 1, 3). This is a much higher tooth count than early ophiderpetontids such as *Ophiderpeton kirktonense* (Milner 1994).

Both premaxillae are preserved in articulation (Fig. 3). They come together in a narrow point. The maxillary ramus is rather short, occupying only a fraction of the distance covered by the maxilla, and the vomerine process is very short.

A separate palatine is visible in a resample of the small skull fragment (Fig. 3). As preserved, it is an elongate, rectangular bone that runs alongside the maxilla to the choana. Teeth are present in one row paralleling the maxillary tooth row. The cultriform process of the parasphenoid reaches the premaxilla. Lateral to the cultriform process is a short rectangular vomer, which has a posterior recess that forms the anterior margin of the choana. The choana is positioned at the junction of the vomer, palatine, premaxilla, and maxilla. The choanae are close to one another because of the narrow rostrum. The pterygoids approach one another anteriorly, but are prevented from articulation by the cultriform process. It is unknown whether the pterygoids are fused with the epipterygoids and quadrates to form a "palatoquadrate," as in all other aistopods (Carroll 1998*a*; Anderson 2002, 2003*a*, 2003*b*) but does not appear to be the case.

The jaw articulations are posterior to the occiput (Fig. 4), as in "ophiderpetontids" and in contrast with phlegethontiids and *Pseudophlegethontia*. The parasphenoid is shown in greater detail than was figured by Wellstead (1982). The basipterygoid processes are distinct, and the posterior limits of the parasphenoid are more clearly defined in the CT images than

Fig. 1. MCZ 2185, *Lethiscus stocki*. Dorsal slice through main skull fragment of *Lethiscus*. It shows the left jaw folded below the palate, while the right is in articulation. The section passes beneath the palate, through the right jaw, and exposes the medial surface of the lateral wall of the left jaw. Sutures are visible on the medial surface of the left jaw. Note the large number of teeth along the dentary and maxilla. See text section for anatomical abbreviations.

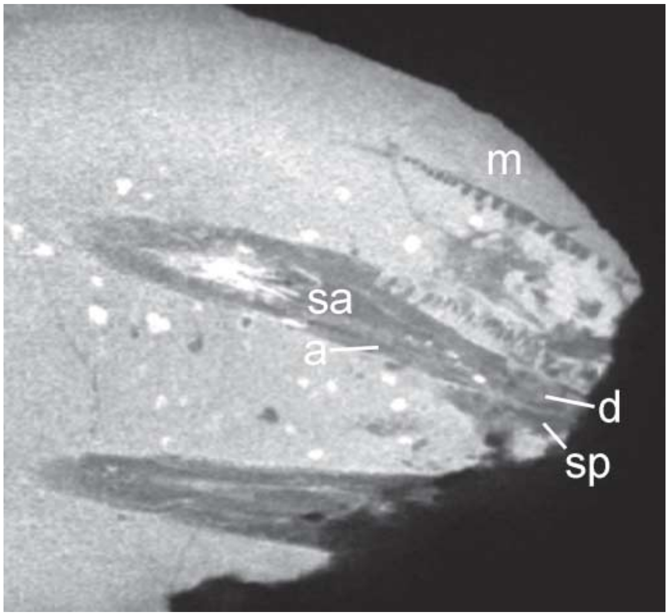


Fig. 2. MCZ 2185, *Lethiscus stocki*. Two sequential slices through the left jaw of *Lethiscus*, with (A) more medial than (B). The medial wall of the "masseteric fossa" is clearly defined, and the articulation is placed above the tooth row, as in *Oestocephalus*. (C) Lower jaw of *Oestocephalus amphiuminus*. Modified from Carroll (1998*a*). See text section for anatomical abbreviations.

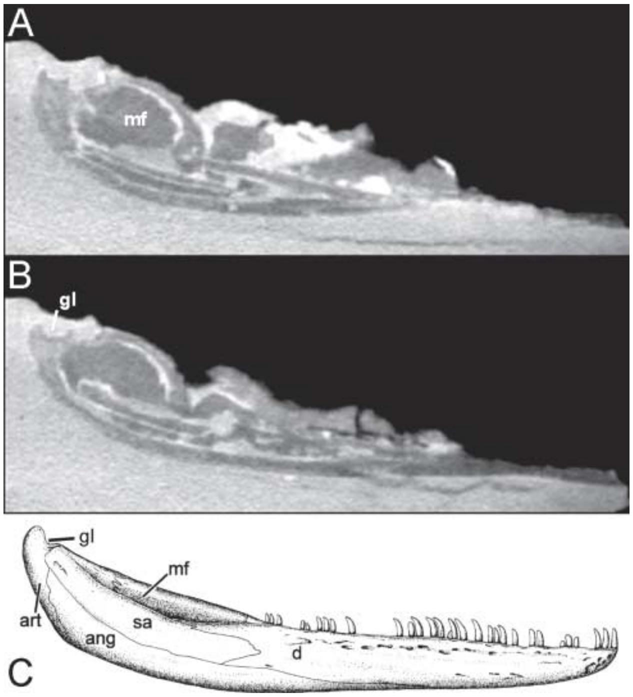
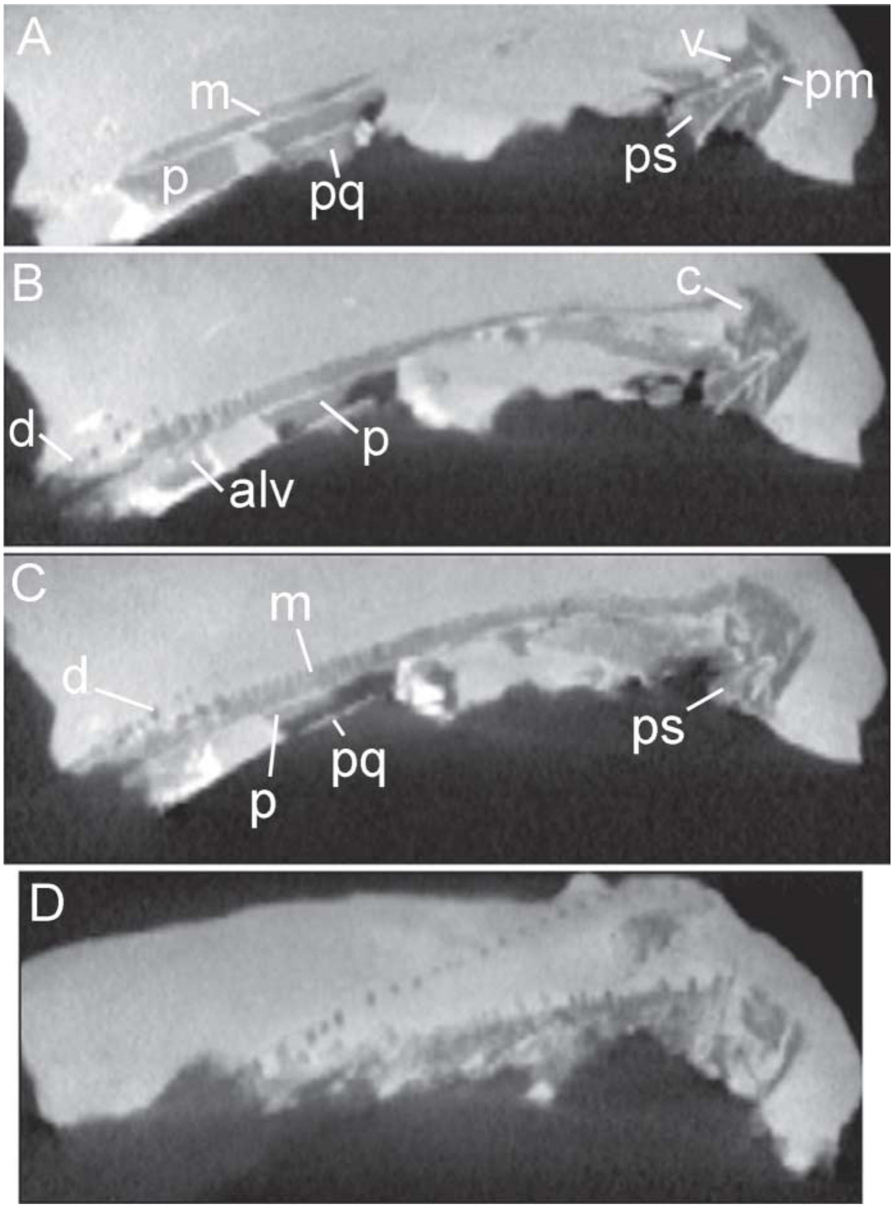


Fig. 3. MCZ 2185, *Lethiscus stocki*. Four progressive slices (A–D) through the anterior skull of *Lethiscus*, showing details of the palate and dentition. See text section for anatomical abbreviations.



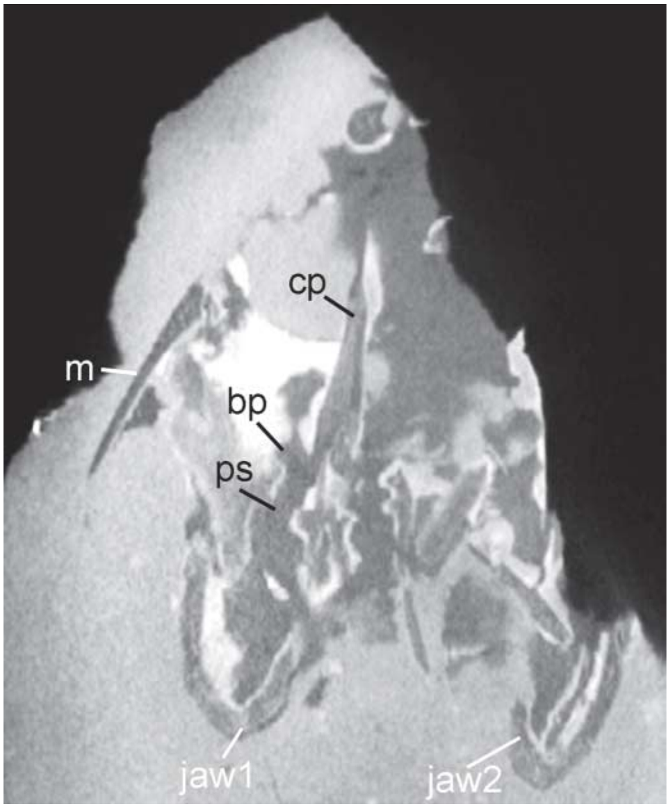
Wellstead's X-ray images. The basal plate is rectangular, rather than widely triangular as figured by Wellstead.

The scans through the anterior vertebral segment did not show the pectoral elements described by Wellstead (1982). Examination of these structures revealed that they have a slightly different colouration and texture from that present on well-defined bone or matrix. Microscopic investigation of these features suggests that they are not skeletal features but are concoidal irregularities on the surface of the matrix caused by sedimentary inclusions with slightly different lithology from the nodule proper. Remnants of other such inclusions present on fragments 11 and 16 are more complete. These additional inclusions have left deep, rounded concavities on the matrix surface; however, most of the inclusions themselves were lost, perhaps as a result of weathering.

Throughout the postcranial skeleton, fractures are centered on the vertebral centrum and pass along the planes of the neural spine and transverse processes (Fig. 5A). This suggests that the unusual (for an aistopod) height of the neural spine described by Wellstead (1982), as he described for vertebra nine, might be a taphonomic artifact. In scans of neural spines that do not have fractures passing through them, the spines have the low morphology more typical of aistopods (Fig. 5B), except for the anteriormost four vertebrae of *Phlegethontia linearis* (Anderson 2002). These vertebrae of *Lethiscus* do not have a deep medial groove on their posterior neural spines.

Transverse processes are as described by Wellstead (Fig. 5B). They seem to have a single rib-bearing facet, which suggests that the "capitulum" figured by Wellstead (1982, text-figs. 10*a*, 10*b*) is an anterior process, which would make the ribs of *Lethiscus* single-headed. A rib in surface exposure on fragment 24 is visible in articulation with the transverse process (Fig. 6). It shows the entire articulation was at one rib "head,"

Fig. 4. MCZ 2185, *Lethiscus stocki*. Dorsal view through the palate. The central structure is the entire parasphenoid, showing basipterygoid processes and long cultriform process. White areas are high density pyrite; the dark grey in the anterior (top) area is calcite, not bone. Jaw1 is folded under the skull and is in lateral view, jaw2 is in a nearly natural position. Also note the jaw articulations are placed posterior to the occiput. See text section for anatomical abbreviations.



here interpreted as the tuberculum, while the other is anteriorly directed. The anterior process of the rib of *Lethiscus* is much shorter and more broadly rounded at the base than in more derived aistopods. All other aistopods have single-headed ribs (Milner 1994; Anderson 2002, 2003*a*, 2003*b*). There is no evidence for the presence of posterior processes on any rib in *Lethiscus*, meaning that the “k-shape” is absent.

Gastralia are similar in shape and size to those found in *Ophiderpeton* and *Oestocephalus* (Fig. 5C). Wellstead (1982) called a series of round to trapezoidal fragments that run along the length of the specimen “gas bubbles,” citing a study by Wood (1977) that stated that these were preserved in other fossils from the Wardie Shales. Wellstead made this determination because the “bubbles” are pyrite surrounding a calcite core. However, crystalline calcite is quite common in the specimen and frequently obliterates bone morphology. Additionally, pyrite coats most bone in the specimen, which suggests that bone was initially present. The “gas bubble” hypothesis also does not explain why the “bubbles” are usually separated from the ventral gastralia (Wellstead 1982, text-figs. 7–9) in discrete layers. We agree with Baird (1964) that these are dorsal osteoderms of an “ophiderpetontid” pattern. Interestingly, the ventral osteoderms are located dorsal to the vertebrae in the anterior part of the specimen. The dislocation of part of the skin agrees with the disarticulation present throughout the skeleton, which suggests that the specimen endured a period of post-mortem degradation before burial.

Phylogenetic analysis

Two most parsimonious trees were found, differing in the position of *Adelogyrinus* and *Asaphestera* at the base of the outgroup (Fig. 7). Since characters were chosen to analyze ingroup relationships the outgroups were left unrooted; rooting the outgroups produces a topology broadly consistent with Anderson (2001). These trees have a length of 44 steps, a consistency index of 0.68, and a retention index of 0.76. Bootstrap support at all nodes was strong (80% or higher), except the placement of *Ophiderpeton* (57%) and the *Oestocephalus–Coloraderpeton* clade (68%). This may be due to character uncertainty stemming from the incompletely known *Ophiderpeton* (18% unknown characters, the highest in the matrix). Additionally, while *Oestocephalus* and *Coloraderpeton* are very similar in skull morphology, their differing dentition may be attracting *Coloraderpeton* toward *Ophiderpeton*, thus reducing the bootstrap support.

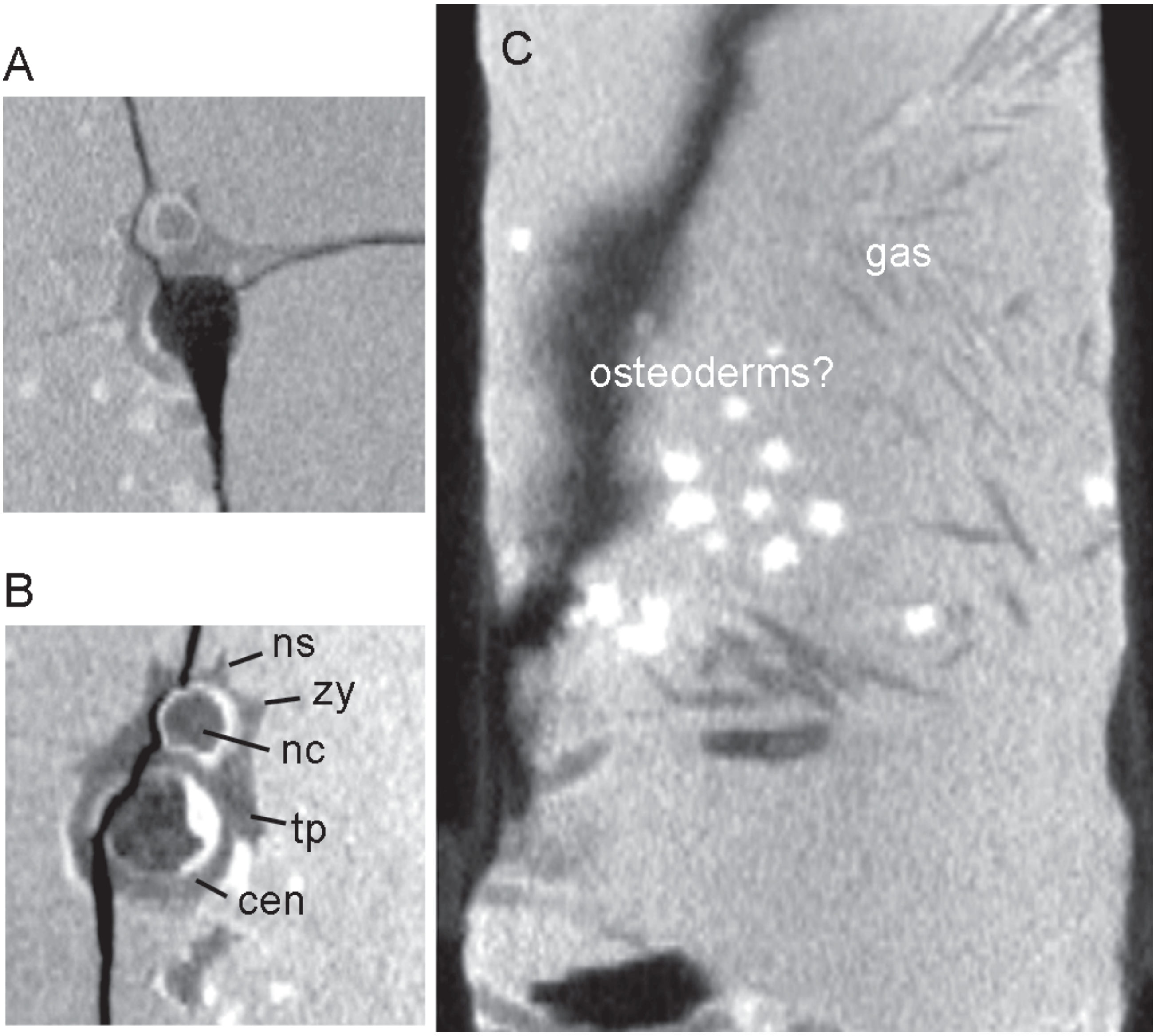
Discussion

Lethiscus has more similarities to “ophiderpetontids” than previously appreciated. The jaw morphology is nearly identical. The apparent single tooth row on the palatine is similar to, although it bears a greater number of teeth than, the single row of teeth on the palatoquadrate of *Oestocephalus* (MCP 323: Carroll 1998*a*). *Coloraderpeton*, in contrast, has three or four rows of teeth on its broad palatoquadrate (Anderson 2003*b*) while *Phlegethontia* has no palatal teeth (Anderson 2002). The pattern of dermal osteoderms is the same as seen in all “ophiderpetontids,” except *Oestocephalus nanum*, which has patches of dorsal osteoderms. The absence of a posterior process of the rib in *Lethiscus* is similar to *Ophiderpeton* and is consistent with their basal position.

The presence of an anterior process in *Lethiscus* suggests that all aistopods have single-headed ribs. This has implications for previous discussions of aistopod vertebral morphology. *Coloraderpeton* and *Pseudophlegethontia* have been described as having remnants of two rib facets on the transverse processes (Gallup 1983; Anderson 2003*b*). Reexamination of *Pseudophlegethontia* in light of the new information from *Lethiscus* has revealed the posteriormost of the doubled shaft of the transverse process to be a lateral spine as in *Oestocephalus* (Fig. 8). This new observation strongly suggests that *Coloraderpeton* also does not have two rib articulations on its transverse process, but rather a lateral spine that is not finished in bone.

Closely spaced marginal teeth are present in many out group taxa, such as *Greererpeton* (Smithson 1982) and *Proterogyrinus* (Holmes 1984), as well as most basal lepospondyls, including adelospondylids (Andrews and Carroll 1991; Carroll and Andrews 1998). Milner (1994) distinguished between *Ophiderpeton* (comprising the Viséan East Kirkton and Jarrow specimens) and *Oestocephalus* (specimens from Nýřany, Linton, and Mazon Creek; see Anderson 2003*b*) in part by dentition. The older, more primitive *Ophiderpeton* has widely spaced teeth, and the Upper Carboniferous *Oestocephalus* has closely spaced teeth. However, with the consideration of more taxa this were available

Fig. 5. MCZ 2185, *Lethiscus stocki*. Two vertebrae of *Lethiscus*. (A) Transverse slice showing the centrum (lower circular structure) and neural arch (dorsal to the centrum). Transverse processes are placed at the neural arch-central junction. Note that the neural spine (projecting from the middle of the top of the neural arch) is short. (B) Slice showing fractures running along the transverse processes and neural arch, centered on the centrum. (C) Gastralia of *Lethiscus*. See text section for anatomical abbreviations.



to Milner, it appears that this character is not as useful as Milner suggested. Widely spaced teeth are present in *Coloraderpeton* (Anderson 2003*b*), which is otherwise very similar to *Oestocephalus.* With *Lethiscus* having closely spaced teeth, it suggests that widely spaced teeth is a derived, not primitive, character in aistopods, present only in *Coloraderpeton* and *Ophiderpeton*.

Phlegethontiidae (assuming *Sillerpeton*, not included in the present analysis, would be placed as sister taxon to *Phlegethontia*), with *Pseudophlegethontia* as its closest outgroup, forms a new taxon, Phlegethontioidea. Ophiderpetontidae sensu lato is a paraphyletic grade, with *Ophiderpeton* placed as sister taxa to the more derived "ophiderpetontids" and phlegethontioids.

Heterochrony and aistopod morphology

The paraphyly of Ophiderpetontidae sensu lato is not surprising. Even within the "family" there seemed to have been a progressive acquisition of characters which, with the description of *Pseudophlegethontia*, approaches the condition of *Phlegethontia*. *Lethiscus* is primitive in possessing a palate with distinct palatines and vomers in addition to the pterygoid. All other aistopods have a palate with a single ossification, the palatoquadrate, although it is unknown whether the epipterygoid and quadrates were co-ossified with the pterygoid in *Lethiscus*. The palatal ramus of the palatoquadrate (or pterygoid) is more broad in advanced aistopods than in *Lethiscus*, and is frequently toothed as in *Oestocephalus* (Carroll 1998*a*) and *Coloraderpeton* (Anderson 2003*b*). This

Fig. 6. MCZ 2185, *Lethiscus stocki*. Camera lucida drawing of a rib of *Lethiscus*. Drawing was taken from the surface and represents broken sections through the bones. Note that only one rib head is formed by a robust swelling, the other, here labeled the anterior process, is a thin process and not a true rib head. Scale bar = 5 mm. See text section for anatomical abbreviations.

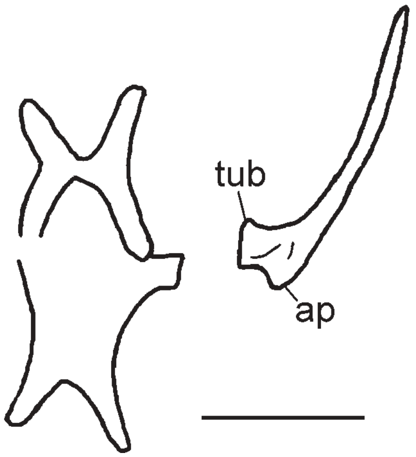


Fig. 7. Strict consensus of two most parsimonious trees, showing hypothesis of aistopod relationships and placement of higher taxonomic names. Mapped onto the tree are several characters suggesting a trend towards loss of dermal ossification. See text for discussion. (a) body elongate, loss of limbs, reduction of girdles. (b) loss of separate palatal ossifications (vomers, palatines). (c) loss of postorbital (d) elongation of skull in parietal region. (e) loss of dorsal osteoderms, reduction of extent of gastralia ossification, rostrum becomes pointed. (f) loss of most skull table elements, hyper ossification of the braincase.

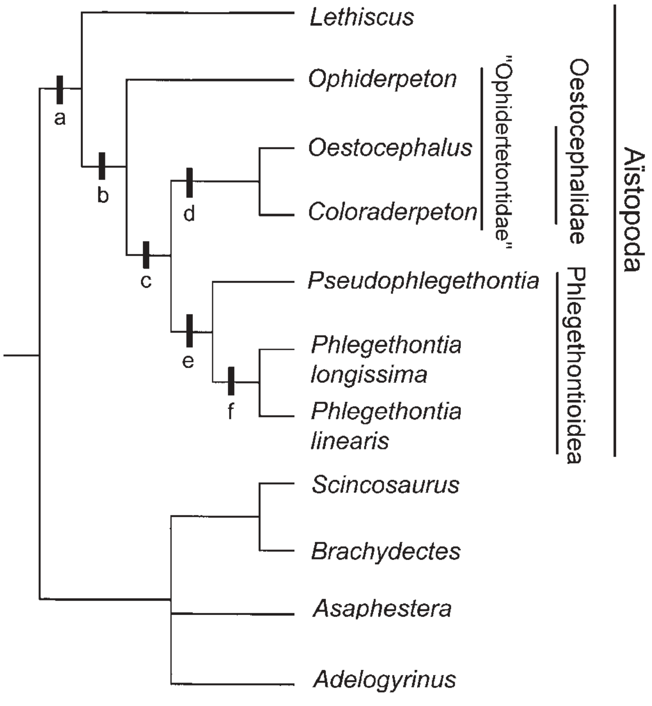
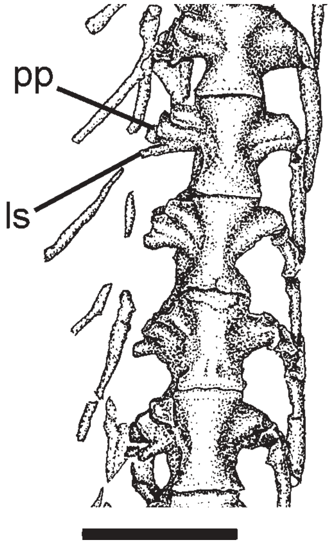


Fig. 8. FMNH PR 281, *Pseudophlegethontia turnbullorum*. Ventral view of vertebrae 23–27 showing the presence of *Oestocephalus*-like lateral spines near the transverse processes of the vertebrae. Scale bar = 2 mm. See text section for anatomical abbreviations.

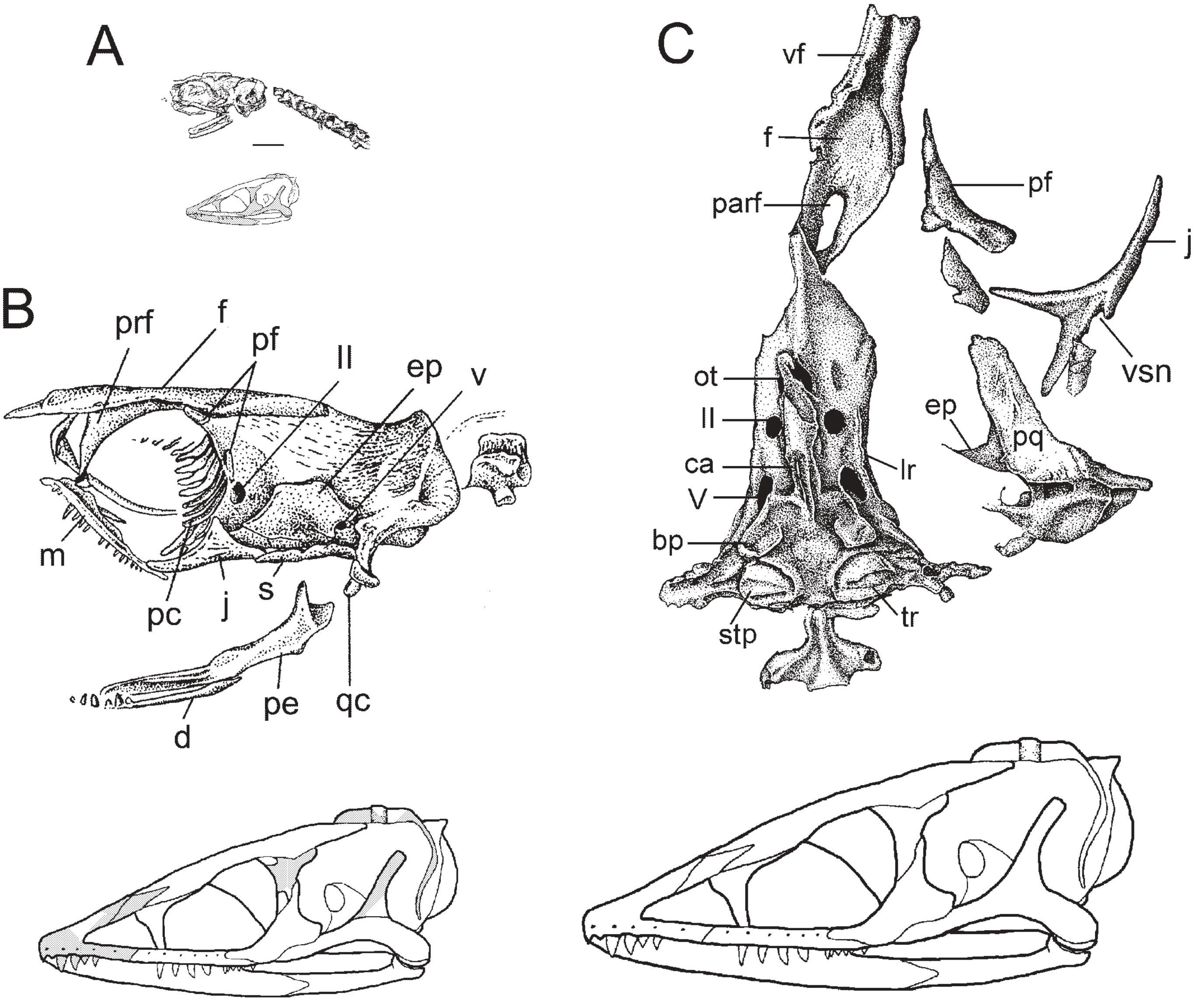


is another example of the progressive loss of dermal ossification common to Paleozoic tetrapods that takes place in aistopods (Anderson 2002, 2003*a*). At the base of Aistopoda, bones covering the temporal fenestra are lost. Between *Lethiscus* and *Oestocephalus* and *Coloraderpeton* (the palate in both species of *Ophiderpeton* is unknown), the vomer and palatines are lost. Between *Ophiderpeton* and all other aistopods, the postorbital is lost. Within phlegethontioids, the postorbital region of the skull becomes shortened, the anterior pointed, dorsal osteoderms are lost, and the gastralia become thin. Finally, within phlegethontiids the braincase becomes a unitary, solidly ossified within even the smallest individuals, and the lacrimal, supratemporal, parietals, postparietals, and tabulars are lost.

A growth series of *Phlegethontia* discussed by Anderson (2002; eight specimens, total skull lengths ranging from 3.36 to 19.8 mm) demonstrates the ontogenetic pattern of ossification within a single species (Fig. 9). First to ossify is the braincase (a single ossification in all specimens of *Phlegethontia*), frontal, and posterior element of the lower jaw (Fig. 9A). Next the dental arcade (dentary and maxilla), prefrontal, and jugal ossify, and the squamosal and postfrontal begin to ossify (Fig. 9B). The squamosal ossifies its lower ramus first, and the postfrontal may ossify from two centres of ossification. The final stage of ossification is completed quickly (Fig. 9C), although the skull depicted in Fig. 9C is highly disarticulated suggesting it is not completely ossified. Unfortunately, discerning the timing of ossification of the premaxilla is impeded by two factors. One, the anterior of the skull tends to be placed near the margins of Mazon Creek nodules, where there is a zone dissolution present. Two, the premaxillae are fine structures, and, should the nodule not break in exactly the right place, they are inaccessible to study without risking destroying visible morphology. Gregory (1948) suggested this was the case in USNM 17097 (Fig. 9B), and it is definitely the case in the only known specimen of *Pseudophlegethontia* (Anderson 2003*a*). Premaxillae are definitely not present in FMNH PR 831 (Fig. 9A) and definitely are present in the skull from Nýřany (NMW 1896 II 34).

The pattern of development of the skull in *Phlegethontia*

Fig. 9. Pattern of development of the skull of *Phlegethontia*. (A) FMNH 831 (B) USNM 17087 (C) MCZ 2204. Skulls drawn to scale. Grey shading shows areas not ossified. See text for discussion. See text section for anatomical abbreviations.



suggests a mechanism for the larger scale acquisition of the unique aistopod skull. The last bones to ossify in *Phlegethontia* are the first bones lost within the aistopod lineage. The first bones lost in the lineage are the palatal and lower temporal bones, and the last lost are the posteromarginal bones; the frontals, the first to ossify in *Phlegethontia*, are never lost. What might be occurring is a progressive cessation of ossification of the dermal bones (paedomorphosis), concomitant with, or possibly driven by, acceleration of ossification of endochondral bones (peramorphosis).

Functional constraints also seem to be present. The posterior marginal bones are only lost within the lineage when the braincase was sufficiently well ossified that it could assume the tasks of supporting the skull and providing sufficient area for the attachment of jaw adductor and epiaxial musculature. Thus, it is only within *Phlegethontia* that the braincase is sufficiently ossified to support the jaw musculature, and the posterior marginal and roofing bones are lost. This freedom of functionally unconstrained elements to become altered or lost has been noted previously within salamanders (Hanken 1984). Within *Pseudophlegethontia*, the sister taxon to *Phlegethontia*, the braincase is incompletely ossified (although more so than within oestocephalids), and the posterior skull roof remains intact (although less so than oestocephalids). This pattern is repeated in the dermal skeleton, where there is a reduction in the amount of ossification of gastralia and loss of dermal ossicles. Within *Lethiscus*, *Ophiderpeton*, and oestocephalids, the gastralia are massively ossified, and dermal osteoderms thickly cover the body. However, within *Pseudophlegethontia* and *Phlegethontia*, gastralia are reduced to gracile ossifications, and dorsal osteoderms are absent.

This pattern of paedomorphosis in one system and peramorphosis in another is documented in modern amphibians (Hanken 1983, 1984) and has been discussed at great length by Gould (1977). Within the salamander *Thorius*, it is hypothesized that it is the peramorphosis within the axial skeleton that ultimately drives miniaturization. When the epiphyses completely ossify to the shafts of the limb bones growth ceases, leaving slower developing systems, such as the dermal skull, in a retarded state of development. For example, the skull of *Thorius* possesses wide fossae and a lack of articulation between elements typical of earlier stages of skull development in other plethodontid salamanders (Hanken 1983, 1984). Similar patterns of morphological change associated with miniaturization have also been described in basal mammals (Rowe 1993) and in squamates (Rieppel 1984), but the specific bones lost vary within each lineage. For instance, within *Thorius* (and all phlethodontid salamanders) the posterior skull elements appear earliest (Hanken 1984), while the posterior elements not otherwise lost are among the last to ossify in *Phlegethontia*. As in *Thorius*, it is possible that hyperossification in the endochondral skeleton of *Phlegethontia* causes a cessation of growth before the entire dermal cranium becomes ossified. This hypothesis explains the order in which skull elements are lost within *Phlegethontia* (and all aistopods). It also suggests that the palatine and vomers identified within *Lethiscus* are not fused to the palatoquadrate as suggested by Anderson (2002) but rather fail to ossify, exemplifying paedomorphosis similar to the marginal skull bones. The discovery of new aistopods can test this hypothesis of a heterochronic origin for the aistopod morphotype.

Classification of Aistopoda

This classification summarizes Anderson (2002, 2003*a*, 2003*b*) and the current phylogenetic analysis. See these works for diagnoses, type specimens, and synonymies. Phylogenetic definitions are provided for some names; however, we are hesitant to provide definitions for all names because of our incomplete knowledge of these animals. For instance, Phlegethontiidae includes *Phlegethontia* and *Sillerpeton* (Anderson 2002), but *Sillerpeton* is only known from a small braincase and a couple of unassociated vertebrae and so is unsuitable for use as an anchor taxon. Similarly, Oestocephalidae currently includes *Oestocephalus* and *Coloraderpeton* (Anderson 2003*b*); using these two taxa as anchors for a node-based definition might exclude other, closely related forms to be discovered in the future, while using them as anchor taxa for a stem-based definition might force the inclusion of a plesiomorphic form, like *Pseudophlegethontia*, within Phlegethontiidae. Although these difficulties arise in part due to the mandatory familial rank, we believe it is best to leave these names undefined at present to prevent creating future nomenclatural difficulties. In accordance with current thinking within phylogenetic taxonomy (Cantino and deQueiroz 2000) formal ranks are abandoned; indentation portrays levels of taxonomic inclusiveness.

Tetrapoda Goodrich 1930
  Lepospondyli Zittel 1888
  Aistopoda Miall 1875

New phylogenetic definition: (Stem) All lepospondyls closer to *Phlegethontia* than to *Diplocaulus*, *Adelogyrinus*, *Brachydectes*, or *Pantylus*.

Note: Multiple anchor taxa were used because lepospondyl relationships are still unstable.

    Lethiscidae Wellstead 1982
      Lethiscus stocki Wellstead 1982
    Ophiderpetontidae Schwartz 1908
      Ophiderpeton brownriggi Wright and Huxley 1866
      Ophiderpeton kirktonense Milner 1994
    Oestocephalidae Anderson 2003*b*
      Oestocephalus amphiuminum (Cope 1868)
      Oestocephalus nanum (Hancock and Atthey 1868)
      Coloraderpeton brilli Vaughn 1969
   Phlegethontioidea New Taxon

Phylogenetic definition: (Stem) All aistopods sharing a more recent common ancestor with *Phlegethontia* than *Oestocephalus*.

    Pseudophlegethontiidae Anderson 2003*a*
      Pseudophlegethontia turnbullorum Anderson 2003*a*
    Phlegethontiidae Cope 1875
      Phlegethontia linearis Cope 1871
      Phlegethontia longissima (Fritsch 1875)
      Sillerpeton permianum Lund 1978
    Phlegethontiidae incertae sedis
      Phlegethontia "phanerhapha" Thayer 1985
   Aistopoda incertae sedis
      "Ophiderpeton" swisshelmense Thayer 1985

Conclusions

Lethiscus is similar to ophiderpetontids in the anatomy revealed by HRCT, but much more remains to be learned about this species. *Coloraderpeton* is very similar to *Oestocephalus* in cranial morphology, but is different in postcranial anatomy. The presence of single rib heads in all known aistopod taxa, including *Lethiscus*, suggests that the second shaft of the transverse process of *Pseudophlegethontia* might be homologous to the lateral spine of *Oestocephalus* (Anderson 2003*b*), which is confirmed by re-examination. Similarly, the previously reported doubled articular facets on the transverse processes of *Coloraderpeton* (Vaughn 1969; Gallup 1983) require further study.

Phylogenetic analysis supports the close affinity of *Pseudophlegethontia* and *Phlegethontia*. "Ophiderpetontids" are paraphyletic, which requires their being separated into two families. There are several, possibly associated, phyletic trends within aistopods. One is the addition of vertebrae to the caudal region, resulting in extremely long tails within *Phlegethontia* (Anderson 2002, 2003*b*). Another is paedomorphosis, including the loss of dorsal osteoderms and many skull roof bones, and the reduction of the degree of ossification of the gastralia and the remainder of the dermal skull. At the same time there is a peramorphic increase in the degree of endochondral ossification, especially in the braincase region, ultimately resulting in the massively ossified braincase of *Phlegethontia*. As our understanding of the genetic mechanisms underlying bone patterning and development increases, it may become possible to infer how aistopods became the most distinctive tetrapods of the Paleozoic.

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Appendix A. Character description and matrix used in this study

1. Snout. 0: blunt; 1: pointed.
2. Parietal-tabular contact. 0: absent; 1: present.
3. Frontals. 0: paired; 1: fused.
4. Postorbital. 0: enters orbital margin; 1: restricted from orbit; 2: absent.
5. Postorbital. 0: contacts supratemporal-tab; 1: no contact with supratemporal.
6. Parietals. 0: present; 1: absent.
7. Parietal foramen. 0: present; 1: absent.
8. Temporal fenestra. 0: absent; 1: present.
9. Occipital condyle. 0: transversely wide; 1: round.
10. Braincase. 0: composed of multiple bones; 1: fully fused.
11. Stapes. 0: columella present; 1: columella absent.
12. Fenestra ovalis. 0: lateral; 1: ventral.
13. Quadrate to occipital condyle. 0: posterior; 1: anterior.
14. Palatoquadrate. 0: absent (distinct pterygoid, quadrate, epipterygoid); 1: present.
15. Marginal dentition. 0: rounded; 1: laterally compressed.
16. Marginal dentition. 0: tightly packed; 1: widely spaced.
17. Proatlas. 0: absent; 1: present.
18. Neural spine. 0: high; 1: low.
19. Transverse process. 0: short; 1: wider than 2 × span of zygapophysis.
20. Spinal nerve foramina. 0: absent; 1: present.
21. Accessory vertebral articulations. 0: absent; 1: present.
22. Pectoral girdle. 0: fully represented; 1: endochondral elements absent.
23. Neural arch. 0: sutured to centrum; 1: fused to centrum.
24. Costal process of rib. 0: absent; 1: present.
25. Posterior process of rib. 0: absent; 1: prominent anteriorly only; 2: prominent throughout trunk.
26. Dorsal osteoderms. 0: present, absent from cheek; 1: present, present in cheek; 2: absent.
27. Ventral gastralia. 0: thick, densely packed; 1: thin, spaced.

Table A1. Data Matrix.

Taxa Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Lethiscus	0	0	0	0	0	0	0	1	1	0	?	?	0	0	0	0	0	1	0	1	0	?	1	1	0	0	0
Ophiderpeton	0	0	0	1	1	0	0	1	1	0	?	?	0	?	0	1	?	1	?	1	?	1	1	0	0	1	0
Oestocephalus	0	1	0	2	-	0	0	1	1	0	1	1	0	1	1	0	1	1	1	1	1	1	1	1	2	1	0
P. longissima	1	-	1	2	-	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	1	1	1	1	2	1
P. linearis	1	-	1	2	-	1	1	1	1	1	?	?	1	1	0	0	?	0	1	1	0	1	1	1	1	2	1
Pseudophlegethontia	1	0	0	1	0	0	0	1	1	0	?	?	1	1	0	0	?	1	1	1	0	1	1	1	2	2	1
Scincosaurus	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Asaphestera	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Adelogyrinus	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Coloraderpeton	0	1	0	2	-	0	0	1	1	0	?	?	0	1	0	1	?	1	1	1	1	1	1	1	2	1	0
Brachydectes	0	1	0	2	-	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	-