

The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution

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ABSTRACT: The postcranial skeleton of *Acanthostega gunnari* from the Famennian of East Greenland displays a unique, transitional, mixture of features conventionally associated with fish- and tetrapod-like morphologies. The rhachitomous vertebral column has a primitive, barely differentiated atlas–axis complex, encloses an unconstricted notochordal canal, and the weakly ossified neural arches have poorly developed zygapophyses. More derived axial skeletal features include caudal vertebral proliferation and, transiently, neural radials supporting unbranched and unsegmented lepidotrichia. Sacral and post-sacral ribs reiterate uncinat cervical and anterior thoracic rib morphologies: a simple distal flange supplies a broad surface for iliac attachment. The octodactylous forelimb and hindlimb each articulate with an unsutured, foraminate endoskeletal girdle. A broad-bladed femoral shaft with extreme anterior torsion and associated flattened epipodials indicates a paddle-like hindlimb function. Phylogenetic analysis places *Acanthostega* as the sister-group of *Ichthyostega* plus all more advanced tetrapods. *Tulerpeton* appears to be a basal stem-amniote plesion, tying the amphibian–amniote split to the uppermost Devonian. *Caerorhachis* may represent a more derived stem-amniote plesion. Postcranial evolutionary trends spanning the taxa traditionally associated with the fish–tetrapod transition are discussed in detail. Comparison between axial skeletons of primitive tetrapods suggests that plesiomorphic fish-like morphologies were re-patterned in a cranio-caudal direction with the emergence of tetrapod vertebral regionalisation. The evolution of digitated limbs lags behind the initial enlargement of endoskeletal girdles, whereas digit evolution precedes the elaboration of complex carpal and tarsal articulations. Pentadactylous limbs appear to have stabilised independently in amniote and amphibian lineages; the colosteid *Greeerpeton* has a pentadactylous manus, indicating that basal amphibian forelimbs may not be restricted to patterns of four digits or less.



KEY WORDS: East Greenland, phylogeny, axial skeleton, girdles, limbs, polydactyly.

Acanthostega gunnari, from the Late Famennian, Upper Devonian of Gauss Halvø, East Greenland, is probably the most completely known of the three Devonian tetrapods preserved in any substantial detail. The first specimens, two incomplete dermal skulls, were discovered by Säve-Söderbergh on Wiman Bjerg, Gauss Halvø, in 1932. However, ill health and Säve-Söderbergh's untimely death delayed the publication of their description for a further 20 years (Jarvik 1952, 1980). No further material was collected until 1970, when John Nicholson discovered numerous specimens while mapping the stratigraphy of Stensiö Bjerg, Gauss Halvø (Friend *et al.* 1976). Surprisingly, the significance of these finds, relative to the extreme rarity of any Devonian tetrapods whatsoever, went unrecognised until they were studied in the mid-1980s by Dr Jenny Clack (1988). Nicholson's discoveries then provided the impetus for further field-work, completed during an Anglo–Danish expedition in 1987 (Bendix-Almgreen *et al.* 1988; Panchen 1988).

Subsequent analyses of the combined Nicholson and Clack collections have vastly increased our knowledge of the formerly nebulous *Acanthostega*, and have yielded a wealth of new data concerning the so-called fish–tetrapod transition. Clack (1988) revised previous descriptions of the dermal skull of *Acanthostega* (Jarvik 1952, 1980); and more recent reconstructions can be found in Clack (1992, 1994a, in press), Clack and Coates (1993)—this includes an inaccurate sutural pattern on the external surface of the lower jaw, and Clack

and Coates (1995). Details of the dermal mosaic surrounding the external naris, a full description of the palate and associated dentition, the choana, and the neurocranial ventral surface are described and discussed in Clack (1994a). The condition of the stapes and discussions of the potential stapedia function in early tetrapods, are provided in Clack (1989, 1992, 1993). Further details of the hyobranchial skeleton were described in Coates and Clack (1991), and an attempted reconstruction appears in Clack and Coates (1993). The neurocranium is now known in exceptional detail; a preliminary description, including details of the fenestra ovalis, in Clack (1994b), has been superseded by a more detailed study including a discussion of the evolution of the auditory region in tetrapods (Clack in press). A detailed description of the mandible is currently in an advanced state of preparation (Clack & Ahlberg, personal communication). Previous publications concerning the postcranial anatomy of *Acanthostega* include Coates and Clack (1990), and Coates (1991, 1993, 1994a,b, 1995), on the origin, early diversification, and developmental evolution of the earliest digitated limbs. Aspects of the axial skeleton have been discussed in Clack and Coates (1993, 1995), Coates (1994a), and Coates and Clack (1995); pectoral and pelvic girdle structure in Clack and Coates (1993, 1995), and Coates and Clack (1995). Early tetrapod palaeoecology, and previous reconstructions of *Acanthostega* appear in Clack and Coates (1993), and Coates and Clack (1995).

Until recently, most information about Devonian tetrapods was based upon *Ichthyostega*, *Acanthostega*'s more famous contemporary, from Gauss Halvø localities and Celsius Bjerg, Ymers Ø (Ymers Island; detailed summaries and maps of the original localities are provided in Jarvik 1952 & 1996; the latter reference also contains a valuable historical review of the various expeditions to East Greenland of relevance to the collection of Devonian tetrapods). *Ichthyostega* was first described by Säve-Söderbergh in 1932, and subsequently researched by Jarvik (summarised in Jarvik 1980, 1996; in the present work *Ichthyostegopsis*, Säve-Söderbergh 1932, known from an incomplete dermal skull, is considered as probably representing a small *Ichthyostega* specimen). However, many apparently specialised features seemed to preclude it from the main path of tetrapod evolution (Jarvik 1980). As a consequence, attempts to resolve the interrelationships of tetrapod-like fishes and fish-like tetrapods tended to shift attention to the increasing diversity of seemingly less specialised Carboniferous taxa (e.g. Milner *et al.* 1986; Long 1990). Nevertheless, other Devonian tetrapod taxa were already being discovered in new field localities or found lurking unrecognised in existing collections. The third Devonian tetrapod known in significant detail, *Tulerpeton curtum* (Lebedev 1984), was collected from the Late Devonian of the Tula region, Pre-Ural Russia. Although consisting mostly of limb and girdle material, detailed description (Lebedev & Clack 1993; Lebedev & Coates 1995) and preliminary phylogenetic analysis already suggests that it is more derived than either of the well known East Greenland taxa (which do not constitute a monophyletic taxon: *contra* Lombard & Sumida 1992). Formerly misidentified fragments plus new material from the Upper Frasnian of Scat Craig in Scotland were recognised as tantalising evidence of an earlier and perhaps more primitive tetrapod, *Elginerpeton* (Ahlberg 1991a, 1995, in press). Another fish-like tetrapod, *Ventastega*, was discovered in the Upper Devonian of Latvia (Ahlberg *et al.* 1994), and this in turn corroborated the previously uncertain tetrapod-like identity of *Metaxygnathus* (Campbell & Bell 1977), an isolated mandible from slightly earlier deposits in Australia. Meanwhile, similarly aged deposits in Pennsylvania have yielded a sixth taxon, *Hynerpeton* (Daeschler *et al.* 1994). The palaeogeographic range of early tetrapods therefore extends from North America, through Europe to Australia, suggesting an almost global Late Devonian equatorial distribution.

Fossil trackways provide further, complementary, evidence of early tetrapod distribution. This alternative data source remains consistent with the skeletal evidence, despite radical reassessments of previously accepted tetrapod trackways during recent years. Examples from the Upper Devonian of Australia (Warren & Wakefield 1972) are now supplemented by possible tetrapod trackways from the Middle Devonian of Scotland (Rogers 1990), and Ireland (Stössel 1995). However, trackways reported from the Lower Devonian of Australia (Warren *et al.* 1986) are now thought to be not of tetrapod origin, and an isolated footprint from the Devonian of Brazil Leonardi 1983) is considered as probably misidentified (Clack 1994a; in preparation, personal communication). Trackway evidence raises further questions about the palaeoecology of Devonian tetrapods, but these are mostly beyond the scope of the present study. Nevertheless, it is worth noting that the sedimentological context of *Acanthostega* specimens (Bendix-Almgreen *et al.* 1990) supports the anatomical evidence (discussed in section 5.1.), indicating that this was primarily

an aquatic animal, occupying the active parts of a vegetation-choked, meandering fluvial channel system. Published data concerning the palaeoenvironments of other Devonian tetrapods are limited, but indicate some diversity. *Tulerpeton* is known from shallow marine deposits (Lebedev 1984, 1985, 1990), while the apparently terrestrially-adapted *Hynerpeton* originates from non-marine floodplain sediments (Daeschler *et al.* 1994) rich in faunal and floral remains (Woodrow *et al.* 1995). Concise summaries and discussions of these and further new data concerning questions of tetrapod origin, terrestrialisation, and the changing picture of Upper Devonian terrestrial environments can be found in Shear (1991), Lombard and Sumida (1992), Ahlberg and Milner (1994), Coates and Clack (1995), and Daeschler and Shubin (1995).

The focus of this paper, however, is restricted to the detailed description of the postcranial skeletal anatomy of *Acanthostega*, including the vertebral column, caudal fin, ribs, girdles, and limbs. These data are (then) combined with an expanded database developed from that which was assembled for the analysis of the *Tulerpeton* postcranium (Lebedev & Coates 1995), and used to generate a phylogeny incorporating all of the recently discovered Upper Devonian tetrapods plus selected Carboniferous and Permian species. Character choice, as in the *Tulerpeton* analysis, places greater emphasis on postcranial features, an area which has often been neglected in previous works. The contentious question of what actually constitutes a tetrapod is re-examined (cf. Lebedev & Coates 1995), and a 'total group' (Patterson 1993a,b) definition is used throughout the text.

1. Materials and methods

The *Acanthostega gunnari* material described in this paper comes from Stensiö Bjerg of the Britta Dal Formation of the *Remigolepis* Group *sensu* Nicholson and Friend (1976). The *Remigolepis* Group forms part of the Mount Celsius Supergroup, which also includes Wiman Bjerg and the Britta Dal Formation. It has been dated as Fammenian (Bendix-Almgreen 1976), on the basis of faunal characteristics and correlation with more confidently dated deposits. The fossiliferous Aina Dal and Britta Dal Formations yield a variety of limbed and finned stem-tetrapods including *Acanthostega*, *Ichthyostega* and *Eusthenodon*, plus the porolepiform *Holoptychius*, the dipnoan *Soederberghia*, the placoderm *Remigolepis*, and isolated ctenacanth fin spines (J. Long, personal communication; Bendix-Almgreen 1976; Clack 1994a). The sedimentary, faunal and palaeoecological contexts of this material are discussed in detail in Bendix-Almgreen *et al.* (1988, 1990). The best articulated specimens are now known to come from a single, small lens of fossil mud-cracked matrix within an apparently actively flowing channel deposit preserved in point bar sediments. Mostly isolated bones were collected from similar deposits above and below this particular cache. The bone surfaces retain a finely detailed outermost layer which, combined with the high degree of skeletal articulation (Figs 1–4), indicates that each corpse travelled only a short distance prior to burial and fossilisation. Other *Acanthostega* specimens, including the holotype, MGUH A33 (Jarvik 1952), have been collected from the talus of Wiman Bjerg, Celsius Bjerg, and the Aina Dal Formation (Bendix-Almgreen *et al.* 1990). The particular *Ichthyostega* specimen referred to in the description comes from the scree from the upper part of the Aina Dal Formation (Bendix-Almgreen *et al.* 1988).

Figure 1 *Acanthostega gunnari*. MGUH f.n. 1227, individual X. This, the most complete specimen, lies directly above individuals Y and Z, as depicted in Figure 2.



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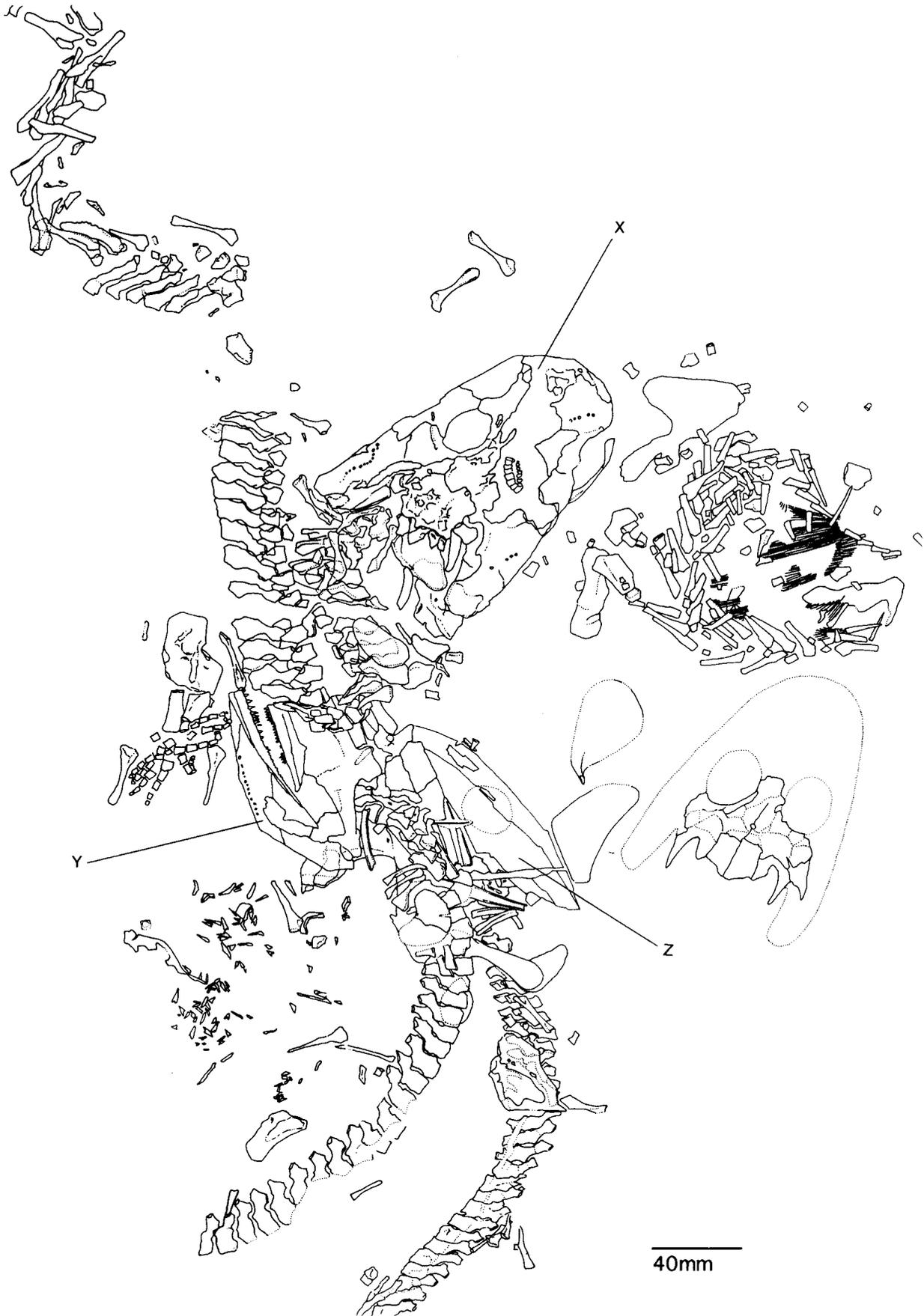


Figure 2 *Acanthostega gunnari*. MGUH f.n. 255, 1227, 1258, UMCZ T1300. Line drawing of individuals X, Y, & Z (see labelled cranial material) plus associated skeletal material as formerly located *in situ*, prior to field collections in 1970 (Friend *et al.* 1976) and 1987 (Bendix-Almgreen *et al.* 1987).

Most of the described material belongs to the Museum Geologicum Universitatis Hafniensis (=Geological Museum, University of Copenhagen), and is identified by the

abbreviation MGUH. When returned to Copenhagen, the numbers of these specimens will have the prefix VP. At present, all of the specimens currently retain their field

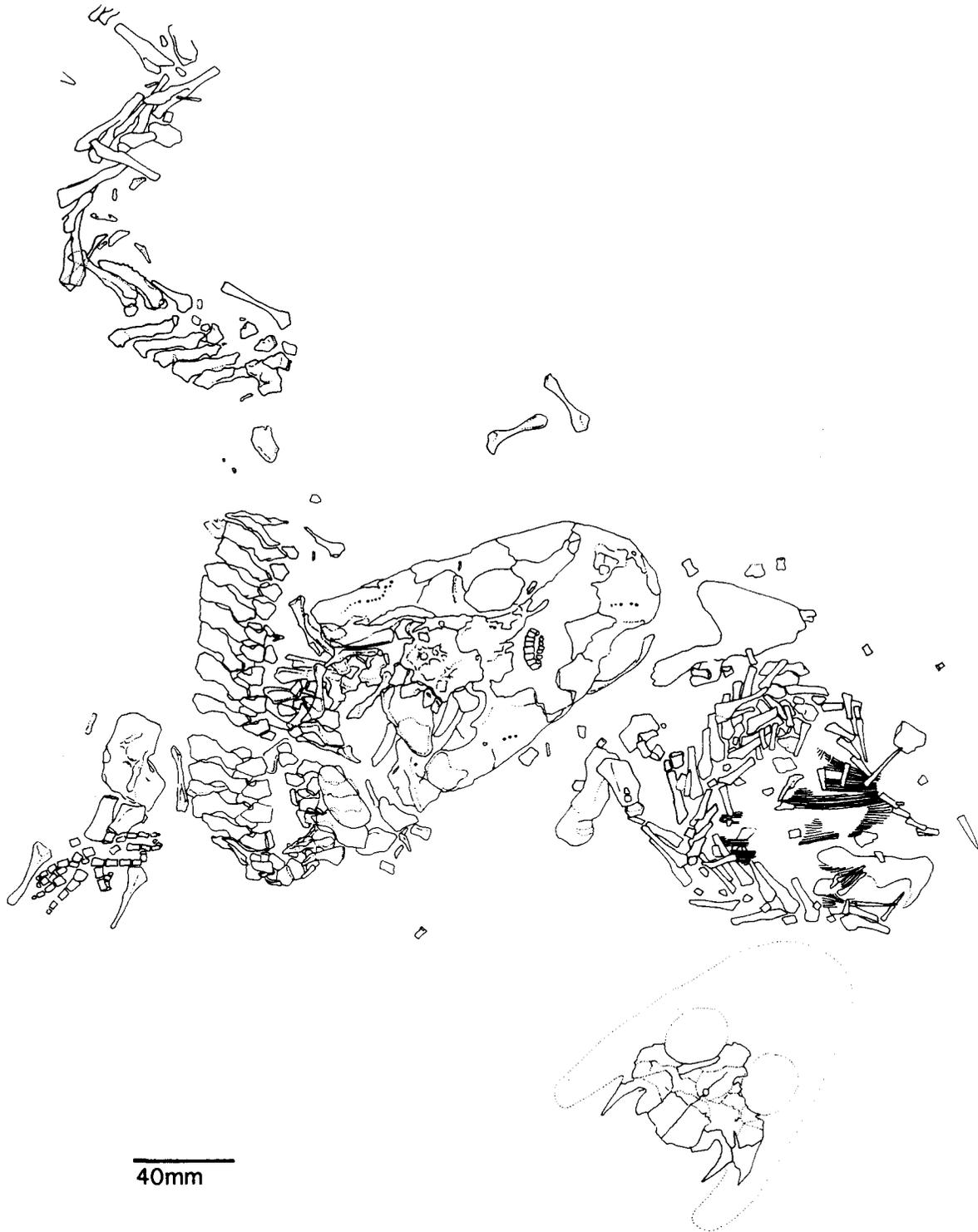


Figure 3 *Acanthostega gunnari*. MGUH f.n. 255, 1227. Individual X plus nearby pelvic, hindlimb, and caudal material.

numbers and are therefore prefixed with f.n. Specimens collected in 1970 (Clack 1988) belong to the University Museum of Zoology, Cambridge (abbreviation: UMZC), and bear the prefix T. Other abbreviations preceding specimen numbers refer to the following collections: CMNH: Cleveland Museum of Natural History, Cleveland, Ohio, U.S.A.; FM: Field Museum of Natural History, Chicago; MCZ: the Museum of Comparative Zoology, Harvard; PIN: the Palaeontological Institute of the Academy of Sciences of Russia; YPM-PU: the Peabody Museum, Yale (formerly within the Princeton University collections).

The following list comprises all of the *Acanthostega* material

referred to in the description, and the single *Ichthyostega* specimen.

MGUH f.n. 252. Almost complete array of ventral trunk scales (gastralia), plus pelvic plate. Previously figured by Bendix-Almgreen *et al.* (1988 fig. 3; 1990 fig. 3).

MGUH f.n. 255. Part of tail endoskeleton with dermal rays, plus incomplete pelvis and hindlimb. Fits onto edge of block MGUH f.n. 1227.

MGUH f.n. 272. Isolated humerus. Previously figured by Bendix-Almgreen *et al.* (1990 fig. 3).

MGUH f.n. 260. Pelvic girdle with femur articulated in acetabulum.



Figure 4 *Acanthostega gunnari*. MGUH f.n. 1258, UMCZ T1300. Individuals Y and Z.

MGUH f.n. 1227. Large block consisting of 11 parts (Figs 1–3). Includes the most complete specimen of *Acanthostega* (individual X: see discussion below), consisting of a dorsoventrally crushed skull with brain case, sclerotic ring, palate, stapes, branchial arches and pectoral girdle; octodactylous left and incomplete right forelimbs; vertebral column extending from cervical to mid-caudal region, plus incomplete rib series. MGUH f.n. 1227 also contains a further skull, and the pelvic, hindlimb, and caudal skeleton (with dermal rays) of a third individual (extending onto MGUH f.n. 255). MGUH f.n. 1227 connects with UMCZ T1300. Parts of MGUH f.n. 1227 have been previously figured in Bendix-Almgreen *et al.* (1990 fig. 4); Clack (1989 fig. 1; 1992 fig. 1; 1994a figs 1 & 9); Coates and Clack (1990 fig. 1; 1991 fig. 1); Coates (1991 figs 1 & 3; 1993 fig. 1; 1994b fig. 4).

MGUH f.n. 1258. Multi-part block which connects with specimen UMCZ T1300. Includes branchial arches, ribs and neural arch series of two individuals (Y & Z: see discussion below). Cleithrum of individual Z includes clear postbranchial lamina. Palatal material also present. Previously figured in Coates and Clack (1991 fig. 2); Clack (1994a fig. 8).

MGUH f.n. 1300. Multipart block including excellent caudal lepidotrichia with few endoskeletal bones. Also includes important palatal material and a uniquely, almost 'in-the-round' skull. Cranial material previously figured in Clack (1994a figs 2, 3 & 10).

MGUH f.n. 1336. Skull and pectoral girdle including natural mould of interclavicle.

MGUH f.n. 1358. Clavicle plus scapulocoracoid with ventral portion of cleithrum.

MGUH f.n. 1375. Hindlimb with near-articulated tarsus and digits.

MGUH f.n. 1396. *Ichthyostega* scapulocoracoid with cleithrum.

UMZC T1291. Pelvic girdle and caudal rib. Previously figured in Clack (1988 fig. 12).

UMZC T1300. Composite block including three skulls with branchial arches and pectoral girdles. Fits between blocks MGUH f.n. 1227 and 1258. Skulls labelled as 'B' and 'C' in Clack (1988) associated with postcrania of individuals Z and Y respectively (MGUH f.n. 1258). Previously figured in Clack (1988 figs 1–5, 7, 10 & 11; 1994b fig. 1); Bendix-Almgreen *et al.* (1990 fig. 4).

MGUH f.n. 1324. Composite block including caudal endoskeleton and a sacral rib.

The relation between specimen catalogue numbers and individual examples of *Acanthostega* is complicated because of the sequence of field collections and subsequent laboratory preparation. This rich lens of material is now known to include at least three partially complete individuals (Fig. 2 shows their overlapping arrangement in the matrix), parts of which were collected during the course of both 1970 and 1987

expeditions. These are referred to as individuals X, Y, and Z in the following text.

Mechanical techniques were employed for almost all of the specimen preparation. These included mounted needle, dental mallet, and pneumatic pen. Acid preparation was used only locally to etch-out a clean natural mould of the interclavicle (MGUH f.n. 1336). A Well diamond wire saw with 0.3 mm diameter wire was used to trim and section specimens. The matrix enclosing the fossils consists of an intractable, micaceous sandy siltstone of a variable character (see Clack 1988 for a more detailed discussion). The relative difficulty and frustration of working with such material (for example, when first exposed, the periosteal and perichondral bone frequently blisters away from the underlying bone and then disintegrates) serves to emphasise the importance of Sarah Finney's contribution, as preparator, to the success of this research.

Most specimen drawings were completed with the use of a camera lucida.

2. Systematic palaeontology

Genus *Acanthostega* Jarvik, 1952

Type species *Acanthostega gunnari* Jarvik, 1952

Amended diagnosis (revised from Clack 1988; most cranial characters incorporated from Clack 1994a,b). Unique features (relative to other stem-tetrapods): arrow-shaped supratemporal spanning skull table–cheek junction; deeply embayed tabular with long lateral horn; maxillary bearing about 44 teeth; premaxillary bearing about 13 teeth; dentary bearing about 70+ teeth; sixth caudal vertebra with anteriorly serrated haemal arch plus spine; first neural radial extends from eighth caudal vertebra, and first haemal radial extends from fifteenth caudal vertebra; manus with phalangeal formula of 3,3,3,3,4,4,4,3. Derived characters relative to panderichthyids and lower stem-tetrapods: spade-shaped snout with enlarged bilateral pair of nasals; stapes and fenestra ovalis present; lateral commissure absent; operculogular series absent; foraminate parasymphysial plate with tooth row; Meckelian bone concealed dorsal to prearticular; vertebral column rhachitomous with 30+ presacral segments; narrow zygapophyses present; caudal fin lepidotrichia elongate, unsegmented and unbranched; anterior thoracic and posterior cervical ribs unciniate; single pair of elongate sacral ribs; limb girdles with enlarged endochondral plates; pectoral girdle separated from skull; ischial pelvic symphysis; biramous ilium; humerus with subrectangular entepicondyle; femoral adductor blade present; limbs dactyloous; fibulare articulates directly with digits. Retained primitive characters include: preopercular bone; lateral otic fissure continuous with vestibular fontanelle/fenestra ovalis; parasphenoid terminates anterior to ventral cranial fissure; basisphenoid and parasphenoid excluded from vestibular rim; large ceratohyal and 3+ deeply grooved, ossified branchial arches; intercentra paired; anocleithrum present; cleithrum with broad postbranchial lamina; endochondral girdles unsutured; scapulocoracoid lacks substantial infraglenoid buttress; caudal lepidotrichia present; postacetabular buttress more prominent than supra-acetabular buttress; radius near-spatulate distally; short ulna without olecranon process.

3. Description

3.1. Vertebrae

The most complete vertebral column is preserved in MGUH f.n. 1227: X. This consists of an uninterrupted vertebral series extending from the atlas to presacral segment 29 (counting

from anterior to posterior). The series then resumes more posteriorly as haemal arches plus spines, and continues from the sacral intercentrum to caudal segment 13 (Figs 1–3 & 5a). This is the only individual in which neural arches remain in articulation with centra. Two other less complete individuals, Y and Z underlie individual X (Figs 2, 4 & 5b,c). In total, these three individuals incorporate parts of specimens MGUH f.n. 255, 1227 & 1258, plus UMZC T1300. Individuals Y and Z also preserve continuous series of neural arches, consisting of presacral segments 1–30 and 2–28 respectively.

The vertebrae are rhachitomous with an unconstricted notochordal canal. The degree of central ossification resembles that of *Eusthenopteron* (Andrews & Westoll 1970a; Jarvik 1980), *Ichthyostega* (Jarvik 1980, 1996), and to a lesser extent *Whatcheeria* (Lombard & Bolt 1995). Most presacral vertebrae consist of an anteroposteriorly broad neural arch, paired, tiny pleurocentra and paired, large intercentra. Transverse processes and zygapophyses are only weakly developed, in the sense that both structures display minimal lateral development, and that the craniocaudal zygapophyseal dimension is barely equal to and usually less than that of the neural arch at the same level (cf. Lombard and Bolt's characterisation of *Whatcheeria*). The combined vertebral series of individuals X, Y, and Z are most consistent with a presacral count of 30 vertebrae. The caudal skeleton consists of around 32 vertebrae, and includes a well developed tail fin supported by lepidotrichia plus neural and haemal radials. The best caudal endoskeleton (Fig. 6a) is coiled next to the snout of individual X (MGUH f.n. 255, 1227). Complementary data were obtained from MGUH f.n. 1324 (Fig. 6b) and the tail of individual X (MGUH f.n. 1227). An almost complete dermal fin is preserved in MGUH f.n. 1300, (Fig. 6c). Other substantial areas of lepidotrichia are present in MGUH f.n. 1227 & 255, and MGUH f.n. 1324. The restored vertebral column, including the caudal fin and radials, is shown in Figure 7.

3.1.1. Presacral vertebrae. Each multipartite centrum includes a large but thinly ossified intercentrum which in anterior view is crescentic, with wedge-shaped upturned sides wrapping around the notochordal channel (cf. *Ichthyostega*, Jarvik 1980, 1996; *Greererpeton*, Godfrey 1989) (Figs 5a, 7, 8 & 9a–d). The external surface is covered almost entirely with perichondral bone, while the remaining surfaces are rugose and unfinished. The perichondral bone is pitted, with slight muscle scarring anterior to the weakly developed parapophyses. Each rib articulation is directed posterolaterally, and is dorsally continuous with the posterior intercentral rim. The facet is preceded posteroventrally by a perichondrally lined shallow groove, which Jarvik (1980 fig. 157) (igr, Fig. 8d,e) identified in *Ichthyostega* as a channel for the intermetameric artery. The ventral intercentral surface is flattened or slightly concave, roofing the path of the dorsal aorta. There are no prominent protuberances or tubercles such as those which Godfrey (1989: *Greererpeton*) and Holmes (1989: *Archeria*) interpreted as hypaxial muscle insertions (e.g. atlantal intercentrum, Fig. 8e). Overall, intercentra show little regional variation in the presacral region (except where noted below), and in this respect resemble those of *Eusthenopteron* (Andrews & Westoll 1970a). Such intercentral uniformity, especially in the cervical region, is unusual for limbed tetrapods. The equivalent region of *Ichthyostega* is unknown, and the closest comparison among more advanced tetrapods is *Greererpeton*. Furthermore, in *Acanthostega* most intercentra appear to consist of unfused antimeres (cf. *Crassigyrinus*, Panchen 1985), with two notable exceptions: the atlantal and sacral intercentra are fused firmly along the ventral midline (Fig. 8d,e). Thus none exhibit the ventral consolidation found in intercentra such as those of *Whatcheeria* (Lombard & Bolt 1995). The degree of fusion in

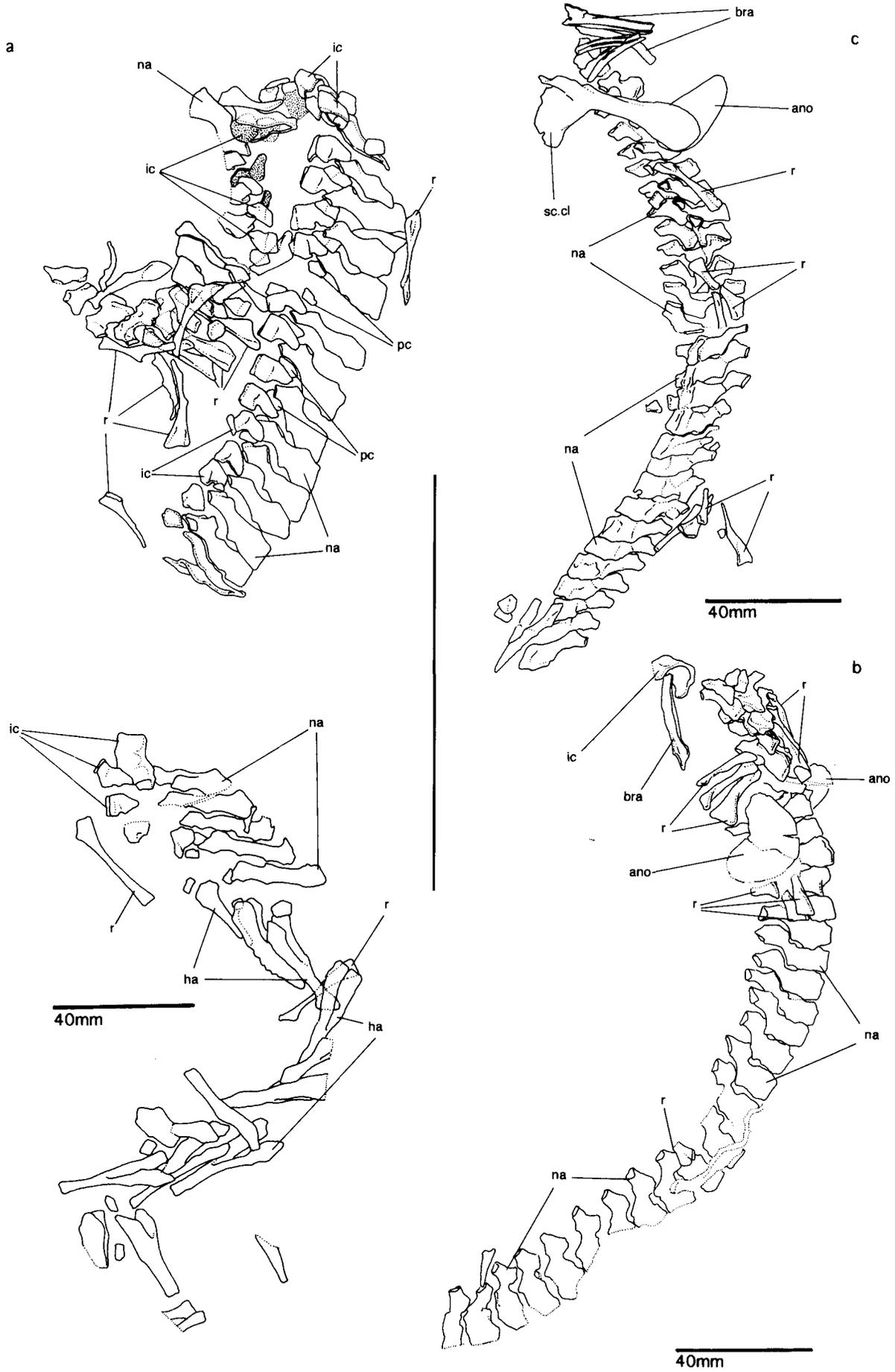


Figure 5 *Acanthostega gunnari*. (a) MGUH f.n. 1227. Axial skeleton of individual X. (b) MGUH f.n. 1258 and UMCZ T1300. Axial skeleton of individual Y. (c) MGUH f.n. 1258 and UMCZ T1300. Axial skeleton of individual Z.

presacral segments 2–6, 17–21, and 24–29, is unknown (first and second caudal intercentra are divided, resembling those of the mid-trunk region).

Pleurocentra have a restricted distribution within the vertebral column, extending from the eighth presacral to around the twenty-second caudal segment (Fig. 7). Like the intercentra, these pleurocentra are little more ossified than those of *Eusthenopteron* (Andrews & Westoll 1970a). Where present, each vertebral segment has a pair of these rounded, subpentagonal plates (Figs 5a, 7, 8f & 9c,d), divided externally into approximately equal dorsal and ventral regions by a faint horizontal ridge. Unlike those of Andrews and Westoll's (1970a) description of *Eusthenopteron*, the pleurocentra bear perichondral bone. However, personal observation of a moderately large specimen of *Eusthenopteron* (CMNH 8160; Fig. 33c) found those pleurocentra which were visible to have perichondral bone, resembling the condition in *Acanthostega*. In *Acanthostega* and *Eusthenopteron* the pleurocentral dorsal external surface may bear a shallow groove, possibly associated with spinal nerves. The 'interdorsals' of *Ichthyostega* (Jarvik 1980) are significantly better ossified and more clearly notched and grooved than the pleurocentra of *Acanthostega*.

Neural arches and spines (Figs 7, 8a–c & 9) display the greatest variation along the presacral column. The spines are squared-off dorsally as in *Ichthyostega* and more recent tetrapods. This contrasts strongly with basal stem-tetrapods and other osteichthyans where they tend to be rounded or acute, although in *Eusthenopteron* the ten most anterior spines have somewhat straighter, near-horizontal apices. Cervical arches are shorter and more highly differentiated nearer to the occiput (Fig. 8a–c). The atlas arch (well preserved in MGUH f.n. 1227, X; MGUH f.n. 1258, UMCZ T1300, Y) consists of barely more than a pair of anterodorsally grooved perichondral subrectangles. These may have sandwiched a cartilage plug, or abutted directly above the neural canal. The transverse processes are minimal, and the diapophyses indistinct. Narrow, weakly developed prezygapophyses indicate the presence of an otherwise unknown proatlas. There is no anteromesial finger-like process, as in *Pholidropteron* (Clack 1987). Each half of the neural arch bears a posterodorsally ascending groove, lateral to the anterodorsal angle. The postzygapophyses are more distinct, but the precise angle of articulation between the atlas and axis arches is uncertain, and restored to resemble *Greererpeton*. With this degree of inclination there appears to have been only limited atlantal–axial overlap.

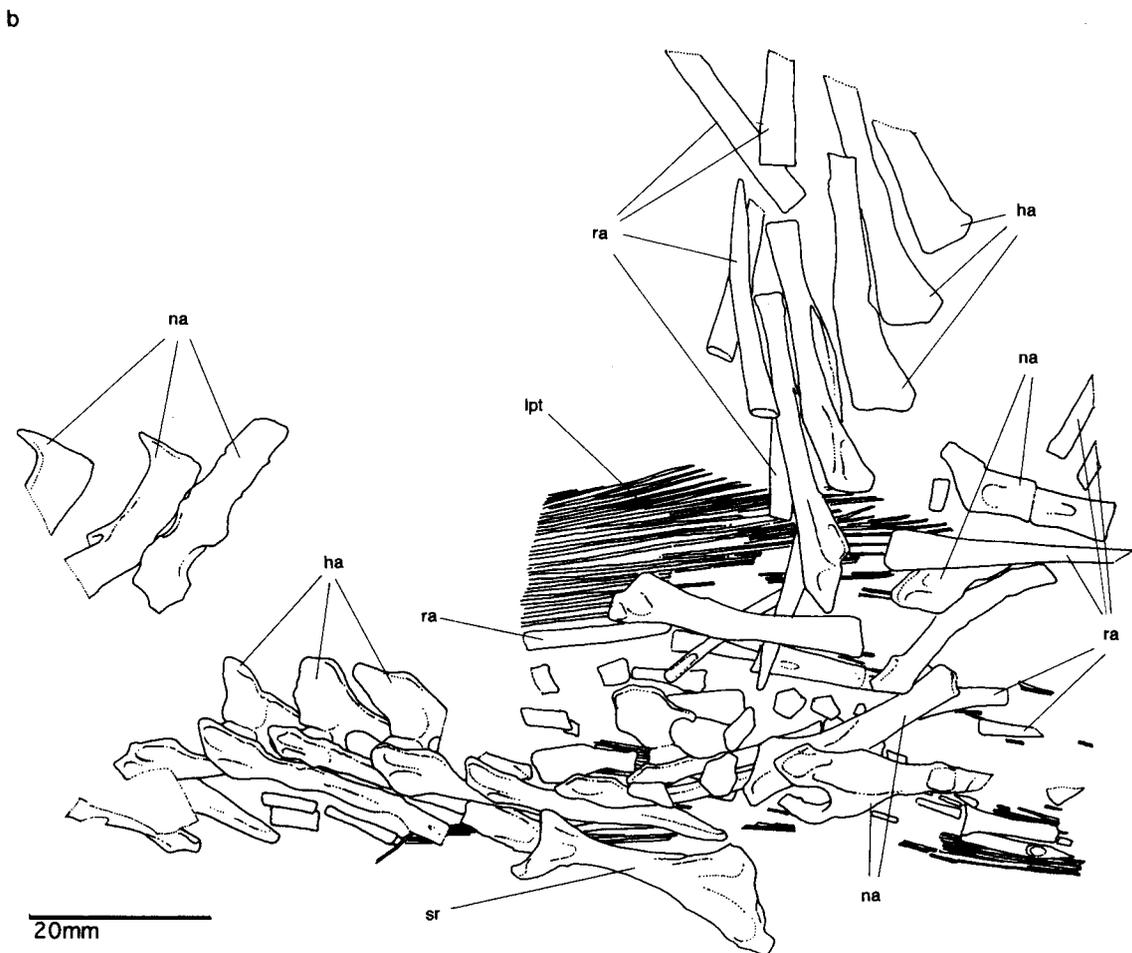
The axial arch, like the atlantal, is paired (Fig. 8a–c). The transverse processes are much better developed than in the atlas, and resemble those of all more posterior neural arches. Similarly, the pre- and postzygapophyses are more clearly differentiated, likewise resembling those of more posterior neural arches. Above the neural canal, the spine is elongated craniocaudally, projects forwards, and the entire structure appears to be tilted slightly anteriorly. In this respect it resembles a less extreme version of the anteriorly curved axial arch in *Proterogyrinus* (Holmes 1984) and *Pholidropteron* (Clack 1987). Like *Greererpeton* (Godfrey 1989), the axial spine extends as a thickened but posteriorly truncated sagittal crest; flanking troughs divide this from large lateral ridges. These ridges enlarge posterolaterally, project above the postzygapophyses, and appear to engage with the third neural arch.

The third neural arch is taller and more slender than the axial, with a crimped apex and smaller lateral ridges. Once again, the arch and spine are paired (MGUH f.n. 1227; UMCZ T1300). Bilateral neural arch fusion occurs only from the fourth presacral to around the 22nd caudal vertebra. Many subsequent details of presacral neural arch diversity are

presented in Figures 2–5, and 7. All arches are only loosely associated with their intercentra. The atlas and axis arches are simply butted against posterodorsal intercentral edge. However, from presacral segment 3 to caudal segment 4, a small flange projecting from beneath each prezygapophysis appears to form a closer association with the intercentral rim. Each arch increases in height until presacral segments 14 or 15, and the arches extend posterodorsally so that the neural spines project extensively above posteriorly preceding intercentra. The degree of posterior overlap is significantly greater than that of *Ichthyostega*, and among early limbed tetrapods, only *Greererpeton* resembles *Acanthostega* in displaying such an otherwise fish-like characteristic. Lateral ridges, like those on the axial and third neural spines, are present in at least segments 4, 7, 9, 10, 12, 14, 15, and 30. These are less prominent than those of the axial, and may be associated with tendinous inter-arch bracing. Similar structures are preserved in individual Y (UMZC T1300), extending across arches 19–26 (Fig. 5b). Alternatively, such ridges may mark myoseptal attachment sites. In the similarly notochordal vertebral column of the extant actinopterygian fish *Polypterus senegalus* (Bartsch & Gemballa 1992) myosepta in much the same orientation extend across three or more neural spines. In *Acanthostega* most presacral spines (segments 6–24; less so from 24 to caudal 2 or 3) are sufficiently broad, craniocaudally, to interarticulate above the level of the zygapophyses. The extent to which a xenarthrous-like condition was achieved is uncertain, and there are no facets or signs of wear on the anterior or posterior surfaces of the neural spines. The zygapophyses, however, are poorly developed: their craniocaudal dimension is less than that of the neural arch at the same level (cf. better developed zygapophyses in *Whatcheeria*, Lombard & Bolt 1995). They may have provided insufficient bracing by themselves for semi-emergent trunk support.

Anterior and posterior aspects of the neural arches are best known from posterior trunk segments 25–28 (Y: MGUH f.n. 1258) (Fig. 9a,b). Once again, the condition is intermediate between *Eusthenopteron* (Andrews & Westoll 1970a) and *Ichthyostega* (Jarvik 1980). Like the inter- and pleurocentra, the neural arches are only thinly ossified, resembling *Eusthenopteron* more closely than *Ichthyostega*. The notochordal and neural canals are confluent, and are continuous dorsally with a supraneural canal, which is assumed to have housed a dorsal ligament. A perichondral strap above the anterior and posterior supraneural canal openings connects the lateral surfaces. Anterior and posterior edges of the neural spines are otherwise unossified, and apparently connect along only the dorsal edge. In disrupted specimens neural arches are often splayed with complete separation of the left and right sides. Such separation is complete in *Panderichthys* (Vorobyeva & Schultze 1991) and *Crassigyrinus* (Panchen 1985), occasional in *Eusthenopteron*, but absent in *Ichthyostega* and other more recent tetrapods.

3.1.2. Sacral and caudal vertebrae; caudal fin. The sacral segment is not highly differentiated relative to neighbouring vertebrae. The intercentrum is slightly longer, craniocaudally, than its neighbours. The intercentral halves are fused ventrally, and, like *Eusthenopteron* (Andrews & Westoll 1970a), bear enlarged parapophyses (Figs 5a, 7 & 8e). The caudal count of around 32 segments is more than *Eusthenopteron* (25), but less than *Ichthyostega* (36) (Jarvik 1952, 1980). The caudal fin is more extensive than that of *Ichthyostega*, originating at caudal segment 8 instead of 12, dorsally, and 15 instead of 29–30, ventrally. In *Acanthostega*, caudal intercentra 1–3 remain divided, but are fused from segment 4. Parapophyseal rib facets are born by caudal intercentra 1–4, and the fourth intercentrum is the most anterior to show a distinct, incomplete



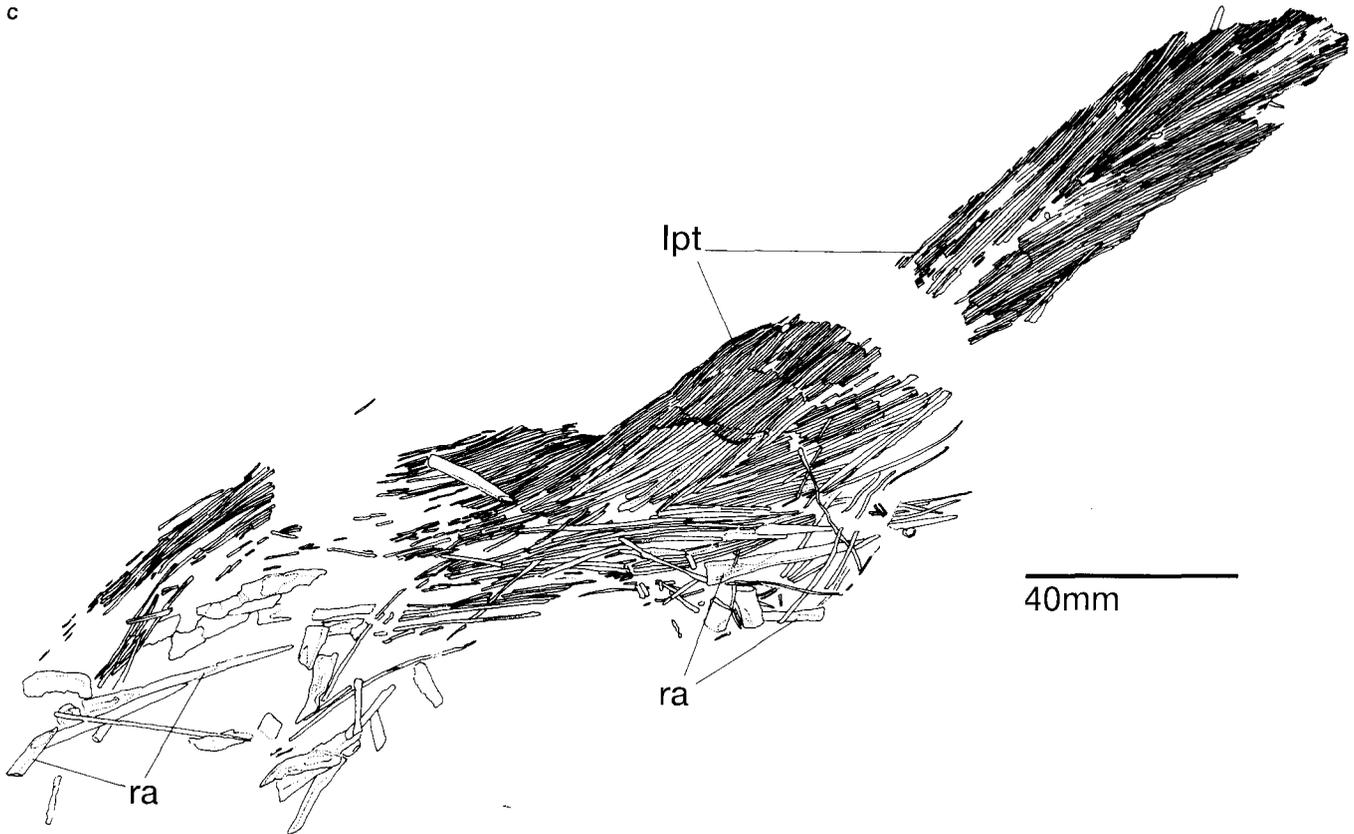


Figure 6 *Acanthostega gunnari*. (a & b left, c above, d overleaf.) (a) MGUH f.n. 255, 1227. Caudal skeleton coiled next to snout of individual X. (b) MGUH f.n. 1324. Caudal skeleton with sacral rib. (c) MGUH f.n. 1300. Caudal fin lepidotrichia plus disarticulated endoskeletal supports. (d) MGUH f.n. 1227. Caudal endoskeleton showing specialised most anterior haemal arches and spines: numbers indicate position in caudal series. (di) Exposed surface of specimen; (dii) reverse of block, showing complete extent of arches and spines.

haemal arch. However, posteriorly enlarged ridges flanking the dorsal aortic groove are already apparent on the sacral intercentrum. All haemal arches are fused to the intercentra. The first three complete haemal arches (caudal intercentra 5–7) are specialised and fit closely together (Figs 5a, 6a,d & 7). Three specimens (MGUH f.n. 255, 1227 & 1324) display this unusual, and apparently conserved, morphology. The first haemal arch bears almost no spine, and fits within the slightly concave anterior face of the second arch and spine. The walls of the second haemal arch are broader anteroposteriorly, and the broad spine, which is directed more posteriorly than the arch, has an acute, serrated leading edge. This arch and ‘steak knife’ spine, in turn, fit neatly into the anterior of the third haemal arch. The walls of the third haemal arch are perforated by a foramen opening externally into an anterodorsally directed groove, and the substantial spine expands distally to form a rounded, anvil-shaped apex. The ossified bridge, separating haemal from notochordal canals in these and all more posterior arches, consists of incompletely fused ledges extending from the lateral wall of each arch (Figs 6b & 9e: clearly visible in MGUH f.n. 1324). These persistently divided bridges resemble unfused intercentra in more anterior regions of the vertebral column. The haemal spines of caudal segments 8–14 are slender, laterally fluted, and terminate in a slightly expanded spear-like apex. More posterior haemal arches and spines become gradually shorter as they near the caudal terminus. These spines have a flattened apex which articulates with radial fin supports (Figs 6b, c, 7 & 9e). The most posterior haemal ossifications are rod-like median structures with barely any remaining proximal arch. None of the haemal arches bears any projection resembling incipient zygapophyses like those of the most anterior caudal neural arches.

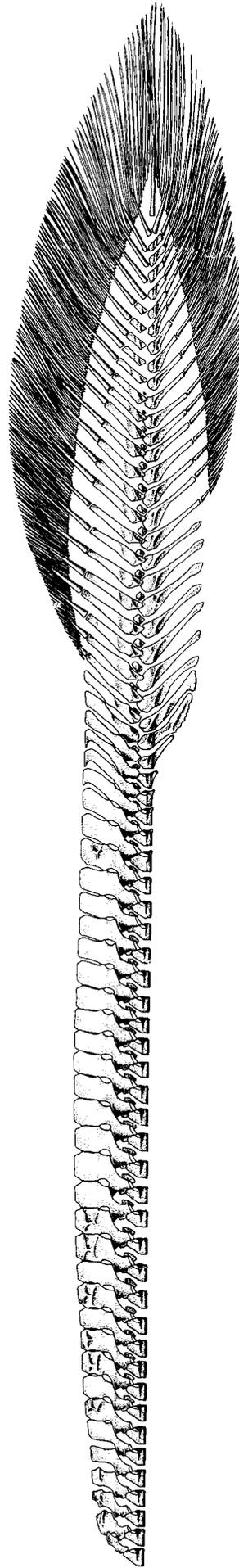
The neural arch and spine of caudal segment 1 is unspecialised, but those of segments 2–4 occupy a transitional zone where they become reoriented to a greater posterodorsal slope which is maintained throughout the tail. Caudal neural spines 2–4 also bear specialised apices, with anteriorly projecting prongs (X, MGUH f.n. 1227, and MGUH f.n. 1324) (Figs 5a, 6b & 7). The zygapophyses become less distinct, and disappear by caudal segment 6, although a more dorsal anterior projection suggests some accessory interarticulation. Caudal neural arch and spine 8 is the first to support a radial, as do all more posterior neural ossifications until about caudal segment 27. Beyond this point a series of radial-cum-neural spines support the remainder of the tail. Pleurocentra cease at about caudal segment 22. The urostyle (Fig. 7) is restored after *Ichthyostega* (Jarvik 1952, 1980, 1996), and, like *Ichthyostega*, distinct neural arches end before the haemal arches/spines. However, unlike *Ichthyostega* (Jarvik 1952-fig. 13E), in *Acanthostega* the supraneural canal is absent in the caudal region (Fig. 9d). The neural radials are simple, elongate conical rods. None is divided into proximal and distal radials as Ahlberg and Trewin (1995) describe in the lungfish *Dipterus*, and as Jarvik restores in caudal vertebrae 15–23 of *Ichthyostega* (1980, 1996; these were not identified in Jarvik’s 1952 restoration and description).

The lepidotrichia resemble those of *Ichthyostega*, although in *Acanthostega* they are more numerous, encompass a greater part of the tail, and are relatively longer. The best lepidotrichial array is preserved on specimen MGUH f.n. 1300 (Fig. 6c), but other examples include the coiled tail adjacent to the snout of individual X (MGUH f.n. 255 & 1227, Fig. 6a), and the fragment of caudal skeleton on specimen MGUH f.n. 1324 (Fig. 6b). These dermal rays are neither segmented or branched,



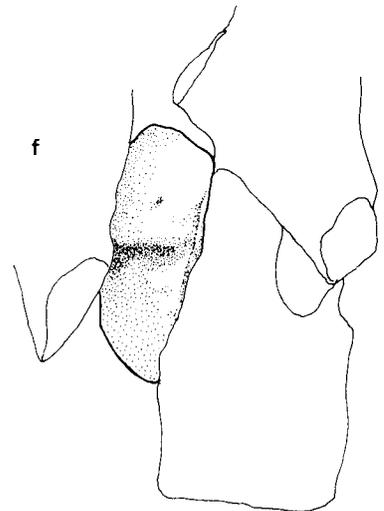
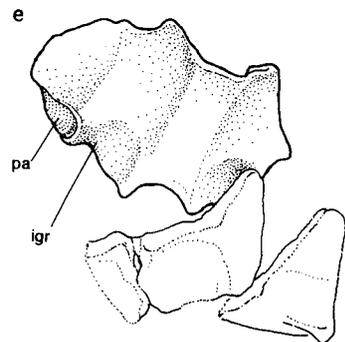
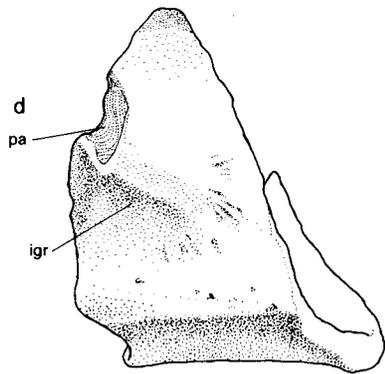
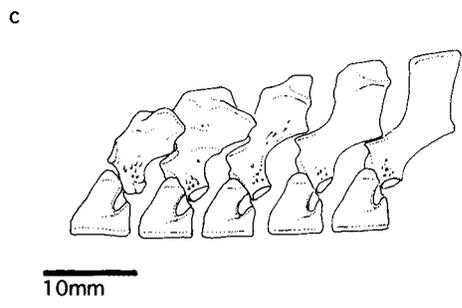
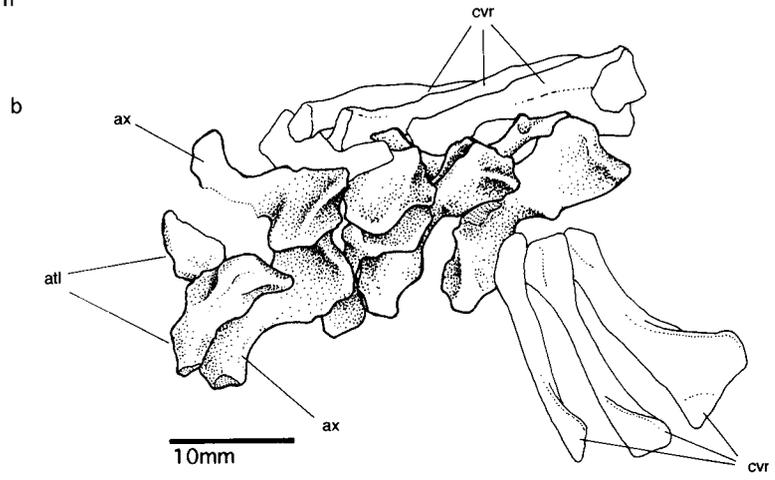
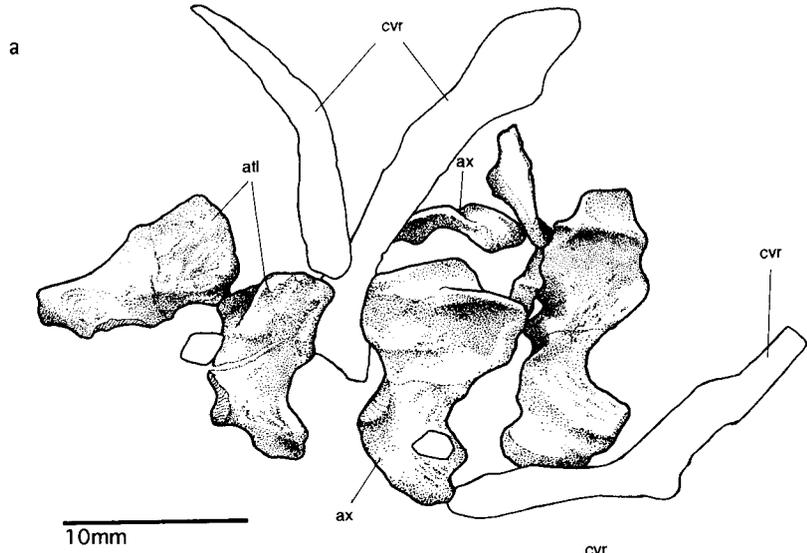
unlike those of *Eusthenopteron* (Jarvik 1980) or *Panderichthys* (Vorobyeva & Schultze 1991). Jarvik (1952) records a ratio of about 1:5 or 6 between radials and lepidotrichia for *Ichthyostega*; in *Acanthostega* this appears to lie between 1:6

and 1:8. *Acanthostega* exhibits none of the apparent tail fin subdivision which Jarvik (1980 fig. 156; 1996) relates to the underlying region of segmented neural radials and attributes to the coalescence of dorsal and caudal fins.



40mm

Figure 7 *Acanthostega gummari*, reconstructed vertebral column with caudal radials and lepidotrichia.



3.2. Ribs

No individual specimen of *Acanthostega* preserves an entire set of ribs. In order of completeness, most are found in individual X, MGUH f.n. 1227, individual Y, UMZC T1300 & MGUH f.n. 1258, individual Z, UMZC T1300 & MGUH f.n. 1258. A sacral rib is present on MGUH f.n. 1324 (Figs 6b & 11a–d). The presence of parapophyses and diapophyses with well developed rib facets indicates that ribs were present from the atlas to the fourth caudal vertebrae. All ribs (Fig. 10) have an enlarged spatulate head which is 'not conspicuously bicipital' (Milner & Sequeira 1994) like those of primitive temnospondyls such as *Balanerpeton*, and primitive stem-amniotes such as *Whatcheeria* (Lombard & Bolt 1995). The capitulum can only be distinguished from the tuberculum by an inter-facet angle. Most ribs are very different from those of *Ichthyostega*: none is strongly curved ventrally, and none bears a prominent and/or imbricating uncinatous process. Only the rudimentary ribs of the immediately presacral region in *Acanthostega* resemble those of *Ichthyostega*. This characteristic is almost certainly plesiomorphic, cf. *Eusthenopteron* (Jarvik 1980; Andrews & Westoll 1970a). In *Acanthostega* the ribs are mostly short, and only atlantal, axial, and caudal rib lengths exceed significantly the height of the neural arches plus spines. The short condition of the ribs is probably plesiomorphic relative to more recent tetrapods. In *Eusthenopteron* rib length is equivalent to no more than intercentral height (Andrews & Westoll 1970a), and in *Panderichthys* it (also) matches only neural arch plus spine height (Vorobyeva & Schultze 1991).

Anterior thoracic and cervical ribs are expanded distally (Fig. 8a,b; see also reconstructed rib series in Fig. 33b). The atlantal rib has a long, slightly posteroventrally curved shaft which expands only at its most distal extremity. The posterodistal surface is gently concave, and the acute dorsal crest of the expanded region descends proximally onto the anterior face of the shaft. From axial to eighth vertebrae the distal expanded region enlarges and the central shaft becomes correspondingly shorter. The anterior thoracic ribs of *Balanerpeton* (Milner & Sequeira 1994), and to a lesser extent *Eldeceon* (Smithson 1994) plus many other basal crown group tetrapods, are expanded distally in a similar fashion. From vertebrae 9 to 16 the distally expanded region decreases until reduced to a small flange in an increasingly proximal location on the dorsal surface of the shaft. Posterior to these, the remaining presacral ribs are straight and spinous, diminishing in length until they have only a rudimentary, short, posteriorly curved shaft (depicted in lateral view in Fig. 33b, and dorsal view in Fig. 31). These ribs are little more than half the relative length of neural arch plus spine height.

The sacral rib (Fig. 11a–d) of *Acanthostega* was present, uniquely, on MGUH f.n. 1324 (Fig. 6b). Extracted from the surrounding matrix, it clearly resembles an enlarged reiteration of the rib morphologies associated with presacral vertebrae 4–9 (Fig. 33b). It is quite unlike the stubby sacral ribs of *Proterogyrinus* (Holmes 1984), *Archeria* (Holmes 1989), or *Eogyrinus* (Panchen 1966), resembling instead the less specialised examples of *Greererpeton* (Godfrey 1989) and especially the more truncated pattern of *Eryops* (Olsen 1936) (Fig. 11e). Thus in *Acanthostega* the sacral rib bears a series of rugose ridges scarred by ligamentous attachments to the ilium. The

most prominent ridge originates on the anterior, lateral surface of the capitulum, and extends diagonally to the posterodorsal, distal extremity of the spatulate shaft (Fig. 11b). Again like *Eryops*, a second crest originates below the midpoint of the dorsal ridge (Fig. 11c), and this extends to the anteroventral distal extremity. The anterolateral face of the distal, spatulate region is convex, and the posteromesial surface is concave (Fig. 11b & a respectively). In both *Eryops* and *Acanthostega* the dorsodistal apex of the rib is proximal relative to the level of the ventrodistal extremity. It is worth noting at this point that Jarvik (1996, fig. 39C) illustrates a 'postsacral' rib of *Ichthyostega* which resembles quite closely the sacral rib of *Acanthostega*. Personal observation of *Ichthyostega* material suggests that this is quite unlike other postsacral ribs, which, surprisingly, resemble the bladed postpectoral pattern (*contra* Jarvik 1996). It seems likely, therefore, that this may be the sacral rib of *Ichthyostega*.

The caudal ribs are slightly longer than the most fully developed presacral ribs. Of the four pairs, the most anterior are about 20% longer than the height of their associated neural arch plus spine. The elongated rib shafts have a slight posteromesial curvature, and a much reduced distally expanded region relative to the sacral or anterior thoracic ribs. In certain specimens (e.g. UMZC T1291, Fig. 10k) a horizontal groove lies near to the dorsal edge of the convex anterolateral face of the expansion.

3.3. Pectoral girdle

The pectoral girdle consists of broad, thin scapulocoracoids, tall cleithra, anocleithra, clavicles and a median interclavicle (Fig. 14). As a limb-bearing girdle, it displays an unusual combination of fish-like, plesiomorphic characteristics combined with those which are present in more derived taxa such as *Hynerpeton* (Daeschler *et al.* 1994), *Tulerpeton* (Lebedev & Coates 1995) and *Whatcheeria* (Lombard & Bolt 1995). Only two specimens of the rather thinly ossified scapulocoracoid preserve the coracoid region (UMZC T1300 and MGUH f.n. 1227: Fig. 12a, b). Like *Ichthyostega* (Jarvik 1980), *Hynerpeton* (Daeschler *et al.* 1994), and *Tulerpeton* (Lebedev & Coates 1995), no growth lines or sutures are discernible, so the boundaries of contributing bones are uncertain. The glenoid, preserved most clearly in UMZC T1300 (Fig. 12a), is slightly longer than the greatest width of the humeral head—reversing the condition in stem reptiliomorphs such as *Pholiderpeton* (Clack 1987) and *Archeria* (Romer 1957). Glenoid orientation is posterolateral, and the strap-shaped, strongly concave fossa is slightly helical ('screw-shaped': Romer 1922). The coracoid region is uniformly thin, and where preserved has formed, *post mortem*, a crushed eggshell-like form to the sheet of bone. In life, the coracoid appears to have curved mesially and quite sharply just below the level of the glenoid, following the clavicular profile which it contacts anteriorly. In this respect it resembles closely the coracoid of *Greererpeton* (Godfrey 1989). In *Acanthostega*, two foramina pierce the coracoid beneath the anteroventral glenoid corner (Fig. 12a: foramina D & E). Similarly sited paired foramina associated with the glenoid canal are found in many other early tetrapods including microsaur (Carroll & Gaskill 1978), *Proterogyrinus* (Holmes 1984), *Pholiderpeton* (Clack 1987), *Hynerpeton* (Daeschler *et al.* 1994) and *Panderichthys* (Vorobyeva &

Figure 8 *Acanthostega gumari*. (a) MGUH f.n. 1227, individual X: most anterior three cervical neural arches. (b) MGUH f.n. 1258 & UMZC T1300, five cervical neural arches and associated ribs of individual Y. (c) Reconstruction of five most anterior (cervical) vertebrae. (d) UMZC T1300, atlantal intercentrum, right side. (e) MGUH f.n. 1227, sacral intercentrum (stippled) in ventral view showing slightly prominent parapophyses, accompanied by two preceding incompletely exposed intercentra (anterior towards top of figure). (f) MGUH f.n. 1227, pleurocentrum (stippled), left side.

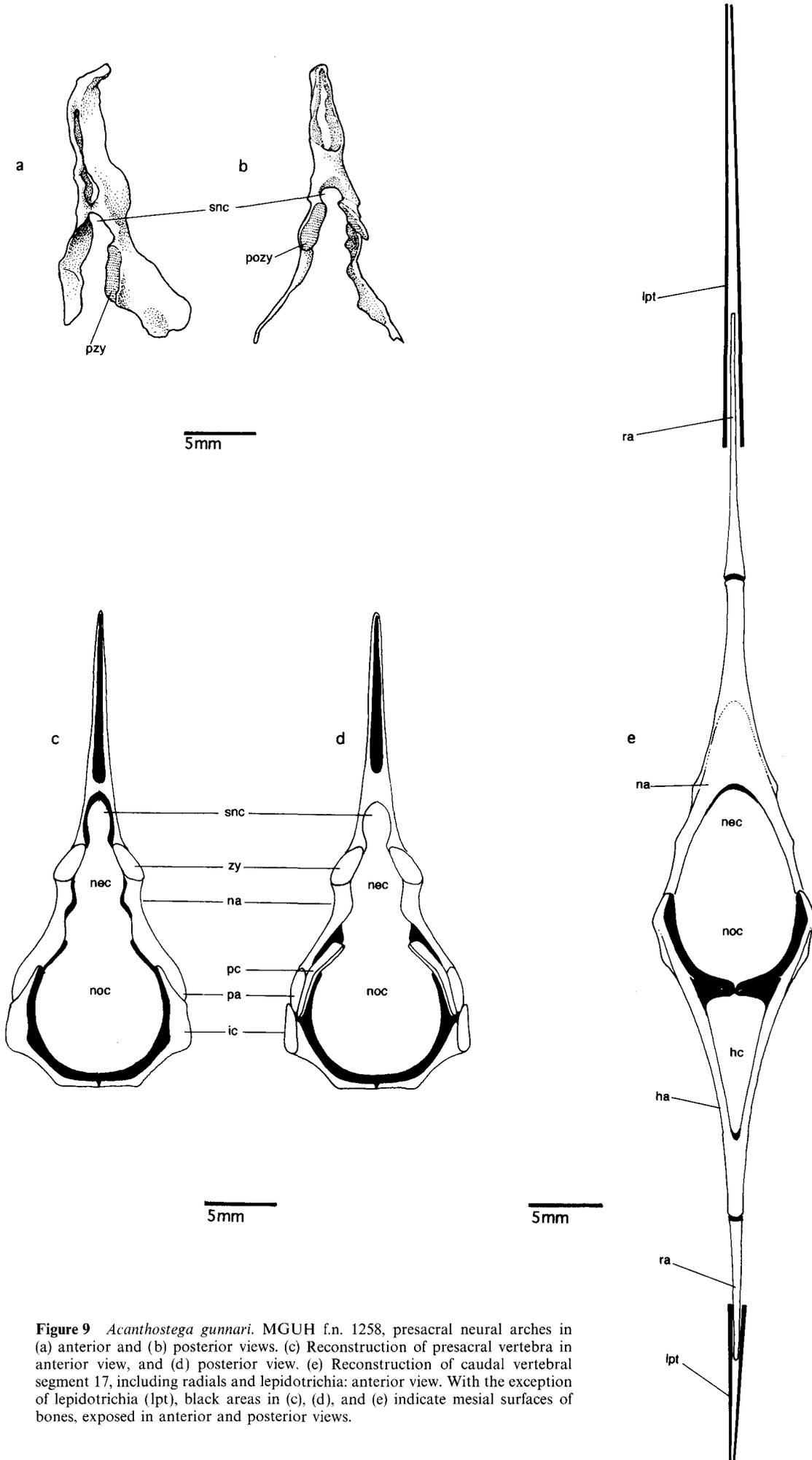


Figure 9 *Acanthostega gunnari*. MGUH f.n. 1258, presacral neural arches in (a) anterior and (b) posterior views. (c) Reconstruction of presacral vertebra in anterior view, and (d) posterior view. (e) Reconstruction of caudal vertebral segment 17, including radials and lepidotrichia: anterior view. With the exception of lepidotrichia (lpt), black areas in (c), (d), and (e) indicate mesial surfaces of bones, exposed in anterior and posterior views.

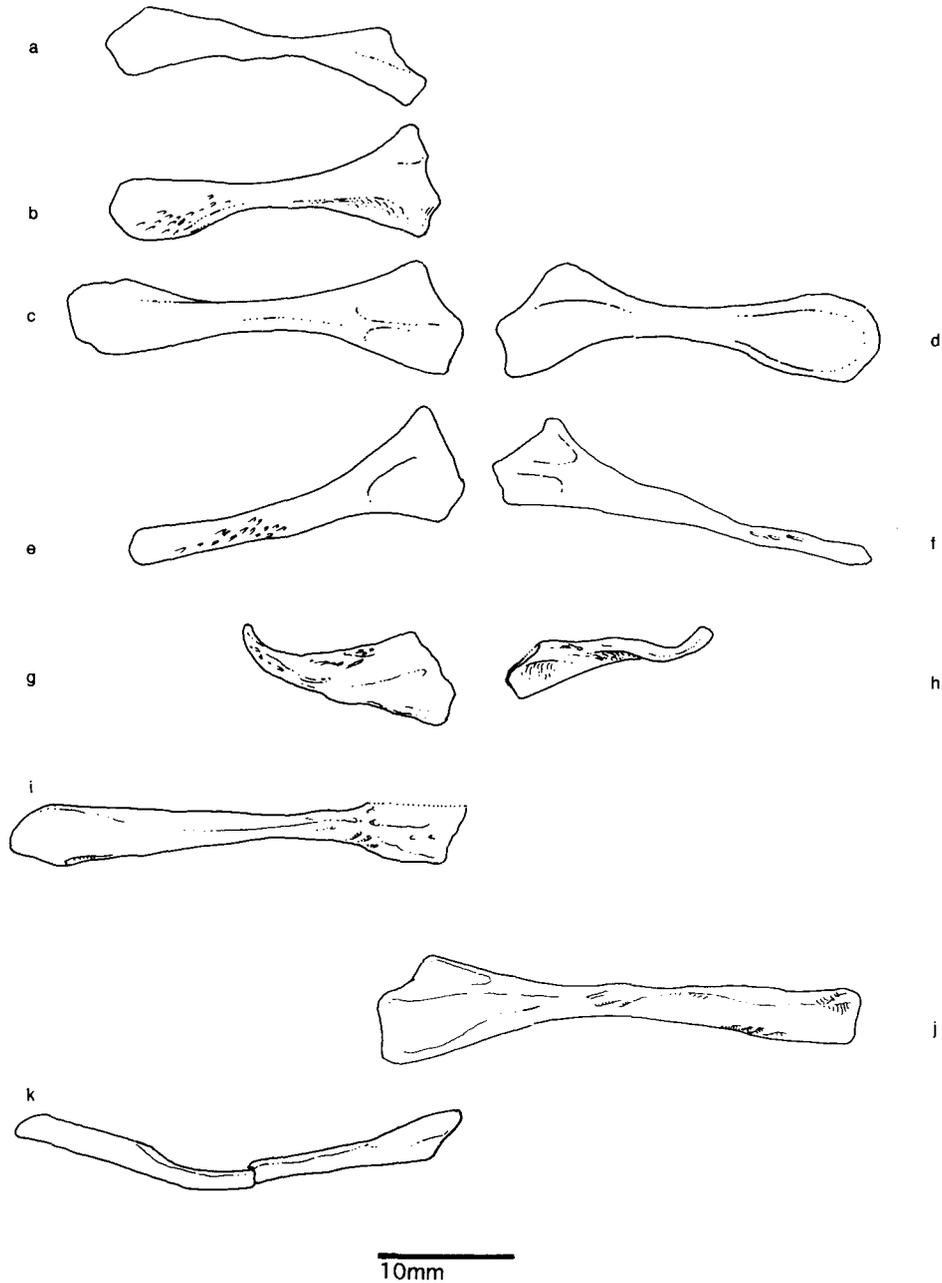


Figure 10 *Acanthostega gunnari*, presacral and caudal ribs, all illustrated as if from right side. (a), (b) & (c) Anterior thoracic ribs, anterior surface; (d) anterior thoracic rib, posterior surface; (e) mid trunk rib, anterior surface; (f) mid trunk rib, posterior surface; (g) posterior trunk rib, anterior surface; (h) posterior trunk rib, dorsal surface; (i) caudal rib, anterior surface; (j) caudal rib, posterior surface; (k) caudal rib, dorsal surface. All ribs from individual X, MGUH f.n. 1227, except (f) MGUH f.n. 1258, and (k), UMZC T1291. For cervical ribs see Figure 8, and sacral rib, see Figure 11.

Schultze 1991). This corroborates Holmes' (1980) hypothesis that such foramina are primitive for (crown-group) tetrapods. The thin bony sheet anterodorsal to the glenoid is pierced on the external surface of UMZC T1300 by at least three foramina (Fig. 12a: A–C). Of these, foramina A and C appear to be present on a second specimen, MGUH f.n. 1358. The foraminate condition of the mesial surface is more variable, with four or more present in MGUH f.n. 1227 (Fig. 12b: i–iv), but only a single foramen present in MGUH f.n. 1358 (Fig. 12d). This triangular arrangement of foramina A–C as apparent in specimens MGUH f.n. 1258, 1358, & UMZC T1300, is quite unlike published descriptions of any other scapulae. However, foramen C, located just behind the cleithral anterodorsal process is also present (but undescribed) in *Ichthyostega* (personal observation: MGUH f.n. 1396; undescribed in Jarvik 1996, but clearly visible in his plate 48, part

1), *Watcheeria* (personal observation: FM PR 1704) and perhaps *Hynerpeton* (Daeschler *et al.* 1994 fig. 1).

The triangular posterodorsal face of the well ossified supraglenoid buttress is entirely smooth (tra: Figs. 12b & 14a). No specimen provides a view of the scapulocoracoid mesial surface equivalent to that of the external surface as shown in Figure 12a, but several important features can be identified in specimens MGUH f.n. 1227 and MGUH f.n. 1358, as shown in Figure 12. In mesial aspect, the supraglenoid buttress is continuous with a substantial anterodorsal crest (adc: Fig. 12b, d), the pair uniting smoothly to form an arch at the base of the cleithrum-cum-scapular blade. Although the mesial surface of the glenoid is thickened, there is no evidence of a well ossified ventral footing which could constitute a substantial infraglenoid buttress. This absence of an infraglenoid buttress is unique among limb-bearing scapulocoracoids, and makes a

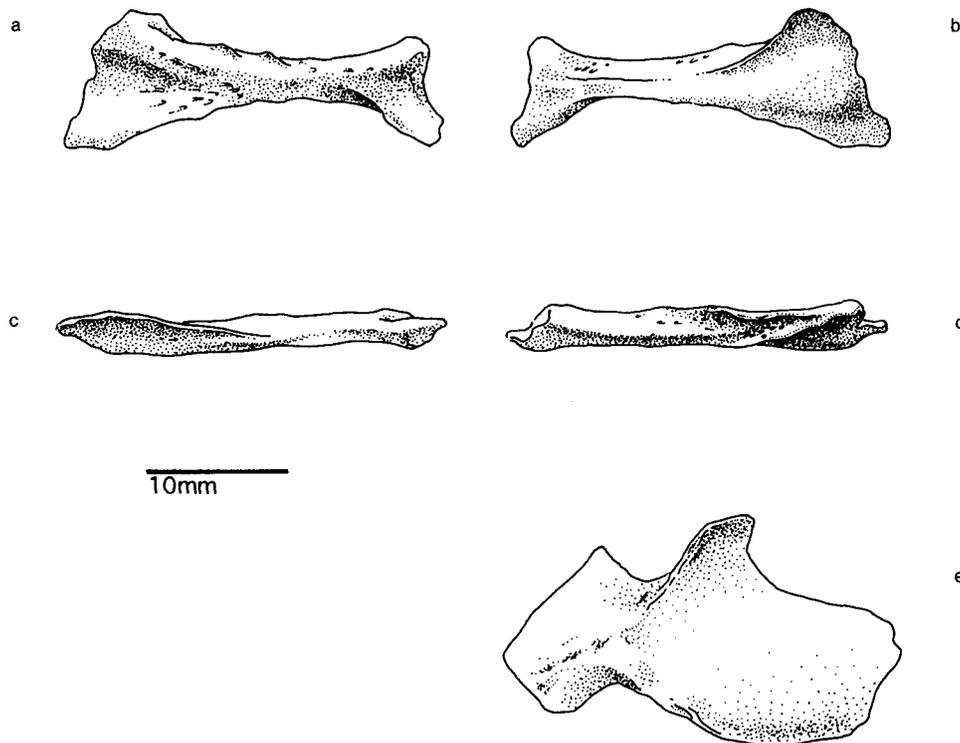


Figure 11 *Acanthostega gunnari*. MGUH f.n. 1324, sacral rib, left side. (a) Posteriomesial surface; (b) anterolateral surface; (c) ventral surface; (d) dorsal surface. (e) *Eryops*, sacral rib, left side, anterolateral surface (adapted from Olsen 1936).

striking contrast with those of *Ichthyostega* (Jarvik 1980, 1996), *Tulerpeton* (Lebedev & Coates 1995), *Hynerpeton* (Daeschler *et al.* 1994), and post-Devonian tetrapods. Elsewhere, the scapular region in *Acanthostega* is ossified as thinly as the coracoid, except where the thick, anterodorsal crest is applied closely to the rear of the cleithral anteroventral process. Similarly thickened areas of scapulo-cleithral attachment occur in *Ichthyostega*, *Hynerpeton* and *Panderichthys*. A deep, well defined groove passes up the anterior of this crest indicating its division from the cleithrum. Ventrally, the groove probably embraced the ascending, dorsal clavicular process. Vorobyeva and Schultze (1991 fig. 17) depict a similar groove in *Panderichthys*, and Daeschler *et al.* (1994 fig. 1B) describe this as the 'anteromedial depression' in *Hynerpeton*. In *Acanthostega* and *Hynerpeton* scapulo-cleithral fusion is complete dorsal to the anterodorsal crest. Only the rudimentary nubbin of an incipient scapular blade appears to be present in *Acanthostega*, and this is almost entirely enveloped by the lower regions of the cleithrum (Fig. 12e, f). *Ichthyostega* and *Hynerpeton* probably exhibit similar conditions. In *Acanthostega* sections through the base of the cleithrum/scapular blade reveal a striking pattern of highly vascularised dermal bone-like histology flanking more broadly trabecular endochondral bone. Ventrally, the dermal bone occupies the anterior and lateral surfaces; in a more dorsal section it passes around the anteromesial angle, occluding most of the apparently endochondral bone from exposure on the mesial surface.

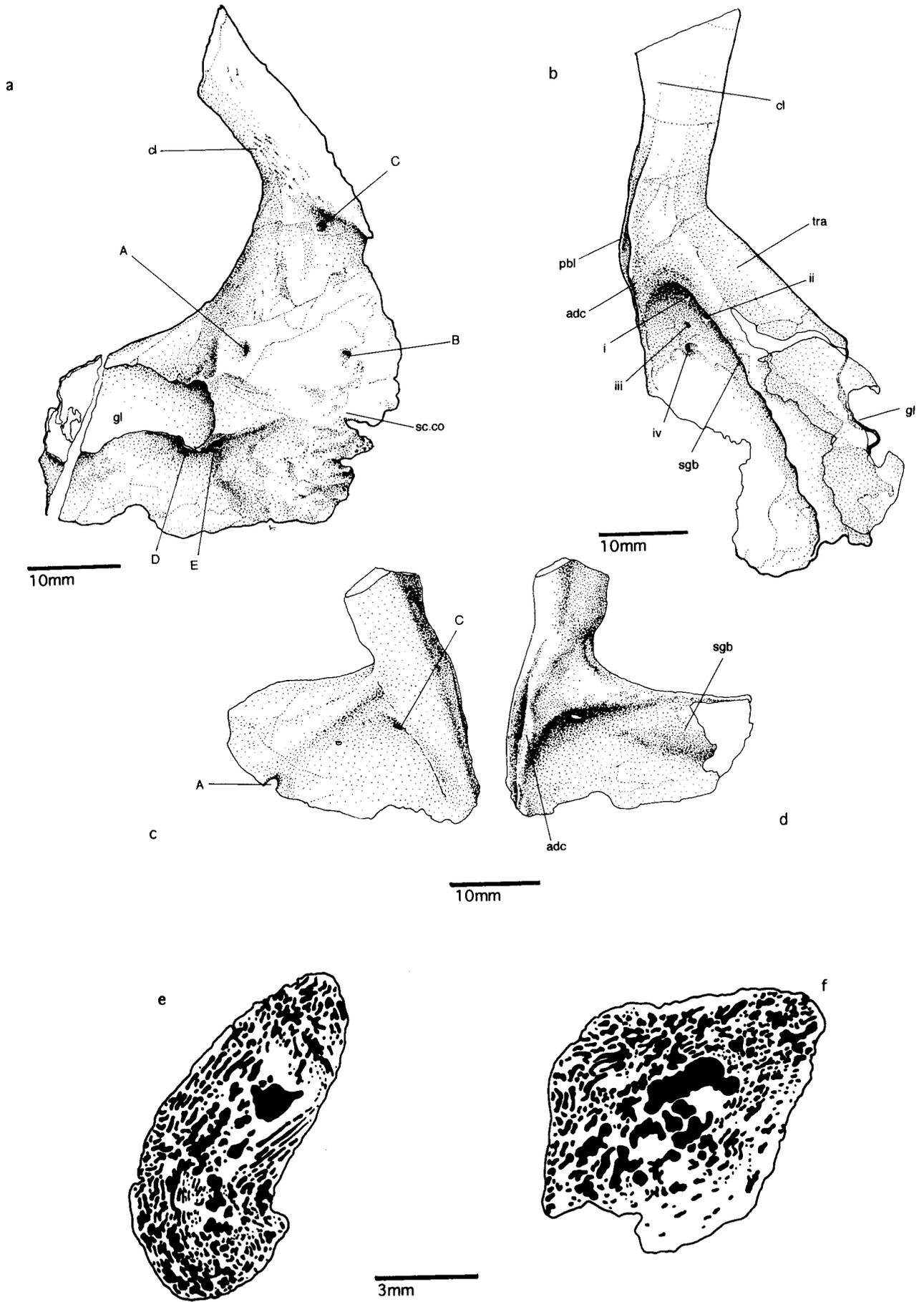
The cleithrum, as previously described (Coates & Clack 1991), is tall, expanded dorsally, has an anteroventral process

and a broad postbranchial lamina (Fig. 13a, b). This is significantly broader and more dorsally extensive than the laterally narrow, lamina-like flanges of *Ichthyostega* (Jarvik 1980, 1996, described as an 'anteromedial depression'), *Hynerpeton* (Daeschler *et al.* 1994) and *Whatcheeria* (Lombard & Bolt 1995). No dermal ornament is present, and muscle scarring is faint and limited to an area just above foramen C. The anteroventral process is well developed, and must have been overlapped by the posterior lamina of the clavicular ascending process. As noted in *Whatcheeria*, the postbranchial lamina does not extend onto the clavicle.

The pear-shaped anocleithra (Figs 5b,c & 13a-c) are almost entirely smooth. Like those of *Eusthenopteron* (Jarvik 1980; Andrews & Westoll 1970a) they are overlapped posteroventrally by the cleithra, and oriented anterodorsally towards the rear of the skull table. The exposed anterodorsal surface is slightly raised, and the posterior margin of this area is perforated, anteroventrally, by a small slot of unknown function. The posterior edge of each anocleithrum is serrated, from which originate a band of short, shallow grooves. Similar serrated zones border the more anteroventrally sited anocleithra of *Tulerpeton* (Lebedev & Coates 1995). Although the *Acanthostega* anocleithral shape most closely resembles those of *Neoceratodus* (Jarvik 1980), they do not appear to have shared the unusual, mesially reflected orientation of this dipnoan example.

The clavicles (Fig. 13d-h) in most respects resemble those of *Tulerpeton* (Lebedev & Coates 1995) or *Greererpeton* (Godfrey 1989). Each has a broad, rounded subtriangular

Figure 12 *Acanthostega gunnari*. (a) UMZC T1300, right scapulocoracoid and ventral portion of cleithrum, lateral surface. (b) MGUH f.n. 1227, right scapulocoracoid plus incomplete cleithrum, mesial surface exposed from posterodorsal aspect (composite figure combining data from two fractured surfaces beneath skull of individual X). (c) MGUH f.n. 1358, incomplete right scapulocoracoid plus cleithrum: lateral surface, and (d) mesial surface. (e) MGUH f.n. 1358, section through cleithro-scapular bone level with apex of 'triangular area', and (f) through cleithral shaft at apex of specimen. Black areas represent matrix infill of endochondral/vascular spaces.



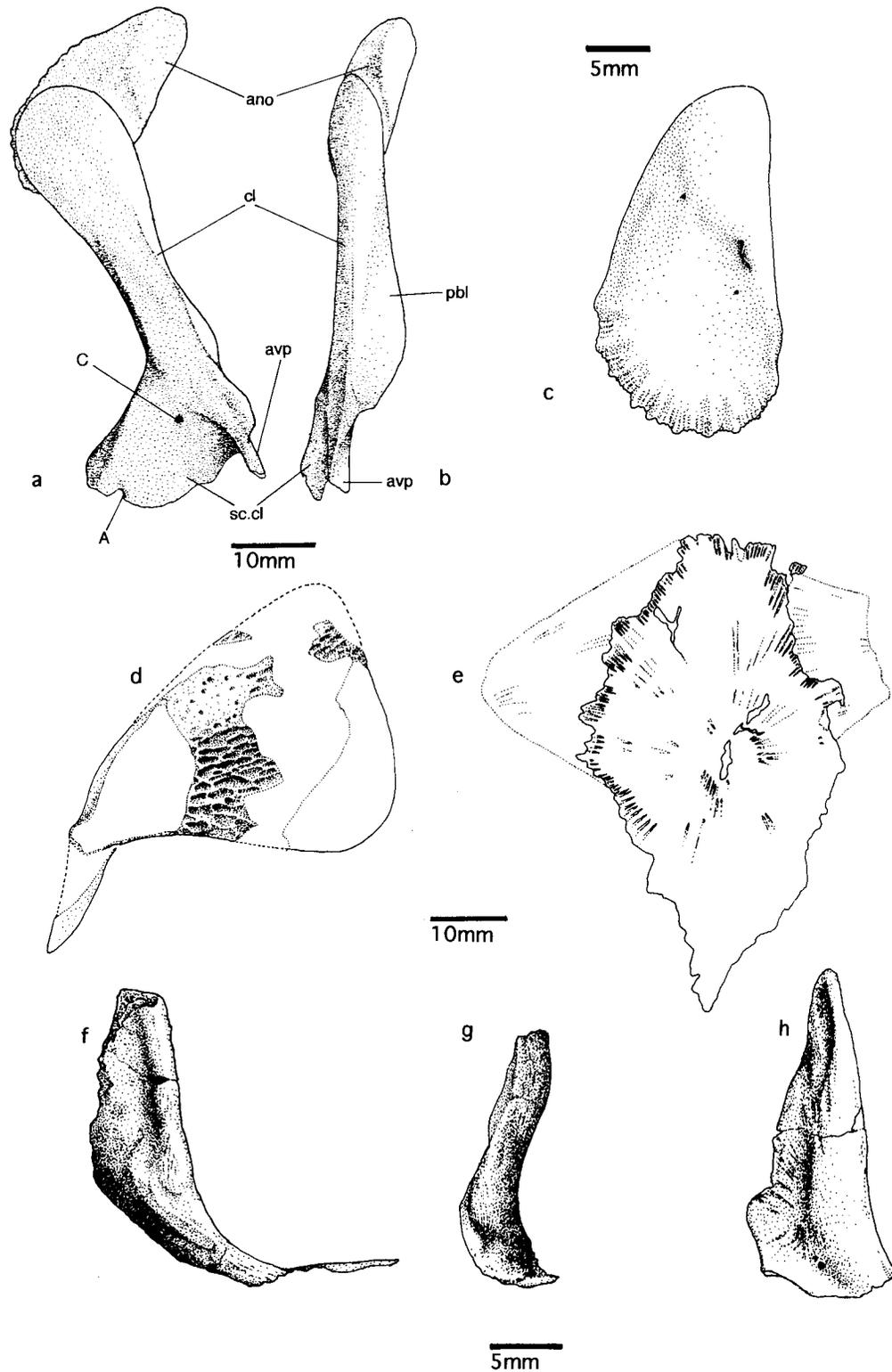


Figure 13 *Acanthostega gunnari*. MGUH f.n. 1258, right cleithrum and anocleithrum plus scapulocoracoid (incomplete) in (a) lateral and (b) anterior views. (c) MGUH f.n. 1227, right anocleithrum. (d) MGUH f.n. 1227, right clavicle, ventral surface. (e) MGUH f.n. 1330, interclavical and incomplete clavicles. MGUH f.n. 1358 right clavicle, dorsal process with posterior lamina: (f) lateral and (g) anterior surfaces. (h) MGUH f.n. 1300 left clavicle, dorsal process with posterior lamina: mesial surface.

ventral plate and a rod-like ascending, dorsal process. The ventral external surface bears a reticular ornament of ridges and pits behind a broad, smooth anterior margin. Unlike *Greererpeton* none of the ornament is visible in lateral view. The dorsal clavicular process in *Acanthostega* is recurved dorsomesially, so that in anterior view it is almost S-shaped, seen most clearly in MGUH f.n. 1358a (Fig. 13g). This resembles the corresponding processes of *Ichthyostega* (Jarvik

1980, 1996) and *Ventastega* (Ahlberg *et al.* 1994). In lateral view the dorsal process has a well developed posterior lamina and a complex arrangement of shallow grooves surrounding a sharply defined, low crest.

The interclavicle is known from a variety of incomplete specimens, the best of which is MGUH f.n. 1336 (Fig. 13e) and appears to have been approximately kite-shaped. All interclavicles are preserved with the internal, dorsal surface

exposed. Dermal ornament morphology is uncertain, but appears to match that of the clavicles. Radiating grooves on the dorsal surface originate from the inferred centre of growth. The orientation and degree of clavicular overlap is estimated from MGUH f.n. 1336. This indicates the presence of a well developed, broad parasternal process, similar to that in *Pholiderpeton* (Clack 1987) and quite unlike the narrow processes of *Ichthyostega* and *Whatcheeria*. The degree of clavicular overlap is probably similar to that of *Ventastega*. Interclavicular contact appears to be occluded by a medial, ornamented strip of the interclavicle.

3.4. Forelimb

3.4.1. Humerus. The general morphology of the humerus (Figs 15, 16 & 18) and the remainder of the forelimb has been described briefly in earlier publications (Coates & Clack 1990; Coates 1990). The humerus, known mostly from specimens MGUH f.n. 272 (Bendix-Almgreen *et al.* 1990 Fig. 3B) and 1227, is L-shaped and dorsoventrally compressed, with a

prominent ectepicondylar ridge and large entepicondyle, as found in most basal crown-group tetrapods (Figs 15 & 16). The long axis of the proximal articular surface lies at an angle of only 30° to a plane projected through the radial and ulnar condyles. This relatively flat morphology is shared with *Ichthyostega* (Jarvik 1980, 1996), but quite unlike *Tulerpeton* (Lebedev & Coates 1995), *Greererpeton* (Godfrey 1989), and *Proterogyrinus* (Holmes 1984). An elliptical caput humeri wraps around the proximal surface, extending slightly further onto the proximoposterior edge than onto the anterior edge. The proximodorsal (extensor) surface is dominated by a large, anterodorsally directed depression which may be the insertion site for a scapulohumerus-like muscle. Note that here and elsewhere in this description, unless stated otherwise, inferred areas of muscle insertion follow what Lombard and Bolt (1995) aptly describe as 'Romerian convention' (with reference to influential publications such as Romer 1956 and 1957). Interpretations of musculature for extremely primitive limb skeletons need to be treated with caution, because the degree

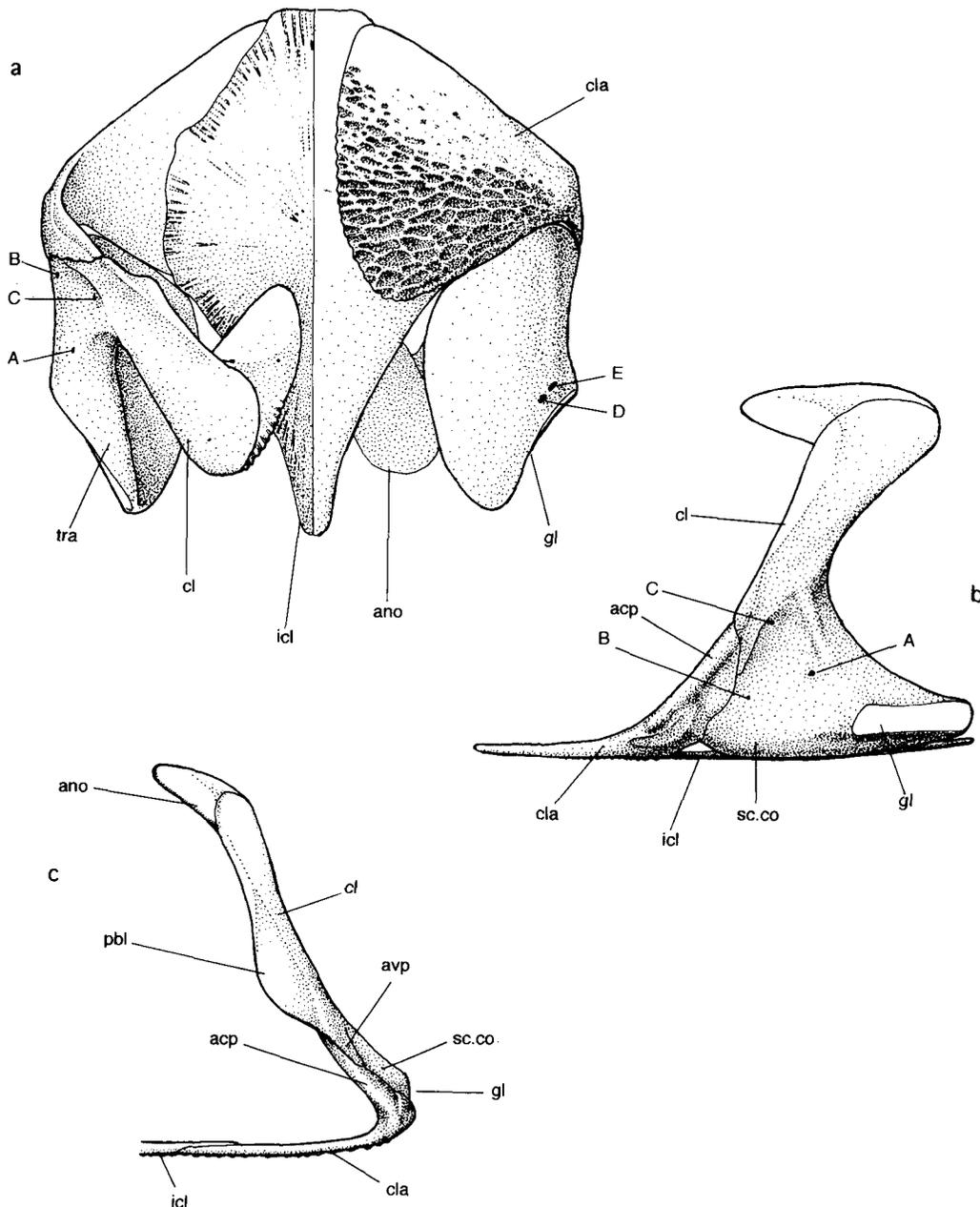


Figure 14 *Acanthostega gumari*. Reconstructed pectoral girdle. (a) Left side of figure: dorsal view; right side of figure: ventral view. (b) Lateral surface; (c) anterior surface, left side.

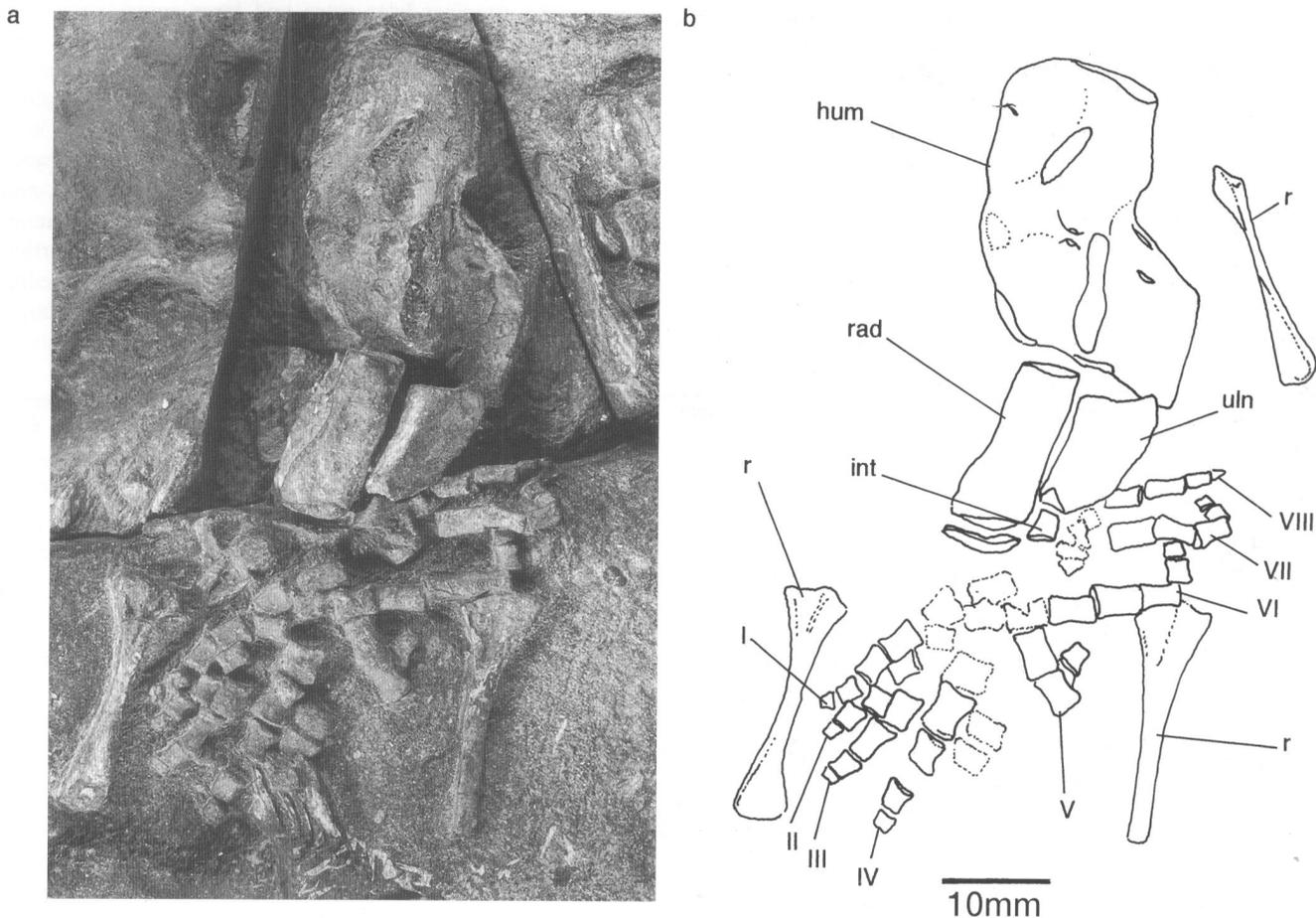


Figure 15 *Acanthostega gunnari*. MGUH f.n. 1227, individual X, octodactylous forelimb: (a) photograph; (b) line drawing of specimen, including nearby ribs. Dotted outlines in carpus indicate osteoderm-like plates.

of muscular differentiation which had evolved from that of paired sarcopterygian fins is most uncertain.

The posterodistal boundary of the scapulohumerus depression rises into a prominent, elongate ridge interpreted as the insertion for the latissimus dorsi muscle. A single foramen piercing the anterodorsal surface resembles a similarly sited foramen in *Eusthenopteron* (Andrews & Westoll 1970a). Bendix-Almgreen *et al.* (1990) plus Coates and Clack (1990) identified this ridge, probably incorrectly, as the deltoid process. The misinterpretation was based upon Andrews and Westoll's (1970a) description of the humeral ridges of *Eusthenopteron*, and Rackoff's (1980) similarly-influenced analysis of the humerus of *Sterropterygion*. In fact, the interpretation presented here is far more consistent with Jarvik's (1980 fig. 103) description of *Eusthenopteron*. Jarvik, and Andrews and Westoll interpret fin humeri (or first axial mesomeres, A1) after the complex humerus of *Eryops*, but far simpler comparisons can be made with early tetrapod humeri such as those of *Greererpeton* (Godfrey 1989), *Tulerpeton* (Lebedev & Coates 1995), and *Archeria* (Romer 1957).

The area posterior to the latissimus dorsi ridge is mostly smooth, with only limited muscle scarring next to the trailing edge, terminating distally as an acute process facing one or more proximal openings of the entepicondylar canal. Jarvik (1980) identified a similar structure as process 2 in *Ichthyostega*, and a similarly well developed example is present in *Eoherpeton* (Smithson 1985: described as a flange of unknown function). A low, rounded prominence interpreted as the supinator process in *Acanthostega* lies in-line anterodistally with the latissimus dorsi ridge (again consistent with Jarvik's 1980 interpretation of *Eusthenopteron*). A low crest extending

posteriorly from the supinator process towards the ectepicondyle usually bridges a short, wide ectepicondylar canal, equivalent to canal A of *Ichthyostega*. In *Acanthostega*, specimen MGUH f.n. 1227, while this ectepicondylar canal or foramen is present in the left humerus, it is reduced to a short, deep sulcus on the right humerus. The apex of the ectepicondyle is missing from all known specimens, and the restoration (Fig. 16) is estimated from other, more advanced, early tetrapod humeri—with the notable exception of *Ichthyostega* in which a subrectangular ectepicondyle bears a distinct proximal process: the 'dorsal ridge' and process 1 in Jarvik (1980 fig. 166). In *Acanthostega* the posterior ectepicondylar surface is deeply scarred by extensor muscle insertions which extend onto the base of the entepicondyle.

The thickened medial edge of the subrectangular entepicondyle forks distally to produce processes 3 and 4, resembling those of *Ichthyostega*. Two large canals penetrate the dorsal surface, although their precise paths and relationships with the foramina on the ventral surface are uncertain. All of these foramina appear to be related to Jarvik's canals b and c in *Ichthyostega*, and the more proximal openings may represent several foramina of a primitively ramose entepicondylar canal. The clearly defined radial and ulnar facets are separated by a broad strip of perichondral bone. In contrast to the condition in more derived tetrapods—e.g. *Tulerpeton* (Lebedev & Coates 1995), these epipodial facets are in a relatively anterior position: the ulnar facet lies predominantly below the ectepicondyle, from which the radial facet is well separated, lying terminally across the humeral anterodistal corner. The subcircular ulnar facet faces laterally with only a slight ventral inflection. A distinct groove divides ectepicondylar base from

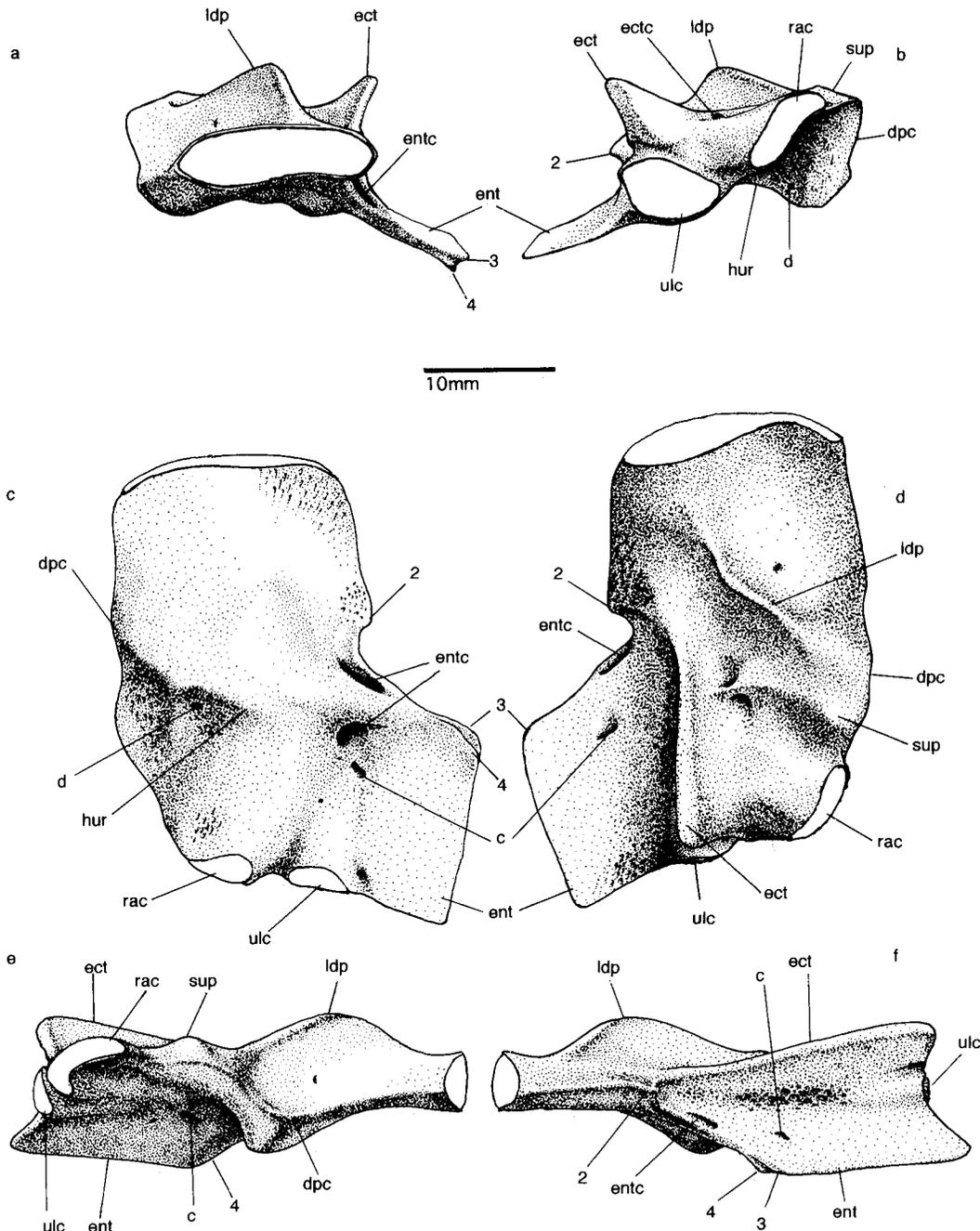


Figure 16 *Acanthostega gunnari*. Right humerus, restored: (a) proximal surface; (b) distal surface; (c) ventral surface; (d) dorsal surface; (e) anterior surface; (f) posterior surface.

the ulnar facet, passing from the proximodorsal entepicondylar surface to the broad inter-epipodial space. The elliptical or strap-shaped radial facet is divided horizontally into lateroventrally and anterodorsally directed areas. If the cartilaginous cap was thin in life, then the radial facet may have been functionally bipartite, with the radius stable in two principal postures: flexed laterally, or extended anteriorly. The condition of these facets is somewhat peculiar relative to those of more derived tetrapods, in which the ulnar facet is generally strap-shaped, and the radial facet is bulbous and subcircular. Functionally, the significance of these contrasting morphologies is uncertain.

The dorsally convex anterior keel extends for barely half of the total anterior humeral edge, like those of *Greererpeton* (Godfrey 1989) and *Tulerpeton* (Lebedev & Coates 1995). Moreover, like *Acanthostega*, each of these taxa also has a deltopectoral crest oriented almost vertically relative to the near-horizontal flange extending proximally to the humeral

head. In reptiliomorphs such as *Proterogyrinus* (Holmes 1984), *Archeria* (Romer 1957), or *Westlothiana* (Smithson *et al.* 1994), the deltopectoral crest is more compact, and situated more proximally, beyond which a long dorsally concave anterior keel extends towards the radial condyle. Such long anterior keels may incorporate an indistinct supinator process. These keels and processes are distinctly absent in microsauro humeri (Carroll & Gaskill 1978).

The proximal ventral (flexor) surface is divided into a smooth anterior region, possibly associated with the insertion of the supracoracoideus, and a faintly scarred, slightly concave posterior region upon which the coracobrachialis may have inserted. Further scarring, associated with the subscapularis, lies on the ventral surface of process 2 (Fig. 16c). The distal portion of the ventral surface, like the proximal region, is mostly smooth. Perhaps the most unusual feature is a broad, shallow groove extending proximally from the widely-spaced epipodial facets. A low, rounded ridge extends posteriorly

from the deltopectoral crest, dividing the distal from proximal regions of the ventral surface (Fig. 16c, hur) and forming a gently rounded bridge between the proximally and distally directed openings of the entepicondylar canal (Jarvik's 'canals b & d' in 1980, 1996) before blending into the medial entepicondylar edge. The distal entepicondylar canal opening, and a smaller foramen which resembles the ventral opening of Jarvik's 'canal c' (1980) in *Ichthyostega*, are similar to those of *Greererpeton* (Godfrey 1989). In agreement with Smithson's (1985) description of the humerus in *Eoherpeton*, this low ridge probably corresponds to the humeral ridge of *Eusthenopteron* (Andrews & Westoll 1970a fig. 10; Jarvik's 'ventromedial crest' in 1980 fig. 103) and a similar, unnamed ridge in *Ichthyostega* (Jarvik 1996 fig. 45F: extending between processes 4 and 6). In *Acanthostega* a single foramen pierces the distal surface, resembling 'canal d' of *Ichthyostega*. Again, this feature (Fig. 16c, foramen d) resembles the more numerous foramina piercing the humeral ridge of *Eusthenopteron* (Andrews & Westoll 1970a). The near-perpendicular orientation of the ridge relative to the anterior edge may be plesiomorphic compared with more derived humeri (in these, vestigial ridges extend posterodistally from proximally sited deltopectoral crests, e.g. *Proterogyrinus*, Holmes 1984 fig. 26). Scarring probably indicates insertion points for radial flexor musculature on the anterodistal ridge surface. A further foramen lies next to the posteroventral rim of the ulnar facet.

3.4.2. Epipodials and manus. The ulna (Fig. 17g-l; MGUH f.n. 1227) is flattened dorsoventrally and only two-thirds the length of the radius. The outline, in dorsal aspect, resembles that of *Ichthyostega*, (Jarvik 1996 fig. 46) both having straight anterior and convex posterior edges, and both being broader

proximally and narrower distally, with no distinct shaft or narrowed mid-region. Both also have a clearly defined anterior surface, whereas posteriorly each finishes as a narrow flange. In *Acanthostega* the ulna lacks an olecranon process. The distal surface, in dorsal or ventral profile, is notched posteriorly, so that the narrow posterior portion is offset proximally relative to the broader anterior facet for articulation with the intermedium. Similar posteriorly notched distal surfaces are present in *Ichthyostega* and *Tulerpeton* (Lebedev & Coates 1995).

The radius (Fig. 17a-f; MGUH f.n. 1227) is subcylindrical proximally and flattened distally, resembling a slightly shortened version of the spatulate radial morphologies found in sarcopterygian pectoral fins, such as those of *Eusthenopteron* (Andrews & Westoll 1970a; Jarvik 1980). This similarity is reinforced by the predominantly anterodistal expansion of the dorsal (extensor) radial surfaces in both of these taxa. In *Acanthostega* the ventral (flexor) and anterior radial surfaces are gently concave. Similarly concave surfaces are present in *Ichthyostega* and *Tulerpeton*. The anteroventral angle is drawn into an elongate crest which resembles that of the truncated radius in *Ichthyostega* (Jarvik 1996 fig. 46), and may be related to the prominent ventral radial process in *Eusthenopteron* (Andrews & Westoll 1970a: fig. 13). The posterior radial surface in *Acanthostega* is mostly smooth, although incised by a shallow channel crossing from proximovenral to dorso-distal surfaces.

As described previously (Coates & Clack 1990), the wrist and articulated digits are preserved solely in individual X, on specimen MGUH f.n. 1227 (Fig. 15). The restoration (Fig. 18) differs from that in Coates and Clack 1990 (figs 1c & 2e)

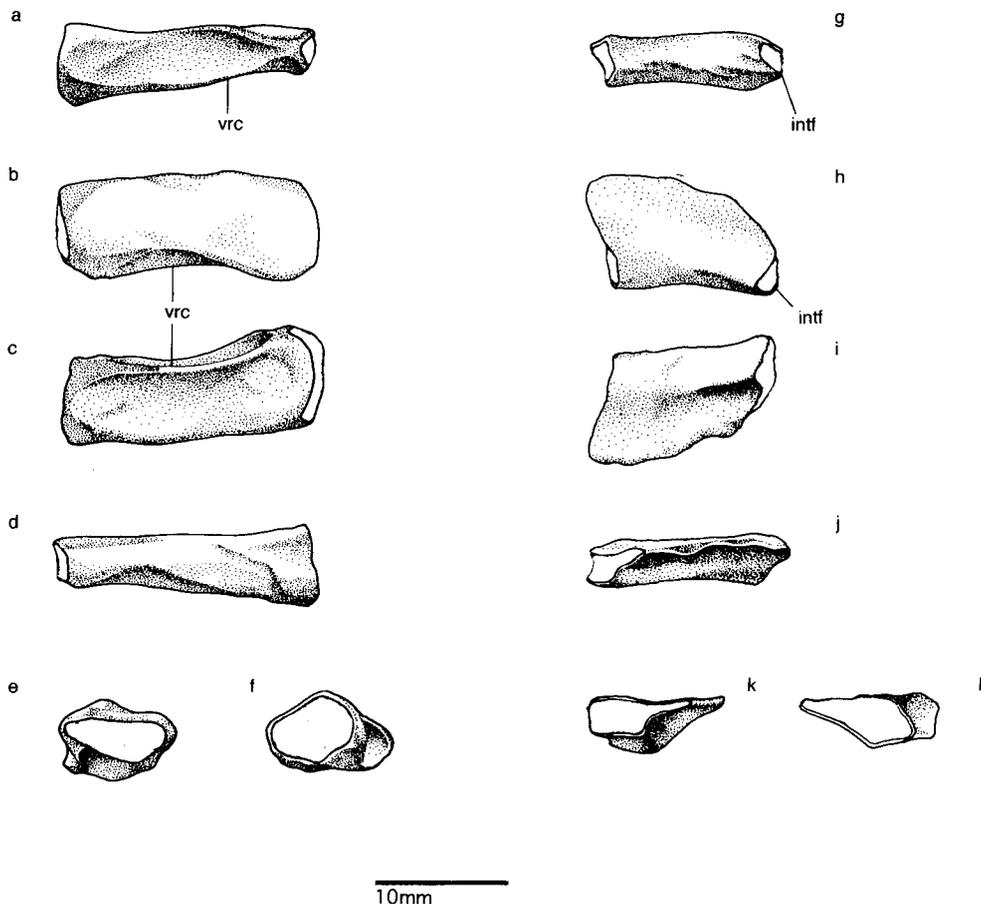


Figure 17 *Acanthostega gumari*. MGUH f.n. 1227. Left radius in (a) anterior, (b) dorsal, (c) ventral, (d) posterior, (e) distal, and (f) proximal views. Left ulna in (g) anterior, (h) dorsal, (i) ventral, (j) posterior, (k) distal, and (l) proximal views (dorsal surface towards top of page in e, f, k & l).

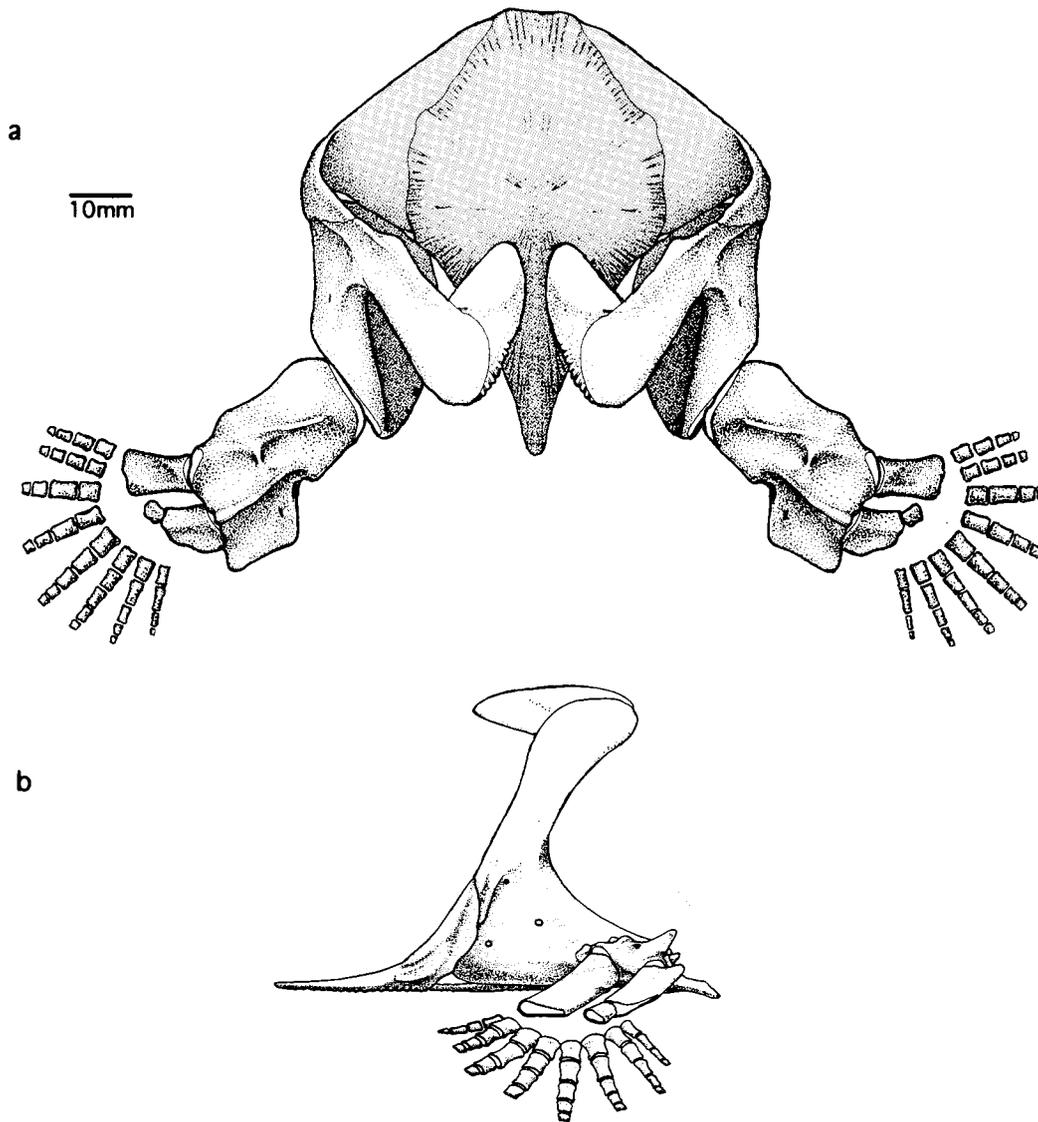


Figure 18 *Acanthostega gunnari*. Restored pectoral girdle and articulated forelimb in (a) dorsal view, and (b) lateral view. Note that forelimbs are slightly flexed, and that radius and ulna therefore appear foreshortened in dorsal view.

because of the clearer picture of the limb obtained after more detailed preparation. The wrist includes only one endochondrally ossified bone, the intermedium. This is subcylindrical, expanded distally, and sheathed, with the exception of proximal and distal surfaces, in perichondral bone. Other elements in the region of the wrist consist of rectangular plates of thinly ossified dermal or perichondral bone. They may originate from mostly cartilaginous wrist elements, or represent thin scutes from the dorsal or ventral surfaces of the manus.

The phalangeal formula, counting from anterior to posterior and disregarding the most proximal phalanx (equivalent to the metacarpal) in each digit, is 3:3:3:3:4:4:4:3 (instead of 3:3:3:4:4:5:5:4, as previously reported). Digit eight is the most slender, even when compared with the short anterior digits one to three. Individually, each phalanx is spool-shaped, with a slightly constricted shaft. Variations in dimensions change gradually across the digit series, except for phalanx two (counting from proximal to distal) of digit three, which is significantly longer than equivalents in digits one and two.

3.5. Pelvic girdle

The pelvic girdle is best preserved in specimens MGUH f.n. 252, 260, 1227, 1258, and UMZC T1291 (Fig. 19). Each half consists of a completely ossified plate with no traces of sutures

between the pubis, ilium, and ischium as found in more derived tetrapods (Figs 19, 20, 23). Similarly sutureless conditions are found in *Ichthyostega* (Jarvik 1980, 1996), *Whatcheeria* (Lombard & Bolt 1995), and *Eoherpeton* (Smithson 1985). Specimen UMZC T1291 (illustrated in Clack 1988 fig. 12B), an almost entire pelvic plate, shows most clearly the biramous dorsal portion of the iliac region (Fig. 19a, b). The anterior, dorsal iliac process was concealed at the time of Clack's (1988) description, resulting in a misleadingly close comparison with temnospondyl pelvises. In fact, the iliac region is equally similar to those of anthracosaur pelvises (e.g. *Proterogyrinus* Holmes 1984; *Archeria* Romer 1957). The narrow iliac neck is imperforate (unlike *Ichthyostega*) and in an unusually posterior position, bifurcating above the rear of the acetabulum, and well behind the supra-acetabular buttress, to produce a stout dorsal process and a spatulate posterior blade. The morphology of these structures is variable (Fig. 19). The dorsal process is neither broad and thin like those of *Proterogyrinus* and *Archeria*, nor squat like that of *Ichthyostega*. Instead, it thickens dorsally until slightly bulbous, and the anterodorsal surface bears a broad slot with an unfinished granular endochondral lining. Like *Eoherpeton* (Smithson 1985), which has a similarly biramous ilium with a club-shaped dorsal process, this is assumed to have been

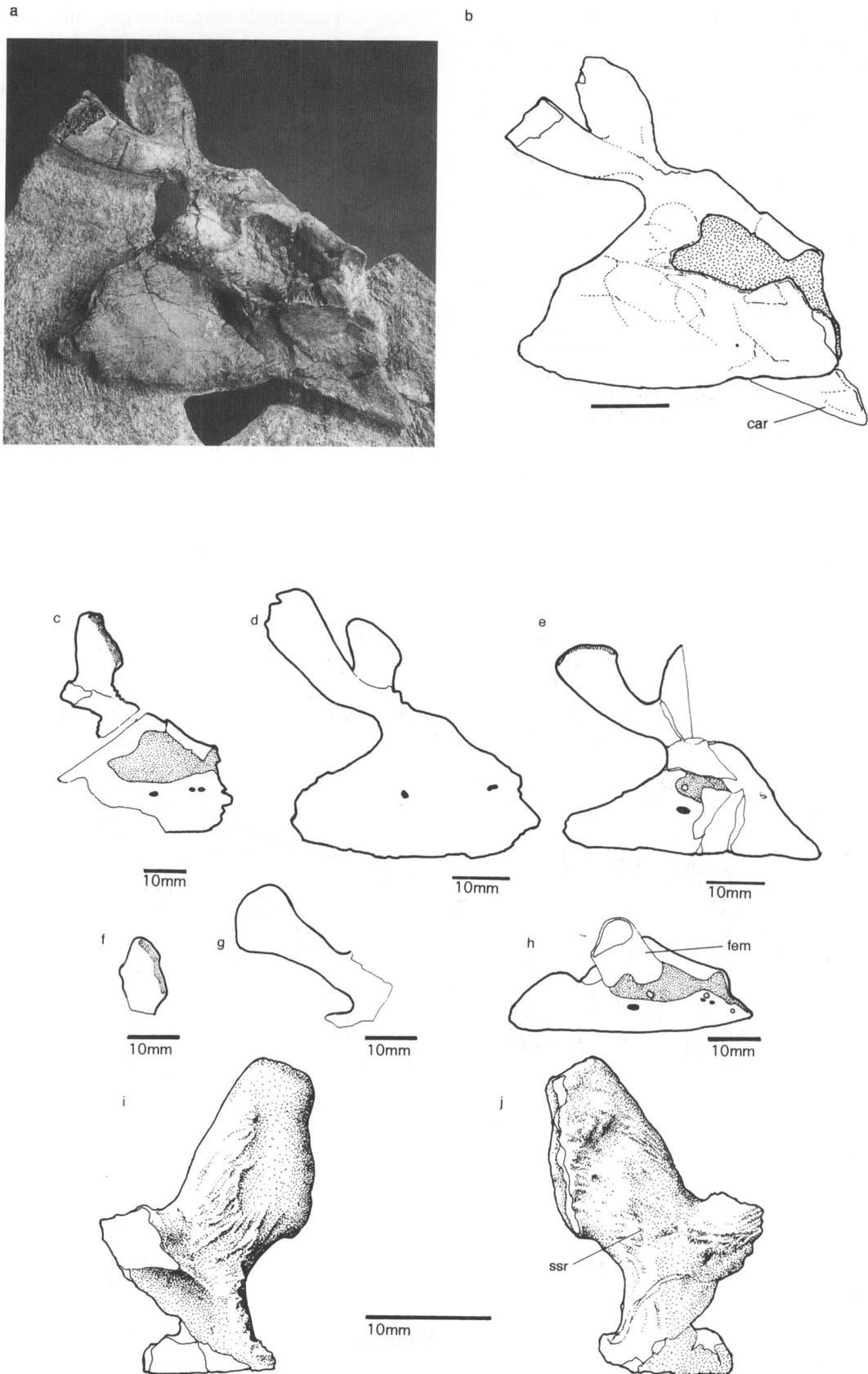


Figure 19 *Acanthostega gunnari*. Pelvic girdles: (a) UMZC T1291, photograph of lateral surface, right side (proximal head of caudal rib adjacent to ventral edge); (b) UMZC T1291, drawing of specimen; (c) MGUH f.n. 1258, lateral surface (see also h & i); (d) MGUH f.n. 1227, mesial surface; (e) MGUH f.n. 252, posterior part is lateral surface, anterior part is natural mould of mesial surface; (f) MGUH f.n. 1227, isolated anterior iliac process from individual X; (g) MGUH f.n. 267, posterior iliac process; (h) MGUH f.n. 260, lateral surface of pelvic plate with proximal portion of femur articulated *in situ* with acetabulum; (i) MGUH f.n. 1258, detail of rugose ornament on lateral surface of iliac dorsal process; (j) MGUH f.n. 1258, mesial surface. Solid black foramina indicate structures on near side; open foramina on far side.

cartilage-capped in life (cf. extant frogs and salamanders: Francis 1934). Less complete but perhaps similar processes are present in *Tulerpeton* (Lebedev & Coates 1995), and *Crassigyrinus* (Panchen & Smithson 1990). The anterioromedial face of the ilium in *Ichthyostega* bears a similarly unfinished, but somewhat broader, surface (Jarvik 1996 plate 56). This is the area which Jarvik interprets as the sacral rib attachment site, although no corresponding rib morphology has been found to fit this concavity. Four different kinds of acanthostegid dorsal process are illustrated in Figure 19. Small specimens are almost smooth, but larger examples bear prominent rugosities, predominantly on the lateral surface (Fig. 19i, j; MGUH f.n. 1258). Unlike Jarvik's interpretation of *Ichthyostega*, the site of sacral rib attachment lies on the smoother mesial surface, and there is no distinct facet or marked perimeter for this zone.

The posterior iliac blade is offset laterally relative to the origin of the dorsal process. Subelliptical in cross-section proximally, the blade becomes an extremely thin bony lamina distally. Once again, blade morphologies vary between individuals (Fig. 19). In a large specimen (MGUH f.n. 252) the blade is short, broad and incomplete distally, terminating as an unfinished bony concavity (and presumably finished with a cartilaginous plug in life). However, the blade in the pelvic reconstruction (Fig. 20), as based upon that of MGUH f.n. 1227, is finished distally with a narrow, gently serrated edge with complete perichondral covering. All blades are smooth except for ventromesial striations extending onto the base of the dorsal iliac process, thought to be associated with an iliofemoralis insertion.

A 'transverse line' (Romer 1957) bisects the iliac neck, extending as a prominent ridge from a point above the anterior of the acetabulum until continuous with the leading edge of the posterior blade. The ridge bears a series of aponeurotic crests anterior and lateral to the iliac neck, from which it is usually separated by a shallow trough. A similarly smooth, U-shaped trough is described in *Whatcheeria* (Lombard & Bolt 1995). However, in one specimen of *Acanthostega*, MGUH f.n. 1258 (Fig. 19i, j), the crested ridge climbs the anterior edge of the dorsal process, separated by a short gap from a further ridge associated with the broken stump of a posterior blade. Such ridges and crests are thought to be associated with pelvic insertion within the hypaxial trunk musculature. The iliac surface below the transverse line is relatively broad.

The puboischiadic plate is relatively long, and, as noted in Smithson *et al.* (1994), corresponds to the length of about six trunk vertebrae. The entire acetabulum is in an unusually anterior position relative to the iliac processes, when compared with other early tetrapod pelvises. Consequently, the supra-acetabular buttress, which in living tetrapods receives the primary femoral thrust, lies unusually far forwards of the base of the iliac neck. Furthermore, the supra-acetabular buttress is significantly less prominent than the well developed postacetabular buttress (Fig. 20). The rounded, subtriangular and horizontally elongate acetabulum resembles those of *Ichthyostega* (cf. photographs in his fig. 160, rather than reconstructions, in Jarvik 1980; fig. 49 in Jarvik 1996) and *Whatcheeria* (Lombard & Bolt 1995), especially because of the continuity with the unfinished leading edge of the puboischiadic plate. However, it is worth noting that in a single *Ichthyostega* specimen, (Jarvik 1996 fig. 49D) the anterior pubic acetabular rim is finished. Each of the *Acanthostega* pelvises, and most of those pertaining to *Ichthyostega*, therefore have a characteristically flared perichondral rim where the granular endochondral acetabular surface broadens anteriorly onto the leading edge of the pubic

region. The posterior tongue-like projection into the acetabulum of *Ichthyostega* corresponds very simply to the perichondral projection between the supra- and postacetabular buttresses in *Acanthostega* (and likewise many other Palaeozoic tetrapods). The anterior tongue-like projection in *Ichthyostega* (Jarvik 1980 fig. 160; 1996 fig. 48) may correspond to the anterior, ventral-most projection of the dorsal perichondral acetabular rim. The lower acetabular lip is the most thickly ossified region of the pelvis in *Acanthostega*, and is continuous with the prominent postacetabular buttress. The lateral face of the pubo-ischiadic plate is pierced by three foramina below the acetabular lip. Two lie in the position normally occupied by the obturator canal, at the most anterior corner preceding the unfinished anterior edge. The largest foramen lies just anteroventral to the posterior acetabular buttress, although the position varies between individuals (NB: Fig. 19c–e, h). Specimen UMZC T1291 has a further, small foramen close to the ventral midline (as in reconstruction: Fig. 20). Jarvik (1980) interpreted both puboischiadic foramina of *Ichthyostega* as obturator canals; some variability in the number of puboischiadic foramina is apparent in Jarvik (1996), where certain specimens have a single, large, external foramen which is confluent with the paired foramina on the medial surface. Holmes (1984), however, interpreted only the largest and most anterior as an obturator canal, out of the three *Acanthostega*-like puboischiadic foramina present in *Proterogyrinus*.

Most of the puboischiadic plate lies behind the acetabulum. This area is only thinly ossified, although the lateral surface is scarred extensively up to the level of the postacetabular buttress by insertions for ischiofemoralis and/or ischioacaudalis musculature. Neither is the dorsal acetabular rim reinforced as in *Proterogyrinus* (Holmes 1984), *Greererpeton* (Godfrey 1989), or *Crassigyrinus*, where Panchen and Smithson (1990) interpret scarring as dermal ornament. The smooth mesial puboischiadic surface bears a broad, rounded ridge where the anterior portion turns outwards, providing a broad insertion area for the puboischiofemoralis internus (Wettstein 1931; Francis 1934; Romer 1957; Holmes 1984). A large foramen, continuous with the most posterior of the three visible on the lateral surface, lies anterior to this mesial ridge. Two foramina pierce the out-turned pubic area: the dorsal foramen appears to be continuous with *both* of the associated lateral foramina; the ventral foramen is probably nutritive. The symphyseal region is deepest at the foot of the broad mesial ridge. It consists of deep, perichondrally finished vertical striations with no unfinished endochondral surface. This suggests that the symphyseal junction consisted of fibrous tissue rather than an ossified sutural union.

3.6. Hindlimb

3.6.1. Femur. The femur (described briefly in Coates 1991) is best known from specimen MGUH f.n. 1227 (Fig. 21a–f), and several less complete but complementary specimens (notably MGUH f.n. 260, in which a distally incomplete specimen remains articulated with the acetabulum: Fig. 19h). The femur is about 25% longer than the humerus, and resembles most closely those of *Tulerpeton* (Lebedev & Coates 1995), *Ichthyostega* (Jarvik 1980) plus an undescribed specimen from the Horton Bluff Formation (YPM-PU 20103: Carroll *et al.* 1972). The most striking difference from femora such as those of *Archeria* (Romer 1957), *Proterogyrinus* (Holmes 1984), *Greererpeton* (Godfrey 1989), *Crassigyrinus* (Panchen & Smithson 1990), or the enigmatic *Papposaurus* (Watson 1914; full description and attribution to *Proterogyrinus pancheni* in Smithson 1986), is the more distally sited pattern of muscle insertions along the ventral surface. In *Acanthostega*

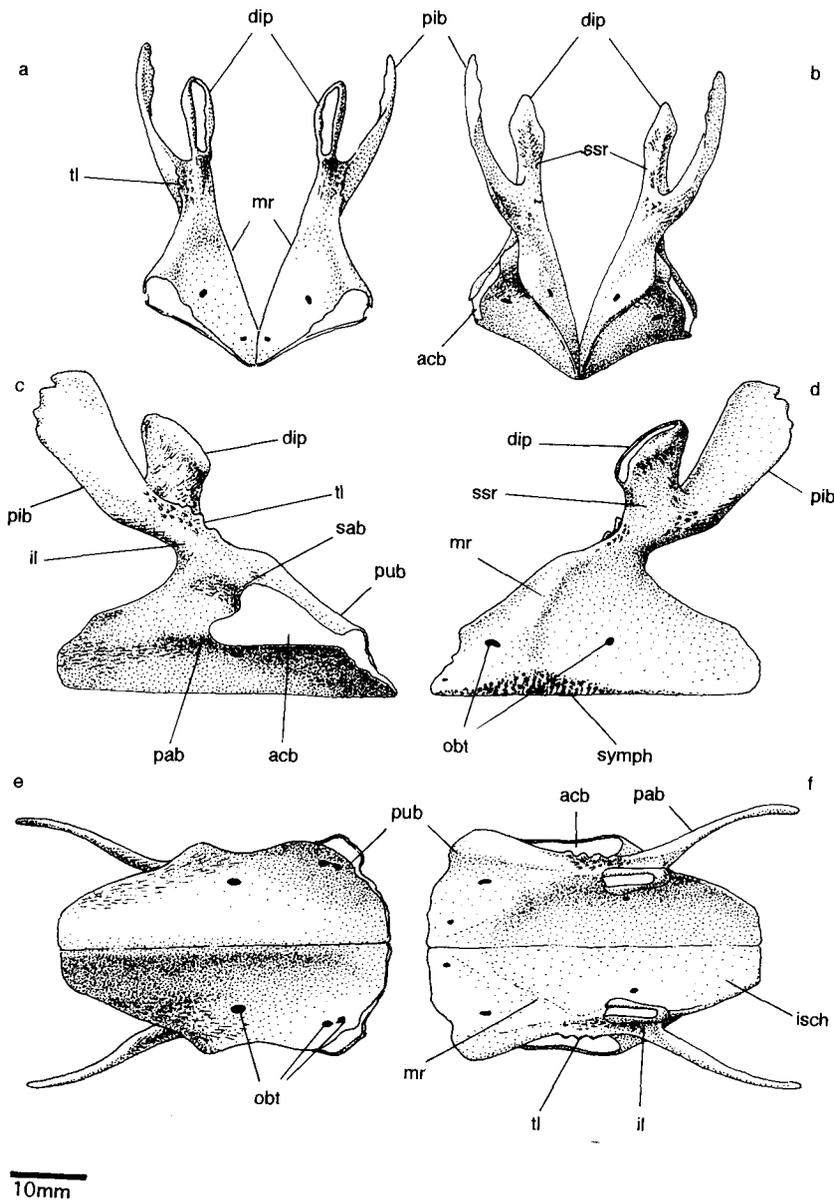


Figure 20 *Acanthostega gunnari*. Reconstruction of pelvic girdle in (a) anterior, (b) posterior, (c) lateral, (d) mesial, (e) ventral, and (f) dorsal views.

the uniquely elongate adductor blade extends for almost 50% of the total femoral length, the trochanters are spaced more distantly along its length, and considerable anterior torsion ($\sim 75^\circ$) results in the intercondylar fossa facing anteriorly when the long axis of the femoral head is oriented horizontally. The term 'adductor blade' (cf. Lebedev & Coates 1995, on the femur of *Tulerpeton*; Fig. 21, adb) is used here to distinguish the prominent ridge bearing fourth and internal trochanters, from the more acute, and what appears to be primitively short, adductor crest (Fig. 21, adcr). Figure 36 illustrates the considerably greater proximodistal extent of the adductor crest in more advanced tetrapod femora. Note that in Jarvik's (1996) description of the femur of *Ichthyostega*, most of the curiously bulbous blade on the ventral surface is described as an adductor crest (unlike the portion labelled as such in Fig. 36l).

In *Acanthostega*, the proximal articular femoral surface is anteroposteriorly broad, and, like the distal articulating surfaces, is visible mostly from the ventral (flexor) surface. As in other early femora, the posterior portion of the proximal surface recedes relative to the anterior. The gently concave intertrochanteric fossa has no rugosities indicating the extent

of the joint capsule or ligamentous attachments, and, unlike *Tulerpeton* and *Ichthyostega*, it encloses only two foramina (Fig. 21d, l), interconnected by a shallow groove. However, like *Tulerpeton*, the proximal femoral region is more extensively ossified than those of *Archeria* and *Proterogyrinus*, and the articular surface is separated from the base of the internal trochanter by a broad perichondrally finished surface. The maximum femoral head width is 37% of the total length, whereas in the relatively shorter femur of *Ichthyostega* it is 51%. Thus *Acanthostega* has a proportionately longer femoral shaft, which Romer (1957) considered important for a broad femoro-tibialis insertion. Comparison with extant amniote and amphibian musculature (Wettstein 1931; Francis 1934) suggests that it is equally important for caudo- and iliofemoralis insertion.

The proximodorsal (extensor) surface is convex and smooth, marked only by a shallow depression close to the posterior edge, which may be associated with the insertion of a femur-iliac ligament (cf. *Salamandra*, in Francis 1934). The distal articulations are well ossified: the posterior (lateral) condyle is elevated somewhat prominently above the anterior, and, as in *Ichthyostega*, the intercondylar fossa encloses two foramina

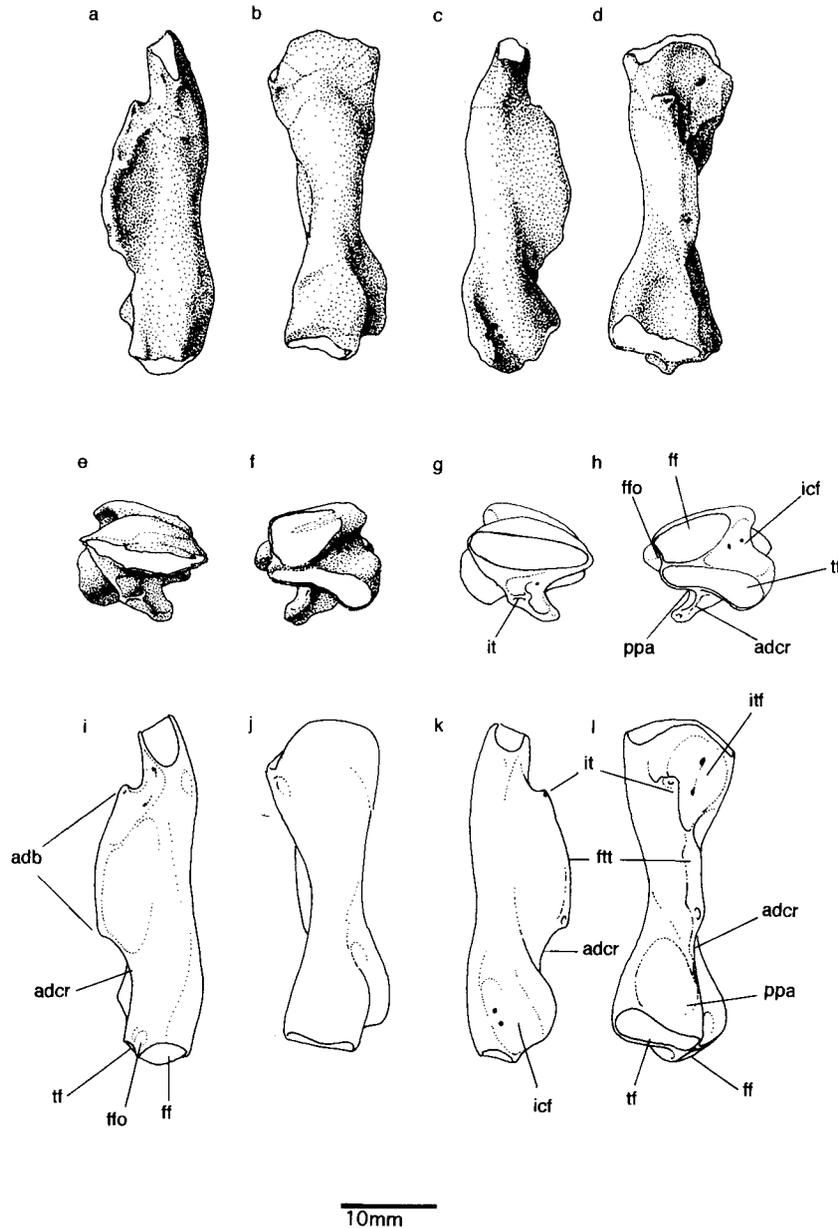


Figure 21 *Acanthostega gunnari*. MGUH f.n. 1227. Right femur in (a) posterior, (b) dorsal, (c) anterior, (d) ventral, (e) proximal, and (f) distal views. Restored right femur in (g) proximal, (h) distal, (i) posterior, (j) dorsal, (k) anterior, and (l) ventral views.

(Fig. 21c, f, h, k). The tibial facet is restricted to the anterior condyle, and the fibular to the posterior condyle. The relative positions of the condyles causes the angle subtended within the intercondylar fossa to be acute: $\sim 60^\circ$. In distal aspect, if the intercondylar fossa faces anteriorly, then the popliteal area faces ventrally. There is no uniquely fibular fossa; instead, a shallow fossa lies between the posterior extremities of both tibial and fibular facets. The tibial articular surface faces anteroventrally and the fibular posterolaterally; the boundary between consists of a perichondral strip (otherwise known only in *Ichthyostega*), and both surfaces fit closely to the proximal epipodial heads.

An exceptionally well developed adductor blade (mislabelled as the adductor crest in Coates 1991) dominates the ventral surface. It extends well past the femoral midpoint and terminates level with the distal condylar expansion (Fig. 21). The blade includes internal and fourth trochanters, providing insertions for the ischiofemorals plus puboischiofemorals muscles proximally, and the caudifemorals distally. As in *Tulerpeton* (Lebedev & Coates 1995), *Greererpeton* (Godfrey

1989), *Crassigyrinus* (Panchen & Smithson 1990), and *Westlothiana* (Smithson *et al.* 1994), the internal trochanter is separated from the femoral head and projects proximally above a short groove (also noted by Jarvik 1980 figs 162 & 163, beneath the proximal end of the 'oblique ridge' or adductor blade in *Ichthyostega*). The internal trochanteric boss bears a shallow pit, and distal to this the rounded apex of the blade narrows before expanding at the union with a low, acute ridge passing proximally across the blade's posterior surface. This secondary ridge and junction marks the distal boundary of the intertrochanteric fossa, and it divides a smooth, proximal area of the posterior surface of the adductor blade from a distal, fluted region. *Tulerpeton* exhibits a very similar distribution of smooth and fluted surfaces. Furthermore, the confluence of this secondary ridge with the adductor blade (although much reduced) is similarly clear in a pelycosaur femur (Romer & Price 1940), where it marks the proximal limit of the fourth trochanter. In *Acanthostega* the fourth trochanter is assumed to occupy the remainder of the apex of the adductor blade, terminating distally as a similar but

slightly less prominent boss (also pitted). This, in turn, precedes a short, acute, adductor crest extending towards, but not quite reaching, the tibial facet rim. The broad, shallow, popliteal area or space lies entirely on the ventral surface of the anterior, tibial condyle.

3.6.2. Epipodials and pes. The anteroposteriorly broad tibia of *Acanthostega* (MGUH f.n. 1227: Figs 22–25) resembles those of *Ichthyostega* (Jarvik 1980, 1996), *Whatcheeria* (Lombard & Bolt 1995), and, to a lesser extent, *Crassigyrinus* (Panchen & Smithson 1990). Like *Ichthyostega*, but unlike more derived tetrapods, the tibia is significantly longer than the fibula. This also resembles *Eusthenopteron*, in which the tibia is about twice the fibular length (excluding the entepicondyle-like flange, Jarvik 1980). Tibial length is less than half (~45%) that of the femur, closely resembling equivalent proportions in *Tulerpeton* (Lebedev & Coates 1995) and *Crassigyrinus*, but quite unlike *Ichthyostega*, where it is about 68% of femoral length. A well developed but rounded cnemial crest extends along the entire anterior edge of the dorsal (extensor) surface (Figs 22, 25a), resembling the more acute crests of *Ichthyostega* and *Tulerpeton*. Like these taxa and *Crassigyrinus*, there is no rugose excavation or supplementary crest for insertion of the triceps tendon or puboischiotibialis

(cf. *Proterogyrinus* Holmes 1984), and the surface posterior to the cnemial crest is remarkably smooth. In dorsal view the anterior and posterior edges are almost straight, showing none of the concavities producing the shaft or interepipodial space present in more derived tetrapod tibiae; neither is there any torsion along the proximodistal axis, associated with forward turning of the foot.

The ventral (flexor) surface is pierced proximally by a small foramen. A shallow depression occupies the lower half of this surface, the upper margin of which appears to be equivalent topographically to the flexor rugosities of other early tibiae. There is no trace of the peculiar triangular boss present in *Crassigyrinus* (Panchen & Smithson 1990 fig. 7b,c). The posterior (lateral) tibial edge is shorter and narrower than the anterior, and in life was overlapped by the anterior (mesial) edge of the fibula (Figs 23–25). The anterior edge is marked distally by a series of muscle scars, and, more visible from a dorsal perspective (Fig. 25a), a small, shallow depression close to the proximal head. The distal articular surface is slightly L-shaped because of the terminal projection of the cnemial crest (cf. *Tulerpeton* Lebedev & Coates 1995), and divided into two distinct facets for the intermedium and the tibiale. This also resembles the pattern of *Ichthyostega* (Jarvik 1980,

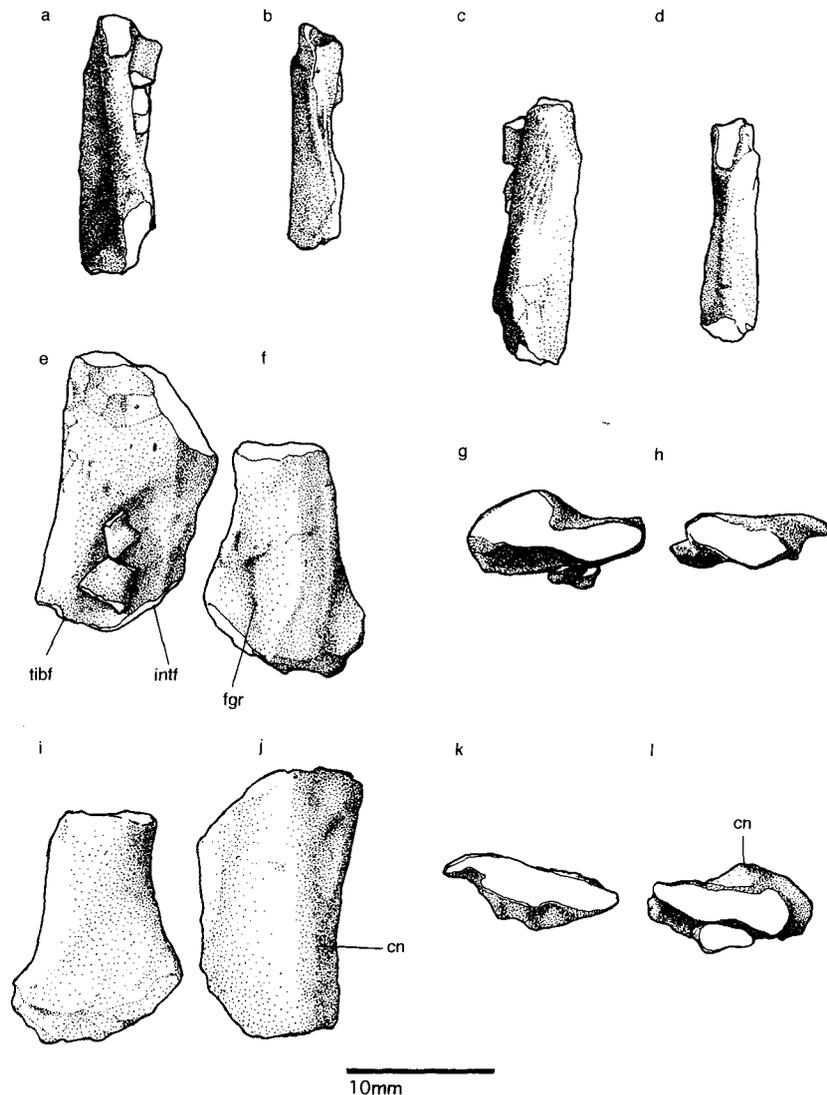


Figure 22 *Acanthostega gunnari*. MGUH f.n. 1227. Right hindlimb epipodials, showing tibia in (a) posterior, (c) anterior, (e) ventral, (g) proximal, (j) dorsal & (l) distal views. Fibula in (b) posterior, (d) anterior, (f) ventral, (h) proximal, (i) dorsal & (k) distal views. a–d, distal surface towards top of page; e, f, i & j, distal surface towards bottom of page; g, h, k & l, dorsal/extensor surface towards top of page. Note distal phalanges of digit 2 attached to ventral surface of tibia, visible in a, c, e, g & l.

1996), although in *Acanthostega* none of the tibial articulation is exposed on the ventral surface.

The fibula (MGUH f.n. 1227; Figs 22–25) is about 20% shorter than the tibia, similarly broad and dorsoventrally thin, but with slightly more concave anterior and posterior edges. In contrast to the squat, rounded fibular outline of *Ichthyostega* (Jarvik 1980, 1996), in *Acanthostega* the slightly waisted shape may indicate the emergence of a proximal shaft as in more derived fibulae. A broad, flat topped ridge extends along the ventral (flexor) surface next to the posterior edge (Fig. 22f,k), resembling similar ridges in *Crassigyrinus* (Panchen & Smithson 1990), *Eoherpeton* (Smithson 1985), and a more tubercular crest in *Tulerpeton* (Lebedev & Coates 1995). A strikingly similar tubercular crest is present but currently undescribed in *Whatcheria* (personal observation, specimen FM PR 1635). In *Acanthostega* and *Crassigyrinus* the confluence of the ventral ridge and the posterior fibular edge creates similarly narrow, shallow pockets, visible in posterior view (Fig. 22b). The anterodistal corner is divided from the remainder of the ventral surface by an oblique fibular groove,

as in *Benthosuchus* (Bystrov & Efremov 1940), *Crassigyrinus* and *Tulerpeton*. All surfaces are smooth, with no areas of muscle scarring.

The dorsoventrally narrow proximal fibular head is linear when viewed from the extensor or flexor surfaces, whereas the distal surface is strongly convex, like those of *Ichthyostega* Jarvik (1980, 1996) and *Whatcheria* (Lombard & Bolt 1995), rather than the near-sigmoid curvature of other early fibulae. In contrast to the tibia, the fibula exhibits a limited amount of axial twist, amounting to about 25° (Fig. 22h,k), as in *Tulerpeton*. The greater degree of fibular twist noted in *Crassigyrinus*, which remains considerably less than in more derived tetrapods, is thought to orient the plantar surface vertically to assist hindlimb function as a paddle (Panchen & Smithson 1990). Pelvic limb and girdle articulation in *Acanthostega* corroborates this interpretation. Figure 23 illustrates the extent of distal limb-reorientation (note also the contribution of femoral axial twist), and the degree of fibular-tibial overlap obscuring the limited interepipodial space (which is visible only in anterior and posterior views). Similar

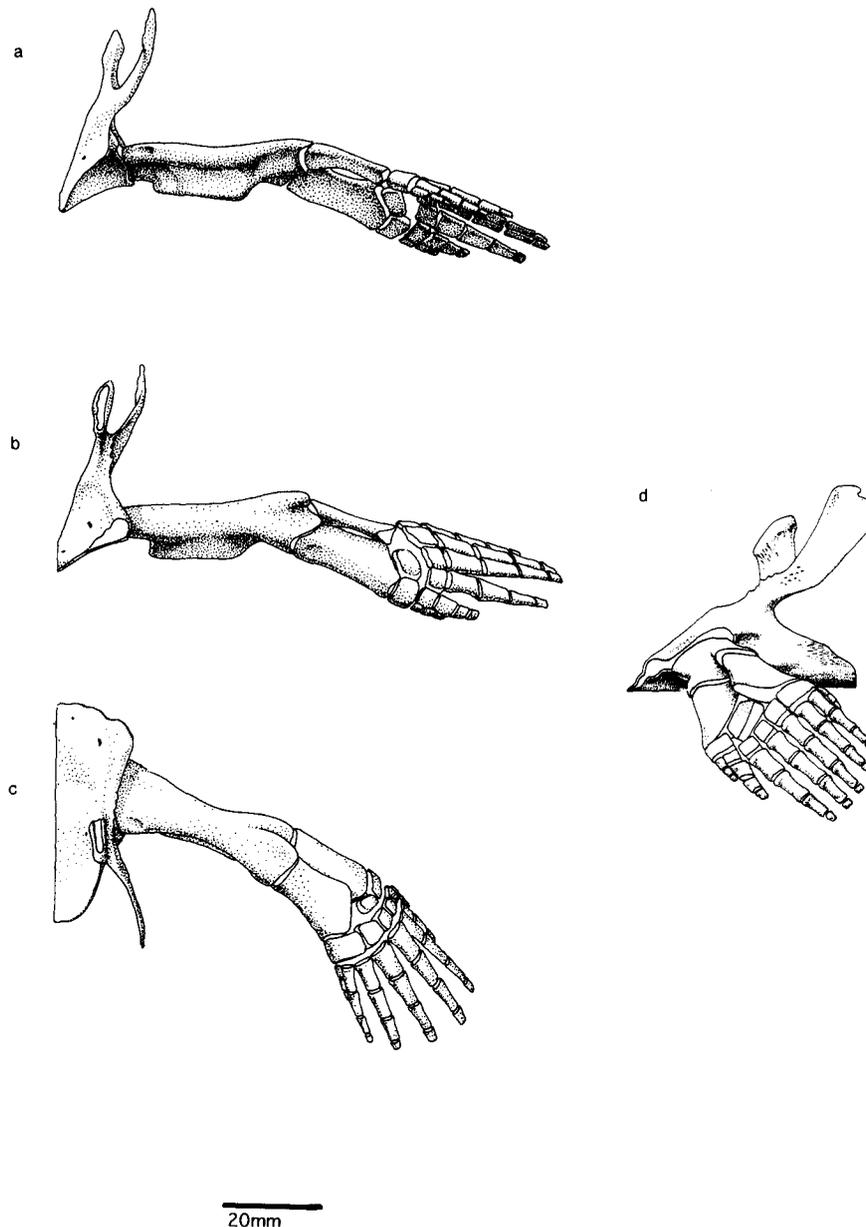


Figure 23 *Acanthostega gunnari*. Reconstructed hindlimb in articulation with pelvis: (a) posterior view; (b) anterior view; (c) dorsal (extensor) view; (d) lateral view. Right side shown in (a) and (c), left side shown in (b) and (d).

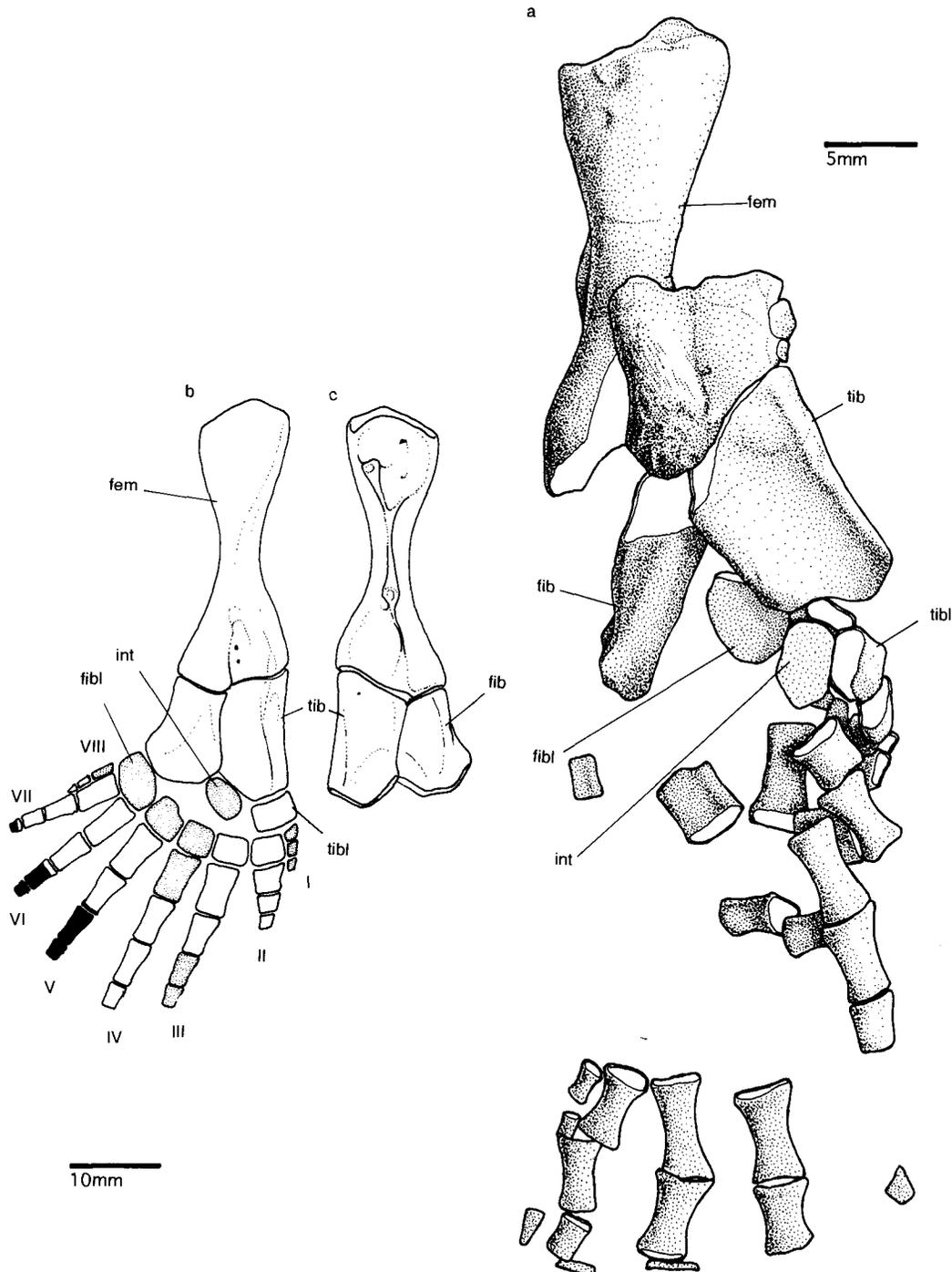


Figure 24 *Acanthostega gumari*. Right hind limb: (a) MGUH f.n. 1375, right hindlimb specimen, drawn as if all matrix removed, dorsal view; (b) dorsal (extensor) surface of restored limb, with unshaded bones indicating articulated preservation, stipple indicating disarticulated preservation, and black indicating complete restoration; (c) ventral (flexor) surface of femur, tibia and fibula.

epipodial spatial relationships in *Ichthyostega* have always appeared to consist of close contact between the tibial and fibular edges (Jarvik 1980 fig. 164; Coates & Clack 1990 fig. 1). However, if interpreted after the rearticulated *Acanthostega* epipodials, this now appears to be a preservational artefact.

The ankle and digits are described from a single, semi-articulated specimen, MGUH f.n. 1375 (Figs 24a & 25b–f). Other less complete specimens are known, but add no further details to the structure of the pes. The specimen consists of a right limb exposed principally from the ventral (plantar) surface (Fig. 25b). The proximal portions of three large and one tiny digit remain articulated at the distal edge of the matrix, relative to limb orientation (Fig. 25d–f). The tarsus

appears to have been wrenched apart in a proximodistal direction, and an aggregation of digit and ankle bones extends from the distal tibial surface towards the four articulated toes (Fig. 24a). Few bones appear to have been lost: the aggregation consists of succeeding digits, with each folded over the plantar surface of its posterior neighbour. The interpretation of each bone has been encoded in Figure 25, with the cluster illustrated in ventral (plantar), posterior, dorsal (extensor), and anterior views. The reconstruction (Fig. 24b) identifies restored, repositioned, and articulated elements, and the eight-digit pattern represents a fairly conservative hypothesis relative to the hind limb of *Ichthyostega* (Fig. 37b), in which the third of a seven-digit array is the smallest member (Coates & Clack 1990).

The tarsus (Figs 23–25) is ossified far more comprehensively than the carpus. The rectangular tibiale is finished perichondrally on only dorsal, ventral, and the anterior surfaces. It is preserved in close association with the tibial anterodistal surface in specimens MGUH f.n. 1375 and 1227. The ovoid intermedium and larger, polygonal fibulare each consist of an endochondral plate, finished only on the extensor and flexor surfaces. The fibulare and intermedium resemble their proportionately larger equivalents in *Ichthyostega* (Coates & Clack 1990; Jarvik 1980, 1996). Like *Ichthyostega* and *Tulerpeton* (Lebedev & Coates 1995), the fibulare supports more than one digit. No identifiable centrale bones have been found. A series of four large, subrectangular, dorsoventrally compressed distal tarsals lie at the bases of digits II–V; whether the most proximal bone of digit I is a distal tarsal or metatarsal is uncertain. The distal tarsal at the base of digit V is distinguished by the presence of a shallow notch in the anteroproximal corner. The phalanges are mostly much larger than those of the manus, with the exception of those restored to the diminutive digits I & VIII. Those of digit II are unusually broad proximally and tapered distally: a second example of these bones is preserved attached to the ventral tibial surface in MGUH f.n. 1227 (Fig. 22e). The digit distribution is shown in Figures 23 and 24a, and the restored phalangeal formula is 1,2,3,3,3,3,2, listed from anterior to posterior.

3.7. Scales

Scales of *Acanthostega* have been found scattered around most specimens, and MGUH f.n. 252, (Fig. 26a; figured previously in Bendix-Almgreen *et al.* 1990) includes a particularly well preserved patch of articulated gastralia. There is no evidence of dorsal scales or osteoderms, and certainly none resembling the thin cycloid caudal scales present in *Ichthyostega* (Jarvik 1952, 1980). The gastralia are spindle-shaped, deeply grooved mesially, and externally smooth. The posterior edge is more convex than the anterior, and when articulated the thinner apices are oriented towards the ventral midline. Similarly shaped gastralia are present in *Crassigyrinus* (Panchen 1985), the early aïstopod *Lethiscus* (Wellstead 1982), and adelogyrinids (Andrews & Carroll 1991). The ventral squamation pattern of *Acanthostega* is *en chevron*, with opposing rows meeting at the ventral midline at an acute angle (Fig. 26d). No enlarged or specialised scales occur on or near to the midline (cf. *Proterogyrinus*, Holmes 1984; *Pholiderpeton*, Clack 1987; *Greererpeton*, Godfrey 1989). There are approximately ten imbricating scales per row on either side of the midline: the mesial grooves of the ventral-most scales enclose the ventral apices of more dorsal members. The degree of inter-scale overlap is uncertain. From specimen MGUH f.n. 252 there appear to be 30–32 scale rows within the length of the puboischadic symphysis. The ventral midline of this specimen is split open so that the mesial surface of the right side emerges from beneath the external surface of the left side scales. This probably records abdominal rupture following *post mortem* fermentation of the gut contents.

Another form of scale or osteoderm has been found associated with articulated limb material. The forelimb, MGUH f.n. 1227, and the hindlimb, MGUH f.n. 1375, both include rectangular, thinly ossified scutes (Fig. 26e,f). These appear to consist of a perichondral layer overlying a thin sheet of compact bone. The situation of these osteoderms suggests that they may have reinforced the plantar and palmar surfaces of these paddle- or flipper-like limbs.

4. Phylogenetic relationships

4.1. Phylogenetic analysis

Results of the phylogenetic analysis are summarised as: (1), a classification (section 4.2); (2) a cladogram (Fig. 27); (3) a

consensus tree (Fig. 28); and (4) an X-tree (Fig. 29). The data set (76 characters: see sections 7 & 8) is an expanded version of that which was used for the *Tulerpeton* analysis (43 characters: Lebedev & Coates 1995). New characters were formulated from the detailed anatomy of *Acanthostega*, and adapted from recent publications on early tetrapod phylogeny (Ahlberg & Milner 1994; Milner & Sequeira 1994; Ahlberg 1995). In addition to the recently discovered Devonian taxa, genera selected for inclusion in the analysis represent each of the major early tetrapod clades. The monophyly of these genera is well-established, whereas that of the larger clades within which they are usually classified remains open to question. Furthermore, most of the genera in the analysis are known from relatively complete skeletal material, whereas conjectural, primitive, character states for more inclusive taxa are correspondingly less certain. Loxommatids were therefore excluded from the analysis (although their possible relationships are discussed below), because their postcranial anatomy is currently undescribed. Detailed published descriptions are available for all of the included genera, and each has been inspected at first-hand, with the exception of *Panderichthys*, of which only pectoral girdle material has been examined directly. As in other recent studies (e.g. Lombard & Bolt 1995), it is taken as axiomatic that osteolepiform sarcopterygians constitute a valid outgroup for assessing the polarity of character transformation in more advanced tetrapods (*contra* Forey *et al.* 1991). Character states in the designated outgroup, *Eusthenopteron foordi*, were scored from published descriptions (Andrews & Westoll 1970a; Jarvik 1980), with corroborative personal observation of Stockholm, Cleveland and Cambridge specimens.

For an initial analysis of the data set (section 8) with PAUP 3.0 (Swofford 1990), all characters were weighted equally, the DELTRAN option was used for character optimisation, and all characters were treated as unordered. A search completed using the branch and bound algorithm produced a set of twelve trees, each of 138 steps. Strict and Adams consensus trees of these results are identical, resembling the tree in Figure 28, but with a total of three polytomies: the first includes *Elginerpeton*, *Ventastega* plus *Metaxygnathus*, and *Acanthostega* plus all more advanced tetrapods; the second includes stem-amphibians *Eryops*, *Balanerpeton*, and *Saxonerpeton*; and the third includes stem-amniotes *Westlothiana*, *Proterogyrinus*, and *Archeria*. Improved resolution was achieved if character types were treated as ordered. This produced a set of six trees, each of 139 steps. Consensus trees were identical, each retaining the stem-tetrapod and stem-amphibian polytomies, but gaining the resolved stem-amniote sequence (Fig. 28). Successive character weighting (Farris 1969), when applied to the data set (using PAUP options: base weight of 1000, and values proportional to rescaled consistency index with best fit), further reduced the set of trees to three, and removed the stem polytomy from the consensus trees (Fig. 28). The tree with the closest congruence between branching sequence and taxonomic stratigraphic occurrence (Fig. 27) was selected as the best supported for X-tree construction (requiring fewest additional *ad hoc* assumptions about range extensions: Smith 1994) (Fig. 29). The consistency index is 0.83, and the retention index 0.89. A search for bootstrap values of a 50% majority rule consensus tree (unweighted data) generated significant results for nodes B/C (99%), D (54%), E (52%), F/G (50%), L (92%), N (73%), and O (57%); B/C and F/G indicate polytomies combining these nodes in the consensus tree.

The Tetrapoda are defined as a total-group within this discussion, including all crown- and stem-members, as in Coates 1994b (*contra* Lebedev & Coates 1995, where the total-

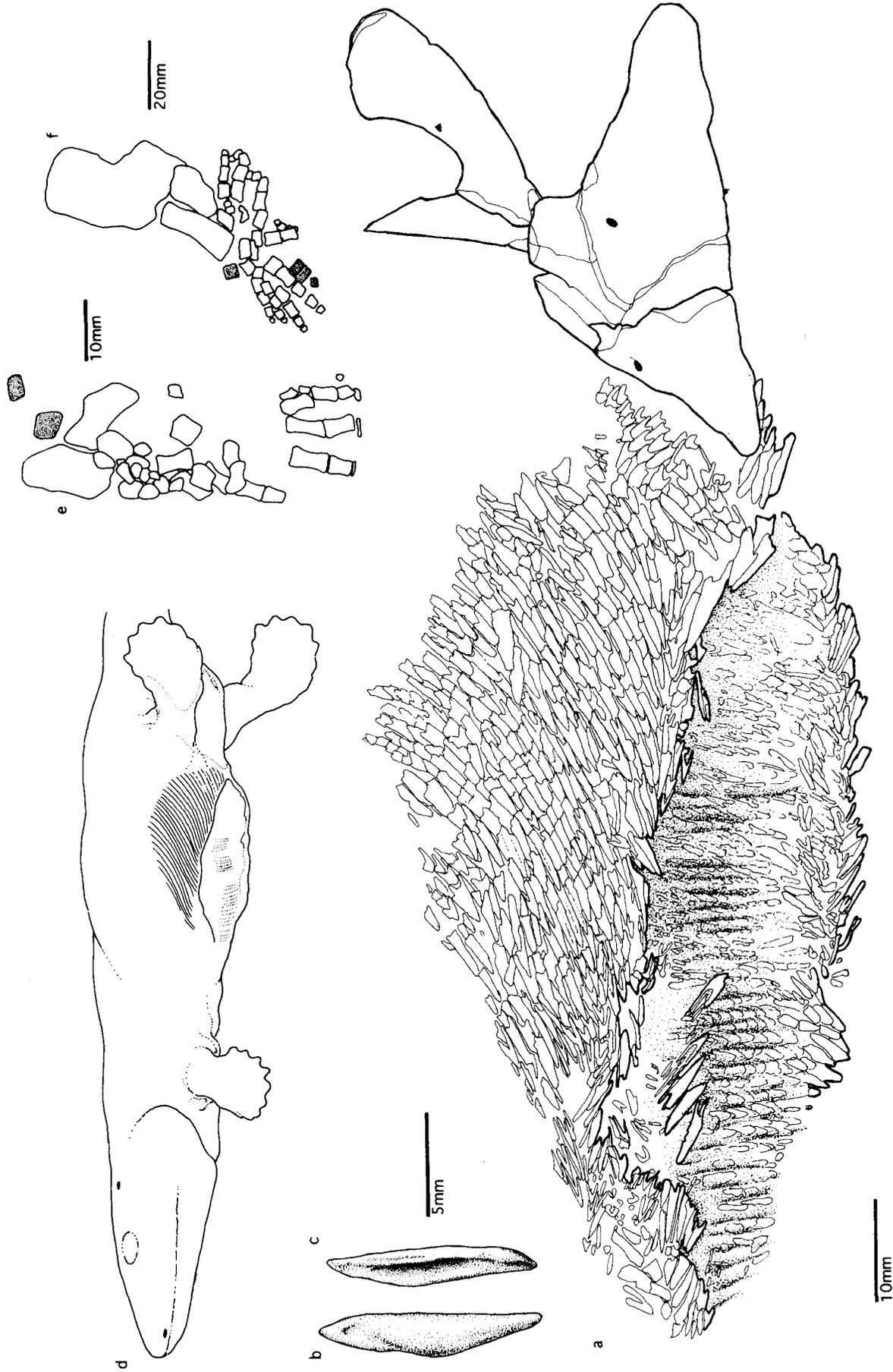


Figure 26 *Acanthostega gannari*. MGUH f.n. 252. (a) Ventral squamation of trunk region (gastralia), disrupted along midline, with associated pelvic girdle. (b) Single gastralia in mesial view, and (c) external view. (d) Orientation of scale rows from MGUH f.n. 252, with diagrammatic restoration of *Acanthostega* (minus tail) showing area covered by specimen, including abdominal rupture. (e) MGUH f.n. 1227, forelimb with associated osteoderms (stippled). (g) MGUH f.n. 1375, hindlimb with associated osteoderms (stippled).

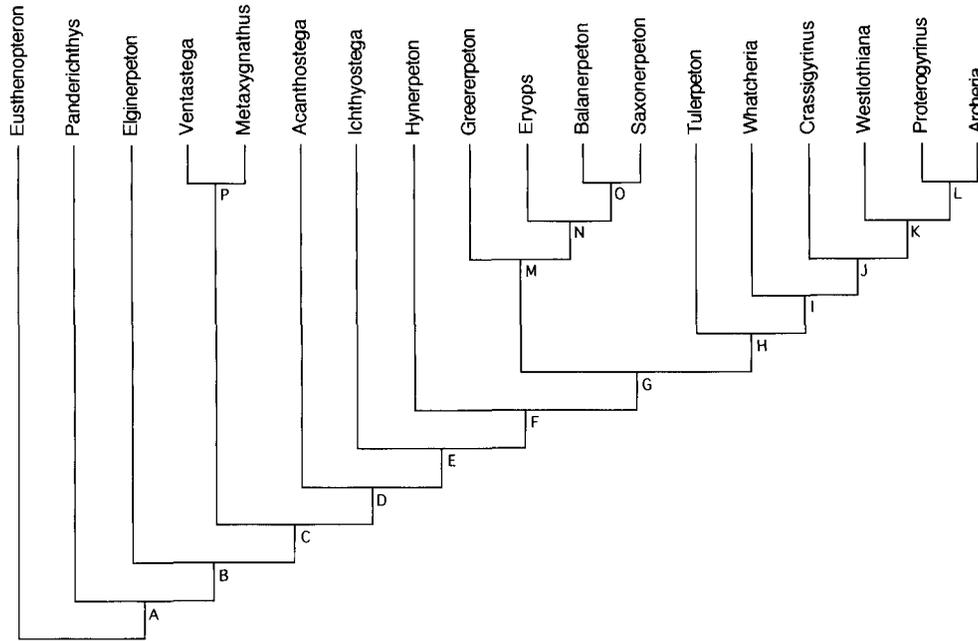


Figure 27 Cladogram of selected early tetrapod genera with greatest congruence between node sequence and stratigraphic occurrence of included taxa.

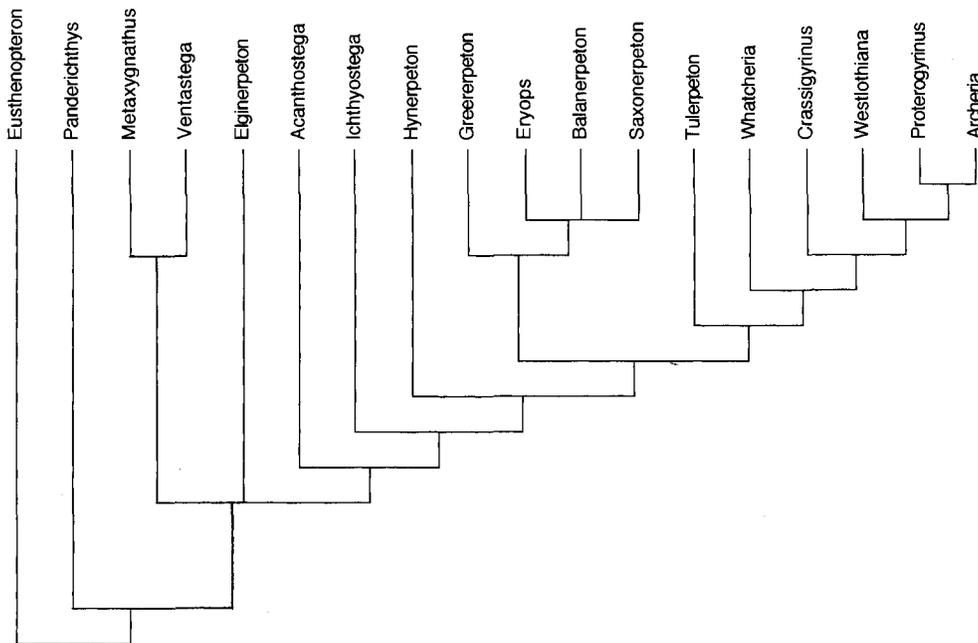


Figure 28 Strict and Adams consensus trees (identical configuration) of three most parsimonious solutions to phylogenetic analysis.

group was named Osteolepiformes, and Tetrapoda was restricted to the crown-group). Crown-group Tetrapoda therefore appear to have originated before the end of the Devonian, as indicated by the phylogenetic position of *Tulerpeton* (suggested previously in Lebedev & Coates 1995, and corroborated here). However, the tetrapod stem-group, extending from the divergence of their ancestry from that of the Dipnoi, their living sister-group, (see Meyer 1995 for a concise review of morphological and molecular evidence concerning this still contentious issue) probably dates from at least the early Devonian (some 40 million years earlier). Porolepiformes supply a valuable stratigraphic marker for this fundamental phylogenetic divergence, irrespective of whether they are considered to be stem-group lungfish (e.g. Ahlberg 1991;

Cloutier & Ahlberg 1995) or basal members of the osteolepiform plus tetrapod clade (Schultze 1994).

Ahlberg (in press) argues for restriction of the term 'Tetrapoda' to the crown-group (cf. de Queiroz & Gauthier 1992; Lebedev & Coates 1995), because details of the basal phylogenetic split from lungfish ancestry remain subject to intense debate. Furthermore, the name 'stem-tetrapod' is then restricted to those taxa primitively possessing limbs (although the definition of what might constitute a limb *versus* fin is avoided). This special definition, although acknowledged as informal, of a stem-group therefore refers to an, at most, post-panderichthyid grade of organisation (panderichthyids being the closest known finned relatives of limbed tetrapods: Ahlberg & Milner 1994; Cloutier & Ahlberg 1995). Alternatively, de

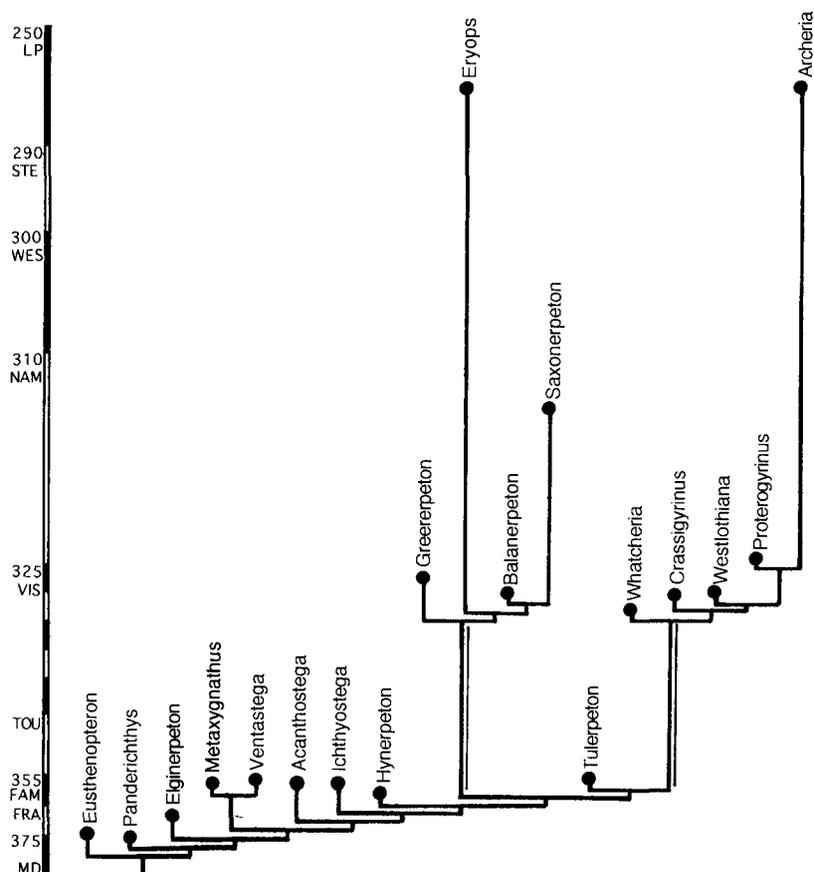


Figure 29 X-tree, derived from cladogram in Figure 27. Key: MD, Middle Devonian; FRA, Frasnian; FAM, Famennian; TOU, Tournasian; VIS, Viséan; NAM, Namurian; WES, Westphalian; STE, Stephanian; LP, Lower Permian. Double lines indicate significant ghost lineage.

Queiroz and Gauthier (1992) advocate naming stem-groups quite separately from crown-groups, and the tetrapod stem thus becomes (somewhat confusingly) the Osteolepida, which must include panderichthyids and the most primitive limbed tetrapods. However, none of these solutions are accepted in the present work. Ahlberg's formulation is rejected because it remains focused upon limb possession as the key characteristic of stem- plus crown-tetrapods, although this character will inevitably fragment as increasingly intermediate and incomplete limb-like fossils are discovered. Furthermore, such a truncated stem-group contributes to the proliferation of ranks inserted almost arbitrarily between fundamental cladogenic events, and subsequent originations of crown-group diversity—cf. Altangerel *et al.* (1993), *versus* Patterson (1993a); discussion in Lebedev and Coates (1995). As an alternative, the classification of Tetrapoda as a total group is simpler, and independent from preselected key characters. Differences with Lebedev and Coates' classification are minor: the number of hierarchical ranks is reduced; the name 'Osteolepiformes' is released for more precise and traditional taxonomic usage; Amphibia and Amniota as total-groups are sufficient for marking the extent of crown-group Tetrapoda, and the subdivisions 'Reptiliomorpha' and 'Batrachomorpha' (both after Säve-Söderbergh 1934) become redundant. Similarly, de Queiroz and Gauthier's (1992) special, uniquely stem-group definitions of Osteolepida, Anthracosauria (for stem-amniotes), and Temnospondyli (for stem-amphibians) can also be removed from the classification, and reserved for basal, extinct monophyletic radiations which resemble most closely those groups for which they were intended originally. The use made by Gauthier *et al.* (1988) of Anthracosauria, as exemplified in

Lombard and Bolt's (1995) interpretation of *Whatcheeria*, is not adopted in the current classification for the same reasons.

The *scala naturae*-like topology of the base of the cladogram (Fig. 27) reflects no more than the rarity of relevant material, rather than an implicit hypothesis of ancestor-descendent relationships. Similarly, the persistent stem-tetrapod polytomy in the consensus trees (Fig. 28) results from the fragmentary remains of *Elginerpeton* (Ahlberg 1995, in press), *Ventastega* (Ahlberg *et al.* 1994), and *Metaxygnathus* (Campbell & Bell 1977). Their interchanging positions are the most varied feature between the trees resulting from the analysis using ordered, equally weighted characters. *Hynerpeton* (Deaschler *et al.* 1994), however, retains a stable location throughout all of the analysis, situated between *Ichthyostega* and the base of the tetrapod crown-group. Predictably, when *Elginerpeton*, *Ventastega*, and *Metaxygnathus* are removed from the weighted data set, and with them the basal polytomy, only a single most parsimonious solution emerges. These fragmentary Devonian taxa have little effect on the general tree topology. As an approximate measure of their significance relative to the current analysis, missing data amounts to 92% in *Metaxygnathus* and *Hynerpeton*, 74% in *Ventastega*, and 66% in *Elginerpeton*. In the last two taxa it should be noted that the associations of postcranial with cranial material were not challenged for the purposes of the analyses. These percentages were recalculated with respect to the data missing from steps preceding their point of insertion in the phylogenetic reconstruction (Fig. 29), and the revised results were 82%, 93%, 42% and 20% respectively. This may supply a better assessment of their contribution, with *Elginerpeton* appearing

to provide the greatest proportion of its phylogenetically useful data and *Hynerpeton* the least.

Hynerpeton illustrates clearly the spurious sense of accuracy created by instances of consistency between otherwise differing tree morphologies. Although *Hynerpeton* always emerges as the sister-group of crown-tetrapods, this result is based solely on the absence of a broad postbranchial lamina (character 43) from this isolated pectoral girdle. Consequently, bootstrap values for Node F (Fig. 27) are unknown and probably negligible. Moreover, reduction of postbranchial laminae may have occurred earlier in tetrapod phylogeny, as suggested by the uncertain condition in *Ichthyostega*. Furthermore, the missing data content in such early examples of (apparently) limbed, stem-tetrapods is difficult to predict. Isolated fragments of *Acanthostega* and *Ichthyostega* would not have indicated such unanticipated morphologies as those now described for the ribs, tails, limbs, and gills. Laurin (1996) suggests that a similar phenomenon occurs in the *Tulerpeton* analysis (Lebedev & Coates 1995), where *Tulerpeton* emerges as a basal stem-amniote (cf. Figs 27 & 28). Significantly, this suggestion arose after Laurin identified inconsistencies between the published data-matrix and phylogenetic results. The cause of this is a typographical error: the *Tulerpeton* data-matrix mis-codes character 43 (presence of interpterygoid vacuities) for *Balanerpeton* as '?' (Lebedev & Coates 1995), whereas it should read '1'. Laurin reports that further analysis of relative node strength (Laurin & Reisz 1995) demonstrates that a strict consensus derived from trees of only one extra step, relative to the shortest obtained from the *Tulerpeton* data, removes *Tulerpeton* to a basal crown-group polytomy. The same operation applied to the present data set (unweighted) has the same effect, and the number of trees increases dramatically from 6 to 138. The association between *Tulerpeton* and basal stem-amniotes, although maintained through both analyses, is therefore fairly weak, consistent with the distribution of boot-strap values listed earlier.

In comparison with Lebedev and Coates' (1995) cladogram, the crown topology (Figs 27–29) is resolved far more clearly. In this earlier work the amniote and amphibian branching sequences were highly varied, and an Adams consensus tree presented a tetrapod crown-group consisting of an amniote polytomy, emerging from a trichotomy with *Greererpeton* and the amphibian stem. Here, however, despite the potentially confounding effects of additional taxa, *Greererpeton* is placed consistently as the basal sister-group of Amphibia; thereby corroborating the general structure of cladograms in Panchen and Smithson (1988) and Smithson (1985), which first suggested the profound extent of the amphibian–amniote dichotomy. Recurrence of *Tulerpeton* within the Amniota (albeit a somewhat tenuous result) further implies the existence of stem-amphibian and -amniote lineages extending throughout the Tournasian. Resolution of the amniote polytomy with *Tulerpeton* as the most primitive known stem-amniote might also have been expected to produce a *Stufenreihe* (Abel 1911, in Panchen 1992) with *Westlothiana* at the apex. Instead, the embolomeres *Proterogyrinus* and *Archeria* cap the series, perhaps indicating the root of a discrete anthracosauroid radiation.

Finally, it is worth including a brief comparison of the current results with other recently published analyses of early tetrapod interrelationships. Bolt (1990) and Lombard and Bolt (1995) place *Crassigyrynus* as the outgroup to *Whatcheeria* plus Anthracosauria (*sensu de Quieroz & Gauthier 1992*), and it is worth noting that the crownward location of *Crassigyrynus* relative to *Whatcheeria* in Figure 27 is not strongly supported. However, a laboured and speculative refutation of Lombard and Bolt's hypotheses is inappropriate in the absence of more

detailed descriptions (especially of the *Whatcheeria* postcranium). At present, confirmation of the status of *Whatcheeria* as an unusually primitive and well preserved stem-amniote is perhaps the most significant result from this part of the analysis. Carroll (1995) has produced a large-scale analysis of early tetrapods (18 taxa; 184 characters) which results in trees of a radically different topology relative to those presented here. No tetrapod crown-group is specified, because no link is considered to be established sufficiently between extant amphibians and Palaeozoic tetrapods, thus challenging Milner's (1988) and Bolt's (1991) hypotheses of amphibian monophyly and relation to fossil temnospondyls. Carroll explores thoroughly the viability of the solutions to his data set (which are more robust than the results presented here), and the results are of significant interest. The basal sequence of taxa from *Eusthenopteron* to *Ichthyostega* resembles the tree in Figure 27. The interrelationships of more advanced tetrapods differ strongly, however. Colosteids plus temnospondyls, anthracosaurs, and seymouriamorphs, are successive sister groups to a pair of radiations: *Westlothiana*, diadectomorphs, and amniotes on the one hand, and lepospondyls on the other. A detailed analysis of Carroll's data is beyond the scope of the current study, but it is clear that the coding of postcranial characters differs strongly from those presented here. Future analyses, addressing the relation of Carroll's data set to the tetrapod crown group, and incorporating more of the new data emerging from work on Lower Carboniferous and Devonian tetrapods, will be of considerable interest.

4.1.2. *Caerorhachis*. *Caerorhachis bairdi*, thought to originate from the Namurian of the Scottish Midland Valley, was described in 1977 by Holmes and Carroll as a dendrerpetontid temnospondyl, i.e. stem-amphibian. It is the focus of particular attention in this discussion because of the uncertainty surrounding this classification; especially those diagnostic characters which have been obtained from the cranial remains. The postcranium, however, is fairly well preserved, including clear axial and appendicular skeletal morphologies. This appears, therefore, to be an appropriate place in which to reconsider the affinities of *Caerorhachis*, given the emphasis on postcranial characters within this phylogenetic analysis.

Milner (1980) first questioned the temnospondyl interpretation of *Caerorhachis*, and argued for it to be excluded from a cladistically defined Dendrerpetontidae. Godfrey *et al.* (1987) then considered it to be the sister taxon to all temnospondyls, excluding colosteids. Milner (1990) subsequently treated it similarly as the most plesiomorphic temnospondyl. In 1994 Milner and Sequeira suggested the most significant reinterpretation when they challenged the placement of *Caerorhachis* within the stem-amphibia altogether. Instead, they suggested that it might be understood better as either a stem-tetrapod or stem-amniote. Holmes and Carroll's diagnosis of *Caerorhachis* as an amphibian was found to be based upon a series of questionable character state interpretations including: (1) dermal ornament and skull features, reinterpreted as plesiomorphic for crown-tetrapods; (2) absence of anterior iliac process, and cheek fusion to skull table, reinterpreted as of ambiguous polarity or possibly convergent; (3) valuable diagnostic characters such as otic region, cultriform process, humerus, and manual digit count completely absent; (4) palatal vacuities reconstructed from too severely crushed material; (5) gastrocentrous vertebrae usually associated with stem-amniotes.

The results of the analysis presented in this paper mostly corroborate Milner and Sequeira's (1994) reinterpretation, especially the removal of *Caerorhachis* from the stem-amphibia. Such gastrocentrous vertebrae, including considerably reduced intercentra and enlarged, ventrally fused pleurocentra, are

more stem amniote-like than those of *Whatcheeria* (Lombard & Bolt 1995). They resemble most strongly a more notochordal version of the vertebrae in *Proterogyrinus* (Holmes 1984) (character 60). The abrupt change between cervical and anterior thoracic rib morphologies (character 34) in *Caerorhachis* is also widespread among stem-amniotes. Similarly, the extreme reduction or near absence of an anterior iliac process also resembles the condition of stem-amniotes. Unlike the condition of *Greererpeton* (Godfrey 1989) or other stem-amphibians, the anterodorsal iliac surface retains a narrow, but anteroposteriorly rounded crest, which could represent a truncated version of the taller crest found in *Proterogyrinus* (character 14, state 2), or the less acute process of *Hylonomus* (Carroll 1969). Slightly more convincingly, the iliac transverse line of *Caerorhachis* passes directly onto the ventral edge of the posterior process (character 69). This follows the uniquely stem-amniote patterns of *Hylonomus*, *Proterogyrinus*, and *Archeria* (Romer 1957). Likewise, the L-shaped intermedium (character 52) in *Caerorhachis* also appears, so far, to be a non-homoplastic synapomorphy of stem-amniotes (Lebedev & Coates 1995). Thus *Caerorhachis* may be inserted as high as Node L on the amniote stem (Fig. 27), which amounts to a qualified suggestion that it may be a basal embolomere. This does not necessarily preclude the significance of Milner and Sequeira's observed similarities between the figured, unreconstructed anterior palate and that of the loxomatid *Baphetes* (Beaumont 1977). Panchen and Smithson's (1988), suggestion that loxomatids are basal amniotes is corroborated by the centrally depressed and posteriorly expanded portion of the parasphenoid of genera such as *Baphetes* (Fig. 30; character 64: Node J), and the phylogenetic distribution of other taxa with similarly angled orbits (*Whatcheeria*, Lombard & Bolt 1995; *Crassigyrynus*, Panchen 1985). Such palatal similarities may therefore represent persistent transitional characters of basal stem-amniotes.

4.2. Classification

This 'stem-based' (de Queiroz & Gauthier 1992) classification summarises the results of the phylogenetic analysis, and follows the conventions of Patterson and Rosen (1977).

INFRACLASS Tetrapoda (Goodrich 1930)

- Plesion Rhizodontidae (Jarvik 1942)
- Plesion Osteolepidae (Jarvik 1942)
- Plesion Panderichthyida (Vorobyeva & Schultze 1991)
- Plesion *Metaxygnathus*
- Plesion *Elginerpeton*

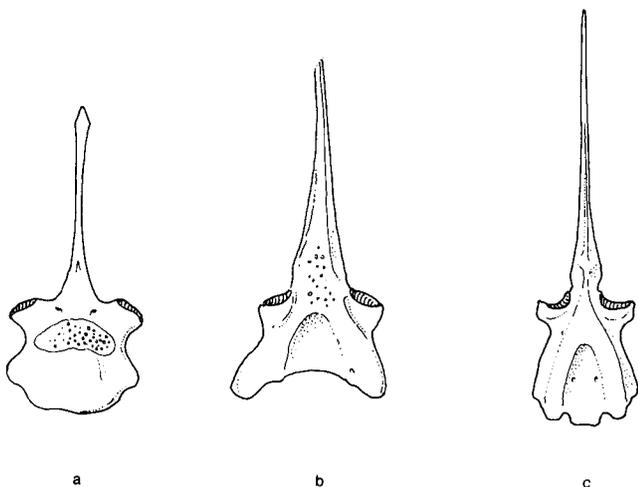


Figure 30 Parasphenoids of early crown-group tetrapods: (a) *Balanerpeton*, after Milner and Sequeira (1994); (b) *Baphetes*, after Beaumont (1977); (c) *Archeria* after Holmes (1989).

- Plesion *Ventastega*
- Plesion *Acanthostega*
- Plesion *Ichthyostega*
- Plesion *Hynerpeton*
- DIVISION Amphibia (Linnaeus 1758)
 - Plesion *Greererpeton*
 - Plesion *Eryops*
 - Plesion *Balanerpeton*
 - Plesion *Saxonerpeton*
- DIVISION Amniota (Goodrich 1916)
 - Plesion *Tulerpeton*
 - Plesion *Whatcheeria*
 - Plesion *Crassigyrynus*
 - Plesion *Westlothiana*
 - Plesion *Proterogyrynus*
 - Plesion *Archeria*

4.3. Distribution of character states

Node A: *Panderichthys* and more crownward tetrapods. (1) Marginal position of the external naris; (2) separate dorsal fin lost; (3) humerus with anterior keel; (4) platybasic skull; (5) enlarged scapulocoracoid plate.

Node B: *Elginerpeton* and more crownward tetrapods. (6) Tooth row on parasymphysial plate; (7) parasymphysial foramina; (8) Meckelian bone concealed dorsal to prearticular; (9) humeral epipodial facets separated; (10) rudimentary sacrum; (11) femoral adductor blade; (12) L-shaped tibial distal articular surface; (13) pre- and postzygapophyses; (14) biramous ilium with a stout, unfinished anterodorsal process; (15) large nasals.

Elginerpeton apomorphies: (16) supraneural canal for dorsal ligament canal closed; (17) ilium neck canal.

Node C: *Ventastega* plus *Metaxygnathus* and more crownward tetrapods. (18) Bony enclosure of infraorbital sensory canal interrupted by external naris; (19) jugal–quadratojugal contact excludes squamosal–maxilla contact; (20) spade-shaped snout.

Node P: *Ventastega* plus *Metaxygnathus*. (21) Coronoid fangs in tooth row.

Node D: *Acanthostega* and more crownward tetrapods. (22) Fenestra ovalis; (23) stapes (cf. Smithson & Thomson 1982); (24) ischia contribute to pelvic symphysis; (25) fore and hind limb epipodials are parallel, and both articulate with carpus/tarsus; (26) carpus/tarsus with skeletal elements articulating laterally as well as proximodistally; (27) dactyl: manus/pes with series of digits; (28) single bilateral pair of nasal bones; (29) pectoral girdle detached from skull; all dermal bones dorsal to anocleithrum lost; (30) presacral neural spines oriented vertically, and squared-off dorsally; (31) neural radials; (32) rugose fourth trochanter restricted to adductor blade crest; (33) multiple obturator foramina; (34) presacral ribs with uncinate processes; (35) coronoid fangs absent.

Node E: *Ichthyostega* and more crownward tetrapods. (29) Anocleithrum absent; (37) latissimus dorsi process of humerus in-line with ectepicondyle; (38) dark dentine; (39) olecranon process present, and ulna equal to or greater than radial length; (40) ventromesially extended infraglenoid buttress; (41) rib length exceeding combined height of centrum, neural arch and spine; (42) supra-acetabular buttress most prominent.

Ichthyostega apomorphies: (17) ilium neck canal; (36) humeral processes 3 & 4.

Node F: *Hynerpeton* and more crownward tetrapods. (43) Loss of postbranchial lamina.

Node G: Crown group *Tetrapoda*. (2) All dermal fin rays absent; (9) humeral/femoral epipodial facets rejoined by perichondrally unfinished isthmus; (44) wrist and knee hinged,

ankle rotary; (45) scapulocoracoid separate from cleithrum; (46) rod-like ascending clavicular process; (47) waisted fibula with sigmoid profile distally; (48) tarsus with two or more centralia; (49) haemal radials absent; (50) humeral ectepicondylar and 'd' canals absent; (51) posteriorly expanded parasphenoid; (31) neural radials lost.

Node H: total group *Amniota*. (52) Tarsus with L-shaped intermedium; (53) large supraglenoid foramen lateral to triangular area of scapulocoracoid.

Tulerpeton apomorphies: (29) anocleithrum present; (54) flanged tibia; (55) strongly convex radial condyle; (56) tuberculate fibular posterior edge.

Node I: *Whatcheeria* and more crownward amniotes. (4) Tropibasic skull; (12) ovoid distal tibial articular surface; (14) ilium with short, blade-like anterodorsal process; (20) loss of broad, spade-shaped snout; (57) nature of dermal ornament; (58) tabular horn with superficial and deep component; (59) large scapular blade.

Whatcheeria apomorphies: (37) latissimus dorsi process offset relative to ectepicondyle; (56) tuberculate fibular posterior edge; (60) pleurocentral enlargement.

Node J: *Crassigyrinus* and more crownward amniotes. (11) Femoral adductor blade reduced distally; (61) post temporal fossae closed; (62) clavicles separated by interclavicle anteriorly; (63) sutured puboischiadic plate; (64) parasphenoidal posterior expansion depressed centrally, with prominent ventrolateral margins.

Crassigyrinus apomorphies: (1) External nostril high on snout; (13) postzygapophyses lost; (21 + 35) coronoid fangs in tooth row; (39) olecranon process absent, and ulna shorter than radius; (50) ectepicondylar foramen present.

Node K: *Westlothiana*, *Proterogyrinus*, and *Archeria*. (3) Humeral keel elongate; (33) single obturator foramen; (34) abrupt change between cervical/pectoral and anterior thoracic ribs; (55) strongly convex radial condyle; (60) pleurocentral enlargement; (65) pentadactylous forelimb; (66) tabular-parietal suture.

Westlothiana apomorphies: (4) platybasic skull; (14) uniramous ilium; (16) dorsal ligament canal closed; (32) loss of distinct fourth trochanter; (54) flanged tibia; (67) waisted humerus.

Node L: *Proterogyrinus* and *Archeria*. (32) Rugose fourth trochanter extending onto anterior surface of internal trochanter; (68) proximo-anteriorly directed pectoral crest; (69) transverse pelvic ridge directed towards ventral edge of posterior iliac process.

Proterogyrinus apomorphies: (29) anocleithrum present.

Archeria apomorphies: (36) humeral processes 3 and 4; (53) supraglenoid foramen within triangular area.

Node M: total group *Amphibia*. (12) Tibial distal articular surface ovoid; (14) ilium uniramous; (63) sutured puboischiadic plate; (70) immobile basal articulation; (71) exoccipital-postparietal suture; (72) incipient interpterygoid vacuities.

Greererpeton apomorphies: (11) femoral adductor blade reduced distally; (33) single obturator foramen; (43) postbranchial lamina present; (65) pentadactylous forelimb (see below, section 5.2.3.).

Node N: *Eryops* and more crownward amphibia. (60) Pleurocentra enlarged; (73) cultriform process contacts vomers; (74) four digit manus.

Eryops apomorphies: (16) dorsal ligament canal closed; (36) humeral processes 3 and 4; (55) convex radial condyle; (60) pleurocentra enlarged.

Node O: *Balanerpeton* and *Saxonerpeton*. (62) Clavicles separated by interclavicle anteriorly; (75) 'propeller-blade' humerus.

Saxonerpeton apomorphies: (3) humerus with rounded

leading edge; (15) ilium biramous; (20) loss of broad snout; (34) abrupt change between cervical/pectoral and anterior thoracic ribs.

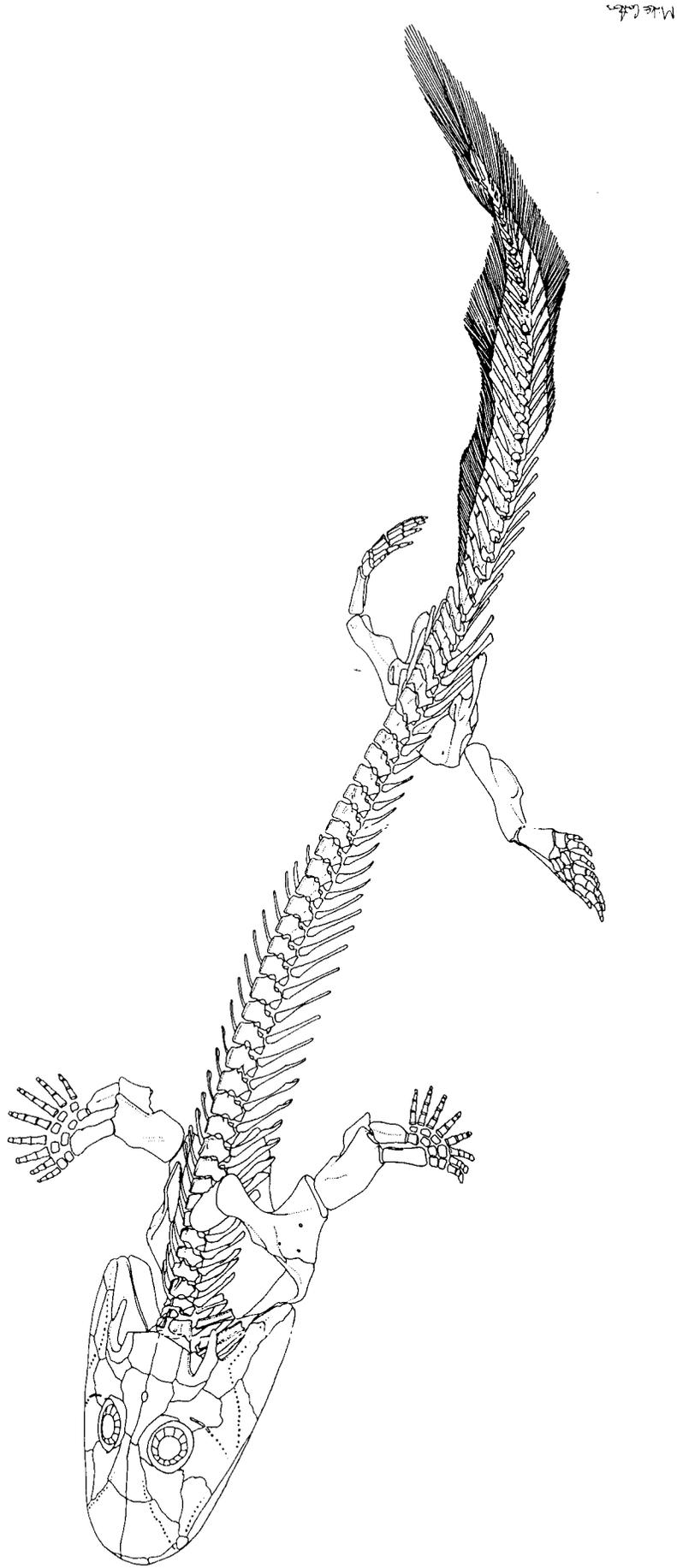
5. Discussion

5.1. Skeletal reconstruction and mode of life

The exceptionally complete nature of the *Acanthostega* material has enabled the production of a detailed skeletal reconstruction (Fig. 31). Although this is a composite based upon data drawn from several specimens, it mostly represents MGUH f.n. 1227, individual X. The reconstruction was attempted initially as part of a collaborative project with the American Museum of Natural History, New York, to produce skeletal and enflashed models for their renovated fossil vertebrate displays. The sculptor, Mr Elliot Goldfinger, posed a series of invaluable questions about the three-dimensional properties of much of the material which were important for assessing rib orientation, lateral dimensions of the girdles, and their positions relative to the vertebral column.

The mode of life of *Acanthostega* has been discussed in greater detail elsewhere, primarily in the context of a scenario-review concerning theories of vertebrate terrestrialisation and tetrapod origin (Coates & Clack 1995). Although this review remained 'in press' between 1992 and 1995 (thereby becoming somewhat dated, relative to the emergence of more recent data concerning early tetrapods), the principal conclusions remain relevant. In comparison with *Ichthyostega* and *Tulerpeton*, *Acanthostega* is the most anatomically adapted for an aquatic existence. Moreover, this is consistent with the sedimentological analysis which suggests deposition within active regions of a meandering fluvial channel system (Bendix-Almgreen *et al.* 1990). Large lycopod branches (50 mm diameter) indicate an abundant vegetation local to these channels, and the palaeoclimate is interpreted as monsoonal. In fact, seasonality is indicated quite dramatically by the fossil mud cracks disrupting the otherwise fairly undisturbed remains of individual X (Figs 1–3), MGUH f.n. 1227. Thus *Acanthostega* is envisaged as an occupant of stagnant, vegetation-choked backwaters. Here it could cope with partial emergence into moist, shady conditions, but otherwise remain below the water surface, air-gulping, and using its limbs for submerged walking (perhaps using a 'walking-trot', Pridmore 1995), and to clamber through knotted roots and stems. Ahlberg and Milner (1994) comment that this aquatic interpretation of *Acanthostega* is in itself uncontroversial. However, they consider the argument (Edwards 1989; Coates & Clack 1990, 1991) that this aquatic existence was primary instead of secondary (i.e. descended from more terrestrial precursors) as altogether more contentious, because it requires that digitated limbs, sacral ribs, enlarged pelvic girdles, and operculogular series loss, all evolved underwater.

An answer to this challenge is simply to note that in the absence of more terrestrially adapted but less crownwardly derived stem-tetrapods, the 'primitively aquatic' interpretation of *Acanthostega* is the most parsimonious. The 'secondarily aquatic' hypothesis requires that a whole series of fish-like features were either sustained in hypothetical terrestrial ancestors, or represent reversed character states in *Acanthostega*. These include an extensive, bone-enclosed, cranial sensory canal network (Clack 1988; Clack & Coates 1993); a hyoid arch with a large ceratohyal (Coates & Clack 1991) which implies suction feeding rather than mechanical prey transport (Reilly & Lauder 1990); 3+ ossified, deeply grooved branchial arches which are more conventionally fish-like than those of *Neoceratodus* the only non-obligate



40mm

Figure 31 Skeletal reconstruction of *Acanthostega gunnari*.

airbreather among living lungfish (Coates & Clack 1991); a notochordal occipital–vertebral junction, related to the lack of a functional neck, barely differentiated cervical neural arches, presence of a functioning internal gill chamber, and persistence of postbranchial laminae (and anocleithra); and a radial-supported tail-fin with closely packed, elongate lepidotrichia. Such a fin is extremely likely to have been able to generate muscular waves throughout its length in both cranial and caudal directions as in living lungfish (personal observation). This would have been advantageous for a primarily aquatic organism, but may have been something of a handicap on dry land.

Conversely, fin-walking using a tetrapod-like gait, sometimes associated with the evolution of pseudo-digitated limbs, has evolved repeatedly in entirely aquatic taxa, from epaulette sharks to antenarid teleosts (Edwards 1989; Pridmore 1995; and reviews therein). Likewise, operculogular bones have been reduced and lost in numerous fishes, including extant lungfish and various teleosts such as stomiids and anguillids (most notably the morays, which also have their pectoral girdle detached from the skull; thus qualifying as yet another convergence with tetrapods: see Panchen & Smithson 1990 on morays as analogues of *Crassigyrinus*). Tetrapod-like sacra are, however, absent in extant fish. Nevertheless, in certain ‘walking’ teleosts the pelvis is attached directly to the anteroventral portion of the pectoral girdle, and is therefore functionally analogous, at least in part, to tetrapod pelves.

Finally, while it remains clear that no extant taxon is individually sufficient as an analogue of *Acanthostega*, *Arapaima gigas* provides an intriguing alternative to the more usual suggestions (e.g. lungfish or giant salamanders). *Arapaima*, the ‘pirarucu’ of Brazil and other parts of tropical South America, is an osteoglossid teleost retaining primitive continuity between the gut and swim-bladder or rudimentary lung. The conserved ability to breath air confers a considerable adaptive advantage upon this large predator, especially over non-airbreathing prey whose habitat also extends beyond seasonally flooded forest floors and into vegetation-choked, anoxic backwaters (Kodera 1994). With the exclusion of the paired fins, the postcranial skeleton exhibits several features (obtained from personal observation of a ~1.5 m specimen displayed in the Museum of Comparative Zoology, Harvard University) which are unexpectedly similar to those of basal or near-crown-tetrapods. The pectoral girdle has an enlarged endoskeletal component including an extensive, broad coracoid plate (but no scapular enlargement). The pectoral radials are substantial and fused via interdigitating sutures into a single proximal appendicular element. A substantial pelvis, lying below vertebral segments 23–27, has anterior and posterior symphyseal regions (but there is no bony sacral attachment). The vertebral column is well ossified, with neural arches fused to ring centra, pre- and postzygapophyses, and well developed transverse processes. Each process bears an elongate posterior groove which forms a sleeved-hinge, articulating with the specialised heads of well ossified, posteriorly concave and distally expanded pleural (ventral) ribs. The transverse (dorsal) ribs are relatively small. Finally, the long-based dorsal and anal fins combine with the caudal fin to produce a tail with proportions resembling closely those of *Acanthostega*. It is probably significant that this, once again, is a taxon without a record of spending significant periods out of water (Sayer & Davenport 1991; Goulding *et al.* 1988) but which exhibits several osteological characters which have previously been used to bind limbed-tetrapod evolution to terrestrialisation.

5.2. Evolution of the tetrapod postcranial skeleton

5.2.1. Axial skeleton. Godfrey and Riesz (1991), while redescribing the vertebral morphology of the stem-amniote

Gephyrostegus, hypothesised a series of conditions for the primitive atlas–axis complex. They suggested that these were either diagnostic for the Tetrapoda (including *Ichthyostega* and *Crassigyrinus*) or more plesiomorphic, occurring in ‘some panderichthyid osteolepiform fish’. These conditions (listed below in italics) can now be tested against information obtained from *Acanthostega* and the results of the phylogenetic analysis.

1. *Proatlantal and atlantal arches are always smaller than the relatively massive axial arch.* The condition in *Acanthostega* tends to support this conclusion, although the morphological distinction between atlantal (the proatlas is unknown) and axial arches is less pronounced, and the axial arch is hardly ‘massive’. Nevertheless, in comparison with *Eusthenopteron* (Andrews & Westoll 1970a) which has cervical neural arches that are significantly less individually distinguishable, the reduced atlas–axis differentiation of *Acanthostega* is marginally derived; i.e. more conventionally tetrapod-like.

2. *The proatlantal and atlantal arches are paired, while the axial arch is a unitary structure.* In *Acanthostega* the atlantal, axial, and at least third neural arches are paired. In comparison with the paired neural arches and spines described in *Panderichthys* (Vorobyeva & Schultze 1991) and *Elpistostege* (Schultze & Arsenault 1985) this probably represents a more primitive condition than that hypothesised by Godfrey and Riesz. However, axial regional variation in panderichthyids is undescribed. In *Eusthenopteron* Andrews and Westoll (1970a) describe the neural arch halves of vertebrae 1–5 as fused, with unfused arches and spines occurring only sporadically, and always more posteriorly. However, those of at least segments 4 and 6 out of a series from 3–7, appeared to be unfused or broken in the well preserved Cleveland specimen discussed elsewhere in this text (CMNH 8160, Fig. 33c). Moreover, the presence of separate neural arch halves in *Crassigyrinus* (Panchen 1985; Panchen & Smithson 1990), whether secondarily ‘degenerate’ or otherwise, illustrates the broad distribution of this character around the crown-group tetrapod radiation.

3. *The atlas intercentrum and pleurocentrum are paired and unossified dorsally and ventrally.* *Acanthostega* is strikingly inconsistent with this assumption. Although unossified dorsally, the atlantal intercentrum is sufficiently well fused ventrally to preserve no trace of the midline suture (unlike its slightly smaller posterior neighbours), and there is no evidence of ossified atlantal pleurocentra. The panderichthyid condition remains unknown, but in *Eusthenopteron* intercentra 1–5 are described as *always* having their right and left halves coossified, (Andrews & Westoll 1970a; my emphasis; CMNH 8160 uninformative), and the associated pleurocentra are particularly large. Fusion of the *Acanthostega* atlas intercentrum is therefore considered decidedly primitive relative to Godfrey and Riesz’s hypothesis.

4. *The axis intercentrum is crescentic and paired, and accompanied by paired pleurocentra.* All *Acanthostega* intercentra are crescentic, but the degree of fusion of the axis intercentrum and the presence of paired axial pleurocentra are unknown.

5. *Cervical intercentra have ventrolaterally directed tubercles.* As mentioned in the description, these are absent throughout the *Acanthostega* vertebral column.

Acanthostega is therefore plesiomorphic relative to points 1, 2, and perhaps 5 of the condition suggested by Godfrey and Riesz (1991). If this hypothetical stage is assumed to have occurred, then it is extremely unlikely that this primitive cervical pattern was exhibited by any panderichthyid. Alternatively, it seems possible that points 1–5 may approximate more closely to the cervical patterns of basal crown-group tetrapods, and stem-amniotes in particular. However,

point 3, concerning the condition of the atlantal intercentrum, presents the deepest inconsistency with Godfrey and Reisz's hypothesis, and suggests that conflicting trends of neural arch and central consolidation occurred quite independently. Further progress on the question of early cervical patterning will have to await the publication of new data. Relevant vertebrae are quite unknown in *Ichthyostega* and *Tulerpeton*, but more detailed descriptions of *Panderichthys* and especially the basal stem-amniote *Whatcheeria* (Lombard & Bolt 1995) may clarify the situation.

More topographically extensive attempts to characterise the primitive condition of (limbed) tetrapod axial skeletons (and obtain some insight into conditions close to the fish-tetrapod transition) have often tried to quantify changes in terms of regional vertebral counts. Totals of between 23 and 30 presacral vertebrae have been suggested as the primitive complement for crown-tetrapods (e.g. Romer 1956), and intercentral counts of *Eusthenopteron* (Andrews & Westoll 1970a), *Acanthostega*, *Whatcheeria* (Lombard & Bolt 1995), and *Crassigyrinus* (Panchen 1985) more or less support this hypothesis. However, *Ichthyostega* (Jarvik 1980) and *Greererpeton* (Godfrey 1989), with presacral counts of 22 and 41 respectively, indicate wide variation within the somewhat sparse primary data closest to the node of crown-tetrapod divergence. Alternatively, the proliferation of caudal relative to presacral vertebrae may present a slightly more robust characteristic of advanced tetrapods relative to fish-like stem-tetrapods (Fig. 32). The porolepiform *Glyptolepis* (Andrews & Westoll 1970b) provides outgroup comparison for stem-tetrapod conditions, and has a pre- to postsacral vertebral ratio of around 36:37. In the basal stem-tetrapod osteolepiform *Osteolepis* the ratio is about 28:35, and in the more derived *Eusthenopteron* the ratio is around 30:25 (Andrews & Westoll 1970b). In *Panderichthys* the details are undescribed although gross restorations consistently show a caudal length of less than half the pectoral-pelvic distance (Vorobyeva 1992). The following list provides a similar but contrasting set of pre- to postsacral ratios for early limbed tetrapods: *Acanthostega*, 30:32; *Ichthyostega*, 22:36 (Jarvik 1980, 1996); *Greererpeton*, 41:40 (Godfrey 1989); *Eryops*, 22:34 (Moulton 1974); *Proterogyrinus*, 32:~45 (Holmes 1984); *Archeria*, 37:~80 (Holmes 1989); *Seymouria*, 24:~40 (White 1939). Once again, *Acanthostega* seems to occupy an intermediate position in this apparent morphocline of fish-tetrapod axial morphology.

The absence of strong regionalisation in the presacral axial skeleton of *Acanthostega* relative to crown-tetrapods is strikingly plesiomorphic, as implied in the discussion of cervical patterning. Within the vertebral column, only the atlantal and sacral intercentra are individually identifiable, and most variation within this domain is expressed in the neural arches and spines (Fig. 32a). In comparison with the precaudal arches and spines of fish-like stem-tetrapods such as *Osteolepis* (Andrews & Westoll 1970b) or the incomplete series known in *Panderichthys* (Vorobyeva & Schultze 1991) and *Elpistostege* (Shultze & Arsenault 1985), those of *Acanthostega* are fairly derived (vertically oriented, subrectangular, and with horizontal apices; thus resembling those of more advanced tetrapods). It may be significant, therefore, that (so far) the neural arches which resemble most closely those of *Acanthostega* are the most anterior of *Eusthenopteron* (Andrews & Westoll 1970a text-fig. 20) in which the square-headed arches around segment 3 (Fig. 33c) contrast with the more rounded, narrower, and posteriorly-raked arches and spines of segments 26+ (Fig. 32a). Moreover, in *Acanthostega* the degree of neural arch posterior overlap relative to subjacent and preceding centra is also unusually fish-like, and matched only by *Greererpeton* (Godfrey 1989) from among higher

tetrapods. Thus posterior slope of the neural arches may provide some further insight into the axial morphological transition between features usually thought of as either strictly fish- or tetrapod-like.

Almost all neural arches and spines are inclined posteriorly in a fish-like taxon such as *Eusthenopteron*, with a slightly increased slope towards the caudal end of the vertebral column (Fig. 32). This gradual reorientation occurs throughout the vertebral series (Andrews & Westoll 1970a text-figs 20 & 23) whereas in early limbed-tetrapods an equivalent transformation occurs more restrictedly, sandwiched between the near-vertical arches of the trunk and more posteriorly inclined arches in the caudal region. Although the relation between arch plus spine orientation and myoseptal attachment may not be straightforward (cf. *Polypterus senegalus*, described in Bartsch & Gemballa 1992), the caudally accentuated slope most probably reflects an increased degree of myotome infolding. In *Acanthostega* the transition from near-vertical to more posteriorly inclined arches occurs between presacral segments 27 or 28 and the most anterior caudal segments with haemal arches. *Ichthyostega* is restored with a more gradual transition (Jarvik 1980, 1996), but no individual specimen preserves an uninterrupted sacral to caudal vertebral series and the reconstruction is somewhat idealised. Of the crown-tetrapods, stem-amphibians such as *Greererpeton* tend to resemble more closely *Acanthostega* and *Ichthyostega* in these respects (a smooth transition encompassing the sacral region), whereas in stem-amniotes such as *Proterogyrinus* (Holmes 1984) the transition is more abrupt and displaced posteriorly to around caudal vertebra 15 (*Caerorhachis*, Holmes & Carroll 1977, shows a similarly discontinuous pattern in the anterior caudal region). It therefore appears that the fish-like characteristics of the vertebral column were displaced caudally during the early tetrapod evolution. Furthermore, caudal displacement of fish-like axial patterns appears to have diversified after the divergence of amphibian and amniote stem-lineages, and may prove to be a valuable source of taxonomically useful characters.

Such patterns of caudal displacement are repeated in at least two further sequences of axial morphological transformation: first, the posterior extent of zygapophyseal development; and second, radial plus lepidotrichial distribution. Incipient zygapophyses are restricted anteriorly to the trunk region in *Eusthenopteron* (Andrews & Westoll 1970a). However, zygapophyseal development extends posteriorly to caudal segments 5 or 6 in *Acanthostega* and *Ichthyostega*, 12+ in *Greererpeton*, 31 in *Eryops*, 22+ in *Proterogyrinus*, and 47 in *Archeria*. Caudal fin development is less easily compared between the arrangement in *Eusthenopteron* and higher stem-tetrapods. Nevertheless, it is probably significant that in *Eusthenopteron* the anterior dorsal fin inserts above presacral vertebrae 26–28, the second dorsal and anal fins insert around caudal vertebra 5, haemal radials extend from caudal vertebra 11, and the lepidotrichia from 13 ventrally and 15 dorsally. In *Acanthostega* neural radials originate at caudal segment 8, haemal radials at segment 15, dorsal lepidotrichia at segment 8, and ventral lepidotrichia at segment 15, whereas in *Ichthyostega* neural radials originate at caudal segment 14, haemal radials at segment 21, dorsal lepidotrichia at segment 14, and ventral lepidotrichia at segment 32. When combined with the robust phylogenetic topology (Fig. 28), in which *Ichthyostega* is located consistently crownwards of *Acanthostega* (see similar results in Ahlberg & Milner 1994; Lebedev & Coates 1995; Ahlberg in press), the changing distributions of these morphological features add corroborative support to the hypothesis that tetrapod repatterning of the primitively fish-like axial skeleton proceeded in a cranio-caudal direction.

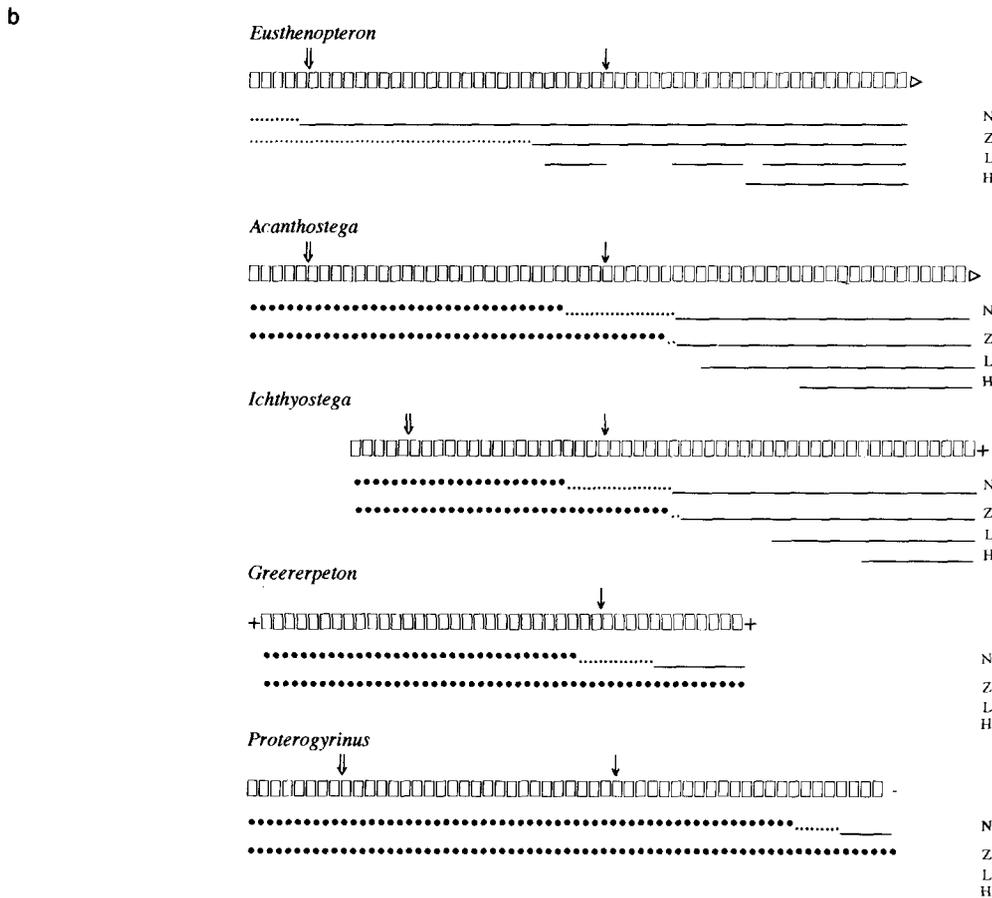
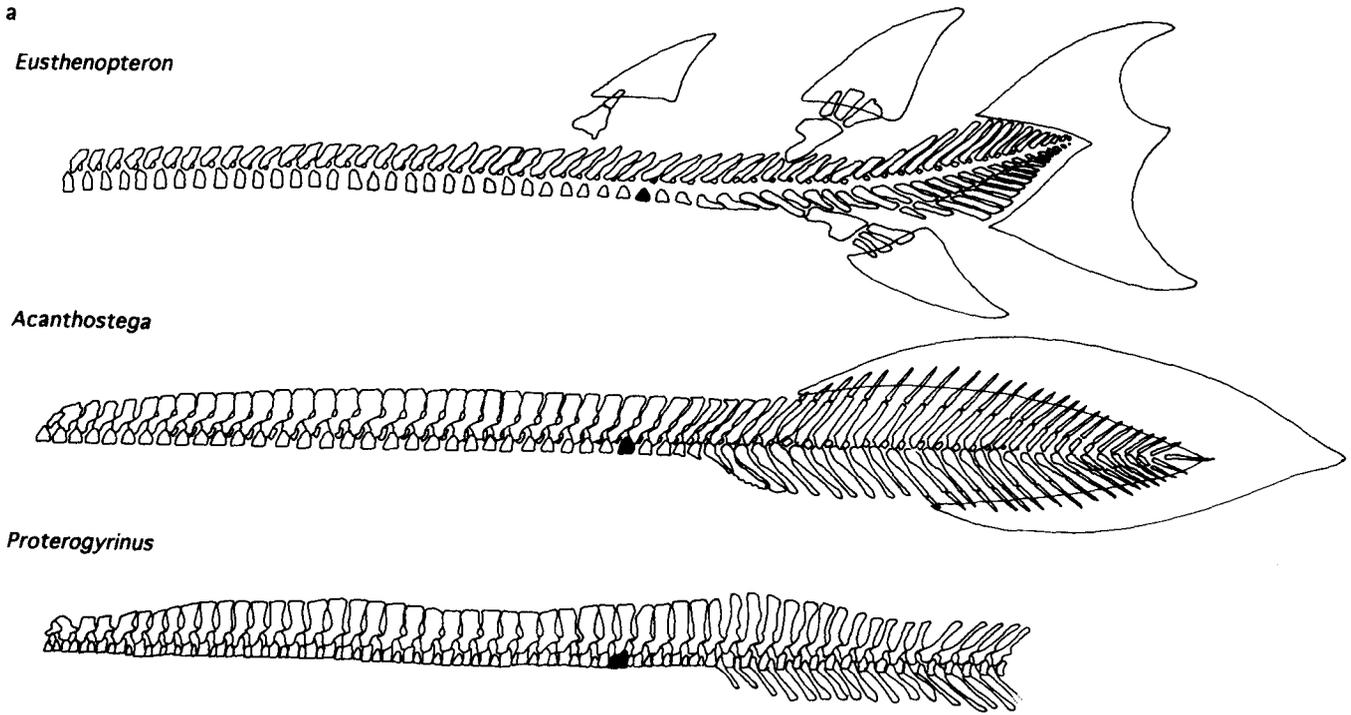


Figure 32 (a) Axial skeletons (minus ribs) of *Eusthenopteron* (after Andrews & Westoll 1970a), *Acanthostega*, and *Proterogyrinus* (adapted from Holmes 1984). Black centra indicate sacral segment. (b) Diagrammatic representations of stem and basal crown-tetrapod axial skeletons, illustrating the caudal displacement of fish-like morphologies. Rectangles represent vertebral segments; bold outlines in presacral region. ↓, relative position of pectoral girdle; ↓ position of pelvic girdle; +, continuation of vertebral series and or incomplete data; ▷, terminus of vertebrae; horizontal line, expression of fish-like character; dotted line, incomplete or transitional character expression; bold dotted line, tetrapod character; N, posteriorly inclined neural (and haemal) arches; Z, absence of zygophyses; L, lepidotrichial outgrowth; H, haemal radials.

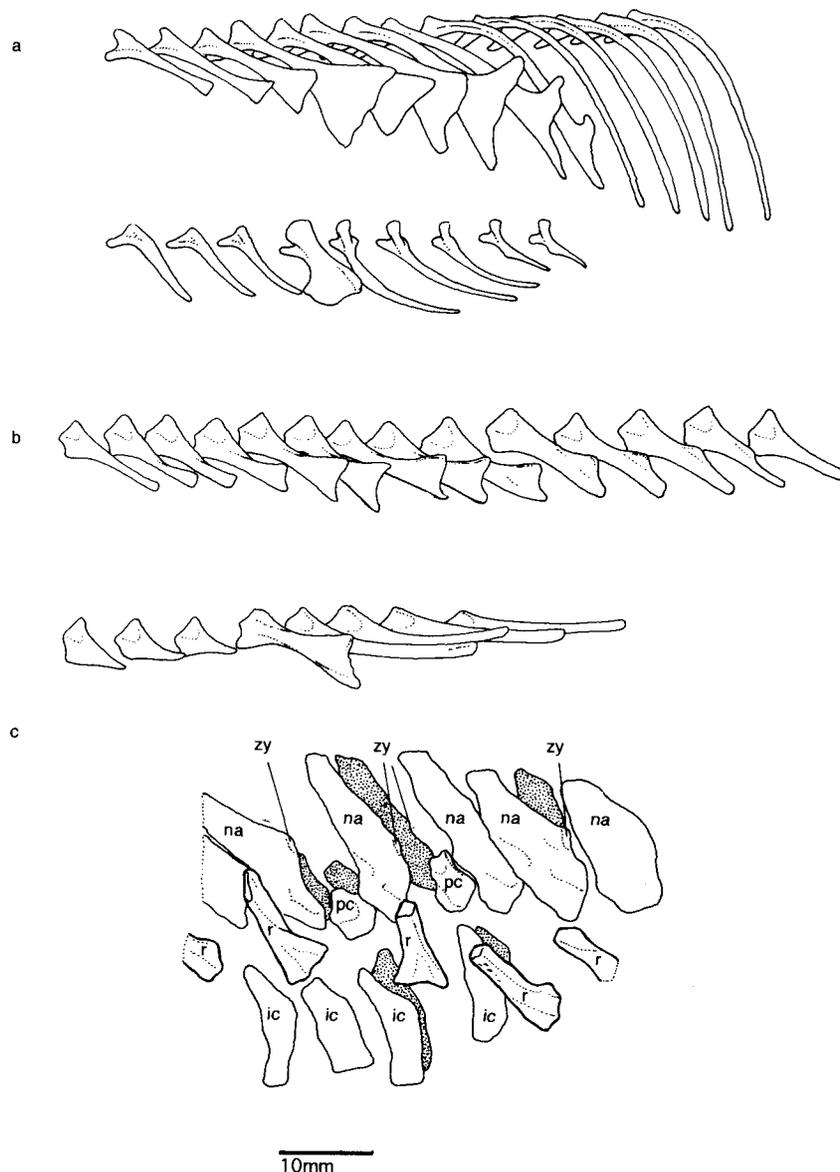


Figure 33 Rib morphologies: (a) cervical and thoracic ribs 1–14, and pre- to postsacral ribs 24–32 from the seymouriamorph stem-amniote *Kotlassia* (after Bystrov in Romer 1956, fig. 137); (b) *Acanthostega*, cervical and thoracic ribs 1–14, and pre- to postsacral ribs 28–35. Anterior to left of figures. (c) *Eusthenopteron foordi*, CMNH 8160, showing anterior vertebrae and ribs of segments 3–8; anterior to right of figure; interior surfaces of antimeric structures stippled.

It appears increasingly likely that such fundamental changes in vertebrate skeletal morphology are causally linked to the shifting expression boundaries of *Hox* genes (Burke *et al.* 1994, 1995; Gaunt 1994; Sordino *et al.* 1995). All four *Hox* clusters, *A*, *B*, *C*, and *D* (known primarily from amniote-centred experimental research) were probably present in the last common ancestor of living osteichthyans (Pendleton *et al.* 1993; Ruddle *et al.* 1994), where they would have been expressed colinearly in a craniocaudal progression. Systematic comparison of homologous *Hox* expression domains in a variety of taxa should therefore provide useful insights into the evolution of vertebral regionalisation. Already, a consistent association has been identified between the anterior expression boundary of *Hoxc-6* and the transposed (Goodrich 1906) cervical–thoracic vertebral transition in mice, chicks and *Xenopus* (Gaunt 1994; Burke *et al.* 1995). This strongly suggests that the association between *Hoxc-6* and the cervical–thoracic transition is conserved from an early stage in tetrapod evolution. However, recognition that *Hoxc-6* also marks the emergence of the brachial plexus in the non-regionalised anterior axial skeleton of the teleost actinopterygian *Danio*

erio (Molven *et al.* 1990) demonstrates that such expression boundaries are not necessarily linked to, or manifest as, skeletal differentiation (Burke *et al.* 1995). The condition in *Danio* may be primitive relative to tetrapods, but it remains untested by outgroup comparison. Absence of a clear cervical–thoracic vertebral boundary therefore indicates that *Acanthostega* may precede the establishment of *Hoxc-6* regulated skeletal axial differentiation (if indeed they are causally linked), and that morphologies like this illustrate a more primitively generalised (perhaps *Danio*-like) condition. However, lack of osteological clues concerning the emergence of the brachial nerves (except for the relative position of the pectoral girdle) prevents the formulation of any clearer inferences about the early polarity of *Hoxc-6* expression boundary changes.

Other associations noted by Burke *et al.* between axial expression boundaries and anatomical landmarks in chicks and mice include all four *Hox-10* paralogues with the sacrum, *Hoxd-9* with the end of the lumbar vertebrae, and the remaining *Hox-9* paralogues with the thoracic–lumbar transition. These indicate a suite of ancestral expression patterns

conserved from early amniotes, and provided clues about axial expression domains at even earlier nodes in tetrapod phylogeny (as implied by the presence of rudimentary sacrum in *Acanthostega*, and perhaps an incipient sacrum in *Eusthenopteron*: Andrews & Westoll 1970a). The operational evolution of these genes may be inferred, therefore, from sequences of morphological change such as the caudally directed tetrapod repatterning of a fish-like plesiomorphic axial skeleton (Fig. 32). Moreover, it is fairly likely that as products of cluster duplication, all members of a paralogous *Hox* group primitively shared the same anterior expression boundary (Ruddle *et al.* 1994; Burke *et al.* 1995), and subsequent boundary differentiation facilitated morphological diversification. The data presented in Figure 32 suggest, therefore, that the differential expression of development-regulating genes in the evolution of tetrapod axial skeletons evolved in a gradual, anteroposteriorly directed sequence. However, none of the morphological characteristics mapped in Figure 32 has been linked, as yet, to the expression zones of any *Hox* (or closely related) gene. Tests of this speculative inference will have to await further results from *Danio rerio* or other, more phylogenetically informative outgroups of tetrapods (such as dipnoans, cladistians or chondrosteans, and chondrichthyans).

The caudal fin skeletons of advanced stem-tetrapods and recent lungfish share several features. In particular, the combination of unbranched and unsegmented caudal lepidotrichia with finless paired appendages in *Acanthostega* parallels closely the pattern of campotrichial development in *Lepidosiren* (Goodrich 1904; discussed further in Coates 1994b). The axial endoskeleton of *Acanthostega* (or *Ichthyostega*), however, is more heavily ossified than in recent dipnoans, and resembles more closely the condition in *Eusthenopteron*. As yet it is unclear whether the peculiar and somewhat more consolidated vertebrae of *Panderichthys* and *Elpistostege* (Vorobyeva & Schultze 1991; Schultze & Arsenault 1985) are apomorphic for panderichthyids, or represent a transitional tetrapod stem condition. While lungfish have long been used as analogues for early tetrapod structure and function, in several respects the aberrant actinopterygian *Polypterus* provides an equally informative alternative. *Polypterus* also has a leaf-shaped caudal fin, well ossified vertebrae and ribs, and a partially modified cervical region allowing limited head movement (plus paddle-like pectoral appendages specialised for slow propulsion). Bartsch and Gemballa's (1992) description of polypterid caudal ontogeny illustrates clearly how such a tail pattern can be remodelled from a primarily heterocercal arrangement. This includes the secondary generation of dorsal radials, a feature which clearly evolved convergently in several osteichthyan lineages, including stem-tetrapods, dipnoans, and cladistian actinopterygians. Paradoxically, such dorsal radials, normally thought of as a decidedly piscine characteristic, are within the context of this discussion a derived feature of advanced stem-tetrapods. Such radials must have originated after *Eusthenopteron* and perhaps before the panderichthyids, whose tails appear to resemble those of *Acanthostega* and *Ichthyostega*. *Polypterus* also lacks a supraneural ligament, and thus exhibits a characteristic which (as indicated by supraneural canal closure) is usually associated with change of vertebral function. In early tetrapods this may be associated with some increased degree of terrestriality; hence the importance which may be attached to the phylogenetically early canal loss in *Elginerpeton* (Ahlberg *in press*). However, while this ligament contributes to vertebral elastic recoil during swimming (Symmons 1979), loss may also be associated with exclusively aquatic specialisations. For example, Bartsch and Gemballa attribute ligament absence in *Polypterus* to the demands of increased flexibility

required for movement within a restricted aquatic environment, which is consistent with the mode of life suggested for *Acanthostega* in section 5.1.

The most phylogenetically informative characteristics of the ribs in *Acanthostega* are probably the distally flared or flanged shafts (Figs 10 & 33). These flanges are ubiquitous among anterior thoracic and posterior cervical ribs of basal crown-tetrapods. Examples are known in taxa such as *Crassigyrinus*, *Balanerpeton*, adelospondyls (Andrews & Carroll 1991), microsaur (Carroll & Gaskill 1978), *Greererpeton* (Godfrey 1989) and *Proterogyrinus* (Holmes 1984). Variation in flange development is considerable, but the clearest phylogenetic signal emerges from the patterns of flange reduction within individual rib series. In stem-tetrapods (cf. *Acanthostega*), stem-amphibians (cf. *Greererpeton*) and perhaps basal stem-amniotes, reduction occurs gradually, resembling the gradual vertebral transitions discussed earlier. Alternatively, in slightly more derived stem-amniotes and microsaur (character 34; Nodes K & O) flange reduction is abrupt and usually occurs close to the rear of the pectoral girdle. Within the present phylogenetic scheme this similarity (at Nodes K & O) is considered convergent (it would be interesting to know how this abrupt rib transformation relates to the rib regionalisation present in more recent amniotes). In fact, a third example of transformed rib morphology may occur at an altogether deeper node in tetrapod phylogeny: in *Eusthenopteron*. Andrews and Westoll (1970a text-figs 19 & 23) illustrate an apparently consistent variation between the most anterior three pairs of short and broad ribs (segments 6–8), just posterior to the pectoral girdle, and the distinctly narrower ribs of the remaining, more caudal, series. Personal observation of a previously undescribed specimen (CMNH 8160; Fig. 33c) corroborates this description. Such anterior ribs are weakly bicapital, with short, broad shafts, and are significantly more substantial than those described and illustrated in Jarvik (1980). It seems possible that these rib morphologies may represent the rudimentary early expression of axial regionalisation as recognised in crown-tetrapods, and would therefore corroborate the general observation that tetrapod axial characteristics are manifest earliest in the anterior parts of fish-like skeletons.

The relation between distally expanded ribs and those with uncinat processes has become unclear. Milner and Sequeira (1994), while describing expanded ribs in the temnospondyl *Balanerpeton*, implied that these two morphologies were nonhomologous by concluding that 'uncinate processes are never present'. Similarly, Lombard and Bolt (1995), while describing the stem-amniote *Whatcheeria*, draw a distinction between uncinat processes and distal flanges. However, Romer (1956) described uncinat processes as simply posterior projections which are present on the posterior cervical and anterior thoracic ribs, providing attachment for axial muscles including those inserting on the scapula. The seymouriamorph *Kotlassia*, used to illustrate Romer's description (Fig. 33a), shows a sequence of distally expanded ribs which represent only a moderately exaggerated version of those found in earlier stem-amniotes. This suggests that there is no fundamental difference between distally expanded ribs and those which are uncinat. This provides a simpler interpretation than Milner and Sequeira's, because no *ad hoc* hypothesis is required for additional originations of uncinat-like morphologies. Furthermore, the distribution of such minor uncinat processes is consistent with the suggested functional role of anchoring the pectoral girdle to the axial musculature (Romer 1956). And thirdly, the relation between sacral and (clearly) uncinat anterior thoracic ribs in *Eryops* as recognised by Olsen (1936), is consistent with the even closer resemblance between sacral and anterior thoracic ribs in *Acanthostega*

(Fig. 33). Uncinate processes are therefore concluded to be a derived stem-tetrapod character, emerging between nodes A and D of the cladogram (Fig. 27). Uncinate processes subsequently diversified independently into the more extreme examples displayed by taxa such as *Ichthyostega*, *Eryops* and *Whatcheeria*. Sacral rib evolution was probably linked intimately to the emergence of uncination. The earliest examples appear to have been abrupt re-expressions of anterior thoracic or posterior cervical rib morphologies, and both served a similar role of supplying anchorage for soft tissue attachment between girdle and axial skeleton. Subsequent sacral rib evolution consists mostly of shaft reduction and consolidation, with the butt-joint probably characteristic of stem-amniotes (e.g. *Archeria*, Holmes 1989). The presence of this more derived pattern of sacro-iliac attachment in *Ichthyostega* is disputed, because there is no convincing example of a distinct iliac sacral facet as restored in Jarvik's description (1980, 1996; personal observation).

5.2.2. Girdles. The origin of limbed tetrapods is associated with substantial transformations affecting pectoral and pelvic girdles. Massive endochondral expansion affects both, while pectoral evolution is accompanied by loss of dermal elements and pelvic evolution is characterised by origination of an ischium and sacral attachment to the axial skeleton. Pectoral endochondral expansion appears to have been initiated before the diversification of panderichthyids (Node A, Fig. 27), in which the scapulocoracoids already possess supraglenoid and infraglenoid buttresses, plus broad coracoid plates. However, it is unclear, from both original material (personal observation: PIN 3547/19) and conflicting reconstructions (Vorobyeva & Schultze 1991; Vorobyeva 1992) whether the plesiomorphic, spatially restricted tripod areas of scapulocoracoid-dermal attachment, as present in *Eusthenopteron* (Jarvik 1980) are reduced in *Panderichthys* to two, or to a single plate as in more advanced tetrapods. The narrow groove separating early scapular growth from the ventromesial lip of the postbranchial lamina in *Acanthostega* (Fig. 12) is already apparent in *Panderichthys*, and persists at least as far as Node G (Fig. 27). This groove indicates incomplete fusion during ontogeny, and probably represents an early stage in the general phylogenetic trend of cleithral separation from the scapulocoracoid. The fates of the major pectoral foramina present in a fish-like girdle such as that of *Eusthenopteron* are uncertain. The incomplete rear of the panderichthyid pectoral girdle preserves only a broad supracoracoid canal of fish-like proportions. This passes anterodorsally into the area inferred to become the subscapular fossa in more derived tetrapods, while the condition of the supraglenoid canal in *Panderichthys* is somewhat conjectural (restored in Vorobyeva & Schultze 1991, figs 17 & 18, but absent in Vorobyeva 1992, fig. 60A).

The shoulder fragment attributed to *Elginerpeton* (Ahlberg in press) is the most recognisably limbed-tetrapod-like piece of the Scat Craig postcranial assemblage. This is the earliest example yet of a thickly ossified, triradiate confluence between an incipient scapular blade, postcleithral buttress and supraglenoid buttress. The most advanced feature of this specimen is the subscapular fossa perforated apically by several small foraminae, and this may constitute a supplementary transitional stem-character for Node B. In these respects *Acanthostega* and *Hynerpeton* resemble *Elginerpeton* quite closely. However, the persistent, visible suture between the scapular apex and cleithrum indicates weaker development of an incipient blade in *Elginerpeton*; thereby corroborating the systematic analysis which places it at a (considerably) lower node on the phylogenetic tree.

Acanthostega is the most primitive tetrapod with a pectoral girdle detached from the skull (character 29), and this clearly precedes loss of a fish-like cleithrum (character 43) and

detachment from the scapulocoracoid (character 45). However details of other major pectoral transformations remain unknown: the broad supraglenoid and supracoracoid canals of fin-supporting girdles are already substituted by several small foraminae (assuming that the foraminae and canals are in some sense equivalent), and the glenoid fossa already resembles those of more derived tetrapods. *Ichthyostega* (Node E) adds little to the emerging picture of pectoral evolution. Here, the extent of the postbranchial lamina is greatly reduced and less than that suggested by the reconstructions in Jarvik (1980, 1996). The scapulocoracoid has an unusually broad infraglenoid buttress for an early limbed tetrapod (such a buttress appears to be absent in *Acanthostega*), and the supraglenoid plus supracoracoid canals are significantly smaller and less *Eusthenopteron*-like than those in published reconstructions (Jarvik 1980, fig. 165; personal observation and work in progress on MGUH f.n. 1396; canal proportions reduced in Jarvik 1996, fig. 42). The apparently apomorphic supraglenoid process is probably a taphonomic artefact. The most simply interpreted character at this node is therefore absence of an anocleithrum (i.e. further dermoskeletal reduction). Anocleithra, however, reappear at least twice, and on both occasions in stem-amniotes: *Tulerpeton* and *Pholiderpeton* (hence the positive score for *Proterogyrinus* in the data matrix; see discussion in Lebedev & Coates 1995). *Hynerpeton* (Node F), at the apex of the tetrapod stem, has more or less lost the postbranchial lamina altogether, suggesting that this less fish-like interpretation of *Ichthyostega* may be correct. Postbranchial lamina loss therefore appears to have occurred before scapulocleithral separation (character 45) and the crown-tetrapod radiation (Node G).

Unfortunately, this apparently tidy sequence of pectoral girdle evolution is not sustained within the tetrapod crown-group. Although the single pectoral specimen of the first stem-amniote plesion, *Tulerpeton*, exhibits scapulocleithral separation and absence of any postbranchial lamina (Lebedev & Coates 1995), the second plesion, *Whatcheeria*, displays only occasional scapulocleithral separation and Lombard and Bolt (1995) consider a postbranchial lamina to be present. However, *Whatcheeria* has a less well developed lamina-like flange than *Hynerpeton* (Daeschler *et al.* 1994), in which this structure is considered absent. Moreover, in contrast to *Tulerpeton*, the several specimens of *Whatcheeria* display a range of conditions, from complete separation of the cleithrum, scapula and coracoid, to fusion of the cleithrum to a sutureless scapulocoracoid. The scapular blade is well developed in both of these taxa, and it is important to note that characters 40 (a ventromesially extended infraglenoid buttress) and 53 (large, laterally directed supraglenoid foramen lateral to the triangular area) are scored as present in *Whatcheeria* (personal observation: specimens FM PR 1766 and FM PR 1706 respectively).

Alternatively, in the basal stem-amphibian *Greererpeton*, a postbranchial lamina is always associated with a cleithrum detached from a short bladed, unsutured scapulocoracoid (Lebedev & Coates 1995). The pattern of pectoral girdle evolution is more complicated, therefore, than that suggested by Lebedev & Coates (1995). Fusion between pectoral dermal and endoskeletal bones appears to have been sustained within basal crown-group tetrapods. Such fusion probably persisted longer in amniote than in amphibian stem lineages, whereas scapular blade development is an earlier feature of stem-amniotes relative to stem-amphibians. Postbranchial laminae are probably not a persistently primitive characteristic of any crown-tetrapods. Instead, the presence of these laminae in certain stem-amphibians may represent a character reversal (possibly a paedomorphic condition: A. R. Milner, personal communication). These conclusions are not, however, inconsistent with those of Brainerd *et al.* (1993) or Lebedev and

Coates' scenario of airbreathing evolution. Amniotes still appear to have placed greater and phylogenetically earlier emphasis upon airbreathing, while gills retained a more significant role in early amphibians (although there is increasing evidence of external gill breathing in juvenile stem-amniotes: Klembara 1995).

Different patterns of parasphenoidal posterior expansion (characters 51 & 64) in the amphibian and amniote basal lineages may be related to these (hypothesised) alternative routes towards air breathing. Back-growth of the parasphenoid probably serves primarily to reinforce the basisphenoidal-basioccipital junction, as in early actinopterygians (Patterson 1975). However, as a novel feature relative to crown-tetrapods, the elaboration of this region is taxonomically distinctive to each of the phylogenetic rami. In early stem-amniotes the posterior portion of the parasphenoid tends to be slightly arched or concave relative to the buccal cavity, with prominent ventrolateral margins and a concave posterior edge (cf. *Crassigyrinus*, Panchen 1985; *Eoherpeton*, Smithson 1985; *Proterogyrinus*, Holmes 1984; *Westlothiana*, Smithson *et al.* 1994; and note *Baphetes*, Beaumont 1977) (Fig. 30). Early stem-amphibians display a quite different morphology, consisting of a flat plate with a central denticulated area, and usually a straight or convex posterior margin. Examples include *Balanerpeton* (Milner & Sequeira 1994), *Doleserpeton* (Bolt 1977), and to a lesser extent *Greererpeton* (Smithson 1982). Adelospondyls display similarly plate-like conditions (Andrews & Carroll 1991), as do microsaurians (Carroll & Gaskill 1978). It seems possible that the central denticle field records a persistent pharyngeal bite within early amphibians, which was opposed by tooth-plates supported on the ventromedial, basibranchial components of a persistent cartilaginous gill skeleton (cf. numerous living actinopterygians). In support of this hypothesis, it is worth noting that Hook (1983) reports the presence of numerous small toothplates, resembling those which are usually associated with branchial skeletons, scattered in the throat region of *Colosteus scutellus*, a close relative of *Greererpeton*.

The pelvis of *Acanthostega* already displays most features associated with crown-group tetrapods: large size; extensive ossification; rudimentary sacrum; and puboischiadic symphysis (although this is fibrous and/or ligamentous). Most changes associated with the fish-tetrapod transition (sacral origination; ischial origination; puboischiadic plate enlargement; closely united symphyseal margins) therefore occurred prior to the divergence of *Acanthostega* from the main tetrapod stem. In the absence of pelvic data from *Panderichthys*, plesiomorphic comparison is limited mostly to Andrews and Westoll's (1970a; as favoured here) versus Jarvik's (1980) conflicting interpretations of the pelvis in *Eusthenopteron*. These alternatives are opposed by 180°, so that the ilium as recognised by Andrews and Westoll, is identified by Jarvik as an ischium. The prominent postacetabular buttress and sutureless condition are the most strikingly *Eusthenopteron*-like feature of the acanthostegid pelvis (Fig. 34). The development of a broad ischium (as discussed in Panchen & Smithson 1990; Lebedev & Coates 1995) may be the most significant advanced pelvic novelty of *Acanthostega*. Otherwise, the clearest morphological peculiarity of the pelvis in *Acanthostega* which is shared with other primitive limbed tetrapods is the continuity of the acetabulum with the anterior pubic edge. *Whatcheria* and most specimens of *Ichthyostega* share this feature, but apart from representing a transitional stem-crown tetrapod condition, the significance of this acetabular pattern remains obscure. So far, the only non-*Acanthostega* clues about early limb-bearing pelvis concern elaboration of the ilium. *Elginerpeton* (Ahlberg in press) (Node B) already seems to

have had an immensely robust iliac neck which may have been biramous and perforated with a small neck canal, cf. *Ichthyostega* (Fig. 34c), whereas *Ventastega* (Node C) may have had an ilium with a blade-like portion closely resembling that of *Acanthostega* (Ahlberg *et al.* 1994).

Pelvic evolution crownwards of *Acanthostega* is clearer than in previous phylogenies. The association of biramous ilia with the earliest sacral pelvis indicates that basal amphibian uniramous ilia such as those of *Greererpeton* (Godfrey 1989) (Fig. 34d) are derived (character 14, Node M, with various reversals). Supra-acetabular buttresses are more prominent than postacetabular buttresses in *Ichthyostega* plus all more recent tetrapods (character 42, Node E), and pelvic sutures become an established feature prior to Node G, the crown-group radiation (consistent with occasional presence of an identifiably separate pubis in *Ichthyostega*: Jarvik 1996). Smithson *et al.* (1994) have already commented that the considerable length of the puboischiadic plate in *Acanthostega* (encompassing around six vertebrae) is (also) probably primitive relative to crown tetrapods. When combined with the prominent postacetabular buttress and the posteriorly sited iliac neck, all of these characteristics appear to be related to the possession of a paddle-like hindlimb with a posteriorly directed power-stroke. Other pelvic transformations include the coalescence of small foramina into a single large obturator foramen, resembling a similar trend in pectoral evolution. Although occurring in certain *Ichthyostega* specimens, this seems to have stabilised independently in amniote and amphibian stem-lineages; only the largest and anteriormost pubic foramen in *Proterogyrinus* (Fig. 34f) is considered to be homologous with the unambiguously single obturator foramina of *Archeria* (Holmes 1984; Romer 1957) and *Westlothiana* (Smithson *et al.* 1994). Similarly, anterior iliac processes are reduced independently in both primary crown-tetrapod lineages. In small stem-amniotes this may result in a uniramous morphology which is superficially indistinguishable from that of certain stem-amphibians (e.g. *Westlothiana*, Smithson *et al.* 1994). In others, however, anterior iliac processes are reduced to a distinctively narrow crested morphology (cf. *Caerorhachis*, Holmes & Carroll 1977, or *Proterogyrinus*, Holmes 1984) (Fig. 34e), although this is clearly absent in some taxa omitted from the analysis (e.g. *Eoherpeton*, Smithson 1985). Romer's transverse pelvic ridge is also modified in basal stem-amniotes, as exemplified in the embolomeres *Proterogyrinus* and *Archeria* (character 69, Node L). The significance of these changes and how they reflect modified muscular insertions in and around the pelvic girdle are uncertain.

5.2.3. Limbs. Tetrapod limbs can be characterised as vertebrate paired appendages in which an anteriorly directed digital arch with free (i.e. ray-less) segmented postaxial radials is associated with a laterally and proximodistally articulated carpus or tarsus. This unwieldy and probably insufficient definition consists of a list of 'key' limb characteristics, all of which emerged at phylogenetic loci which were neither coincident with the tetrapod crown-group radiation or the cladogenic split from dipnoan ancestry. From the current and previous analyses of tetrapod limb evolution (Coates 1991; Lebedev & Coates 1995) it is quite clear that most limb (versus fin) characteristics, bar the stabilisation of pentadactyly, accumulated throughout the duration of the stem-group. Many of the broader aspects of the fin-limb transition, especially those concerning the evolution of limb development, are discussed in greater detail elsewhere (suggested references include: Shubin & Alberch 1986; Tabin 1992; Coates 1994b, 1995; Morgan & Tabin 1994; Shubin 1995, and Sordino *et al.* 1995). In summary, these fall into the three following subject areas: (a) the transformation of embryonic fin-bud apical

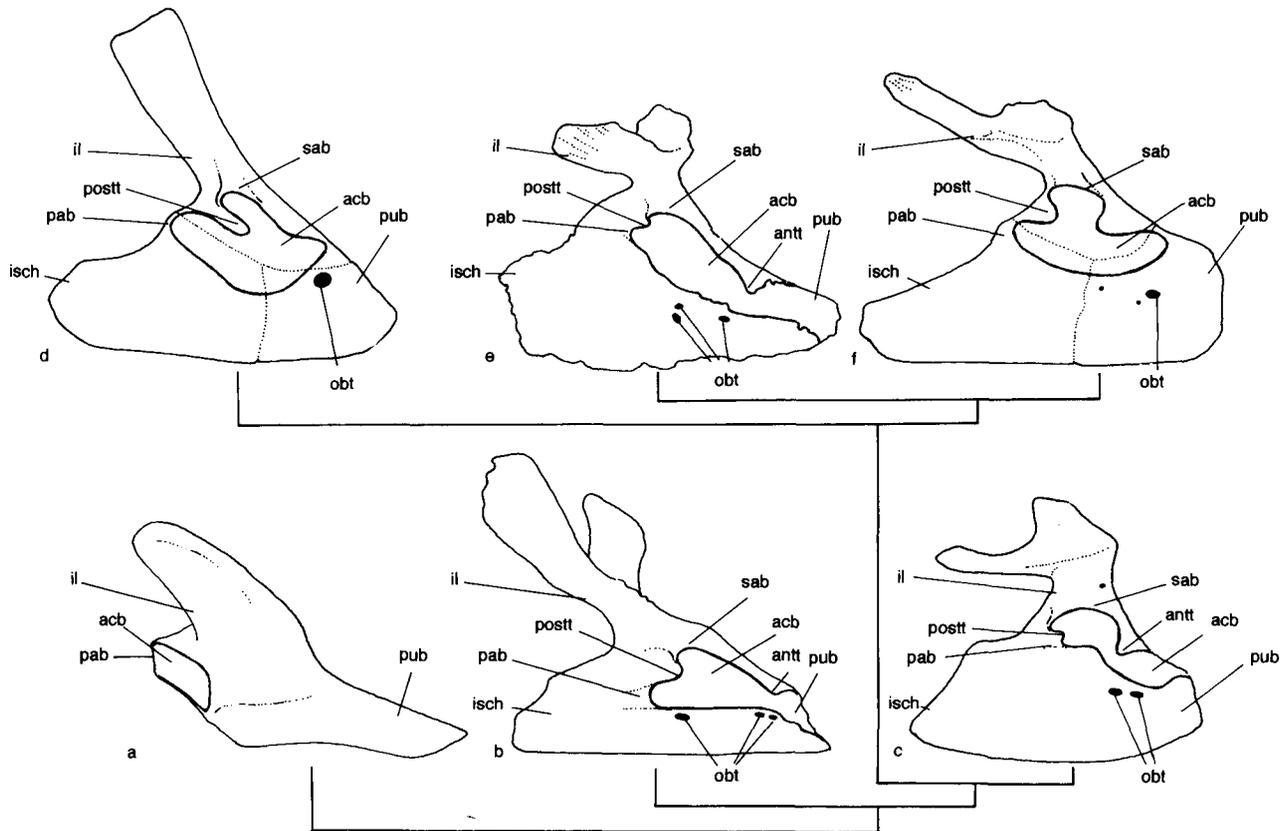


Figure 34 Line drawings of pelves, all right side, lateral views. Dendrogram illustrating relationships derived from phylogenetic tree in Figure 27. Note retention within basal amniote ramus of multiple obturator foraminae and continuity between acetabulum and pubic rim. (a) *Eusthenopteron* (after Andrews & Westoll 1970a, fig. 14a); (b) *Acanthostega*; (c) *Ichthyostega* (after Jarvik 1980, fig. 162A); (d) *Greererpeton* (after Godfrey 1989, fig. 22a); (e) *Whatcheeria* (after Lombard & Bolt 1995, fig. 8; specimen somewhat crushed laterally) (f) *Proterogyrinus* (after Holmes 1984, fig. 30a).

ectodermal folds into limb-bud apical ectodermal ridges (associated with dermal ray loss and changed regulation of bud out-growth); (b) distal mesenchymal proliferation (associated maintenance of bud outgrowth, and extension of, or outgrowth beyond, an evolutionarily conserved metapterygial axis); and (c) a change from monophasic to polyphasic regulatory gene expression in the fin or limb bud, altered distal tissue response to developmental signalling networks (associated with the formation of a digital arch), and the relation between gene expression boundaries and limb morphology. Some of these developmental transformations may be informed by phylogenetic patterns of morphological change.

The lower part of the tetrapod stem (Fig. 27) shows that by Node A, flat, anteriorly keeled humeri (character 3) were associated with enlarged scapulocoracoids (character 5). A similar correlation occurs at Node D, where the earliest femur with a well developed adductor blade plus fourth trochanter (character 32) accompanies the first record of an ischiadic plate (character 24). Thus primary remodelling of proximal limb bones is linked closely (and predictably) to major changes in girdle structure. The extensively restored femur and *Ichthyostega*-like iliac fragments attributed to *Elginerpeton* (Ahlberg in press) are quite consistent with this hypothesis. Similarly, the flattened humerus of *Elginerpeton*, although superficially like those of *Panderichthys* (Vorobyeva 1992) and rhizodonts (Andrews & Westoll 1970b; Long 1989) may have an *Ichthyostega*-like ventral radial facet (revised relative to Ahlberg's 1991 interpretation), and is likewise associated with an enlarged scapulocoracoid (Ahlberg in press). However, certain features of this humerus may be apomorphic relative to other primitive limb humeri, including the immense,

subtriangular entepicondyle; the prominent pectoral crest; the linear insertion of the ectepicondyle (with no apparent evidence for a separate latissimus dorsi insertion); and the absence of any ventral ridge or crest.

Acanthostega provides the most complete evidence of primitively digitated limbs and girdles. Unlike the tantalising fragments from taxa at nodes B, C, and P, these are unambiguously paddle-like appendages which retain several fin-like features such as polydactyly, multiple humeral canals (discussed in Lebedev & Coates 1995), epipodial proportions, and humeral epipodial facets situated in an unusually anterior position. In *Acanthostega* these facets appear to represent a midpoint in the phylogenetic posteriorisation of epipodial articulations, culminating in early crown-tetrapods where the ectepicondylar ridge projects above the radial facet (e.g. *Archeria*, Romer 1957) (Fig. 35). Within this framework the flattened humeri of *Panderichthys*, *Elginerpeton*, *Acanthostega*, and *Ichthyostega* clearly resemble those of basal crown-group taxa such as *Tulerpeton* or *Greererpeton*. But perhaps the most striking transformation affecting the proximal bones of all early limbs concerns the sustained proximalisation of major points of muscle insertion. This process is inseparable from the early development of humeral and femoral shafts. In *Acanthostega* the latissimus dorsi process is situated anterodistally relative to the proximal end of the ectepicondyle (Figs 16 & 35) to which it remains connected by a long low ridge. In taxa such as *Eusthenopteron* these processes are situated at either end of the same elongate tuberosity (see Andrews & Westoll 1970a and Jarvik 1980 for conflicting interpretations). Subsequently, in taxa ascending both principal crown-group rami, the latissimus dorsi process diminishes and migrates

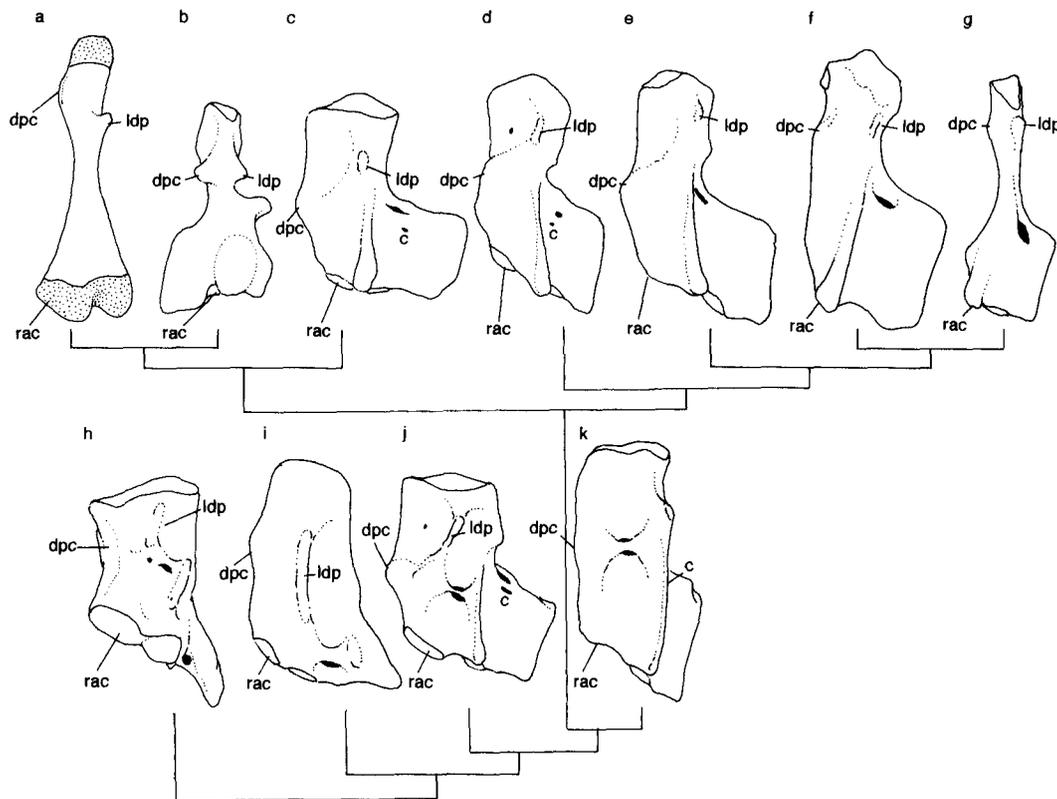


Figure 35 Basal crown-tetrapod and stem-tetrapod humeri (all drawn from left side; all viewed from dorsal surface except (b): shown in anterior/ventral view) showing changing patterns of major muscle insertion points. Dendrogram illustrating relationships derived from phylogenetic tree in Figure 27. (a) *Salamandra* (Francis 1934); (b) *Eryops* (adapted from Andrews & Westoll 1970a); (c) *Greererpeton* (Godfrey 1989); (d) *Tulerpeton* (Lebedev & Coates 1995); (e) *Eoherpeton* (Smithson 1985); (f) *Archeria* (Romer 1957); (g) *Westlothiana* (Smithson *et al.* 1994); (h) *Eusthenopteron* (Andrews & Westoll 1970a); (i) *Panderichthys* (Vorobyeva 1992); (j) *Acanthostega*; (k) *Ichthyostega* (personal observation; Jarvik 1980, 1996).

proximally until it lies close to the posterodorsal rim of the humeral head, in-line with the ectepicondyle (Fig. 35). Likewise, the pectoral crest migrates proximally along the ventral surface until it lies close to the anteroventral rim of the humeral head. Early femora display remarkably similar patterns of shifting muscle insertions, which in this case are indicated mostly by transformations affecting the adductor blade (Fig. 36). The extensive subrectangular blade is reduced distally, the acute adductor crest elongates as the fourth trochanter becomes more compact, and the internal trochanter is transformed into a prominent boss projecting close to the femoral head. Within the stem-amniotes the fourth trochanter either migrates around the internal trochanter until it extends onto the anterior face (as in *Archeria* and *Proterogyrus*) or remains located slightly more distally (*Westlothiana* and more advanced taxa). Alternatively, in stem-amphibians the fourth trochanter becomes increasingly difficult to identify, thus paralleling an apparently apomorphic characteristic of *Westlothiana*. However, as noted by Smithson *et al.* (1994), such similarities may be related to smaller size rather than taxonomic affinities.

Like the humerus and femur, the epipodials of *Acanthostega* also display unusual mixtures of primitive and derived characteristics. Pre-axial radial homologues (radius and tibia) which are significantly longer than their axial relatives (ulna and fibula), are almost certainly primitive relative to more advanced tetrapods (cf. *Eusthenopteron*, Andrews & Westoll 1970a; *Barameda*, Long 1989), whereas articulation with a carpus or tarsus (character 25) is clearly derived. Similarly, the fibula has no twist along the proximodistal axis indicating in-turning of the foot, suggesting that fibular torsion may be a crown-tetrapod synapomorphy (including *Tulerpeton*,

Lebedev & Coates 1995). Such remodelling surely relates functionally to a greater degree of terrestriality. Absence of clearly defined fibular and ulnar shafts, as also found in *Ichthyostega*, appears to be a further crown-tetrapod characteristic; broad, flat hindlimb epipodials (which may recur in *Whatcheeria*: Lombard & Bolt 1995) represent a transitory condition which mostly preceded the crown tetrapod radiation. There remains little doubt that such limb bone morphologies functioned as flippers or paddles in life. Although these broad epipodials articulate with extensively bladed femora (character 32) of the kind previously assumed to represent a terrestrial adaptation (Carroll *et al.* 1972), extant analogues suggest that if such blades provide broad distal muscle insertions, then these are likely to be aquatic specialisations for more effective power stroke generation (Ashley-Ross 1992; further discussion in Lebedev & Coates 1995). Moreover, similarly flattened epipodials have evolved convergently in several aquatic extant tetrapod lineages. When combined with the extreme distal torsion along the femoral shaft and the location of the fibular facet directly above the tibial, the epipodial pair provide an effective paddle-blade held perpendicular to the craniocaudal axis (Figs 23, 31), and are thoroughly consistent with the aquatic functional interpretation of the pelvis.

The unossified condition of the *Acanthostega* carpus is shared with most other early limbed tetrapods. The only hint of wrist elaboration is provided by the ossified intermedium. However, this is subcylindrical with only proximal and distal surfaces exposing unfinished endochondral bone, and thereby resembles, disconcertingly, equivalent pre-axial radials in various non-tetrapod sarcopterygians (Shubin 1995). The intermedium has no articular facets indicating lateral interarticulation to complement proximodistal interarticulation be-

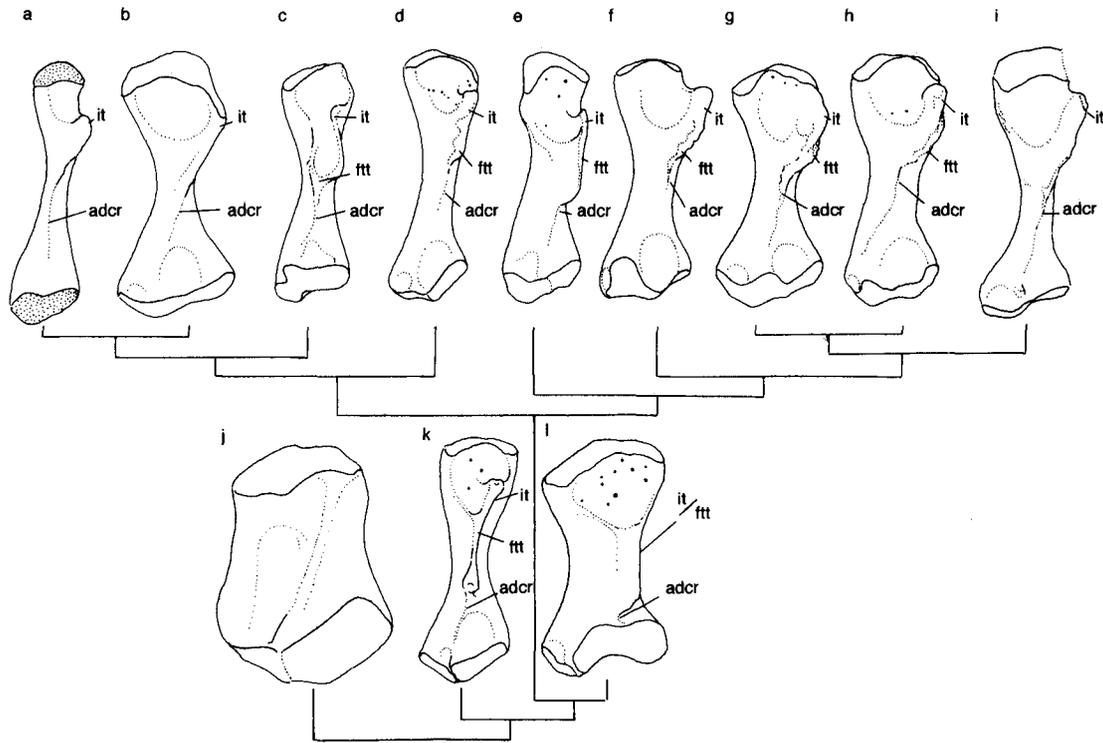


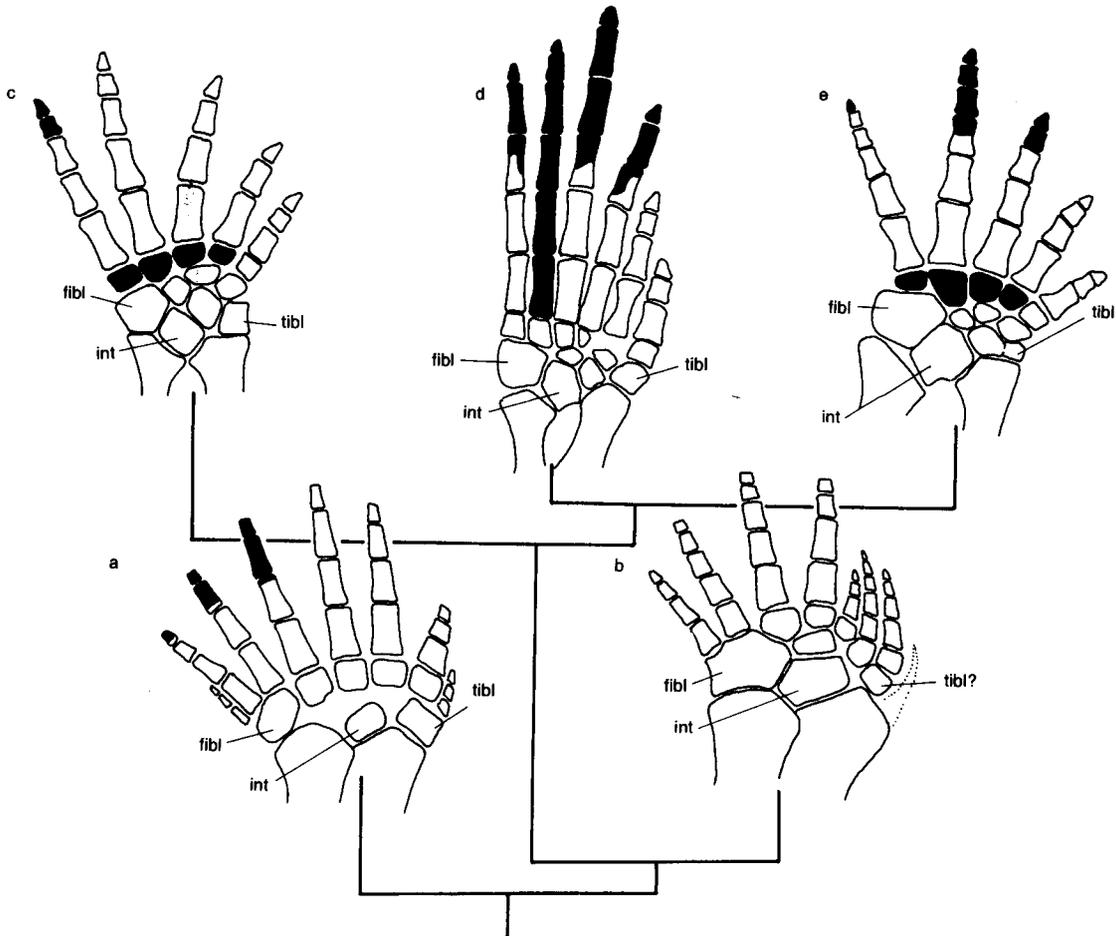
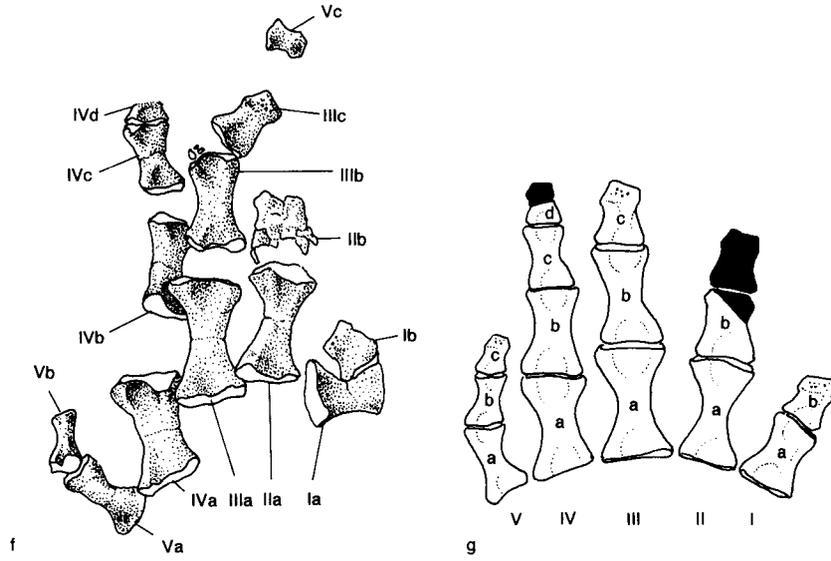
Figure 36 Basal crown-tetrapod and stem-tetrapod femora (all drawn as from left side; all viewed from ventral surface) showing changing patterns of major muscle insertion points. Dendrogram illustrating relationships derived from phylogenetic tree in Figure 27. (a) *Salamandra* (Francis 1934); (b) *Trachystegus* (a tuditanomorph microsauro, c.f. *Saxonerpeton*: Carroll & Gaskill 1978); (c) *Eryops* (adapted from Romer & Parsons 1977, and personal observation of cast in UMZC); (d) *Greererpeton* (Godfrey 1989); (e) *Tulerpeton* (Lebedev & Coates 1995); (f) *Crassigyrinus* (Panchen & Smithson 1990); (g) *Proterogyrinus* (Holmes 1984); (h) *Archeria* (Romer 1957); (i) *Westlothiana* (Smithson *et al.* 1994); (j) *Eusthenopteron* (Jarvik 1980); (k) *Acanthostega*; (l) *Ichthyostega* (Jarvik 1980; in 1996 redescription muscle insertions agree with this interpretation, but entire ventral blade is labelled as adductor crest).

tween proximal wrist bones, and suggests the presence of a significantly more plesiomorphic wrist joint than those known in any other tetrapod forelimbs. Note that the carpus of *Acanthostega* as illustrated in Carroll (1995, fig. 6c) is inaccurate, with wrist bones reconstructed mistakenly from an outline reconstruction of osteoderm distribution (see section 3.7; Fig. 26e,f). However, the tarsus of *Acanthostega* follows a more conventional trend of robust construction as found in more derived tetrapod hind limbs (Fig. 37). And like *Ichthyostega* (Jarvik 1980, 1996; Coates & Clack 1990), the tarsus is dominated by a huge fibulare. In *Acanthostega* this articulates directly with three digits, whereas in *Ichthyostega* the fibulare articulates with two, and connects with a third via a distal carpal. In *Tulerpeton*, although present, the large fibulare is occluded from the digits by a series of distal tarsals, providing the limb with an altogether more sophisticated and flexible ankle joint. This feature, when added to characters 44 (hinged wrist and knee; ankle rotary: Rackoff 1980) and 48 (2+ tarsal centralia: Lebedev & Coates 1995), plus the in-turned fibular shaft, presents a radically different kind of distal limb morphology from those present in its Devonian contemporaries. It is therefore apparent that phylogenetically, wrist and ankle elaboration lags behind the evolution of digits.

Such well articulated limbs as those of *Greererpeton* and *Tulerpeton* (even if hexadactylous) are far closer to the textbook conception of 'the primitive tetrapod limb', and correspond quite closely to the *Trematops*-like *Ichthyostega* hindlimb illustrated in Carroll (1988, fig. 9–10a). It is probably worth re-emphasising that this restoration is incorrect. It has subcylindrical instead of flattened epipodials, plus five new bones inserted into the tarsus (thus conflating wrist and ankle elaboration with the origin of digits), and is attributed to

Jarvik's 1952 description of 'The fish-like tail in ichthyostegid stegocephalians'. The same reconstruction also appears in Benton's (1990) *Vertebrate Palaeontology*, where it is attributed to Jarvik (1955). In fact, this restoration appears in none of Jarvik's publications. Jarvik (1996, fig. 51B), however, includes a hindlimb restoration resembling superficially that which appears in Figure 37b. This revised version, although bearing seven digit-like structures, remains interpreted by Jarvik as pentadactylous. It should also be noted that the tarsus of this new version contains fewer elements than the pattern presented here, and the phalangeal formulae are reduced. Significantly, this may represent some variability in the hindlimb structure of *Ichthyostega*, although the specimen forming the basis of this reconstruction GGU (Grønlands Geologiske Undersøgelse) A166 is less complete than that described by Coates and Clack (1991).

Detailed discussions about the significance of the eight, seven, and six digit limbs of *Acanthostega*, *Ichthyostega*, and *Tulerpeton* have been published elsewhere (e.g. Coates & Clack 1990; Cook 1990; Coates 1991; Tabin 1992; Coates 1993; 1994b; Shubin 1995). In summary, such limbs challenge the evolutionary primacy of pentadactyly, and highlight inadequacies within previous theories concerning the evolution of tetrapod limbs from sarcopterygian fins. The 8- and 7-digit morphologies of *Acanthostega* and *Ichthyostega* appear as successive plesions on the tetrapod stem, while the 6-digit *Tulerpeton* lies at the base of the amniote stem. Polydactyly therefore appears to persist within basal crown-tetrapods, and Node K (*Westlothiana* plus embolomeres) is the least derived point at which amniote forelimb and hindlimb pentadactyly (character 65) can be identified with any degree of confidence. There is no equivalent evidence of persistent polydactyly



within stem-amphibians, and until recently there appeared to be a robust phylogenetic pattern of pentadactylous hindlimbs, and forelimbs with never more than four digits. However, it now appears that pentadactylous forelimbs were also (transiently) present. Two specimens of the colosteid stem-amphibian *Greererpeton burkemorani* at the Cleveland Museum of Natural History include a partially preserved manus. One of these is on public display (CMNH 11036), and shows parts of four digits. These include a diminutive posteriormost digit which matches the composition of the homologous member in the apparently near-complete digital array of CMNH 10938 (Fig. 37f). This second specimen has a 5-digit manus, with the phalangeal formula 1:2:2:3:2.

Of these two specimens only CMNH 11036 is listed by Godfrey (1989), and it is unclear if the material in its present, prepared condition was available at the time of his research. CMNH 10938 consists of a well articulated postcranium with a complete forelimb including the preserved manus. In certain respects this resembles that of the closely related *Colosteus scutellus*, which Hook (1983) restored with the phalangeal formula of 2:2:3:3. Personal inspection of MCZ casts of the *Colosteus* material confirm Hook's interpretation. The phalanges are altogether more elongate and slender than those of *Greererpeton*, and there is no trace of a fifth digit. Digits II, III, and IV of *Greererpeton* seem to share the same phalangeal formulae as those of *Colosteus*, although the most posterior digit (V) in *Greererpeton* is significantly smaller, relative to the remainder of the digital series. An alternative restoration of the *Greererpeton* manus (Fig. 37f) could interpret digit I as the distal part of digit II (despite a poor correspondence between bone diameters), thus presenting a more conventionally amphibian-like 4-digit pattern. However, if this is adopted, then the result is an unlikely phalangeal formula of 3:2:3:2 (although such an unusual formula is hardly more bizarre than the hindlimb of *Ichthyostega*), and close congruence with the *Colosteus* phalangeal formula is lost. The restoration of *Greererpeton* presented in Figure 37g is fairly conservative; it requires minimal bone redistribution, and the shortest digit (I) lies where it might be predicted, at the distal end of the digital arch (cf. Shubin and Alberch's 1986 analysis of tetrapod limb morphogenesis; discussed below). The pentadactylous condition of *Greererpeton* corroborates the view that distal limb patterns remained unstable in the early phases of both stem-amphibian and stem-amniote lineages. These five digits might be regarded as transitional with respect to the 4-digit (or less) manus of more derived amphibians. Re-coding characters 27, 65 and 74, as a single transformational ordered series does not alter the conclusions of the phylogenetic analysis in terms of either resultant numbers of trees, tree morphologies/branching sequences, or character distributions. Pentadactylous forelimbs remain independently derived within each crown-tetrapod lineage (Nodes K & M: Fig. 27), and

4-digit (or less) amphibian forelimbs are apparent by Node N (if not earlier).

These diverse early limb patterns and their relation to sarcopterygian fins can be explained at the morphological level most parsimoniously by Shubin and Alberch's (1986) model of prechondrogenic skeletal patterning (Coates & Clack 1990). In their analysis, tetrapod limbs are characterised as the products of dynamic morphogenetic processes (focal condensation, asymmetric segmentation and bifurcation) occurring within limb bud mesenchyme. In amniotes and anurans, digits branch sequentially from the posterior to anterior edges of the limb. This is inferred as a primitively conserved sequence, relative to the more variable patterns of digit morphogenesis observed in urodeles (see also Blanco & Alberch 1992). Therefore, when applied to polydactylous Devonian limbs (and the manus of *Greererpeton* relative to subsequent amphibians) the smallest and most anterior digits appear to be those which arose (ontogenetically) last, and therefore those which fail to emerge under pentadactylous (or less) conditions. The proximal part of tetrapod limbs develops as a continuous sequence of segmenting and anteriorly branching precartilaginous foci. This is redirected in a posterior to anterior direction across the distal domain of most limb buds, where it is characterised as the 'digital arch' (Shubin & Alberch 1986), and from which digits branch distally/postaxially. Consequently, the similarity between proximal, preaxially branched portions of tetrapod limbs and the paired fin skeletons of fish-like stem-tetrapods such as *Eusthenopteron* and *Panderichthys* may be explained as phylogenetically conserved manifestations of the same morphogenetic processes. Furthermore, Shubin and Alberch characterised the metapterygial axis of (gnathostome) fins as a continuous sequence of segmenting and bifurcation, with the implication that this is sustained, distally, in tetrapod limbs to become the digital arch (NB: unlike tetrapod limbs, at the time of writing metapterygial morphogenesis has not been observed experimentally in any non-tetrapod taxon, and only inferred from comparative embryological descriptions and adult fin morphologies). Thus the limbs of *Acanthostega* may be described as peramorphic (*sensu* McNamara 1986) relative to the characteristic short axis of stem-tetrapod fins, with metapterygial axial development sustained and apparently redirected anterodistally.

The significance of this apparently redirected axis and the pre- to postaxial flip in branching events producing digits is uncertain. Nevertheless, the failure of development regulating gene expression in tetrapod limbs to correspond to simple orthogonal axes (Lewis & Martin 1989) may be related to the axial transformation in the fin-limb evolutionary transition (Coates 1991; Duboule 1994). The triphasic pattern of *Hox* gene expression in amniote limbs corresponds to the major divisions of skeletal development, although the distalmost phase fails to correlate in any simple way with sequences of digit development (Nelson *et al.* 1996). Moreover, only an

Figure 37 (a)–(e) Pedes, all drawn as from left side, dorsal surface: (a) *Acanthostega*; (b) *Ichthyostega*; (c) *Greererpeton* (after Godfrey 1989, fig. 26b); (d) *Tulerpeton* (after Lebedev & Coates 1995, fig. 12b); (e) *Proterogyrinus* (after Holmes 1984, fig. 36). Dendrogram illustrating relationships derived from phylogenetic tree in Figure 27. Note that Jarvik (1996) maintains that the *Ichthyostega* hindlimb is pentadactylous. The anteriormost digit cluster (b) is interpreted as consisting of a prehallux, followed by digit I, with the shortest (digit III in the present work) being an interdigital, web-supporting rod; the remaining four stout digits are numbered II–V, and a postminimus is sketched-in at the posterior margin.

(f) Manus of *Greererpeton burkemorani*: CMNH 10938, previously undescribed digits of right forelimb, viewed from ventral (plantar) surface. Lettering identifies individual bones as moved minimally for restoration in adjacent diagram. Terminal phalanges lack a distal articular surface and have a distally pock-marked surface (nutritive foraminae?). Bone Vc is moved to position of best-fit on digit V, where the total digit morphology resembles closely that of the complete posteriormost digit on the manus of CMNH 11036 (not figured). It is possible that this may be the terminal phalanx of digits IV or II, but this requires either an extended digit IV or a extreme distal narrowing of (crushed) phalanx IIb. (g) *Greererpeton*, reconstructed forelimb digits: solid black indicates restored bone, roman numerals indicate conventional digit numbering; letters correspond to specimen in (f).

equivalent proximal phase of *Hox* expression occurs in the paired fins of the teleost *Danio rerio*, corroborating the inference that distal developmental domains enclosing the digital arch and wrist/ankle are neomorphic relative to a primitively finned condition (Sordino *et al.* 1995; Coates 1995). However, to describe the manus and pes as simply 'new' because of the associated developmental changes (Ahlberg & Milner 1994) may be insufficient. Relative to fin skeletons, digits are serial homologues of secondary radials, although redeployed in a new orientation within a new morphogenetic domain (Coates 1995). The major differences from radials such as those in extant lungfish (see Haswell 1882 for clear illustrations of their remarkably variable morphology), are developmental redirection across the digital arch, implied changes in response to gene regulation, and the apparent imposition of digit 'individualisation' (Wagner 1989).

Relative to pentadactylous limbs, primitive patterns of seven or eight digits suggest a broader distal domain in the earliest limb buds, and may reflect some transitional condition in the changing role and proportions of the thickened apical ectodermal ridge or fin fold during the evolution of limbs from rayed-fins (see further discussion in Thorogood 1991, and Sordino & Duboule 1996). Moreover, the digit series of *Acanthostega* may represent a primitively generalised condition, in which no individual member shares a specific relation to any of the five (or less) present in extant examples. The relationship may consist of no more than the shared potential to generate digits serially across a digital arch, with more precise homologies (i.e. digit identities) being derived gradually with the evolutionary acquisition of (apomorphic) developmental controls. An early example of this may be apparent in the hindlimb of *Ichthyostega*, where several specimens demonstrate conservation of the peculiar, anterior digit cluster (Fig. 37b) (Coates & Clack 1990; Jarvik 1996). In this respect the condition of the forelimb of *Acanthostega* parallels the condition of the axial skeleton (section 4.4.1), where the absence of morphological landmarks present in more derived tetrapods suggests a primitively, less highly differentiated pattern of morphogenetic regulation (Coates 1993). The limbs in *Acanthostega* may therefore have shared the same, phased *Hox* gene expression patterns as found in recent limbs, but without the derived expression boundaries or detailed, developmentally downstream, regulatory interactions known to govern extant digit domains (Tickle & Eichele 1994; Tickle 1995). Although such speculative hypotheses are not directly testable, they suggest that similar differences may be identified in the development of various non-tetrapod paired appendages.

6. Acknowledgements

My sincere thanks to Dr Jenny Clack for the invitation to work on the postcranium of *Acanthostega* while at the University Museum of Zoology, Cambridge U.K., where the initial part of this research was completed. Sarah Finney deserves particular thanks for her exceptional dedication and good humoured preparation of the fossil material. Thanks also to Professors Jarvik and Bjerring for friendly discussions and unhindered access to the vertebrate palaeontological collections in Stockholm. I am grateful to Drs A. L. Panchen, T. R. Smithson, J. Bolt, E. Lombard, M. Laurin, P. E. Ahlberg, A. C. Burke, and C. Nelson, for discussion and suggestions of numerous improvements to the manuscript, and the staffs of the Zoology Museum, University of Cambridge, the Field Museum of Natural History, Chicago, the Museum of Comparative Zoology, Harvard, the Cleveland Museum of Natural History, Cleveland, and the Royal Museum of Scotland, Edinburgh for help and access to collections. The Carlsberg

Foundation (Copenhagen), The Geological Survey of Greenland, Denmark, NERC, and the University Museum of Zoology, Cambridge, funded the 1987 Greenland expedition, led by Svend E. Bendix-Almgreen. This research was funded by NERC project grant GR3/7215'A, and BBSRC advanced research fellowship B/94/AF/1945.

7. Explanation of Figure lettering

acb	acetabulum	adb	adductor blade
adc	anterodorsal crest	adcr	adductor crest
ano	anocleithrum	atl	atlas neural arch
ax	axis neural arch	avp	anteroventral process
bra	branchial arch	car	caudal rib
cl	cleithrum	cn	cnemial crest
cvr	cervical rib	dc	distal tarsal
dcp	dorsal clavicular process	dip	dorsal iliac process
dpc	deltpectoral crest	ect	ectepicondyle
ectc	ectepicondylar canal	ent	entepicondyle
entc	entepicondylar canal	fem	femur
ff	fibular facet	ffo	fibular fossa
fgr	fibular groove	fib	fibula
fibl	fibulare	ftt	fourth trochanter
gl	glenoid	ha	haemal arch
hc	haemal canal	hum	humerus
hur	humeral ridge	ic	intercentrum
icf	intercondylar fossa	icl	interclavicle
igr	groove for intermetameric artery	il	ilium
int	intermedium	intf	intermedial facet
isch	ischium	it	internal trochanter
itf	intertrochanteric fossa	ldp	latissimus dorsi process
lpt	lepidotrichia	mr	mesial ridge
na	neural arch	nec	neural canal
noc	notochordal canal	obt	obturator foramen
pa	parapophysys	pab	postacetabular buttress
pbl	postbranchial lamina	pc	pleurocentrum
pib	posterior iliac blade	pozy	postzygapophysis
ppa	popliteal area	pub	pubis
pzy	prezygapophysis	r	rib
ra	radial	rac	radial condyle
rad	radius	sab	supra-acetabular buttress
sc.cl	scapulocleithrum	sc.co	scapulocoracoid
sgb	supraglenoid buttress	snc	supraneural canal
sr	sacral rib	ssr	site of sacral rib attachment
sup	supinator process	symph	symphyseal surface
tf	tibial facet	tib	tibia
tibf	tibiale facet	tibl	tibiale
tl	transverse line	tpr	transverse process
tra	triangular area	ulc	ulnar condyle
uln	ulna	vrc	ventral radial crest
zy	zygapophysis		

8. Characters used in cladistic analysis

Capital letters in brackets refer to source of character: EG, Gaffney 1979; V,HPS, Vorobyeva & Schultze 1991; F,G,P, Forey, Gardiner, & Patterson 1991; ALP,TRS, Panchen & Smithson 1988; PA,AM, Ahlberg & Milner 1994; AM,SS, Milner & Sequeira 1994; PA, Ahlberg 1995; OL,MC, Lebedev & Coates 1995.

Character	Character description
1.	External naris high on snout: separated from gape by lateral rostral and posterior portion of premaxilla (0); marginal position (1) (V,HPS); separated from gape by lachrymal: premaxilla contact (2).
2.	Separate dorsal and caudal median fins (0); distinct dorsal fin absent (1) (V,HPS); all fins absent (2).
3.	Humerus with rounded leading edge (0); anterior keel (1); anterior keel long (2) (OL,MC).
4.	Tropibasic skull (0); platybasic skull (1) (ALP,TRS).
5.	Enlarged scapulocoracoid plate: absent (0); present (1).
6.	Tooth row on parasymphysial plate (or subsequent modification): absent (0); present (1) (PA).
7.	Parasymphysial foramina (or subsequent modification): absent (0); present (1) (PA).
8.	Meckelian bone unexposed dorsal to prearticular: absent (0); present (1) (PA).
9.	Humeral/femoral epipodial facets: continuous (0); separated (1); joined by perichondrally unfinished isthmus (2) (OL,MC).
10.	Pelvic girdle attached by specialised (i.e. regionally differentiated) rib to axial skeleton: absent (0); present (1) (EG).
11.	Femur with extensive adductor blade: absent (0); present (1); blade reduced distally (2) (OL,MC).
12.	Tibial distal articular surface: absent (0); L-shaped (1); ovoid (2) (OL,MC).
13.	Pre- and postzygapophyses: absent (0); present (1).
14.	Ilium uniramous: (0); biramous with stout, unfinished anterodorsal process: (1); with short, blade-like anterodorsal process: (2).
15.	Large nasals: absent (0); present (1) (PA).
16.	Supraneural canal for dorsal ligament: open (0); closed (1).
17.	Ilium neck canal: absent (0); present (1).
18.	Bony enclosure of infraorbital sensory canal continuous with ethmoid commissure (0); canal enclosure interrupted at naris (1) (F,G,P).
19.	Up to 7-plate cheek; jugal: quadratojugal contact excluding squamosal: maxilla contact: absent (0); present (1) (ALP,TRS).
20.	Broad spade-shaped snout: absent (0); present (1) (PA).
21.	Coronoid fangs in tooth row: absent (0); present (1) (PA).
22.	Fenestra ovalis: absent (0); present (1) (EG).
23.	Stapes (as defined in Smithson and Thomson 1982): absent (0); present (1) (EG).
24.	Pelvic symphysis exclusively anterior to acetabulum (0); ischial contribution to symphysis (1) (EG).
25.	Epipodials diverge and only axial element articulates with distal carpal/tarsal-like structures (0); epipodials parallel; both articulate with carpus/tarsus (1) (EG).
26.	Skeletal elements distal to epipodials unelaborate, articulating only proximally and distally (0); carpus/tarsus with skeletal elements articulating laterally as well as proximodistally (1) (EG).
27.	Distal segmented radials associated with lepidotrichia (0); dactyly: manus/pes with digits: lepidotrichia-free postaxial segmented radials, generated in accordance to a constant ratio with the prechondrogenic axial segments (1) (EG).
28.	Single bilateral pair of nasal bones: absent (0); present (1) (ALP,TRS).
29.	Dermal component of pectoral girdle attached to rear of skull roof, including post-temporal, supracleithrum and anocleithrum (0); bony cranio-pectoral linkage absent, post-temporal and supracleithrum absent (1); anocleithrum absent (2) (OL,MC).
30.	Presacral neural spines oriented vertically; squared-off crest: absent (0); present (1).
31.	Neural radials: absent (0); present (1).
32.	Rugose fourth trochanter: absence of distinct zone (0); restricted to crest of adductor blade (1); extends onto anterior surface of internal trochanter (2).
33.	Obturator foramina: absent (0); multiple (1); single (2).
34.	Ribs spinous: (0); presacrals with uncinat process (1); abrupt change between cervical/ pectoral and anterior thoracic series (2).
35.	Coronoid fangs lost: absent (0); present (1) (PA).
36.	Humerus with processes 3 & 4: absent (0); present (1).
37.	Latissimus dorsi process: off-set anteriorly relative to ectepicondyle (0); in-line with ectepicondyle (1) (OL,MC).
38.	Tooth histology (presence of dark dentine): absent (0); present (1) (ALP,TRS).
39.	Ulna with olecranon process, and of equal or greater length than radius: absent (0); present (1) (PA,AM).
40.	Ventromesially extended infraglenoid buttress: absent (0); present (1).
41.	Rib length exceeds centrum plus neural arch and spine height: absent (0); present (1).
42.	Supra-acetabular more prominent than postacetabular buttress: absent (0); present (1).
43.	Post-branchial lamina: present (0); absent (1).
44.	Wrist and knee hinged; ankle rotary: absent (0); present (1) (Rackoff 1980) (EG).
45.	Scapulocoracoid: co-ossified with cleithrum (0); separate from cleithrum (1) (OL,MC).
46.	Rod-like ascending clavicular process: absent (0); present (1) (OL,MC).
47.	Fibula waisted, with distal sigmoid profile: absent (0); present (1) (OL,MC).
48.	Tarsus with two or more centrale bones: absent (0); present (1) (OL,MC).
49.	Haemal radials: present (0); absent (1).
50.	Ectepicondylar foramen and 'd' canal: present (0); absent (1) (PA,AM).
51.	Parasphenoid expanded posteriorly: absent (0); present (1).
52.	Tarsus with L-shaped intermedium: absent (0); present (1) (OL,MC).
53.	Large, laterally directed supraglenoid foramen lateral to triangular area: absent (0); present (1) (OL,MC).
54.	Tibia with flange on posterior edge: absent (0); present (1) (OL,MC).
55.	Strongly convex radial condyle: absent (0); present (1) (OL,MC).

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