

THE FIRST STEM TETRAPOD FROM THE LOWER CARBONIFEROUS OF GONDWANA

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ABSTRACT. The first stem tetrapod from Gondwana, *Ossinodus pueri* gen. et sp. nov., is described from fragmentary material that includes a skull table and many important parts from the postcranial skeleton. It was recovered together with a typically non-marine to marginal (near) marine fish fauna from the Lower Carboniferous (mid Viséan) Ducabrook Formation, Queensland, Australia. Phylogenetic analysis hypothesises that *Ossinodus* belonged to a clade that includes *Whatcheeria* and *Pederpes*, positioned on the stem of the crown tetrapods, one step crownward of *Tulerpeton*. Hind limb morphology suggests that small specimens of *Ossinodus* were primarily aquatic but that larger ones were less so.

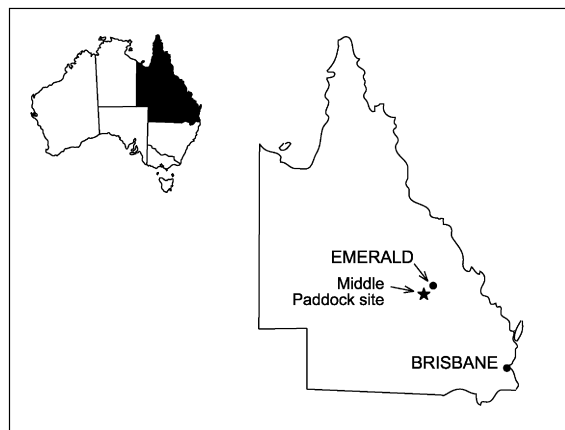
KEY WORDS: stem tetrapod, Lower Carboniferous, Gondwana, Australia, phylogeny, terrestrialisation, WhatcheerIIDae.

REMAINS of the earliest tetrapods are now known from both the Laurasian and Gondwanan landmasses in the uppermost Devonian. Comprehensive accounts have been published of the East Greenland forms *Acanthostega* (e.g. Coates and Clack 1990, 1991; Clack 1994; Coates 1996) and *Ichthyostega* (Jarvik 1996), the Latvian *Ventastega* (Ahlberg *et al.* 1994) and Russian *Tulerpeton* (Lebedev and Coates 1995). In addition to the European taxa, Late Devonian tetrapods have been recovered from eastern North America (Daeschler *et al.* 1994; Daeschler 2000). While all of these tetrapods are from the Famennian, even earlier, fragmentary Frasnian tetrapods from Scotland have been described as *Elginerpeton* (Ahlberg 1995, 1998), while *Panderichthys* from the Frasnian of Russia has been recognised as the tetrapod sister group (Vorobyeva and Schultze 1991; Cloutier and Ahlberg 1995). In contrast to the relative abundance of northern occurrences, in Gondwana finds of Late Devonian tetrapod remains have been sparse to date. Undisputed tetrapod footprints in the Upper Frasnian–Famennian Genoa River Beds of north-eastern Victoria (Warren and Wakefield 1972; Clack 1997) and a mandible, *Metaxygnathus*, from the Frasnian Cloghnan Shale of New South Wales (Campbell and Bell 1977) indicate the presence of Devonian tetrapods in the Australian part of the southern landmass.

Despite these Late Devonian occurrences, until recently few tetrapods have been recovered from the lowermost Carboniferous, and the scant evidence of later Carboniferous tetrapod life has been restricted to the eastern United States of America and Western Europe, a region known as the Mississippian Tetrapod Province (Milner 1993). The earliest tetrapods now known from the Carboniferous are: *Pederpes*, an articulated specimen from the upper Tournaisian (Ivorian, Tn3c) Ballagan Formation, Dumbarton, Scotland (Clack 2002a); and the fragmentary mid-Tournaisian (Ivorian) tetrapods from the Horton Bluff Formation, Nova Scotia (Clack and Carroll 2000).

Carboniferous tetrapods were thus unknown from outside Euramerica, although Turner (1993) predicted an Australian Early Carboniferous tetrapod fauna in the Drummond Basin of south-east Queensland. This forecast was based on the presence of a microvertebrate fauna, designated the *Ageleodus/xenacanthidid*/hybodontiform assemblage, which is commonly found in non-marine and marginal marine environments in Euramerican Late Devonian and Carboniferous deposits that also contain tetrapods. Examples of these are: the Famennian Catskill Formation at Red Hill, Pennsylvania (ST, pers. obs. 2001); the Tournaisian at Horton Bluff, Nova Scotia (ST, pers. obs. 2001); the mid Viséan Burdiehouse Limestone and Wardie Shales (Turner 1993), both in Scotland; and late Viséan deposits near Delta, Iowa (Turner 1993).

The first tetrapods from the Lower Carboniferous of Gondwana, from the Middle Paddock site in the Ducabrook Formation of the Drummond Basin, Queensland (Text-fig. 1), were collected as surface scrap



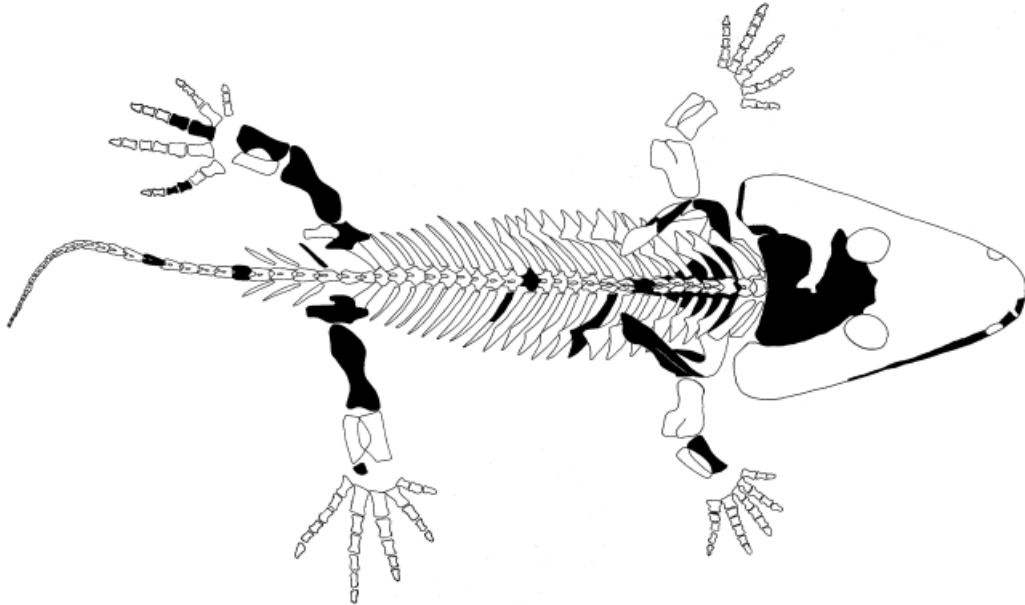
TEXT-FIG. 1. Locality map. The Middle Paddock site is 23°56'S, 147°23'E, approximately 80 km south-west of Emerald.

(Thulborn *et al.* 1996). Six subsequent field trips have produced additional tetrapod material from excavations of the sediments.

The initial interpretation by Thulborn *et al.* (1996) suggested the presence of three tetrapod taxa at the Middle Paddock site: an anthracosaur, based on the presence of an ilium with a postiliac process; a colosteid, determined by a premaxilla with a tusk; and a possible temnospondyl. Further discoveries, especially of more complete cranial material, have led to the conclusion that the tetrapod remains belong to a single taxon, based on the similar pattern of ornamentation of all the dermal bones. A new taxon is described below from the cranial material and the postcranial material is referred to that taxon.

EARLY TETRAPOD RELATIONSHIPS

The phylogenetic position of the Middle Paddock tetrapod is discussed below but some clarification of terminology is necessary here. The Tetrapodomorpha (Ahlberg 1991) encompasses Rhizodontida, Osteolepiformes and Panderichthyidae, as well as stem tetrapods and the crown group Tetrapoda. In phylogenetic analyses of early tetrapods *Ichthyostega* and *Acanthostega* consistently fall outside the Tetrapoda (Goodrich 1930), that is, on the tetrapod stem. Most phylogenies concur that the crown group Tetrapoda consists of two sister groups, a crown clade including temnospondyls (and lissamphibians), usually with baphetids, and a second crown clade including anthracosaurs and amniotes (e.g. Panchen and Smithson 1988; Lebedev and Coates 1995; Coates 1996; Clack 1998). The positions of taxa such as *Crassigyrinus* (Clack 1998), *Greererpeton* (Smithson 1982), *Caerorhachis* (Ruta *et al.* 2002) and *Whatcheeria* (Lombard and Bolt 1995) vary from stem tetrapods to taxa on the amphibian or amniote stems. It is assumed in these analyses that lissamphibians are more closely related to temnospondyls than to the amniote clade (Bolt 1969) although that relationship was not tested. Laurin and Reisz (1997) and Laurin *et al.* (2000) have produced a phylogeny that reaches very different conclusions based on a much wider spectrum of taxa, most far crownward of those discussed in this paper. Most recently Clack (2002a) included a number of 'lepospondyls' in an analysis of stem tetrapods. Her results showed that these were more closely related to temnospondyls and baphetids than to anthracosaurs. We have followed Coates' (1996, contra Lebedev and Coates 1995) terminology for the crown groups forming the dichotomy in the Tetrapoda. Thus Amphibia (Linnaeus 1758) is used rather than Batrachomorpha (Säve-Söderbergh 1934) for the crown clade including temnospondyls and extant Amphibia, and Amniota (Goodrich 1916) is used instead of Reptiliomorpha (Säve-Söderbergh 1934) or Anthracosauria (*sensu* Gauthier *et al.* 1988) for the crown clade including anthracosaurs and Amniota. A new phylogenetic definition of the taxon Anthracosauria by Laurin *et al.* (2000) is not used in the present paper.



TEXT-FIG. 2. Diagram to show the different tetrapod bones (shaded black) recovered from Middle Paddock. Drawing based on *Eucritta* (Clack 2001, fig. 8) with some modification to the skull and limbs. Adult *Ossinodus* would have been much larger than *Eucritta*, c. 1.5 m in length.

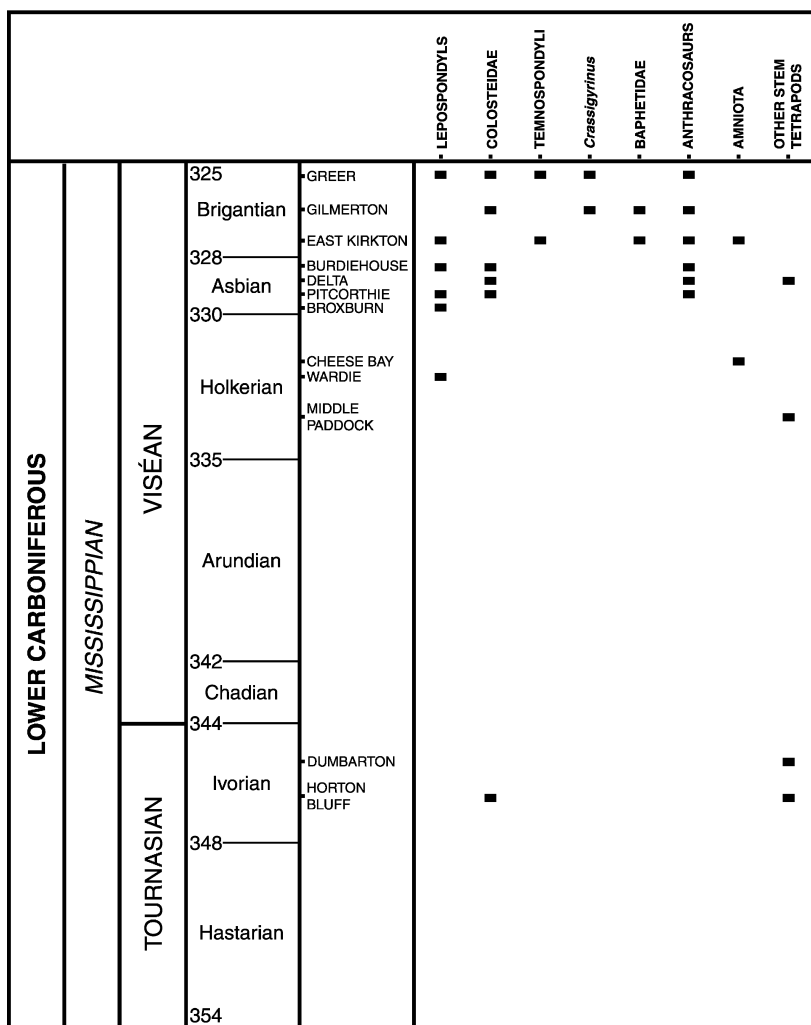
GEOLOGICAL SETTING

The site

The most productive area to date, the Middle Paddock site (Queensland Museum Locality L1117; 23°56'S, 147°23'E) consists of an eroded drainage area at the head of a minor stream system. The site was discovered in 1995 by local landowners who sent tetrapod and gyraacanth spine fragments to the Queensland Museum. A later visit by scientists was made when surface scrap including tetrapods was collected over a four-hour period. A second, five-day trip in 1996 established the area over which scrap was weathering and searched the immediate area for further exposures. Several strata rich in palaeoniscoids were located but none containing the larger fish or tetrapod elements found at the main site. Minor excavation of the apparently most productive area was carried out to investigate the state of preservation of *in situ* bone. Several extremely well-preserved tetrapod postcranial elements were recovered from an area known as Middle Rise. During the 1997 field trip the productive area was gridded with iron stakes at 10 m intervals, to be left permanently in place. The grid, measuring 60 m north–south and 70 m east–west, covers the area from which bone has been collected on the surface. All material recovered is now designated as to grid square for future taphonomic analysis and entered onto an ACCESS database. A more extensive excavation was begun at Middle Rise with minor excavations elsewhere, again in order to determine productive areas. Excavation continued in 1998. In 1999, 2000 and 2001 the Middle Rise area was further subdivided into 1-m squares from which all bone found was recorded in detail. These 22 weeks of fieldwork have produced some 60 tetrapod bones representing a minimum of four individuals. A representation of the different bones recovered is shown in Text-figure 2.

Age of the Ducabrook Formation

Playford (1977, 1978, 1985) studied the palynoflora of the Ducabrook Formation and correlated it with the north-west Australian *Anapiculatisporites largus* Assemblage, dating the formation as late Viséan.



TEXT-FIG. 3. Distribution of the principal Early Carboniferous tetrapod faunas. The approximate positions of the faunas have been taken from the original literature and fitted to the time scale of Jones (1995).

Thulborn *et al.* (1996) correlated the Middle Paddock fauna with the oldest last appearance of the *A. largus* Assemblage, providing a mid Viséan age (V3a), rather than the youngest last appearance, as other spores present have been additionally recorded from older Tournaisian palynofloral assemblages (Text-fig. 3). Preliminary papers on the lungfish (Turner *et al.* 1999) and rhizodont (Johanson *et al.* 2000) support a post-Tournaisian age. Both are closest to Laurentian taxa from the mid Viséan or later in the Carboniferous.

Geology and palaeoenvironment

The unit containing the tetrapod bones at Middle Paddock marks the transition between two environments. It is here designated the Tetrapod Unit. Below the unit, the alternation of siltstone and wave-influenced sandstone and oolitic limestone represent episodic shallowing and deepening of a saline lagoon, while

above the unit, sedimentary analysis indicates cyclic flood plain and channel-fill deposition in a fluvial environment. The overall sequence represents a progradational deltaic system (Parker 2001). The Tetrapod Unit itself consists of two conglomeratic horizons with the lower grading into the sandstone that separates the two conglomerates. These khaki green, mostly friable rocks are compositionally uniform with respect to mineralogy and clast type, with differences occurring in percentages and sizes of clasts. They consist of granules and pebbles of calcareous sedimentary rock fragments and sand-sized grains of quartz, plagioclase, alkali-feldspar and accessories. A feldspathic arenite matrix is heterogeneously distributed, as is the generally calcitic cement. The entire unit has a maximum thickness of 0.24 m. The tetrapod and associated fish fossils in the Tetrapod Unit were deposited by a twin-peaked flood event on a tidal channel floor (Parker 2001) and most were disarticulated prior to transport (Turner *et al.* 1999). Further detail of the depositional environment and geology will be published elsewhere.

Fauna of the Tetrapod Unit at the Middle Paddock site

An abundant fish fauna is present at the site with preliminary papers published on the lungfish, *Ctenodus* (Turner *et al.* 1999), and a rhizodont, cf. *Strepsodus* (Johanson *et al.* 2000). Pectoral elements and spines of the acanthodian, *Gyracanthides* sp. nov., are common (Warren *et al.* 2000). Also present are several taxa of palaeoniscoids, and sharks including *Ageleodus* comparable with that from the older Raymond Formation (Turner 1993), a new species of xenacanthid, a possible ctenacanthid and three taxa of hybodontoids. A fragmentary unidentified ostracod is a rare invertebrate component of the fauna. We could also expect osteolepiforms and other acanthodians. An osteolepiform, *Cladarosymblema narrienense*, has been described from the early Viséan Raymond Formation of the Drummond Basin (Fox *et al.* 1995), but to date no osteolepiform material has been found at Middle Paddock. The Raymond Formation also contains an extensive fish microfauna with acanthodian scales and invertebrates including *Spirorbis* (Turner 1993). Palaeoniscoids have been reported from the Star of Hope Formation that lies stratigraphically between the Raymond and Ducabrook formations (Turner and Long 1987).

MATERIAL AND METHODS

All specimens from Middle Paddock site are housed in the fossil collections of the Queensland Museum, Brisbane, Australia. The poorly cemented nature of both the conglomerates and fossiliferous sandstone made removal of the fossil elements relatively easy. This was achieved with an Aro engraver and sharpened carbide rods held in pin vices. The specimens were consolidated when necessary with Paleobond, and joined with Jurassic Gel. Fragile specimens were backed by carbowax (polyethylene glycol 4000) with an outer shell of plaster of Paris.

Institutional abbreviations. FM, Field Museum of Natural History, Chicago, Illinois; KUV, Museum of Natural History, The University of Kansas, Lawrence, Kansas; QM, Queensland Museum, Brisbane, Queensland; YPM-PU, The Peabody Museum, Yale University (formerly within the Princeton University collection).

SYSTEMATIC PALAEONTOLOGY

TETRAPODAMORPHA Ahlberg, 1991
WHATCHEERIIDAE Clack, 2002a *incertae sedis*

OSSINODUS gen. nov.

Derivation of name. Latin *ossis*, bones and *nodus*, puzzle.

Type and only known species. *Ossinodus pueri* sp. nov.

Remarks. Derived features of the Whatcheeriidae present in *Ossinodus* are the presence of a massive tooth on the maxilla about position 5 or 6, and a very broad interclavicle with acutely angled lateral corners. Primitive features of the Whatcheeriidae present in *Ossinodus* are the supratemporal-postparietal contact;

probable fang pairs on the vomers, palatines and ectopterygoids with a row of some smaller accessory teeth on each (presence on the ectopterygoid implies presence on the vomer and palatine); row of coronoid teeth nearly continuous; at least some lateral lines in tubes through bone; and ilium with postiliac process and dorsal iliac blade. Features of uncertain polarity shared with other members of the Whatcheeridae are the pronounced angle between the skull table and cheek in transverse section, and trunk ribs with expanded distal flanges.

Diagnosis. Large stem tetrapod with a skull table almost square in shape; intertemporal present; reduced tabular without a ventral extension and reduced temporal embayment; elongate postparietal-supratemporal suture; the parietal-postparietal and parietal-supratemporal sutures together form an almost transverse line across the skull table, reflecting the narrow anterior part of the postparietal; and one or more enlarged premaxillary teeth. Postcranial skeleton with robust neural arches; cleithrum reduced and unsutured to a scapulocoracoid with a well-ossified blade; interclavicle with a parallel-sided parasternal process; clavicle with grooved anterior margin; pelvis with large postiliac process in which the transverse line does not approach the ventral border; femur with extensive adductor blade and crest; tibia flattened with an L-shaped distal end. While most of these characters are primitive for stem tetrapods, some are derived in relation to *Ichthyostega* and *Acanthostega*. None is autapomorphic but together serve to differentiate *Ossinodus* from other stem tetrapods.

Ossinodus pueri sp. nov.

Text-figures 4–13

Derivation of name. Latin *pueri*, boys (named for each ‘boy’ associated with the initial discovery: Hastings, Cameron and Mitchell Hawkins; Tony and Guy Thulborn; Tim and Angus Hamley; and for Bryan Currie who found the holotype).

Holotype. Queensland Museum Fossil QM F 37414, a skull table (Text-fig. 4A–C).

Locality and horizon. Queensland Museum Locality L1117, Middle Paddock, central Queensland, Australia; Ducabrook Formation, Drummond Basin; Early Carboniferous (mid Viséan, V3a).

Referred cranial and mandibular material. Posterior skull table margin (QM F 34621, QM F 37444); maxilla (QM F 34281, QM F 34600, QM F 37433); premaxilla (QM F 37417, QM F 37452); ectopterygoid (QM F 37453); quadrate (QM F 34601, QM F 34284, QM F 36937); quadratojugal (QM F 37441, QM F 36932, QM F 37450); prefrontal (QM F 37439); QM F 37449 ornament with suture and orbital margin; ornament (QM F 34622); probable coronoid (QM F 34282); posterior end of left mandibular ramus (QM F 37440).

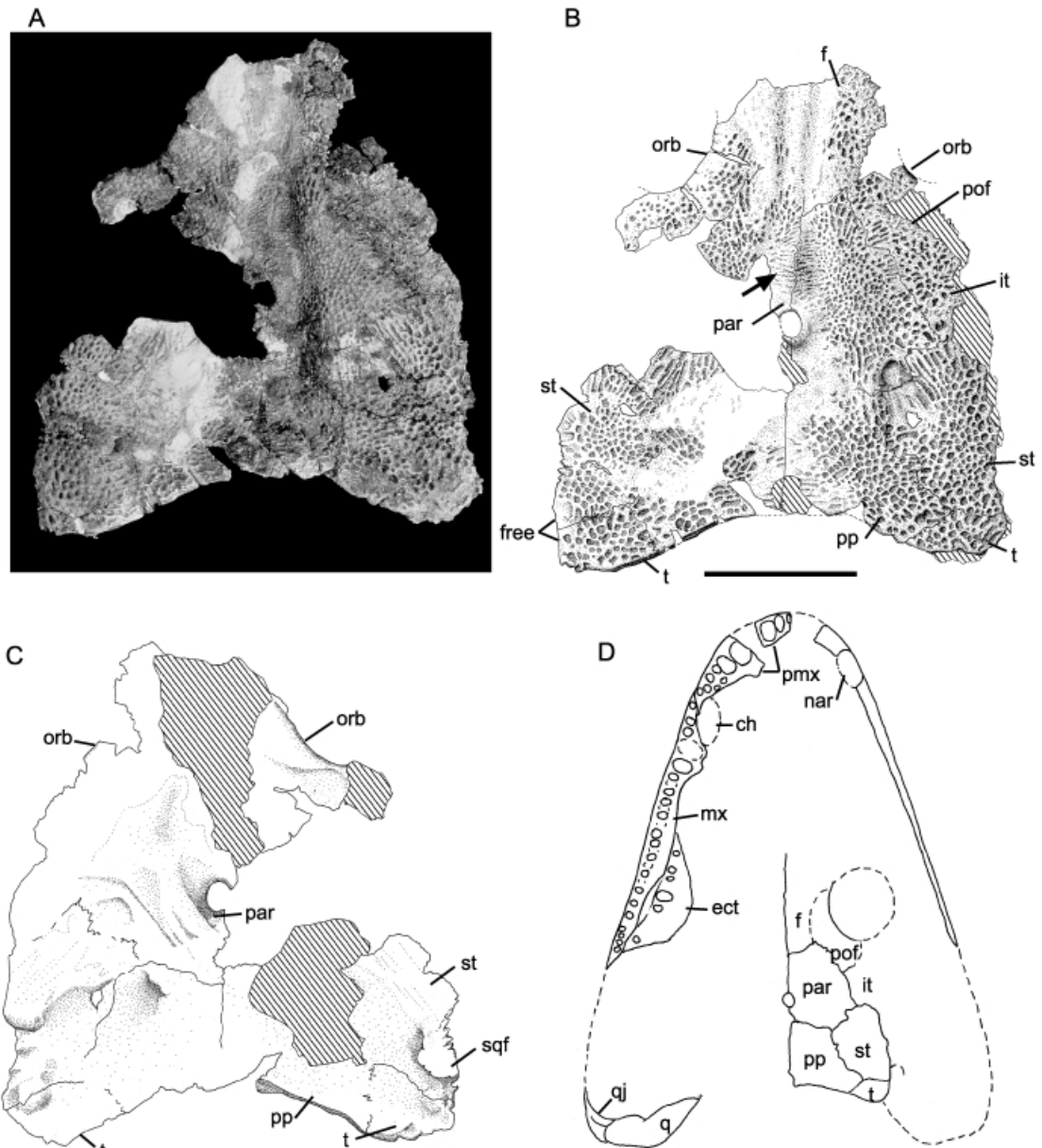
Referred postcranial material. Neural arch (QM F 36903, QM F 37418, QM F 37420); rib (QM F 37427, QM F 37426, QM F 34616); scapulocoracoid (QM F 37405, QM F 37434); interclavicle (QM F 34610); clavicle (QM F 36907); cleithrum (QM F 34607, QM F 37429); pelvic girdle (QM F 37431, QM F 34280, QM F 36955); femur (QM F 37415, QM F 37416, QM F 37432); tibia (QM F 37406, QM F 37404); fibulare? (QM F 37436); metapodial (QM F 34285, QM F 36916); phalange (QM F 36935, QM F 36912, QM F 37437).

Diagnosis. As for the genus.

DESCRIPTION

Cranial and mandibular skeleton

Ornament and sensory canal system. All of the cranial material bears a similar pattern of ornamentation suggesting its derivation from the same taxon. Pits separated by robust ridges are accompanied by rare areas with elongate ridges separated by grooves (Text-figs 4A–B, 5A, D, 6A, G, 7F, I). In the holotype (Text-fig. 4A–B), an area with finer ornament consisting of mostly transverse ridges is present in a depressed midline strip, especially on the parietals anterior to the parietal foramen. Sensory grooves are not evident on the maxilla and no continuous grooves appear on the skull table.



TEXT-FIG. 4. *Ossinodus pueri* skull. A–C skull table (QM F 37414). A, photograph in dorsal view. B, drawing of A. C, drawing of ventral surface. D, reconstruction of the skull of *Ossinodus pueri* in ventral (left) and dorsal (right) views. In B arrow points to area of finer ornament in the midline. In D the maxilla has been lengthened in relation to the premaxilla, skull table and quadrate because they come from larger individuals. Cross hatching in B and C represents areas restored with epoxy. Scale bar represents 50 mm. All specimens in Text-figures 4–13 are of *Ossinodus pueri* gen. et sp. nov. from the Ducabrook Formation, Queensland.

A sensory canal composed of part open groove, part enclosed canal and part pit is present on the premaxilla (QM F 37452, Text-fig. 6i). A short groove is preserved on an isolated piece of ornament (QM F 34622), while a pit line penetrates the surangular (QM F 37400, Text-fig. 7p).

The ornament pattern in *Ossinodus* is unlike anthracosaurian ornament which is typically poorly expressed, but more closely resembles that of the Baphetidae (Beaumont 1977) and Colosteidae (Smithson 1982), or that of some temnospondyls. This pattern in *Ossinodus* differs from the other members of the Whatcheeriidae. In *Whatcheeria* the dermal bones are almost devoid of ornament (Lombard and Bolt 1995). In *Pederpes* the skull table shows a unique pattern of reticulate ornament in which the pitted areas towards the centre of each bone are extended by short ridges that do not reach the sutures. The pits are smaller in *Pederpes* than in *Ossinodus* but this aspect would change with the size of the specimen. Elsewhere on *Pederpes* the ornament is reduced (J. A. Clack, pers. comm. 2002).

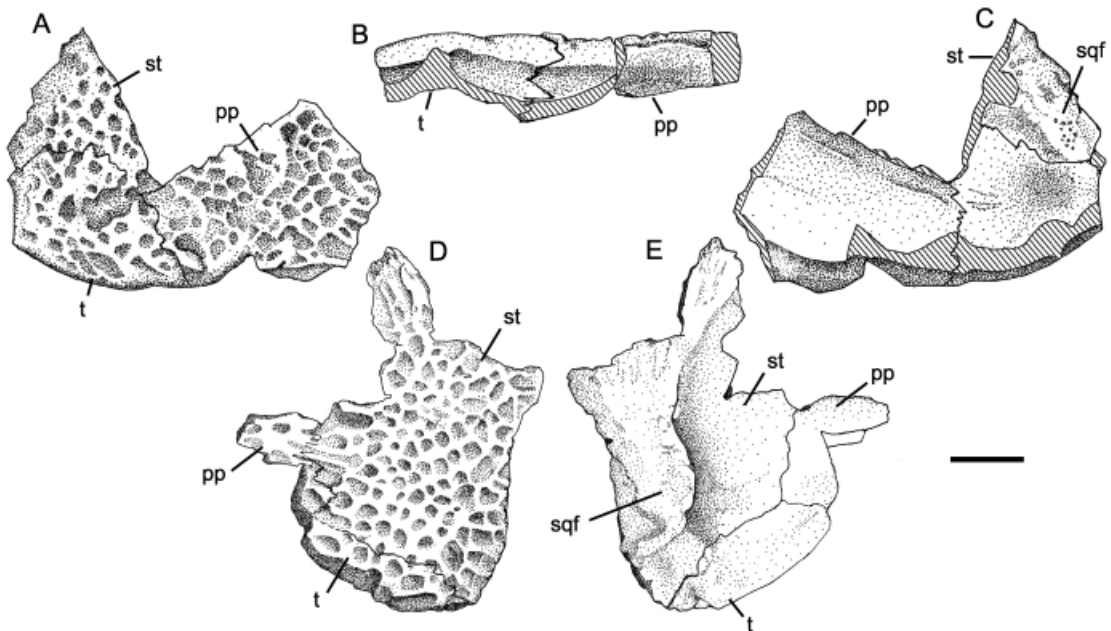
Skull table (Text-fig. 4). The holotype is a skull table (QM F 37414, Text-fig. 4A–C) that includes a large part of the postero-mesial margin of the left orbit, a small part of the right orbit, the pineal foramen and a part of the posterior border of the skull. The table is depressed in a wide band along the midline except in the area immediately surrounding the parietal foramen, which is raised. An elongate supratemporal-postparietal contact, preserved in full on the right, is primitive and suggests *Ossinodus* is non-anthracosaurian (Smithson 1985), although in the analysis of Clack (2002a), this character appeared to be homoplastic. A small length of suture on the right indicates that a bone was present between the postfrontal and supratemporal. This is hypothesised to be an intertemporal because a suture between the postorbital and the parietal is found only in colosteids (Smithson 1982) and some Dvinosauria (Warren 1999). All sutures delimiting the tabulars are preserved and show that the tabulars are reduced compared with most early tetrapods. The presence of a slight posterior projection of the tabular and associated temporal embayment is indicated by an area of unbroken edge on the lateral side of the left tabular and supratemporal. This area is preserved better in QM F 37444 (Text-fig. 5D–E). In *Ossinodus* this free lateral margin of the tabular is shorter than the otherwise quite similar tabular margin from an undetermined tetrapod from the Devonian of Andrejevka (Lebedev and Clack 1993). Small tabulars (much smaller than postparietals) are shared with the other whatcheeriids, colosteids (Schultze and Bolt 1996; Smithson 1982) and *Caerorhachis* (Holmes and Carroll 1977) while in some temnospondyls the tabulars are reduced together with the postparietals (Sequeira and Milner 1993).

In *Ossinodus*, the postparietal-parietal and supratemporal-parietal sutures form an almost transverse line across the skull table, rather than these suture pairs meeting at a marked angle. This suture line does not reflect a reduced temporal embayment as the transverse line is not present in colosteids where that embayment is even more reduced (Schultze and Bolt 1996) than it is in *Ossinodus*. The presence of a transverse line is shared with *Whatcheeria* but not *Pederpes* (Clack 2002a).

On the ventral surface of the supratemporal, all three specimens with the tabular-supratemporal area preserved show an area for contact with the squamosal (Text-figs 4c, 5c, e). Although the area is not completely preserved it appears as a loose suture, suggesting that the posterior part of the cheek had some mobility. A similar area is present in *Crassigyrinus* (Panchen 1985, fig. 8). An unsutured cheek (butt joint) is now known in colosteids (Schultze and Bolt 1996) and may be primitive for Tetrapoda, but a supratemporal with a deeply interdigitated suture to the squamosal is characteristic of the Whatcheeriidae (Clack 2002a). The best preserved supratemporal (QM F 37444, Text-fig. 5D–E) appears to have a free edge, lateral to the squamosal suture, and extending anteriorly and posteriorly beyond that suture. This free edge on the supratemporal suggests the cheek region of *Ossinodus* formed a sharp angle with the skull roof as it does also in *Whatcheeria* (Lombard and Bolt 1995), *Pederpes* (Clack 2002a), *Crassigyrinus* (Panchen 1985; Clack 1998) and anthracosaurians (Smithson 1985).

No rugosities marking the opisthotic contact are preserved on the ventral surface of the tabular. However, the presence of double facets (Clack 1998) appears to be linked with ‘anthracosaur type’ (Panchen 1985) tabular horns that are thickened by a marked posteroventral extension (*Crassigyrinus* and anthracosaurs) and the tabular is too reduced in *Ossinodus* for this to have been present.

The occipital surface of the skull table (Text-fig. 5b) consists of a shallow shelf traversed by a groove that is marked in QM F 34621 but less marked in the larger holotype. In QM F 34621 the groove is interrupted for a few millimetres on the tabular. Above the postparietal part of the groove is a small posteriorly-directed flange that stops short of the skull midline. In both specimens the ventral margins of the tabulars have a narrow strip of broken bone that is too thin to have supported the ventral tabular flange found in anthracosaurs. The ventral margin of the postparietal in QM F 34621 is complete for a short distance, indicating the upper margin of an opening. This margin slopes downwards away from the midline, rather than down towards the midline as does the dorsal surface of the posttemporal fossa in *Whatcheeria* (Lombard and Bolt 1995). This finished bone surface seems too close to the midline to be the margin of a posttemporal fossa. Clack (2003) has suggested that openings in this position in *Pederpes* and *Whatcheeria* were not for the posttemporal fossa but for an occipital artery. This could be true in *Ossinodus* although in this case the openings



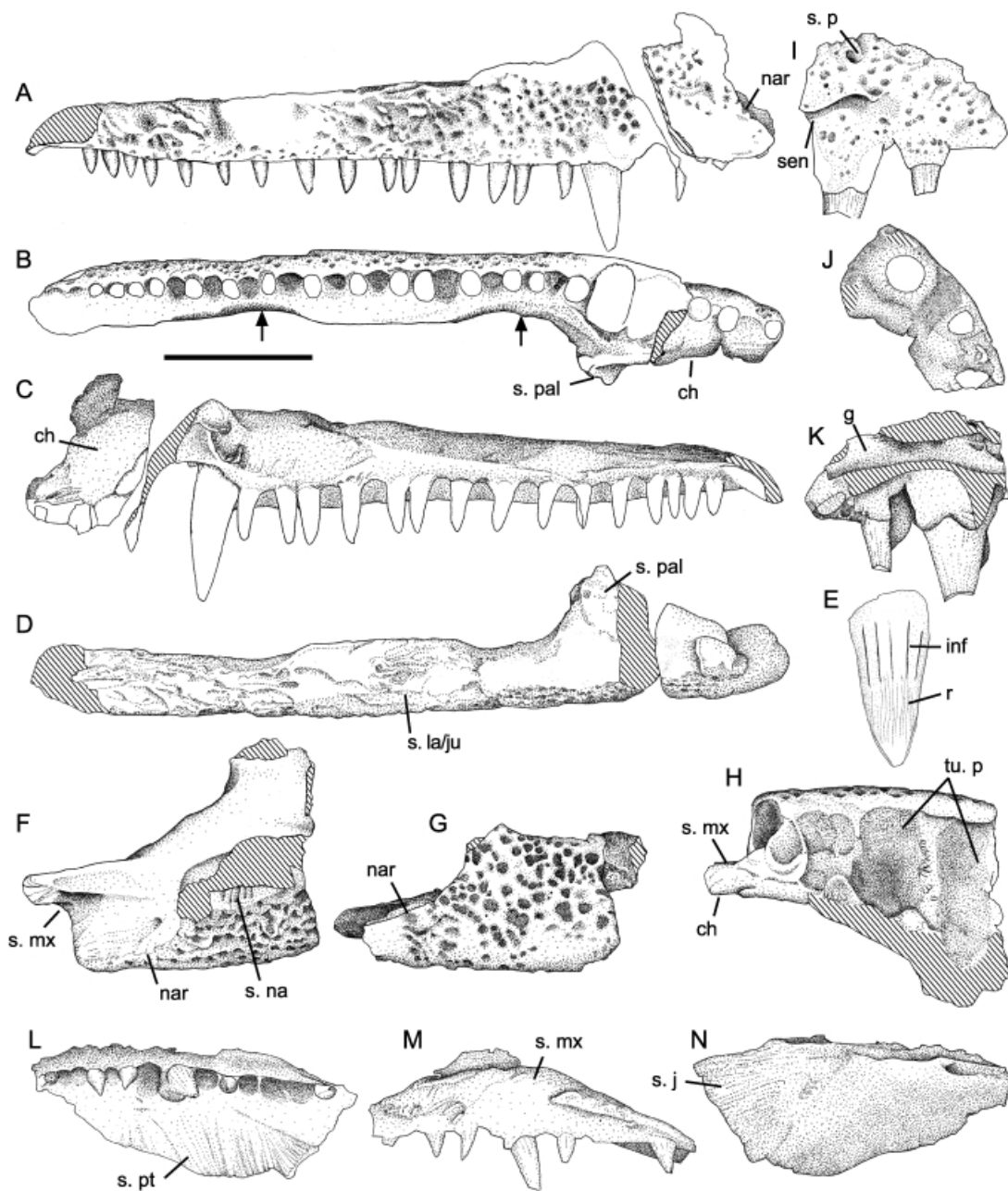
TEXT-FIG. 5. Skull table. A–C, QM F 34261 in A dorsal, B occipital and C ventral views. D–E, QM F 37444 in D dorsal and E ventral views. Scale bar represents 10 mm.

would not be contained by the opisthotic, instead being roofed by the tabulars. The presence or absence of more laterally placed posttemporal fossae and tabular buttons (Clack 1998) is not determinable.

Maxilla. Ornament on the lateral surface of the maxilla (QM F 34281, Text-fig. 6A) is finer than on the bones of the skull table and there are no sensory pits or grooves. The dentition, consisting of 34 teeth and a tusk pair, is described further below. The posteroventral wall of the naris is preserved on the anterior end of the maxilla, close to the tooth row (Text-fig. 6A), while the posterolateral wall of the choana is preserved on the anterior inner surface (Text-fig. 6B–C). Posterior to the choana is a rugose medial projection marking the position of contact with the palatine. Immediately posterior to this the medial surface is markedly recurved, expands and recurves again (Text-fig. 6B–C). These concavities may mark the lateral borders of fenestrae or could be areas adjacent to the palatine and ectopterygoid tusks. An elongate foramen between the palatine and the maxilla was found in *Eogyrinus* (Panchen 1972) and *Proterogyrinus* (Holmes 1984). The maxilla was loosely attached to the adjacent bones with no interdigitating sutures. This is similar to the situation in *Ventastega* (Ahlberg *et al.* 1994) and *Acanthostega*, which was described by Clack (1994, 2002b) as having poorly imbricated butt joints to the jugal and lacrimal. Clack noted that, in *Acanthostega*, the maxilla was frequently missing or disarticulated, again indicating a loose attachment to the adjoining bones.

Premaxilla. Two premaxillae have been found representing different parts of the bone. The posterior part of a premaxilla (QM F 37417, Text-fig. 6F–H) has fine ornament similar to that on the maxilla but is from a larger specimen. A few millimetres above the tooth row the anteroventral margin of the large external nostril is preserved, while a smooth area on the posteromesial part of the palatal surface is part of the lateral border of the choana. In dorsal view (Text-fig. 6F), a part of the suture with the nasal or internasal is preserved lateral to a broken area, while mesial to this the smooth dorsal surface of the bone curves ventromedially. A posteriorly directed prong, which is laterally recessed, indicates an area of overlap with the maxilla. The ventral surface of QM F 37417 (Text-fig. 6H) is largely occupied by tooth loci, with two large loci anteriorly and three or more smaller loci posteriorly. A mesial strip of broken bone suggests the premaxilla may have continued ventrally for a few millimetres before suturing with the vomer.

A piece of curved tooth-bearing bone is most probably a premaxilla (QM F 37452, Text-fig. 6I–K), from near the symphysis. One end of the bone has a smooth, rather than broken, edge suggesting it may be from the midline. If so, the midline suture is not interdigitated, at least anteriorly. Externally the fragment is ornamented and bears a sensory canal



TEXT-FIG. 6. Maxilla, premaxilla and ectopterygoid. A-E, right maxilla (QM F 37433) in A lateral, B ventral, C mesial and D dorsal views. E, enlargement of maxillary tooth. F-H, right premaxilla (QM F 37417) with part of external nostril in F dorsal, G lateral and H ventral views. I-K, right premaxilla (QM F 37452) from near the symphysis in I anterolateral, J ventral and K posteromesial views. L-N, left ectopterygoid (QM F 37453) in L ventral, M lateral and N dorsal views. Arrows indicate recurved areas of the inner surface of the maxilla. Scale bar represents 10 mm.

that is partially enclosed. A large sensory pit is present, connecting to an enclosed length of canal, followed by an open section. Internally a canal divides the lower, tooth-bearing part from the upper part that is ridged for the suture with the nasal. The tooth row includes a tusk and, more medially, two smaller teeth and two empty loci.

Ectopterygoid. An isolated but complete bone (QM F 37453, Text-fig. 6L–N) is most likely an ectopterygoid. QM F 37453 has no part of the choanal margin, which should be present if the bone was a vomer or palatine. The bone is extensively underlain by the pterygoid as evidenced by a ridged sutural area covering over half the ventral surface (Text-fig. 6L). The posterior surface of the bone adjacent to the tooth row is not ridged ventrally. Instead, the dorsal surface has a series of smoothly curved ridges suggesting a suture with the jugal (Text-fig. 6N). There is no indication of the smooth edge that would mark the border of the sub-temporal fossa. Exclusion of the ectopterygoid from the sub-temporal fossa is a character of *Crassigyrinus* and embolomeres (Clack 1998) and of some temnospondyls, compared with more primitive Devonian tetrapods. Six teeth with nine additional loci are preserved along the lateral margin, with an enlarged locus and a small tusk at locus 7 and 8 (Text-fig. 6L). The mesial side of the bone extends horizontally from the tooth row, rather than rising up. The lateral surface of the ectopterygoid is rugose. A flange extends dorsally just medial to the lateral surface.

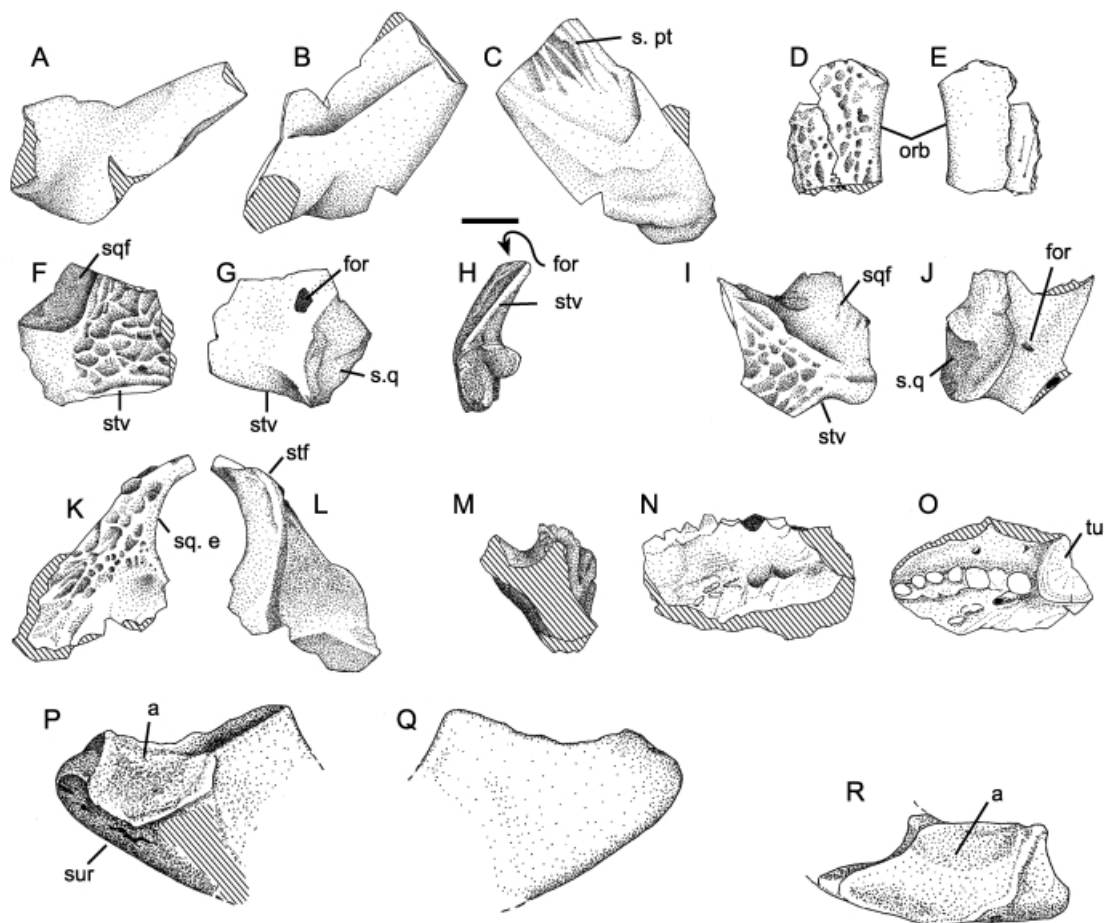
Dentition. The maxilla (QM F 37433) has loci for circa 34 bullet-shaped although distally-keeled (lanceolate) teeth, with a maxillary tusk and adjacent tusk pit (Text-fig. 6A–C). The tusk and pit lie at approximately position 6 and 7 on the tooth row. Each tooth (Text-fig. 6E) has a number of longitudinal grooves extending from one-third to one-half of the height from the base and marking the infolds of dentine. More distally, fine longitudinal ridges traverse the surface of the tooth (Text-fig. 6E). These ridges are more numerous than the dentine infolds, and are especially densely distributed on the maxillary tusk where they originate well down in the infolded area. The ridges appear to be unrelated to the infolds. Occasionally the ridges bifurcate or anastomose. Although they are present also on the external (labial) surface of the teeth, here they are not as marked; the ridges disappear towards the tooth tip on both external and mesial surfaces. Other elements in which the teeth are preserved distally, such as the ectopterygoid (QM F 37452), premaxilla (QM F 37453) and a fragment of dentary (QM F 37403), have similarly ridged teeth. In all cases the bone of attachment extends further up the external surface of the tooth than it does up the lingual surface.

Tooth sockets with scant remnants of tooth bases are present on the premaxilla (QM F 37417, Text-fig. 6H). Two greatly enlarged tusk pits appear anteriorly, with the loci for four smaller teeth posterior to them adjacent to the labial margin of the bone. The two teeth closest to the tusks may have been larger than shown, especially lingually. It is also possible that two smaller teeth were present lingual to these. The more anterior fragment of premaxilla (QM F 37452) has an enlarged tusk posteriorly and four smaller teeth or loci towards the symphysis. Together these fragments of premaxilla indicate an area of enlarged teeth towards the middle of the bone with smaller teeth both anteriorly and posteriorly. The complete ectopterygoid (QM F 37453, Text-fig. 6L–M) has a small tusk with adjacent pit situated mid way along the bone. Anterior to the tusk are three small teeth and three loci, while posteriorly are two teeth and six loci. A large tusk base and a row of seven smaller teeth are present on the partial coronoid (QM F 34282, Text-fig. 7o).

While no teeth from *Ossinodus* have yet been sectioned basally, some detail of their histology is apparent on the surface of broken teeth. The teeth are polyplacodont (Schultze 1969) with no bone entering between the infolds of dentine. The infolds are themselves folded into primary bends with no evidence of secondary bends or side branches (Warren and Davey 1992). The number of infolds varies from approximately 26 in a tooth of 4 mm diameter to approximately 60 in a tusk of 11 mm diameter. All *Ossinodus* teeth have dark dentine associated with the primary bends (figured in QM F 34281 by Thulborn *et al.* 1996, fig. 3c, d). This condition was recognised by ST as close to that found in *Eogyrinus* (Atthey 1876) and led her to conclude that tetrapods were present at the Middle Paddock site.

Keeled teeth are known in baphetids but markedly enlarged maxillary and premaxillary teeth are not. Baphetids also lack additional teeth on the inner row of the palate (Beaumont 1977). The only known early tetrapods with similar dental arrangement (premaxillary and maxillary tusks, tusks on the inner bones of the palate as well as an inner row of smaller teeth) are *Whatcheeria* (Lombard and Bolt 1995) and some anthracosaurs (e.g. *Eogyrinus*, Panchen 1972). An enlarged maxillary tusk at about position 5 or 6 is a synapomorphy of the Whatcheeridae (Clack 2002a). Some marginal teeth are enlarged on the premaxilla and maxilla of colosteids (Smithson 1982; Hook 1983) and some temnospondyls have premaxillary tusks. The teeth in *Pholiderpeton* were described as having fine irregular sculpturing above the infolded area around the base (Clack 1987), a morphology that may be comparable to the finely ridged surface of *Ossinodus* teeth.

Dark dentine is present in all embolomeres in which the histology is known, *Crassigyrinus* (Panchen 1985), *Metaxygnathus* (Cambell and Bell 1977), *Whatcheeria* (FMNHPR1747; AW, pers. obs. 1999) and in some temnospondyls. It is absent in colosteid material from Goreville (Schultze and Bolt 1996; KUVPI26314; AW, pers. obs. 1999) and *Tulerpeton* (Lebedev and Clack 1993).



TEXT-FIG. 7. Cranial and mandibular bones. A–C, right quadrate (QM F 34601) in A ventral, B internal and C external views. D–E, circumorbital bone with suture (QM F 37449) in D dorsal and E ventral views. F–H, right quadratojugal (QM F 37441) in F lateral, G internal and H ventral views. I–J, left quadratojugal (QM F 37448) in I lateral and J internal views. K–L, left prefrontal (QM F 37439) in K posterior and L internal views. M–O, coronoid (QM F 34282) in M posterior, N mesial and O dorsal views. P–R, posterior end of right mandibular ramus (QM F 37440) in P lateral, Q mesial and R dorsal views. Scale bar represents 10 mm.

Quadrate. The best preserved quadrate (QM F 34601, Text-fig. 7A–C) shows a markedly screw-shaped condyle with the larger, inner condyle projecting further anteriorly than is common in Carboniferous tetrapods. The mesial surface is traversed by deeply impressed grooves between longitudinal ridges marking a strongly interdigitating suture with the pterygoid. Internally, a deep groove above the condyle separates it from the more dorsal part of the quadrate.

Quadratojugal. All three quadratojugal fragments are of the posterolateral portion. The most complete (QM F 37448, Text-fig. 7I–J) is from a left quadratojugal and shows a large ovate rugose area which abutted the quadrate. Latero-dorsally a recessed area marks the overlap with the squamosal. Towards the anterior, the most ventral part of this overlap shows evidence of an interdigitating suture. All three specimens have a small foramen on the internal surface just dorsal to the articular area for the quadrate. In two of them (QM F 37448, QM F 37441) these foramina clearly connect internally with a foramen that exits a few millimetres below the edge of the subtemporal vacuity. A foramen in a similar position in some baphetids exits from the quadratojugal and runs forward in a groove along its internal face (Beaumont 1977, accessory paraquadrate foramen). The quadrate-quadratojugal area most resembles that of baphetids

in the shape of the articulation, the position of the quadratojugal-squamosal suture and the internal foramen in the quadratojugal.

Prefrontal. QM F 37439 (Text-fig. 7K–L) is a roughly triangular bone with one side of the triangle concave. The bone is thin except along this margin which is thickened and triangular in section. This specimen is most likely to be part of the circumorbital series, especially a left prefrontal, although the thickening along the concave margin is greater and more abrupt than the slightly thickened areas surrounding the more posterior margin of the orbit on the preserved skull table. QM F 37439 is similar also to an isolated squamosal from *Palaeoherpeton* (Panchen 1964, fig. 4).

Ornamented bone with orbital margin. An ornamented fragment (QM F 37449, Text-fig. 7D–E) has a suture parallel to the orbital margin. It is slightly thickened beside the margin, with the suture marking the edge of the thickening. It could be a part of a postfrontal or, less likely, prefrontal.

Mandible. The posterior end of a right mandibular ramus (QM F 37440, Text-fig. 7P–R) and a coronoid bone (QM F 34282, Text-fig. 7P–R) were the only mandibular material recovered. The concave glenoid fossa fits closely the convex articular facets on a separate quadrate (QM F 34601). No sutures are determinable on the mandible but the presence of a probable short sensory line on the lateral surface confirms the presence of the surangular as well as the articular. The glenoid is markedly raised above the level of the remainder of the ramus, especially lingually, in that the anterior border of the articular is almost vertical. This raised articular resembles restorations of *Crassigyrinus*, *Ventastega* and *Megalocephalus* by Ahlberg and Clack (1998) and *Eoherpeton* (Panchen 1975) but is unlike other early tetrapods. Also unusual is the presence of a posterior flange of surangular, presumably the homologue of the postglenoid area of many more recent tetrapods. This was present also in *Ventastega* (Ahlberg and Clack 1998) and *Eoherpeton* (Panchen 1975; Smithson 1985).

The partial left coronoid (QM F 34282, Text-fig. 7M–O) was described as an ectopterygoid (Thulborn *et al.* 1996) before the discovery of the complete ectopterygoid (above). Specimen QM F 34282 includes a tooth row of six small teeth, one tooth pit and part of a large tusk. These teeth are positioned above an almost vertical wall of bone with a rugose surface, presumably the mesial side of the coronoid. Lateral to the tooth row the surface of the bone rises towards a suture with the dentary. This bone is unlike the ectopterygoid (QM F 37453) in that the tusk is much larger compared with the marginal teeth and the bone on the mesial side of the tooth row slopes away from the tooth row.

Postcranial skeleton

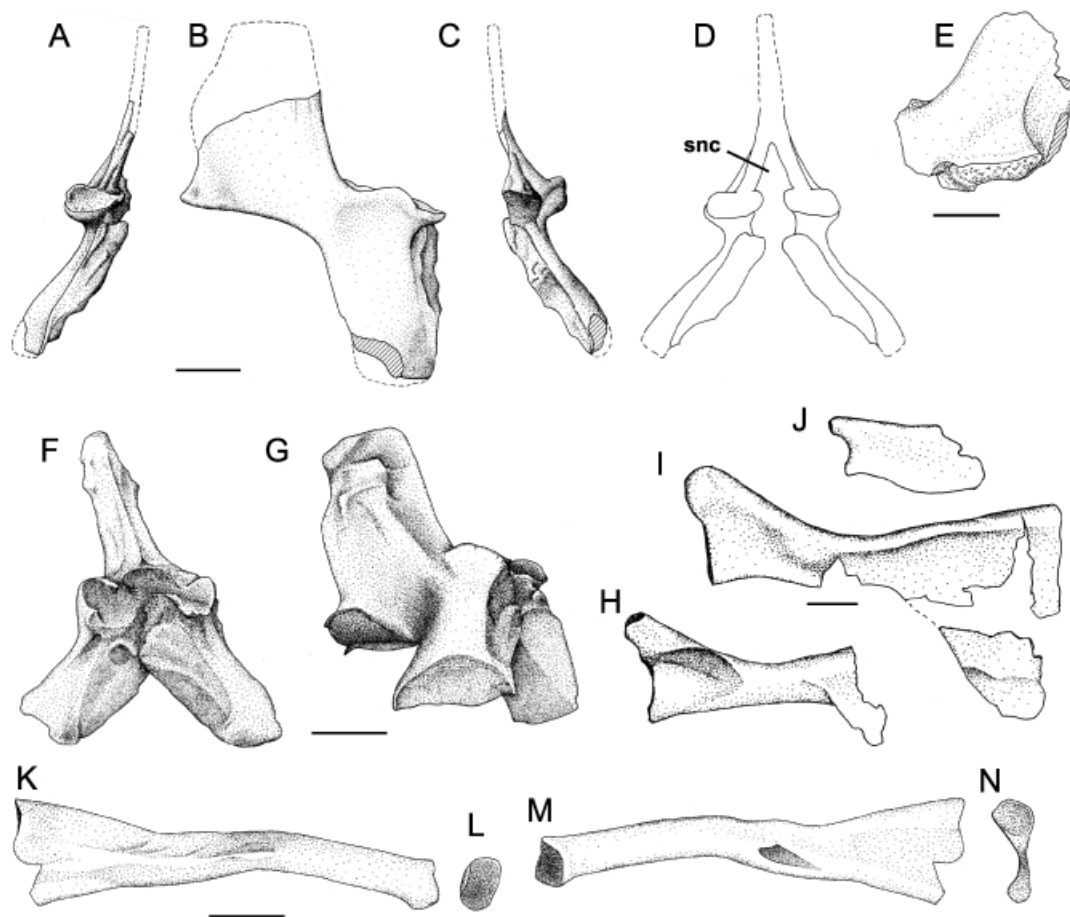
In the description of postcranial elements most terminology follows that used by Lebedev and Coates (1995) for *Tulerpeton* or Coates (1996) for *Acanthostega*.

Neural arch. Presacral neural arches QM F 36903 and QM F 37418 (Text-figs 8A–D, F–G) are well preserved and robust. Their neural spines are ‘squared off’ dorsally as in *Ichthyostega*, *Acanthostega* and more recent tetrapods (Coates 1996) but the most dorsal part of the spine is narrower craniocaudally than it is just above the zygapophyses. Both neural spines are upright without the posterior slope found in *Acanthostega*.

In other features the neural spines differ from one another. A slight ridge traverses the spine of QM F 37420 from its anteroventral to near its posterior margin where this increases in anteroposterior length (Text-fig. 8G). At this point a series of horizontally aligned tuberosities is present on the neural spine. In QM F 37418 the left and right halves of the neural spine are not separated by a perichondral strap as they are in *Acanthostega*; in QM F 36903 a strap may have been present. In QM F 36903 the pre- and postzygapophyses are robust and craniocaudally elongate (equal to or greater than the base of the neural spine) as they are in *Whatcheeria* (Lombard and Bolt 1995) in contrast to *Acanthostega* (Coates 1996); in QM F 37418 they are still robust but their craniocaudal dimension is less than the base of the neural spine. The prezygapophyses are shorter than the postzygapophyses. Heavy buttressing of the prezygapophyses is marked in QM F 37418 with the thickened buttress continuing along the transverse processes.

The transverse process of QM F 36903 is short, is directed more ventrally than laterally and has no diapophysis. These features are indicative of neural arches from the caudal region but the specimen appears to be too robust for that. In contrast the transverse processes of QM F 37418 are laterally directed and the right process has an expanded diapophysis.

The medial surface of the half of QM F 36903 preserved shows little detail but a reconstruction (Text-fig. 8D) suggests a large supraneural canal was present. A small supraneural canal may be present between the postzygapophyses of QM F 37418 but these are crushed. It is absent between the prezygapophyses as it may have been also in *Greererpeton* (Godfrey 1989, fig. 7).

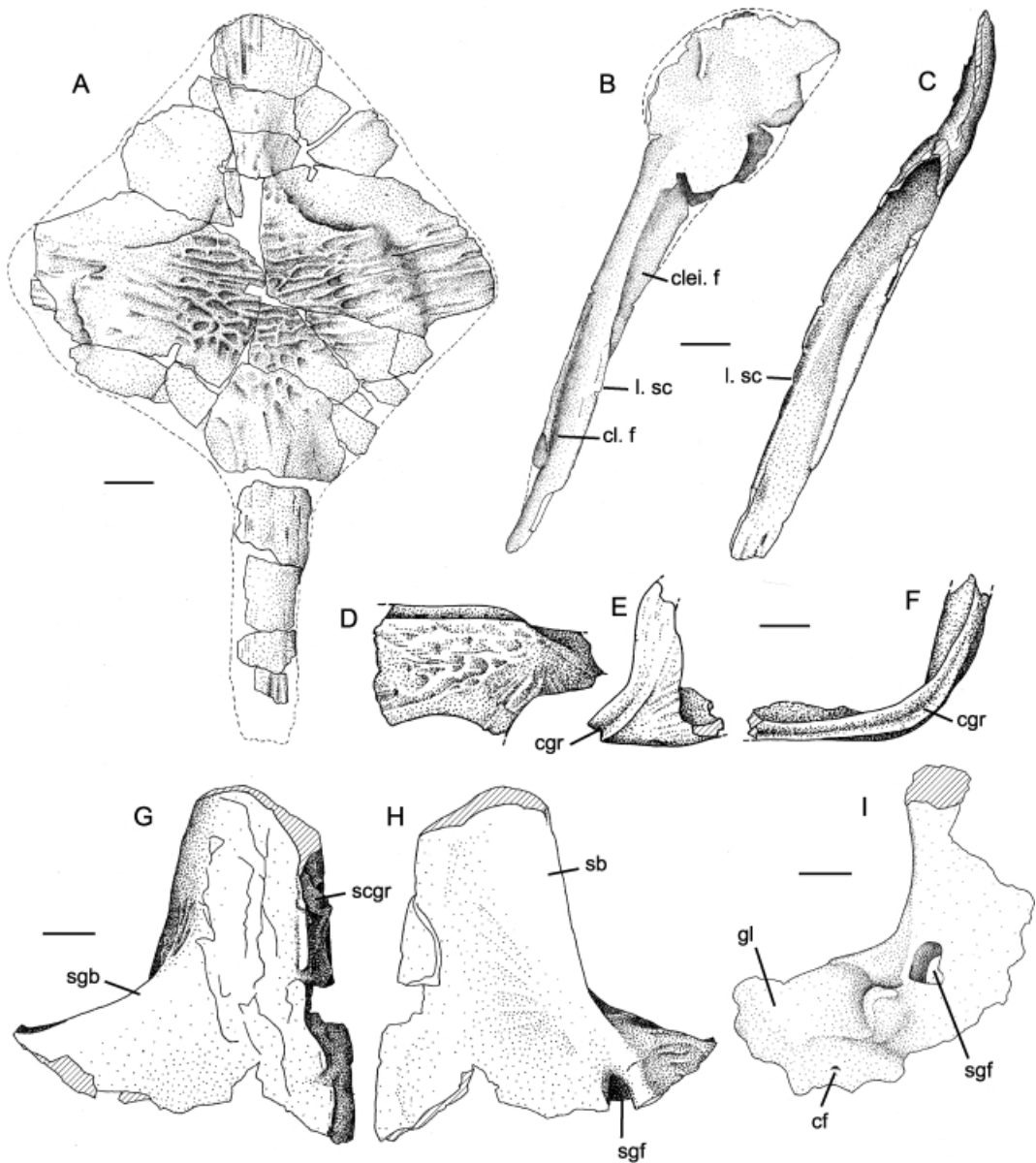


TEXT-FIG. 8. Neural arches and ribs. A–G, neural arches; H–J, anterior trunk ribs; K–N, posterior trunk rib. A–D, QM F 36903 in anterior, right lateral, posterior, and restored anterior views. E, QM F 37420 in right lateral view. F–G, QM F 37418 in anterior and right lateral views. H, QM F 37427, rib with complete proximal end. I, QM F 37426, rib with almost complete proximal end. J, QM F 34616. K–N, QM F 37451, complete rib from a posterior position in the trunk in K anterior, L distal, M posterior and N proximal views. Scale bars represent 10 mm.

A third partial neural arch, QM F 37420 (Text-fig. 8E), is shaped quite differently and is less well ossified. Most of the neural spine is missing so that the specimen consists of a well-developed but weakly buttressed prezygapophysis and a small transverse process that is rounded in lateral outline.

Other vertebral elements. No positively identifiable intercentra or pleurocentra have been found.

Ribs. Four well preserved partial ribs (Text-fig. 8H–N) have been found as well as several portions of rib shaft. Rib QM F 37427 (Text-fig. 8H) has a narrow capitulum and robust tuberculum preserved proximally and the beginning of a marked process distally. The rib is thickened on both its leading and trailing edges with the leading edge especially thickened in the region of the process. Rib QM F 37426 (Text-fig. 8I) is preserved from immediately behind the proximal end. It includes a large, triangular process but is missing the most distal end. This rib is most similar to the cervical rib of *Proterogyrinus* (Holmes 1984, fig. 23a). A probable immediately presacral rib of *Crassigyrinus* (Panchen 1985, fig. 19b) has a similar process. Rib QM F 34616 (Text-fig. 8J) is much smaller than the ribs described above. It consists of an undivided proximal end and an elongate process that is 'primitive or close to *Whatcheeria*' (M. I. Coates, pers. comm. 1996). Whether any of the processes arising from the above ribs are uncinat or expansions



TEXT-FIG. 9. Pectoral girdle. A, interclavicle QM F 34610 in ventral view. B-C, right cleithrum QM F 34607 in mesial and posterior views. D-F, left clavicle QM F 36907 in ventral, lateral and posterior views. G-I, scapulocoracoid. G-H, QM F 37434 in internal and external views; I, QM F 37405 in external view. Scale bars represent 10 mm.

of the distal end of the rib cannot be determined. A complete rib without processes, QM F 37451 (Text-fig. 8K-N), is short, and uncurved. At the proximal end, a small, narrow tuberculum is clearly separated from a larger capitulum by a narrowing of the connecting bone. The distal end is subcircular in outline. A small ridge traverses a third of the anterior side of the middle part of the rib, while a large foramen penetrates the posterior surface. Apart from the foramen, this rib is similar to that illustrated as a first thoracic in *Proterogyrinus* (Holmes 1984, fig. 23b) except that in the *Ossinodus* rib the capitulum does not project beyond the tuberculum.

Scapulocoracoid. Partial right and left scapulocoracoids (Text-fig. 9G–I) were not co-ossified with a cleithrum as occurs in Devonian tetrapods. The right scapulocoracoid, QM F 37405 (Text-fig. 9I), is poorly ossified except in the region of the glenoid, as is the case in most other early tetrapods. Ossification is greatest in the area of the supraglenoid buttress which forms a large triangular area on the medial surface. On its lateral face the buttress is marked by two ridges which arise from a bifurcation posterior to the supraglenoid foramen, with the more anterior ridge running to the anterior margin of the glenoid and the more posterior forming the curved anterior edge to the scapulocoracoid. The glenoid consists of an anterior posterolaterally facing portion and a posterior laterally facing portion but there is little preserved twisting between the two. The coracoid is thickened below the glenoid, indicating the presence of an infraglenoid buttress, but this area is poorly preserved. Among early tetrapods the specimen resembles *Tulerpeton* (Lebedev and Coates 1995) and anthracosaurs in the large supraglenoid foramen which is directed laterally. Two or more smaller foramina are present in Devonian tetrapods. An indentation below the glenoid may be a single coracoid foramen; this area is so badly preserved that additional foramina may have been present.

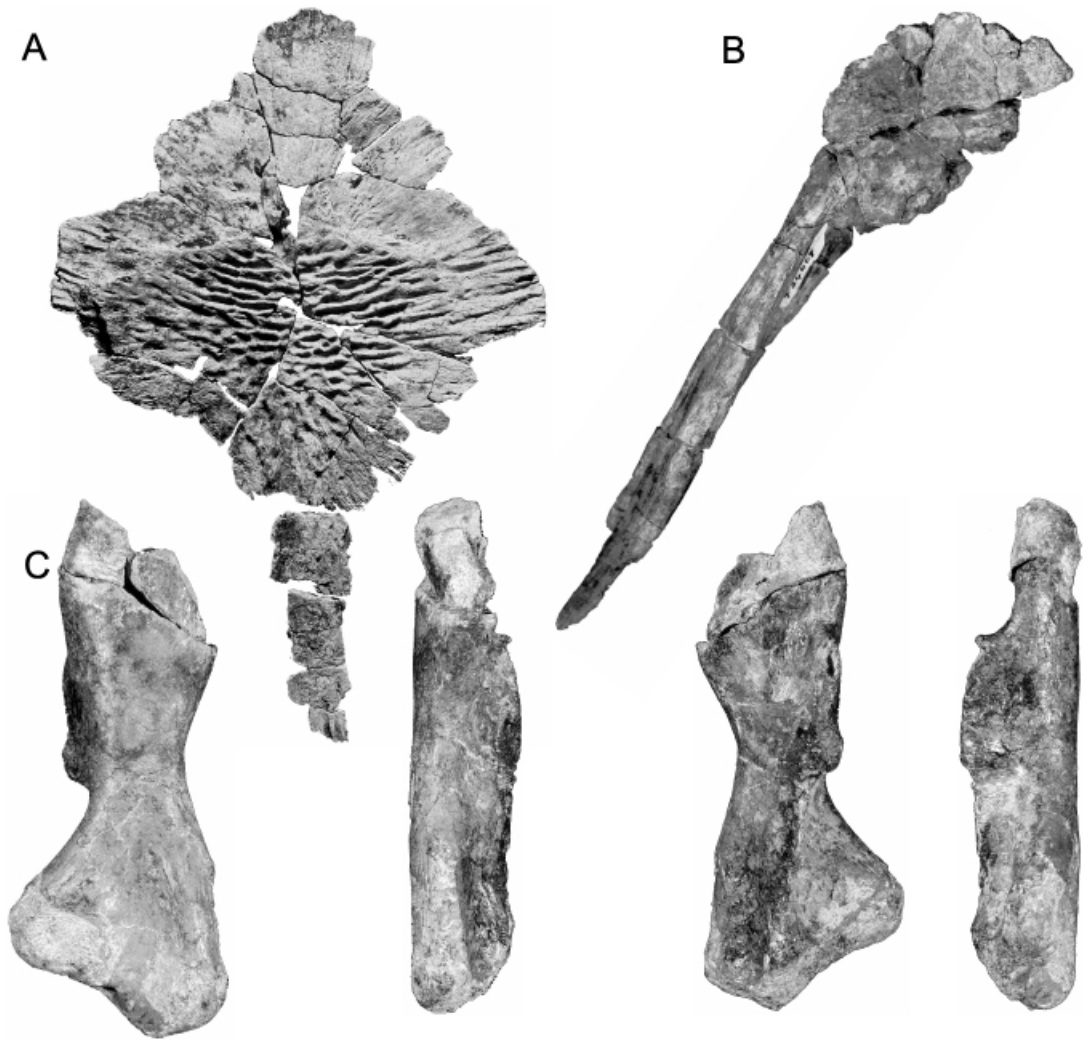
In the larger specimen, QM F 37434 (Text-fig. 9G–H), the scapular blade is fully ossified except for the dorsal margin which may have been broken or finished in cartilage. The posteromedial margin of the scapula carries a wide groove, marked by a ridge on the medial side, into which the stem of the cleithrum fits. This area is rarely ossified in early tetrapods or later temnospondyls. The supraglenoid foramen faces laterally rather than posterolaterally. The specimen was broken below the scapula and no part of the coracoid plate or glenoid were recovered. Whether the scapula and coracoid were ossified separately as in *Pederpes* (Clack 2002a) and some specimens of *Whatcheeria* (Lombard and Bolt 1995), or formed a single ossification as is usually the case, is not determinable in *Ossinodus*.

Interclavicle. The single interclavicle found (QM F 34610, Text-figs 9A, 10A) is strongly stemmed posteriorly (parasternal process). The posterolateral borders of the interclavicle are markedly concave so that the stem is almost parallel-sided, while the anterolateral borders are almost straight. Articular facets for the clavicles are impressed onto the ventral surface of the interclavicle, mirroring the shape of the lateral margin of the clavicle. These facets are smoothly convex anteriorly but a posterior facet is rugose and set at an angle to the anterior facet, resulting in a bowed clavicular margin. The centre of ossification of the interclavicle is at the same level as the rugose facet for the clavicle and the ornament is unusual in that it radiates mostly transversely towards these facets. The clavicles must have met in the anterior midline as this area of the interclavicle is unornamented. Posterolaterally the margins of the interclavicle are unornamented. The interclavicle as a whole is thickened along three ridges which can be seen on its otherwise undistinctive dorsal surface: two lead from the centre of ossification laterally beneath the rugose clavicular facets, while the third extends posteriorly onto the anterior end of the parasternal process. A parasternal process is present in most Devonian tetrapods, anthracosaurs, microsaurs, and some terrestrial temnospondyls (e.g. Yates 1999); it is absent in the Devonian *Ventastega* (Ahlberg *et al.* 1994), colosteids (Godfrey 1989), most temnospondyls and probably baphetids (Milner and Lindsay 1998). The parasternal process is narrower and more elongate in *Ossinodus* than in any early tetrapod except *Ichthyostega* (Jarvik 1996) and *Whatcheeria* (Lombard and Bolt 1995). In *Whatcheeria* the process is robust and thickened but this is not so in *Pederpes* (J. A. Clack, pers. comm. 2002) while in *Ossinodus* the process is a little thickened, especially anteriorly.

Clavicle. Ornamentation of the same type as the interclavicle covers what remains of the left clavicular blade of QM F 36907 (Text-fig. 9D–F). An unusual, strongly developed unornamented groove leads along the anterolateral margin of the clavicle, extending a little way up the dorsal process. This groove (Text-fig. 9E–F, cgr) is pierced by a number of small foramina that lead into the bone. The dorsal process of the clavicle (clavicular stem) is subtriangular in section with a short, posteriorly directed flange marking the lateral border of the articular area for the cleithrum. Judging from the extent of the obverse facet on the cleithrum, the dorsal process of the clavicle was about twice as long as the part preserved. A similar, less pronounced, groove on the anterolateral margin of the clavicle is present in *Tulerpeton* (Lebedev and Coates 1995) where it is described as a smooth anterolateral edge, suggesting the insertion of soft tissue. This character shared by *Tulerpeton* and *Ossinodus* was used in the diagnosis of the Tulerpetontidae (Lebedev and Coates 1995).

Cleithrum. The most complete cleithrum (QM F 34607, Text-figs 9B–C, 10B) has an expanded head and tapered tail with facets for articulation with the scapulocoracoid and clavicle. The posteroventral part of the head is divided into two flanges which, although incomplete, appear equally developed: one continues the line of the external surface of the cleithral head while the other is continuous with the internal surface of the head and the ridge delineating the scapulocoracoid articular area from the clavicular articulation area (= lamina suprascapularis of Bystrow and Efremov 1940). The deep recess formed by these flanges presumably clasped the anterodorsal part of the scapula. A pronounced, rounded ridge is present near the anterior margin of the internal surface of the cleithral head (Text-fig. 9B).

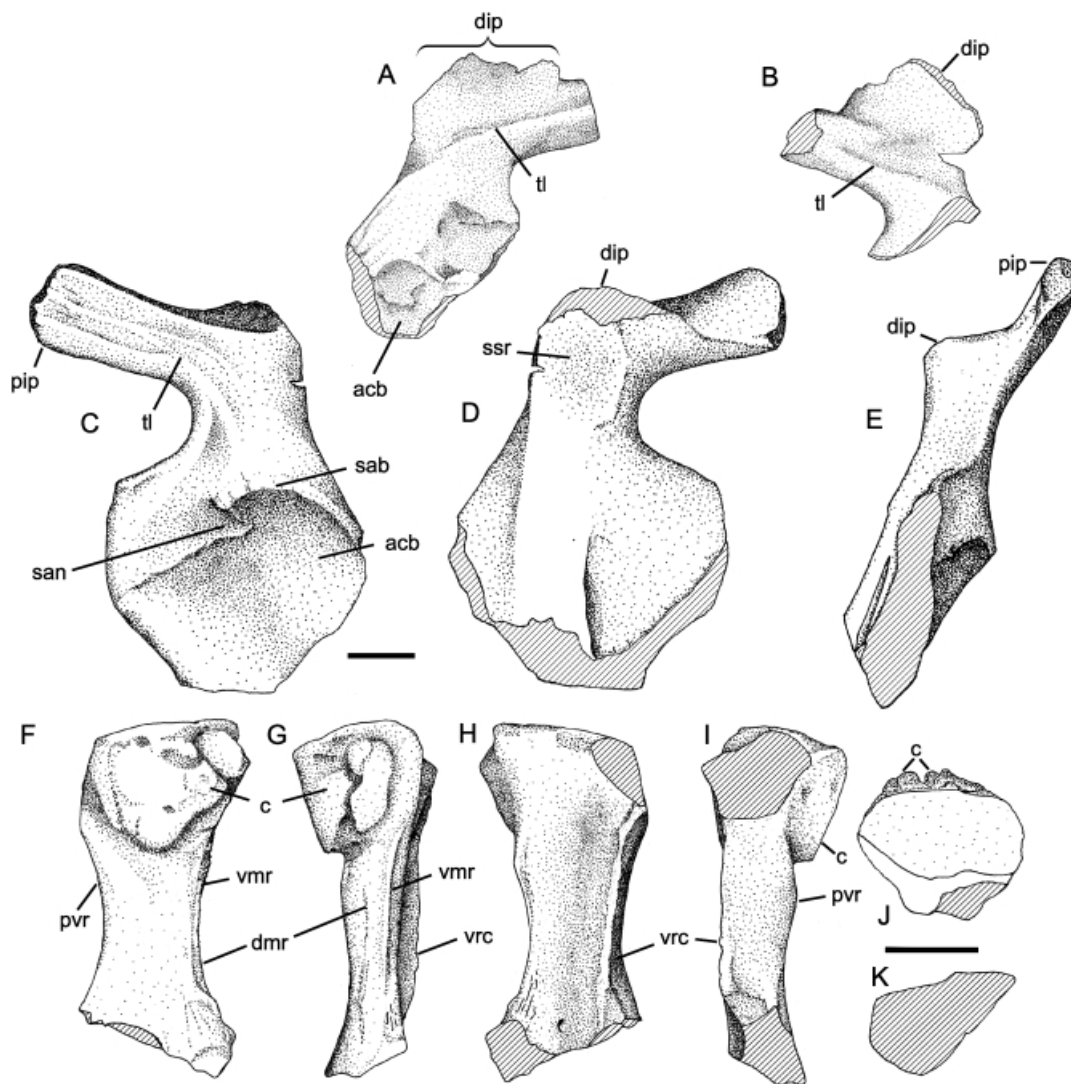
Overall the cleithral head is similar to *Pederpes* (Clack 2002a). A less extensive recess on the cleithral head was



TEXT-FIG. 10. *Ossinodus pueri*, photographs. A, interclavicle (QM F 34610) in ventral view; $\times 0.7$. B, cleithrum (QM F 34610) in mesial view; $\times 0.8$. C, 3 femur (QM F 37415) in, from left to right, extensor, posterior, flexor, and anterior views; $\times 0.8$.

present in the Triassic stereospondyls *Benthosuchus* (Bystrow and Efremov 1940), *Parotosuchus pronus* (Howie 1970) and *Metoposaurus ouazzoui* (Dutuit 1976). Cleithra of *Greererpeton* (Godfrey 1989), *Tulerpeton* (Lebedev and Coates 1995), and *Whatcheeria* are not described as recessed. Clack (1987, fig. 28) figured internal and lateral views and sections of the cleithrum of the embolomere *Pholiderpeton*, showing no flanged areas of the head and hence no recess.

Radius. The radius (Text-fig. 11F–K) is well preserved overall but lacks a segment from the proximoventral surface and the distal end has been abraded. The proximal surface would have been subcircular, while the distal outline is drop-shaped with the apex of the drop towards the lateral surface. In common with other early tetrapod radii a system of ridges is present towards the edges of the extensor and flexor surfaces. Four of these are the most prominent. The ventral radial crest described in *Acanthostega* (Coates 1996, fig. 17a, c) is equally well developed in *Ossinodus* and *Baphetes* (Milner and Lindsay 1998, fig. 10). Three other ridges have been named (Warren and Ptasznik 2002) to assist



TEXT-FIG. 11. Pelvic girdle and radius. A–E, pelvic girdle. A, QM F 34280 in lateral view. B, QM F 36955 in lateral view. C–E, QM F 37431 in (left to right) lateral, mesial and posterior views. F–K, right radius (QM F 37451) in F dorsal, G mesial, H ventral, I lateral, J proximal and K distal views. In F–I proximal is to the top of the page; in J–K the dorsal surface is to the top. Scale bars represent 10 mm.

in comparison with other early tetrapod radii. A pronounced ventromesial ridge is present in *Baphetes*, *Acanthostega* and *Ossinodus* (Text-fig. 11F–G, vmr). The prominent ridge on the middle portion of the dorsomesial surface of *Baphetes* occurs as a slight rise on the *Ossinodus* radius (Text-fig. 11F–G, dmr) and is absent in *Acanthostega*. However, *Acanthostega* and *Baphetes* share the presence of a proximoventral ridge on the posterior surface opposite the ventral radial crest (Text-fig. 11F, I, pvr). This ridge is barely discernible in *Ossinodus*. The *Ossinodus* radius is thus plesiomorphic in its overall shape, which is less waisted and elongate than radii from the colosteid, *Greererpeton* (Godfrey 1989) and the anthracosaurs. When compared with other early tetrapods the radius referred to *Ossinodus* most closely resembles those of *Acanthostega* (Coates 1996), *Pederpes* (Clack 2002a), *Baphetes* (Milner and Lindsay 1998), and *Ichthyostega* (Jarvik 1996), in that these radii are short and less waisted compared to *Greererpeton* (Godfrey 1989) and the anthracosaurs *Proterogyrinus* (Holmes 1984), *Pholiderpeton* (Clack 1987) and *Archeria*

(Holmes 1989; Romer 1957). It most closely resembles the radius of *Baphetes* in its shape and the distribution of ridges, but differs in that the ridges on the extensor side of the bone are less prominent.

The *Ossinodus* radius is unique in the presence of a complex swelling near the proximal end. This abnormality covers the whole width of the extensor surface, and continues onto the mesial surface. The surface of the bone appears spongy and irregular, with several pits and smaller swellings, the whole delineated from the normal bone surface by a marked groove. This has been shown by X-ray to be a callus associated with a comminuted fracture of the radius (Warren and Ptasznik 2002).

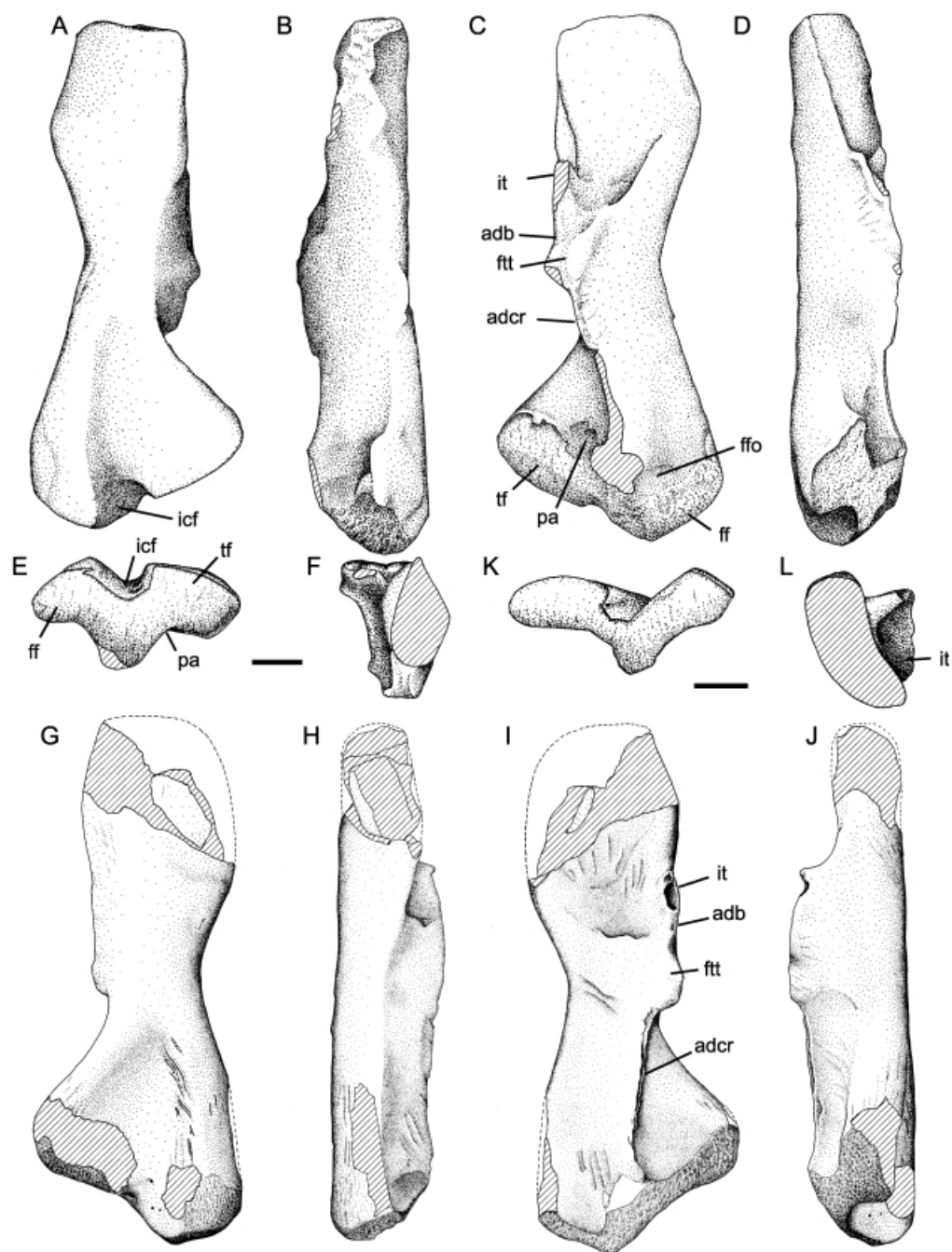
Pelvic girdle. The most complete specimen (QM F 37431, Text-fig. 11C–E) consists of an ilium with a broad iliac neck, a complete postiliac process, partially preserved iliac (dorsal) blade, and most of the acetabular area. The specimen appears to be co-ossified, that is, no sutures are preserved between ilium, ischium or pubis. The iliac neck bifurcates above the posterior margin of the supra-acetabular buttress, forming a parallel-sided postiliac process and a blade-like dorsal iliac process. This dorsal iliac process, which is more complete in QM F 36955 (Text-fig. 11B), is displaced towards the medial side posteriorly while the anterior part is aligned with the postiliac process. A strip of unfinished bone forms the dorsal surface of the dorsal iliac process and dips down a little onto the posteromedial surface. A transverse line (Romer 1922) traverses the lateral surface of the postiliac process from an origin above the supra-acetabular buttress but does not approach the ventral surface. In QM F 37431 the line is barely discernible but may be represented by two low ridges that diverge from the base of the iliac neck, while a third and fourth ridge traverse the upper edge of the postiliac process from the base of the dorsal iliac process. In QM F 34280 and QM F 36955 the line is a pronounced swelling of the lateroventral surface of the postiliac process. In the former specimen it continues across the neck of the ilium to the anterior border of that bone, at least to the level of the acetabulum. On the medial surface of QM F 37431 a marked facet for the sacral rib occupies two-thirds of the width of the iliac neck (Text-fig. 11D); this facet is not discernible in the other specimens. Beneath the facet a broad ridge divides the medial surface of the ilium. Running vertically beside this ridge, adjacent to its posterior border, is a deep groove that may have been enclosed in the intact specimen. The pelvis is incomplete in this area and obviously abraded.

Although not fully preserved, the acetabulum in QM F 37431 appears to have been more extensive in area, especially posteriorly and ventrally, than in other early tetrapods. A supra-acetabular notch (Smithson 1985 = posterior tongue-like projection of Coates 1996) partially separates the smaller dorsal part of the acetabulum from the more extensive ventral part. The posterior border of the acetabulum is separated from the posterior edge of the ilium by a broad strip of perichondral bone. There is no post-acetabular buttress. The most ventral part of the pelvis preserved retains the same thickness as the neck of the ilium, and curves laterally, perhaps representing the lower edge of the acetabular rim.

A single ossification in the pelvis is found in *Acanthostega*, *Ichthyostega*, *Whatcheeria* and *Eoherpeton*, while a wide separation between the posterior border of the ilium and the acetabular border is found in *Acanthostega* and *Whatcheeria*. The broad iliac neck in *Ossinodus* is found in *Elginerpeton* (Ahlberg 1998) but not *Acanthostega* (Coates 1996). An iliac neck positioned above the acetabulum is characteristic of *Ichthyostega* (Jarvik 1996) and *Whatcheeria* (Lombard and Bolt 1995) but not *Acanthostega*. The iliac blade is reduced in both crown groups but remains fan-shaped in QM F 36955, *Eogyrinus* (Panchen 1972), *Pederpes* and *Whatcheeria*, although in these three taxa it is smaller than in *Acanthostega*. In the anthracosaurs *Proterogyrinus* (Holmes 1984) and *Archeria* (Romer 1957) the dorsal iliac process is almost in the same longitudinal plane as the postiliac process, whereas in *Ossinodus* and other early tetrapods the blade is offset medially in relation to the postiliac process. *Ossinodus* shares with other stem tetrapods like *Acanthostega* and *Tulerpeton* (Coates 1996) a transverse line on the postiliac process that does not approach the ventral border of that process. The converse is found in embolomeres and *Caerorhachis* (Ruta *et al.* 2002) in which the distal part of the line follows the ventral edge of the postiliac process.

Femur. Detail of the femur is best seen on QM F 37415 (Text-figs 10C, 12G–L). As in most early tetrapods the adductor blade is prominent and elongate and separated from the femoral head by a groove (Coates 1996). This separation reflects a greater ossification of the femoral head, as Coates surmised. Distally the adductor blade of *Ossinodus* continues to approximately half-way along the length of the femur, an elongation exceeded only by *Acanthostega* (Coates 1996) and *Tulerpeton* (Lebedev and Coates 1995). It is extended by an elongate adductor crest, which ends on the broad ridge separating popliteal and fibula fossae, just short of the distal end of the fully ossified bone. In QM F 37415 the proximal end of the adductor blade, which forms the internal trochanter, has a deep pit in a similar position to one reported in *Acanthostega* (Coates 1996). Distal to this the remainder of the adductor blade (representing trochanter 4) is marked by a slight thickening proximally, while the most distal part of the ridge is markedly thickened. In the larger specimen (QM F 37432, Text-fig. 12A–D) this expansion marks the junction of a low ridge on the posterior face of the adductor blade, with the apex of the blade. A similar ridge is present in *Acanthostega* (Coates 1996).

Little of the fluting on the posterior surface of the adductor blade found in *Tulerpeton* (Lebedev and Coates 1995) is



TEXT-FIG. 12. Femur. A-F, right femur QM F 37432 in A extensor, B posterior, C flexor, D anterior, E distal and F proximal views. G-L, left femur QM F 37415 in G extensor, H posterior, I flexor, J anterior, K distal and L proximal views. Scale bars represent 10 mm.

present on either specimen. Marked fluting traverses the distal end of the adductor crest in QM F 37415 and a number of ridges mark a muscle insertion on the posterior wall of the intercondylar fossa. These flutings may have been abraded from the surface of QM F 37415. This specimen shows an additional muscle insertion in the form of a pronounced ridge at the posterodistal corner of the flexor surface.

The *Ossinodus* femora differ from *Acanthostega* in lack of torsion of the tibial facet in relation to the head of the femur. In the *Ossinodus* femora and in other early tetrapods these lie almost in the same plane, whereas in *Acanthostega* the tibial facet is rotated ventrally so that in distal view the articular facets for the tibia and fibula lie at 60 degrees to one another (Coates 1996); in other early tetrapods the long axes of the facets are more nearly in line.

A prominent adductor crest, which terminates between the popliteal and fibula fossae, is present in all early tetrapods and most reptiles (Romer 1922). In the few temnospondyls where the femur is described [e.g. *Eryops* (Cope and Mathew 1915), *Mastodonsaurus* (Schoch 1999), *Parotosuchus* (Howie 1970) and *Ecolsonia* (Berman *et al.* 1985)] the adductor crest is often less pronounced distally and bifurcates, sending a ridge along the anteroventral side of the femur to terminate at the ventral margin of the tibial facet. This second ridge may be a derived feature of temnospondyls but unfortunately femora of the earliest described temnospondyls, those from East Kirkton, are not preserved on the ventral surface (Milner and Sequeira 1994).

The femur is closest in overall morphology to *Tulerpeton* (Lebedev and Coates 1995) and to the femur from the Horton Bluff Formation (YPM-PU 20103, Clack and Carroll 2000).

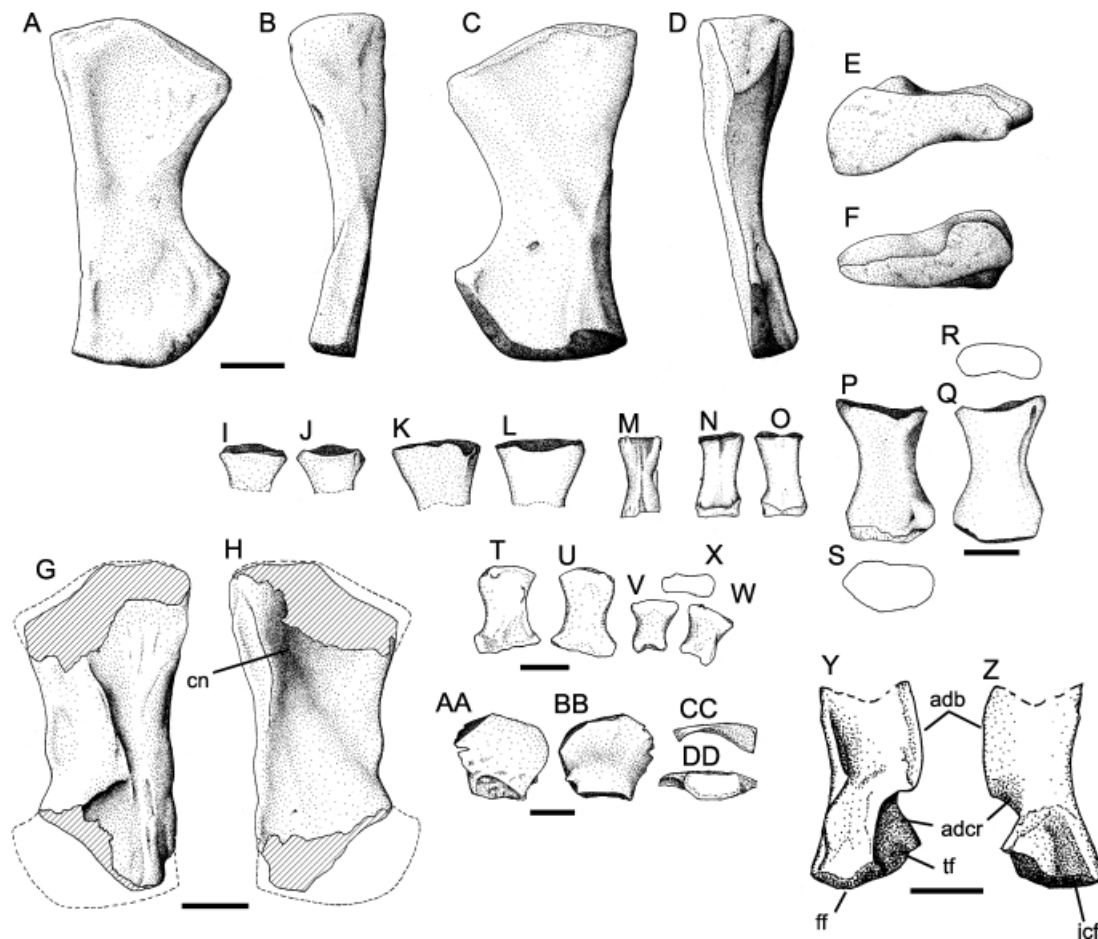
The third *Ossinodus* femur (QM F 37416, Text-fig. 13Y–Z) is one-quarter as large as the others. It is incomplete proximally, lacking the internal trochanter and the femoral head and has a more extensive adductor blade than the other specimens. This blade not only extends further away from the body of the femur but also more distally and has a less well-defined fourth trochanter. The posterior surface of the adductor blade is grooved along its length just below the apex. On the dorsal surface the distal part of the bone is depressed, leaving a transverse ridge. This ridge appeared to be an artefact but may be a real feature of the bone as it appears also in one Horton Bluff femur (YPM-PU 20103).

Tibia. Of the two tibiae, QM F 37406 (Text-fig. 13A–F) is the better preserved. It appears undistorted in shape but abraded on the flexor and extensor surfaces. The bone is dorsoventrally flattened with a markedly concave posterior border and no evidence of torsion between the proximal and distal ends. On the extensor surface, the cnemial crest is poorly developed although possibly eroded as it is more pronounced in QM F 37404 (Text-fig. 13G–H). An anterodistally elongate rugose area central to the flexor surface, reported in *Tulerpeton* (Lebedev and Coates 1995), is represented by the junction of a Y-shaped ridge system which originates near the two proximal extremities of the tibia, with the tail of the Y continuing as a prominent thickening of the anterior distal side of the flexor surface and terminating at the facet for articulation with the tibiale. Both anterior and posterior surfaces of the tibia are drawn out into low flanges. The distal articulating surface of the tibia (Text-fig. 13F) is L-shaped with the short, external branch of the L forming the articulation for the tibiale.

The tibia is more dorsoventrally flattened overall than in other early tetrapods except *Whatcheeria* (Lombard and Bolt 1995) and *Pederpes* (Clack 2002a). Otherwise it most closely resembles tibiae of *Tulerpeton* (Lebedev and Coates 1995), *Proterogyrinus* (Holmes 1984) and *Eoherpeton* (Smithson 1985). Broad, flat, hind-limb epipodials are characteristic of pre-crown group tetrapods. As in *Acanthostega* there is no evident torsion between the articular areas of the proximal and distal ends, but unlike that taxon and in common with more derived tetrapods, the posterior side of the tibia is concave. Both anterior and posterior surfaces of the tibia are drawn out into low flanges that are slight compared with those in *Westlothiana* (Smithson *et al.* 1994) or the posterior flange in *Crassigyrinus* (Panchen and Smithson 1990), their height being closer to the posterior flange of *Tulerpeton* (Lebedev and Coates 1996). The L-shaped distal articulating surface of the tibia is shared with *Tulerpeton* (Text-fig. 13F).

Fibulare? QM F 37436 (Text-fig. 13AA–DD) may represent a fibulare. The bone is roughly pentagonal, is flattened on one surface, recurved on the opposite. The flattened side has a series of irregular pits resembling weathered ornament. Of the five faces, four are flattened and unfinished where they articulated with the presumed fibula and carpals, while one tapers to a finished ridge. One unfinished edge is much deeper than the others. This element is unlike the fibulare found in *Acanthostega* (Coates 1996) but is closer to *Tulerpeton* (Lebedev and Coates 1995) and *Proterogyrinus* (Holmes 1984).

Metapodials and phalanges. Three larger specimens (QM F 37438, Text-fig. 13T–U; QM F 34283, Text-fig. 13P–S; QM F 36916, Text-fig. 13K–L) may represent metapodials. They are flattened, slightly expanded proximally and distally, and a little concave on one surface. The most complete (QM F 37438) has a rugose scar close to one end and one side is drawn out into a marked ridge in the same position as the double ridges in *Ichthyostega* (Jarvik 1996, fig. 52). Two of the metapodials, (QM F 34283, Text-fig. 13P–Q; QM F 37438, Text-fig. 13T–U) are bilaterally and proximodistally asymmetrical, a morphology associated with pentadactyly (Clack 2002a). The best-preserved

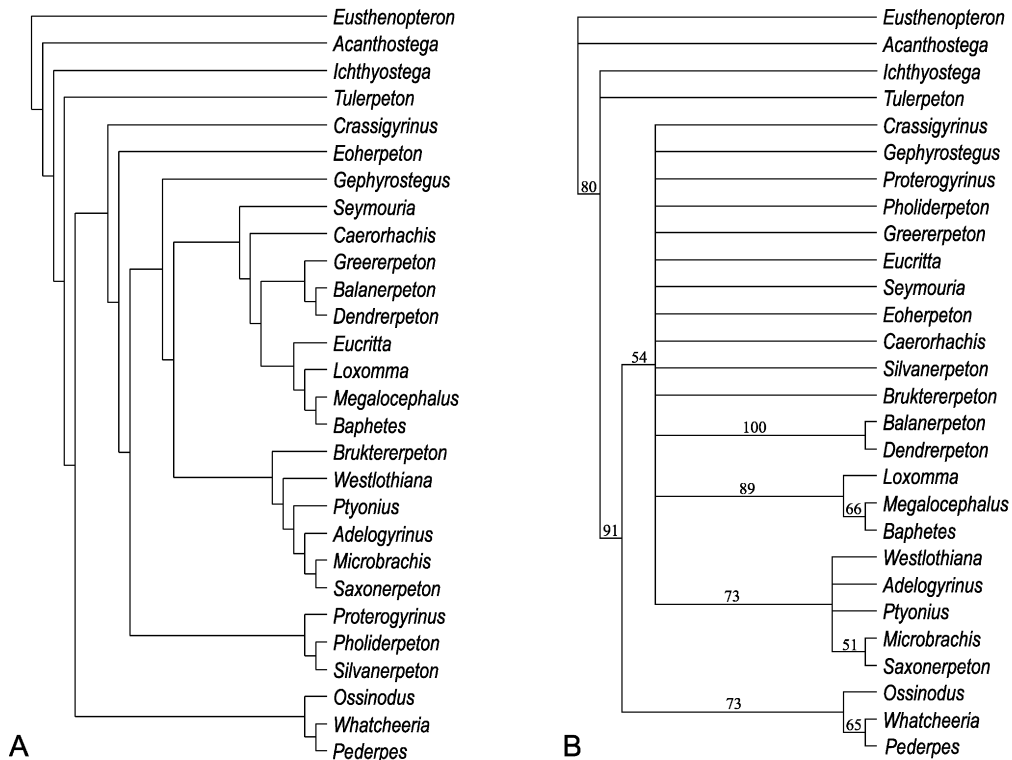


TEXT-FIG. 13. Hind limb and phalanges. A–F, left tibia QM F 37406 in A extensor, B anterior, C flexor, D posterior, E proximal and F distal views. G–H, left tibia QM F 37404 in G flexor and H extensor views. I–X, metapodials and phalanges: I–J, QM F 36935; K–L, QM F 36916; M, QM F 36912; N–O, QM F 37437; P–S, QM F 34283; T–U, QM F 37438; V–X, QM F 37447. Y–Z, femur QM F 37416 in Y flexor and Z extensor views. AA–DD, ?fibulare QM F 37436. Scale bars represent 10 mm.

probable phalanx, QM F 37437 (Text-fig. 13N–O) is also a little concave on one surface and the proximal and distal ends of this surface are notched. A tiny knob projects from one of the lateral surfaces. QM F 36912 (Text-fig. 13M) is more waisted and has a groove running between the proximal and distal ends.

PHYLOGENETIC ANALYSIS

As the material of *Ossinodus* is, as yet, fragmentary, this analysis was performed in order to indicate its probable phylogenetic position among early tetrapods, rather than to test relationships among the early tetrapods in general. Thus, more derived members of the crown Tetrapoda were excluded. We have used a data matrix of 141 characters and 26 taxa provided by Clack (2002a), deleted two uninformative characters (51 and 64), added two taxa, *Tulerpeton* (Lebedev and Coates 1995) and *Ossinodus*, a cranial character (142) and two postcranial characters (143, 144). The added characters were not placed in the logical position in the list to avoid confusion and for the same reason characters 51 and 64 are left in the list



TEXT-FIG. 14. Phylogenetic hypotheses of *Ossinodus pueri* and other early tetrapods. A, single tree recovered by PAUP 4.0b8 from a heuristic search of 27 taxa and 14 characters. B, bootstrap values for the analysis in A.

(although not used in the analysis). *Tulerpeton* was included as an early tetrapod with a well-preserved postcranial skeleton that could be compared with *Ossinodus*. Data were entered into a NEXUS Data Editor (Page 2001), analysed using PAUP 4.0b8 (Swofford 2000), and printed using Treeview (Page 1996). Characters were unordered and of equal weight.

The matrix was analysed using the heuristic search algorithm and deltran optimisation, resulting in a single most parsimonious tree of 521 steps (C.I. = 0.3724; R.I. = 0.5557) (Text-fig. 14A). In it *Ossinodus* forms the sister taxon to *Whatcheeria* + *Pederpes*, the three taxa forming a clade that is sister to the other Carboniferous tetrapods. The Devonian tetrapods are stem taxa to this clade with *Tulerpeton* the closest stem taxon. A bootstrap analysis (Text-fig. 14B) showed reasonably strong support for the separation of the Carboniferous tetrapods into two clades, one consisting of *Ossinodus*, *Whatcheeria* and *Pederpes* and the other of the remaining Carboniferous tetrapods, but weak support for branches within these two clades. In this analysis, *Tulerpeton* forms a trichotomy with *Ichthyostega* and all of the more crownward tetrapods.

When *Tulerpeton* was deleted from the matrix ten most parsimonious trees resulted. Of these, five showed *Ossinodus* as the sister group to *Whatcheeria* and *Pederpes*, while five showed *Ossinodus* as the stem of *Whatcheeria* plus *Pederpes* and the other Carboniferous tetrapods. In the strict consensus tree a trichotomy was formed by *Ossinodus*, *Whatcheeria* + *Pederpes*, and the remaining Carboniferous tetrapods.

Excluding all postcranial characters from the analysis did not change the relationship between *Ossinodus*, *Whatcheeria* and *Pederpes*, although it changed the overall topology of the tree. The inclusion of *Tulerpeton* introduced stability to the analysis and indicates that it may be a stem tetrapod rather than a reptiliomorph as suggested by Lebedev and Coates (1995).

DISCUSSION

The fauna from the Middle Paddock site in the Ducabrook Formation falls towards the end of period of some 30 myr known as Romer's Gap (Coates and Clack 1995) in which tetrapods are almost unknown. In this gap two events fundamental to early tetrapod history took place: at least some tetrapods became terrestrial, and the stem tetrapods gave rise to the Amphibia and Amniota. Before the gap, the Devonian tetrapods appear to have been primarily aquatic, while at East Kirkton in Scotland during the mid Viséan at least some of the tetrapods were terrestrial. A probable stem amniote with a terrestrially adapted postcranial skeleton, *Casineria* from the Cheese Bay Shrimp Bed, Scotland (Paton *et al.* 1999), is just younger than *Ossinodus* while the first lepospondyls are known from the Wardie Shales, Scotland, at the same time (Wellstead 1982) (Text-fig. 3). Hence *Ossinodus* is important not only as the first tetrapod from the Lower Carboniferous of Gondwana, but also as a stem tetrapod from towards the end of Romer's Gap. Such a stem tetrapod could provide phylogenetic evidence to help unravel relationships within the early tetrapods and morphological evidence of the beginnings of terrestriality.

Phylogenetic analysis. The phylogenetic analysis above was carried out to give some indication of the closest relatives of *Ossinodus* and its position among early tetrapods. The skeleton is far from complete and the analysis included other incomplete material, especially *Tulerpeton*, which has little cranial material, and the baphetids, which have little postcranial. The results are not particularly robust but nevertheless the relationships of most taxa are not unexpected. *Acanthostega* and *Ichthyostega* remain on the tetrapod stem. Joining them is *Tulerpeton*, previously a reptiliomorph, the clade consisting of *Whatcheeria*, *Ossinodus* and *Pederpes*, *Crassigyrinus* and, unexpectedly, *Eoherpeton*. The analysis has thus broken up the anthracosaurs, further removing *Gephyrostegus* and *Seymouria*, which becomes a stem amphibian. *Tulerpeton* was considered a reptiliomorph by Lebedev and Coates (1995) and Coates (1996), but a stem tetrapod (Ahlberg and Clack 1998; Clack and Ahlberg in press) in analyses that addressed mandibular characters only. No other computer assisted analysis has considered its position, presumably because most analyses rely on cranial rather than postcranial characters. Ahlberg and Milner (1994) placed *Tulerpeton* between *Ichthyostega* and *Crassigyrinus* on the tetrapod stem in a similar position to the result obtained from our analysis.

The Horton Bluff material (Clack and Carroll 2000) indicates that some of the tetrapod clades present in later Carboniferous deposits were established by the mid Tournaisian. These include the colosteids, represented by a humerus comparable with *Greererpeton*, and a humerus, femora and interclavicles that appear to be reptiliomorph (Clack and Carroll 2000). The presence of *Ossinodus* in the mid Viséan of Australia and of a clade of *Ossinodus*-like tetrapods spanning the Early Carboniferous tropics suggests that some of the reptiliomorph material from Horton Bluff may belong to this clade also.

Habitus of Ossinodus. The overwhelming evidence from both *Ichthyostega* and *Acanthostega* of an aquatic habitat for Devonian tetrapods (e.g. Coates and Clack 1995) leads to speculation as to when tetrapods became primarily terrestrial. Certainly the Brigantian fauna from East Kirkton included a variety of terrestrial tetrapods (e.g. Smithson *et al.* 1994) and *Casineria* from the Scottish Asbian was terrestrial (Paton *et al.* 1999) so that tetrapods must have developed skeletons able to support them out of water in the intervening period of some 30 myr. The single articulated tetrapod from the Tournaisian, *Pederpes*, is the first to show the beginnings of terrestrial locomotion. In particular, *Pederpes* has a reduced digital number, with a pes that is turned forward as indicated by asymmetrical metatarsals (Clack 2002a). *Ossinodus* falls towards the end of this time gap and although the material is incomplete and not articulated its possible habitat should be considered.

Ossinodus cranial material is not helpful in this respect and no elements that could be interpreted as grooved ceratobranchials associated with gill breathing have been found. Additionally there is no evidence for the postbranchial lamina on the cleithrum associated with gill breathing (Coates and Clack 1991). The lack of preserved intercentra and pleurocentra could reflect their poor ossification and hence a non-supporting function. However poorly ossified centra are also found in baphetids (Milner and Lindsay 1998), *Crassigyrinus* (Panchen 1985) and *Greererpeton* (Godfrey 1989), and this state may be plesiomorphic for tetrapods (Milner and Lindsay 1998). Coates (1996) listed several features of the pelvis in

Acanthostega as supporting fully aquatic locomotion. One of these, a posteriorly displaced iliac neck, is not present in the *Ossinodus* pelvis, while the other features are not preserved. Clack (2002a) proposed that the asymmetrical metatarsals found in early tetrapods, such as *Pederpes*, *Greererpeton* and *Proterogyrinus*, are indicative of a realignment of the hind limb from the paddle-like position in Devonian tetrapods to an anteriorly directed stance associated with walking. The two asymmetrical metapodials in *Ossinodus* suggest that its locomotion was similar. On the other hand, two *Ossinodus* postcranial elements do suggest hind-limb assisted locomotion in water.

The Horton Bluff femur (YPM-PU 20103) is closely comparable with that in *Ossinodus*, and also *Tulerpeton* (Lebedev and Coates 1995), in the structure of its elongate adductor blade and crest. The internal trochanter on the proximal end of the adductor blade is separated from the femoral head by a notch (deepest in *Tulerpeton*) and the elongate fourth trochanter is strongly delineated from the adductor crest. The femur of *Whatcheeria* (Lombard and Bolt 1995) is similar in the elongate adductor blade and distal position of the adductor crest but the proximal end is incomplete so that direct comparison of that area is not possible. In *Pederpes* the adductor blade is elongate but not separated from the head of the femur by a notch (Clack 2002a). The trochanters are less distinct in the Horton Bluff femur, and Lebedev and Coates (1995) tentatively interpreted this specimen as being associated with the less differentiated musculature of a powerful swimmer. The small *Ossinodus* femur (QMF 37416) is presumably from an immature individual. It has less well-defined trochanters than the larger specimens and a more elongate blade with a more distal adductor crest. It is thus closest in morphology to the Horton Bluff femur. It is possible that juvenile specimens of *Ossinodus* were more aquatic than adults and that the shorter adductor blade with more robust trochanters found in the femora of larger specimens indicates an enhanced ability to move on land. Finally, the tibia of *Ossinodus* is a broad, flattened, relatively un-waisted element similar to that in *Whatcheeria* (Lombard and Bolt 1995) although considerably better ossified than it is in *Acanthostega* (Coates 1996). Broad, flattened hind limb epipodials were considered by Coates (1996) to function as paddles or flippers, especially when associated with an extensively bladed femur. The preserved hind limb elements found in large specimens of *Ossinodus* suggest that the taxon had progressed beyond the fully aquatic locomotion hypothesised for *Acanthostega*, but the small femur may indicate that small specimens were restricted to an aquatic lifestyle.

Palaeobiogeography. Until the reports from Nova Scotia (Clack and Carroll 2000) and the description of *Pederpes* (Clack 2002a), Tournaisian tetrapods were unknown, the earliest Carboniferous remains being from the mid Viséan of Euramerica. Late Devonian tetrapods are well known from Laurentia and were present during the Late Devonian in the Australian region as evidenced by trackways (Warren and Wakefield 1972) and a mandible (Campbell and Bell 1977), but otherwise no Australian tetrapods are known until the latest Permian (Warren 1997). Possibly the tetrapods from the Australian Devonian were forced to the north during the Tournaisian through advancing glaciation, leaving a remnant population in the mid Viséan of Queensland, before becoming extinct in Gondwana. This is a likely scenario as Australia drifted south. On the other hand some fish from the Middle Paddock site could represent invasions from elsewhere. The lungfish *Ctenodus* sp. nov. (Turner *et al.* 1999) is congeneric with *Ctenodus* from the Lower Carboniferous Calciferous Sandstone Series of Scotland, rather than sharing a close relationship with the more primitive *Delatitia* (Long and Campbell 1985) from the Tournaisian of Victoria. Similarly, *Strepsodus* from Middle Paddock is probably the earliest east Gondwanan member of the Rhizodontidae, a Laurentian taxon (Johanson *et al.* 2000). Other east Gondwanan rhizodonts such as *Barameda* from the Tournaisian of Victoria (Long 1989) and *Gooloogongia* from the Frasnian of New South Wales (Johanson and Ahlberg 1998) are more primitive, endemic taxa (Johanson *et al.* 2000). In contrast, *Gyracanthides* is a Gondwanan taxon that seems to have dispersed to Laurentia in the Devonian, eventually giving rise to *Gyracanthus* (Jones *et al.* 2000). The fish macrofauna are thus a mix of Laurentian taxa that appeared post Devonian and the Gondwanan *Gyracanthides*. The tetrapod, *Ossinodus*, is most closely related to *Whatcheeria* from the Upper Viséan of Iowa and *Pederpes* from Scotland, and could also be close to some of the Tournaisian material from Nova Scotia. These relatives are all from Laurentia, so present evidence suggests the origin of the Whatcheeriidae was northern, with *Ossinodus* dispersing to Gondwana with *Strepsodus* and *Ctenodus*. This hypothesis must now be tested with further

analysis of tetrapod, rhizodont and lungfish taxa in the Famennian–Viséan timespan. This picture could be clarified with the discovery of more complete cranial material of tetrapods from the Australian Devonian and Lower Carboniferous. Such a scenario supports a connection rather than an oceanic barrier between Laurentia and Gondwana in the Viséan (Jones *et al.* 2000).

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APPENDIX

Abbreviations

a, articular; acb, acetabulum; adb, adductor blade; adcr, adductor crest; c, callus; cf, coracoid foramen; cgr, groove on anterior face of clavicle; cl.fac, facet for clavicle; clei.f, facet for cleithrum; ch, choana; cn, cnemial crest; dip, dorsal iliac process; dmr, dorsomesial ridge; ect, ectopterygoid; f, frontal; ff, fibular facet; ffo, fibular fossa; free, free margin of supratemporal and tabular; for, foramen; ftt, fourth trochanter; g, groove; gl, glenoid fossa; icf, intercondylar fossa; inf, infolding of tooth enamel; int, internal trochanter; it, intertemporal; l. sc, lamina suprascapularis; mx, maxilla; nar, naris; orb, margin of orbit; pa, popliteal area; par, parietal; pip, posterior iliac process; pmx, premaxilla; pof, postfrontal; pp, postparietal; pvr, proximovenral ridge; q, quadrate; qj, quadratojugal; r, ridge; sab, supra-acetabular buttress; san, supra-acetabular notch; sb, scapular blade; scgr, groove on scapular for articulation with cleithrum; sen, sensory canal; sgb, supraglenoid buttress; sgf, supraglenoid foramen; s.j, suture with jugal; s.la/ju, suture with lacrimal/jugal; s.na, suture with nasal; s.mx, suture with maxilla; snc, supraneural canal; s.p, sensory pit; s.pal, suture with palatine; s.pt, suture with the pterygoid; s.q, suture with quadrate; sq.e, squamosal embayment; sqf, facet for squamosal; ssr, site of sacral rib attachment; st, supratemporal; stf, facet for supratemporal; stv, margin of subtemporal vacuity; sur, surangular; t, tabular; tf, tibial facet; tl, transverse line; tu, tusk; tu.p, tusk pit; vmr, ventromesial ridge; vrc, ventral radial crest.

List of characters and character states used in the phylogenetic analysis

Characters 1–141 are from Clack (2002a), character 142 is new, characters 143 and 144 are from Lebedev and Coates (1995).

Skull roof and braincase

1. Anterior tectal (accessory dermal bone associated with naris having surface ornament and no lateral line canal): (0) present; (1) absent.
2. Anterior tectal: (0) narial opening ventral to it; (1) narial opening posterior to it.
3. Basioccipital: (0) indistinguishable from exoccipitals; (1) separated by suture.
4. Basioccipital: (0) ventrally exposed portion longer than wide; (1) ventrally exposed portion shorter than wide.
5. Basioccipital: (0) condyle present; (1) notochordal.
6. Basipterygoid junction: (0) basipterygoid process fits into socket recessed into epipterygoid; (1) pterygoid/epipterygoid forms narrow bar and clasps basipterygoid process fore and aft.
7. Ectopterygoid reaches adductor fossa: (0) no; (1) yes.
8. Exoccipitals meet skull table: (0) no; (1) yes.
9. Exoccipital contributes to condyle: (0) no; (1) yes.
10. Intertemporal: (0) present; (1) absent.
11. Intertemporal lateral edge: (0) not interdigitating with cheek; (1) interdigitates with cheek.
12. Jugal deep below orbit (vs. narrow process): (0) 50 per cent or more of orbit diameter; (1) less than 50 per cent orbit diameter.
13. Jugal alary process on palate: (0) no; (1) yes.
14. Lacrimal contributes to narial margin: (0) no, excluded by anterior tectal; (1) yes; (2) no, excluded by nasal/maxillary or prefrontal/maxillary suture.
15. Lacrimal reaches orbit margin (= prefrontal/jugal suture): (0) yes; (1) no.
16. Maxilla meets quadratojugal: (0) yes; (1) no.
17. Maxilla sutures to vomer: (0) no; (1) yes.
18. Maxilla external contact with premaxilla: (0) narrow contact point, not interdigitated; (1) interdigitating suture.
19. Median rostral (=internasal): (0) mosaic; (1) paired; (2) single; (3) absent.
20. Nasals contribute to narial margin: (0) no; (1) yes.
21. Opisthotic paroccipital process ossified and contacts tabular below post-temporal fossa: (0) no; (1) yes; (2) paroccipital process absent.
22. Parietal meets tabular: (0) no; (1) yes.

23. Postorbital suture to skull table (intertemporal or supratemporal) interdigitating vs. smooth: (0) smooth; (1) interdigitating.
24. Postparietal: (0) longer than wide; (1) approximately square or pentagonal; (2) wider than long.
25. Postparietal occipital exposure: (0) absent; (1) present.
26. Prefrontal/postfrontal suture: (0) anterior half of orbit; (1) middle or posterior half of orbit; (2) absent.
27. Premaxilla posterodorsal process onto snout: (0) absent; (1) present.
28. Premaxilla forms part of choanal margin: (0) broadly; (1) point; (2) not, excluded by vomer.
29. Preopercular: (0) present; (1) absent.
30. Squamosal posterodorsal margin shape: (0) convex; (1) sigmoid or approximately straight; (2) entirely concave.
31. Squamosal contact with tabular: (0) smooth; (1) interdigitating; (2) absent.
32. Squamosal suture with supratemporal position: (0) at apex of temporal embayment; (1) dorsal to apex; (2) ventral to apex.
33. Supratemporal forms part of skull margin posteriorly: (0) no; (1) yes.
34. Supratemporal interdigitating suture with squamosal: (0) absent; (1) present.
35. Tabular lateral horn: (0) absent; (1) button; (2) blade.
36. Tabular emarginated lateral margin: (0) no; (1) yes.
37. Tabular facets/butresses for braincase ventrally: (0) no; (1) single; (2) double.
38. Tabular occipital exposure: (0) absent; (1) extends as far ventrally as does postparietal; (2) extends further ventrally than does postparietal.

Palate

39. Palatine/ectopterygoid exposure: (0) more or less confined to tooth row; (1) broad mesial exposure additional to tooth row.
40. Pterygoids: (0) separate in the midline; (1) meet in the midline anterior to cultriform process.
41. Pterygoids flank parasphenoid: (0) yes; (1) no.
42. Pterygoid quadrate ramus margin in adductor fossa: (0) concave; (1) with some convex component.
43. Pterygoid junction with squamosal along cheek margin: (0) unsutured; (1) half and half; (2) sutured entirely.
44. Parasphenoid: (0) grooved ventrally about half of length; (1) narrow, V-shaped cultriform process along whole length; (2) flat and more or less broad.
45. Parasphenoid depression in body: (0) absent; (1) single median; (2) double.
46. Parasphenoid posterolateral wings: (0) absent; (1) present.
47. Parasphenoid wings: (0) separate; (1) joined by web of bone.
48. Parasphenoid sutures to vomers: (0) yes; (1) no.
49. Parasphenoid carotid grooves: (0) curve around basiptyergoid process; (1) lie posteromedial to basiptyergoid process.
50. Parasphenoid ventral cranial fissure: (0) not sutured; (1) sutured but traceable; (2) eliminated.
51. Vomers separated by parasphenoid: (0) greater than half their length; (1) less than half their length.
52. Vomers separated by pterygoids: (0) for over half their length; (1) less than half their length; (2) not separated.
53. Vomers: (0) as broad as long or broader; (1) about twice as long as broad or longer.

Dentition

54. Ectopterygoid tusk pairs: (0) present; (1) absent.
55. Ectopterygoid row (3+) of smaller teeth: (0) present; (1) absent.
56. Ectopterygoid denticle row: (0) present; (1) absent.
57. Ectopterygoid/palatine shagreen field: (0) absent; (1) present.
58. Maxilla tooth number: (0) more than 40; (1) 30–40; (2) less than 30.
59. Palatine tusk pairs: (0) present; (1) absent.
60. Palatine row of smaller teeth: (0) present; (1) absent.
61. Palatine denticle row: (0) present; (1) absent.
62. Parasphenoid shagreen field: (0) present; (1) absent.
63. Parasphenoid shagreen field: (0) anterior and posterior to basal articulation; (1) posterior to basal articulation only; (2) anterior to basal articulation only.
64. Pterygoid shagreen: (0) dense; (1) a few discontinuous patches or absent.
65. Premaxillary teeth with conspicuous peak: (0) absent; (1) present.
66. Premaxillary tooth number: (0) more than 15; (1) 10–14; (2) fewer than 10.
67. Vomer tusk pairs: (0) present; (1) absent.
68. Vomerine tusk pairs noticeably smaller than other palatal tusk pairs: (0) no; (1) yes.
69. Vomer anterior wall forming posterior margin of palatal fossa bears tooth row meeting in midline: (0) yes; (1) no.
70. Vomerine row of small teeth: (0) present; (1) absent.

- 71. Vomerine shagreen field: (0) absent; (1) present.
- 72. Vomerine denticle row lateral to tooth row: (0) present; (1) absent.
- 73. Upper marginal teeth number: (0) greater than lower; (1) same as lower; (2) smaller than lower.
- 74. Caniniform teeth (about twice the size of neighbouring teeth) on maxilla: (0) absent; (1) present.

Mandibular characters

- 75. Angular mesial lamina suture with prearticular: (0) absent; (1) present.
- 76. Coronoid dentition: (0) fang pair alone; (1) several small teeth and larger fangs in same row; (2) row of small teeth only; (3) absent.
- 77. Coronoid shagreen: (0) absent; (1) present.
- 78. Mandibular sensory canal: (0) present; (1) absent.
- 79. Mandibular canal exposure: (0) entirely enclosed; (1) mostly enclosed; (2) mostly or entirely open.
- 80. Oral sulcus of mandibular canal: (0) absent; (1) present.
- 81. Meckelian bone visible between prearticular and infradentary series: (0) present; (1) absent.
- 82. Parasymphysial tooth plate: (0) present; (1) absent.
- 83. Parasymphysial plate tusk-pair (distinct from other teeth): (0) absent; (1) present.
- 84. Parasymphysial accessory teeth on dentary: (0) present; (1) absent.
- 85. Prearticular denticulated field: (0) defined edges; (1) scattered patches; (2) absent.
- 86. Surangular crest: (0) absent; (1) present.

General skull characters

- 87. Anterior palatal fenestra: (0) single; (1) double; (2) absent.
- 88. Interpterygoid vacuities: (0) border involves vomer; (1) border does not involve vomer.
- 89. Interpterygoid vacuities: (0) absent; (1) at least two times longer than wide; (2) less than two times longer than wide.
- 90. Naris position: (0) ventral rim closer to jaw margin than height of naris; (1) distance to jaw margin similar to or greater than height of naris.
- 91. Naris shape: (0) slit-like; (1) round or oval; (2) upper margin ragged.
- 92. Naris shape: (0) ventrally facing; (1) dorsolaterally facing.
- 93. Naris size relative to choana: (0) less than 50 per cent; (1) same or larger.
- 94. Orbit shape: (0) round or oval; (1) angle at anteroventral corner; (2) angle at posteroventral corner; (3) emarginated margin including jugal, lacrimal and prefrontal.
- 95. Orbit position re snout/parietal outline: (0) centre closer to front than rear; (1) centre near middle; (2) centre closer to rear than front.
- 96. Orbit position re snout/quadrates outline: (0) centre closer to front than rear; (1) centre near middle; (2) centre closer to rear than front.
- 97. Suspensorium proportions: (0) quadrates-anterior margin of temporal embayment about equal to maximum orbit width (discounting any anterior extensions); (1) quadrates-anterior margin of temporal embayment less than maximum orbit width; (2) quadrates-anterior margin of temporal embayment more than maximum orbit width.
- 98. Skull table/cheek junction: (0) smooth profile; (1) square/abrupt profile.
- 99. Skull table shape: (0) longer than broad; (1) approximately square; (2) shorter than broad.
- 100. Ornament character: (0) fairly regular pit and ridge with star-burst pattern at regions of growth; (1) irregular but deep; (2) irregular but shallow; (3) absent or almost absent.

Postcranial

- 101. Centra: (0) rhachitomous; (1) gastrocentrous; (2) holospondylous.
- 102. Centrum (sacral): (0) distinguishable by size or shape from pre- and postsacrals; (1) not so distinguishable.
- 103. Clavicles meet anteriorly: (0) present; (1) absent.
- 104. Cleithrum: (0) co-ossified with scapulocoracoid; (1) separate.
- 105. Cleithrum: (0) smoothly broadening to spatulate dorsal end; (1) distal expansion marked from narrow stem by notch or process or decrease in thickness; (2) cleithrum end simply tapered.
- 106. Cleithrum cross-section at mid section: (0) flattened oval; (1) complex; (2) single concave face.
- 107. Femur: (0) shorter than humerus; (1) same length as humerus; (2) longer than humerus.
- 108. Femur internal trochanter: (0) separate from head; (1) confluent with head.
- 109. Femur adductor blade: (0) distinguished distally from shaft by angle or notch; (1) fades into shaft distally.

110. Femur adductor crest: (0) extends more than half way down shaft; (1) extends half way or less down shaft.
111. Humerus: (0) ends more or less untorted; (1) ends offset by more than 60 degrees.
112. Humerus: (0) L-shaped; (1) waisted but no shaft; (2) humerus with distinct and slender shaft.
113. Humerus accessory foramina: (0) present; (1) absent.
114. Humerus latissimus dorsi process: (0) part of ridge; (1) distinct but low process; (2) spike.
115. Humerus deltopectoral crest position compared with latissimus dorsi process: (0) more distal than head; (1) equidistant from head.
116. Humerus latissimus dorsi process position relative to ectepicondyle: (0) offset anteriorly; (1) in line.
117. Humerus anterior margin: (0) smooth finished bone convex margin; (1) anterior keel with finished margin; (2) cartilage-finished; (3) smooth concave margin.
118. Humerus radial facet position: (0) distal and terminal; (1) anteroventral; (2) ventral.
119. Humerus radial/ulnar facets: (0) confluent; (1) separated by perichondral strip of bone.
120. Iliac blades: (0) posterior process plus dorsal blade; (1) posterior process only.
121. Interclavicle body shape (distinguished from parasternal process): (0) rhomboid, longer than broad, but posterior half longer than anterior; (1) rhomboid, posterior half not longer than anterior; (2) broader than long.
122. Interclavicle parasternal process shape: (0) absent or tapering; (1) parallel sided.
123. Neural arch ossification: (0) paired in adult; (1) single in adult.
124. Neural arch (sacral): (0) distinguishable by morphology of spine; (1) not so distinguishable.
125. Pelvis: (0) single ossification; (1) at least two ossifications per side.
126. Pelvis obturator foramina: (0) multiple; (1) single or absent.
127. Radius: (0) longer than ulna; (1) same length as ulna; (2) shorter than ulna (including olecranon process if present).
128. Ribs (trunk): (0) straight; (1) ventrally curved.
129. Ribs (trunk): (0) no longer than height of neural arch plus centrum; (1) less than 2.5 times height of neural arch plus centrum; (2) more than 2.5 times height of neural arch plus centrum.
130. Ribs (trunk): (0) tapered distally or parallel sided; (1) expanded distally into triangular posterior flanges.
131. Ribs (trunk) bear proximodorsal (uncinate) processes: (0) absent; (1) present.
132. Ribs (trunk) differ strongly in length and morphology along 'thoracic' region: (0) absent; (1) present.
133. Ribs (cervical): (0) flared distally; (1) tapered distally.
134. Rib (sacral) distinguishable by size: (0) shorter than trunk ribs, longer than presacra; (1) same length as presacra.
135. Rib (sacral) distinguishable by shape: (0) broader than immediate presacra but not broader than mid-trunk proximal shafts; (1) broader than mid-trunk proximal shafts.
136. Scapulocoracoid dorsal blade: (0) absent; (1) present.
137. Scutes: (0) tapered and elongate, four or more than four times longer than broad; (1) ovoid, no more than three times longer than broad.
138. Tibia, fibula width at narrowest point: (0) 50 per cent of length; (1) less than 30 per cent of length.
139. Tibia and fibula: (0) meet along length; (1) separated by interepipodial space.
140. Number of digits on manus: (0) more than five; (1) five; (2) fewer than five.
141. Number of digits on pes: (0) more than five; (1) five; (2) fewer than five.

New skull roof character

142. Skull table transverse line: (0) parietal/postparietal (or parietal/postparietal + parietal/tabular) and parietal/supratemporal sutures angled; (1) not angled or slightly angled.

Additional postcranial characters

143. Tibia: (0) distal articular surface absent; (1) L-shaped; (2) ovoid.
144. Pelvic ridge : (0) directed towards ventral edge of postiliac process absent; (1) present.

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