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Pederpes finneyae, AN ARTICULATED TETRAPOD FROM THE TOURNAISIAN OF WESTERN SCOTLAND

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SYNOPSIS The Tournaisian tetrapod *Pederpes finneyae* is described in detail, from the holotype and only specimen. The specimen derives from the Ballagan Formation, Tournaisian CM palynozone and is the earliest post-Devonian tetrapod known from articulated remains. It is preserved almost complete except for the tail, some skull regions and a few limb extremities. The animal resembles *Whatcheeria deltae* from the Viséan of Iowa, especially in the skull morphology, although the two differ in characters such as the lateral line expression, dermal ornament expression, proportions of the sub-orbital portion of the jugal and several other dermal skull characters. The postcranial skeleton of *Pederpes* shows several unique features, including the structure of the leading edges of the cleithrum and clavicle, the form of the rib flanges and a possible supernumerary digit on the manus. The humerus is also unusual in possessing a spike-like latissimus dorsi process, most like that of *Baphetes*. An investigation of the phylogenetic position of the whatcheeriiids is carried out by comparing the results from two recently published databases. The clade lies very close to the base of the tetrapod stem group, although according to the dataset employed, the whatcheeriiids compete with *Crassigyrinus* for the next most basal node after the Devonian forms. Possible whatcheeriiids also occur in the Viséan of Australia and the Tournaisian of Ireland and less certainly elsewhere, making the whatcheeriiids a long-lasting clade, widely distributed in time and space.

KEY WORDS anatomy, Carboniferous, Calciforous Sandstones, phylogeny, skeleton, whatcheeriid

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INTRODUCTION

Pederpes finneyae (Clack 2002a) is the first almost complete and fully articulated tetrapod to be described from the earliest part of the Carboniferous, the Tournaisian epoch. Only a few limb and girdle fragments from Nova Scotia, Canada (Clack & Carroll 2000) and a partial lower jaw from Ireland (Clack & Ahlberg 2004) are otherwise known from the entire Tournaisian. This time-period combined with the earlier part of the Viséan epoch are colloquially referred to as 'Romer's Gap' (Coates & Clack 1995). During the time represented by this 15 – 20 million year gap in the fossil record, tetrapods developed full terrestriality and the roots of the crown groups were established, but little is known about the sequence, timing or location of these events (Clack 2002b). Information from an almost complete tetrapod from this epoch is therefore of great importance. This paper describes the specimen, Glasgow Hunterian Museum (GLAHM) specimen 100815 (Fig. 1), augmenting the initial publication (Clack 2002a) with further anatomical details, a phylogenetic investigation comparing the cladogram produced in the original description with another recently produced, together with further details of the locality and palaeogeography.

MATERIAL AND METHODS

The specimen was collected in 1971 by Peder Aspen, then of Glasgow University, as an isolated *in situ* nodule from a horizon in cementstone sequences. It was identified initially as the rhizodont fish *Strepsodus*, but only a little of the specimen was visible in the clayey limestone nodule that enclosed the animal, so that this identity was based partly on size and partly on the presence of eroded 'labyrinthodont' teeth visible anteriorly (in addition, since no-one had ever discovered tetrapod material in these or any other Scottish Tournaisian sequences, neither Aspen nor the Museum staff nor other palaeontologists who examined the specimen were expecting to find one). Key to its re-identification as a tetrapod in 1996 were comma-shaped sections through gastralia, visible in the cross-sections of the nodule, and large flat plates of bone visible in section at the posterior end.

The specimen is compressed laterally and has been prepared largely from the left side, which was covered by thinner and somewhat softer matrix than the right. All of the

right side of the skull roof is missing. The right lower jaw is present but its outer face is badly eroded and the inner face is visible only in section. The left lower jaw lacks its outer face and the prearticular is present largely as a natural mould. Both premaxillae and most of the midline series of bones except the postparietals are also missing. These parts of the skull appear to have fallen or been eroded off the nodule before collection. The otic capsule and basioccipital are also missing, although these seem to have been lost during preservation, or were unossified.

The skull has been laterally flattened but also crushed a little dorsoventrally and has lost its anterior end. The left side of the palate is almost intact, whereas the right side has been crushed so that the pterygoid now lies vertically with its lateral edge downwards and the ectopterygoid is missing. The right palatine is partially visible in dorsal view and both vomers are present although crushed. The block containing the skull consists of several separate pieces that can be assembled in various combinations to give different views of the palate, braincase and teeth.

Parts of the right side have been selectively prepared and this has exposed the right forelimb and two digits and most of the right hindlimb. It would be possible to prepare more of the specimen in the future if time and resources allow.

The specimen was prepared mechanically using, in decreasing order of force, a Chicago pneumatic pen, a dental mallet with a reciprocating handpiece holding sharpened tungsten carbide rod and a pin vice, all under a binocular microscope with up to 50× objectives. The bone, which consists of a well consolidated periosteal layer over a very delicate spongy layer (often rotten or hollow inside) was consolidated with dilute Paraloid B72 in acetone. In places, the specimen was cut using a Well diamond wire saw with a wire diameter of 0.3 mm, to enable preparation of parts of the specimen that would otherwise be inaccessible, such as the stapes. Although this cut through several bones, such as the interclavicle and right clavicle, it simultaneously revealed their presence and also facilitated estimation of their extent by giving the thickness of the bones at various points.

A small block from the specimen, which it was hoped might contain additional digits from the right manus, was taken to the University of Texas Computed Tomography Laboratory, at Austin, TX (UTCT). This yielded fair results and further elements were clearly visible in the specimen (Fig. 2). However, the CT scan showed up mainly voids in



Figure 1 *Pederpes finneyae* Clack, 2002a. **A**, photograph of left side of entire specimen. **B**, Map of exposed surface of specimen. Vertebrae and ribs are numbered according to their preserved positions. Scale bar for **B** = 10 mm. For abbreviations used, see the text.

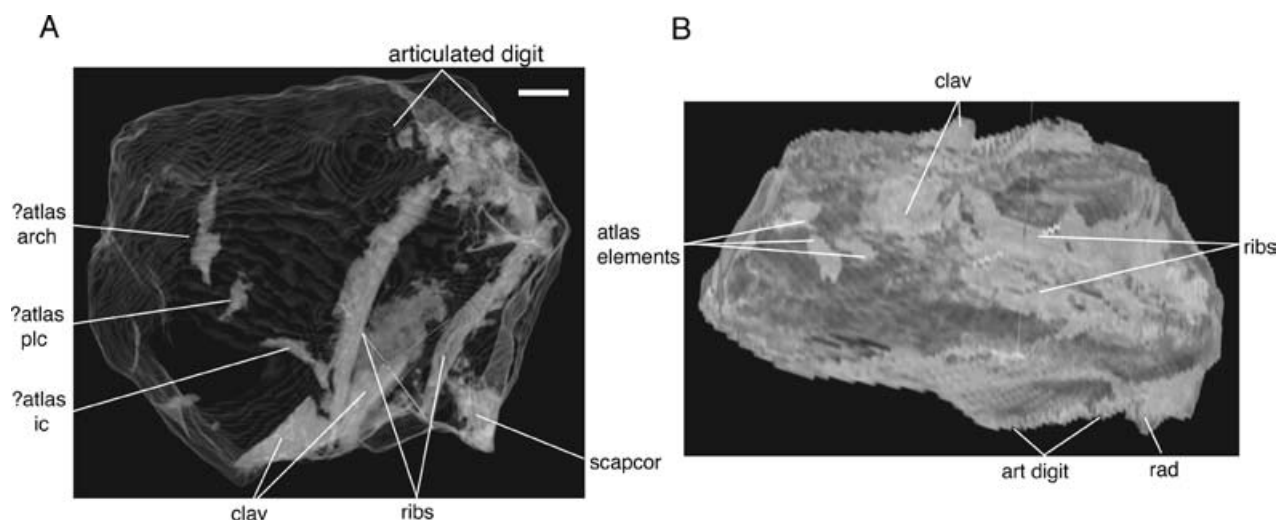


Figure 2 *Pederpes finneyae* Clack, 2002a: image produced from CT scanning of the block containing the right clavicle stem and one of the digits. **A**, view from the upper surface. This shows a probable atlas arch and centrum, as well as parts of at least two ribs that cannot be seen on the surface. **B**, view along the plane of preservation. This shows that most of the bones lie in approximately the same plane, although the distal end of the right radius and the articulated digit appear more superficially. Scale bar = 10 mm.

the bone, rather than the periosteal layers, so that the picture that emerged was not very detailed. Elements such as an atlas arch and its possible centrum, ribs from the right side and part of the right clavicle were identifiable, although no more digits were found. As a guide to what else lies within the specimen, this technique could prove useful for further preparation but, at present, is no substitute for mechanical techniques.

The specimen was photographed using a Nikon D1 digital camera and figures were initially drawn in pen and ink from these or with a camera lucida attached to a Wild M3 microscope. These were then scanned and finished using Adobe Photoshop 6 and a Wacom graphics pad attached to an Apple Macintosh G4 computer.

LOCALITY, GEOLOGICAL CONTEXT AND PALAEOGEOGRAPHY

The specimen was found at a height of 44.3 m above the level of the stream in Auchenreoch Glen, north of Dumbarton, Scotland (Figs 3A, B). The location is given as 44 m 'below (i.e. downstream of) Lot's Wife', the latter being a columnar formation of intrusive igneous rock, possibly related to a basalt dyke that runs vertically through the sequence close to where the specimen was collected (Fig. 3D). Detailed field notes have been provided by Dr Aspen (Fig. 3A), who described the specimen as having lain between two even and flat cementstone horizons. Below the specimen horizon lay a bed containing plants, bivalves and *Spirorbis* shells and another containing ostracods. Aspen (unpublished field notes, 1971) also reported arthropod cuticle from the same horizon. During preparation many plant fragments, *Spirorbis* shells and a few fish scales were also found. Many of the specimens collected by Aspen are now housed in the collections of the Hunterian Museum, including scales of the rhizodont *Strepsodus*, actinopterygian scales, ostracods, *Spirorbis*, bivalves and plants. A single isolated brachiopod is also in the collection, found loose 30 m upstream from Lot's Wife. The collection repres-

ents a fairly typical fauna for the Cementstone sequences (Cameron & Stephenson 1985; Paterson *et al.* 1990; Guion *et al.* 2000).

The sequence of cementstones and shales from which the specimen came lies within the Ballagan Formation, part of the Cementstone Group that was formerly known as the lower part of the Scottish Calciferous Sandstone Measures. These Measures include lithologies that vary from fluvial sandstones and lagoonal cementstones to marine limestones and shales, and also include non-marine limestones, oil-shales and volcanic formations (Cameron & Stephenson 1985). More recent terminology places the Ballagan Fm within the Inverclyde Group (Fig. 3B). In the area north of Dumbarton, the Ballagan Fm reaches a thickness of up to 140 m (Paterson *et al.* 1990) and is exposed in a series of glens, including Auchenreoch Glen, that feed into Murroch Glen (Fig. 3C). The rocks are exposed in almost horizontal beds along the steep-sided glens and stream cuttings, so that little of any one horizon is accessible. A search of the area in 1997 by J. A. C. with Dr Aspen and colleagues failed to find any more of the tetrapod specimen or other fossil material. More recent visits have produced a lungfish rib (University Museum of Zoology, Cambridge, UMZC 2003.58), the only record of a lungfish from this cementstone sequence and a, so far unidentifiable, sarcopterygian scale.

Palynological samples gave a suggested date of claviger-macra (CM) palynozone, Tournaisian Tn3c, Courceyan, Dinantian, Early Carboniferous (Clack 2002a), which accords with the Tournaisian age usually assigned to the Cementstone sequences (Paterson *et al.* 1990).

During the late Dinantian, the area around Dumbarton stood on the edge of one of a series of basins that spanned what is now the Scottish Midland Valley and what were then adjacent areas in Northern Ireland. The Dumbarton locality lay north of and approximately midway between what are called the Ayrshire and Central Basins (Guion *et al.* 2000). Westward lay the Ulster Basin and to the north of that lay the locality from which the jaw of *Occidens portlocki*, an Irish Tournaisian tetrapod, derived (Clack & Ahlberg 2004). The basins appear to have become separated during the Viséan

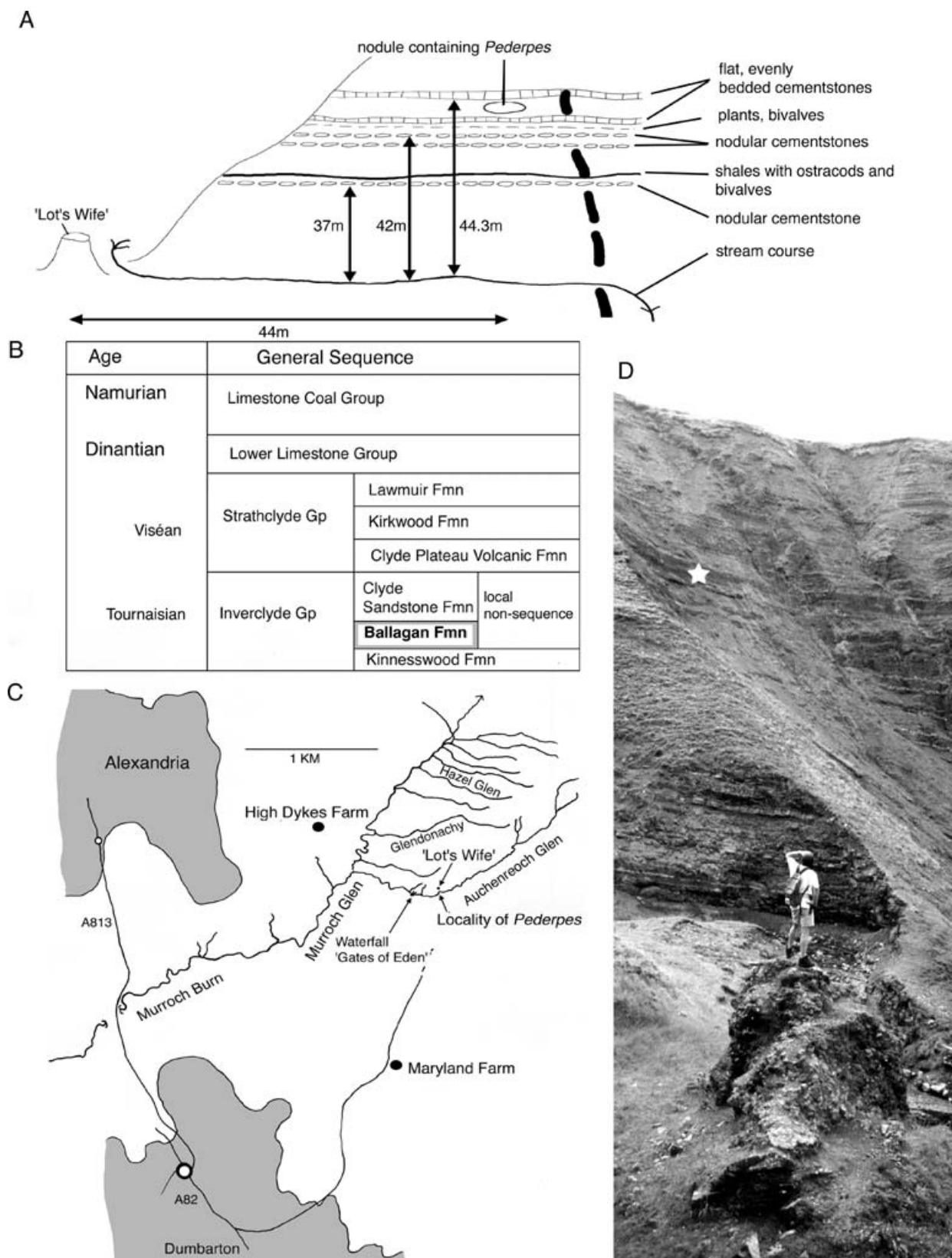


Figure 3 Stratigraphic context of *Pederpes* and the Ballagan Formation. **A**, sketch adapted from field notes made by Peder Aspen to show the position of 'Lot's Wife' and the site from which *Pederpes* derived. The nodule was located between two flat-bedded cementstone horizons in a west-facing scarp by a right angled bend in the burn. **B**, Position of the Ballagan Formation in the Lower Carboniferous of the Greenock area (from Paterson *et al.* 1990). **C**, Map to show locality of *Pederpes* showing position of Auchenreoch Glen relative to Dumbarton and site from which *Pederpes* was recovered. **D**, photograph of the locality where *Pederpes* was found, with 'Lot's Wife' in the foreground (with R. N. G. Clack for scale). White star indicates approximate position of the *Pederpes* nodule.

(Guion *et al.* 2000), but may have been part of a continuous basin in earlier times. Both localities show some evidence of marginal marine conditions, although in the western part of the Scottish region, fully marine conditions only developed in the upper part of the Calcareous Sandstone Measures (Cameron & Stephenson 1985: for *Occidens*, see Clack & Ahlberg 2004). However, both *Pederpes* and *Occidens* are isolated finds and may not have lived in the areas in which they are preserved. The coincidence of two similar and probably contemporary tetrapods in what were geographically close localities suggests that further collecting in these deposits would nevertheless be profitable, especially given the rarity of Tournaisian tetrapod material.

The completeness and lack of disarticulation between the elements in the skeleton of *Pederpes* suggests that the carcass had probably dried out and been 'mummified' prior to being swept into marginal marine conditions before preservation. In the Dinantian, the climate of the region appears to have been monsoonal, that is, dry with seasonal wetting (Falcon-Lang 1999; Guion *et al.* 2000), possibly conducive to mummification of the carcass before transport.

ABBREVIATIONS USED IN FIGURES

4th t, fourth trochanter; **add cr**, adductor crest; **Ang**, angular; **art**, articulation; **Bsph**, basisphenoid; **ch**, choana; **clav**, clavicle; **cleith**, cleithrum; **Cor**, coronoid; **Dent**, dentary; **dpc**, deltoid process; **Ect**, ectopterygoid; **ectep**, ectepicondyle; **entep**, entepicondyle; **Epipt**, epipterygoid; **fem**, femur; **fen**, fenestra; **fib**, fibula; **fib fos**, fibular fossa; **for**, foramen; **gast**, gastralia; **hum**, humerus/humeral; **ic**, intercentrum; **icf**, intercondylar fossa; **iclav**, interclavicle; **il**, ilium; **int t**, internal trochanter; **Intemp**, intertemporal; **isch**, ischium; **Jug**, jugal; **l**, left; **Lacr**, lacrimal; **ldp**, latissimus dorsi process; **llc**, lateral line canal; **lr jaw**, lower jaw; **mt**, metatarsal; **mus**, muscle; **Mx**, maxilla; **Nas**, nasal; **Pal**, palatine; **Par**, parietal; **Pbsph**, parabasisphenoid; **ped**, pedal; **phal**, phalanx; **plc**, pleurocentrum; **Pmx**, premaxilla; **Pofr**, postfrontal; **pop sp**, popliteal space; **Popar**, postparietal; **Porb**, postorbital; **posn**, position; **posr**, postsacral rib; **Preart**, prearticular; **Prefr**, prefrontal; **Preop**, preopercular; **Psph**, parabasisphenoid; **Pt**, pterygoid; **Quadjug**, quadratojugal; **r**, right; **R**, rib; **rad**, radius; **scap**, scapular; **scapcor**, scapulocoracoid; **skr**, skull roof; **Squ**, squamosal; **Surang**, surangular; **Sutemp**, supratemporal; **Tab**, tabular; **tars**, tarsus/tarsal; **tib**, tibia; **ung**, ungula; **Vo**, vomer.

SYSTEMATIC PALAEONTOLOGY

TETRAPODOMORPHA Ahlberg, 1991

WHATCHEERIIDAE Clack, 2002a

DIAGNOSIS. Derived states: narrow, steep-sided skull with orbit deeper than wide; ?intertemporal–squamosal contact; massive tooth on maxilla about position 5 or 6; light dermal skull ornament; dorsal branch of mandibular lateral line running along surangular; very broad interclavicle with acutely angled lateral corners.

Primitive states: grooved, denticulated parasphenoid; closed palate with denticulated surface; supratemporal–postparietal contact, fang pairs on vomers, palatines and ectopterygoids with a row of some smaller accessory teeth on

each; row of coronoid teeth nearly continuous; at least some lateral lines in tubes through bone; rhachitinous vertebrae; no differentiated sacral neural arch, ilium with posterodorsal process and dorsal iliac blade.

Uncertain polarity: supratemporal with deeply interdigitated suture to squamosal; small tabular with 'button' terminating in ornamented surface; steeply angled suspensorium with deeply excavated temporal notch, pronounced angle between skull table and cheek in transverse section; scapulocoracoid ossified in two portions; about 28 presacral vertebrae; trunk ribs with expanded distal flanges.

Genus *PEDERPES* Clack, 2002a

DIAGNOSIS. Whatcheeriid with the following apomorphies: intertemporal–squamosal contact a narrow process (c.f. broad contact in *Whatcheeria deltae*); trunk ribs with at least vertebrae numbers 4–9 bearing accessory processes and/or foramina at dorsal edge of acutely triangular terminal expansions and about numbers 10–12 with flared ends; short presacral ribs with accessory processes; minute lateralmost digit on manus; deep striations on anterior edge and anterior region of external surface of stem of clavicle and cleithrum; ovoid dorsal blade of cleithrum with fimbriated edge.

SPECIES INCLUDED. Only the type species, *Pederpes finneyae*.

REMARKS. *Pederpes* is distinguished from *Whatcheeria deltae* by the following: low but distinct ornament on dermal bones including shoulder girdle, punctate and pitted on tabular, postparietal and supratemporal (other skull table bones not known); downturned occipital flange of tabular and postparietal lacking ornament and sharply set off from rest of skull table by a crest; maxilla narrower than in *W. deltae* (maximum width about 4% of skull length in *Pederpes*, about 6% in *W. deltae*); in *Pederpes*, nasal lacks notch in narial margin present in *W. deltae*; jugal narrower below orbit than *W. deltae* (jugal depth less than 20% of orbit diameter in *Pederpes*, about 30% in *W. deltae*) with only a narrow spike anterior to orbit (c.f. antorbital expansion in *W. deltae*); lacrimal contributes at least a quarter of anterior orbit margin (c.f. possible short contribution in *W. deltae*); no conspicuous thickening of prefrontal orbit margin c.f. *W. deltae*; suspensorium greatly elongated (about same length as maximum orbit width in *W. deltae*, about 25% longer than maximum orbit width in *Pederpes*); postorbital–postfrontal suture very short in *Pederpes* and almost overlain by intertemporal, not so in *W. deltae*; postorbital contributes more than half of distance between temporal embayment and posterior orbit margin; skull table slightly wider relative to its length in *Pederpes* (width about 1.8 times length in *Pederpes*, about 1.6 times in *W. deltae*); *Pederpes* lacks depressions in postparietals present in *W. deltae*; no lateral lines visible in grooves on skull roof (exposed only in pores c.f. grooves on jugal and postorbital of *W. deltae*); interclavicle with thin parasternal process (of unknown length) but not thickened and robust c.f. *W. deltae*; cleithrum without conspicuous posterior notch (c.f. *W. deltae*); ilium with dorsal blade and short posterior process (c.f. broadened blades in *W. deltae*); metatarsals and pedal phalanges longer than broad (c.f. broader than long in *W. deltae*); conspicuous, spike-like latissimus dorsi process on humerus resembling that of *Baphetes*; unossified pubis; ventral armour of numerous elongate oval gastralia (none in *Whatcheeria*).

DESCRIPTION

(In the following description all comparative information about *Whatcheeria* is from Lombard & Bolt (1995) unless otherwise stated, with additional information from Bolt & Lombard (2000) and pers. obs.)

Skull roof

The skull roof pattern of *Pederpes* is in many ways similar to that of *Whatcheeria deltae* from the Viséan of Iowa, USA, but shows many differences in detail. Figure 4 gives a drawing of the assembled skull. One of the most conspicuous differences lies in the dermal ornament. In *Whatcheeria* it is more or less completely absent and although *Pederpes* shows reduced ornament compared to most other Carboniferous or Devonian tetrapods, it is nevertheless present. It is fairly regular, consisting of small round pits at the centres of the bones, with elongated grooves and ridges towards the bone margins. Dermal ornament is well-defined on the skull table, where the pits form a reticulate pattern in places, but is less well-defined elsewhere, being least on the jugal. The much larger *Ossinodus pueri* from Australia, suggested as a *whatcheeriid* or a close relative by Warren & Turner (2004) shows much deeper, more regular ornament, distributed over the entire skull table without grooves or ridges peripherally on the individual bones.

Lateral line grooves are not obvious on the preserved parts of the skull roof of *Pederpes*, in contrast to *Whatcheeria* where they are represented by grooves (Lombard & Bolt 1995: fig. 2). *Pederpes* shows larger-than-average pores on the lacrimal, jugal and postorbital in the places where a lateral line might be expected, but the jugal also shows a row of six much smaller, deeper pores in a regular row along its ventral edge that might also indicate a lateral line expression. The right lower jaw shows the natural mould of a surangular lateral line groove, the only groove on the skull. A surangular lateral line is also found in *Whatcheeria* and some embolomeres (e.g. *Eogyrinus* Panchen, 1972; *Pholiderpeton* Clack, 1987a).

At the front of the snout on the left are the remains of a crushed bone showing the eroded roots of two or more teeth. This might be the premaxilla or the vomer exposed in dorsal view and is not otherwise informative. The maxilla is narrow, relatively more so than in *Whatcheeria*, particularly anteriorly where the smoothly concave narial margin sweeps down almost to the jaw margin. A process that probably bounded the choana can be seen within the external naris. The maxilla is incomplete posteriorly, so it is not clear whether it contacted the quadratojugal to exclude the jugal from the jaw margin. In *Whatcheeria*, Lombard & Bolt described the jugal as being excluded from the jaw margin, but their fig. 1 shows it as contributing. This may be a variable feature that changes during ontogeny, with differences between individual specimens. A scatter of pores of varying sizes marks the external face of the maxilla. It is not clear whether any of these are lateral line pores or enlarged dermal ornament.

The left nasal is partially preserved and shows a ragged or 'fimbriate' (Lombard & Bolt 1995) edge where it bounds the external naris, as in *Whatcheeria* and embolomeres. It has a deeply interdigitating suture with the prefrontal, although much of the contact with that bone is obscured where

the lacrimal has been pushed over it. The lacrimal too has a fimbriate edge forming its contribution to the external naris, though it does not have the deeply incised notch at its base seen in *Whatcheeria*. The margin of the lacrimal that contacts the nasal and prefrontal and that which contributes to the orbit are also fimbriate. There is a hint of something similar in *Whatcheeria*, although the sutures around its orbit are unclear. Lombard & Bolt's reconstruction drawing shows the lacrimal excluded from the orbit by an anteriorly expanded jugal, but the specimen drawing appears to show an interdigitated margin with the lacrimal more posteriorly. Having seen the material we agree that it is difficult to interpret this area. In *Pederpes*, it is clear that the lacrimal formed a substantial part of the orbit margin.

The prefrontal is thickened around the orbit margin, of which it forms a small proportion of the dorsal border and at least the dorsalmost part of the anterior border. The corner so formed is quite abrupt, in contrast to *Whatcheeria* in which it is more rounded. The prefrontal has been pushed down beneath the lacrimal to some extent, this is estimated in the reconstruction below. Part of it appears in the interpterygoid vacuity beneath. The anterodorsal corner of the orbit is thickened and marked by almost regular ridges and grooves that curve round into the orbit itself, but there does not seem to be a series of sinuses present, in contrast to *Whatcheeria*. There is a deeply interdigitated suture with the postfrontal, but the contact margin with the frontal has been lost. The postfrontal forms most of the dorsal margin of the orbit, but little else of the bone is available for description. It joins the postorbital just anterior to the posterodorsal corner of the orbit as in *Whatcheeria*, but, whereas in that animal the postfrontal–postorbital suture is clearly visible, in *Pederpes* it is nearly overlain by the (possibly slightly displaced) intertemporal. Like the anterodorsal corner, the posterodorsal corner of the orbit is quite abrupt, giving an almost 'squared-off' appearance to the orbit dorsally. Although incomplete, the postorbital ventral ramus is slightly fimbriate. The postorbital is apparently broader but not much deeper than that in *Whatcheeria*, although the skull figured by Lombard & Bolt (1995: fig. 1) is broken in this area.

The remaining part of the orbit margin formed by the jugal is deeply excavated as in *Whatcheeria* and both resemble the deepened orbit seen in *Anthracosaurus russelli* (Panchen 1977; Clack 1987b). However, despite being almost identical in size to the skull of *Whatcheeria* figured by Lombard & Bolt in their fig. 1 (Field Museum PR1634) the depth of the jugal below the orbit is much less in *Pederpes*. Furthermore in *Pederpes*, the jugal extends only a little way beyond the anterior margin of the orbit and is not expanded into a wedge as in *Whatcheeria* (whichever jugal reconstruction is considered). Most of the posterior margin of the jugal including its contact with the squamosal and quadratojugal and much of that with the postorbital, is represented by eroded bone, although some of the sutural lines can be made out as natural moulds. A vertical row of foramina running up the orbital margin of the jugal may represent a sensory lateral line.

The squamosal is an elongate bone forming much of the suspensorium, relatively longer than in *Whatcheeria* compared with the width of the orbit. It has a deeply interdigitating suture with the supratemporal (which has nevertheless been somewhat pulled apart) as in *Whatcheeria*. There is a shallow groove along the posterior margin of the bone, but no

evidence of any internal flange for contact with the pterygoid/epipterygoid ossifications. It apparently had an open junction at this point as in embolomeres, *Acanthostega* and *Crassigyrinus* (Clack 1987a, 1994a, 1998a, respectively). There is a deeper-than-average ornament-like groove just internal to this that could represent a lateral line groove (see Fig. 4A, upper arrow).

At the extreme posterior end of the suspensorium, the bones have sprung apart a little. There is a clear separation between the quadratojugal and the remaining bones and the squamosal–quadratojugal suture is also fairly clear. Running dorsally from this junction is a further suture that can only define the lateral border of the preopercular. However the dorsal extent of this bone is unclear (Fig. 4). It probably extends to the point at which the posterior groove on the squamosal begins to fade out. A foramen near the base of this bone may be a lateral line pore (Fig. 4A, lower arrow). The preopercular is present in this animal as in some specimens of *Whatcheeria* (Bolt & Lombard 2000), a primitive feature lost in all other post-Devonian tetrapods.

The quadratojugal is represented by its posteriormost section and by a broken fragment forming part of the jaw margin.

The skull table of *Pederpes* is relatively broader than in *Whatcheeria* but otherwise they are very similar in construction. *Pederpes* lacks the depressions seen at the centres of the postparietals in *Whatcheeria* (the parietals are not preserved). The tabular, which is relatively small and essentially rectangular in *Pederpes*, has a slightly extended ornamented region at its posterolateral corner (a ‘tabular horn or button’), similar to that of *Whatcheeria* but somewhat smaller. There are also resemblances to the tabulars from Tula associated with *Tulerpeton* (Lebedev & Clack 1993). The tabular bears a thin vertical flange on its occipital surface, less robust than in *Whatcheeria* and marked out from the skull table by a distinct crest (Fig. 5B). The ornament continues on the lateral border of the tabular, wrapping under the edge. The supratemporal is very similar to that of *Whatcheeria* in being more or less pentagonal except for its posteroventral process that sutures with the squamosal. The supratemporal forms the apex of the temporal notch via a smooth, unornamented and embayed margin similarly in both genera (Figs 4, 5A).

The postparietal is similar to that of *Whatcheeria* in its relative proportions, having about twice the anteroposterior dimension of the tabular and in being roughly pentagonal. Its posterior margin bears a continuation of the crest seen on the tabular that separates the dorsal from the occipital surface and the latter bears a continuation of the flange from the tabular (Fig. 5B). *Pederpes* differs from *Whatcheeria* in its clear demarcation of the two surfaces. In the latter genus, the dorsal and occipital surfaces are confluent. However, on the postparietal of *Pederpes*, the occipital surface terminates a little way from the midline in a margin that is concave (Fig. 5B: for) and probably marks the position of a vacuity, which may have been occupied by the dorsal part of the neurocranium, as in *Whatcheeria*. The entire occipital flange is quite shallow and apart from the midline vacuity, bears no obvious margin for a post-temporal fossa or occipital arteries. However, there may be a very small fossa at the junction of the tabular and postparietal just below the crest, where there is a similar feature in *Whatcheeria* (Clack 2003 q.v. for a discussion of the evolution of the occiput in whatcheeriids and other early tetrapods). There

are also a few very small foramina in the flange itself (Fig. 5B).

The intertemporal and its relationships to the postorbital, supratemporal and squamosal are the most difficult to determine because of the eroded nature of key areas. The anterior margin of the intertemporal over the orbit is clear and its contact with the parietal and supratemporal dorsally can be seen in the natural mould. However, where it meets the supratemporal and postorbital, there seems to be a rather unusual feature and it is not clear whether this is artefactual. There appears to be a long, narrow process reaching between the squamosal and postorbital (Fig. 5A). Contact between the intertemporal and the squamosal is unusual in early tetrapods. This may be a synapomorphy of the whatcheeriids. However, in *Whatcheeria*, the intertemporal–squamosal contact is broader; the shape and finger-like nature of the process in *Pederpes* are unexpected. By contrast, however, in *Whatcheeria*, the intertemporal is produced anteriorly into a process wedged between the postfrontal and parietal, a feature that is almost certainly absent from *Pederpes*.

Palate and braincase

The palate is represented by quite an extensive exposure of natural mould of the dorsal surface and eroded bone of the left side, with elements from the right side crushed and distorted. All elements are denticulated, probably almost entirely, with their dorsal surfaces being marked by radiating ridges and grooves. The pterygoids are long and triangular and probably met in the midline anterior to the parasphenoid, as in *Whatcheeria*. Palatine and ectopterygoid are quite broad at least in dorsal view, but nothing can be made of the shape of the vomers except that there appears to have been an anterior palatal fenestra between them. There is no such fenestra recorded in *Whatcheeria*, so the feature in *Pederpes* may be an artefact, resulting from crushing and separation of the vomers. The anterior margin of the subtemporal fossa, to which the ectopterygoid contributed substantially, is pointed. The interpterygoid vacuities were very narrow, closely matching the outline of the parabasisphenoid.

The parabasisphenoid is well-preserved and has been exposed by preparation (Figs 6E, I). The posterior portion of the cultriform process is narrowly triangular, concave posteroventrally and sparsely denticulate. Fine striations also mark its ventral surface. Further anteriorly its lateral margins coalesce into a more blade-like form (Fig. 6E). Parts of the basiptyergoid processes can be seen where they have been prepared out internal to the left orbit and are typically bifaceted and ‘unfinished’ as in *Whatcheeria* and most other early tetrapods. Just in front of the basiptyergoid processes the dorsal surface of the parabasisphenoid forms low, irregular crests presumably for the insertion of eye muscles. Further anteriorly, the structure is concave, presumably for reception of the sphenenthmoid, which appears to have been unossified.

Posterior to the basiptyergoid processes, the parabasisphenoid is drawn out into paired ‘wings’ separated by an embayment in a similar fashion to those in *Whatcheeria* and *Crassigyrinus* (Panchen 1985; Clack 1998a: Figs 5C, D). Between the wings the surface bears a continuation of the denticulated surface of the cultriform process, with no definite margin to the denticulated area. The wings bear well-marked striations ventrally, but the dorsal surface cannot be

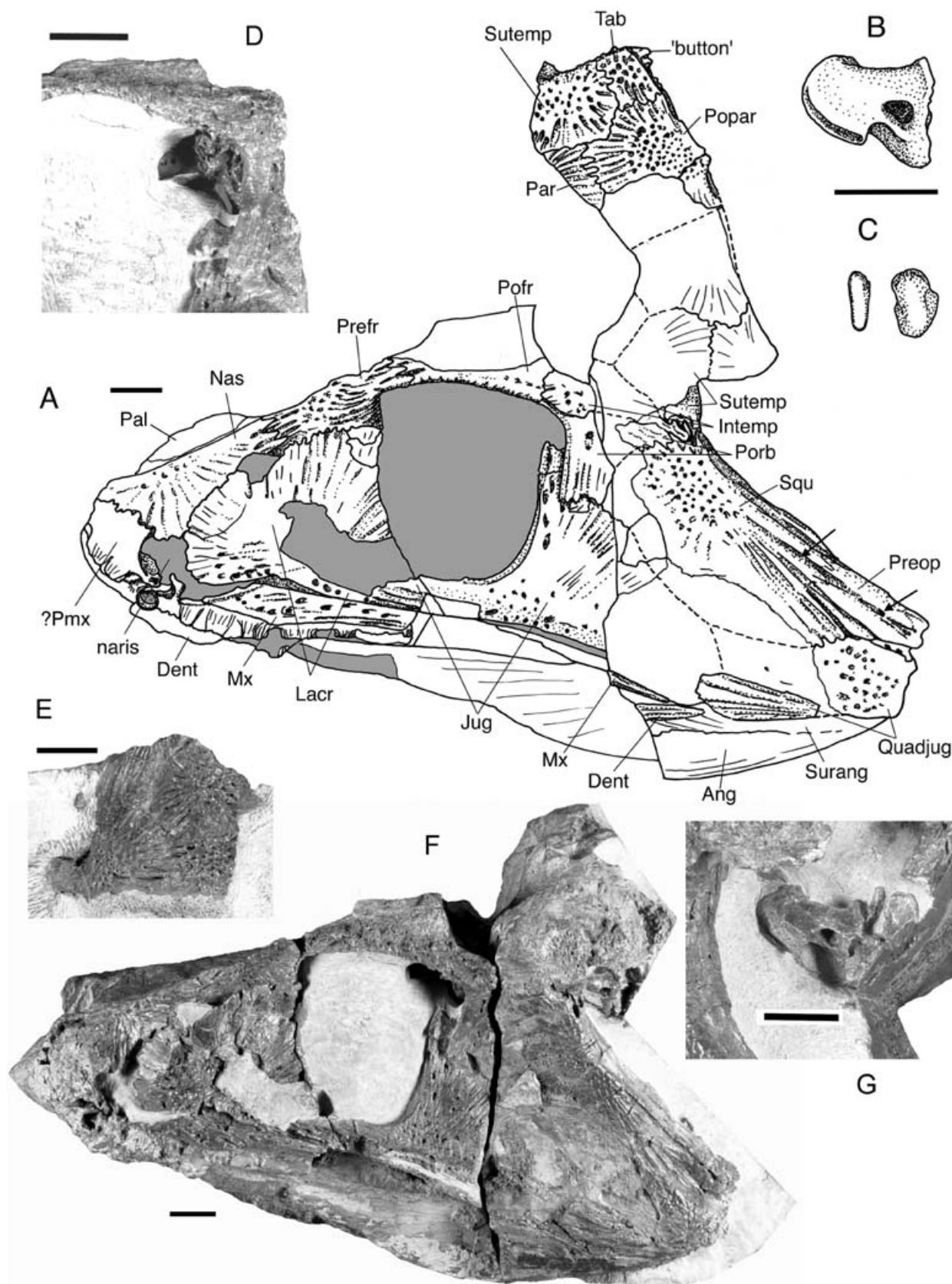


Figure 4 *Pederpes finneyae* Clack, 2002a: skull and hyobranchial skeleton. **A**, skull in lateral view with the skull table in its preserved position. White areas on the skull are natural mould or eroded bone, grey represents matrix. **B**, stapes. **C**, possible proatlantes or parts of the hyobranchial skeleton. **D**, photograph of basisphenoid seen through the orbit. **E**, skull table, midline of the table is towards the left of the photograph. **F**, photograph of entire skull. **G**, close-up of stapes and elements seen in **C**. Scale bars = 10 mm. For abbreviations used, see the text.

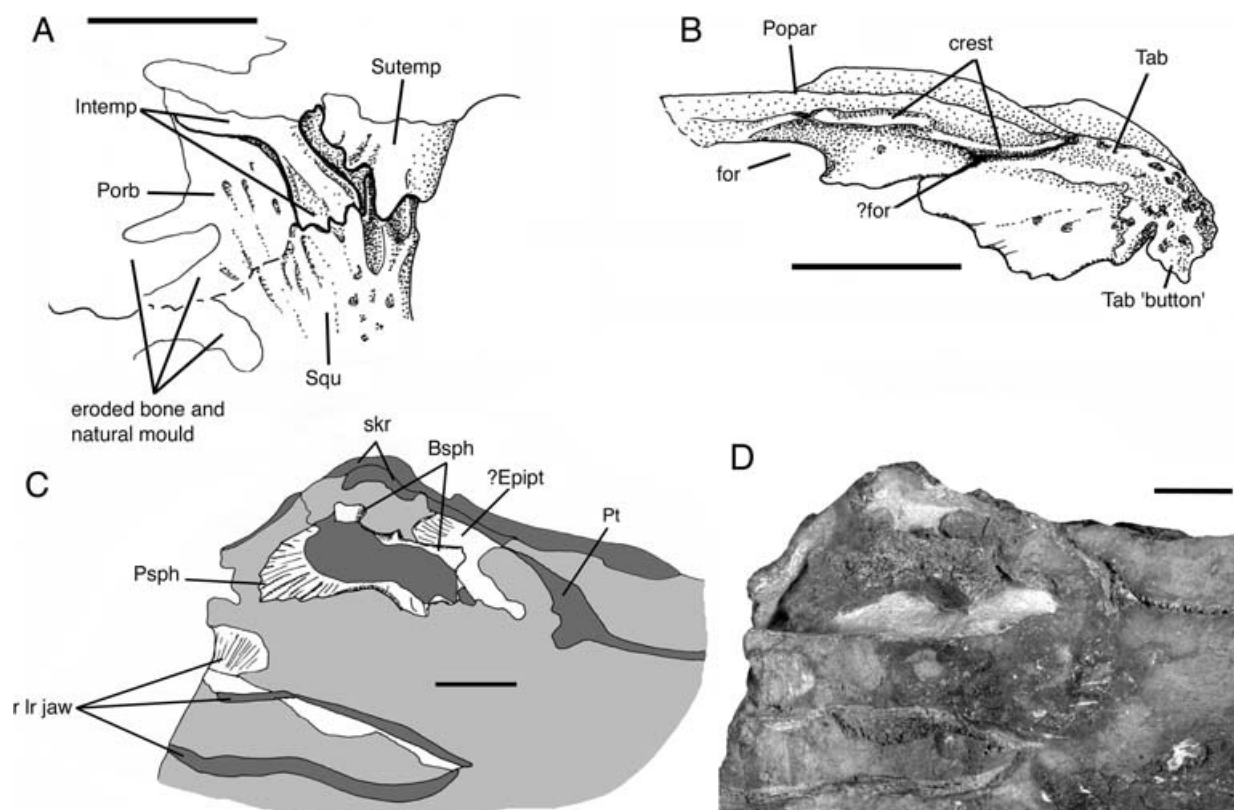


Figure 5 *Pederpes finneyae* Clack, 2002a. **A**, drawing of the junction between the skull roof and cheek to show the process from the intertemporal that contacts the squamosal. **B**, detail of posterior view of the tabular and postparietal to show the ridge that separates the ornamented from the unornamented portion of these bones, the occipital flanges and foramina and the tabular button. **C**, the section of the skull block showing part of the parabasisphenoid, skull roof, pterygoid and part of the right lower jaw. The parasphenoid is seen in deeply oblique view as it passes into the block. Pale grey, matrix; dark grey, section through bone; white, natural bone surface. **D**, photograph of view in **C**. Scale bars = 10 mm. For abbreviations used, see the text.

seen. The basioccipital would have been exposed between them, but probably fell out during preservation along with the otic capsule, suggesting that it was not securely integrated into the braincase, resembling the condition in *Crassigyrinus*. Part of what may be an epipterygoid is visible in the cross-section of the braincase exposed in a major fracture through the skull-block (Fig. 5C), although it consists only of a thin blade-like bone.

Hyobranchial skeleton

The left stapes has been exposed by preparation and is very well preserved in a three-dimensional uncrushed state (Figs 4B, G). It resembles very closely that of *Acanthostega* (Clack 1994b, 1998b, 2002a) and although absolutely larger, is relatively smaller than in that animal. It has a very large stapedial foramen. The surface of the footplate cannot be seen, but appears to have been of the relatively large size typical for early tetrapods. The distal margin is expanded and has an unfinished surface, as in *Acanthostega* and other early tetrapods such as *Greererpeton* (Smithson 1982, Godfrey 1989a) and *Pholiderpeton* (Clack 1983). In *Whatcheeria*, the stapes are all crushed into more or less a single plane, but the shape and size were probably similar.

Beside the stapes lie several small elements of uncertain identity (Figs 4C, G). They may possibly represent proat-

lantes, or small elements of the hyobranchial system. Otherwise, as in *Whatcheeria*, there is no evidence of ossified branchial bars.

Lower jaw

Internal and external faces are represented although preservation is poor throughout, but different views are provided by assembling the block containing the skull in various ways (Fig. 6). The anterior and posterior parts of the dentary and a few anterior teeth are represented by crushed remains on both sides. The posterior end of the dentary bears fine parallel striations on its outer surface, but few other details can be made out. It is not clear whether there was a widening in the dentary midway along its length at the junction with the postsplenial and angular, but this is possible based on the condition in *Whatcheeria*. The infradentary series is represented both by natural mould and some remaining bone of the internal surface, but the external ornament is not visible. The surangular is quite elongate with a narrow anterior process carrying part of the surangular lateral line groove as in *Whatcheeria* (Figs 6B, C). The angular is shallow. The ventral margin is shallowly curved as in *Whatcheeria*. There is no evidence for an inframandibular lateral line groove, although a few foramina may represent it.

Of the internal face of the jaw, coronoids were clearly present and a small part of one of them has been exposed

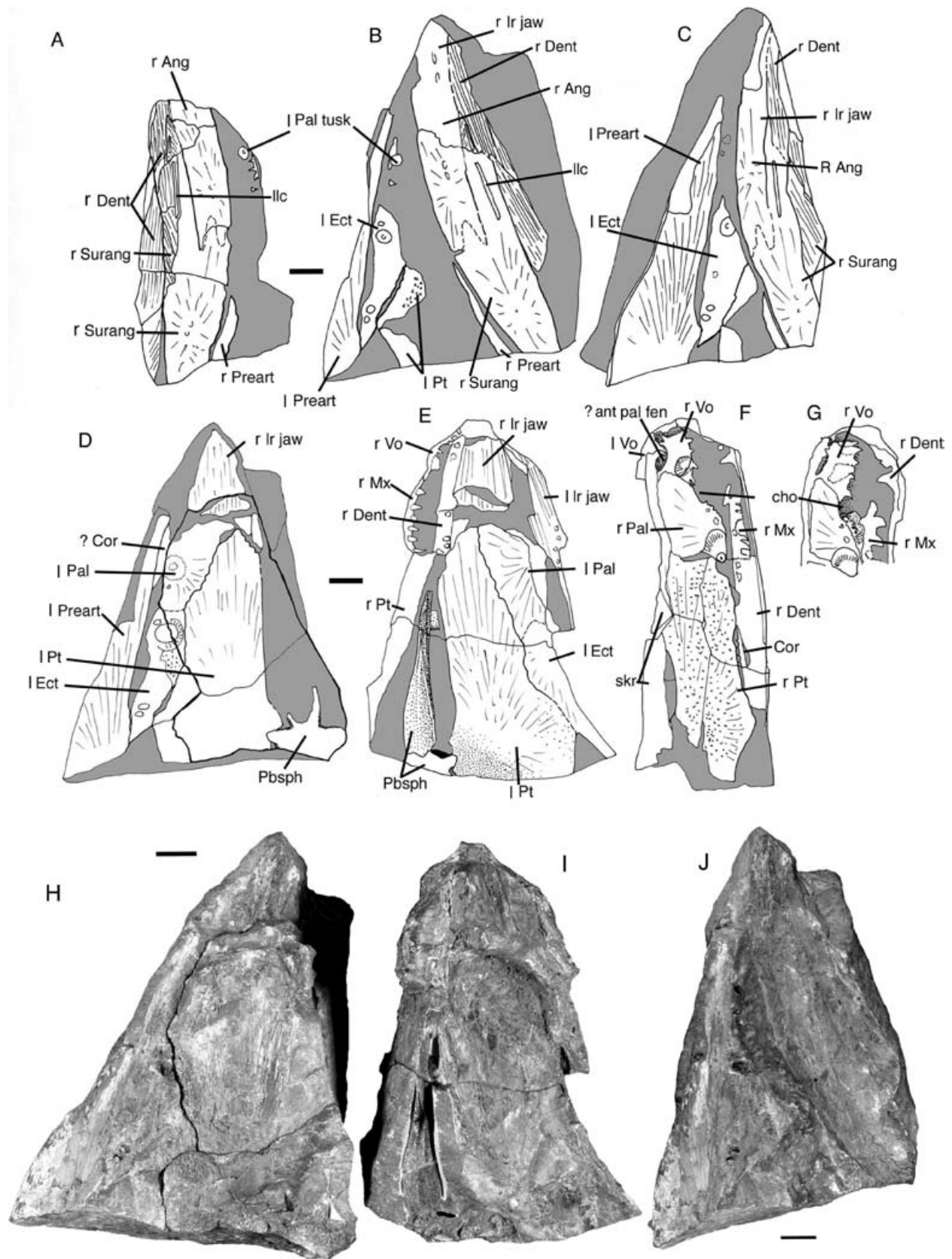


Figure 6 *Pederpes finneyae* Clack, 2002a. **A–G**, different views of the skull block assembled in various ways to show the palate and dentition. **A**, right lower jaw in external view. **B**, counterpart of right lower jaw on block containing part of the palate. **C**, a view of the block shown in **B** slightly rotated to the right to show more of the palate. Dorsal view. **D**, block shown in **B** with its counterpart (seen in **A**) placed in position. The heavy line indicates the dorsal view of the part shown in **A**. **E**, counterpart of **D**, the block bearing the cheek and snout, in ventral view. **F**, block in **E** rotated to the right to show the side of the block. **G**, same, rotated to show more of the vomer. **H–J**, photographs of skull in various views. **H**, same view as **G**. **I**, same view as **E**. **J**, same view as **B**. Scale bars = 10 mm. For abbreviations used, see the text.

by preparation. However, no anatomical details are available. The prearticular can be seen from the natural mould not to have borne any denticle fields in the visible portion, although this does not include the posteriormost section. As its ventral border is very simple and delicate, it clearly did not suture with the surangular or angular and possibly not with the postsplenial. Whether there was any remnant of the Meckelian bone as in *Whatcheeria* is doubtful, since nothing can be seen in the available section through the right ramus.

Dentition

Figure 6 indicates preserved aspects of the dentition. The remains of at least five substantial teeth are preserved on the left maxilla, the largest being the fourth, as in *Whatcheeria*. The natural moulds of a few smaller teeth are visible on the right. Combining all of the available information, a total count of about 17 is suggested, which is similar to that of *Whatcheeria*. The dentary count is more problematical, although it was possibly similar to that of *Whatcheeria*. The shape of the marginal tooth crowns are too poorly preserved to infer their shape. There are a few coronoid teeth preserved and these are quite small and even-sized, again not dissimilar to those in *Whatcheeria*. The palatal dentition is better represented and remains of substantial fangs are present on all three tooth-bearing palatal bones. The palatine and ectopterygoid each bear a large fang and a few smaller teeth, although the number of these is uncertain (Figs 6C, D). The ventral edge of the right vomer has been prepared out to reveal four small teeth and intervening spaces, with the root of a larger fang visible in cross-section. A few small denticle-like teeth are also revealed along this margin, but whether they were part of a row of such denticles or part of a larger denticle field is not clear. Over all, the formula was probably similar to that of *Whatcheeria*.

Axial skeleton

Vertebrae

Twenty-seven neural arches are preserved in an articulated sequence, interrupted only by a sharp kink near the posterior end and a small gap further anteriorly where adjacent arches have come adrift (Fig. 1). The first arch preserved is about 20 mm behind the skull table (which implies a somewhat greater gap between it and the basioccipital region) and is assumed to be the axis. The arches show little in the way of regional differentiation, as found in the Devonian tetrapod *Acanthostega* (Coates 1996). A clearly differentiated axis arch would not therefore be expected, and it seems more parsimonious to assume the first preserved to be the axis (Fig. 7A). That would imply displacement of only one arch in this otherwise complete presacral column. A probable atlas arch is present in the block that was CT scanned (Figs 2, 7B), but there is no evidence for additional arches between this and the first preserved. The atlas arch is similar to those of several other early tetrapods, in particular that of *Archeria* (Holmes 1989) and also that of *Greererpeton* (Godfrey 1989b), in that it seems to lack an anterior zygapophysis.

The apices of almost all the neural spines seem to have been poorly ossified and have been crumpled to various de-

grees (Fig. 7A). An alternative explanation is that the irregularities indicate some kind of soft tissue attachment here, but they seem too random for such a purpose. This feature does not compare closely with the horizontal ridges on the spines of *Acanthostega* that Coates (1996) suggested might have supported tendinous interarch bracing, or indicate the positions of myosepta. The two halves of each neural arch do not always appear to have been sutured together and have been prised apart in several cases. The spines are, in the main, low rectangles. Presacral neural arches are not described in detail for *Whatcheeria*, but those illustrated by Lombard & Bolt (1995) lack the dorsal part of the spine. This could result from poor ossification, concordant with that seen in *Pederpes*.

Anterior zygapophyses are well-developed and conspicuous and, as preserved, appear to be approximately horizontal (Fig. 7). However the posterior ones are not conspicuous and at first glance this may appear as an intermediate condition between *Acanthostega* (Coates 1996), in which zygapophyses are scarcely developed, and other early tetrapods. However, in *Pederpes* this does seem to be an artefact of preservation, since where the posterior face of the arch can be seen in section, the posterior zygapophysis is present and substantial. Some specimens of *Whatcheeria* are similarly preserved (pers. obs.).

Instances of regional variation among the arches consist of a gradual narrowing of the transverse processes towards the posterior end whereas the spines increase very slightly in width (compare Figs 7A and 7C). The five or so immediately presacral spines appear to have better ossified apices and one arch, number 22 of the preserved series, has a foramen through the pedicle of the posterior zygapophysis (Figs 7C, D).

Centra are typically rhachitinous as far as can be seen. None of the centra is preserved in its natural position, but disarticulated inter- and pleurocentra lie scattered in the matrix (Figs 1, 8A, 8C, 9). Intercentra are wedge-shaped in lateral view, bearing a rib facet in typical fashion, while pleurocentra are elongately rhomboidal in outline. There is no evidence for any pleurocentra being fused dorsally as in *Whatcheeria*, but not many can be seen, so this feature could, in fact, be present. Similarly, there is no evidence for intercentra that are split in the midline, but this cannot be ruled out given the split neural arches.

The number of presacral vertebrae is not clear, although it is likely that the sacral arch is present, given the presence and position of both ilia and hind limbs. Arch number 24 of the preserved sequence (probably number 25 in life) has marginally the widest and tallest spine and may be the sacral, although its transverse process is neither specialised nor enlarged, as one might expect of a sacral arch (Fig. 7C). This contrasts with the condition in *Whatcheeria*, in which the sacral vertebra and rib are described as being 'unequivocally identifiable' (Lombard & Bolt 1995: 480). The sacral rib of *Whatcheeria* is robust (Bolt & Lombard 2000) contrasting with the short and pointed presacrals, while the transverse process of the sacral arch is broadened (pers. obs.). Posterior to the possible sacral in *Pederpes*, there are three more arches that lie increasingly out of line and after that the postsacral region and tail have been completely lost. *Whatcheeria* has at least 27 presacral vertebrae (perhaps up to 30: Bolt & Lombard 2000), so that an alternative possibility is that in *Pederpes*, the sacral arch is either lost or is

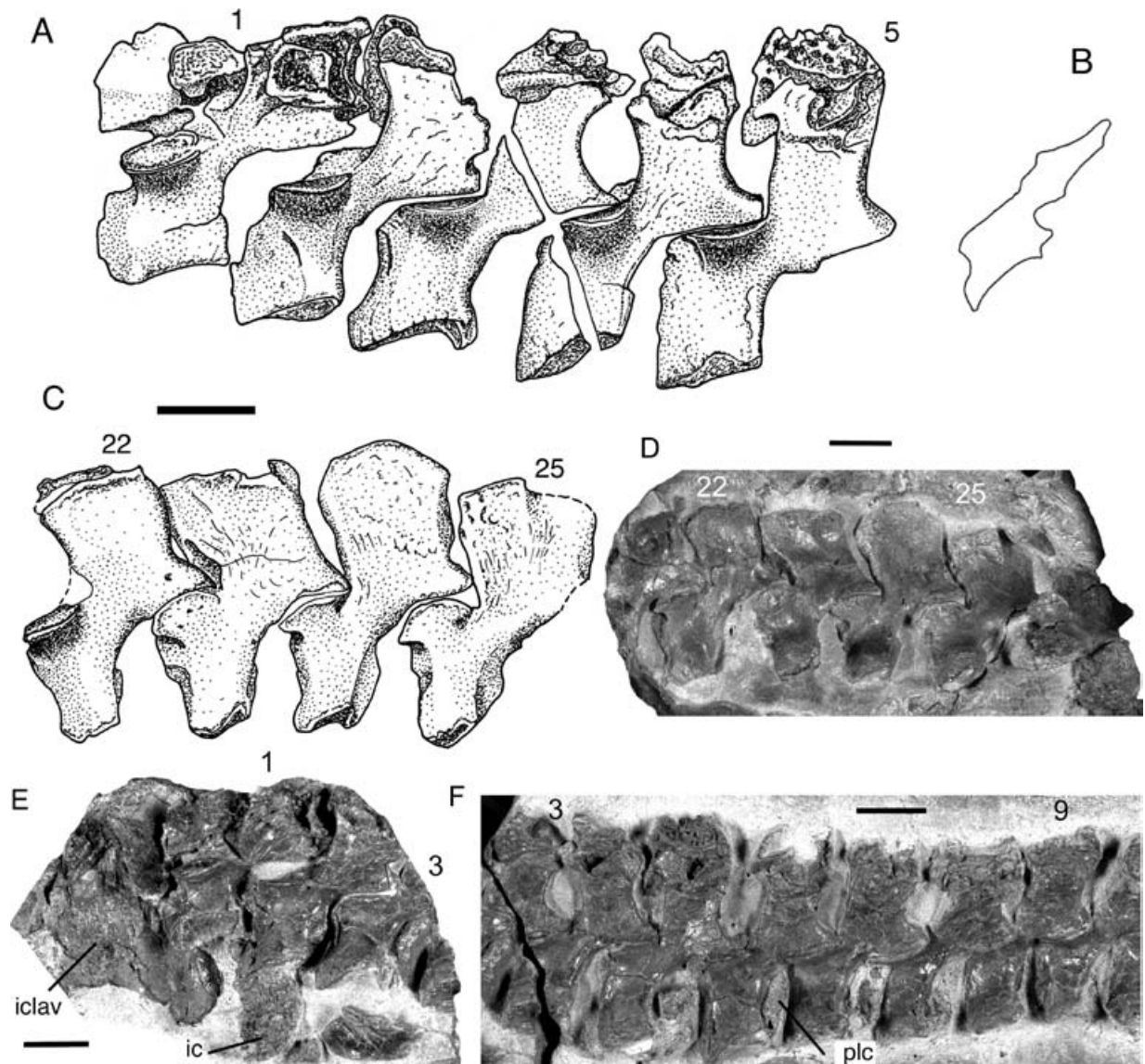


Figure 7 *Pederpes finneyae* Clack, 2002a. **A**, first five neural arches as preserved. **B**, outline of atlas arch from CT-scan. **C**, vertebrae 22–25 as preserved. Number 24 may be the sacral arch. **D**, photograph of same view as show in **C**. **E**, photograph of arches 1–3 (seen also in **A**). **F**, photograph of arches 3–9 (compare 3–5 in **A**). Scale bars = 10 mm.

the 27th preserved, which is exposed only in ventral view. Even in its case, however, the transverse processes are not enlarged.

Ribs

The ribs of *Pederpes* constitute one of its most conspicuous and unusual features, in that a distinctive ‘thoracic’ set bears triangular to rectangular overlapping flanges of unique design, decreasing in size posteriorly (Figs 1, 10). The ‘thoracic’ ribs of *Whatcheeria* likewise carry expanded distal flanges, although they are different in shape and have not been described in detail. The first preserved rib in *Pederpes* is assumed to have been the axial. In their natural sequence posterior to that lies a series of 12 ribs. Posterior to these, at least six have been exposed, but it is not entirely certain whether all belong to the left side or whether

some, that have their proximal ends orientated away from the column, originally belonged to the right side. It is clear that many ribs lie in the matrix on the right and future preparation or CT scanning could clarify this question. In the following description the ribs will be referred to by their numbers in the preserved sequence. The first appears to expand distally and bears a bifurcated end, although it is poorly preserved. Rib 2 is slightly expanded distally but un-notched, whereas rib 3 is not only slightly expanded but is also incised by a notch at its posterodistal corner. Rib 4 begins a series of increasingly unusual and expanded distal ends, having a slender posterodorsally pointing process extending from about 12–13 mm from its distally expanded and otherwise rectangular end. Ribs 5 and 6 each have a large, almost rectangular distal expansion and each carries a slender process that lies parallel to the proximal edge of the flange and contacts or nearly contacts it posteriorly to leave an opening between the process

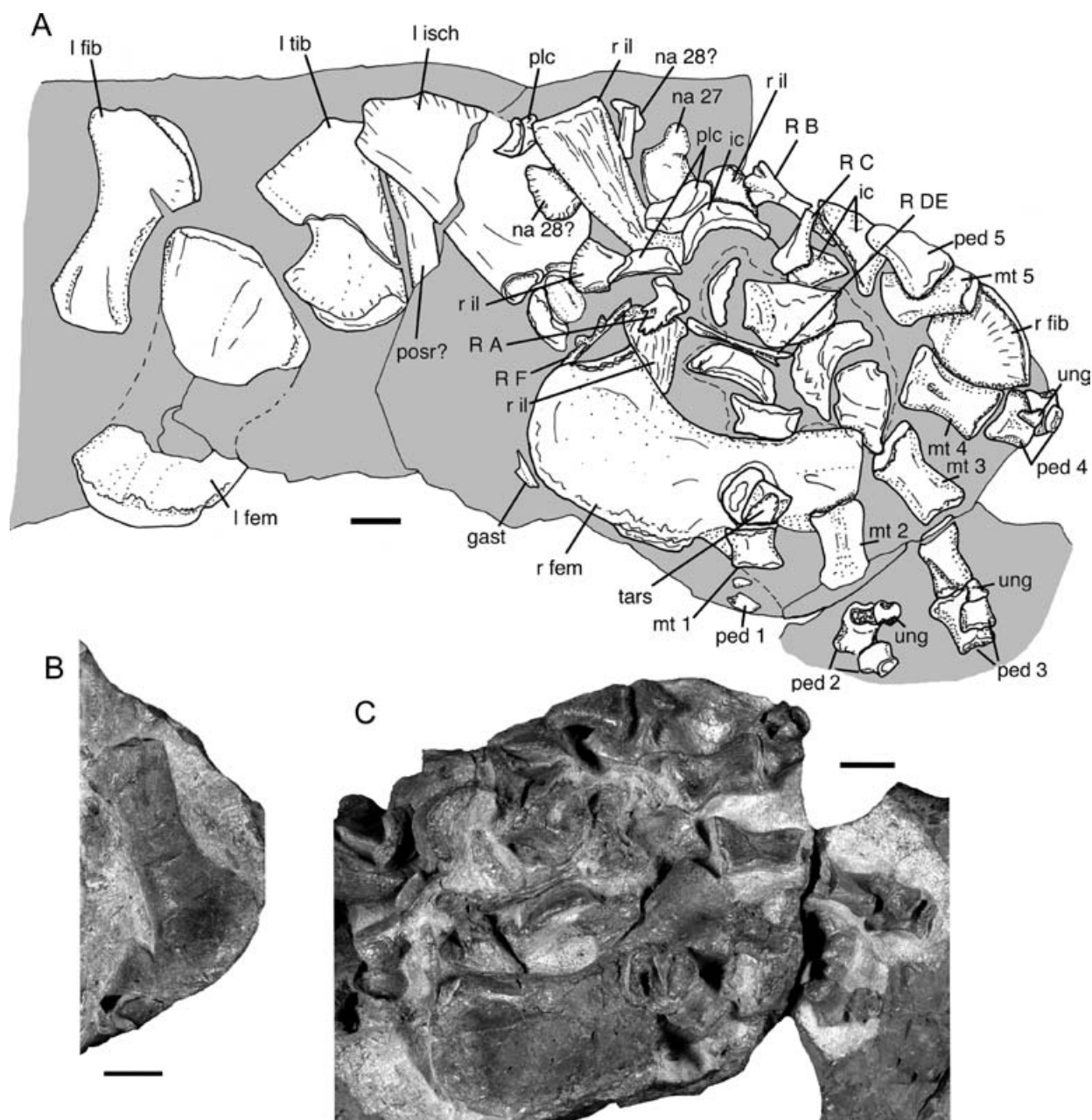


Figure 8 *Pederpes finneyae* Clack, 2002a: elements from the region of the hind limb. **A**, map of the hind limb region from the underside of the specimen. Dotted line indicates position of the group of centra shown in Fig. 9. R A, R B, R C, R DE and R F are presacral ribs shown in Fig. 10. **B**, right tibia (see Fig. 16D). **C**, photograph of right femur and digits, seen in **A**. Scale bars = 10 mm. For other abbreviations used, see the text.

and the rectangular flange (Figs 10G, H). There is nothing similar reported in *Whatcheeria*, nor any other tetrapod to our knowledge with the exception of *Ichthyostega*. Jarvik (1996: pl. 44) figured similar openings in some isolated ribs of *Ichthyostega*. In other respects, such as the thin and irregular posterior edge of the expanded portion and the overlap between ribs, those of *Pederpes* most closely resemble those of *Ichthyostega*, although the former are much shorter and less robust (see Discussion, below for further consideration of the rib morphology).

From rib 10 to rib 12 the posterior expansion reduces in size, its shape distally becomes more rounded, although there is a distal notch in its margin (Fig. 10I). Each rib also

bears one or two small pointed processes along the anterior or posterior margins of the shaft. Posterior to rib 12 the ribs become more or less parallel-sided. No more ribs are preserved in situ but the block containing the hind limb and pelvic girdle shows some extraordinary short ribs that bear a variety of processes and flanges best conveyed by illustrations (Figs 10A–F). These could be immediately presacral or postsacral ribs, but parts of long, robust ribs, presumably postsacral, are preserved in the region of the pelvic girdle and hindlimb. Short pointed presacral ribs occur in *Crassigyrinus* (Panchen 1985).

Like those of *Whatcheeria*, the ribs of *Pederpes* are bicipital in the sense of having articulations with both the

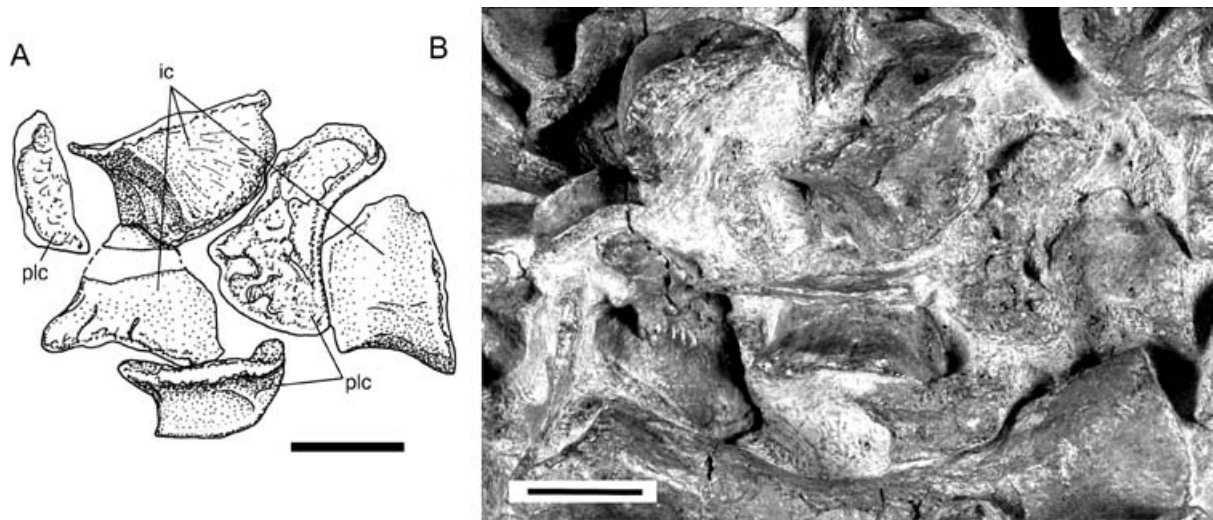


Figure 9 *Pederpes finneyae* Clack, 2002a: central elements. **A**, detail of elements outlined in Fig. 8A. **B**, close-up photograph of the same central elements, with ribs RA and RDE (see Figs 8 & 10) also visible. Scale bars = 10 mm. For other abbreviations used, see the text.

transverse process and the intercentrum, but the two heads are joined by a web of bone and are not clearly differentiated.

Appendicular skeleton

Pectoral girdle

Most of the pectoral girdle is represented, including both clavicles, both cleithra (probably) and the interclavicle, together with parts of both scapulocoracoids (Figs 1, 11). All elements are probably complete and lie almost in their natural position, but it has not been possible to expose all parts.

The clavicle is rather unusual in several respects. Conspicuously, the anterior margin is deeply striated, ridged and grooved, which is unlike anything described in other early tetrapod clavicles (Figs 11D, E). More usually, the anterior clavicular margin is smooth and unornamented, as in *Tulerpeton* (Lebedev & Coates 1995) or is marked by a simple groove as in *Crassigyrinus* (Panchen 1985). The striations in *Pederpes* diverge from approximately the mid-point of the anterior margin, where there is a tiny process. The striations appear most like those of an interdigitating sutural surface and, indeed, they are also found on the internal surface of the narrow dorsal clavicular blade at the point where it probably clasped the cleithrum, while matching striations are present at the base of the stem of that bone. However, the anteroventral margin of the dermal girdle does not suture with any other bone in tetrapods, so these striations in *Pederpes* must be for some other purpose. Where dermal bone is sunk into soft tissue, the surface usually becomes smooth (e.g. the anterior edge of the clavicle in *Tulerpeton*: Lebedev & Coates 1995) rather than ornamented, so the reason for the striations in *Pederpes* is unknown. The remainder of the external surface of the ventral plate bears elongate ridges and grooves similar to those on the suspensorium. The external surface of the clavicle in *Whatcheeria* is unornamented, as on the dermal skull roof.

The overall shape of the clavicle is also slightly unusual, being a rather elongate wedge with no sharp distinction between the ventral plate and the dorsal process. In this,

it resembles *Whatcheeria*, although the bone is relatively narrower overall. It has been flattened into a single smooth open curve, but probably there was more acute curvature where the ventral plate passed into the dorsal process. The dorsal process is roughly triangular in cross-section, having two striated planes (anterior and posterior) and one smooth and convexly rounded (mesial: only visible on the right side). This contrasts with at least one specimen of *Whatcheeria* (unnumbered, pers. obs.) in which anterior and posterior faces are grooved. Clavicles whose ventral plates are comparably narrow occur in *Crassigyrinus* (Panchen 1985), *Eucritta* (Clack 2001) and *Baphetes* (Milner & Lindsay 1998), although that in *Pederpes* lacks anything like the boss on the anterior margin of the latter. The dorsal process of the right clavicle has also been exposed and shows its anterior and mesial faces.

The cleithrum (Figs 11A, B) is also unique, sharing some characters with several Carboniferous tetrapods but being closest in shape to that of *Ossinodus* (Warren & Turner 2004). It has a narrow, tapering stem with a short expanded dorsal plate. It does not resemble that of *Whatcheeria*, which has a relatively much larger dorsal plate, marked by a deep notch in its posterior margin. In *Pederpes*, much of the posterodorsal margin is overlain by ribs, but a small notch is visible, although not comparable in size to that of *Whatcheeria*. Almost the entire dorsal margin of the blade is fimbriated and is marked off from the stem by a small notch in the anterior margin. Much of the external surface of the stem is finely striated and grooved and its anterior edge bears a deep groove similar to that in *Pholiderpeton* (Clack 1987a). It presumably housed some soft tissue such as a ligament securing the suture between clavicle and cleithrum (whichever of two alternative sutural relationships obtained—see below). There is no postbranchial lamina anteriorly and the posterior edge of the stem is drawn out into a knife-edge, giving an essentially triangular cross-section not unlike that of *Pholiderpeton* (Clack 1987a; Fig. 11B x–y). The interarticulation between cleithrum and clavicle is discussed further below.

There appears to be no anocleithrum, although this is not quite certain. Part of a thin oval-shaped bone with fimbriated

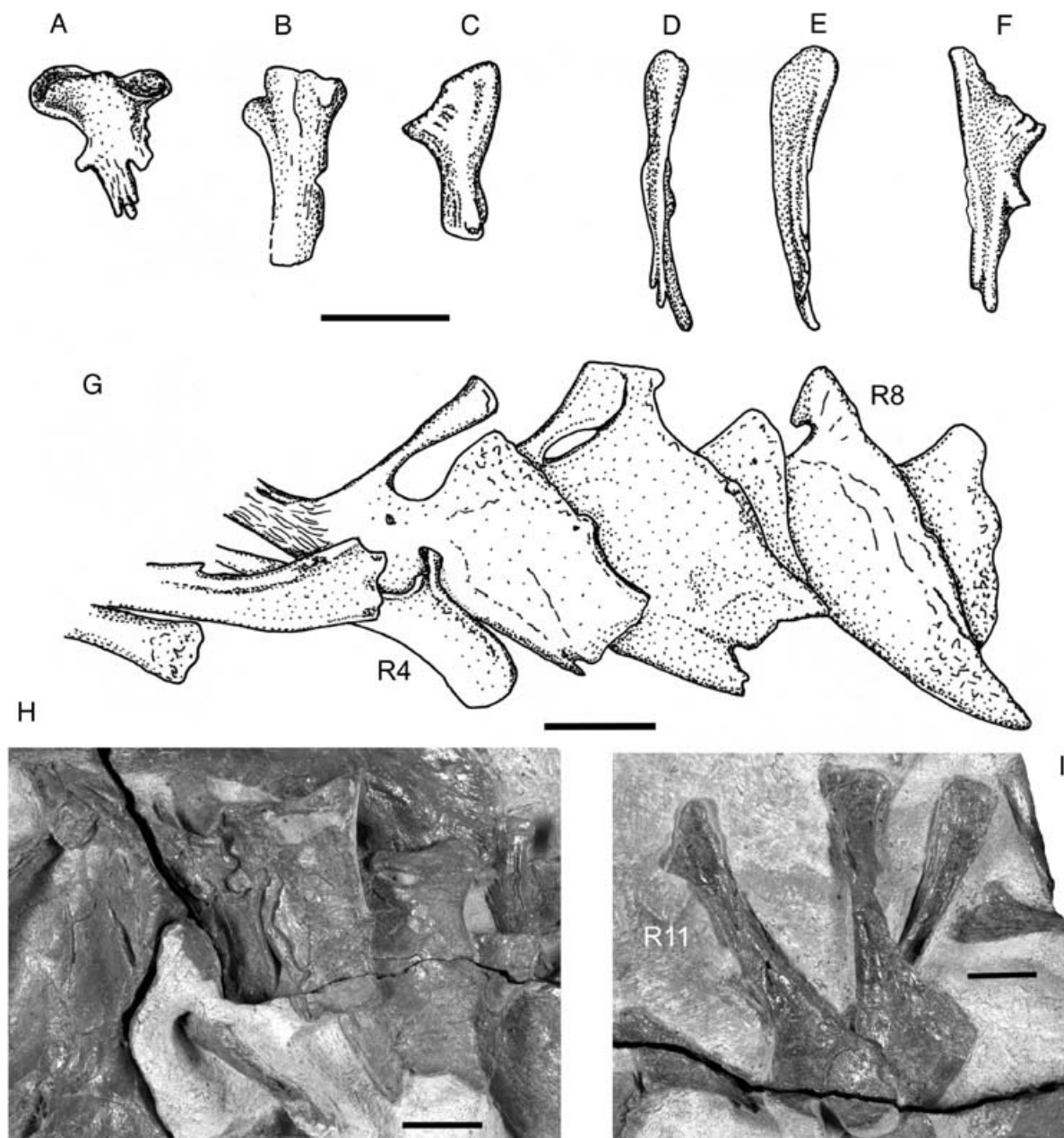


Figure 10 *Pederpes finneyae* Clack, 2002a: ribs. **A–F**, presacral ribs seen in Fig. 9; **D** and **E** are two views of the same rib. **G**, ribs 2–9. **H**, photograph of flanges on ribs 4–9. **I**, ribs 11–13. Scale bars = 10 mm.

edges from the right side lies close to the right humerus, but has been exposed from the upper surface of the specimen. It has been interpreted as part of the right cleithrum (Fig. 1). However, there is no evidence of a stem associated with this bone and close to it, exposed on the underside, lies a robust bone with a notch in it. This has been interpreted as part of a rib. Alternatively, the 'right cleithrum' may be part of an anocleithrum and the notched bone the cleithrum. Unfortunately because any cleithral stem would lie between forelimb and vertebral elements, it would be impossible to prepare out. CT scanning may resolve this issue.

The interclavicle (Figs 11F, G) is very broad and although much of it is inaccessible, sections through the bone show it to be substantial, allowing extrapolation of its size in

conjunction with visible true edges. Its ventral surface centrally is marked by small pits lying in transverse grooves, whereas anterior and posterior to this the orientation changes to longitudinal ridges and grooves. Further towards the edges, the ridges and grooves radiate outwards towards the margins. The slightly depressed area formerly occupied by the left clavicle can be seen, while the right clavicle lies more or less in its natural position: this suggests that the clavicles did not meet (or at most, met only at their anterior tips). The main body of the bone is rhomboidal and is tucked up very close to the head between the suspensoria, probably close to its natural position. The posterior part of the bone is drawn out into a narrow parasternal process whose full length can not be estimated. However, it is relatively thin and flat, unlike

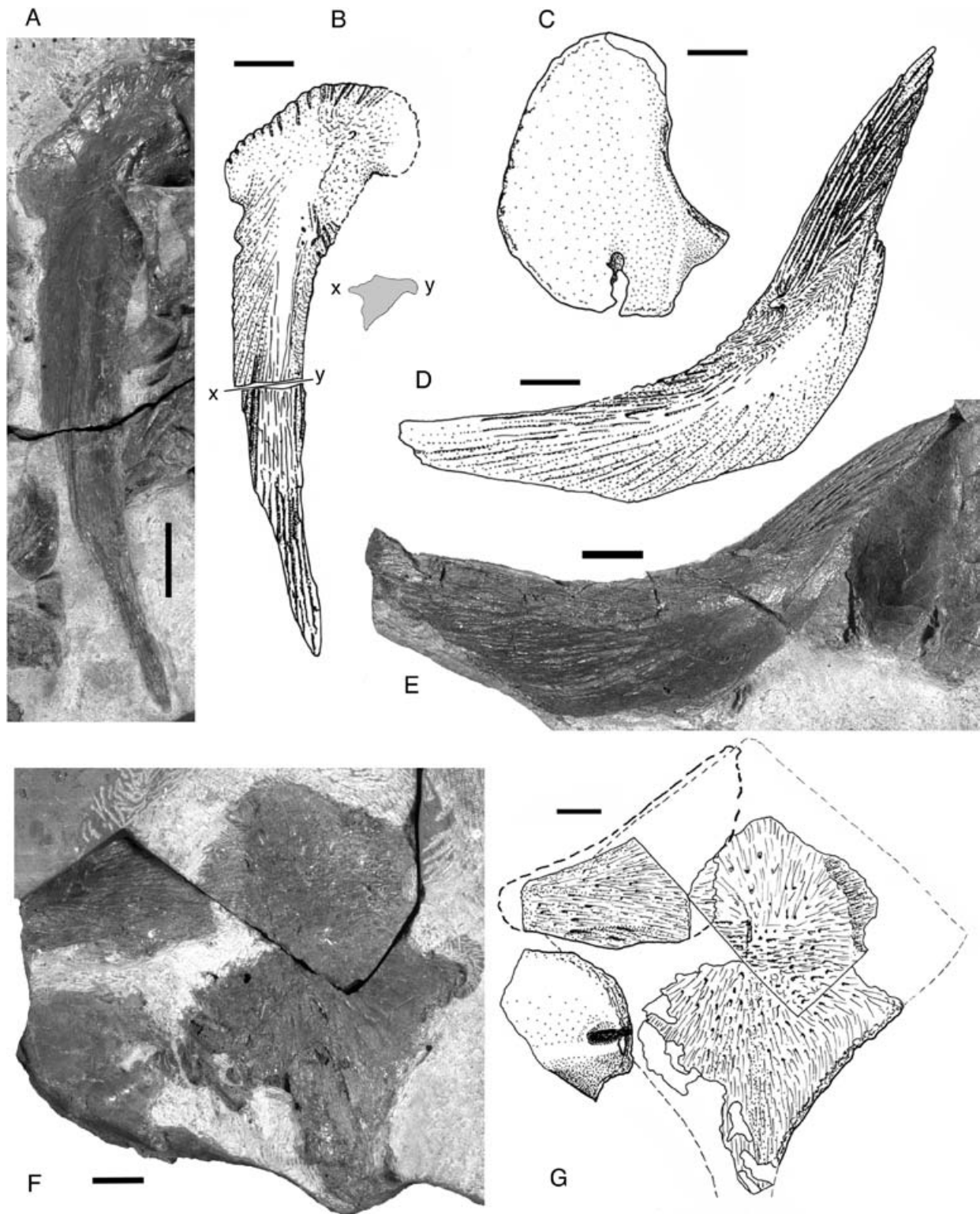


Figure 11 *Pederpes finneyae* Clack, 2002a: pectoral girdle. **A**, photograph of left cleithrum. **B**, drawing, with inset cross-section x-y. **C**, left scapulocoracoid. **D**, left clavicle. **E**, photograph of left clavicle and part of scapulocoracoid. **F**, photograph of interclavicle, right clavicle and scapulocoracoid, in their preserved positions. **G**, drawing of view shown in **F**. Light broken line is the inferred outline of the interclavicle; heavy broken line is the inferred outline of the ventral clavicular plate. Scale bars = 10 mm.

the robust parasternal process in *Whatcheeria*. There is no doubt that, measured from the centre of radiation, the anterior portion of the interclavicle was shorter than the posterior, a condition that seems to be primitive for tetrapods. It is pos-

sible that the anterior part of the rhombus was actually shorter than estimated here, giving it a shape more comparable with that of *Whatcheeria*, however, the bone is so thin and friable that it was judged wiser not to prepare it further. The

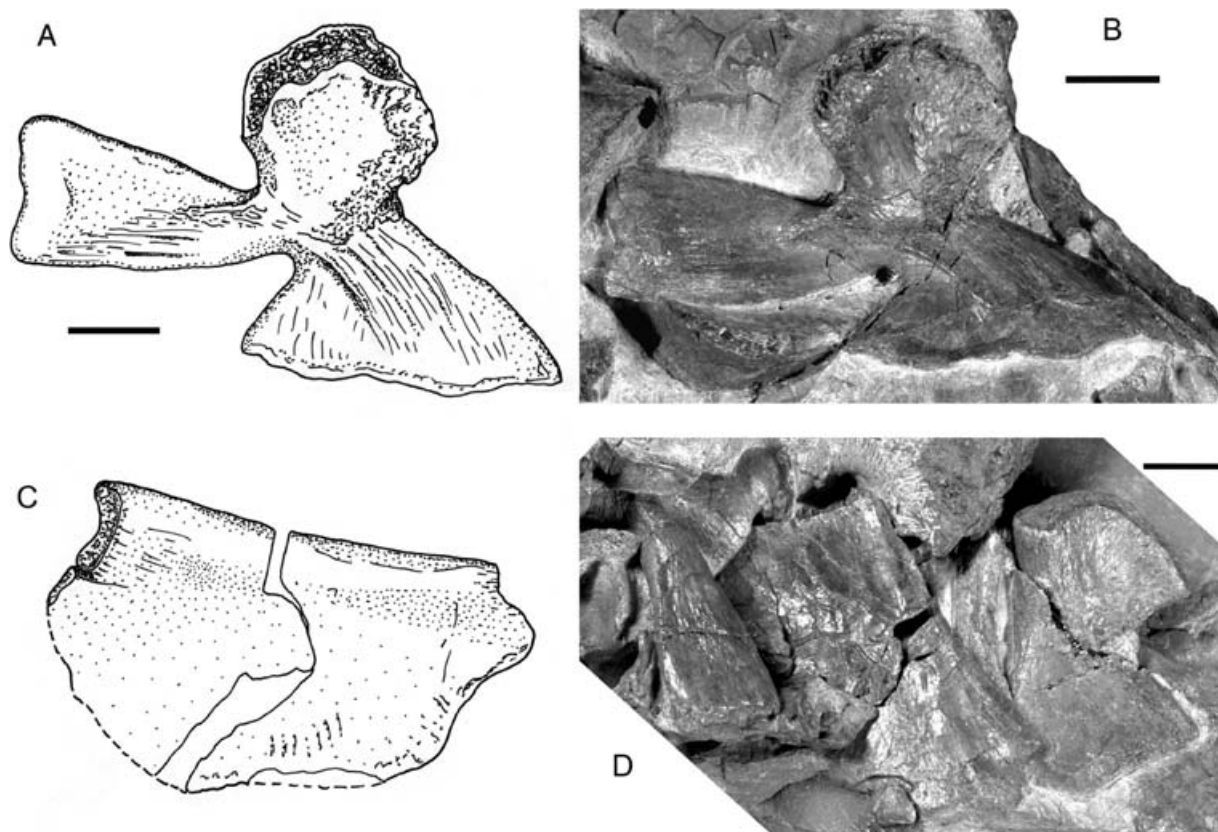


Figure 12 *Pederpes finneyae* Clack, 2002a: pelvic girdle. **A**, left ilium in mesial view. **B**, photograph of left ilium. **C**, left ischium in lateral view. **D**, photograph of left ischium with postiliac process of right ilium seen on the left and the left tibia seen on the right (see also Fig. 8A). Scale bars = 10 mm.

interclavicle of *Ossinodus* (Warren & Turner 2004) is similar in shape to that envisaged here for *Pederpes*.

Only the scapular portion of the endochondral pectoral girdle is preserved, as an apparently separate entity from the coracoid, the latter not being represented as an ossification (Fig. 11C). The coracoids may have been entirely cartilaginous; since all other parts of the girdle and both humeri remain close to life position, it seems unlikely that the coracoids have been lost from the specimen. Separate scapular and coracoid ossifications are found in *Whatcheeria* (at least in some specimens). There is a supraglenoid foramen in *Pederpes*, but because the glenoid region of the scapular appears not to have been ossified (both sides show this), the foramen is open ventrally. This is also seen in one of the scapulocoracoids attributed to *Ossinodus* (Warren & Turner 2004). The supraglenoid buttress is broad and robust, visible along one of the fractures across the nodule.

Pelvic girdle

Both ilia are present: the left is exposed in internal view and the right in external, although only small parts of the latter are visible. The left ischium is preserved and exposed in lateral view (Fig. 12). There is no evidence of an ossified pubis, a phenomenon frequently encountered in early tetrapods eg. *Silvanerpeton* (Clack 1994c), *Eldeceeon* (Smithson 1994), *Eucritta* (Clack 2001) and *Crassigyrinus* (Panchen & Smithson 1990). This is not the case in the figured specimen of *Whatcheeria* (Lombard & Bolt 1995), in which the pelvis

appears as a single ossified unit. However, in some specimens (pers. obs.) the three pelvic ossifications are separate.

The ilium (Figs 8A, 12A, B) has both a dorsal blade and a posterior iliac process, as has *Whatcheeria* and as seems to be primitive for tetrapods. However, the shapes of the blade and process are rather different from those of *Whatcheeria*. In the latter animal, both features are rather broad, whereas in *Pederpes* they are more compact. The dorsal blade is fan-shaped, with a relatively narrow neck and an unfinished dorsal margin. It is set off mesially from the plane of the posterior process and the two are separated by a smooth groove, as in *Whatcheeria*. However, whereas in *Whatcheeria* the two features overlap anteroposteriorly in lateral or mesial view, they are entirely separate in *Pederpes*. The posterior process expands slightly proximodistally and apart from the distal face, the margins are smooth. There are fine striations along the length of the posterior process but not the deep ridges found there in *Whatcheeria*. A sacral rib may have attached at the base of the dorsal blade, at a region of rugose bone near the anterior margin, but there is no other evidence for a point of attachment on the blade itself. This position for a sacral rib attachment is similar to that suggested by Coates (1996) for *Acanthostega*. Nothing of the acetabulum can be seen on the ilium.

The ischium (Figs 8A, 12C, D), roughly D-shaped, has a robust dorsal margin but is very thin and delicate for the most part. It shows a pair of facets along its proximal margin, that are separated by a groove. Presumably this would have allowed passage of a blood vessel or nerve, but the hole so

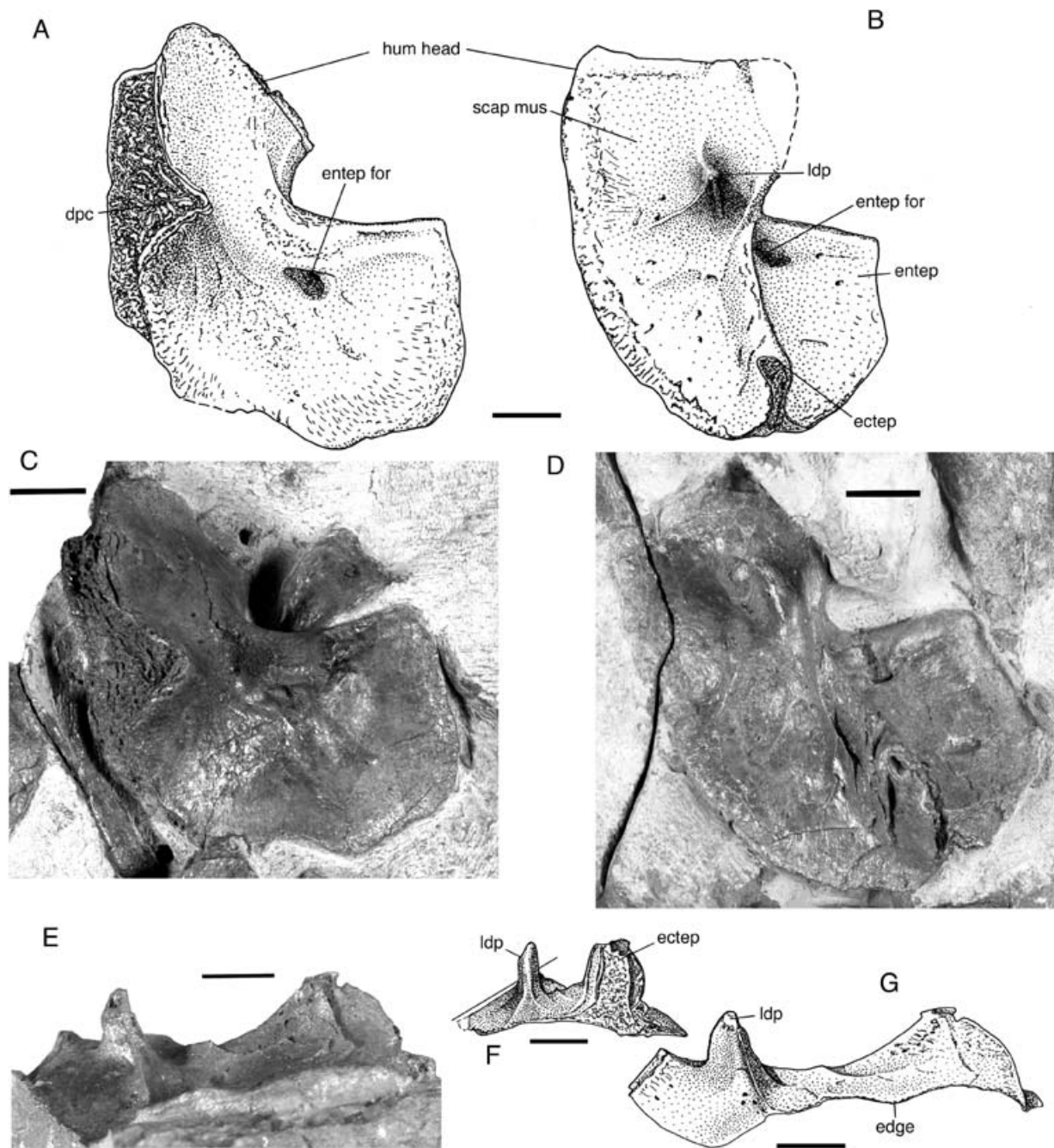


Figure 13 *Pederpes finneyae* Clack, 2002a: forelimb. **A**, right humerus in flexor view. **B**, left humerus in extensor view. **C**, photograph of right humerus in flexor view. **D**, photograph of left humerus in extensor view. **E**, photograph of left humerus from anterior to show latissimus dorsi process. **F**, drawing of humerus from anterodistal viewpoint to give another view of the latissimus dorsi process and showing the angle of the caput humeri (oblique line). **G**, drawing of same view as that shown in **E**. Scale bars = 10 mm. For abbreviations used, see the text.

formed does not seem to be one of the obturator foramina, which usually lie in the pubic plate. The facets might have formed part of the acetabulum, but as with the ilium, the shape of the acetabulum cannot be inferred.

Forelimb and manus

Both humeri, the right radius and ulna and two digits from the right manus are preserved. Fortunately, the humeri show both dorsal (extensor) and ventral (flexor) surfaces between them (Fig. 13). The humerus has the typical L-shape found

in early tetrapods, with an anteroposteriorly broad, squarish caput humeri, a large, more or less rectangular entepicondyle with an entepicondylar foramen, a prominent ectepicondyle and a large deltopectoral crest. There are no accessory foramina (c.f. *Acanthostega* (Coates 1996), *Ichthyostega* (Jarvik 1996), *Tulerpeton* (Lebedev & Coates 1995) and *Crassigyrinus* (Panchen 1985)). The right and left humeri are 68 and 60 mm long, respectively.

On the extensor surface there is an anterodorsal depression that is probably for the scapulohumeralis muscle (see Coates 1996 for terminology and caveat in interpreting

muscle anatomy of very early tetrapods). This depression is bounded distally by a slight ridge, which is confluent with the most conspicuous feature of the humerus, a spike-like latissimus dorsi process (Figs 13B, E–G). Only one other early tetrapod humerus approaches this condition, that being *Baphetes* (Milner & Lindsay 1998), but some specimens of *Whatcheeria* had a process in a similar position (pers. obs.). However, most of these are crushed, so it is not possible to estimate the height of the process. Posterior to the latissimus dorsi process, the extensor surface is smoothly concave. Distal to the latissimus dorsi process, again the surface is mainly smooth, with a very low ridge separating a pair of very shallow depressions. Tiny nutrient foramina pierce the surface, which is otherwise essentially featureless, lacking any trace of a supinator process. There is no equivalent to ‘process 2’ of *Ichthyostega* (Jarvik 1996) or *Acanthostega* (Coates 1996). The latissimus dorsi process is a little offset from the course of the ectepicondyle: to have them in line is a feature of more derived tetrapods (Coates 1996). In *Acanthostega*, *Ichthyostega* and closely related tetrapodomorph fishes, the latissimus dorsi region is positioned noticeably anterior to the line of the ectepicondyle, but in *Baphetes*, *Whatcheeria* and *Pederpes*, the process is only slightly more anterior.

The ectepicondyle rises steeply from the anterodorsal surface into a prominent buttress with an unfinished distal termination. It does not protrude beyond the distal margin (Figs 13B, D, F, G). The entepicondyle has a thickened and rounded proximal margin, but the posterior and distal margins were unfinished, judging by the well-defined edge to the perichondral surface. It has not proved possible to prepare the unfinished surfaces of the entepicondyle in either humerus.

The anterior and distal margins of the humerus are confluent with the head and form an almost smooth curve whose surface is unfinished throughout. This surface is also confluent with the distal aspect of the ectepicondyle and also appears to pass into the distal and posterior margins of the entepicondyle. It seems unlikely that the radial and ulnar condyles were separately defined surfaces and were most likely distal in position, judging from the two available views of the humerus. The margins of the perichondral bone are pitted and striated.

On the flexor surface, the most prominent feature is the deltopectoral crest, which rises from the anterior margin as a triangular expansion to the unfinished surface, similar to that in *Baphetes*. The process continues on the flexor surface, diminishing rapidly until it is marked only by a low humeral ridge (Figs 13A, C). Distal to the ridge, the surface is marked by slight rugosities and pits.

The caput humeri is set at an angle of about 35 degrees to the distal condyles, as far as can be established (there does not seem to have been any dorsoventral compression in this humerus, given the state of the latissimus dorsi process). A low angle is found in many early tetrapods, ranging from about 25–30 degrees in *Acanthostega* (Coates 1996) and *Greererperton* (Godfrey 1989b), through 37–40 degrees in *Proterogyrinus* (Holmes 1984) and 45 degrees in *Eoherpeton* (Smithson 1985).

Radius and ulna are preserved in ventral (flexor) aspect and their distal articular surfaces are visible (Fig. 14). Radius and ulna are of approximately the same length, as in *Tulerpeton*, but there is no olecranon process on the ulna of *Pederpes*, in contrast to *Tulerpeton*. The radius is about 62%

of the length of the humerus, this being relatively longer than in *Baphetes*, where the figure is 49% (Milner & Lindsay 1998). Otherwise, the radius of *Pederpes* closely resembles that of *Baphetes*. It is slightly waisted with expanded proximal and distal ends, although as with *Baphetes* it is less slender than those of many Carboniferous tetrapods such as the embolomeres *Proterogyrinus* (Holmes 1984), *Pholiderpeton* (Clack 1987a) and *Archeria* (Romer 1957), or *Greererperton* (Godfrey 1989b). The flexor surface is marked by a small foramen and bears rugose ridges along both anterior and posterior margins. Although only the flexor surface is visible, a break through the bone shows that the cross-section is rectangular (Fig. 14A, beneath). This suggests that, like the flexor surface, the extensor surface was also marked by longitudinal ridges as in *Baphetes* (Milner & Lindsay 1998), *Ossinodus* (Warren & Turner 2004) and embolomeres. The flexor surface is concave and the distal surface reflects this (Fig. 14C).

The ulna is of similar proportions to the radius, although its anterior (as preserved) surface is more concave. Like the radius, it is stouter than those of most other early tetrapods. There is a rugose region mid-way along the shaft on the posterior surface, that does not seem to be found in other early tetrapods (Fig. 14B). However, the distal articular surface is oval in section and bifaceted in typical early tetrapod fashion. Radius and ulna are not described for *Whatcheeria*, but several specimens preserve them. Their proportions are quite similar to those of *Pederpes*, but some are more flattened. Those associated with the uncatalogued humerus noted above and labelled ‘24’ are particularly similar to those of *Pederpes* (pers. obs.).

Pederpes has the shortest ulna relative to the radius of any early tetrapod whose measurements are available, with the exception of *Acanthostega*. Using illustrations from the literature and measuring at the midline (discounting the olecranon where present), the following figures were obtained for the ulna as a percentage of radius: *Acanthostega* 1.36% (Coates 1996), *Pederpes* 95%, *Crassigyrinus* 93% (Panchen 1985), *Silvanerpeton* 92% (Clack 1994c), *Proterogyrinus* 92% (Holmes 1984), *Archeria* 84% (Romer 1957), *Eldeceon* 84% (Smithson 1994), *Pholiderpeton* 82% (Clack 1987a), *Gephyrostegus* 82% (Godfrey 1989b), *Ichthyostega* 82% (Jarvik 1996). It is not clear whether a shorter ulna is primitive or associated with an aquatic lifestyle.

Two manual digits, one articulated and one slightly disarticulated, are preserved and have been described previously (Clack 2002a). There is also a possible ungual from a third digit, although it is very elongate (Fig. 14D). If correctly interpreted, it suggests considerable variation among the manual digits. The articulated digit is short and stout and somewhat flattened, with three phalanges, wider than long, whose proximal and distal margins are flared (Figs 14D, 15B, E). There are no obvious grooves in the proximal or distal margins for ligamentous attachments (c.f. *Casinaria*: Paton *et al.* 1999). The ungual is very small. A metacarpal and a carpal are associated with this digit, so that its phalangeal formula is clear. Articulated digits similar in proportion to this are seen on the holotype of *Whatcheeria* and other articulated specimens, however, it is not clear which of these are manual and which pedal digits. In the holotype they are found in association with the tibia and fibula, but in at least one other specimen they appear to be associated with the radius and ulna (pers. obs.).

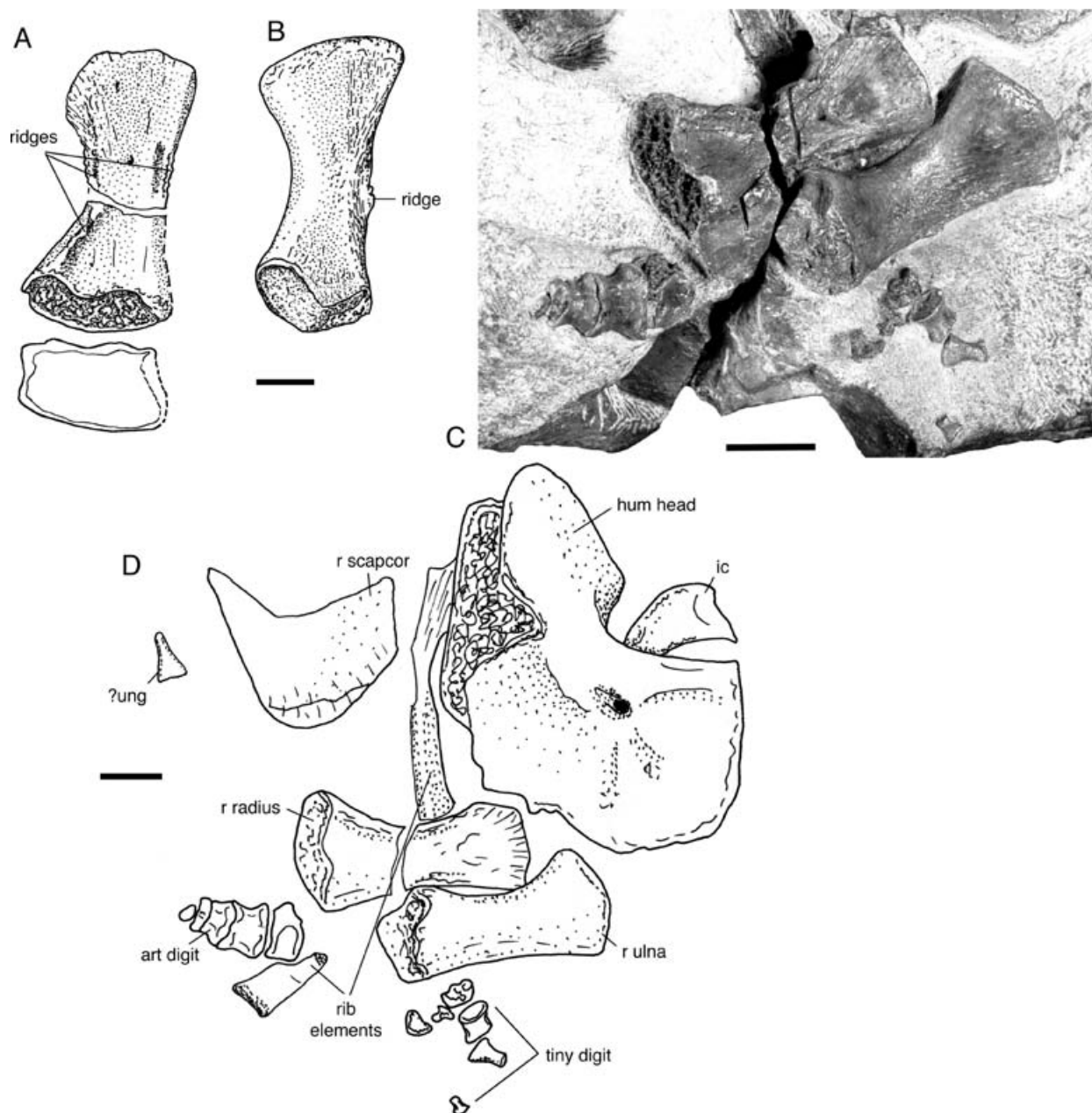


Figure 14 *Pederpes finneyae* Clack, 2002a: forelimb elements. **A**, right radius in flexor view. **B**, right ulna in flexor view. **C**, photograph of radius ulna and manual digits as preserved. **D**, drawing of right humerus, radius, ulna, digits and additional elements as preserved. Scale bars = 10 mm. For abbreviations used, see the text.

The disarticulated manual digit of *Pederpes* is tiny (Figs 15A, D). The ungual is not preserved, but the smallest phalanx present bears an articular surface for an additional element. Only an ungual has been restored, judging by the size of the facet. One of the three spool-shaped bones may be a metacarpal, but there are also three other ossifications of unusual shape which may rather be the remains of metacarpals or strangely shaped carpals (Figs 14D, 15A). One of these is a crescent-shaped perichondrally sheathed element. It was suggested (Clack 2002a) that this digit may represent a supernumerary as in the manus of *Tulerpeton* (Lebedev & Coates 1995) or in the pes of *Ichthyostega* (Coates & Clack 1995) or *Acanthostega* (Coates 1996). It lies close to the ulna,

as does the sixth digit of the manus of *Tulerpeton*. Figure 15 (D, E) shows the restored digits to the same scale to emphasise the minute proportions of the possible supernumerary digit. The digits are further discussed below.

Hindlimb and pes

Femora, tibiae and fibulae from both sides are preserved (Figs 8A, 8C, 16). The left femur is badly fractured and lacks much of its central portion, but it has been possible to remove it from the matrix, as with the left fibula. Part of the flexor surface of the right femur is exposed, as is the whole of the extensor surface of the right fibula: the left tibia is exposed

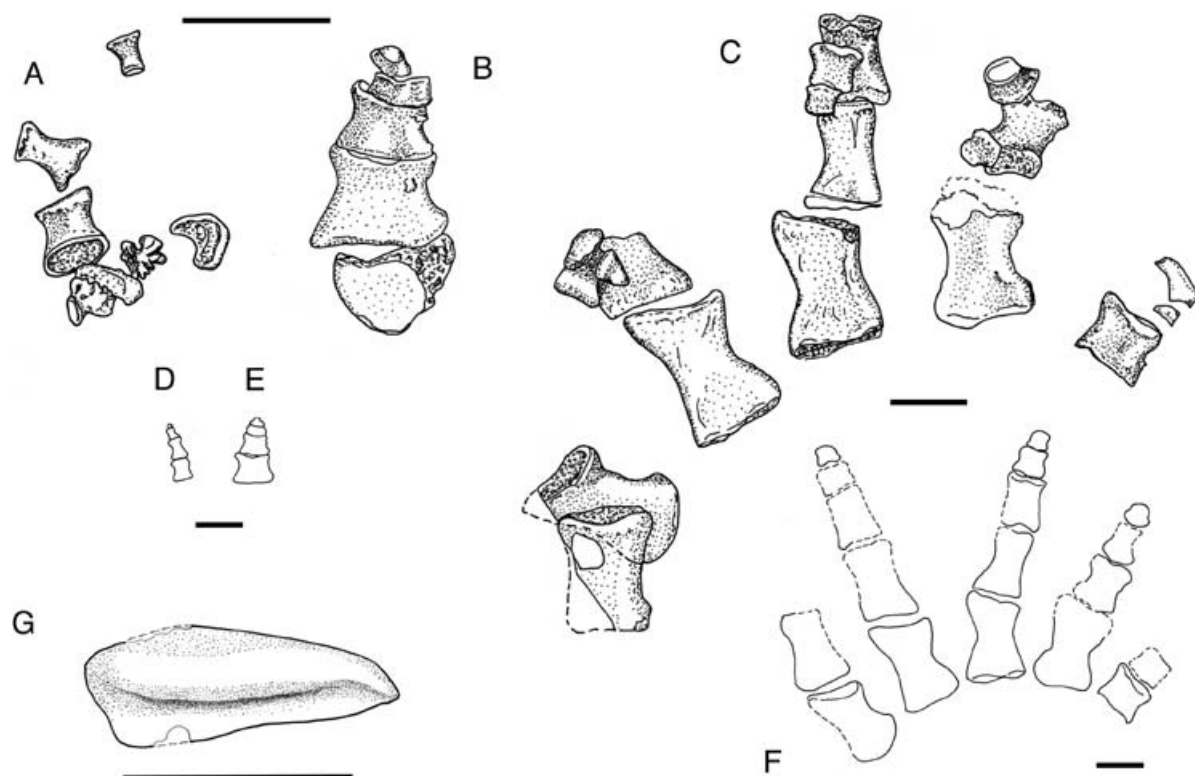


Figure 15 *Pederpes finneyae* Clack, 2002a. **A**, possible supernumerary manual digit. **B**, articulated manual digit with carpal bone. **C**, pedal digits in flexor view. **D**, **E**, **F**, restorations of the digits shown in **A**, **B** and **C** respectively, drawn to the same scale. **G**, gastralium in internal view. Scale bars = 10 mm.

in flexor view. The right tibia is preserved close to the end of the right femur but lies vertically in the block. It has been proximodistally compressed and only the proximal third is informative. Five digits of the right pes are represented and have been described previously (Clack 2002a). In three of them most phalanges and unguals are represented (Figs 8A, 8C, 15C, 15F), preserved with their tips flexed under.

As with the humeri, right and left femora reveal complementary aspects of the bone, although they do not provide a complete picture (Fig. 16). The right femur is 65 mm long and the left is 60 mm, a discrepancy similar to that found between the right and left humeri. This discrepancy may result from differential distortion, but may also indicate 'right-handedness' in the animal. Godfrey (1989b) records dimensions for the limb elements of *Greererpeton* and they show inconsistent discrepancies between left and right sides, so caution must accompany such an interpretation.

Despite its damage, the complete length of the left femur seems to be represented. The head of the left femur is 30 mm wide, but the corresponding measurement for the right is hard to estimate as its boundaries are unclear. The femur is short and stout, being about the same proximodistal length as the humerus, a condition that is found not only in *Whatcheeria* (Bolt & Lombard 2000), but also in *Proterogyrinus* (although some of the length of the humerus in the latter is accounted for by the distally angled entepicondyle: Holmes 1984). In the Devonian tetrapod *Acanthostega*, the femur is about 25% longer than the humerus (Coates 1996) and is relatively a little longer in *Tulerpeton* (Lebedev & Coates 1995). The relative proportions of humerus to femur in *Ichthyostega*

is still unknown (Coates & Clack 1995) so the primitive condition for this character is uncertain. In more derived tetrapods, the femur is often substantially longer than the humerus.

The femur of *Pederpes* is very broad for its length and, in this, most closely resembles the femur of *Ichthyostega*. In addition to its unusual proportions, the femur of *Pederpes* is also unusual in that the head passes without separation into the adductor blade, with internal and fourth trochanters not clearly demarcated. The adductor blade stretches about half the length of the entire femur and there is little in the way of an adductor crest. The articulating surface of the head, seen best in the left element, is convex, broadest anteriorly and diminishing to a crest posteriorly. The intertrochanteric fossa is completely preserved in the right element: it is shallowly concave and is marked by a few nutrient foramina. Both femora show a broad, shallow fibular fossa, but the popliteal area is visible only on the left element, being hidden by phalanges on the right. Like the fibular fossa it is broad and shallow. The extensor surface can be seen only on the left element, which shows a broadly convex area proximally and a shallow intercondylar fossa. Articular surfaces, seen best on the left element, are all visible from the flexor surface.

The overall shape of the femur of *Pederpes* is not dissimilar to that illustrated for *Whatcheeria* (Lombard & Bolt 1995), although the head of the *Pederpes* femur is more rounded in profile. The distal articular surface is almost identical. However, there are many femora in the collection of *Whatcheeria* material, showing a great deal of variation, so

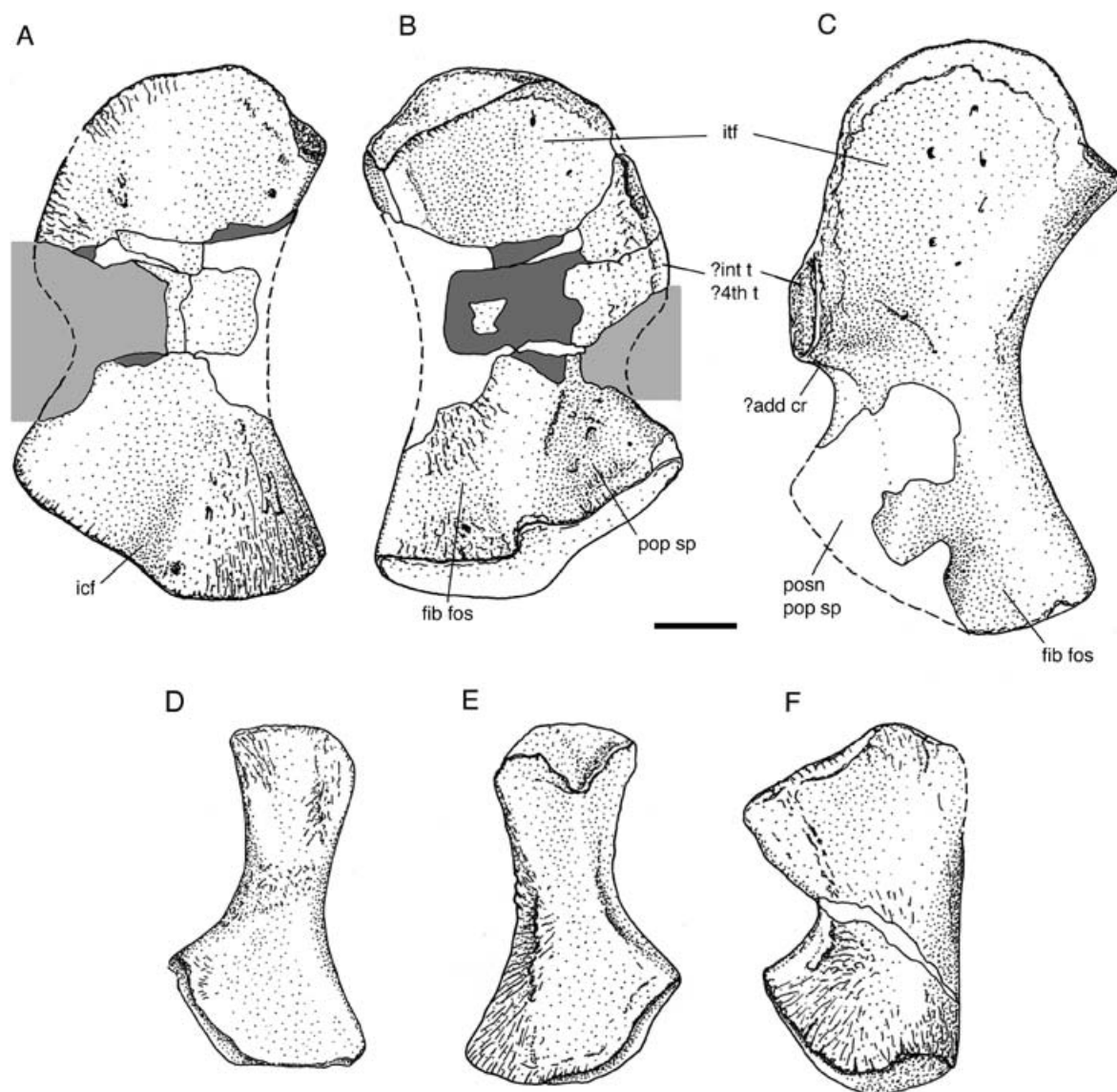


Figure 16 *Pederpes finneyae* Clack, 2002a: hindlimb. **A**, extensor and **B**, flexor surfaces of left femur. **C**, extensor surface of right femur. **D**, extensor surface of left fibula. **E**, flexor surface of left fibula. **F**, flexor surface of left tibia. Scale bars = 10 mm. For abbreviations used, see the text.

until this material is fully analysed, it is not clear how significant the comparison can be. The *Pederpes* femora also resemble a small, presumed juvenile femur associated with the material of *Ossinodus* (Warren & Turner 2004). Confluence of the head with the adductor blade and trochanters is also seen in juvenile specimens of *Greerpeton* (Godfrey 1989b); these regions became separated as the animal grew. It is also true of some *Archeria* (Romer 1957) and *Proterogyrinus* (Holmes 1984) femora, although in their case, the extent of the combined head and blade is much less, reaching only just over a third of the length of the bone. Coates (1996) suggested that a distal position for fourth and internal trochanters could be associated with aquatic locomotion, but lack of separation between the head and adductor blade could indicate a juvenile condition. This could be expected to correlate with an aquatic phase in the lives of early tetrapods up to a point, but a possible interpretation of the digits suggests that *Whatcheeria* was more fully aquatic than *Pederpes* (see

below). It is hard therefore to disentangle some of the influences at work here.

The tibia (Figs 8A, 16F) is short and broad, with proximal and distal expansions that are roughly equal in size and the narrowest point falling about halfway along the length. This contrasts with most other early tetrapods, in which the narrowest point is closer to the distal end and the proximal end is broader than the distal. Closest to *Pederpes* are the tibia associated with *Ossinodus* (Warren & Turner 2004); a juvenile specimen of *Greerpeton* (Godfrey 1989b); and in these latter two features, also *Whatcheeria*. The tibiae of *Ichthyostega* and *Acanthostega* are scarcely waisted and that of *Ichthyostega* bears a conspicuous longitudinal crest on the extensor surface, lacking in all other early tetrapods. In contrast to *Acanthostega* (Coates 1996) and *Ichthyostega* (Jarvik 1996), but like all other tetrapods, there is an open interepipodial space between tibia and fibula.

Tibia and fibula are of approximately equal length, which contrasts with *Acanthostega* and *Ichthyostega* in which the fibula is substantially shorter than the tibia and most other tetrapods in which the fibula is longer than the tibia. Exceptions to this are *Tulerpeton* (Lebedev & Coates 1995), *Whatcheeria* and *Crassigyrinus* (Panchen & Smithson 1990), in which, like *Pederpes*, they are roughly equal.

Like the tibia, the fibula (Figs 16D, E) is distinctly waisted, with the narrowest point about halfway along the shaft. The distal end is much broader than the proximal, as is typical for tetrapods. The flexor surface bears a rugose ridge along its posterior margin. The bone lacks the axial twist seen in *Acanthostega* (Coates 1996) and *Crassigyrinus* (Panchen 1985). The distal articular surface is distinctly bifaceted, marking surfaces to meet a fibulare and an intermediate, which, however, are not preserved. Tibiae and fibulae are much more flattened in cross-section than the radius and ulna, even the fibula preserved in a vertical orientation, such that the flattening is probably natural rather than a result of preservation. Despite the flattening, they are substantially more slender in extensor/flexor view than those figured for *Whatcheeria*, although again some examples from the *Whatcheeria* collection are little flattened and are much more slender than those figured. The tibiae and fibulae of *Pederpes* seem to fall between those illustrated for *Whatcheeria*, *Ichthyostega* and *Acanthostega* and those of most other early tetrapods in terms of these proportions. In terms of tibial length compared to femoral length, *Whatcheeria* and *Pederpes* have tibiae about 60% of femoral length, whereas in other tetrapods the figures are: *Ichthyostega* 68% (Jarvik 1996), *Acanthostega* 45% (Coates 1996), *Tulerpeton* 45% (Lebedev & Coates 1995), *Crassigyrinus* 45% (Panchen & Smithson 1990), *Proterogyrinus* 52% (Holmes 1984), while in *Greererpeton* (Godfrey 1989b) it varies between about 42% and 53% (figures from illustrations in the above monographs). *Ichthyostega* and *Acanthostega* both have paddle-like hind limbs, so the discrepancy between them is hard to account for, but certainly *Pederpes* and *Whatcheeria* are unusual in their proportions, more closely resembling *Ichthyostega* than other tetrapods.

Five pedal digits are represented (Figs 8A, 8C 15C, 15F). Most of the phalanges and metatarsals are longer than wide, slightly waisted and with flared articular ends. Unguals are preserved in digits II, III and IV. They are bluntly rounded in outline. A possible ungual is preserved on the left (upper) surface of the specimen (Fig. 14D), but it is rather flat and pointed in comparison, so the identity must remain in doubt. Preserved elements include all metatarsals plus: in digit I, a broken phalanx and an ungual; in digit II, two phalanges including an ungual; in digit III, four phalanges including an ungual; in digit IV parts of three phalanges including an ungual; and in digit V a single phalanx. This could give a conservative pedal phalangeal formula of 2,3,4,4,?(>2) and this is shown in the reconstruction (Fig. 15F). However, digit IV may be missing some elements. Digit V has been restored with 4 phalanges like *Greererpeton*, whose proportions the pes of *Pederpes* most closely resembles.

The flexor surface shows no notches for attachments of ligaments as seen in the Viséan tetrapod *Casineria*, in which it was suggested (Paton *et al.* 1999) that such notches indicated that the pes of *Casineria* was capable of a grasping action. However, there are small paired rugose processes at the articular margins of the phalanges of digits 3 and 4,

which may indicate muscular or ligamentous attachments between them. Cross-sections through some of the phalanges show that the flexor surface was more concave than the extensor. Three of the metatarsals and some of the phalanges of *Pederpes* are anteroposteriorly and proximodistally asymmetrical, which Clack (2002a) suggested might indicate that the foot was orientated anteriorly to facilitate terrestrial locomotion, in contrast to the more cylindrical or poorly distinguishable metatarsals of the known Devonian tetrapods. This asymmetry is sometimes 'edited out' of reconstruction drawings despite its presence in specimens (compare for example Holmes (1984) fig. 35 with Fig. 36, digits 2–4). Its presence seems to be significant and deserves further attention.

The flexion of the digits is one of the indications that the carcass might have dried up prior to burial. Similar flexion is seen in the manus of *Acanthostega*, although in its case, the body is not thought to have been transported very far (Coates 1996).

Gastralia

Sections through the nodule show that there was an extensive covering of gastralia (scutes or dermal scales) ventrally, as in most other early tetrapods. The gastralia are about 9–10 mm long and about 2 mm wide with a long oval outline (Fig. 15G). One end, assumed to be that that lay closest to the midline, is slightly more pointed than the other. The external or ventral surface is gently convex and the internal or dorsal surface is concave with a ridge along one edge, hence the comma-shaped cross-section noted above. This shape is fairly typical for an early tetrapod scale, although the proportions vary from very elongate as in *Crassigyrinus* (Panchen 1985), through moderately elongate and quite similar to *Pederpes* in *Acanthostega* (Coates 1996), to broader as in embolomeres (Clack 1987a) and *Casineria* (Paton *et al.* 1999). The surface is unornamented, as found in *Acanthostega*, embolomeres and *Greererpeton* (Godfrey 1989b) and unlike that in *Tulerpeton* (Lebedev & Coates 1995). *Pederpes* differs significantly from *Whatcheeria*, which appears to lack gastralia altogether.

RECONSTRUCTION

The palatal reconstruction (Fig. 17B) was based on the exposed pterygoid–palatine–ectopterygoid view (Fig. 6E), which was freely duplicated and reversed using Adobe Photoshop 6. The vomers, maxilla and premaxilla are notional. The length and width of the subtemporal fossae was based on a projection of the preserved anterior segment and fitted to the known length of the suspensorium. The palatal view so produced was narrowed slightly to allow for some bowing of the palate that would have been likely in life.

The dorsal view (Fig. 17A) was projected from the palatal view, with the skull table fitted in its natural position, the position of the orbits projected from the lateral view. The resulting shape bears a strong resemblance to *Whatcheeria*, with the narrow frontals of that animal emerging. In *Whatcheeria*, the frontals narrow to an elongate point between the nasals, but this has not been reconstructed for *Pederpes*, in which the region is not preserved. The overall skull shape appears to be rather deep and triangular, with a narrow snout and expanded

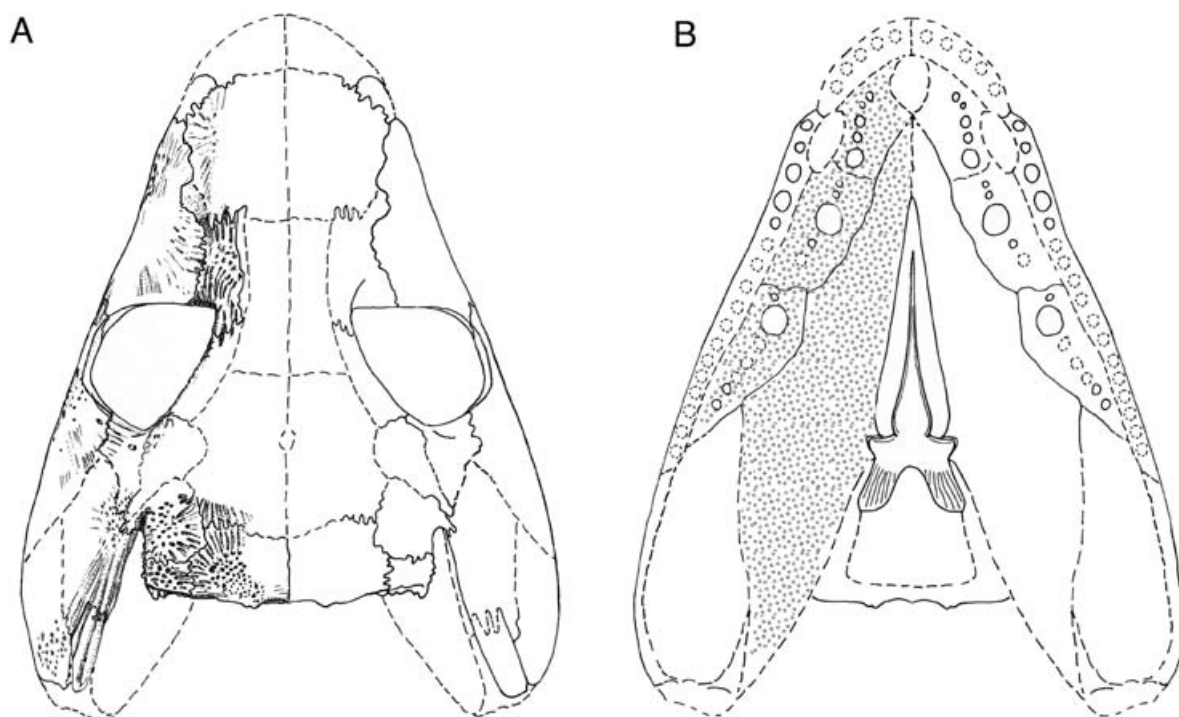


Figure 17 *Pederpes finneyae* Clack, 2002a: reconstruction of the skull in **A**, dorsal and **B**, palatal views. The distribution of denticles is shown schematically, because it has been inferred from a few selectively prepared areas.

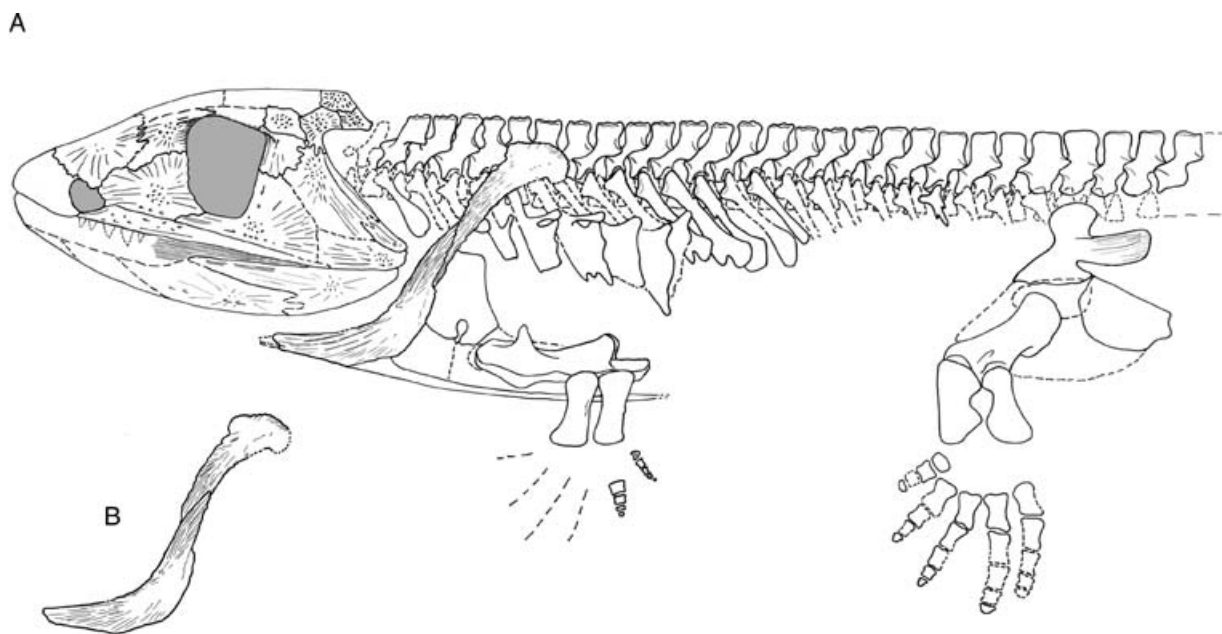


Figure 18 *Pederpes finneyae* Clack, 2002a. **A**, skeletal restoration. **B**, alternative position of clavicle relative to cleithrum.

cheek region, rather unusual among early tetrapods. The relatively short tooth row with a count of probably less than 20 in the maxilla is also unusual among known Devonian and Carboniferous forms, being seen most strikingly in *Ichthyostega*. A low premaxillary count has been reconstructed as in *Whatcheeria*.

The lateral view of the skull (Fig. 18A) was based very closely on the exposed surface, but the orbit was stretched along its long axis to allow for the compression it has under-

gone, shown by the underlap of the prefrontal and postorbital beneath the lacrimal and jugal, respectively. A premaxilla was added but its dimensions are notional. In practice this gives a skull about 170 mm long, very similar in size and proportion to FM PR 1634 with the exceptions noted above.

For the skeletal reconstruction (Fig. 18A), the vertebral column was straightened and the ribs added in the sequence in which they appear with very little change in orientation. In a few cases the length of the rib is known and this was

taken as a guide. The ribs are shown in planar view, but in reality would have been foreshortened in lateral view as they encompassed the body. It was considered that to attempt to show this would only add to the sources of error. Only a single (atlas) arch has been added at the anterior end, assuming that the first preserved arch is the axis. The first rib preserved is assumed to have been the axial rib and it is further assumed that all subsequent ribs of the left side are present up to the 12th. After that, it becomes less clear whether what is preserved is from the left or right sides.

Positioning of the girdles was suggested by reconstructions of other Carboniferous tetrapods such as *Crassigyrinus*, *Greerpeton* and *Proterogyrinus* (but see below for a discussion of the contact between cleithrum and clavicle). The manus is shown with the tiny digit as a supernumerary at the trailing edge of the limb, similar to that on the manus of *Tulerpeton*, with four additional digits and their phalangeal count hypothesised. (See below for a discussion of the manual digits.) The other preserved manual digit has been placed as digit 5. This formula is not to be taken as definitive.

DISCUSSION

Phylogenetic Investigation

In the original description of *Pederpes* Clack (2002a) carried out a phylogenetic analysis to assess its significance for early tetrapod phylogeny. It emerged as the sister taxon to *Whatcheeria deltae*, the pair representing the next most primitive tetrapod clade after the Devonian forms. This fitted well with the stratigraphical position of *Pederpes* as well as with its morphology. The analysis was not particularly robust, however, and it was shown by a reverse constraint analysis that trees only four steps longer placed *Crassigyrinus* as the next most primitive clade after the whatcheeriiids. Another peculiarity of this analysis was the crown clade topology, in which *Seymouria* appeared as a sister taxon to the temnospondyls, *Greerpeton* and *Caerorhachis*, with *Eucritta* and the baphetids as the most derived clade. That made the appropriateness of the dataset itself suspect.

More recently, Ruta *et al.* (2003) have attempted an overarching analysis of early tetrapods including stem and primitive crown group taxa, comparing their results with other recent analyses that show conflicting results. Their chief interest was in the relationship of the crown groups Lissamphibia and Amniota to fossil taxa and, in particular, in the position of the so-called 'lepospondyl' groups with respect to the crown group. Controversy surrounds the relationships of these groups. Some analyses (e.g. Laurin 1998; Laurin & Reisz 1999) have produced results placing the lepospondyls as closest relatives of both lissamphibians and amniotes, a non-traditional arrangement, which contrasts with more 'conventional' groupings of lissamphibians with temnospondyls and amniotes with anthracosaurs (e.g. Panchen & Smithson 1987). Ruta *et al.*'s (2003) final analysis tended to support the latter groupings, however, the base of their tree also showed conspicuous differences from earlier analyses, including that of Clack (2002a: which is referenced throughout the following discussion). Their analysis did not include *Pederpes*, but did include *Whatcheeria*, which was placed above the colosteids and *Crassigyrinus*. We therefore de-

cided to compare the datasets and results from Ruta *et al.* (2003: which is referenced throughout the following discussion) with Clack in detail to try to establish the cause of the differences at the base of the tree and, in particular, the position of the whatcheeriiids.

It is usually rather difficult to compare conflicting cladograms directly because of non-overlapping datasets. Therefore, in order to compare the original *Pederpes* analysis with that of Ruta *et al.*, we performed a set of experiments. The principal objective was, having modified each dataset to provide as closely comparable sets as possible, to interrogate the datasets for the character choices and distributions that might have been key to the differences that our respective analyses produced. A PAUP (4.0b10) analysis using the parsimony ratchet as in Ruta *et al.* (see Nixon 1999 and Quicke *et al.* 2001 for a description of the method), a more exhaustive search than a simple heuristic search, was performed on all the datasets, using accelerated transformation (ACCTRAN).

The data matrix used by Ruta *et al.* consisted of 90 taxa coded for 319 characters (224 cranial and 95 postcranial), whereas the much smaller dataset of Clack consisted of 25 taxa and 141 characters (100 cranial and 41 postcranial). The single most parsimonious tree (MPT) produced by Clack is shown in Fig. 19A. Of the 25 taxa used by Clack, the 22 that were also used by Ruta *et al.* appear in the consensus tree (out of 64 MPTs) of Ruta *et al.* with the relationships being shown in Fig. 19B.

To make the datasets comparable, we first deleted from the dataset of Ruta *et al.* all of the taxa not used by Clack. From the remaining data, we deleted all invariant characters, leaving a total of 239. Of these, 64 were parsimony uninformative. The majority of deleted or uninformative characters were those that applied either to lepospondyls only, lissamphibians only, amniotes only or to individual small clades such as colosteids or dissorophids.

A cladogram from this reduced dataset (Dataset 1: Supplementary Data, Appendix 1) produced three MPTs, the consensus of which is shown in Fig. 19C. Run unrooted, this data gives the unusual result of placing *Eusthenopteron* and *Ichthyostega* as sister-taxa one node crownward of *Acanthostega*, which appears as the most primitive taxon. It shows other significant differences from that produced by Ruta *et al.*'s full dataset. For example, *Greerpeton* appears as the sister-taxon to *Adelogyrinus*, allied successively with *Ptyonius* (a nectridean) and the two temnospondyls, *Balanerpeton* and *Dendrerpeton*. Defining *Eusthenopteron* as the outgroup places it, *Ichthyostega* and *Acanthostega* plus all more crownward taxa in an unresolved polytomy, but does not change the topology of the rest of the tree. Other aspects of the original Ruta *et al.* tree are more or less maintained. *Eucritta* appears as a stem taxon basal to baphetids and all other tetrapods, while *Gephyrostegus* sits one node crownward to the three 'anthracosaurs' *Eoherpeton*, *Pholiderpeton* and *Proterogyrinus*. These MPTs have a length of 466, a Consistency Index (CI) of 0.425, a Retention Index (RI) of 0.546, a rescaled Consistency Index of 0.232 (RC) and a Homoplasy Index (HI) of 0.590.

Following this, *Pederpes*, *Loxomma* and *Silvanerpeton* (used by Clack but not included by Ruta *et al.*) were added to Dataset 1 and scored for the remaining 239 characters (Dataset 2: Supplementary Data, Appendix 2). A few data points were modified at this stage, where the scoring seemed

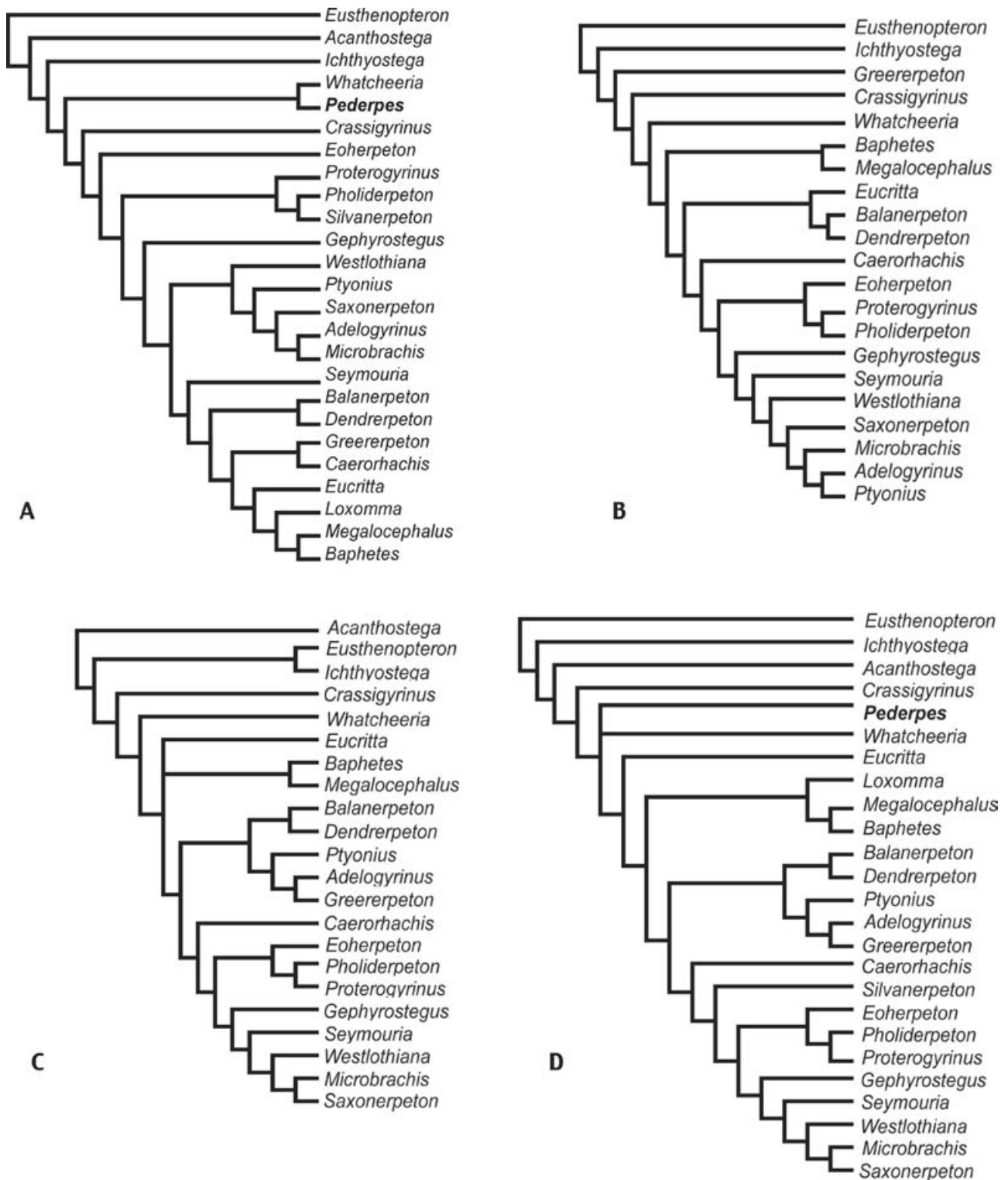


Figure 19 **A**, single most parsimonious tree (MPT) from Clack (2002a). **B**, relationships of 22 taxa common to Clack (2002a) and Ruta *et al.* (2003), as they appear in the latter's consensus cladogram. **C**, consensus of three MPTs from Dataset 1. **D**, consensus of two MPTs from Dataset 2.

to be incorrect (see Supplementary Data, Appendix 3). Some data from *Silvanerpeton* was taken from work in progress by J. A. C. and M. Ruta. This new dataset was then analysed, using *Eusthenopteron* as the user-defined outgroup. The analysis found two MPTs of length = 556, CI = 0.475,

RI = 0.544, RC = 0.259 and HI = 0.540. In one of these, *Whatcheeria* appeared as the sister-taxon to *Pederpes* and this clade sat one node above *Crassigyrinus*, while in the other MPT, the three occupied successive nodes, with *Crassigyrinus* basal to *Pederpes* and *Whatcheeria*,

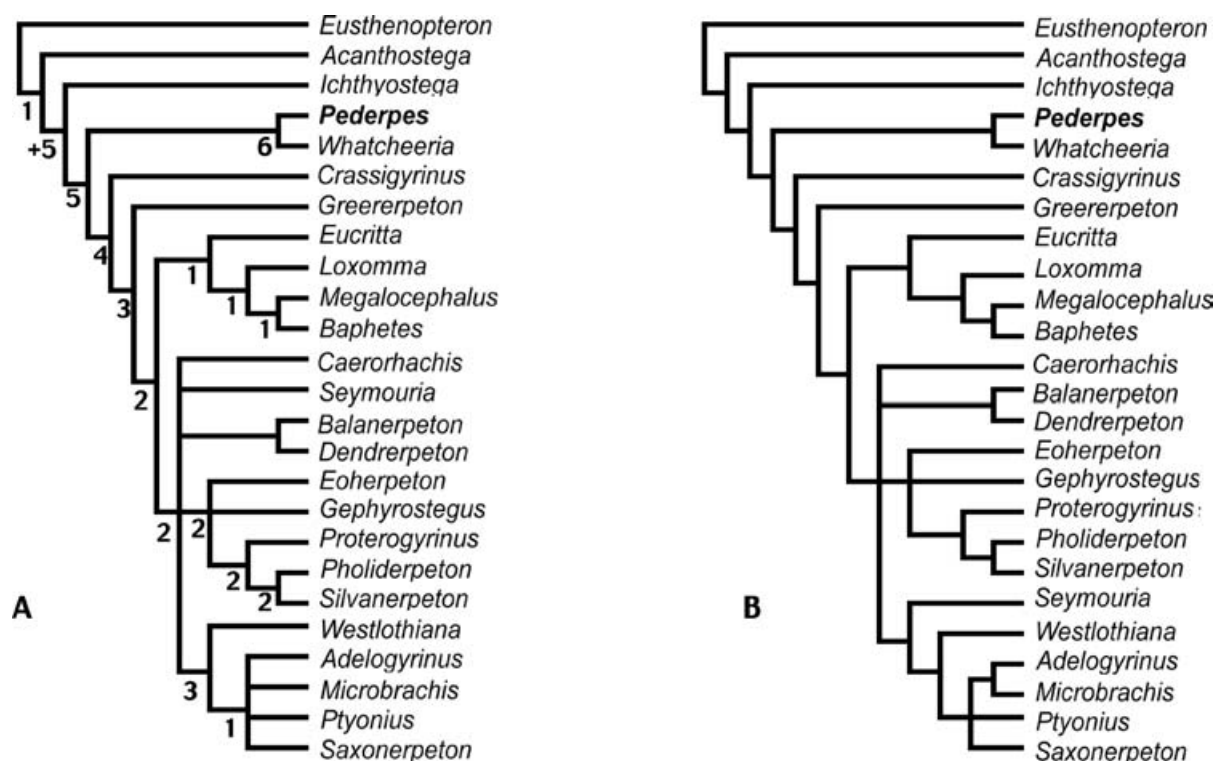


Figure 20 A, strict and B, Adams consensus of six most parsimonious trees from Dataset 3, with Bremer support values given for A.

respectively. There were no other differences in topology between these two trees, whose consensus is shown in Fig. 19D. The topology of the rest of the tree was maintained unchanged, except that *Silvanerpeton* appeared as a stem taxon basal to the three ‘anthracosaurs’, while *Loxomma* sat as the basal member of the baphetid clade.

The next step was to build a new dataset based on that of Clack but to include a suite of applicable characters derived from Ruta *et al.* that covered aspects of anatomy not featured by Clack. To do this, we first compared both sets of characters to find which of those of Clack had equivalents in the large Ruta *et al.* set. Of their 239 variant characters, 32 cranial and nine postcranial characters from the set of Clack had exact equivalents in Ruta *et al.*, while 18 cranial and seven postcranial characters had partial equivalents in Ruta *et al.* Of these partially equivalent characters, some of those from Clack were represented by two or more separate characters in Ruta *et al.*, while some were stated in a slightly different way and so could have been scored differently in the two datasets. This means that nearly 50% of Clack’s original cranial characters and 60% of her postcranial characters had no equivalent in the Ruta *et al.* character list, while about 72% of the relevant characters from Ruta *et al.* had no equivalent in Clack’s.

From the list of 239 possibly applicable characters from Ruta *et al.*, we chose 35 cranial and 19 postcranial characters that applied widely to the taxa included in Clack’s analysis and omitted some that were restricted to small clades such as nectrideans, microsaurids, colosteids, dissorophids or other temnospondyls. We modified, restated or rescored four of them and created a third dataset (Dataset 3: Supplementary Data, Appendix 4). The resulting character list consisted of 36% characters unique to Clack, 36% which overlapped or

partly overlapped between the two analyses and 28% taken from Ruta *et al.* Appendix 5 (Supplementary Data) gives this character list with its modifications indicated.

While doing this, several factors contributed to the ease or difficulty of comparison and the former could be adopted as a beneficial practice for future studies. First, Ruta *et al.* listed taxa in alphabetical order in their matrix, whereas ours were originally listed in tree order. For ease of comparison when trees vary, alphabetical order is to be preferred and we changed Clack’s list accordingly. Second, the order in which characters are described varies much between authors, Ruta *et al.* using an approximately front to rear route around the skull, as is often used in bone descriptions. However, since there is no consistency about what this order should be, again, an alphabetical listing, as recommended by Bolt & Lombard 2001, is much easier to use. Within each character, components are also listed in alphabetical order. Thus ‘tabular – squamosal contact’ would always appear as a character of the squamosal, could not be duplicated under tabular and would always appear in a consistent place in the list. Ruta *et al.*’s code number for each character is useful as datasets change but characters are reused, however, we suspect that the minutely atomised system of character description recommended by Bolt & Lombard (2001) would be found too laborious for most authors.

Dataset 3 consists of 25 taxa and 195 characters divided into 135 cranial and 60 postcranial. It contains three characters that are parsimony uninformative (34, 72, 87). Six MPTs were discovered, of length = 657, CI = 0.382, RI = 0.536, RC = 0.205 and HI = 0.618. The strict and Adams consensus of these trees are given in Fig. 20, with Bremer support values for each node of the strict consensus tree. Note that these two consensus trees differ mainly in the position of *Seymouria*.

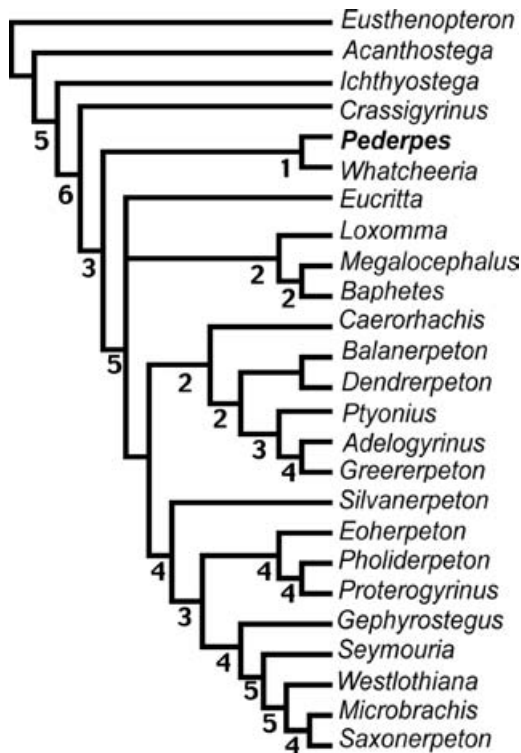


Figure 21 Strict consensus of two most parsimonious tree from Dataset 4, with Bremer support values for each node.

The results show a broad overlap with those of Clack, with some notable exceptions, in the positions of *Greererpeton*, *Caerorhachis*, the relationships of the ‘anthracosaurs’, and the position of the baphetids. *Greererpeton* retreats to its more conventional position as a stem tetrapod, above *Crassigyrinus* and below the baphetids, the latter now appearing as a more primitive clade remote from temnospondyls. In the strict consensus tree, *Seymouria* appears in an unresolved polytomy with *Caerorhachis*, temnospondyls, a *Westlothiana*–lepospondyl clade and the anthracosaur taxa, whereas in the Adams consensus tree, it appears as the basal member of the *Westlothiana*–lepospondyl clade, remote from either temnospondyls or anthracosaurs. There are some minor differences in the relationships found among the lepospondyls, but otherwise these consensus trees are similar.

A fourth dataset was then created and analysed by adding to Dataset 2 the suite of 73 characters from Clack that had no equivalent in Ruta *et al.*’s original list (Dataset 4: Supplementary Data, Appendix 6 as characters 240–312). This set of 312 characters was scored for the 25 taxa and 67 proved to be parsimony uninformative. Two MPTs were found of length = 803, CI = 0.453, RI = 0.538, RC = 0.244 and HI = 0.557. The trees maintained much of the topology produced by Dataset 2 including the positioning of the whatcheeriids above *Crassigyrinus* and of *Greererpeton* with *Adelogyrinus* and *Ptyonius*. Figure 21 gives the strict consensus of these two trees with the Bremer support for each node.

Note that the trees from Dataset 4 are generally more robust in terms of Bremer support than those from Dataset 3, particularly towards the crown, requiring several extra steps to break the nodes. However, near the base of the tree, for

the nodes supporting the sister-taxon relationship between *Pederpes* and *Whatcheeria* and the placing of the whatcheeriids with respect to *Crassigyrinus*, the trees from Dataset 4 are much less strongly supported than those from Dataset 3. This is significant given that *Pederpes* and *Whatcheeria* were initially suspected by the authors to be possibly the same taxon, with only quite subtle differences separating them. It is hard to see how a dataset that accurately reflects this similarity can break down so easily. Furthermore, the unusual association of *Greererpeton* with *Adelogyrinus* is maintained for four extra steps in the trees from Dataset 4. In the trees from Dataset 3, *Seymouria* seems to be the ‘rogue’ taxon, having the most labile distribution.

In order to assess the performance of different character sets on the final topologies retrieved by Clack and Ruta *et al.*, we performed several tests. We first compared the two trees deriving from Dataset 4 with the six trees retrieved from Dataset 3. A Templeton test showed that the latter trees are only a slightly worse fit for the Dataset 4 character set than the topologies yielded by Dataset 4 (*P* values ranged from 0.3311 to 0.067). We then compared the results from Dataset 3 with those from Dataset 2. In this case the topologies implied by Dataset 2 were a much worse fit for the data than the Dataset 3 trees (*P* = 0.0091). Finally, the Ruta *et al.* topology was imposed on Dataset 3. Comparisons between the two trees yielded by Dataset 3 with the Ruta *et al.*’s arrangement indicated that the latter differed significantly from the most parsimonious topologies of Dataset 3 (*P* = 0.0257).

To investigate character distribution at the basal nodes, we took the first tree in the list from each of the sets generated by Datasets 3 and 4 and analysed the origin of the characters supporting the nodes between *Ichthyostega* and the next taxon and between this taxon and the rest of the tree. In Dataset 3 the taxon following *Ichthyostega* is *Pederpes* + *Whatcheeria*, while in Dataset 4 tree 1 it is *Crassigyrinus*; in each case the next successive taxa are these two in reverse. From Dataset 3, 37 characters appear to support the node from *Ichthyostega* to the whatcheeriids, of which 17 are ‘Clack’s’ (had no equivalent in Ruta *et al.*’s original list), 14 are ‘shared’ (i.e. had equivalents or partial equivalents in each list) and six are ‘Ruta’s’ (i.e. unique to Ruta *et al.*’s original list). From Dataset 4, 52 characters appear in this position, 18 Clack’s, 14 shared and 19 Ruta’s. Of these characters, 27 overlap in distribution. Four of these are Ruta’s, six are shared and 17 are Clack’s. A slightly higher percentage of supporting characters are postcranial from Dataset 4 (73% versus 61%) and a slightly higher percentage of characters from Dataset 4 have a CI = 1.00 (32.5% versus 29%). Appendices 6 and 7 (Supplementary Data) give the character distributions and apomorphies at the basal nodes of tree 1 from each of the two datasets.

At the next node, 21 characters from Dataset 3 and 23 from Dataset 4 support their respective positions; from Dataset 3, seven characters are Clack’s, 12 are shared and two are Ruta’s, compared with Dataset 4 from which seven are Clack’s, 11 are shared and five are Ruta’s. Only two characters overlap. A total of 21% of characters from Dataset 4 are postcranial, compared with 53% from Dataset 3. Only three characters from each dataset have a CI = 1.00 (Dataset 3: 33, position of the anterior margin of the parietal; 46, preopercular; 99, angular prearticular suture condition. Dataset 4: 111, basioccipital condition; 172, entepicondylar foramen; 182, accessory foramina).

Next, we compared character scores for *Crassigyrinus* and *Pederpes*. Dataset 3 contains eight characters in which *Crassigyrinus* is scored as more primitive compared with 11 for which *Pederpes* is more primitive. Dataset 4 contains nine characters in which *Crassigyrinus* is scored as more primitive, compared with 10 for which *Pederpes* is more primitive. In all other characters, either the two show similar states, or the state is not known in one of the two taxa. Whereas of the 11 characters in Dataset 3 for which *Pederpes* is more primitive, 10 appear at the node which places it below *Crassigyrinus* in the MPTs, only a single one of the Dataset 4 characters of this polarity appears at the node that places *Crassigyrinus* below *Pederpes*, so that it is not obvious why Dataset 4 places *Crassigyrinus* below the whatcheerids, despite it including a suite of Clack's characters.

Because of the statistical way in which PAUP deals with characters, it does not seem possible to extract information about which precise characters swing the balance from one tree to the other, which is what, as anatomists, we would like to know. Perhaps theoreticians can perform comparable exercises to elucidate disruptive characters in a parallel way to that for individual taxa (Wilkinson 2003). Are there individual characters that are pivotal to the structure of the tree such that omitting them would produce very different tree topologies?

Although inconclusive, the above exercise does seem to show that there is some unconscious bias in the way characters are selected and formulated. Characters that we perceived as suggesting *Pederpes* to be more primitive than *Crassigyrinus* are 'swamped out' by those employed by Ruta *et al.* to produce the reverse result produced by their much larger dataset, even though in Dataset 4 there are approximately equal numbers of characters on each 'side' and only three of those placing *Pederpes* as more primitive are 'Clack's'. One further observation may be made, which is that towards the crown of the trees produced by both Dataset 3 and Dataset 4, there is an increasing proportion of 'Ruta's' characters supporting the nodes, suggesting more interest on their part and less on mine in resolving the relationships of more crownward taxa. This discrepancy may be one of the influences reflected by the Bremer support values for the trees from Datasets 3 and 4 as noted above.

Comparative Anatomy and Functional Morphology

Comparison with *Whatcheeria*

On first acquaintance, the skull of *Pederpes* was scarcely distinguishable from that of *Whatcheeria*. As study progressed, it became clear that a suite of subtle characters differ between the taxa. These include the ornament type, exposure of the lateral line, the shape of several individual bones and, most strikingly, the proportions of the jugal. *Pederpes* has a much shallower ramus beneath the orbit than in *Whatcheeria*, which is also much shorter anterior to the orbit. The depth of the jugal beneath the orbit is one of the features that can increase proportionally during ontogeny in early tetrapods and in related sarcopterygian fish (eg. *Greererpeton*: Godfrey (1989a); *Eusthenopteron*: Schultze (1984)) but the skulls of *Pederpes* and the holotype of *Whatcheeria* are similar in size. Therefore, even if the anterior extent of the jugal and its depth below the orbit increased ontogenetically, the contrast represents different ontogenetic trajectories in the two animals, indicating a taxonomic distinction between them.

There are other more obvious differences in the postcranial skeleton, including the shape of the dermal shoulder girdle elements, the ilium and the rib flanges. The shape of the phalanges in *Whatcheeria* has not yet been fully described and there is some uncertainty in partially articulated specimens as to which are pedal and which are manual elements. However, there are at least two sets of articulated digits, one associated with a radius and ulna and one with a tibia and fibula (pers. obs.). Taken at face value this might be an indication that both manus and pes of *Whatcheeria* had phalanges broader than long, as in the articulated manual digit of *Pederpes*. It could suggest that the pes of *Whatcheeria* was more greatly modified into a paddle-like limb than that of *Pederpes* and that *Whatcheeria* had a more fully aquatic lifestyle, but this remains uncertain pending detailed description of the *Whatcheeria* material.

Ribs

Among the most conspicuous features of *Pederpes* are the greatly expanded distal flanges on the 'thoracic' ribs. Much has been written about the homology and function of rib flanges, with a detailed discussion in Coates (1996). Coates concluded that 'uncinate processes' referred to by several authors, should not be treated separately from more distal expansions of the ribs, whether 'thoracic' or 'cervical'. All are probably associated with the area of origin of intercostal musculature that aids in maintaining the shape of the body cavity. There is no necessary connection between these muscles and costal ventilation as is typical for many amniotes. Brainerd *et al.* (1993) showed that non-amniotes do not use intercostals in lung ventilation and that the transverse abdominus muscle, which is unique to tetrapods and lies internal to the ribs, functions only in exhalation in non-amniotes. Inhalation takes place by buccal pumping and this is a probable mode for primitive as well as more crownward non-amniote tetrapods (Janis & Keller 2001; Clack 2002b). Uncinate processes and other flanges or rib expansions are therefore unlikely to be associated with ventilation in the earliest tetrapods, but were probably involved with other functions including locomotion and anchoring of the shoulder girdle. Broad distal flanges resembling those in *Pederpes* are found widely distributed among early tetrapods, including such disparate forms as the Devonian tetrapod *Ichthyostega* (Jarvik 1996), the seymouriamorph *Kotlassia* (Bystrow 1944) (although not in its relative *Seymouria*) and the only distantly related temnospondyls *Eryops* (Moulton 1974) and *Mastodonsaurus* (Schoch & Milner 2000). In many other cases, expanded rib-ends are confined to the cervical area e.g. the anthracosaurs *Eldeceon* (Smithson 1994) and *Archeria* (Holmes 1989), the baphetid *Eucriita* (Clack 2001) and the microsaurs *Pantylus* (Carroll & Gaskill 1978). In yet others, the processes are confined to short dorsally placed spikes, such as in the colosteid *Greererpeton* (Godfrey 1989b). It seems unlikely that the flanges, processes or expansions are fulfilling the same function in this whole range of tetrapods. It further seems unlikely, given their scattered distribution among both terrestrial and aquatic, early and late and primitive and derived forms that they had a single origin. In order to test this it seems more reasonable to define each type carefully and to separate it from others in terms of shape and position, in other words to treat them *a priori* as non-homologous. That said, as described above, those of *Pederpes* show the closest

resemblance in some details to those of *Ichthyostega*, with which they share features such as the presence of a foramen near the dorsal edge of the distal expansion. Work in progress on *Ichthyostega* (Clack *et al.* 2003a,b) suggests a highly specialised aquatic predator with a very peculiar (in its original sense), possibly seal-like terrestrial gait that might have involved increased rigidity of the rib cage and severely restricted lateral bending. In this case the rib flanges were most probably used in quite a different manner from that of *Pederpes*, whose hind limb shows a more conventional walking foot. The term 'uncinate process' thus seems inadequate to cover all of the different morphologies and positions of rib flanges seen in early tetrapods.

Humerus

The humerus of *Pederpes* is most similar to that of *Baphetes*, matching it in almost every respect except that in *Pederpes* the latissimus dorsi process is even more exaggerated and spike-like than that of *Baphetes* (Milner & Lindsay 1998). Some humeri of *Greererpeton* (Godfrey 1989b) also resemble those of *Pederpes*, especially in general outline, and some of the crushed specimens of *Whatcheeria* are also similar (uncatalogued specimen on a block, labelled as '24', pers. obs.). The significance of the similarities is unclear, since *Pederpes* shows no unequivocally close relationship to *Baphetes* or *Greererpeton*.

The latissimus dorsi and deltoideus muscles are derivatives of the dorsal muscle mass that runs from the body wall and shoulder girdle to the fin in fishes. A corresponding ventral mass runs to the underside of the fin. In tetrapods, these masses are differentiated into many separate muscles, that become very complex especially in amniotes, although their respective undifferentiated origins are evident in early embryogenesis (Romer 1956). The evolution of differentiated musculature may well have taken place gradually with increasing terrestrial capabilities, but the very earliest tetrapods may have retained quite an unspecialised fish-like system.

The deltoideus muscle originates on the scapula blade in modern amniotes and amphibians, but in the earliest tetrapods there was no scapula blade, or the blade was relatively small. The deltoideus muscle may have been correspondingly small, or not well differentiated from the latissimus dorsi that originates in the epaxial musculature. In *Ichthyostega*, the latissimus dorsi process (ldp: Jarvik's (1996) process 1) and deltopectoral crest (dpc: Jarvik's (1996) process 2) are essentially opposite ends of a ridge running across the dorsal surface of the humerus. This condition might indicate that the two muscles were still more or less a single unit. In *Acanthostega*, however, although the ldp rises as an elongate, low process from the dorsal surface of the humerus, the dpc is essentially a thickening of the anterior margin. This condition suggests the beginning of a differentiation between these two muscles. However, in *Pederpes* and other tetrapods with a prominent ldp, the latissimus dorsi was evidently well-differentiated from the deltoideus.

The pectoralis muscle originates on the clavicle and also inserts on the dpc, but in *Pederpes* this feature is poorly ossified, although its major exposure is directed ventrally, towards the area of insertion of the pectoralis. This may suggest that the deltoideus muscle itself was relatively small or poorly differentiated, although the pectoralis was probably

large. One of the latter's main functions would have been to pull the humerus downwards and forwards. In later tetrapods, the ldp and dpc become increasingly separated and come to occupy disjunct positions on the humerus (Coates 1996). Coates also noted that the ldp moves, in phylogenetic terms, into increasing alignment with the ectepicondyle and this is nearly so in *Pederpes*. There is no supinator process recognisable in *Pederpes*, a process that usually lies ventral and distal to the deltoid in tetrapods.

In more primitive humeri of fish such as *Eusthenopteron* and *Panderichthys*, in the Devonian forms *Acanthostega* and *Ichthyostega* and in a recently described humerus from the Devonian of Pennsylvania (Shubin *et al.*, 2004), the ventral surface bears a ridge that appears to divide proximal from distal muscle blocks. In the fishes, the ridge runs diagonally from the proximoanterior corner to the posterodistal corner, whereas in the tetrapods, it runs approximately at right angles to the long axis of the humerus. Shubin *et al.* link this to the changing orientation of the appendage with respect to the body that is characteristic of the laterally orientated tetrapod limb. In later tetrapods, the ridge is reduced in height especially in the more distal regions until, as in *Pederpes*, only the pectoralis portion remains. The reduction could be another indication of the concentration of muscular insertion points from broader and less-differentiated regions as in the fish condition.

Manual digits

The small size of the disarticulated manual digit was commented on by Clack (2002a), who suggested that its proportions were more compatible with a supernumerary digit such as is found in the Devonian forms, rather than with a typical manual digit. The inference drawn was that the manus of *Pederpes* could have been polydactylous. In an attempt to test and quantify this suggestion, we made measurements of comparable elements in a range of early tetrapods in which manus and pes were adequately known. In each case we measured the probable metapodials of each digit present in the articulated manus or pes. Measurements were made along the midlines of the elements, to offset the bilateral asymmetry found in some of them.

Pederpes, *Acanthostega*, *Ichthyostega* (pes only), *Silvanerpeton* (holotype and NMS (National Museums of Scotland) 1994.16.1) and *Eldeceon* (holotype) were measured directly from specimens; *Tulerpeton* was measured from specimen drawings in Lebedev & Coates (1995); *Balanerpeton* was measured from 2.5 × specimen drawings of the holotype in Milner & Sequeira (1994) (magnified for ease of measuring); *Proterogyrinus* was measured from reconstruction drawings in Holmes (1984). *Greererpeton* was not used because manus and pes are not figured from a single individual and detailed reconstruction drawings to the same scale were not available. Note that, similarly, the manus and pes of *Acanthostega* are from different individuals. However, these specimens all derived from the same horizon and skulls from this locality do not vary much in size (Clack 2002c). The pedal elements measured for *Acanthostega* follow the interpretation of Coates (1996) but note that because of the disrupted nature of the specimen, identities as phalanges or metatarsals or even to which digit each belongs, could be disputed in some cases. In the case of *Tulerpeton* the metatarsal of digit 6 is incomplete and was not included in the count.

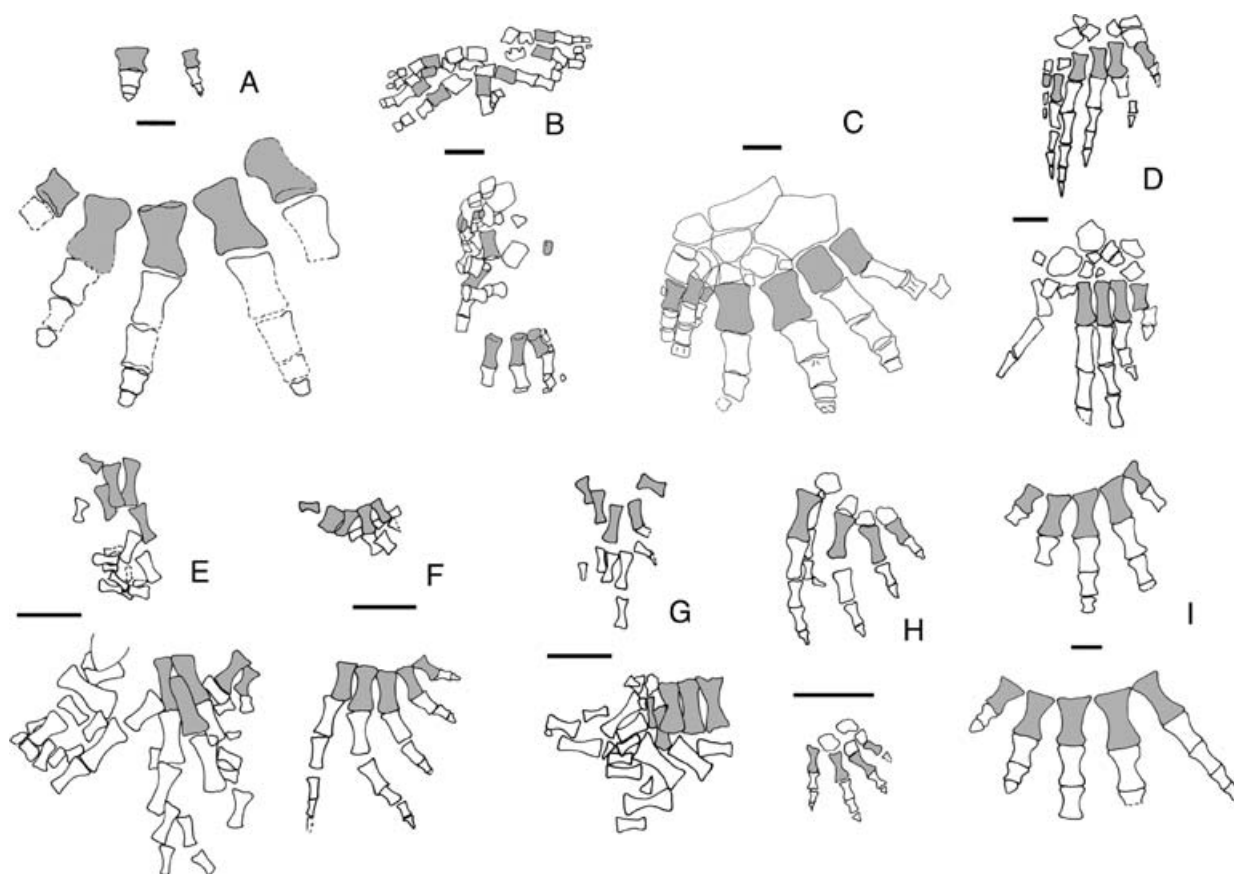


Figure 22 Manus (above) and pes (below) of early tetrapods to show proportions of elements; shading indicates the elements measured in Table 1. **A**, *Pederpes finneyae*; **B**, *Acanthostega gunnari*, from MGUH (Geological Museum, Copenhagen) 1227 (manus) and MGUH 1375 (pes); **C**, *Ichthyostega pes* from MGUH 1349; **D**, *Tulerpeton curtum*, from specimen drawing in Lebedev & Coates (1995); **E**, *Eldeceeon rolfei*, from holotype, NMS (National Museums of Scotland) 1986.39.1; **F**, *Silvanerpeton miripedes*, from holotype, UMZC (University Museum of Zoology, Cambridge) T1317; **G**, *Silvanerpeton miripedes*, from NMS 1994.16.1; **H**, *Balanerpeton woodi* from specimen drawings in Milner & Sequeira (1994); **I**, *Proterogyrinus scheelei*, from reconstruction drawings in Holmes (1984).

In the case of *Eldeceeon*, both peses are superimposed on one another and are difficult to disentangle. In *Balanerpeton*, only four pedal elements are measurable. Measurements of specimens were made with Vernier calipers. Figure 22 shows which elements were measured and gives drawings of manus and pes from the sources cited, to the same scale, for each of the taxa described. Table 1 gives the measurements in each case.

We calculated the average length of the proximal cylindrical elements in each manus and pes. To give an idea of the size of the manus relative to the pes, we expressed the average manual element length as a percentage of the average pedal length. We then calculated the length of the smallest manual and pedal digits as a percentage of the average pedal element length. This allowed comparison between the smallest digit and the size of the pes in *Pederpes* and the other tetrapods. To calculate the average element length in the pes of *Acanthostega* and *Ichthyostega*, and the manus of *Tulerpeton*, we deliberately omitted the very small digits found in those taxa (values in square brackets in Table 1). In *Acanthostega*, these lie at the leading and trailing edges of the foot, in *Ichthyostega* it lies at position three from the leading edge and in *Tulerpeton* it is in the manus associated with the ulna. We also calculated the figures for *Ichthyostega*

when the first two leading edge digits were also excluded (values in round brackets in Table 1). The starred values in the table are the figures for the proportions of the first two digits. In the manus of *Acanthostega*, all digits are comparable in size, so all were included in the averaging process, as were all measurable pedal elements of *Tulerpeton*.

The results are quite clear. The disarticulated digit in the manus of *Pederpes* is even smaller, relative to the size of the average pedal element (25.9%) than is the tiny third digit in the pes of *Ichthyostega* (31.5% without or 36.9% with the two leading edge digits included). The other preserved manual digit is also relatively very small (36.4%). This could either mean that both digits are supernumeraries and part of a polydactylous manus, or that the whole manus was disproportionately small in this animal. The inference here would be extreme specialisation, in contrast to plesiomorphy as suggested by polydactyly. The relatively large size of the humerus compared to the femur would make a disproportionately small manus potentially unlikely, but the presence of a possible elongate ungual could argue in favour of some form of specialisation. The relatively very broad articulated manual digit in *Pederpes* might be a supernumerary if only its length is considered, although in fact it more closely resembles the short, broad, digit II in the pes of *Acanthostega*

Table 1 Measurements of pedal elements in early tetrapods.

Taxon	LM	AvM	LP	AvP	%M/P	LsM	LsP	LsM%AvP	LsP%AvP
<i>Pederpes</i>	3.7, 5.2	–	15.4, 16.5, 16.0, 16.0, 7.4	14.26	–	3.7	7.4	25.9 and 36.4	51.8
<i>Acanthostega</i>	3.7, 4.2, 4.0, 4.3, 4.3, 3.7, 3.5, 3.5	3.9	3.1, 6.1, 7.6, 6.9, 6.6, 7.2, 3.7, 2.4	5.45	71.5	3.5	2.4	64.2	44
<i>Ichthyostega</i>	–	–	[6.6, 6.6][3.8], 10.4, 13.3, 12.0, 13.0	12.07 (10.3)	–	–	3.8, 6.6	–	(31.5), 36.9 (51.7)*, 64.0*
<i>Tulerpeton</i>	[4.1], 8.0, 7.4, 9.0, 9.6, 7.8	8.36	6.5, 11.5, 12.5, 12.3	10.7	78.1	4.1	6.5	38.3	60.7
<i>Eldeceeon</i>	4.5, 4.8, 5.1, 3.1	4.4	5.7, 7.1, 8.0, 8.4	7.3	60.2	4.5	5.7	42.4	78.0
<i>Silvanerpeton</i> Ht	3.4, 4.3, 4.5, 4.5, 3.5	4.05	4.1, 5.1, 6.6, 7.0, 5.9	7.0	70.4	3.4	4.1	59.1	71.3
NMS 1994.16.1	3.9, 6.4, 5.7, 5.7, 3.9	5.12	5.3, 7.6, 8.9, 8.6, 8.2	7.7	66.3	3.9	5.3	50.5	68.6
<i>Proterogyrinus</i>	9.1, 13.1, 14.0, 13.0, 7.6	11.36	15.0, 17.6, 15.5, 13.8, 10.0	14.4	78.9	7.6	10.0	52.7	69.4
<i>Balanerpeton</i> *2	5.9, 8.2, 8.6, 7.4	7.5	7.2, 11.2, 13.8, 15.7	11.9	63.0	5.9	7.2	49.5	60.5

For sources, see legend to Fig. 22. Shaded boxes draw attention to proportions of the supernumerary digits in the Devonian forms and in *Pederpes*.

LM, lengths of proximal manual elements; AvM, average lengths of proximal manual elements; LP, lengths of proximal pedal elements; AvP, average lengths of proximal pedal elements; %M/P, average manual element length as a percentage of average pedal element size; LsM, length of smallest manual element used in the comparison; LsP, length of smallest pedal element used in the comparison; LsM%AvP, length of the smallest manual element as a percentage of the average length of the pedal elements; LsP%AvP, length of the smallest pedal element as a percentage of the average length of the pedal elements; square brackets around figures, smallest elements omitted from calculation of average value; round bracket around figures, figures excluding the two smaller leading edge digits from the pes of *Ichthyostega*; *, size of the two leading edge digits in the pes of *Ichthyostega*.

as reconstructed by Coates (1996) and the articulated digits seen in *Whatcheeria* (Lombard & Bolt 1995; pers. obs.).

A few more points are noteworthy. The two leading edge digits in the pes of *Ichthyostega* are comparable to the smallest pedal digit in other tetrapods, rather than to smaller supernumeraries. Although Lebedev & Coates (1995: 326) describe the pedal elements as ‘much larger’ than those of the forelimb in *Tulerpeton*, according to the current calculation, the forelimb elements are 78% of the size of those of the hind, a similar figure to *Proterogyrinus*. By contrast, in *Acanthostega* and most of the other early tetrapods, the measured figure is nearer 60–70%. Although by subjective judgement the pes of *Eldeceeon* seems relatively larger than in *Silvanerpeton*, the figures do not bear this out, and the apparent disparity in size and robustness appears confined to the femora (Clack 1994c).

Shoulder girdle articulation

Some comments on the articulation between clavicle and cleithrum are required. Initially in the skeletal reconstruction, the clavicle and cleithrum were positioned so that their deeply grooved and ornamented surfaces met in sutural contact. However, this results in the cleithrum running down the anterior face of the clavicular stem. As Dr Anne Warren pointed out (pers. comm.), this seems unusual among early tetrapod shoulder girdles, in which the cleithrum usually runs posterior to the clavicular stem. Indeed in most Devonian forms, the cleithrum is co-ossified with the anterior edge of the scapulocoracoid, suggesting that this relationship may be plesiomorphic.

An investigation of the literature shows that the situation is more complex than it appears. In many cases the junction between cleithrum and clavicle is uncertainly known and portrayed with dotted lines or ambiguous ones and the cross-sectional shape of the cleithrum is usually unavailable.

In *Whatcheeria*, one specimen shows a partially articulated shoulder girdle. The cleithra lie associated with the scapulocoracoids and, on the left side, the two appear artic-

ulated together. On the right, their relationship is less clear. Personal observation of several specimens shows that the cleithrum is grooved on both its anterior and posterior faces, although there is no ridging comparable to that in *Pederpes*. Panchen (1985), however, reconstructed the shoulder girdle of *Crassigyrinus* with the cleithrum placed anterior to the clavicular stem and specifically describes a posterior area in the ventral portion of the cleithrum for overlap of the clavicular stem. The overlap is described as extensive.

In the embolomere *Pholiderpeton* (Clack 1987a), the cleithrum is complex in cross-section and its essentially triangular shape is grooved along each face to a greater or lesser degree, so that it is not clear where the clavicular stem would have rested. In *Archeria*, Romer (1957) described the clavicular stem as grooved postero-externally for an overlap of the cleithrum and the cleithral shaft was described as triangular in section with flat external and anteroventral surfaces, although grooved posteriorly for articulation with the scapulocoracoid. The illustration, however, shows only a short contact between clavicle and cleithrum, so it is not clear how far internally the cleithrum projects. The anhracosaur *Gephyrostegus*, as seen in the holotype specimen, also has the cleithrum in a groove along the posterior edge of the clavicular stem (pers. obs. of specimen peels).

Most temnospondyls, similarly, are known to have had the cleithrum positioned between the clavicular stem and the scapulocoracoid, fitting posteriorly into a groove or facet on the clavicle and this is particularly well illustrated by Shishkin (1987) for the derived form *Plagiosternum*. It is also clear in an articulated skeleton of *Dendrerpeton* (Holmes *et al.* 1998).

In some seymouriamorphs, although in lateral view reconstruction the cleithrum rises directly from the dorsal end of the clavicular stem, in fact, there is a groove along the anterior edge of the clavicle into which the cleithrum fits, but this cannot be seen in lateral view (M. Ruta, in *Discosauriscus*, pers. comm.). In other examples, the cleithrum sits posterior to the clavicular stem (Klembara & Bartik 2000). Several amniotes have the ‘cleithrum anterior’

configuration, such as that figured and described in *Anthraco-dromeus*. The description specifies that the cleithrum is 'notched posteriorly for attachment to the stem of the clavicle' (Carroll & Baird 1972: 335). In other early amniotes featured in that publication, the cleithrum is shown springing directly from the dorsal end of the clavicular stem and the extent and position of their contacts is unclear. The same 'cleithrum anterior' relationship is reconstructed in *Protorothyris* (Clark & Carroll 1973). Gorgonopsids typically have the cleithrum anterior to the clavicular stem (M. J. Allinson, pers comm.). This whole issue is deserving of more attention and could potentially provide useful characters for cladistic analysis.

In finalising the skeletal reconstruction we made a number of graphical 'experiments' placing the cleithrum and clavicle in different relative positions. In terms of smoothness of fit, the 'cleithrum posterior' appears more comfortable, although that is no necessary indicator of correctness. However, this has been maintained for the final reconstruction (Fig. 18B shows the alternative, 'cleithrum anterior', configuration).

Whatcheeriid Distribution

Whatcheeriids are unequivocally found in Tournaisian (Ivorian) deposits from western Scotland through to the late Viséan (Asbian) of Iowa, USA (Bolt *et al.* 1988). This represents a considerable time-span of some 16 million years (Jones 1995). They are also now beginning to be recognised in other parts of the world, for example, from the mid Viséan (Holkerian) of Australia several elements attributed to *Ossinodus pueri* closely resemble the equivalents in *Pederpes*. Warren & Turner (2004) conservatively attribute all the tetrapod elements from Middle Paddock to this species, but even if this is proved incorrect, at least the cleithrum, maxilla and interclavicle seem indisputably whatcheeriid. *Occidens portlocki*, a tetrapod lower jaw, probably Tournaisian, from Northern Ireland, also clusters close to *Pederpes* and *Whatcheeria* in an analysis (Clack & Ahlberg 2004). It is possible that at least some elements from the Famennian of Russia, associated with *Tulerpeton*, if not *Tulerpeton* itself, could belong to whatcheeriids on re-examination (for example the tabulars). Finally, some recently recognised tetrapod remains from Red Hill in Pennsylvania, of late Famennian age, have been tentatively identified as whatcheeriid (work in progress with E. B. Daeschler). If further study confirms this, it will extend the known range of the family down into the Famennian and give it a timespan of around 30 million years, making the family one of the most widely distributed in time and space among Palaeozoic tetrapods as well as one of the most recently recognised (see also Clack & Ahlberg 2004). An alternative interpretation might be that the whatcheeriids represent a 'grade-group' of generalised plesiomorphic tetrapods whose subsequent unravelling may prove the key to resolving relationships of more crownward forms.

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APPENDICES 1–6: SUPPLEMENTARY DATA

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