CHAPTER 6.
WALKING WITH EARLY TETRAPODS:
EVOLUTION OF THE POSTCRANIAL SKELETON AND
THE PHYLOGENETIC AFFINITIES OF THE
TEMNOSPONDYLI (VERTEBRATA: TETRAPODA)

Abstract. Unlike all previous analyses, this revision of the phylogenetic relationships of early tetrapods differentiates between morphogenetic and phylogenetic variation in the postcranial skeleton, and takes into account the morphogenetic stage of specimens when coding character states, including those of many new postcranial characters. All characters used in this analysis were also subject to rigorous selection criteria to ensure their suitability for phylogenetic analysis. The results of this analysis differ significantly from previous analyses in that the Temnospondyli occupy a novel position as sister taxa to the Neospondyli (Seymouriamorpha plus Cotylosauria plus Lepospondyli) forming a new clade, the Terrapoda. All major clades of early tetrapods are statistically robust and supported by numerous unambiguous postcranial characteristics. Overall, the novel results of this phylogenetic analysis reflects the discovery of a major shift in habitat use within the more derived early tetrapods, from predominantly aquatic to predominantly terrestrial. Three distinct morphotypes of postcranial skeleton, including subtypes, form a morphological transformation series, indicating a series of improvements in the locomotor efficiency of the tetrapod limb associated with an increasing degree of terrestriality in early tetrapods. The first tetrapods with limbs designed more for weight bearing than reducing hydrodynamic drag are the Terrapoda. As the most basal members of the Terrapoda, the Temnospondyli are the first vertebrates capable of efficient terrestrial locomotion. There is no evidence of convergent evolution of the postcranial skeletons of the Temnospondyli and Neospondyli; rather the single cranial and single vertebral characters typically used to unite the Anthracosauria with the Seymouriamorpha are identified as convergent. The distinctive results presented here are most likely due to the increased use of characters pertaining to temnospondyls, increased use of postcranial characters, and differentiation between sources of morphological variation to minimise morphogenetic and phenotypic variation and elucidate true phylogenetic signal.

INTRODUCTION

The phylogenetic relationships of early tetrapods have been the subject of much debate and controversy, particularly in the last decade. Numerous phylogenetic analyses have been published, with conflicting cladogram topologies (analyses up to 2003 summarised in Ruta et al., 2003; Klembara and Ruta, 2004a, 2004b; Vallin and Laurin, 2004; Warren and Turner, 2004; Clack and Finney, 2005; Klembara, 2005). Most recent work on the postcranial skeleton of early tetrapods has focused on the fish to tetrapod (fin to limb) transition (research up to 2002 summarised in Clack, 2002a; Warren and Ptasznik, 2002; Clack et al., 2003a; Clack, 2004; Long and Gordon, 2004; Shubin et al., 2004; Warren and Turner, 2004; Ahlberg et al., 2005; Boisvert, 2005; Clack and Finney, 2005; Ahlberg and Clack, 2006; Daeschler et al., 2006; Shubin et al., 2006). There is universal agreement that Acanthostega gunnari and Ichthyostega stensoei are among the first tetrapods with digits, but the relationships of more derived early tetrapod taxa remain controversial.
Previous phylogenetic affinities of temnospondyls

Phylogenetic analyses of the relationships of early tetrapods have alternatively placed different early tetrapod groups as stem groups to temnospondyls, including colosteids (Smithson, 1985; Panchen and Smithson, 1988; Ahlberg and Milner, 1994; Laurin, 1998a; Laurin and Reisz, 1999; Ruta et al., 2003; Vallin and Laurin, 2004) (Figure 4), baphetids (Ahlberg and Clack, 1998; Laurin, 1998a; Ruta et al., 2003) (Figure 3), and embolomeres (Laurin and Reisz, 1999) (Figure 5). Proposed sister taxa to the Temnospondyli include, alternatively, the Anthracosauria (Embolomeri), stem amniotes and Lepospondyli (Laurin and Reisz, 1997; Laurin, 1998b; Vallin and Laurin, 2004), only the Anthracosauria (Embolomeri), and stem amniotes (Ahlberg and Milner, 1994), colosteids (Carroll, 1995; Laurin and Reisz, 1997; Laurin, 1998b), or lepospondyls (Smithson, 1985; Panchen and Smithson, 1988; Ahlberg and Milner, 1994).

Until the 1980’s the only detailed studies of early tetrapod postcranial that did not belong to the Temnospondyli, Seymouriamorpha, Cotylosauria or Lepospondyli was that of *Ichthyostega stensoei* (Jarvik, 1955), the gephyrostegids *Gephyrostegus bohemicus* (Carroll, 1970) and *Brukkererpeton fiebigi* (Boy and Bandel, 1973), and the anthracosaurs *Archeria crassidiscia* (Romer, 1957) and *Pholiderpeton (Eogyrinus) attheyi* (Panchen, 1966). During the 1980’s the postcranial skeletons of *Crassigyrinus scoticus* (Panchen, 1985), the anthracosaurs *Proterogyrinus scheelei* (Holmes, 1980, 1984), *Eoherpeton watsoni* (Smithson, 1985) and *Pholiderpeton scutigerum* (Clack, 1987a), and the colosteid *Greererpeton burkemorani* (Godfrey, 1989a) were described.

During the 1990’s an explosion of detailed work on the postcranial skeletons of basal tetrapods occurred, as many new taxa were discovered (Coates and Clack, 1990; Panchen and Smithson, 1990; Godfrey and Reisz, 1991; Vorobyeva and Kuznetsov, 1992; Ahlberg et al., 1994; Clack, 1994c; Daeschler et al., 1994; Smithson, 1994; Clack and Coates, 1995; Lebedev and Coates, 1995; Lombard and Bolt, 1995; Coates, 1996; Jarvik, 1996; Clack, 1998a; Milner and Lindsay, 1998; Vorobyeva, 1998). In the 21st century, discoveries of new specimens continues (Clack, 2000, 2001, 2002b; Warren and Ptasznik, 2002; Warren and Turner, 2004; Clack and Finney, 2005; Daeschler et al., 2006; Shubin et al., 2006). Comparison of the postcranial skeletons indicates significant differences between the postcranial skeletons of these plesiomorphic tetrapod taxa and that of temnospondyls.

Other recent work on early tetrapods has resulted in the classification of various early tetrapod taxa of uncertain phylogenetic affinities as ‘reptiliomorph’ using various cranial and postcranial characteristics (Smithson et al., 1994; e. g. Lebedev and Coates, 1995; Paton et al., 1999; Ruta et al., 2002). The phylogenetic affinities of temnospondyls within early tetrapods are subject to debate, temnospondyls never belong to the ‘reptiliomorph’ lineage, but despite this, no one has ever defined ‘non reptiliomorph’ postcranial characteristics. Most disconcertingly, all the postcranial characteristics supposedly apomorphic for stem amniotes are present in at least some temnospondyls (Chapter 5). It is possible that the definition of ‘reptiliomorph’ is based on ignorance or misunderstanding of the characteristics of the temnospondyl postcranial skeleton. The description of phylogenetic variation within the Temnospondyli (Chapter 5) provides a basis for comparison of the postcranial skeleton of temnospondyls with that of other early tetrapods.
Sources of morphological variation

Sources of morphological variation in the postcranial skeleton are both interspecific (phylogenetic) variation, and intraspecific (phenotypic and morphogenetic). None of the previous phylogenetic analyses of early tetrapods has distinguished between these sources of variation. Chapter 4 described the extensive morphogenetic variation of the postcranial skeleton in temnospondyls, particularly in the endochondral postcranial skeleton, and found that the same morphogenetic processes are likely to apply to other groups of early tetrapods. Chapter 4 also found that some of the postcranial characters used in phylogenetic analyses of temnospondyls and early tetrapods describe morphogenetic rather than phylogenetic variation, and others were affected by the morphogenetic stage of the specimens. Potentially the use of non-phylogenetic rather than phylogenetic variation in phylogenetic analysis could increase the amount of homoplasy and mask true phylogenetic signal. In order to elucidate true phylogenetic signal, consideration and assessment of all sources of morphological variation is necessary, so that the effects of non-phylogenetic variation are minimised and phylogenetic analysis is based solely on phylogenetic variation.

The aim of this analysis is to compare the postcranial skeleton of the Temnospondyli with that of other early tetrapods, which may assist in resolving the controversial phylogenetic position of the Temnospondyli within the Tetrapoda.

Taxon sampling effects

Temnospondyls are the largest clade of early tetrapods, but are typically under represented in phylogenetic analyses of early tetrapods (listed above). Many previous analyses of early tetrapods bias their taxon sample towards basal early tetrapod taxa and/or basal amniote taxa. The recent analysis of Ruta et al. (2003) thoroughly sampled basal tetrapods, basal amniotes and lepospondyls, but omitted many basal temnospondyls such as \textit{Capetus palustris}, \textit{Adamantipetron ohioensis}, \textit{Acroplous vorax}, \textit{Dvinosaurus} spp and the tupilakosaurs \textit{Tupilakosaurus} spp. and \textit{Thabanchuia oomie}. Consequently, taxon sampling effects may be a cause of the lack of resolution of the phylogenetic position of the Temnospondyli. Increased taxon sampling has been shown to greatly reduce phylogenetic error (Zwickl and Hillis, 2002), consequently the inclusion of as many basal temnospondyls as possible should be a priority in phylogenetic analysis of early tetrapods. Although many of the omitted basal temnospondyls are incomplete, they are more complete than many other taxa included by Ruta et al. (2003). Inclusion of less complete taxa may be important for resolution of the phylogenetic position of problematic clades such as the Temnospondyli, and for circumventing problems with phylogenetic analysis such as taxon long-branch attraction (Anderson, 2001; Wiens, 2005).

The main aim of this study is to use additional data, particularly postcranial characteristics, to reassess the phylogenetic affinities of the Temnospondyli within early tetrapods. Characters previously used in phylogenetic analysis of early tetrapods need revision, in light of recent work on sources of morphological variation in the postcranial skeleton. This study also aims to summarise the extent of phylogenetic variation within the postcranial skeleton of early tetrapods using characteristics employed in phylogenetic analysis.
MATERIALS AND METHODS

Data sources

Although many specimens were examined personally, this study was mainly literature based. Terminal taxa used in the phylogenetic analysis are listed, along with specimens examined and repository information, in Appendix 12. Reinterpretations of specimens described in the literature are listed in Appendix 13.

Abbreviations used in text


Main phylogenetic analysis

Because many previous phylogenetic analyses of early tetrapods exist (listed above), the comprehensive analysis of Ruta et al. (2003), and an analysis of the ‘higher’ temnospondyls (Yates and Warren, 2000) were combined as a basis for analysis. Additional characters were taken from various sources (Sequeira and Milner, 1993; Carroll, 1995; Lebedev and Coates, 1995; Coates, 1996; Paton et al., 1999; Anderson, 2001; Damiani, 2001a; Gardner, 2001; Clack, 2002b; Clack and Ahlberg, 2004; Klembara and Ruta, 2004b; Pawley and Warren, 2004; Sequeira, 2004; Clack and Finney, 2005; Pawley and Warren, 2005). Most of these analyses are based on cranial characteristics; consequently, emphasis was placed on revising and upgrading postcranial characters.

The McClade (Macintosh) built matrix of Ruta et al. (2003) was converted into a PC format acceptable to Nexus Data Editor (NDE) (Page, 2001), and additional data was input using NDE. Many characters in this matrix were recoded due to errors and changes to character states. The character state list (Appendix 14) and data matrix (Appendix 15) presents 72 new characters (ten cranial and 62 postcranial) not previously used in phylogenetic analysis of early tetrapods (marked in bold in the character state list).

The unique character identifiers (e.g. INTCLA 1) were originally used in phylogenetic analysis of early tetrapods by Ruta et al. (2003), the unique character identifiers used here are consistent in that they are either the same characters, or new characters with numbering additional to that of Ruta et al. (2003). The unique character identifiers are also consistent with those of a new analysis of the Temnospondyli (Chapter 5). Phylogenetic trees were prepared for publication using TreeView (Page, 1996).

Some cranial characters employed by Ruta et al. (2003) were omitted because they are subject to character state change with progressive morphogenetic stages (Bystrow and Efremov, 1940; Milner, 1980a; Godfrey, 1989b; Milner and Sequeira, 1994; Shishkin and Rubidge, 2000; Steyer, 2000 and references therein; Steyer, 2002; Werneburg and Steyer, 2002; Steyer, 2003). Other characters, including postcranial characters, were omitted
because they are proportion based (the proportional variation described is continuous rather than forming discrete character states within the taxa sample used in this analysis), not independent (e.g. prezygapophyses cannot exist without postzygapophyses), or because they are phylogenetically uninformative. The main analysis employed 349 characters, of which 201 were cranial characters (58%) and 148 postcranial characters (42%).

Choice of ingroup taxa

To reduce *a priori* assumptions of monophyly, species level terminal taxa were used as much as possible. Where this was not possible genus level terminal taxa were used, occasionally it was necessary to use family level taxa. Preferably all members of the group being considered should be included (Schultze, 1987; Hopson, 1991), so the taxon sample was as complete as possible to minimise the possibility of taxon sampling effects, but some pruning was necessary to keep the main analysis to a manageable level. The main purpose was to clarify the phylogenetic position of the Temnospondyli, consequently, after initial analysis indicated that some early tetrapod groups were unlikely to be close relatives of temnospondyls based on postcranial evidence (Lysorophia, Aistopoda, Adelospondyli, Lissamphibia), they were excluded from the main analysis in order to reduce its size. These excluded groups were retained in the test analyses, and their phylogenetic positions (Appendix 16: Figure 88) do not differ from those obtained in the larger preliminary analysis. As phylogenetic variation in the postcranial skeleton of the Temnospondyli was subject to a separate analysis (Chapter 5), the more derived Temnospondyli were removed, and all basal taxa retained. The phylogenetic positions of taxa within the Temnospondyli presented in the main analysis are the same as those of the separate analysis of temnospondyls (Chapter 5).

Although some taxa in this analysis lack associated postcranial material, they were included for the sake of completeness and to facilitate comparison with other analyses. Taxa with postcranial skeletons of larval morphology (Chapter 4) were not included (e.g. branchiosaurus, *Eucritta melanolimnetes*), because their postcranial skeletons are so morphogenetically immature that they are almost devoid of identifying characteristics. Bolt (1974d) considered that *Broiliellus brevis* may be an immature morphogenetic stage of *Dissorophus* spp., pending further study *Broiliellus brevis* was included. The state of preservation of *Solenodosaurus janenschi* creates difficulties in interpretation. The postcranial skeleton, particularly the vertebrae, is most consistent with that of a derived captorhinomorph grade stem amniote (Carroll, 1972a). Both cranial reconstructions (Carroll, 1970; Laurin and Reisz, 1999) may have misinterpreted the midline of the skull, although anteriorly the midline nasal suture, and posteriorly the supraoccipital, are correctly aligned, the ‘pineal foramen’ of Laurin and Reisz (1999) appears to be the posterodorsal margin of the left orbit, and the ‘tabular’ may be the right postparietal. Pending further investigation, the main analysis excluded *Solenodosaurus janenschi*.

Selection and coding of postcranial characters

It is important that phylogenetic character states, and the coding of these states, refers to interspecific (phylogenetic), rather than intraspecific (morphogenetic or phenotypic) variation. Consequently, the morphogenetic stage of specimens (Chapter 4) was taken into account when coding the matrix. Specimens with morphogenetically immature postcranial skeletons are denoted in the taxon list (mi). Postcranial character states known to be affected by the morphogenetic stage of the specimen (Chapter 4) are denoted ‘m’ in
the character state list, and are accompanied by selection criteria to facilitate identification of immature specimens in which the derived state is indeterminate. If it was possible that a derived postcranial characteristic may be absent in a particular specimen due to the morphogenetic immaturity of the specimen, then the character state was coded ‘?’, to avoid confusing morphogenetic immaturity with the plesiomorphic state.

Analysis of matrices

Analysis of matrices was performed using PAUP 4.0 beta WIN10 (Swofford, 2003), on a Pentium 4 PC. All characters were parsimony informative, and unweighted, five characters are ordered. Parsimony analysis employed the heuristic search algorithm with the following settings: uninformative characters excluded, character state changes optimised with ACCTRAN, random addition sequence with ten replicates, and the TBR (tree bisection-reconnection) branch-swapping algorithm. Bootstrapping used the same options, but with 100 replicates, the number of trees held in memory per replicate was limited to 10,000 in order to limit branch swapping on suboptimal trees. For calculating Bremer node values, used 10 replicates, and a limit of 100,000 trees per replicate was set.

The ‘parsimony ratchet’ employed by Ruta et al. (2003) was tested, but comparison with the heuristic search used here indicated that the parsimony ratchet took much longer to produce a result, and produced longer trees of lower resolution. Consequently, all analyses employed a standard heuristic search. Three separate analyses were run, one main analysis and two separate test analyses, in order to compare the results of the main analysis with those of Ruta et al. (2003).

Tests of degrees of character inclusion

The effect of including postcranial characters was tested by excluding all postcranial characters, (Casineria kiddi deleted). Preliminary analyses removing all cranial characters and taxa without postcranial material (Megalocephalus pachycephalus, Anthracosaurus russelli, Chenoprosopus milleri, Cochleosaurus spp., Saharastega moradiensis, Nigerpeton rieqlesi, Adamanterpeton ohioensis, and Capetus palustris) resulted in a complete lack of resolution after 100,000 trees and consequently were deemed unviable. The effect of removing vertebral characters that have historical significance for temnospondyl taxonomy, but may reflect only differing degrees of ossification of an originally cartilaginous amphicoelous centra (Chapter 4), was tested by removing the relevant characters (TRU VER 8, TRU VER 8, TRU VER 14), and another analysis run where TRU VER 33 was additionally excluded. The results of these analyses are presented in Appendix 16.

Tests of phylogenetic stability

Constraint trees were built to assess alternative phylogenetic relationships of the Anthracosauria. The results of these analyses are presented in Appendix 16.

Comparative phylogenetic analyses

Analysis using matrix of Ruta et al. (2003), postcranial characters changed

This test was designed to test the effect of changing the postcranial characters. It used the same taxa and cranial characters (coding unchanged) as the matrix of Ruta et al. (2003),
but the postcranial characters and coding were changed to that of the main analysis. This analysis used a total of 90 taxa and 376 characters, of which 220 are cranial and 156 postcranial. The results of these analyses are presented in Appendix 16. An analysis excluding postcranial characters from their matrix was performed by Ruta et al. (2003: figure 8).

Analysis using taxa of Ruta et al. (2003)

A separate data matrix was constructed using the same terminal taxa as Ruta et al. (2003), but employing the characters and coding used in the main analysis, in order to test the effect of taxon sampling. This analysis used a total of 90 taxa and 376 characters, of which 217 are cranial and 156 postcranial. This analysis was also reanalysed after re-weighting all characters by their consistency indices [as in Ruta et al. (2003)], and the initial analysis was re-run excluding postcranial characters. The results of these analyses are presented in Appendix 16.

RESULTS OF MAIN PHYLOGENETIC ANALYSIS

The main analysis resulted in nine trees of 832 steps (93 taxa, 349 characters, CI = 0.4387, RI = 0.8560, RC = 0.3755), a consensus tree is shown in Figure 62. Bootstrap and Bremer node values (Figure 63) are consistently high throughout, with few nodes having bootstrap values less than 50% or Bremer node values of one or less. The nine trees result from the unresolved relationships between Casineria kiddi and Caerorhachis bairdi, and Tuditanus punctulatus and Asaphestera intermedia, which are most likely caused by the identical coding of these pairs of taxa. Note that the test of expected consistency index used by Sanderson and Donoghue (1989) is only applicable to analyses of 60 taxa or less, so these have not been calculated here, contra Ruta et al. (2003). Phylogenetic distributions of all character states are provided in the character state list (Appendix 14), and lists of synapomorphies and state changes for each clade are listed in Appendix 17.

Taxonomic definitions

The results of the analysis presented here are unique in that this analysis identifies several new groups of early tetrapods (Figure 62), based on characteristics of the postcranial skeleton (see below). This has necessitated clarification of some existing taxonomic definitions, and creation of some new definitions, in order to facilitate discussion of the results of this analysis.

The recent debate over the taxonomic principles that should be applied to early tetrapod relationships is exemplified by the debate regarding which taxa should be included within Tetrapoda (apomorphy-based vs. crown group vs. stem group vs. total group definition) (Gauthier et al., 1988; Clack, 1997; Coates et al., 2000; Laurin et al., 2000; Anderson, 2002b; Laurin, 2002; Ruta et al., 2003; Laurin and Anderson, 2004). The contents of other early tetrapod groups, including ‘stem-tetrapods’, ‘batrachomorphs’ (stem lissamphibian lineage), and ‘reptiliomorphs’ (stem amniote lineage) are also subject to frequent and dramatic fluctuation, mostly due to the use of crown clade definitions and the disagreement over the phylogenetic affinities of the Lissamphibia, most recently discussed by Anderson (2002b), and Ruta et al. (2003).
FIGURE 62. Results of the main phylogenetic analysis of early tetrapods. Strict consensus of nine trees of 832 steps (93 taxa, 349 characters, CI = 0.4387, RI = 0.8560, RC = 0.3755).
FIGURE 63. Bremer node and bootstrap values for main phylogenetic analysis of early tetrapods. Left numbers are bootstrap values, right and single numbers are Bremer node values.
Two recent phylogenetic analyses (Laurin, 1998b; Ruta et al., 2003) have used a crown clade definition of ‘Tetrapoda’. These analyses use ‘stem tetrapod’ to refer to all taxa basal to the crown clade composed of the last common ancestor of reptiles and amphibians. Unfortunately, the contents of these ‘Tetrapoda’ differ drastically from each other, and do not agree either with the informal definition of ‘tetrapod’, because many taxa with digit bearing limbs are excluded.

The debate over the contents of ‘Tetrapoda’ also affects the contents of the stem plesion, or ‘stem-tetrapods’. The term ‘stem tetrapod’ is typically used informally to include only the most basal tetrapods such as *Acanthostega gunnari*. Application of an apomorphy-based definition of ‘Tetrapoda’ creates further confusion about the definition of ‘stem tetrapod’. Currently, all of the taxa informally termed ‘stem tetrapods’ possess digit bearing limbs. Under an apomorphy-based definition of ‘Tetrapoda’, the term ‘stem tetrapods’ would be restricted to taxa that do not possess digit bearing limbs, for example *Panderichthys rhombolepis* and *Tiktaalik roseae*. Unfortunately restricting the use of the term ‘stem tetrapod’ to refer only to these taxa would be contrary to typical use, and only add to the confusion. Similar issues apply to the definitions of ‘batrachomorph’ and ‘reptiliomorph’, which refer to taxa belonging to the amphibian and amniote lineages, respectively. The content of the Batrachomorpha is extremely inconsistent (Laurin and Reisz, 1995, 1997, 1999; Vallin and Laurin, 2004), and Reptiliomorpha has previously included taxa which are now considered ‘stem tetrapods’ (Lebedev and Coates, 1995; Coates, 1996).

The use of crown group definitions results in an unstable content of these groups, and consequent fluctuation in the morphological characteristics that are present within these groups. This taxonomic insecurity obstructs communication about the comparative morphology of early tetrapods, which is the purpose of this analysis. Consequently, to facilitate ease of discussion and promote taxonomic stability, apomorphy-based definitions (de Queiroz and Gauthier, 1990) are preferred and used here. In, in this context ‘Tetrapoda’ (four legs), and ‘tetrapods’, refers to the clade of vertebrates that possess four digit-bearing legs, in agreement with Clack (1997; 2002a), Ahlberg (1998), and Ahlberg and Clack (1998). In this context, the most basal taxon definitely within Tetrapoda is *Acanthostega gunnari* (note that in this is not a formal taxonomic definition, as the content of the Tetrapoda is not the focus of this analysis). Although the terms ‘stem-tetrapod’, ‘batrachomorph’, and ‘reptiliomorph’ are typically used to define various groups of early tetrapods, they are abandoned here, not only due to difficulties in definition, but because they imply phylogenetic affinities with derived taxa, which is not the aim of this analysis.

**Anthracosauria**

In this context, ‘Anthracosauria’ is applied sensu stricto, following Panchen (1970), to refer to the clade containing the type taxon, *Anthracosaurus russelli*. This clade includes all taxa colloquially named ‘embolomeres’ plus Gephyrostegidae. The postcrania, skeletons of the Seymouriamorpha are morphologically distinct form those of the Anthracosauria sensu stricto. As the Seymouriamorpha do not form the sister taxon to the Anthracosauria in the phylogenetic analysis presented here, the taxon ‘Batrachosauria’ is abandoned, as discussed above.
ICHTHYOGESTEAMORPH

This informal term refers to a stem plesion or ‘grade’ of tetrapods, with ‘Ichthyostega-morphotype’ postcranial skeletons, in which the cleithral shaft is plesiomorphically absent, and the cleithrum is co-ossified with the scapulocoracoid. This morphotype is named for the first tetrapod with this type of postcranial skeleton to be described, *Ichthyostega stensoei*.

ARCHERIA-MORPH

This informal term refers to a stem plesion or ‘grade’ of tetrapods, with ‘Archeria-morphotype’ postcranial skeletons, in which a long cleithral shaft is present, but the humerus is not waisted. This morphotype is named for the first tetrapod with this type of postcranial skeleton to be described, *Archeria crassidisca*.

TERRAPODA

The phylogenetic hypothesis presented here is novel in that the Temnospondyli are sister taxa to stem amniotes and lepospondyls. The new term ‘Terrapoda’ (land legs) defines this clade and morphotype of tetrapods possessing the apomorphic condition of limbs that are indisputably capable of terrestrial locomotion, characterised by the unambiguous synapomorphy (among many others, see below) of a waisted humerus with the proximal and distal ends set at approximately right angles. The type taxon for the Terrapoda is *Dendrerpeton acadianum* Owen 1853. Within tetrapods, the acquisition of limbs is not synonymous with the origin of terrestrial locomotion (Coates and Clack, 1991; Clack and Coates, 1995; Coates, 1996), the term ‘Terrapoda’ formally distinguishes between the origin of tetrapods with limbs *per se*, and the origin of tetrapods with limbs definitely capable of terrestrial locomotion.

NEOSPONDYLI

The new term ‘Neospondyli’ (new vertebrae) refers to the most consistent synapomorphy of this clade, the possession of vertebrae that are essentially of the same basic design to those of the majority of extant tetrapods, in that they are essentially monospondylous and pleurocentrum dominated, with the neural arch fused to the centra. The type taxon for the Neospondyli is *Seymouria baylorensis* Broili 1904. Monospondylous, pleurocentrum dominated vertebral centra are not an exclusive synapomorphy of the Neospondyli, because this vertebral type also occasionally occurs within the more derived Temnospondyli (Chapter 5). Panchen (1977a) discussed the lack of a name for this taxon, a situation that has persisted despite the widespread recognition of this large clade in prior phylogenetic analyses (Carroll, 1995; Laurin and Reisz, 1997; Ahlberg and Clack, 1998; Laurin, 1998b; Laurin and Reisz, 1999; Paton et al., 1999; Anderson, 2001; Ruta et al., 2003; Vallin and Laurin, 2004).

**EVOLUTION OF THE TETRAPOD POSTCRANIAL SKELETON**

This analysis found three distinct morphotypes of postcranial skeleton within the early tetrapod group presented here (Table 1), forming a morphological transformation series. The three morphotypes are ichthyostegamorphs (node Terrapoda), archeriamorphs, and
terrapods. There are clear transitions between these postcranial morphotypes, which may represent changes in locomotor style (Figure 81). All of the nodes between these morphotypes have bootstrap support of 100%, and Bremer node values of a least five.

Terrapods divide further into the Temnospondyli and Neospondyli, which includes the more derived Lepospondyli and Nectridia. The major nodes of the Temnospondyli, Neospondyli, Lepospondyl, and Nectridia are all robustly supported statistically, by both bootstrap and Bremer node values ((Figure 63). The results of the phylogenetic analysis are presented as a cladogram (Figure 62) as lists of postcranial character states (below), and pictorially (Figure 64-81). The phylogenetic distributions of all character states are also provided in the character state list (Appendix 14), and lists of synapomorphies and state changes for each clade are listed in Appendix 17.

**TABLE 1. EVOLUTIONARY TRANSITIONS IN THE POSTCRANIAL SKELETON OF EARLY TETRAPODS**

<table>
<thead>
<tr>
<th>CHARACTERISTIC</th>
<th>FIRST PHYLOGENETIC APPEARANCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Limbs with digits</td>
<td>Tetrapoda (ichthyostegamorphs)</td>
</tr>
<tr>
<td>Jointed elbow and knee</td>
<td>archeriamorphs</td>
</tr>
<tr>
<td>Weight bearing limbs</td>
<td>Terrapoda</td>
</tr>
</tbody>
</table>

In the lists of character states (below), a unique character identifier denotes the relevant character (e.g. INTCLA 1), which is listed in its complete form in the character state list (Appendix 14). Character states in plain type (e.g. TRU VER 1) were previously published and their distribution discussed in Ruta et al. (2003). Characters used in other previously published analyses (see Materials and Methods) have only the numbers in bold (e.g. TRU VER 28). New characters, not previously used in phylogenetic analyses of early tetrapods, are entirely in bold (e.g. INTCLA 7.). The letter ‘m’ prefacing a unique character identifier indicates that the characteristic is subject to morphogenetic development and variation, as discussed by Pawley (Chapter 4). The character states for the morphological transformation series listed below are marked ‘¨’ in the character state list (Appendix 14). References are provided only for taxa not included in the phylogenetic analysis, references for included taxa are in Appendix 12.

The following are unambiguous synapomorphies, unless otherwise noted.

**Tetrapodomorph fish**

This morphotype, here represented by *Panderichthys rhombolepis* and *Tiktaalik roseae*, is characterised by robust fins that plesiomorphically retain lepidotrichia (DIG 1), the synapomorphy of an enlarged coracoid foramen (m SCACOR 18), and the derived characteristic of an enlarged coracoid plate (relative to other tetrapodomorph fish such as *Eusthenopteron foordi*).

**Tetrapoda (ichthyostegamorphs)**

This morphotype contains *Acanthostega gunnari*, *Ventastega curonica*, and *Ichthyostega stensoeit*, and is characterised by the apomorphic, or perhaps transitional, condition of the scapulocoracoid being indistinguishably fused to the cleithrum (SCACOR 20). This clade also contains all taxa with digit bearing limbs.
Synapomorphies: Pre- and postzygapophyses present on trunk vertebrae (TRU VER 20, Figure 64). Pre- and postzygapophyses present on proximal tail vertebrae (CAU VER 5, Figure 64). Sacral vertebrae/ribs: present (SAC VER 1, Figure 67). Anocleithrum unornamented (ANOCLE 2). Cleithrum unornamented (CLE 12). Humeral process 2 present (m HUM 23, Figure 72). Radius shorter than humerus (RAD 1). Digits present (DIG 1). Femur as long as humerus (FEM 5).

Ichthyostega

The postcranial skeleton of *Ichthyostega stensoei* is distinguishable from the more plesiomorphic postcranial skeletons of *Acanthostega gunnari* and *Ventastega curonica* by several derived features which unite it with more derive tetrapods.

Synapomorphies: Ribs ventrally curved (RIB 3, Figure 67). Ventromedially extended infraglenoid buttress present (m SCACOR 4, Figure 71). Presence of olecranon process (m ULNA 1, Figure 75). Supracetabular iliac buttress more prominent than postacetabular buttress (ILI 6, Figure 76).

Archeriamorphs

This morphotype contains *Tulerpeton curtum*, Whatcheeriidae, *Crassigyrinus scoticus*, Colosteidae, Baphetidae, and Anthracosauria plus Gephyrostegidae. The most distinctive characteristics of their postcranial skeletons compared to more plesiomorphic tetrapods are the long cleithral shaft and the interepipodial space between the tibia and fibula.

Synapomorphies: Pre- and postzygapophyses on distal tail vertebrae present (CAU VER 7). Loss of supraneural spines (CAU VER 10, Figure 64) [Also present in an undescribed embolomere (Clack, 2002a)]. Uncinate processes present on anterior trunk ribs (m RIB 5, Figure 67). Long ventral cleithral shaft present with expanded dorsal process (CLE 3, Figure 70). Loss of anteroventral process of cleithrum clasping dorsal clavicular process of clavicle (CLE 11, Figure 70). Loss of accessory foramina in coracoid (m SCACOR 19). Loss of ectepicondylar foramen (except *Crassigyrinus scoticus*) (HUM 6, Figure 72). Distal extremity of ectepicondylar ridge aligned between ulnar and radial condyles (m HUM 9, Figure 72). Latissimus dorsi process of humerus a knob on extensor surface of humerus (HUM 20, Figure 72). Femur longer than humerus (FEM 5). Fibula waisted, interepipodial space present (FIB 1, Figure 79). Ossified proximal edge of separate tarsal intermedium asymmetrical notch, with the fibulare side longest (m TAR 3, Figure 80). Distal tarsals between fibulare and digits present (m TAR 4, Figure 80). Distal tarsals between tibiale and digits present (m TAR 5, Figure 80).

Archeriamorphs more derived than Tulerpeton

This morphotype contains all known post Devonian tetrapods, Whatcheeriidae, *Crassigyrinus scoticus*, Colosteidae, Baphetidae, and Anthracosauria plus Gephyrostegidae.

Synapomorphies: Presence of no more than five digits in manus (DIG 2, Figure 81). Proximal ends of metacarpals/tarsals asymmetrical (m DIG 5). Radius as long as ulna without olecranon process (RAD 2).
**Anthracosauria plus Gephyrostegidae**

The most distinctive feature of this clade is the ventrally fused trunk vertebrae, a characteristic shared with some temnospondyls and all Neospondyli.

**Synapomorphies:** A majority of trunk pleurocentra ventrally fused (m TRU VER 8, Figure 65) (reversed in basal Temnospondyli). Latissimus dorsi process aligned with ectepicondyle (HUM 1, Figure 72). Radial condyle visible in flexor view only (ventral) (m HUM 11, Figure 72, Figure 73). Loss of accessory foramina in humerus (HUM 17, Figure 72). Loss of dorsal iliac ridge (ILI 4, Figure 76). Transverse pelvic ridge present (ILI 7, Figure 76). Tibial distal articulation surface ovoid (m TIB 1, Figure 78).

**Terrapoda**

This morphotype contains the Temnospondyli plus the Neospondyli, which contains the Seymouriamorpha, Cotylosauria, and Lepospondyli. This large clade displays many adaptations of the postcranial skeleton that are likely to be related to a derived change in locomotor style, particularly characterised by the waited humerus with the proximal and distal ends set at right angles to each other.

**Synapomorphies:** Supraneural canal (m TRU VER 28, Figure 64) does not penetrate neural arch. Atlantal neural spine: reduced to cylindrical spinous process (CER VER 5, Figure 66) (reversed in Microsauria). Atlantal rib absent (reversed in Neospondyli more derived than Seymouriamorpha) (RIB 1). Uncinate processes absent (m RIB 5, Figure 67) (reversed in derived Temnospondyli). Posteroventral edge of (first) sacral rib thickened and distinct from main body of rib (RIB 9, Figure 67). Distal expansion of (first) sacral rib strongly posteriorly recurved (RIB 10, Figure 67). Posterior border of dorsal clavicular process (posterior lamina); posteriorly expanded dorsal to center of ossification at the junction with the ventral blade (CLA 6, Figure 69). Loss of medially directed flange (sometimes enlarged into postbranchial lamina) along medial cleithral shaft (CLE 2, Figure 70). Loss of anterior clavicular recess of the cleithral shaft (CLE 9, Figure 70). Loss of lateral cleithral ridge (CLE 10, Figure 70). Scapular blade dorsally flared (m SCACOR 6, Figure 71). Canal of supraglenoid foramen oriented anteroposteriorly (SCACOR 7, Figure 71). Supraglenoid fossa present (m SCACOR 8, Figure 71). Posterior end of glenoid twisted so that the posterior most surface is oriented almost dorsally (m SCACOR 11, Figure 71). Infraglenoid ridge of scapulocoracoid present (m SCACOR 12, Figure 71). Infraglenoid recess of scapulocoracoid present (m SCACOR 13, Figure 71). Loss of scapular ridge on the postero medial surface of the supraglenoid buttress (SCACOR 14, Figure 71). Anterior edge of the supra/infraglenoid buttress dorsally oriented (m SCACOR 15, Figure 71). Anterior border of glenoid: aligned with the posterior edge of the scapular blade (m SCACOR 17, Figure 71) (reversed in Microsauria). Supinator process present (m HUM 2, Figure 73) (reversed in Amphibamidae, Captorhinomorpha, Microsauria). Distal extremity of ectepicondylar ridge aligned with radial condyle (m HUM 9, Figure 73). Humerus waisted (HUM 10, Figure 73). Proximal and distal articulation surfaces of humerus set at approximately right angles to each other (HUM 19, Figure 73). Anterior humeral keel originates distal to deltopectoral crest (HUM 22, Figure 73). Loss of humeral process 2 (m HUM 23, Figure 73). Latissimus dorsi process of humerus flattened towards the surface of the humerus and proximally directed (HUM 24, Figure 73). Ectepicondylic projects anterior to radial condyle (m HUM 26, Figure 73). Loss of dorsomedial radial ridge (RAD 3, Figure 74). Loss of proximoventral radial ridge (RAD 4, Figure 74). Mesial iliac ridge aligned with iliac neck (ILI 5, Figure 76). Loss of accessory pelvic foramina (m PUB 1, Figure 76).
Posterior intertrochanteric ridge joins at the junction of the adductor blade and adductor crest (FEM 7, Figure 77). In distal view, intercondylar fossa aligned with the midline of the popliteal area (FEM 9, Figure 77). Loss of posterior tibial keel (TIB 2, Figure 78). Loss of cnemial extensor flange (TIB 3, Figure 78). Junction of anterior and posterior tibial flexor crests with distal tibial flexor crests: on ventral midline of shaft, distal tibial flexor crest passes down the midline of the shaft (TIB 4, Figure 78). Flexor surface of fibula concave below femoral articulation surface (FIB 2, Figure 79).

Neospondyli

The Neospondyli are distinguishable from all more plesiomorphic tetrapods, and particularly from the Temnospondyli, by the derived characteristics of their vertebrae, which have a grossly enlarged pleurocentrum fused to the neural spine.

Synapomorphies: Neural spines with distinct convex “swollen” lateral surfaces (TRU VER 10, Figure 64). Neural spines of trunk vertebrae suturally attached or fused to centra (m TRU VER 11, Figure 64). Anterior and posterior surfaces of neural spines converge dorsally to form a triangular outline (m TRU VER 29, Figure 64). Trunk centra monospondylous, pleurocentra dominant, intercentra highly reduced or absent (gastrocentrous) (TRU VER 33, Figure 65).

Lepospondyli

The postcranial skeletons of the Lepospondyli are distinguished for the more basal Neospondyli mainly by derived characteristics of the atlas and axis. The Lepospondyli also contains the Nectridia.

Synapomorphies: Atlantal neural spines dorsally fused (m CER VER 1, Figure 66). Atlantal neural arch and atlantal centrum fused (m CER VER 2, Figure 66). Axial centrum with strong anterior (odontoid) process (CER VER 6, Figure 66). Anterior articulating surface of atlas centrum laterally expanded (CER VER 7, Figure 66).

Nectridia

The postcranial skeletons of the Nectridia are characterised by their distinctive vertebrae

Synapomorphies: Extra articulations above zygapophyses in at least some trunk and caudal vertebrae present (TRU VER 1, Figure 64). Neural and haemal spines rectangular to fan-shaped in lateral view (TRU VER 2, Figure 64). Dorsal neural spine crenulated (TRU VER 30, Figure 64). Neural and haemal spines facing each other dorsoventrally present (CAU VER 1). Caudal intercentra absent, haemal arches attached to pleurocentra (CAU VER 9, Figure 64). Cervical ribs without expanded distal ends (RIB 2).
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FIGURE 72. Early tetrapod humeri: ichthyostegamorphs and archeriamorphs. 1, *Acanthostega gunnari*, in 1.1 extensor, 1.2 anterior, 1.3 flexor, and 1.4 distal views, in 1.4 extensor surface is uppermost, after Coates (1996). 2, *Proterogyrinus scheeli*, in 2.1 extensor, 2.2 anterior, 2.3 flexor, and 2.4 distal views, after Holmes (1984). Scale bar = 25 mm
FIGURE 73. Early tetrapod humeri: Terrapoda. 1, *Eryops megacephalus*, in 1.1 extensor, 1.2 flexor, 1.3, anterior, 1.4 posterior and 1.5 distal views, in 1.5 extensor surface is uppermost, from Pawley and Warren (2006). 2, *Limnoscelis dynatis*, in 2.1 extensor, and 2.2 flexor views, after Berman and Sumida (1990). Scale bar = 25 mm
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FIGURE 78. Early tetrapod tibia. All left tibiae in .1 extensor, .2, anterior, .3, flexor, and .4 posterior views.
DISCUSSION

Phylogenetic affinities of the Temnospondyli

The hypothesis of relationships of early tetrapods presented here is novel in that the Temnospondyli are more derived than the archeriamorph groups Anthracosauria and Gephyrostegidae (Figure 62). The results presented here, including the comparative analyses (Appendix 16) consistently place the Temnospondyli as sister taxa to the Neospondyli and the Anthracosauria as a stem group to the Terrapoda. There can be no doubt that the postcranial skeleton of temnospondyls is more derived than that of archeriamorphs, and in vertebral characteristics less derived than that of the Neospondyli (Figure 64 - 81).

This hypothesis of early tetrapod relationships was first proposed after preliminary analysis by Pawley and Warren (2002). An analysis by of limb characteristics (Coates et al., 2002) produced a similar topographical arrangement, but was based on few taxa and did not include cranial characters. The only previous large scale analysis to produce a similar result is the bootstrap tree of Laurin and Reisz (1999) that placed the Anthracosauria basal to the Temnospondyli, but the Gephyrostegidae as the derived sister taxa to the Seymouriamorpha, and the lower jaw analysis of Ahlberg and Clack (1998).

Phylogenetic analysis

There are three main reasons for the novel position of the Temnospondyli presented here: increased use of characters pertaining to temnospondyls (both cranial and postcranial), the increased use of postcranial characters, and differentiation between sources of morphological variation in order to minimise the confounding effects of non-phylogenetic variation (Chapter 4) and promote true phylogenetic signal. Other additional causes for the unique results of this analysis may be the taxon sample used in the main analysis, or increased use of data pertaining to the basal Neospondyli. Clack and Finney (2005) also performed a series of tests comparing their analysis with that of Ruta et al. (2003), but their results did not differ significantly form those of Ruta et al. (2003).

Increased use of temnospondyl characters

This analysis has included many more cranial and postcranial characters pertaining to temnospondyls than any other previous phylogenetic analyses of early tetrapods. The emphasis placed on temnospondyl characteristics may have played a major role in producing in the hypothesis of early tetrapod relationships presented here, but the effect of this increased use of temnospondyl characters is difficult to objectively assess, because many temnospondyl characters are also phylogenetically significant for many other taxa. Both the new analyses presented here that excluded postcranial characters (Appendix 16: Figure 87, Figure 90) essentially retained the same tree topology as the comparable analyses that included all characters, indicating that the choice of cranial characters and coding employed here has definitely assisted in producing the novel phylogenetic position of the Temnospondyli, and the results of the main analysis (Figure 62, Figure 63) cannot be solely attributed to the increased use of postcranial characters.

Replacing the postcranial characters of Ruta et al. (2003) (Appendix 16: Figure 91) produced a tree supporting the existence of the Terrapoda, which when re-weighted (Appendix 16: Figure 92) resulted in a rearrangement of the major clades into a topology similar to that of the main analysis (Figure 62). This indicates that postcranial characters
play an important role in phylogenetic resolution of early tetrapods, particularly at higher
taxonomic levels. This combination of the cranial characters of Ruta et al. (2003) with the
postcranial characters of the main analysis dramatically increased the number of trees
(Appendix 16: Figure 91), whilst keeping tree length lower than and consistency indices
higher than the analysis of Ruta et al. (2003). This result may be due to either the higher
level of homoplasy in the cranial characters of Ruta et al. (2003), or to conflict in the
phylogenetic signals of the cranial data of Ruta et al. (2003) with the postcranial data
presented here.

The comparative lack of phylogenetic variation in the postcranial skeleton may
discourage the use of postcranial characters in analyses, but it is important to recognise
that this lack of variation also results in a strong phylogenetic signal. The inclusion of
comparatively invariant postcranial characteristics consequently establishes a strong
‘backbone’, increasing the robustness of the phylogenetic hypotheses.

The effects of increased use of postcranial characters

One important factor in this study is the amount of recent work on the postcranial
skeletons of ichthyostegamorphs and archeriamorphs (Godfrey, 1989a; Lebedev and
Coates, 1995; Lombard and Bolt, 1995; Coates, 1996; Jarvik, 1996; Milner and Lindsay,
1998; Warren and Turner, 2004; Clack and Finney, 2005). Most of the postcranial
descriptions are thorough and detailed, allowing for comprehensive comparison with
more derived taxa, in a way that would have been impossible two decades ago. It is only
through the accumulation of evidence on the plesiomorphic early tetrapod postcranial
skeleton that it has become obvious that the morphology of other early tetrapod taxa such
as temnospondyls is derived. Description of the postcranial skeletons of more derived
early tetrapod taxa now lags behind that of the more plesiomorphic taxa.

The concentration of recent work on the fin to limb transition is reflected in the
phylogenetic characters. Most of the new postcranial characters added in this analysis
(entirely in bold) are only applicable to the more derived early tetrapod taxa, particularly
the Temnospondyli and Neospondyli (Terrapoda). The analysis presented here
complements previous phylogenetic analyses by extending the degree of detailed research
further up the early tetrapod stem. That notion that the unique tree topology presented her
is due to the increased use of postcranial characteristics is supported by the small scale
analysis of Coates et al. (2002), that only used postcranial characteristics of early
tetrapods as a basis for phylogenetic analysis.

Minimisation of the confounding effects of non-phylogenetic variation

The overall level of homoplasy within the data set of Ruta et al. (2003) is much higher
than the one presented here (Appendix 16: Table 17). This may be due to several causes,
including: the use by Ruta et al. (2003) of proportion-based characters that attempt to
partition continuous variation, the inclusion by Ruta et al. (2003) of both cranial and
postcranial characters that describe morphogenetic or phenotypic rather than phylogenetic
variation, or to lack of assessment by Ruta et al. (2003) of the morphogenetic stage of
specimens when coding postcranial characters, thus confusing immaturity with
plesiomorphy (Chapter 4). The results of the main analysis presented here are far more
parsimonious both in tree length and consistency index than the analysis of Ruta et al.
(2003) (Appendix 16: Table 17), which indicates that efforts to minimise the amount of
non-phylogenetic variation (in both cranial and postcranial characters) in the data set of
this analysis were successful.
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Taxon sample

Changing the taxon list from that of the main analysis to that of Ruta et al. (2003) did not result in a marked change in overall tree topology (Appendix 16: Figure 88), indicating that the tree topology produced in this main analysis does not result from the taxon sample, but rather from the characters and coding used in this analysis.

Postcranial material in the basal Neospondyli

Within the early tetrapod taxa represented in the phylogenetic analyses the postcranial skeleton of Temnospondyli most closely resembles that of the basal Neospondyli (Seymouriamorpha and Cotylosauria) (Pawley and Warren, 2006). The lack of published material on the postcranial skeleton of taxa within the Seymouriamorpha and Cotylosauria has been addressed by some recent publications (Berman et al., 1998; Klembara and Bartik, 2000; Berman et al., 2004). The postcranial skeletons of many taxa of basal taxa within the basal Neospondyli are not thoroughly described however, and this analysis benefited greatly from personal observation of postcranial material, especially that of *Seymouria* spp. and the North American *Diadectes* spp. (Appendix 12). The major published description of the postcranial skeleton of *Seymouria baylorensis* (White, 1939) is erroneous and misleading in some respects if the reconstructions of the postcranial skeleton of *S. baylorensis* are compared with the specimens they are based on. Surprisingly, although postcranial material of *Diadectes* spp. is common in museums, a thorough description of the postcranial skeleton has yet to be published, so that most of the coding for the data matrix (Appendix 15) was taken directly from specimens. Previous lack of attention to the postcranial skeletons of temnospondyls, seymouriamorphs and diadectomorphs may have been influenced by the lack of easily available, detailed publications, so that the results of this analysis have been affected by the increased effort made to gather data on the postcranial skeletons of these taxa.

‘Reptiliomorph’ postcranial characters

Several postcranial characteristics have been used to classify taxa of uncertain phylogenetic affinities as ‘reptiliomorphs’ (Carroll, 1970; Smithson et al., 1994; Lebedev and Coates, 1995; Paton et al., 1999; Ruta et al., 2003). As discussed in the taxonomic definitions, ‘reptiliomorph’ is a vague term used to describe taxa considered to be ancestral to the amniote lineage, rather than ancestral to the lissamphibian lineage. As Ruta et al. (2002) pointed out, all of the following ‘reptiliomorph’ character states are also found in temnospondyls: ventrally joined pleurocentra (m TRU VER), dorsally joined pleurocentra (m TRU VER 9), cervical ribs straight and with expanded distal ends (RIB 2, plesiomorphic), curved trunk ribs (RIB 3), parasternal process (INTCLA 1), high degree of humeral torsion (HUM 19), reduced dorsal iliac blade (ILI 3), and the transverse pelvic ridge (ILI 7). The ‘L’ shaped tarsal intermedium (TAR 3) is plesiomorphic for tetrapods more derived than ichthyostegamorphs, and an astragalus (m TAR 6), is an apomorphy of Neospondyli more derived than Seymouriamorpha, but the phalangeal count for the manus 2,3,4,5,4 is unknown in most archeriamorphs and is plausibly plesiomorphic. A separate coracoid and scapular blade is a transitional morphogenetic feature also found in temnospondyls and is probably plesiomorphic for tetrapods (Chapter 4).

Clack and Finney (2005) raised issues concerning the correct articulation of the cleithrum in reconstructions of early tetrapods. In articulated temnospondyl specimens, the cleithral stem is always located between the dorsal clavicular process and the
scapulocoracoid (Chapter 4). Examination of other articulated early tetrapod specimens such as the archeriamorph *Archeria crassidisca* (AMNH 7117), the seymouriamorphs *Seymouria baylorensis* (White, 1939), *Kotlassia prima* (Bystrow, 1944), *Discosauriscus austriacus* (Klembara and Bartik, 2000), the cotylosaurs *Limnoscelis paludis* (Williston, 1911a), *Diadectes absitus* (Berman et al., 2004), *Diadectes* spp. (Case, 1911b), *Orobates pabsti* (Berman et al., 2004), and the microsaur *Pantylus cordatus* (Carroll, 1968) indicates that they all have the pectoral girdle elements articulated in the same way as temnospondyls. The evidence would imply that articulation of the cleithrum between the clavicle and scapulocoracoid is ubiquitous for early tetrapods, including the amniote stem.

**Convergent evolution of the terrestrial postcranial skeleton**

All phylogenetic analyses to date implicitly imply that the similarities of the postcranial skeleton observed in the Temnospondyli and the Neospondyli is convergently derived (analyses up to 2003 summarised in Ruta et al., 2003; Klembara and Ruta, 2004a, 2004b; Vallin and Laurin, 2004; Warren and Turner, 2004; Clack and Finney, 2005; Klembara, 2005), with the exception of the postcranial analysis of Coates et al. (2002). This convergent evolution is based on the unification of the Anthracosauria and Seymouriamorpha, which excludes the Temnospondyli to a more basal position with the early tetrapods. As noted in the introduction, the phylogenetic position of the Temnospondyli within early tetrapods is highly unstable, and no previous author has suggested postcranial characteristics that would exclusively unite the Temnospondyli with any particular group of early tetrapods.

One previous analysis of early tetrapods has questioned the implications that other hypotheses of early tetrapod relationships have on our interpretation of the evolutionary of the early tetrapod postcranial skeleton (Laurin, 1998b). Of all the literature on early tetrapods, only Romer (1957), and Olson (1976) have explicitly stated that they consider the postcranial skeletons of the Temnospondyli and the Neospondyli to be convergently derived, but neither provided any justification for their point of view. No explicit discussion of this problem has ever been published, so that despite the lack of support for the unification of the Temnospondyli and the Neospondyli (Terrapoda) in previous phylogenetic analyses, there is a complete lack of supporting arguments for ‘convergent’ evolution of the postcranial skeleton in these taxa.

The Seymouriamorpha, the most basal taxa within the Neospondyli, are traditionally united with the more plesiomorphic Anthracosauria by the presence of two characteristics that are derived relative to more basal tetrapods: the presence of a parietal-tabular suture, and the relative enlargement of the pleurocentrum. Panchen (1980) argued that the parietal-tabular suture was convergent, and arrived at by different developmental processes, the results of the main analysis (Figure 62) support this observation. The other characteristic, the enlarged pleurocentrum (relative to the intercentrum) is clearly prone to homoplasy within early tetrapods, particularly the Temnospondyli (see above, Chapter 5), and thus cannot be used as an unambiguous synapomorphy uniting the Anthracosauria and Seymouriamorpha.

Convergent evolution in other taxa is clearly marked by the retention of plesiomorphies that allow ancestry to be determined. For example, the Tasmanian tiger, a marsupial, is similar in overall size and shape to a wolf from the northern hemisphere, and displays many of the same adaptations for a similar hunting lifestyle. On casual inspection, the skeletons of the two are highly alike in size and shape. The true ancestry of the Tasmanian tiger, however, is readily determinable by the many characteristics of its skeleton that clearly and unambiguously identifies it as a marsupial, for example, the
Tasmanian tiger possesses epipubic bones, which are ubiquitous in marsupials, but unknown in placental taxa such as wolves.

Within early tetrapods, there is no evidence whatsoever for convergent evolution in the postcranial skeletons of the Temnospondyli and the Neospondyli, particularly when the absence of derived states due to the morphogenetic immaturity of specimens is taken into account. The Anthracosauromorpha possess several apomorphic characteristic of the postcranial skeleton (Appendix 17), none of which are present in the Neospondyli (e.g. HUM 27, SCACOR 10), and which would provide evidence of a relationship between the two if they were present in the Neospondyli and not the Temnospondyli.

Most interestingly, there are no postcranial apomorphies of the Temnospondyli, and all derived postcranial characteristics of temnospondyls, relative to archeriamorphs, are also present in at least the basal Neospondyli. This suggests that the derived characteristics of the postcranial skeleton of the Temnospondyli are plesiomorphic for the Neospondyli. The basal Neospondyli are differentiated from the Temnospondyli by derived characteristics of the vertebrae, which are not present in any archeriamorphs, and are only present (if at all) in derived temnospondyls (e.g. grossly enlarged pleurocentra fused to the neural arch, swollen neural arches).

The evidence suggests that, despite the novel position of the Temnospondyli in this analysis, the derived characteristics of the postcranial skeleton of the Temnospondyli, relative to archeriamorphs, are highly unlikely to be attributable to convergence.

**Cranial characteristics supporting the Terrapoda**

Several cranial characteristics unite the basal Terrapoda (Appendix 17), also listed below. Of particular interest are the characteristics that pertain to changes in the otic region of the skull and the stapes. These cranial characteristics are particularly intriguing, because they may be associated with the development hearing in the terrestrial environment (last reviewed by Clack, 2002a, 2002d), and they are also associated with a large number of changes in the postcranial skeleton, which may also represent increasing adaptation to the terrestrial environment. Although cranial characters are not the focus of this investigation, the characteristics listed below are definitely worthy of further investigation.

**Synapomorphies:** Sensory canals absent (SC SK 1). Sensory canals (where present) not enclosed (SC SK 2). Presence of postparietal-exoccipital suture (POSTPAR 5). Squamosal with broad, concave semicircular embayment (SQU 3). Stapes is a distally elongated rod (STAP 1). Pterygoid with postero-lateral flange (PTE 9). Parasphenoid without posterolaterally directed, ventral thickenings (ridges ending in basal tubera) (reversed in Cotylosauria) (PASPHE 3). Absence of parasympophysial plate (uncertain in Caerorhachis bairdi) (PSYM 1).

**Revision of vertebral taxonomy in early tetrapods**

Laurin and Reisz (1999), proposed that if temnospondyls were sister taxa to their ‘Tetrapoda’ (Seymouriamorpha plus Cotylosauria plus Lepospondyli in the main analysis presented here) rather than stem taxa to the Embolomeri, that a re-evaluation of current ideas about vertebral centrum evolution among early tetrapods would be necessary; in agreement with Laurin and Reisz, a revision is presented here. This analysis supports the traditional view that vertebral structure is the most useful postcranial characteristic for classification of taxa within the Terrapoda, but does not support the traditional taxonomic use of vertebral structure within a larger group that includes more basal tetrapods.
Historically, centrum type is the postcranial characteristic most commonly used for taxonomic purposes (e.g. Watson, 1919; Watson, 1926; Romer, 1947; Panchen, 1967; Parrington, 1967; Panchen, 1977a). Four vertebral types are commonly recognised in early tetrapods, rhachitomous, embolomerous, gastrocentrous, and stereospondylous. Rhachitomous (plesiomorphic) and embolomerous centra (Anthracosauria, Temnospondyli: Tupilakosauridae), are diplospondylous (Arratia et al., 2001), in that each centrum is composed of two components. In gastrocentrous (Neospondyli, some temnospondyls) and stereospondylous (derived temnospondyls) centra, the pleurocentrum, or intercentrum is much larger than its respective counterpart, so that there is one major unit per vertebral segment (essentially monospondylous).

Within the Temnospondyli, departures from the rhachitomous type of centrum always involves an increased degree of ossification, sometimes to the extent that the centra become amphicoelous discs, as in embolomerous, gastrocentrous and stereospondylous centra. Phylogenetically, the most parsimonious explanation for this wide range of morphological variation is that the cartilaginous precursors of the rhachitomous centra formed subequal amphicoelous pleurocentral and intercentral discs (Chapter 4). No major change in morphogenetic development is necessary to derive monospondylous centra from diplospondylous centra, merely changes in the proportions of the vertebral components (Wake, 1970; Chapter 4).

The rhachitomous centrum is consequently best described as a poorly ossified diplospondylous centrum. The same interpretation of the cartilaginous parts of the centrum could apply to all taxa with rhachitomous centra, which implies that all early tetrapods with diplospondylous centra have an essentially similar centrum structure. Other than in temnospondyls, the centra of the Anthracosauria is the only other examples of a high degree of ossification of diplospondylous centra (Figure 65). The morphology of individual amphicoelous centra (both intercentra and pleurocentra) of temnospondyls is similar to that of embolomeres (e.g. Clack, 1987a; Holmes, 1989a), which supports the hypothesis that the only major difference between rhachitomous and embolomeres centra is the degree of ossification. Note that as the neural arch is never known to articulate with or fuse to the intercentrum in early tetrapods (Warren and Snell, 1991; Chapter 5), so the single centrum of lepospondyls is most parsimoniously a pleurocentrum, in agreement with Williams (1959) and Laurin (1998c).

The degree of ossification of diplospondylous centra is subject to morphogenetic as well as phylogenetic variation (Holmes, 1984; Chapter 4), so this characteristic should be treated with caution for taxonomic purposes. The comparative analyses excluding these historically important vertebral characteristics from phylogenetic analysis (Appendix 6) indicate that their removal has no impact on tree topology. Consequently, the most phylogenetically significant characteristic of the centra are the differences between diplospondylous and the two monospondylous centrum types (TRU VER 33).

**Phylogenetic affinities of Caerorrhachis bairdi and Casineria kiddi**

*Caerorrhachis bairdi* is most likely a basal temnospondyl, based on cranial and postcranial characteristics, and none of the features of the postcranial skeleton listed as ‘reptiliomorph’ by Ruta et al. (2002) would preclude it from inclusion within the Temnospondyli (Chapter 5). Characteristics of basal temnospondyls, observable in *Caerorrhachis bairdi*, but absent in most ‘reptiliomorphs’, include: denticle shargreen covering entire palate, reduced vomerine tusks, the presence of interpterygoid vacuities, lack of a parietal-tabular suture, the skull table firmly fused to the cheek, and an ilium with a post-iliac process, but lacking a dorsal extension.
Caerorhachis bairdi (Holmes and Carroll, 1977; Ruta et al., 2002) and Casineria kiddi (Paton et al., 1999) both from the Carboniferous of Scotland, are indistinguishable based on the available evidence. Although the exact locality of the specimen of Caerorhachis bairdi cannot be determined, reasonable estimates place it in the Namurian, which is younger than Casineria kiddi from the Asbian. The localities of the specimens are not the same, but both come from the Edinburgh region of Scotland.

Caerorhachis bairdi and Casineria kiddi are similar in overall size, and particularly similar in vertebral structure. Both have ventrally fused pleurocentra, which have been independently derived within the Temnospondyli at least four times (Chapter 5). The neural arches are of the simple plesiomorphic form found in temnospondyls. They are not swollen or triangular in lateral view, and the arches are not fused to the centra, as is characteristic of the basal Neospondyli, including the Captorhinomorpha, which were proposed as the closest relatives of Casineria kiddi by Paton et al (1999). The centra of taxa within the Neospondyli consist of a grossly enlarged pleurocentrum that takes up almost the whole centrum length (monospondyous) and small or absent intercentra. Diplospondylous centra are unknown within the Neospondyli. The centra of Caerorhachis bairdi and Casineria kiddi are proto-embolomeric (diplospondylous), most resembling those of the basal Anthracosauria, but embolomeric and gastrocentrous vertebral centra are also found in temnospondyls (Chapter 5). The humerus of Casineria kiddi is waisted with a high degree of torsion, indicating that Casineria kiddi is a member of the Terrapoda, and eliminating it from the Anthracosauria and Gephyrostegidae. The form of the ilium of both Caerorhachis bairdi and Casineria kiddi most closely resembles that of the Dendrerpetontidae. The available evidence strongly indicates that both Caerorhachis bairdi and Casineria kiddi are basal temnospondyls.

The phylogenetic analysis (Figure 62) strongly supports this hypothesis; a bootstrap support of 81% and Bremer node value of five for this node indicates that this phylogenetic position is unlikely to be incorrect, despite the incomplete nature of both specimens. As in Caerorhachis bairdi, none of the postcranial characteristics claimed to be ‘reptiliomorph’ in Casineria kiddi are truly apomorphic for the amniote lineage. All are present in temnospondyls (Chapter 5), or potentially may be present in basal temnospondyls (including the five digit manus), because they are plesiomorphic for early tetrapods.

Phylogenetic affinities of the Lissamphibia

The evidence supporting conflicting hypotheses regarding the phylogenetic affinities of the Lissamphibia was most recently discussed by Schoch and Milner (2004). The results of this analysis are consistent with the findings of Schoch and Milner (2004), and do not provide any extra evidence that would assist in clarifying the phylogenetic affinities of the Lissamphibia. Most of the meagre postcranial evidence form this analysis, particularly vertebral structure, supports derivation of the Lissamphibia from within the Lepospondyli (Appendix 16: Figure 89, Figure 91). No postcranial evidence links the Lissamphibia to the Temnospondyli. Most the problems encountered in clarifying the phylogenetic affinities of the Lissamphibia arise from the state of preservation of specimens, but even three dimensional postcranial material (Evans and Borsuk-Bialynicka, 1998; Borsuk-Bialynicka and Evans, 2002) is too derived to be informative as to phylogenetic affinities. Postcranial characters that may be of interest to future researchers are included in the character state list (Appendix 14).
Terrestrial capabilities of early tetrapods

The hypothesis of early tetrapod relationships presented here implies that at least three major evolutionary transitions occurred during the evolution of the postcranial skeleton of early tetrapods. Clusters of phylogenetic characters indicate major changes in the postcranial skeleton, present at the nodes defining the major postcranial morphotypes, which form a morphological transformation series that may be associated with changes in locomotor style. The results of this analysis support the arguments of Eaton (1960) who proposed that the emergence of tetrapods onto land involved a series of gradual changes, rather than one major adaptive event.

One of the major drawbacks of using phylogenetic analysis for interpreting evolutionary patterns is that gradual evolutionary changes do not make good phylogenetic analysis characters, because continuous morphological gradients do not separate neatly into discrete character states. Phylogenetic analysis consequently tends to reinforce the ‘punctuated equilibrium’ theory of evolution, rather than gradual evolution. Many potentially useful postcranial characteristics were discarded during the preparation of this analysis because they did not separate neatly into discrete character states; for example, the cnemial crest is much steeper sided and well developed in the Terrapoda, but is only a low rounded bump in archeriamorphs (Figure 78). The difference between ‘low and rounded’ and ‘large and well developed’ is impossible to define, with some taxa such as Archeria crassidisca (Romer, 1957) somewhat intermediate. Characteristics such as this may have important functional implications for assessment of locomotor capacity. The results of this analysis should therefore be treated with caution if interpretations of locomotor capacity are made on the basis of the data presented here. Keeping these limitations in mind, the evidence presented here supports a series of associated changes in the postcranial skeleton of early tetrapods.

There is no agreement among early tetrapod workers as to the terrestrial capabilities of the earliest tetrapods. Research on the postcranial skeletons of tetrapodomorph fish indicates that their robust fins could have been used to anchor the body in terrestrial locomotion (Boisvert, 2005). In complete disagreement, the first tetrapods are considered to not have weight bearing limbs and most likely evolved their limbs for use in shallow water, only later co-opting them for use on land (Coates and Clack, 1990). The transition from straight, relatively inflexible fins to limbs with elbow and ankle joints is much greater than the simple change in morphology presented here. The functional change that is required is drastic. Fins are not adapted to resist the gravitational forces of gravity, and the main propulsive force in fish comes from the axial muscles. In extant lower tetrapods such as salamanders and primitive reptiles, the limbs support the head, trunk, and tail off the ground and provide part of the propulsive effort. The series of changes to the postcranial skeleton presented here suggests a gradual transition from fish to tetrapods capable of efficient terrestrial locomotion. However, many of the evolutionary steps involved in the evolution of terrestrial locomotion remain vague.

Reconstructions of musculature in temnospondyls and neospondyls (Romer, 1922; Miner, 1925; Olson, 1936b; Holmes, 1977) are based on the musculature of salamanders and lizards, but not that of fish. No reconstructions of musculature exist for more basal early tetrapods. The postcranial skeleton of extant salamanders and lizards is far more derived than that of any early tetrapod included in this analysis, so that the musculature of early tetrapods could be expected to be correspondingly be more plesiomorphic and fishlike. Most reconstructions of musculature was conducted when tetrapods more basal than temnospondyls were unknown (Romer, 1922; Miner, 1925; Olson, 1936b) except for more recent work on the relatively derived captorhinids (Holmes, 1977). The older
reconstructions need revised in the light of the more recent evidence that the postcranial skeleton of early tetrapods is significantly more fish–like than was considered possible 70 or more years ago.

The most serious problem with the current work on the locomotor capabilities of early tetrapods is the complete lack of integration between the fossil data and the extensive experimental literature on biomechanics of locomotion in extant taxa such as fish, salamanders, and lizards. An exhaustive search of the literature failed to find a single example of the application of research into the locomotion of any extant taxon to the specific anatomical characteristics of any fossil taxon, or vice versa. Consequently current statements on the locomotor capacities of early tetrapods are almost entirely speculative. Likewise, experimental studies of the biomechanics of locomotion in extant taxa ubiquitously use salamanders as the closest living examples of early tetrapods, despite the fossil data indicating without doubt this assumption is incorrect, and that extant salamanders are highly derived relative to any early tetrapod. Interpretations of locomotor capacity in early tetrapods need to synthesise the anatomical data presented by the fossil record with experimental data on the biomechanics of locomotion in extant fish and extant basal tetrapods such as salamanders and lizards. The summary of previous work presented here highlights the limitations imposed by the current lack of integration between the fossil data and experimental work on extant taxa, in that many of the published statements of locomotor capacity in early tetrapods are inconsistent with data from extant taxa.

**Locomotor style**

Edwards (1977) and Pridmore (1995) discussed the feasibility of various gait types in the fish to tetrapod transition, conclusively arguing that the plesiomorphic gait in fish and tetrapods is the walking trot (diagonally opposite feet meet the ground together), powered by axial undulation. As the walking trot requires both feet to be lifted from the substrate simultaneously, Pridmore (1995) argued that the walking trot would be only effective in ichthyostegamorphs if the belly was not lifted from the substrate. The evolution of the lateral sequence walk (diagonally opposite feet lifted one at a time) would have coincided with elevation of the trunk from the substrate during terrestrial locomotion.

The lateral sequence walk is the most stable and effective gait for terrestrial locomotion, but is slower than the walking trot. The reduction in friction achieved by reducing contact with the substrate results in an increase in speed that more than compensates for the slower speed of the lateral sequence walk. Increased axial rigidity improves the effectiveness of the lateral sequence walk (Edwards, 1977), but any increase in axial rigidity reduces the effectiveness of the axial undulation necessary for aquatic locomotion. The evolution of changes to the axial skeleton that increase rigidity in early tetrapods may be correlated with decreasing use of aquatic locomotion and increasing efficiency of terrestrial locomotion.

**Axial skeleton**

Ahlberg et al. (2005) proposed that the reduced degree of lateral flexion in the trunk of *Ichthyostega stensoei*, caused by the proximally expanded ribs, may be an adaptation to increase the rigidity of the trunk for terrestrial locomotion. “Two gaits seem theoretically possible: ‘walking’ with diagonally synchronised limb movements and rigid elevated trunk; and a bilaterally symmetrical ‘shuffling’ or ‘inchworm’ movement” (Ahlberg et al., 2005: p 139). The evidence presented above implies that *Ichthyostega stensoei* may
plausibly have used the lateral sequence walk, based on the possibility that it may have been capable of lifting the trunk at least a short distance from the substrate. The evidence does not support the interpretation of ‘inchworm’ locomotion. The evolutionary advantages of ‘inchworm’ locomotion, or how it could possibly have evolved, were not discussed by Ahlberg et al. (2005). It seems implausible that *Ichthyostega stensoei* would go to the evolutionary effort to develop dorsoventral flexion when the plesiomorphic axial undulation suffices for all other lower tetrapods.

The evidence presented in this analysis does not provide any evidence of the locomotor capacities of archeriamorphs. The limbs of archeriamorphs are less paddle-like than those of ichthyostegamorphs, but they are not obviously designed for weight bearing either (discussed below), so that any discussion of locomotor style in archeriamorphs would be entirely speculative.

Weight bearing limbs are present in all temnospondyls (see below), typically associated with the plesiomorphic (for tetrapodomorph fish and tetrapods) rhachitomous vertebrae. Some temnospondyls display a number of modifications of the axial skeleton, including shortening of the trunk, monospondylous (gastrocentrous) centra, expanded ribs, increased height of neural spines and paramedian osteoderms. These modifications may be adaptations to increase locomotor efficiency in terrestrial environments while retaining the degree of lateral undulation necessary for aquatic locomotion. Modifications to improve axial rigidity are present only in medium-sized temnospondyl taxa that lack lateral line sulci and possess well-ossified limbs, and are typically considered terrestrial (Chapter 5). The possession of weight bearing limbs and improved axial rigidity implies the use of the lateral sequence walk, however the evolution of weight bearing limbs in temnospondyls is not correlated with the axial modifications to increase rigidity, these are present only in derived temnospondyls. The evidence implies that temnospondyls were capable of a lateral sequence walk, but most temnospondyls retained the high degree of axial undulation necessary for efficient aquatic locomotion, consistent with an amphibious lifestyle.

All taxa within the Neospondyli possess weight bearing limbs, correlated with increased axial rigidity achieved through the development of functionally monospondylous, rather than diplospondylous, vertebral centra. The reduction of the number of centra per vertebral segment from two to effectively one by dramatically increasing the size of the pleurocentra would effectively reduce the flexibility of the vertebral column. The most basal neospondyls are characterised by laterally expanded “swollen” neural arches and alternation of neural spine height, again, these modifications from the plesiomorphic condition may be associated with a modified locomotor style (Sumida, 1990, 1997). The evidence presented here indicates that the evolution of the lateral sequence walk may be correlated with the development of weight bearing limbs. Modifications to the axial skeleton to improve rigidity involved a trade off with the reduction in the efficiency of aquatic locomotion, and occurred only after weight bearing limbs were present.

*Appendicular skeleton*

The tetrapodomorph fish *Panderichthys rhombolepis* has distinctly fin-like limbs designed for anchoring and substrate traction, but not weight bearing (Vorobyeva and Kuznetsov, 1992; Boisvert, 2005). The paddle-like limbs of ichthyostegamorphs also cannot be flexed from the elbow to lie in a load bearing posture (Coates and Clack, 1990; Coates, 1996; Clack, 1997), and were probably held horizontally from the body (Figure 81.1).
The fish to tetrapod transition involves a change in the proportions of the fore and hind limb. In fish, the forelimb is longer than the hind limb; in tetrapods, the reverse is true. This change occurs between *Panderichthys rhombolepis* (tetrapodomorph fish) and *Acanthostega gunnari* (tetrapod). Boisvert (2005) interpreted *Panderichthys rhombolepis* as ‘front wheel driven’, and tetrapods such as *Acanthostega gunnari* as ‘rear wheel driven’. Evidence from extant salamanders does not support the assumption that all tetrapods are ‘rear wheel driven’. Evans (1946) found that various species of salamanders rely mainly on axial propulsion, only the fore legs provide any propulsive power, and the hind legs are incapable of doing much more than elevating the trunk and tail. Early tetrapods may have plausibly relied mainly on axial undulation to power locomotion, as in fish, with both the fore and hind limbs mainly acting as props. The increase in the length of the hind limb is not necessarily correlated with a transition to ‘rear wheel drive’ locomotion, the propulsive power of the limbs of early tetrapods has yet to be studied.

The change in limb proportions between the fins of *Panderichthys rhombolepis* and the limbs of *Acanthostega gunnari* may also be explained in terms of the necessity to place the fore and hind feet an equivalent lateral distance apart. The feet need to be approximately the same distance apart in obligate quadrupeds that employ a sprawling gait, in order to minimise yaw during forward progression. The body shape of all early tetrapods is similar to that of most fish, which are torpedo shaped with a large head tapering to a narrow tail, a design that maximises hydrodynamic efficiency. The pectoral girdle is wider than the pelvic girdle, and in order for the front and hind feet to be an equivalent distance apart, the hind limbs have to be longer than the forelimbs. The evidence would imply that although the limbs of *Acanthostega gunnari* were paddle like, and not weight bearing, the increase in hind limb length correlates with an improvement in the efficiency of terrestrial locomotion over that of tetrapodomorph fish such as *Panderichthys rhombolepis*.

The distal limb elements of ichthyostegamorphs are dorsoventrally flattened, with the anterior edge slightly thickened, a design which would reduce hydrodynamic drag. [Note, the radial condyle of *Ichthyostega stensoei* is anteroventral (Clack et al., 2003a), contra Jarvik (1996)]. The shoulder joints in both the tetrapodomorph fish *Panderichthys rhombolepis* (Vorobyeva and Schultze, 1991) and the ichthyostegamorph *Acanthostega gunnari* (Coates and Clack, 1995) are hinge like rather than rotary. Ahlberg et al. (2005) proposed that *Ichthyostega stensoei* was an early and ultimately unsuccessful attempt at tetrapod adaptation for terrestrial locomotion. The results of this study support this finding, *Ichthyostega stensoei* is the only ichthyostegamorph or archeriamorph to display some of the derived postcranial characteristics otherwise found only within the Terrapoda. In particular, *Ichthyostega stensoei* has a supraglenoid fossa (m SCACOR 8), and the anterior edge of the supra/infraglenoid buttress is dorsally oriented (m SCACOR 15). These features are otherwise only known in the Terrapoda, and may be adaptations for weight bearing, which supports the hypothesis that it may have employed the lateral sequence walk, discussed above.

The limbs of archeriamorphs are more flexible than those of ichthyostegamorphs, with an apparently rotary shoulder joint, and joints at elbow and knee, however, Romer (1957) and Holmes (1980) both observed that the forelimbs of the archeriamorphs *Archeria crassidisca* and *Proterogyrinus scheelei*, respectively, could not be bent into a right angle at the elbow (Figure 81.2). Romer (1957) considered that the foreleg of *Archeria crassidisca*, with its low degree of humeral torsion was well suited to being retracted against the body during aquatic locomotion, but was not well suited to terrestrial locomotion due to the “greater difficulty of bringing the forearm and front foot forward into proper walking position” (Romer, 1957, p 148). Holmes (1980) disagreed with
Figure 81. Early tetrapod limbs. All left limbs in left lateral view, 1, forelimb, 2, hind limb. 1, Acanthostega gunnari, after Coates (1996). 2, Archeria crassidisca, after Romer (1957). 3, Eryops megacephalus, after Miner (1925), 4, Captorhinus aguti, after Holmes (2003). Not to scale.
Romer’s interpretation, describing the forelimb of *Proterogyrinus scheelei* as permanently flexed, and unable to be retracted against the trunk, which would make it only suitable for terrestrial locomotion. The weight bearing capacity of this type of limb has yet to be determined, but is unlikely to be as effective as a fully flexed limb which positions the manus underneath the elbow, as in the Terrapoda. Archeriamorphs are therefore transitional between the inflexible limbs of ichthyostegamorphs and the fully flexed limbs of terrapods.

Effective bracing against downwardly directed gravitational forces requires that the lower limb align with the force it is resisting, i.e. perpendicular to the ground. The lower limbs are certainly capable of being arranged this position in the Terrapoda. Functional interpretations of locomotion in terrapods (Romer, 1922; Miner, 1925; Schaeffer, 1941; Holmes, 1977, 1984, 2003) indicate that although the humerus undergoes considerable rotation during the step cycle, there are no functional wrist or ankle joints, rather a flexible manus and pes (Holmes, 1977, 2003). These studies indicate that the limbs of the Terrapoda are load bearing (Figure 81.2) and that the style of locomotion was probably similar to that of the sprawling gait of extant salamanders and reptiles. The anterior distal limb elements (radius and tibia) are column shaped rather than flattened, thus increasing the load bearing capacity of the limb.

Only changes to the axial skeleton occur within the Neospondyli. The lack of phylogenetic change in the appendicular skeleton supports the hypothesis that the limbs of the Temnospondyli and Neospondyli were capable of efficient terrestrial locomotion. Note that even Terrapod taxa as derived as pelycosaurs retain a similar appendicular skeleton to that of morphogenetically mature neospondyls (e.g. Romer and Price, 1940). Secondarily aquatic Terrapoda (temnospondyls and nectridians) do not retain, or convergently re-evolve, the plesiomorphic features of the postcranial skeleton observed in ichthyostegamorphs and archeriamorphs. Secondarily aquatic Terrapoda possess a limb structure similar to that of their terrestrial ancestors, the main adaptations of the postcranial skeleton are an anteriorly enlarged interclavicle and clavicles, and reduced ossification of the endochondral postcranial skeleton (paedomorphosis) (Pawley, in press).

The great diversity of the Terrapoda, with the three main lineages of temnospondyls, stem amniotes and lepospondyls, are all present in the Carboniferous, implying that the development of the fully terrestrial limb may have given them an evolutionary advantage, and allowed them to colonise terrestrial habitats previously unoccupied by vertebrates. Of these groups, temnospondyls are the most plesiomorphic, so they are the first fully terrestrial vertebrates.

This analysis also makes one important final point, that fossil material already described and in collections can provide much valuable information for resolution of phylogenetic relationships of early tetrapods. The results of this analysis support the observation by Ruta et al. (2003) that a scrutiny of the available evidence will be the most productive strategy, and that limits to our knowledge imposed by the lack of relevant fossils (Carroll, 2000b, 2001) are no longer a major impediment to our understanding of the evolution of early tetrapods.

**CONCLUSIONS**

The morphological transformation series presented here indicates a series of further modifications to the postcranial skeleton, beyond the development of the tetrapod limb, were necessary before the evolution of efficient terrestrial locomotion. The
Temnospondyli are the most basal members of the most derived group, the Terrapoda, and are the most plesiomorphic vertebrates with weight bearing limbs capable of efficient terrestrial locomotion. The increased inclusion of postcranial characters and the minimisation of the confounding effects of morphogenetic variation provide a strong phylogenetic signal, resulting in a robust and unambiguous interpretation of the phylogenetic relationships of early tetrapods.

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