Chapter 11

Bones, molecules, and crown-tetrapod origins

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ABSTRACT

The timing of major events in the evolutionary history of early tetrapods is discussed in the light of a new cladistic analysis. The phylogenetic implications of this are compared with those of the most widely discussed, recent hypotheses of basal tetrapod interrelationships. Regardless of the sequence of cladogenetic events and positions of various Early Carboniferous taxa, these fossil-based analyses imply that the tetrapod crown-group had originated by the mid- to late Viséan. However, such estimates of the lissamphibian–amniote divergence fall short of the date implied by molecular studies. Uneven rates of molecular substitutions might be held responsible for the mismatch between molecular and morphological approaches, but the patchy quality of the fossil record also plays an important role. Morphology-based estimates of evolutionary chronology are highly sensitive to new fossil discoveries, the interpretation and dating of such material, and the impact on tree topologies. Furthermore, the earliest and most primitive taxa are almost always known from very few fossil localities, with the result that these are likely to exert a disproportionate influence. Fossils and molecules should be treated as complementary approaches, rather than as conflicting and irreconcilable methods.

Introduction

Modern tetrapods have a long evolutionary history dating back to the Late Devonian. Their origins are rooted into a diverse, paraphyletic assemblage of lobe-finned bony fishes known as the ‘osteolepiforms’ (Cloutier and Ahlberg 1996; Janvier 1996; Ahlberg and Johanson 1998; Jeffery 2001; Johanson and Ahlberg 2001; Zhu and Schultze 2001). The monophyletic status of the Tetrapoda and that of its major constituent clades – lissamphibians and amniotes – is supported by a large number of morphological characters and by a wide range of molecular data (e.g. Duellman and Trueb 1986; Panchen and Smithson 1987, 1988; Duellman 1988; Gauthier *et al.* 1988a,b; Milner 1988, 1993; Hedges *et al.* 1990; Carroll 1991; Trueb and Cloutier 1991; Hedges and Maxson 1993; Hay *et al.* 1995; Laurin and Reisz 1997, 1999; Feller and Hedges 1998; Laurin 1998a–c; Hedges and Poling 1999; Pough *et al.* 2000). The early evolutionary history of the lissamphibian and amniote crown-groups has been the subject of detailed scrutiny (e.g. Laurin 1991; Laurin and Reisz 1995; Báez and Basso 1996; Lee 1995, 1997a,b; Rieppel and deBraga 1996; deBraga and Rieppel

1997; Gao and Shubin 2001), but the phylogenetic placement of some groups is not agreed upon, as exemplified by current debates about the position of turtles relative to other amniotes (e.g. Reisz and Laurin 1991; Lee 1993, 1995, 1996, 1997a,b; Laurin and Reisz 1995; Rieppel and deBraga 1996; deBraga and Rieppel 1997; Platz and Conlon 1997; Zardoya and Meyer 1998; Hedges and Poling 1999; Rieppel and Reisz 1999; Rieppel 2000).

The last twenty years have witnessed a revived interest in early tetrapod interrelationships. New discoveries and a refinement of phylogenetic techniques have broadened our understanding of the anatomy and intrinsic relationships of several groups. Research in this field has had a significant impact on the shaping of the tetrapod stem-group (Lebedev and Coates 1995; Coates 1996; Ahlberg and Johanson 1998; Johanson and Ahlberg 2001) and has led to the recognition of a previously unsuspected diversity of Mississippian taxa (e.g. Clack 1994, 1998a–d, 2001, 2002; Milner and Sequeira 1994; Rolfe *et al.* 1994; Smithson 1994; Smithson *et al.* 1994; Lombard and Bolt 1995; Clack and Finney 1997; Paton *et al.* 1999; Bolt and Lombard 2000; Clack and Carroll 2000). However, the interrelationships of the vast majority of Palaeozoic groups are still intensely debated. Lack of congruent results in the most widely discussed, recently published phylogenetic analyses is astonishing. Traditional views on the taxonomic memberships of the lissamphibian and amniote stem-groups (Bolt 1969, 1977, 1979, 1991; Heaton 1980; Panchen and Smithson 1987, 1988; Milner 1988, 1993; Trueb and Cloutier 1991; Carroll 1995; Coates 1996; Lee and Spencer 1997; Sumida 1997; Clack 1998a–d; Paton *et al.* 1999) have been challenged repeatedly, notably in a series of recent papers by Laurin and Reisz (1997, 1999), Laurin (1998a–c) and Laurin *et al.* (2000a,b). As a result, no consensus has emerged on the position of several groups relative to the lissamphibian–amniote phylogenetic split.

The ancestry of lissamphibians, as well as the status and mutual relationships of the three modern lissamphibian orders, are particularly controversial topics (see discussions in Carroll and Currie 1975; Duellmann and Trueb 1986; Duellmann 1988; Bolt 1991; Milner 1988, 1993, 2000; Feller and Hedges 1998; Laurin 1998a–c; Carroll 2000, 2001; Anderson 2001). Several authors have suggested that some or all of the lissamphibian orders are related to dissorophoids, a group of Permo-Carboniferous and Lower Triassic temnospondyls (e.g. Bolt 1969, 1977, 1979, 1991; Lombard and Bolt 1979; Bolt and Lombard 1985; Milner 1988, 1990, 1993, 2000; Trueb and Cloutier 1991; Boy and Sues 2000; Holmes 2000; Rocek and Rage 2000a,b; Yates and Warren 2000; Gardner 2001). However, much discussion centres on the identity of the immediate sister taxon to frogs, salamanders, and caecilians (also known as gymnophionans). The temnospondyl theory of lissamphibian origin has been revived recently by Carroll (2001) and Carroll and Bolt (2001). These authors hypothesize that the ancestry of frogs and salamanders is rooted into two distinct families of dissorophoids, the amphibamids and branchiosaurids, respectively. Caecilians, however, are thought to be related to tuditanomorph microsaurs (one of the most diverse groups of lepospondyls). In particular, the Lower Permian genus *Rhynckonkos* has been regarded as the most derived stem-group gymnophionan (Carroll and Currie 1975; Carroll and Gaskill 1978; Milner 1993; Carroll 2000, 2001). In Laurin's (1998a–c) and Laurin and Reisz's (1997, 1999) analyses, temnospondyls are a plesion on the tetrapod stem-group (see also below), whereas lepospondyls form a paraphyletic array of stem-lissamphibians. Within this paraphyletic array, lysorophids (long-bodied, Pennsylvanian to Lower Permian tetrapods characterized by a broad orbitotemporal fenestration; Wellstead 1991) are considered to be the nearest Palaeozoic relatives of crown-lissamphibians.

The evolutionary implications of alternative hypotheses of early tetrapod relationships will be considered elsewhere together with a new, comprehensive cladistic analysis recently completed by the authors (Ruta *et al.*, in press). A summary of the results of this analysis (Figure 11.1) and a review of the chronology of major events in the evolutionary history of early tetrapods are presented here. We explore the implications of conflicting phylogenetic hypotheses on estimates of the time of divergence between lissamphibians and amniotes, and compare morphology-based 'time trees' (for the use of this term, equivalent to Smith's 1994, X-trees, see Hedges 2001) with those deriving from recent molecular analyses (e.g. Feller and Hedges 1998; Kumar and Hedges 1998; Hedges 2001). Several questions are addressed in this chapter:

(1) Do different morphology-based cladistic analyses of primitive tetrapods imply different chronological estimates of the separation between lissamphibians and amniotes, or the origin of the lissamphibian and amniote crown-groups?
(2) Are palaeontological and molecular time trees in serious conflict with each other, and what is the source of this conflict?
(3) What is the bearing of fossils on time tree reconstruction, especially when integrated with the results of molecular analyses?

Materials and methods

Which consensus for early tetrapods?

In a series of seminal papers, Smithson (1985), Panchen and Smithson (1987, 1988), Milner (1993), and Ahlberg and Milner (1994) discussed the pattern of character disribution in the apical part of the tetrapod stem-group and in the basal portion of the crown-group. A common feature of these studies is the separation of most Palaeozoic tetrapods into two distinct lineages ultimately leading to lissamphibians and amniotes. Several subsequent analyses (Carroll 1995; Lebedev and Coates 1995; Coates 1996; Clack 1998b,d; Paton *et al.* 1999) have supported the basal dichotomy between these two clades (see Laurin 1998a, Laurin and Reisz 1999, Clack 2000, and Clack and Carroll 2000, for a historical perspective on the classification of early tetrapods). Panchen and Smithson's (1988) scheme of relationships is the most eloquent example of a balanced cladogram (*sensu* Smith 1994): major tetrapod clades are equally distributed on the 'batrachomorph' and 'reptiliomorph' branches of the crown-group (equivalent to the lissamphibian and amniote stem-groups, respectively; see Coates 1996). According to Panchen and Smithson (1988), the evolutionary separation between lissamphibians and amniotes is a Late Devonian event, since the Famennian *Ichthyostega* appears as the least derived plesion on the lissamphibian stem-group. Other stem-lissamphibian plesions include, in crownward order, nectrideans (Bossy and Milner 1998), colosteids (Smithson 1982; Hook 1983; Godfrey 1989), microsaurs (Carroll and Gaskill 1978), and temnospondyls (Milner 1988, 1990, 1993). In Panchen and Smithson's (1988) scheme, baphetids (Beaumont 1977; Beaumont and

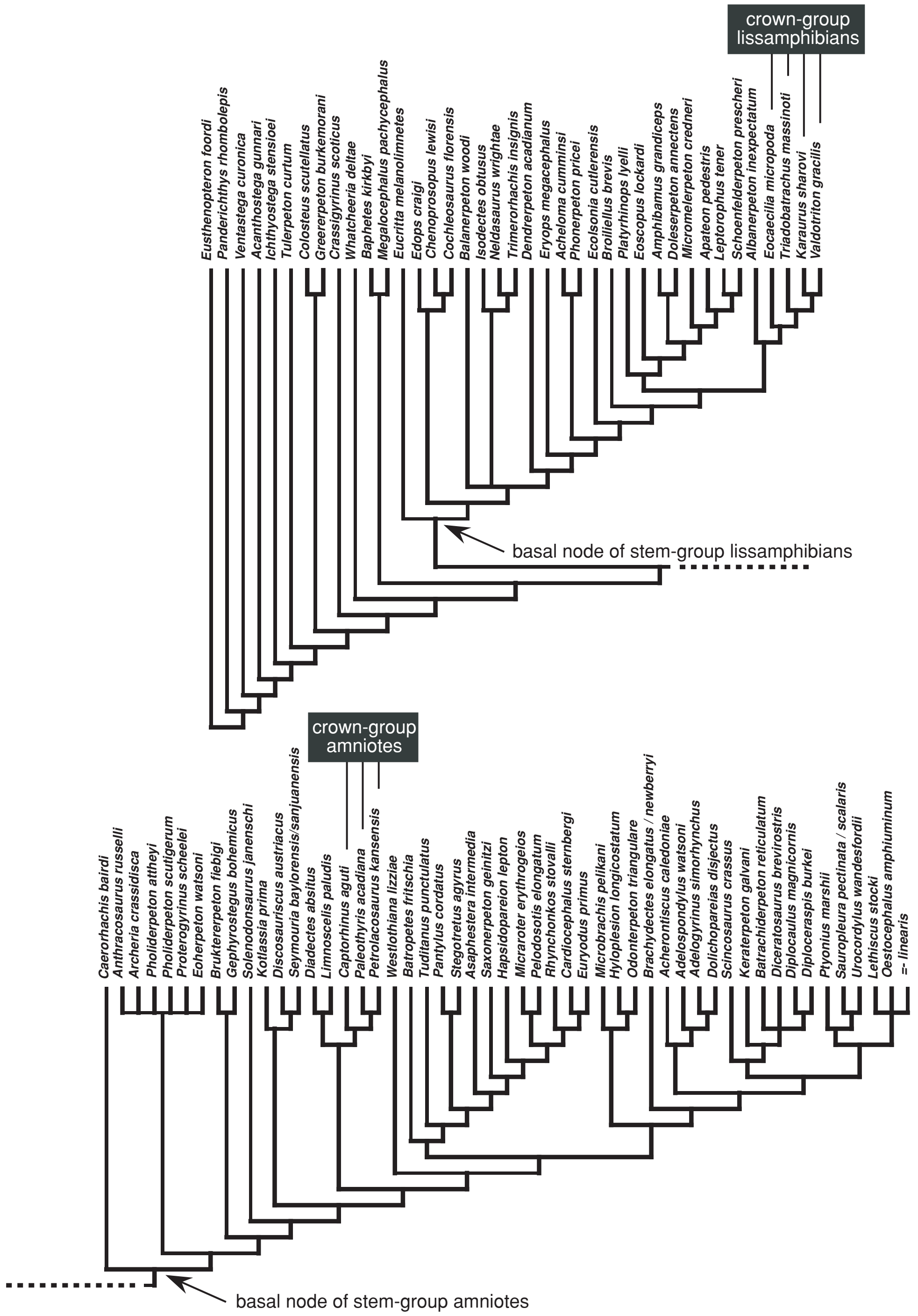

Figure 11.1 Strict consensus of 60 most parsimonious trees derived from a PAUP* analysis (Ruta *et al.* in press). The stem-tetrapod and lissamphibian portions of the trees are in the upper half of the figure, the amniote portion in the lower half.

Smithson 1998; Milner and Lindsay 1998), anthracosauroids (Smithson 1985, 2000), seymouriamorphs (Laurin 2000), and diadectomorphs (Romer 1946; Heaton 1980; Berman *et al.* 1992, 1998; Lombard and Sumida 1992) are progressively more derived stem-amniotes.

A series of key discoveries have been instrumental in redefining our concept of the most primitive tetrapods as well as in our understanding of the pattern of morphological change at the 'fish'–tetrapod transition (e.g. Coates and Clack 1990, 1991; Coates 1996; Jarvik 1996; Clack 1998b). As a result, the stem-tetrapod affinities of most Devonian taxa, including *Acanthostega* and *Ichthyostega*, are now universally accepted (but see Lebedev and Coates 1995, and Coates 1996, for a discussion of the possible stem-amniote affinities of *Tulerpeton*). Regardless of the phylogenetic placement of Devonian taxa, comparisons between the most recent published phylogenies reveal a drastic shift from dichotomously branching to pectinate tree topologies, implying an increase in the number of stem-group branching events. The studies of Ahlberg and Milner (1994), Carroll (1995), Lebedev and Coates (1995), Coates (1996), Clack (1998b,d), and Paton *et al.* (1999) support Panchen and Smithson's (1988) conclusions with regard to the basal dichotomy of Palaeozoic groups. These analyses tackle such diverse problems as the broad pattern of relationships between major tetrapod groups (Carroll 1995), the reconstruction of the sequence of anatomical changes in taxa spanning the 'fish'–tetrapod transition (Lebedev and Coates 1995; Coates 1996), and the placement of various problematic Mississippian tetrapods (e.g. *Crassigyrinus*, *Whatcheeria*, *Eucritta*) known to display a mixture of characters otherwise considered to be unique to separate clades (Clack 1998b,d, 2000, 2001, 2002; Paton *et al.* 1999).

Laurin and Reisz's (1997, 1999) and Laurin's (1988a–c) analyses have cast doubt on the deep separation of Palaeozoic tetrapods between lissamphibian-related and amniote-related taxa. Their cladograms suggest that several early tetrapods, such as *Crassigyrinus*, *Tulerpeton*, *Whatcheeria*, and baphetids, are equally closely related to lissamphibians and amniotes. These results challenge long-recognized patterns of character change and distribution near the base of the tetrapod crown-clade. In particular, traditional groups such as temnospondyls, embolomeres, gephyrostegids, and seymouriamorphs are regarded as discrete radiations preceding the lissamphibian–amniote phylogenetic split. The fossil membership of Laurin and Reisz's (1997, 1999) and Laurin's (1988a–c) crown-group is smaller than in previous works. Importantly, lissamphibians now sit at the crownward end of a paraphyletic assemblage of lepospondyls, in contrast with previous suggestions that the latter may form a highly diverse clade of stem-amniotes (Carroll 1995; but see also Carroll 2001). Anderson's (2001) analysis agrees with Laurin and Reisz's (1997, 1999) and Laurin's (1988a–c) conclusions that lepospondyls are stem-lissamphibians (although only *Eocaecilia* is used in Anderson's work), and that seymouriamorphs, embolomeres, and temnospondyls (represented, respectively, by *Seymouria*, *Proterogyrinus*, and a clade consisting of *Balanerpeton* and *Dendrerpeton*) are progressively less derived stem-tetrapod plesions. The diadectomorph *Limnoscelis* identifies the stem-amniote branch of Anderson's (2001) cladogram (Berman 2000; Clack and Carroll 2000, and references therein).

Very few early tetrapod groups have survived the intense phylogenetic reshuffling of recent analyses. Among those that have, diadectomorphs appear repeatedly as the nearest relatives of crown-amniotes; likewise, the stem-tetrapod affinities of colosteids and most Devonian forms have been retrieved consistently by different authors, despite differences in taxon sample size and the use of contrasting character ordering, weighting, and coding regimes (see also Ruta *et al.*, in press). These data suggest (although not conclusively) that some regions of the tetrapod tree are better corroborated and more stable than others (Panchen and Smithson 1987, 1988; Sumida and Lombard 1991; Berman *et al.* 1992; Lombard and Sumida 1992; Sumida *et al.* 1992; Laurin and Reisz 1997, 1999; Lee and Spencer 1997; Sumida 1997; Berman *et al.* 1998; Berman 2000, Laurin 1998a–c; Paton *et al.* 1999; Clack 2001).

Methodological note

The strict consensus topologies deriving from the most widely discussed published data sets including *Caerorhachis* are considered here (Figures 11.2–11.7). The strict consensus trees resulting from our new analysis (Figures 11.8–11.9) and from experiments of character removal (Figure 11.10) are also illustrated. As in Ruta *et al.*'s (2001) paper, Lebedev and Coates' (1995) and Clack's (1998b, d) analyses have been omitted, since they are superseded by Coates' (1996) and Paton *et al.*'s (1999) works, respectively. Strict consensus trees are plotted on a stratigraphical scale resolved down to stage level (geological timescale based on Briggs and Crowther, 2001, and references therein). For simplicity, stages are drawn to the same length, and not proportional to their actual duration, although dates in millions of years before present (Ma) are appended, where possible, to stage names. In addition, the known ranges of major early tetrapods groups are used (Benton 1993), instead of specific occurrences of individual species. The use of whole ranges permits rapid and easy comparisons between tree shapes, and circumvents the problem of comparing time trees built on different taxon samples for each group. Internodes within monophyletic groups are represented by vertical bars of fixed, arbitrary length (except where ghost ranges are present; Smith 1994). This length represents merely a graphical expedient and does not imply an equal time for the origin of adjacent nodes. It has, however, the inconvenient effect of generating chronologically 'deep' origin events for some groups, depending upon the number of internodes and the placement of the stratigraphically oldest members of a group. Since the actual time occurring between adjacent nodes is unknown, the age of a node leading to two sister taxa is conservatively taken to coincide with the age of the older taxon.

Where species or genera are used as Operational Taxonomic Units (OTUs), it is possible to identify the point of divergence between sister groups, even if whole stratigraphical ranges are employed. For example, in Anderson's (2001) tree, the stem-caecilian *Eocaecilia micropoda* is the sister taxon to brachystelechid microsaurs. Therefore, the divergence of caecilians can be graphically plotted *within* the stratigraphical range of microsaurs instead of at the base of such a range (Figure 11.7). Paraphyletic groups pose problems when whole ranges are used. A possible way around this consists of splitting the ranges of large groups into the smaller ranges in which their component subgroups occurred. For simplicity, however, only total ranges are employed here, whereas paraphyletic groups are denoted by names in inverted commas.

With regards to Coates' (1996) analysis, Ruta *et al.* (2001) pointed out that introduction of corrected scores for digit number and coronoid fangs in some taxa

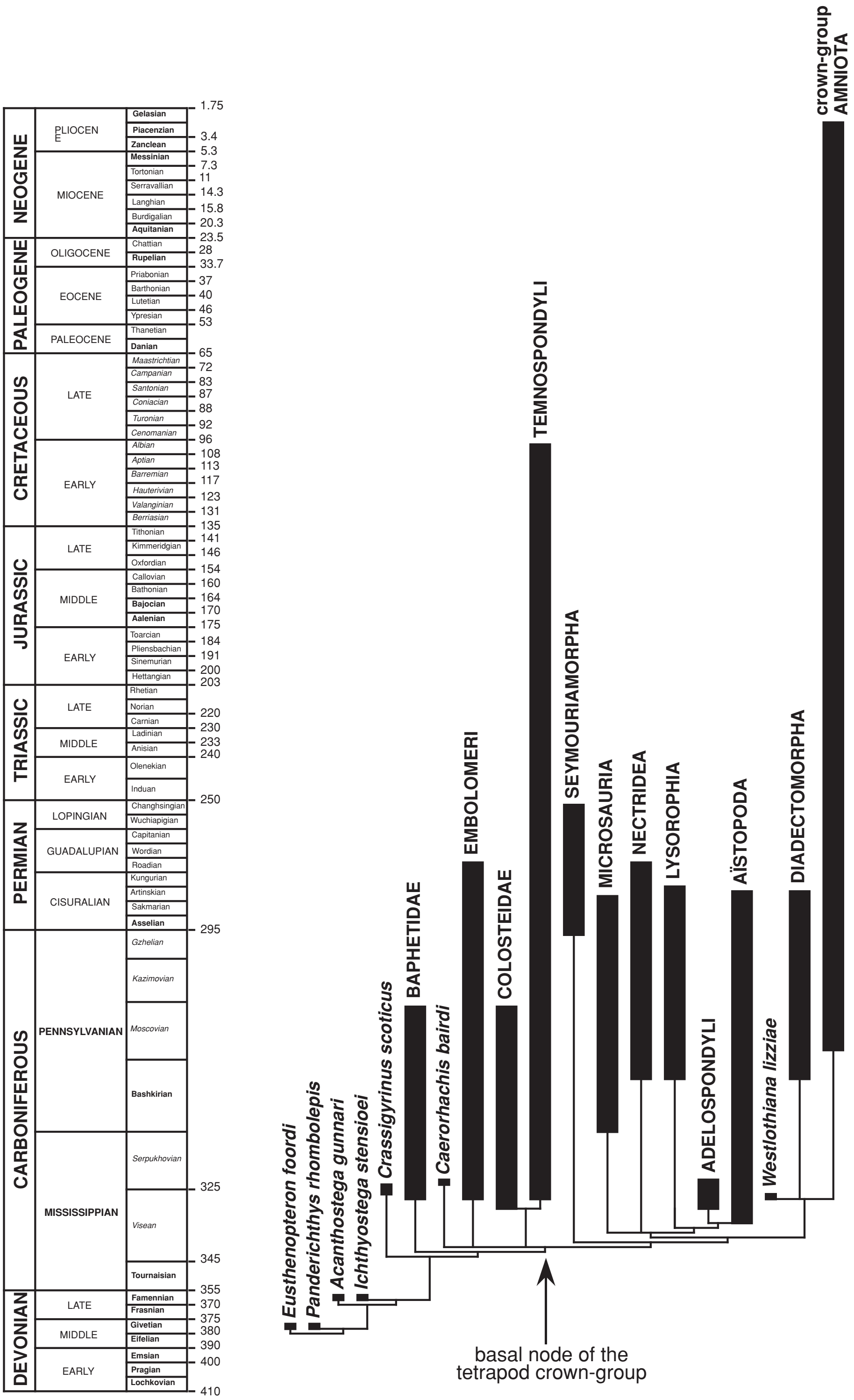

Figure 11.2 Carroll's (1995) analysis plotted on a timescale.

causes loss of phylogenetic resolution among the majority of post-panderichthyid Devonian tetrapods (*Tulerpeton* appears as a basal stem-amniote; Figure 11.3). It can be shown, however, that such poor resolution is due exclusively to the unstable position of *Metaxygnathus* and *Ventastega*. The branching sequence of remaining Devonian taxa is the same as that retrieved by Coates (1996).

Ahlberg and Clack's (1998) analysis (Figure 11.4) poses additional difficulties, because several traditional groups (notably anthracosaurs and temnospondyls) appear as polyphyletic, overlapping arrays of taxa (comments in Ruta *et al.* 2001). However, an expanded version of their dataset (see Appendix 11.1 for a list of the new characters added and their description) retrieves traditional groups after a reweighted run. The strict consensus of the resulting five equally parsimonious trees is discussed here (Figure 11.11), instead of Ahlberg and Clack's original consensus cladogram. A single origin for anthracosaurs and temnospondyls is obtained after analysing their expanded matrix. Lower jaw data can be shown to carry phylogenetic signal in derived portions of the tetrapod tree as well as in the crownward portion of the stem-group. However, the degree to which this signal matches that yielded by other characters is, at present, difficult to evaluate. The impact of lower jaw characters on tree topology must await exhaustive treatment of additional data (e.g. Bolt and Lombard 2001) coded for a larger number of taxa.

Definition and content of Tetrapoda

Any fossil taxon that can be shown, based on a formal character analysis, to be phylogenetically more closely related to extant lissamphibians *and* amniotes than to any other extant monophyletic group is, by definition, a stem-group tetrapod. If a fossil taxon is more closely related to *either* lissamphibians *or* amniotes, it is a crown-group tetrapod (Hennig 1966; Jefferies 1979; Craske and Jefferies 1989). Justification in support of a total-group (or stem-based) clade Tetrapoda will be provided elsewhere (Ruta *et al.*, in press; but see discussions in Ahlberg and Clack 1998, Laurin *et al.* 2000a,b, and Anderson 2001 for alternative nomenclatural solutions).

Briefly, we do not advocate an apomorphy-based definition of Tetrapoda that excludes the 'fish-like' portion of the tetrapod stem-group (Ahlberg and Clack 1998), nor do we restrict the name Tetrapoda to the crown-clade (Laurin 1998a). Instead, we favour an operational definition (Coates *et al.* 2000), whereby all taxa that belong in the total-group of the extant clade Tetrapoda, but which are not members of the crown-group, are simply referred to as stem-group tetrapods (see also Budd 2001; Jeffery 2001).

Fossil evidence for the origin of crown-tetrapods

With few exceptions, published analyses postulate that the origin of the tetrapod crown-group had occurred by the mid- to late Viséan (e.g. Paton *et al.* 1999). A Late Devonian divergence between lissamphibians and amniotes was first proposed by Panchen and Smithson (1987, 1988), who interpreted *Ichthyostega* as a basal stem-group lissamphibian (see also above). Lebedev and Coates (1995) and Coates (1996) also suggested that the origin of the tetrapod crown-group was a Late Devonian event, but in this case, the hypothesized divergence time was based upon their interpretation of the

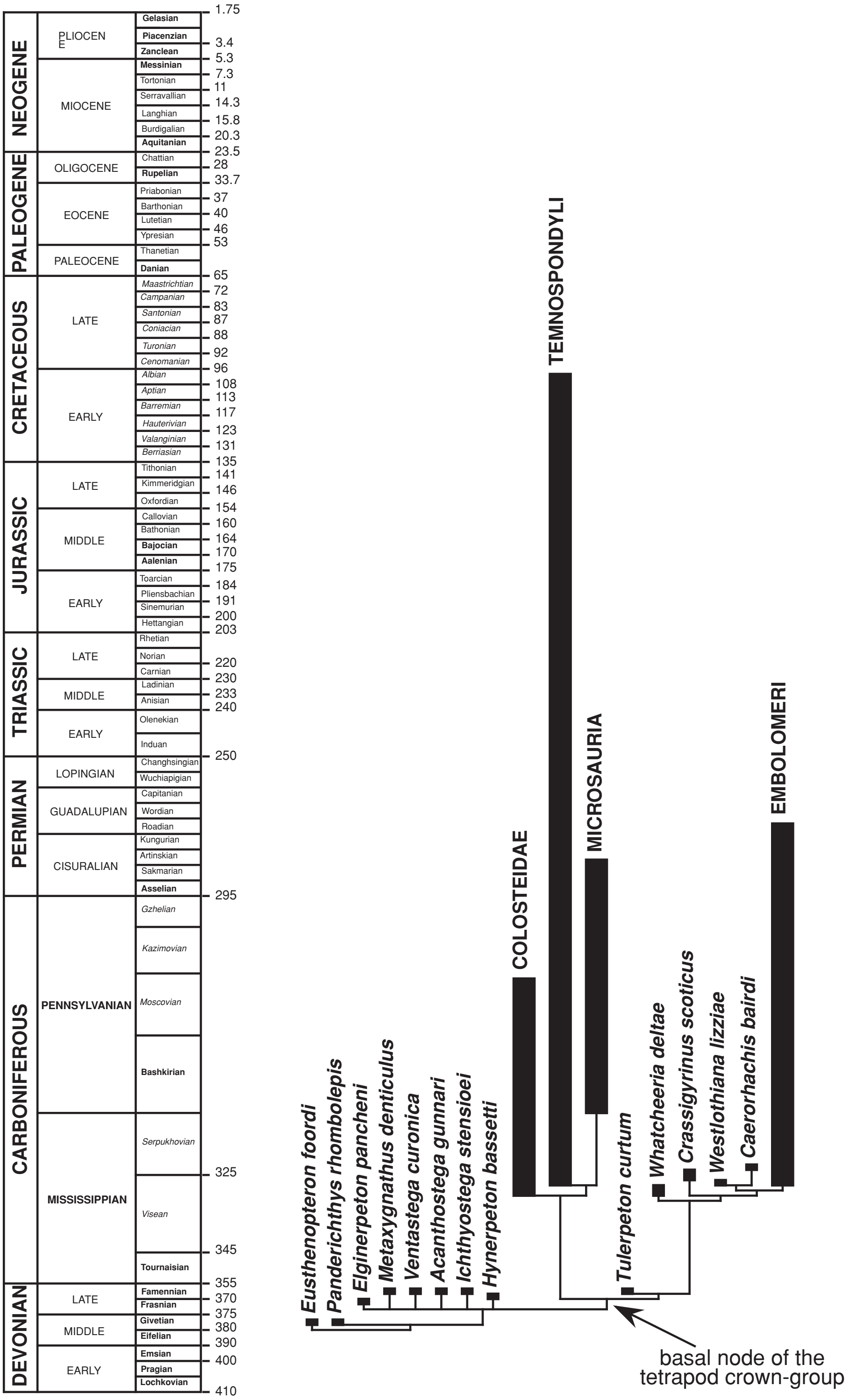

Figure 11.3 Coates' (1996) analysis plotted on a timescale.

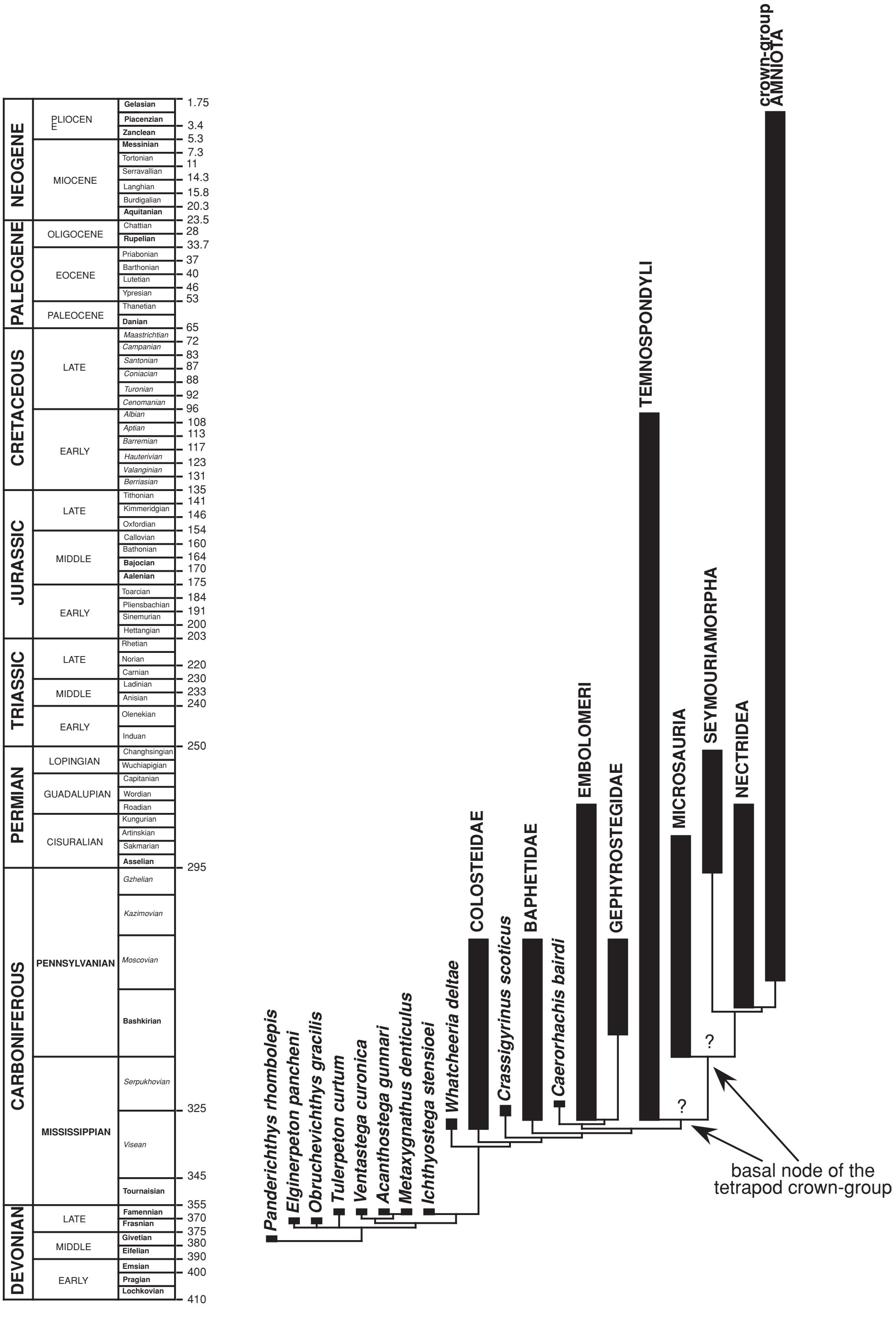

Figure 11.4 Ahlberg and Clack's (1998) analysis plotted on a timescale. The two arrows point to the positions of the basal node of the tetrapod crown-group based upon the derivation of lissamphibians from a lepospondyl or a temnospondyl ancestor.

Famennian *Tulerpeton curtum* (Lebedev 1984) as a stem-group amniote (see also Clack and Carroll 2000). *Tulerpeton* has been neglected in most recent analyses, despite the fact that it is known from well preserved, although incomplete, postcranial material (see Lebedev and Clack 1993 and Ahlberg and Clack 1998 for a discussion of cranial and lower jaw elements attributed to this taxon). However, subsequent studies (e.g. Ahlberg and Clack 1998; Clack 2002; Ruta *et al.*, in press) concur in assigning *Tulerpeton*, as well as all other Devonian taxa, to the tetrapod stem-group. Nevertheless, we acknowledge that hypotheses of a Late Devonian separation between lissamphibians and amniotes are consistent with some recent molecular analyses (e.g. Kumar and Hedges 1998; Hedges 2001).

Mississippian tetrapods are rare. Incomplete remains from the mid-Tournaisian site of Horton Bluff, Nova Scotia (Clack and Carroll 2000), are the oldest documented examples, but these specimens cannot be diagnosed unambiguously as 'batrachomorph' or 'reptiliomorph'. Some isolated humeri appear to be morphologically intermediate between those of *Tulerpeton* (Lebedev and Coates 1995) and the 'anthracosauroid' *Eoherpeton* (Smithson 1985; Clack and Carroll 2000), while others are more similar to colosteid humeri (Godfrey 1989). Additional specimens include femora as well as endochondral and dermal shoulder girdle elements. Recently discovered, mid-Viséan remains from central Queensland represent the only record of Carboniferous tetrapods from East Gondwana (Thulborn *et al.* 1996). Although fragmentary, this fauna is thought to include the earliest known representatives of colosteids and 'anthracosauroids' (*fide* Thulborn *et al.* 1996; Clack and Carroll 2000).

The next oldest Mississippian record is represented by a *Whatcheeria*-like animal from the late Tournaisian of Scotland (Clack and Finney 1997). Like *Whatcheeria* (Lombard and Bolt 1995; Bolt and Lombard 2000), the new tetrapod reveals an array of 'reptiliomorph', 'batrachomorph', and primitive features. The manual character analysis of Lombard and Bolt (1995) and the computer-assisted analyses of Coates (1996), Clack (1998b,d), and Paton *et al.* (1999) concur in assigning *Whatcheeria* to the basal portion of the 'reptiliomorph' branch of the tetrapod tree. Certain recent, comprehensive analyses (Laurin and Reisz 1997, 1999; Laurin 1998a–c; Anderson 2001) have ignored *Whatcheeria*. Other studies, including Ahlberg and Clack's (1998) and our own (Ruta *et al.*, in press), suggest that *Whatcheeria* is a stem-tetrapod. The exceptional preservation and abundant material of *Whatcheeria* provide an important data source for comparative anatomical and phylogenetic studies of early tetrapods. The sequence of branching events in the crownward part of the tetrapod stem-group is the subject of much current debate and may ultimately lead to a re-assessment of the polarity of several characters. A detailed study of *Whatcheeria* and the new *Whatcheeria*-like animal from the Scottish Tournaisian will certainly prove to be crucial in this respect.

Casineria kiddi, a 340 million years old, incomplete skeleton from Gullane, Cheese Bay, Scotland (lower part of late Viséan), is the next animal to be considered. Regarded as the earliest undisputed amniote, it is the oldest tetrapod showing a pentadactyl forelimb, and predates the uppermost Viséan fauna from the Scottish site of East Kirkton (see below). Its relatively low, squared off neural spines are reminiscent of those of such primitive 'anthracosauroids' as *Silvanerpeton* and *Eldeceeon* (Clack 1994; Smithson 1994), whereas its long, curved ribs, separate scapular and coracoid ossifications and proportions of the manus are similar to those of certain embolomeres and various basal crown-group amniotes. However, different combinations of these features have also been observed in other taxa, such as certain microsaurs and *Whatcheeria* (Carroll and Gaskill 1978; Lombard and Bolt 1995; Bolt and Lombard 2000). Although Paton *et al.*'s (1999) cladistic analysis identified *Casineria* as a basal amniote, it is noteworthy that it failed to resolve its position relative to such diverse taxa as *Westlothiana*, *Captorhinus*, *Petrolacosaurus*, and *Paleothyris* (Ruta *et al.*, in press).

Several other taxa with possible 'reptiliomorph' affinities have been included in our analysis. *Westlothiana lizziae* from East Kirkton is usually regarded as one of the most primitive stem-group amniotes (Smithson 1989; Smithson and Rolfe 1990; Smithson *et al.* 1994). However, Laurin and Reisz (1999) placed this taxon as the closest outgroup to the tetrapod crown-clade. Conversely, our analysis strengthens Smithson *et al.*'s (1994) conclusions and offers a novel perspective for interpreting the puzzling mixture of 'lepospondyl' as well as basal amniote features in *Westlothiana* (see also the analysis in Anderson 2001). *Caerorhachis bairdi*, probably from the lowermost Serpukhovian of Scotland, was originally described as a basal temnospondyl (Holmes and Carroll 1977), but has been reinterpreted as a basal stem-amniote by Ruta *et al.*, in press (see also discussion in Milner and Sequeira 1994; Coates 1996).

The late Viséan *Crassigyrinus scoticus* has been the subject of controversy ever since its discovery. Panchen (1985) and Panchen and Smithson (1990) redescribed its cranial and postcranial anatomy. Panchen and Smithson (1988) placed it on the 'reptiliomorph' branch of their tetrapod cladogram, either as sister taxon to 'anthracosauroids', or as sister taxon to a clade encompassing 'anthracosauroids' and seymouriamorph as sister group to diadectomorphs plus crown-group amniotes. Further preparation of the material resulted in a reassessment of the morphology of the palate (Clack 1996), snout, and skull roof (Clack 2000) leading to the recognition of an array of plesiomorphic features. Some recent analyses (Coates 1996; Clack 1998b,d; Paton *et al.* 1999), place *Crassigyrinus* as a basal embolomere, whereas Laurin and Reisz (1997, 1999), Ahlberg and Clack (1998) and Laurin (1998a–c) identify it as a crownward stem-tetrapod. The latter conclusion is also supported by Ruta *et al.* (in press).

The nature of the conflict

From the account above, it is clear that the base of the tetrapod crown-group has uncertain boundaries. In fact, only the amniote affinities of *Casineria* (see also below) remain uncontroversial. The existence of incongruent tree topologies is due to several causes that are not mutually exclusive. The use of incomplete or poorly preserved taxa is likely to result in multiple, equally parsimonious solutions. While implicitly assumed in all fossil-based studies, the influence of such taxa on cladogram topology remains largely unexplored (but see Wilkinson 1995; Anderson 2001; Kearney 2002). However, as demonstrated by Coates (1996), incomplete taxa (e.g. *Hynerpeton*; Daeschler *et al.* 1994) do not necessarily behave as 'rogue' OTUs. Sometimes, the presence of just one unambiguous synapomorphy is sufficient to stablize the affinities of fragmentary material.

Another potential source of character conflict is the fact that various taxa sharing features with two or more different groups deliver confounding signals. In simple cases, variations in the taxon sample are likely to affect the outcome of an analysis through 'attraction' of such 'chimaera'-like taxa. However, the effects of taxon and/or character deletions/inclusions are not predictable. In those cases in which an optimal 'balance' of taxa and characters is achieved, the position of key fossils may remain unresolved. Clack's (2001) analysis provides an excellent example of this taxon/character interplay. Specifically, a clade consisting of *Eucritta* and baphetids forms a trichotomy with temnospondyls and a diverse group including *Crassigyrinus*, *Whatcheeria*, gephyrostegids, and embolomeres (but see also Clack 1998a) in the two equally parsimonious trees discussed by Clack (2001).

Several groups of early tetrapods are so specialized that they provide little or no indication as to their possible ancestry or sister group. Carroll (2001) has emphasized this observation repeatedly, identifying the apparent excess of apomorphies and widespread homoplasy as responsible for obscuring relationships among basal crown-group tetrapods. However, while homoplasy might be widespread, we think it unlikely that the current tetrapod database contains insufficient phylogenetic signal. Thus, a quick inspection of published analyses reveals that the structure of several matrices is not random. A comparison between two of the most comprehensive datasets – Carroll's (1995) and Laurin and Reisz's (1999) – serves to illustrate this point. Despite the use of different taxon and character samples, Carroll's (1995) and Laurin and Reisz's (1999) cladograms are mostly congruent. Crown-lissamphibians are placed among lepospondyls in Laurin and Reisz's study, but are excluded from Carroll's analysis. If lissamphibians are not taken into account, the sequences of branching events in Carroll's (1995) and Laurin and Reisz's (1999) tree topologies are remarkably similar. Minor differences concern the mutual relationships of the lepospondyl orders, the position of *Westlothiana* (grafted to a diadectomorph–amniote clade in Carroll's analysis, but sister taxon to a diadectomorph–amniote–lepospondyl clade in Laurin and Reisz's) and the pattern of sister group relationships between baphetids, colosteids, and temnospondyls (all three groups branch from adjacent nodes in both analyses). It is also noteworthy that (excluding Laurin and Reisz's location of lepospondyls) the branching sequence in the basal stretch of the putative stem-amniote groups (e.g. embolomeres, gephyrostegids, seymouriamorphs, *Westlothiana*) resembles that proposed by several earlier authors (e.g. Lombard and Sumida 1992; Smithson *et al.* 1994; Lee and Spencer 1997; Sumida 1997).

Results

A new analysis for early tetrapods

Recent advances in our knowledge of early tetrapod anatomy have contributed to an expanded and refined database (Trueb and Cloutier 1991; Coates 1996; Laurin and Reisz 1997, 1999; Ahlberg and Clack 1998; Clack 1998b; Laurin 1998a–c; Lombard and Bolt 1999; Paton *et al.* 1999; Bolt and Chatterjee 2000; Schoch and Milner 2000; Yates and Warren 2000; Bolt and Lombard 2001). In our analysis, we have sought to use the maximum practical range of taxon exemplars, consistent with methodological arguments arising from a series of recent studies (Nixon and Davis 1991; Anderson 2001; Prendini 2001; Salisbury and Kim 2001; Ruta *et al.* in press).

The new data matrix encompasses 90 tetrapod species coded for 213 cranial and 94 postcranial characters. The results support the hypothesis of a deep evolutionary split between stem-lissamphibians and stem-amniotes. Further major features of these results are summarized as follows (Figure 11.1):

(1) The post-panderichthyid part of the tetrapod stem-group includes, in crownward order, *Ventastega curonica*, *Acanthostega gunnari*, *Ichthyostega stensioei*, *Tulerpeton curtum*, Colosteidae, *Crassigyrinus scoticus*, *Whatcheeria deltae*, and Baphetidae.
(2) *Caerorhachis bairdi*, embolomeres, gephyrostegids, *Solenodonsaurus janenschi*, seymouriamorphs, a clade consisting of *Westlothiana lizziae* plus lepospondyls, and diadectomorphs are progressively more crownward stem-amniotes.
(3) Within lepospondyls, microsaurs are paraphyletic relative to lysorophids, adelospondyls (including *Acherontiscus*), and a clade encompassing nectrideans plus aïstopods.
(4) *Eucritta melanolimnetes* is basal to temnospondyls, which form a paraphyletic array of taxa relative to crown-lissamphibians.
(5) Albanerpetontids and a diverse dissorophoid clade consisting of branchiosaurids, micromelerpetontids, and amphibamids are successively more outlying sister groups of crown-lissamphibians.
(6) Caecilians are the sister group to a salientian–caudate clade.

The tetrapod crown-group is bracketed at its base by *Eucritta* and *Caerorhachis*, a pair of Scottish taxa noted for their mixture of features otherwise considered to be characteristic of such different groups as temnospondyls, baphetids, and 'anthracosauroids' (Clack 1998b, 2001; Ruta *et al.* 2001). A comprehensive treatment of the characters and results of the new analysis is presented elsewhere (Ruta *et al.* in press). PAUP* 4.0b10 (Swofford 1998; see Ruta *et al.*, in press for details of the search settings used) finds 60 shortest trees at 1303 steps. If *Casineria* (Paton *et al.* 1999) and *Silvanerpeton* (Clack 1994) are included in the analysis, then a strict consensus of the resultant 120 equally parsimonious trees shows considerable loss of resolution in the basal part of the amniote stem-group. The polytomy subtends *Casineria*, *Silvanerpeton*, embolomeres, gephyrostegids, *Solenodonsaurus*, *Discosauriscus*, *Kotlassia*, and *Seymouria*. However, an agreement subtree shows that *Silvanerpeton* branches from the amniote stem between *Caerorhachis* and embolomeres (see also Clack 1994), but that *Casineria* is a 'rogue' taxon. Despite its uncertain placement, *Casineria* emerges, consistently, as a stem-amniote, in partial agreement with Paton *et al.*'s (1999) conclusions.

The new analysis supports traditional views on the amniote affinities of 'anthracosaurs', seymouriamorphs, and diadectomorphs (Panchen and Smithson 1987, 1988; Lombard and Sumida 1992; Lee and Spencer 1997; Sumida 1997), and identifies temnospondyls as a paraphyletic grade group on the lissamphibian stem (Milner 1988, 1990, 1993, 2000). The general results resemble most closely those obtained by Carroll (1995), especially with regards to the monophyly of lepospondyls and their placement on the amniote stem. We are currently evaluating the nature of the lepospondyl groups and the degree of support (morphological as well as statistical) assigned to various nodes within this assemblage (see also Ruta *et al.* in press). Thus, while the position of microsaurs on the amniote stem-group is also retrieved in experiments of taxon and/or character deletion and reweighting, the placement of remaining lepospondyls can be affected drastically. For instance, when post-cranial data are omitted from the analysis, the relationships of remaining lepospondyls change significantly: they are relocated as stem-group tetrapods, as sister group to colosteids. Similar results are obtained if nectrideans and lysorophids are excluded from the dataset. In this case, aïstopods are paired with adelospondyls and, together, they form the sister group to colosteids. The evolutionary implications of these results have yet to be explored in depth. Carroll (1999) has suggested that similarities between lepospondyls and primitive amniotes (especially in the configuration of the vertebrae) represent convergent features related to precocious ossification attained at a small body size. However, the stem-amniote position of microsaurs is not affected by deletion of postcranial characters (Figure 11.10). It is possible that lepospondyl monophyly in the original analysis results from the cumulative effect of implied reversals and optimizations of missing entries related to cranial and postcranial features. Further work in this area is needed.

The results match those of certain previous studies, especially with regards to the position of lissamphibians and the branching pattern in the basal part of the amniote stem. This is unsurprising, because the matrix includes, so far as possible, the majority of characters used in previous analyses (details in Ruta *et al.* in press), as well as further data from smaller morphological sets (e.g. Trueb and Cloutier 1991). As an additional test of the performance of character subsets, we excluded lower jaw data. Removal of these has no major effect on the overall tree topology. The latter matches the results retrieved in the original analysis, except that crown-lissamphibians are more deeply nested in the derived portion of the temnospondyl tree, whereas most tuditanomorphs are collapsed in a large polytomy. We conclude that cranial and postcranial characters are not in conflict with lower jaw data (but see discussion in Ahlberg and Clack 1998).

Elsewhere (Coates *et al.* 2000), we pondered a few of the biological implications of taxon rearrangements in Laurin's (1998a–c) preferred tree topology, in which lysorophids are the hypothesized closest relatives to frogs, salamanders, and caecilians. We concur with Carroll (2001) and Carroll and Bolt (2001) that hardly any feature of crown-lissamphians can be identified as a convincing synapomorphy shared uniquely by lysorophids with each of the three lissamphibian orders. However, Laurin *et al.* (2000b) correctly point out that grafting lissamphibians to temnospondyls is a much worse fit for their data than the topology retrieved from earlier analyses (e.g. Laurin 1998a–c). Prompted by Laurin *et al.*'s (2000b) suggestion that additional phylogenetic analyses should be performed to test the origin of lissamphibians, we have added characters that have been proposed previously as putative shared features of temnospondyls and lissamphibians (e.g. Bolt 1969, 1977, 1979, 1991; Milner 1988, 1990, 1993, 2000; Trueb and Cloutier 1991; Gardner 2001; Ruta *et al.*, in press). Our analysis favours dissorophoids as the closest relatives of lissamphibians among the vast array of Palaeozoic tetrapods.

A recent study by Yeh (2002) on the effect of miniaturization on the skeleton of frogs has shown that, although paedomorphosis is responsible for the loss of several skull bones in miniaturized vertebrates, there is no simple correlation between such losses and small size. However, several bones that ossify late during development, such as quadratojugals, columellae, and palatines, are also those that are lost most frequently. In most anurans, such bones are usually post-metamorphic. Therefore, their loss is plausibly linked to paedomorphosis. In addition, miniaturization may affect members of the same clade in profoundly different ways. Interestingly, the medial skull elements of miniaturized frogs (e.g. parasphenoid) are transversely expanded, whereas the lateral elements (e.g. pterygoids) are laterally compressed. Certain bones are shortened in comparison with their homologues in non-miniaturized frogs (e.g. maxilla, quadratojugal, vomer). Several of these features are also recorded in certain dissorophoids. Striking similarities between the ontogenetic changes in the skull of various modern lissamphibians and those of amphibamids and branchiosaurids add strength to the temnospondyl hypothesis of lissamphibian ancestry (Milner 1988, 1990, 1993, 2000; Schoch 1992, 1995, 1998; Boy and Sues 2000; Carroll 2001). The list of 'absence' features that link lysorophids to lissamphibians in Laurin and Reisz's (1997, 1999) and Laurin's (1998a–c) analyses calls for a cautious treatment of character losses and characters associated with small size. As noted by Milner (1988), examples of convergence among fossil and extant amphibians are widespread. Therefore, the assessment of their relationships cannot rely upon comparisons between very few representatives of Palaeozoic and Recent groups or upon selection of a limited number of putative shared derived similarities. Instead, efforts should be directed towards the recognition of the group in which the internal relationships best reflect the most coherent, inter-nested set of lissamphibian synapomorphies. We argue that temnospondyls show a coherent nested set of this type.

Crown-tetrapod origin and the apex of the tetrapod stem-group

The following analyses were considered: Carroll 1995 (Figure 11.2); Coates 1996 (Figure 11.3); Ahlberg and Clack 1998 (Figure 11.4; see also Figure 11.11 in Appendix 11.1); Laurin and Reisz 1999 (Figure 11.5); Paton *et al.* 1999 (Figure 11.6); Anderson 2001 (Figure 11.7). For each analysis, the inferred minimum age for the lissamphibian-amniote phylogenetic separation is bracketed between 325 and 345 Ma (mid- to late Viséan), in agreement with the conclusions of several previous works (e.g. Clack 1998b,d, 2001, 2002; Paton *et al.* 1999; see also comments in Coates *et al.* 2000). Importantly, divergence time estimates are not affected by the relative positions of unstable/rogue taxa (e.g. baphetids, *Caerorhachis*, *Crassigyrinus*, *Eucritta*, *Whatcheeria*, and various lepospondyl groups) or by the degree of tree balance. For example, comparisons between Laurin and Reisz's (1999) analysis (Figure 11.5) and ours (Figure 11.8) reveal a decrease in stem-tetrapod groups, a decrease in stem-lissamphibian groups, and an increase in stem-amniote groups. Both analyses, however, place aïstopods within the tetrapod crown-group (as stem-lissamphibians or stem-amniotes, respectively). These findings necessarily imply a mid-Viséan age as a minimum hypothesis for the date of the lissamphibian-amniote separation (Figure 11.9). This is largely based on the mid-Viséan occurrence of the earliest known aïstopod, *Lethiscus* (Wellstead 1982).

Stratigraphical data can provide no more than the best approximation of the lissamphibian–amniote divergence time, based on the available sample of fossil material. The absence of an adequate Tournaisian tetrapod record (Coates and Clack 1995; Lebedev and Coates 1995; Coates 1996; Clack and Finney 1997; Paton *et al.* 1999; Clack and Carroll 2000; Clack 2002), relative to that from flanking stages, affects

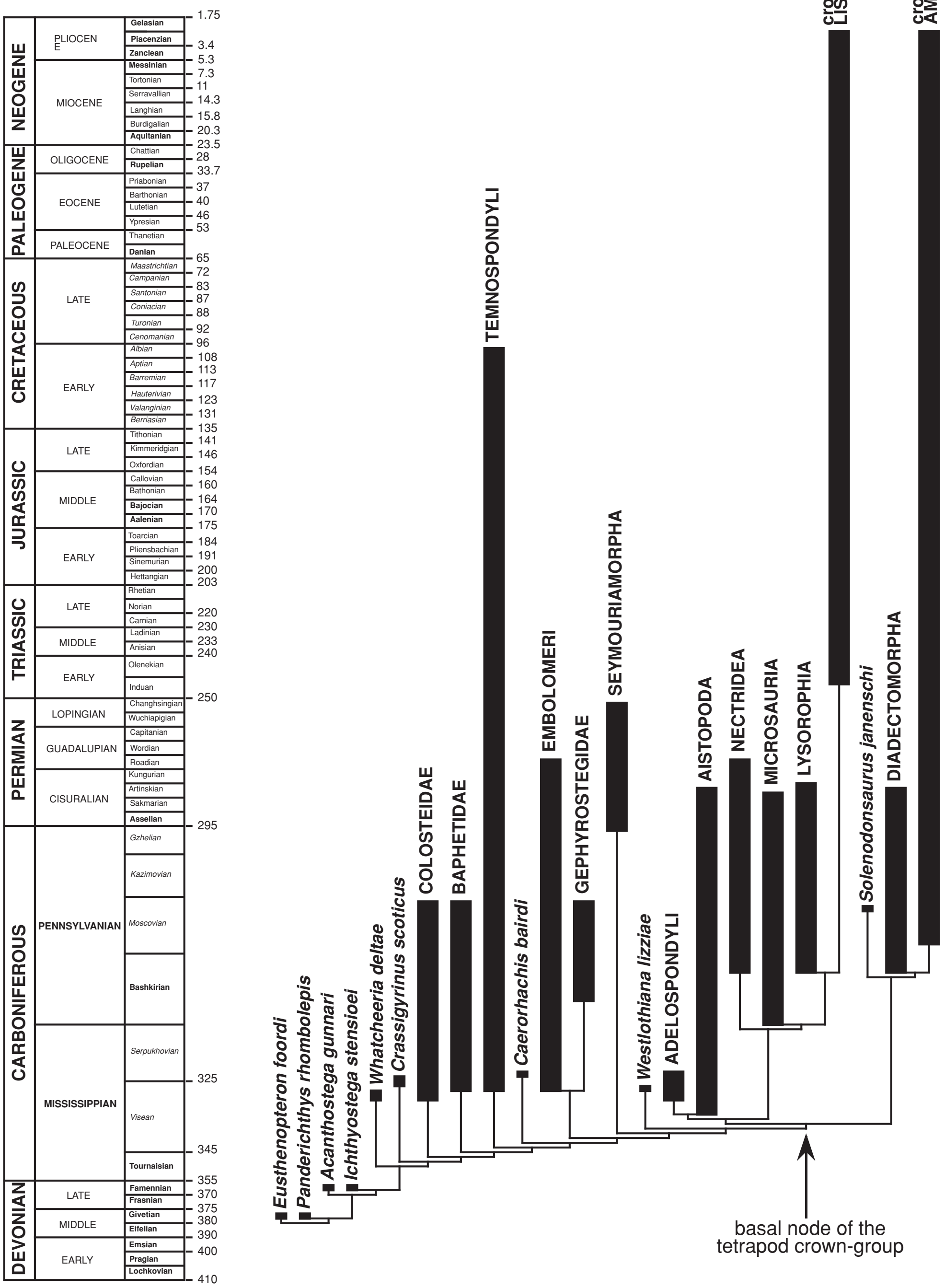

Figure 11.5 Laurin and Reisz's (1999) analysis plotted on a timescale.

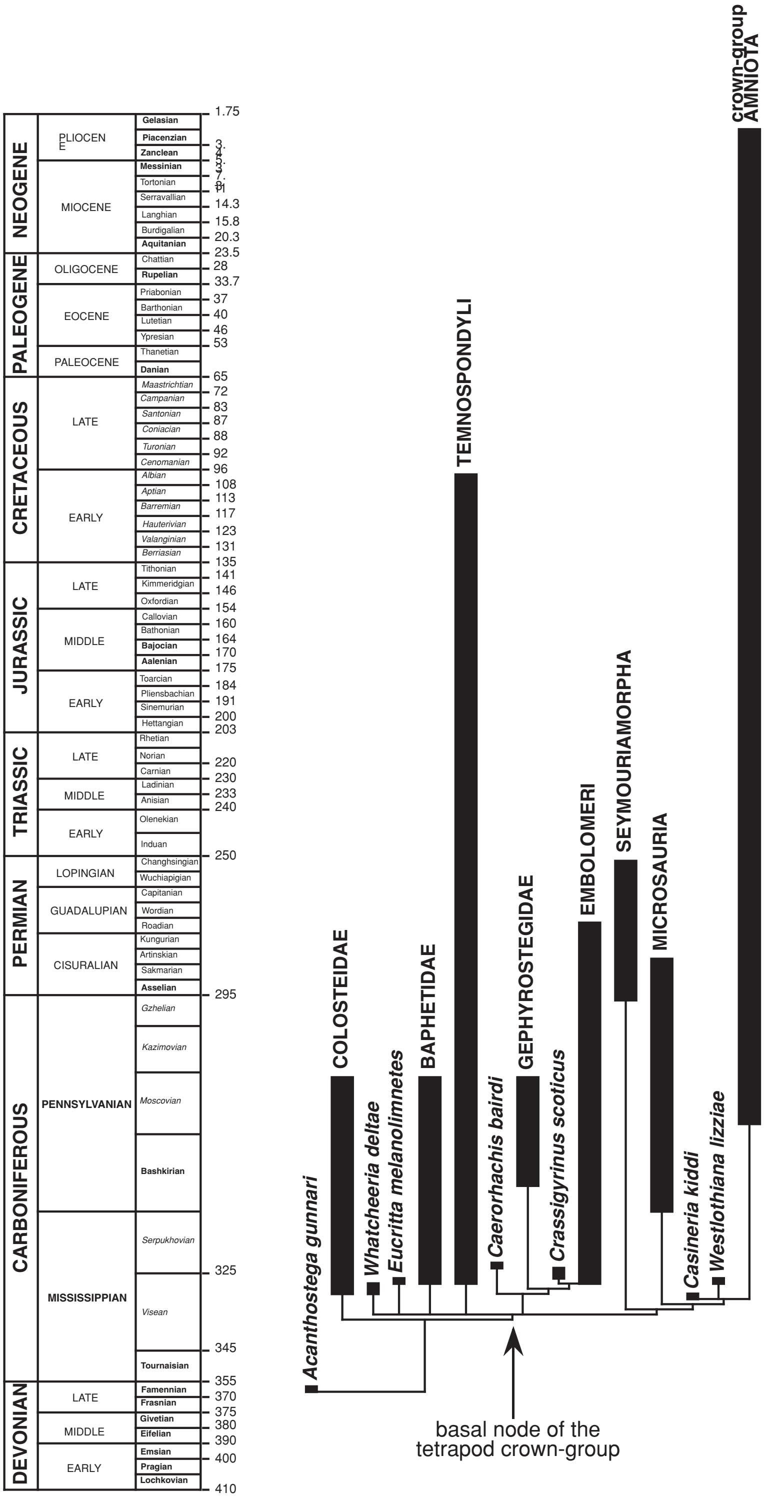

Figure 11.6 Paton *et al.*'s (1999) analysis plotted on a timescale.

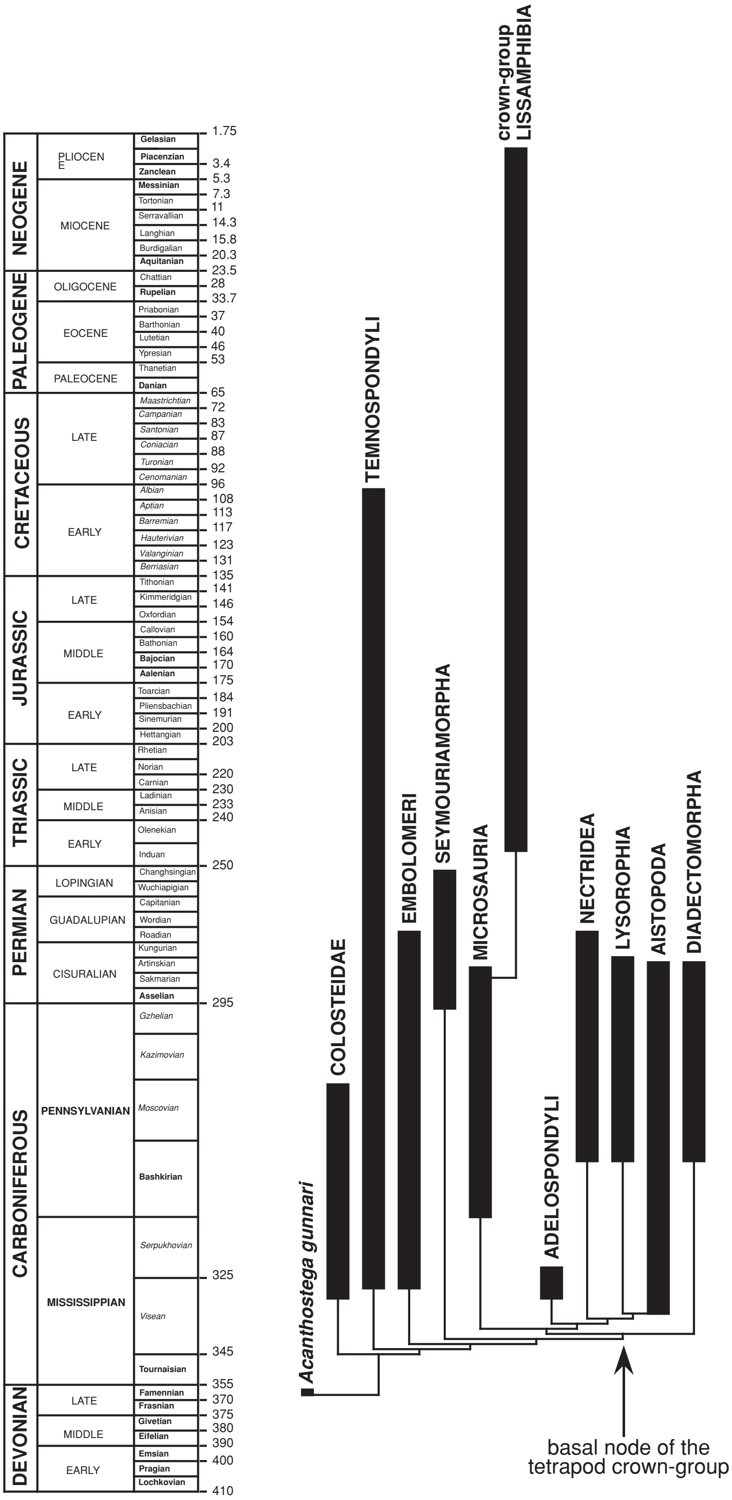

Figure 11.7 Anderson's (2001) analysis plotted on a timescale.

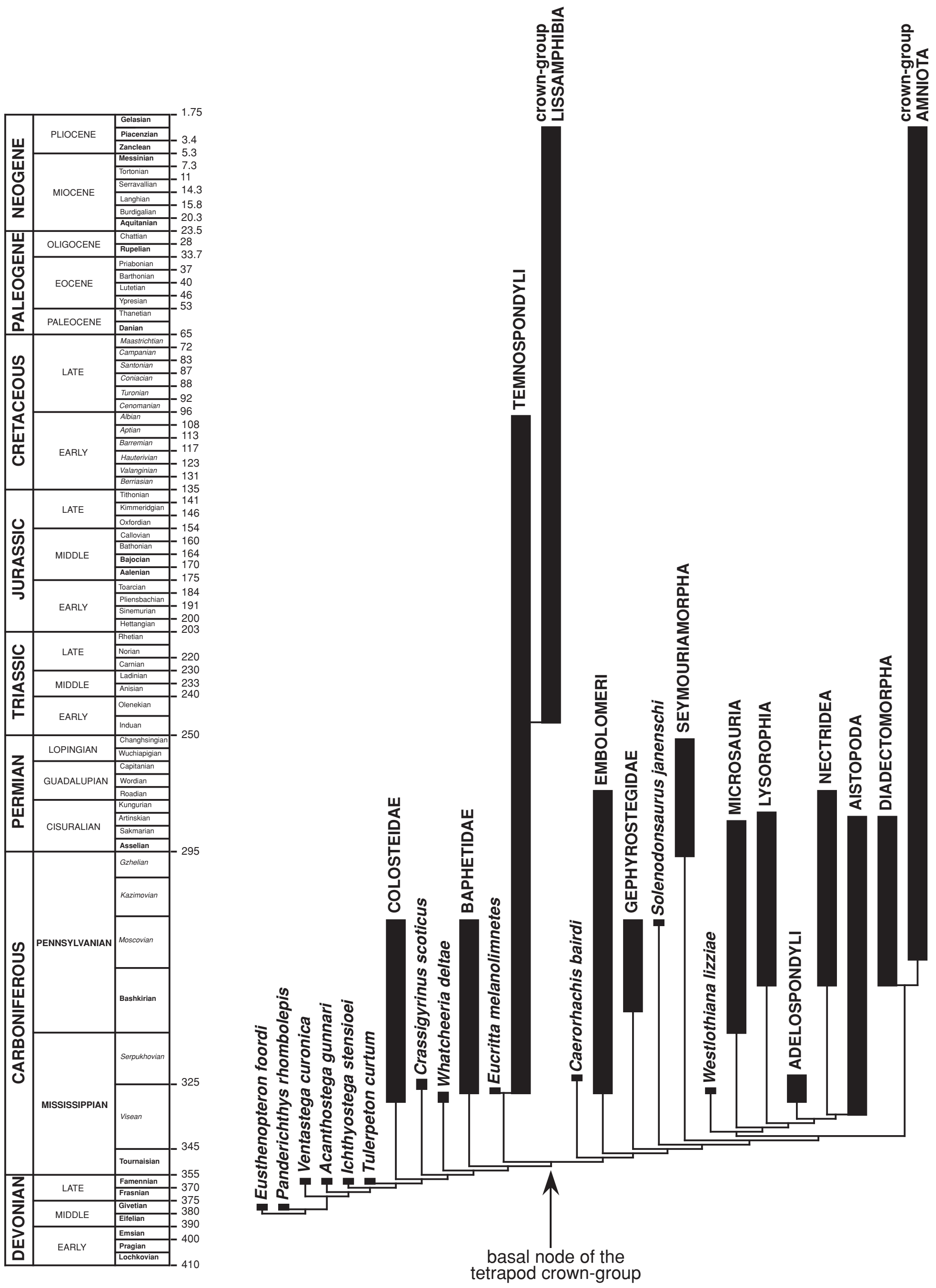

Figure 11.8 New analysis plotted on a timescale (Ruta *et al.* in press).

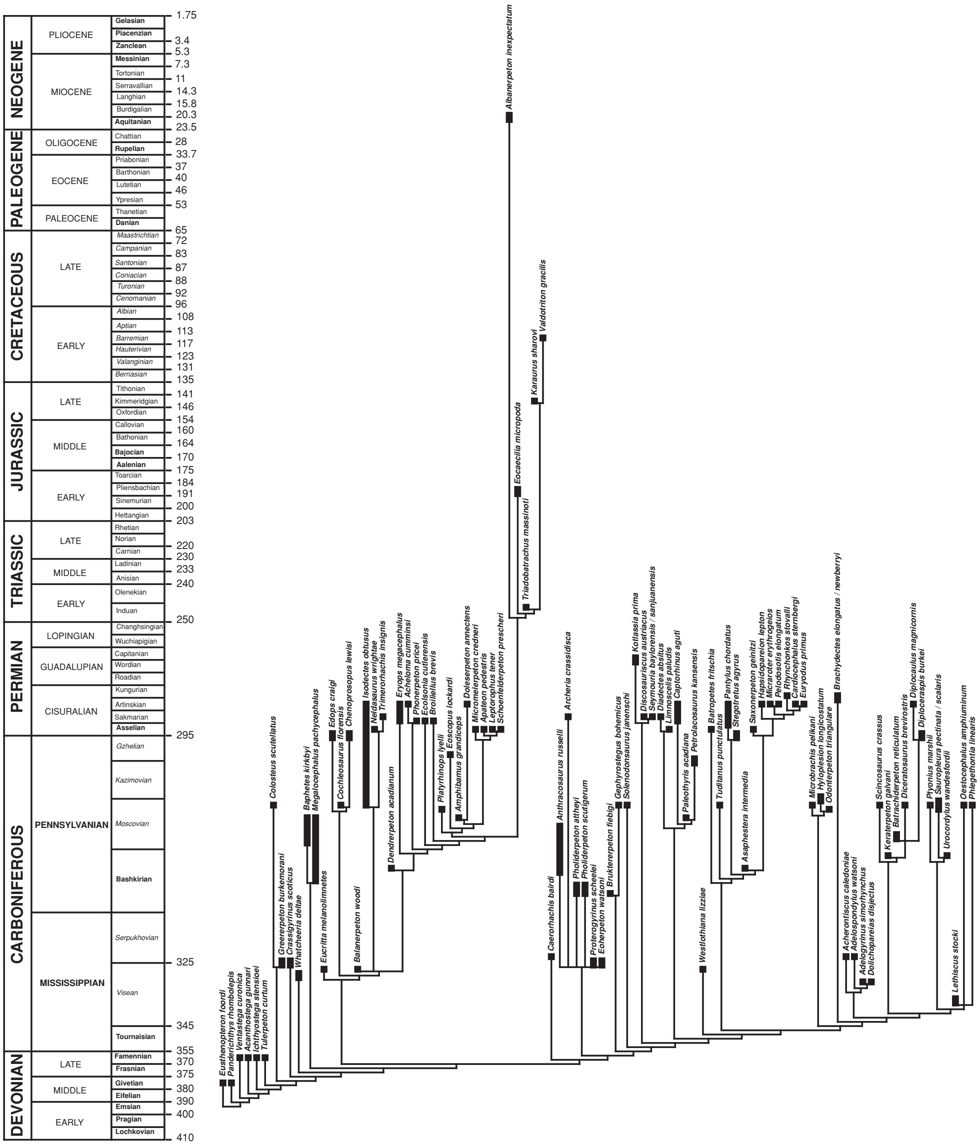

Figure 11.9 Stratigraphical plot of strict consensus of 60 most parsimonious trees at 1303 steps (CI = 0.2357; RI = 0.6744; RC = 0.1641) derived from analysis of cranial and postcranial characters and resolved down to species level (Ruta *et al.* in press).

theories of divergence times, insofar as cladogenetic events can only be plotted within the Viséan and later, or within the Famennian and earlier periods. Therefore, the apparent consensus between widely conflicting tree topologies about the time of origin of the Tetrapoda is only significant because all recent analyses fail to place this event before the Devonian–Carboniferous boundary. However, the observed ‘time signal’ is not exclusively under stratigraphical control, since alternative phylogenies based on novel character and/or taxon combinations could move the crown-tetrapod origin event to either side of the Tournasian gap. The quality of the signal is nevertheless compromised by the patchiness of the contributing data. Consequently, character deletion experiments (see Ruta *et al.*, in press, and discussion above) are likely to have only minimal effects. Thus, while postcranial character removal increases the number of stem-tetrapod taxa (Figure 11.10), this causes only a small change in the minimum estimate of the crown-group divergence time, from mid- to late Viséan.

Crown-lissamphibian origin

There is general agreement on the taxonomic composition of the basal portion of the lissamphibian crown-group (Báez and Basso 1996; Gao and Shubin 2001). The Early Triassic stem-salientian *Triadobatrachus massinoti* from Madagascar is the earliest undisputed crown-lissamphibian, and predates the basal members of the caudate and caecilian orders – *Karaurus sharovi* and *Eocaecilia micropoda* from the Late and Early Jurassic, respectively (Ivakhnenko 1978; Milner 1988, 1993, 2000; Rage and Rocek 1989; Jenkins and Walsh 1993; Carroll 2000; Rocek and Rage 2000b). The Middle Jurassic karaurid caudate *Kokartus honorarius* (Nessov 1988; Nessov *et al.* 1996) is older than *Karaurus*, but is usually regarded as a paedomorphic relative of the latter. Problematic taxa such as *Triassurus sixtelae* Ivakhnenko, 1978, variously interpreted as a Triassic stem-caudate or as a temnospondyl larva (review in Milner 2000), are too poorly known. Likewise, the systematic affinities of various Jurassic 'salamander-like' taxa (e.g. batrachosauroidids and scapherpetontids) remain uncertain (Milner 2000).

The total analysis implies the existence of a mid-Pennsylvanian to Early Triassic ghost lineage connecting albanerpetontids plus crown-lissamphibians with a dissorophoid assemblage consisting of the amphibamid, micromelerpetontid, and branchiosaurid families. The duration of this lineage is disconcertingly longer than that postulated by previous studies (Permian to Early Triassic; e.g. Trueb and Cloutier 1991; Milner 1993) and found also in the cranial analysis, wherein the Early Permian *Broiliellus* is the immediate sister taxon to albanerpetontids and crown-lissamphibians (Figure 11.10). Taken at face value, these results suggest the existence of as yet unknown Permo-Carboniferous taxa into which lissamphibian ancestry is rooted (but see discussion in Ruta *et al.* in press). No crown-lissamphibian has been recorded in the Late Permian. We point out, however, that our analysis does not consider all known dissorophoids (reviewed in Milner 1990), most of which require revision. A resolution of the sister group relationships between the three lissamphibian orders and one or more specific dissorophoid taxa must await a thorough phylogenetic analysis of crownward temnospondyls. Interestingly, Shishkin (1998) discussed a relict and possibly neotenous dissorophoid (*Tungussogyrinus*) from the Permian–Triassic boundary in Siberia. However, the affinities of this fossil are uncertain.

Crown-amniote origin

The earliest known, undisputed crown-amniotes date back to the mid-Pennsylvanian (Carroll 1988, 1991; Benton 1991, 1993, 2001; Carroll and Currie 1991; Hopson

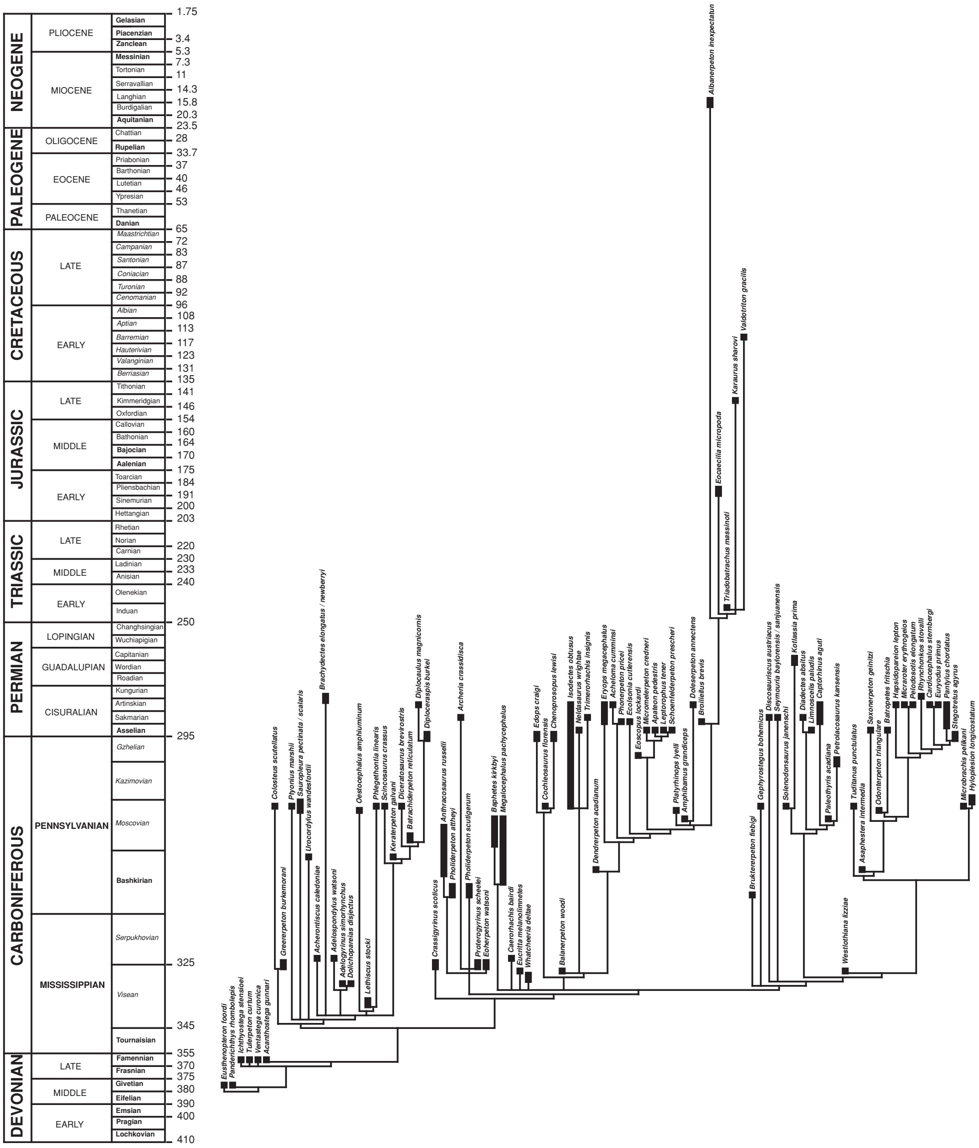

Figure 11.10 Stratigraphical plot of strict consensus of 100 440 most parsimonious trees at 945 steps (CI = 0.2447; RI = 0.6835; RC = 0.17) derived from analysis of cranial characters and resolved down to species level (Ruta *et al.* in press).

1991). Both stem-diapsids and primitive synapsids are represented in the Moscovian (families Protorothyrididae and Ophiacodontidae, respectively) and in the Kasimovian (families Petrolacosauridae and Edaphosauridae, respectively). The divergence between mammals and sauropsids, placed at about 310 Ma in the Pennsylvanian, has been widely used to calibrate molecular clocks (Kumar and Hedges 1998; Hedges 2001; Van Tuinen *et al.* 2001). The timing of this event is not affected by the controversial locations of turtles and of various Permo-Carboniferous and Triassic forms in current amniote phylogenies (e.g. Laurin 1991; Laurin and Reisz 1995; Lee 1995, 1997a, b; Rieppel and deBraga 1996; deBraga and Rieppel 1997; Rieppel and Reisz 1999; Rieppel 2000).

The sequence of branching events in the basal part of the amniote stem-group is not agreed upon. Our analysis reflects established views on the position of such groups as seymouriamorphs and diadectomorphs, but differs from many previous analyses in the relatively basal position of *Solenodonsaurus* (Lee and Spencer 1997; Laurin and Reisz 1999). Virtually no fossils have been proposed as immediate sister groups to amniotes, crownward of diadectomorphs (Sumida and Lombard 1991; Berman *et al.* 1992; Lombard and Sumida 1992; Sumida *et al.* 1992; Laurin and Reisz 1997, 1999; Lee and Spencer 1997; Sumida 1997; Berman *et al.* 1998; Berman 2000, Laurin 1998a–c; Ruta *et al.*, in press).

Dating phylogenetic events

Comparison between morphological and molecular analyses

According to Kumar and Hedges (1998) and Hedges (2001), lissamphibians and amniotes diverged at around 360 Ma ± 14.7 myr in the Famennian (Late Devonian; see also Panchen and Smithson 1987, 1988; Lebedev and Coates 1995; Coates 1996). The upper boundary of this time interval falls within the upper part of the Tournaisian, whereas the lower boundary coincides with the basal part of the Frasnian. In all cases, the lissamphibian–amniote divergence is postulated to have occurred earlier than available fossil evidence suggests. The mismatch between molecular and morphological data cannot be explained easily (see Smith 1999, for a comparable example involving metazoan divergence dates, and other chapters in this volume). However, we note that the mid- to late Viséan separation between lissamphibians and amniotes inferred from morphological analyses falls slightly short of the upper boundary of Kumar and Hedges's (1998) and Hedges' (2001) time interval. As mentioned above, some tetrapod humeri from Tournaisian sediments in Nova Scotia (Clack and Carroll 2000) resemble in their general proportions those of certain Viséan 'reptiliomorphs', notably *Eoherpeton* (Smithson 1985), although the evidence is not compelling. Furthermore, the same sediments have yielded putative colosteid-like humeri, suggesting the occurrence of deeper branching events for at least some tetrapod groups. In addition, the presence of the stem-amniote *Casineria* in the middle part of the late Viséan shows that 'reptiliomorph' diversification was already under way by about 340 Ma (Paton *et al.* 1999).

It is much more difficult to reconcile a Frasnian age for the lissamphibian–amniote phylogenetic split (the lower boundary of Kumar and Hedges' 1998, and Hedge's 2001, time interval) with available fossil data (summary in Coates, 2001). All Devonian tetrapods with limbs postdate fish-like stem-tetrapods, such as *Panderichthys* and *Eusthenopteron*. None of them are currently regarded as a member of the crown-group. Also, the basal node of the tetrapod crown-group cannot be rooted into known Devonian taxa (e.g. Panchen and Smithson 1988) without implying an impressive series of convergent character-changes in the most basal portions of the lissamphibian and amniote stem-groups. However, putative tetrapod trackways recorded in Australia, Ireland, and Scotland (see reviews in Clack 1998a, 2000) could be used to hypothesize the existence of an as yet unrecorded radiation of limbed tetrapods during the Frasnian–Famennian. The dating of several track-bearing sediments is disputed, but in certain cases, a Middle to Late Devonian age has been postulated.

A better agreement between morphological and molecular time-calibrated trees is evident by comparing minimum estimates of crown-lissamphibian origins (see also above). Thus, both morphological analyses and molecular studies (e.g. Báez and Basso 1996; Feller and Hedges 1998; Gao and Shubin 2001) support an early Mesozoic divergence for crown-lissamphibians. According to Feller and Hedges (1998), the Early Triassic age of *Triadobatrachus* implies that the three orders of lissamphibians originated in the Palaeozoic under the traditional hypothesis of a sister group relationship between salientians and caudates. Indeed, the morphology of *Triadobatrachus* appears almost exactly intermediate between that of more derived frogs and various derived dissorophoids (Milner, 1988; Rocek and Rage 2000a,b). Although the gymnophionan–caudate clade [= Procera] proposed by Feller and Hedges (1998) may imply a later evolutionary event for the origin of caecilians and salamanders relative to frogs, this branching sequence is *not* incompatible with the possibility that pre-Jurassic (or even Late Palaeozoic) representatives of caecilians and salamanders may be discovered. Although Feller and Hedges (1998) found morphological support for their Procera, it is at present difficult to propose a suitable candidate for the stem-group membership of this clade (but see McGowan and Evans 1995).

Conflict or compromise?

Agreement between morphology and molecules in reconstructing the timing of major evolutionary events is rare. Discrepancies between different data sources for several taxonomic groups are well documented. In the case of metazoans, birds, and mammals, for instance, molecular analyses indicate that these groups are twice as old as their oldest fossil representatives. Instances of molecular estimates falling short of morphological estimates exist, but are much rarer (e.g. Easteal and Herbert 1997). Several factors have been identified as responsible for the mismatch between molecules and morphology (cf. Cooper and Fortey 1998; Benton 1999; Smith 1999), including the presumed rarity of ancestral forms of major groups (let alone problems with the recognition of ancestors), their preservation potential, and their possible occurrence in places that have not yet been subject to thorough scrutiny. Furthermore, failure to distinguish between the origin of the living members of a Recent clade (crown-group diversification) and the date of separation of the latter from its extant sister group (total-group divergence) may lead to biased assessments of origination times (e.g. Easteal 1999). For instance, assuming the accuracy of our new hypothesis of tetrapod relationships (Ruta *et al.* in press), a time interval of about 30 million years separates the earliest undisputed crown-amniotes from *Casineria*. On the lissamphibian stem, the time interval between the earliest undisputed crown-lissamphibian, *Triadobatrachus*, and the earliest known temnospondyls is about 75 million years (Figure 11.9). Furthermore, as pointed out by van Tuinen *et al.* (2001), fossil-based calibrations of molecular clocks are inevitably sensitive to fossil dating and phylogeny reconstruction (for a comprehensive discussion, see also Wagner 2000). For this reason, they emphasize the importance of introducing confidence limits around such widely used, fossil-based calibration tools as the synapsid–diapsid divergence time (see above).

Another important issue is represented by the erratic behaviour of molecular clocks, a discussion of which was presented by Ayala (1999). Briefly, several factors (e.g. population size, time elapsed between generations, species-specific occurrences of genetic mutations, changes in protein functions, and changes in the adaptation of organisms to their environments) may speed up or slow down molecular clocks (Cooper and Fortey 1998; Benton 1999; Smith 1999). Examination of combined information from a large number of genes has been proposed as an effective tool to reduce drastically the errors introduced by limited sequence data (e.g. Kumar and Hedges 1998; Ayala 1999; Hedges 2001; Stauffer *et al.* 2001). The discussion thus far shows that the most problematic incongruence between molecular and morphological time trees concerns the age of the tetrapod crown-group radiation. This lack of agreement could result from inaccuracies of molecular clock estimates. Smith (1999) has summarized cases in which rates of molecular evolution might change dramatically, both at the start of clade radiation, and in terminal portions of the tree relative to deeper nodes. For example, if genetic changes in a sufficient number of gene families were slowed down at the beginning of the crown-amniote radiation (one of the most widely used calibration points; Feller and Hedges 1998; Kumar and Hedges 1998; Hedges 2001), then molecular data would deliver an excessively early origination date; certainly much older than that estimated from fossils. We note that such a model of varying molecular clock-speed is consistent with the greater agreement between molecular and morphological estimates of crown-lissamphibian origin (since the crown-lissamphibian radiation is far more recent than that of crown-tetrapods).

Sample bias and 'site' effect

Improved molecular methods and techniques (e.g. Hedges 2001), and increased consistency of divergence times, between different gene samples and calibration points (e.g. Stauffer *et al.* 2001), make it appear *a priori* that the mismatch between palaeontological and molecular estimates for divergence times is caused by deficiencies of the fossil record. However, this is strongly disputed in the case of certain groups (notably, birds and mammals; Benton 1999). Sample bias is an important factor when dealing with palaeontological data. Benton and Hitchin (1996) and Benton *et al.* (2000) used cladograms from a wide range of groups to test the quality of the fossil record, which they acknowledge as decreasing dramatically backwards in time. Older fossils are more liable to physical and chemical destruction than younger ones. The former are often more difficult to interpret and to place in a phylogenetic context than the latter. In addition, it is reasonable to assume that taxa that lie phylogenetically close to cladogenetic events are rare.

Benton and Hitchin (1996) and Benton *et al.* (2000) argue that, although the 'completeness' of the fossil record may be lower in the Palaeozoic than in the Cenozoic, its 'adequacy' in recounting major evolutionary events is maintained. Newly discovered taxa are more likely to fit within well-established higher categories, and to redefine only lower ranks (e.g. splitting or clumping genera and species). It follows that differences in fossil dating are only significant at the level of fine chronostratigraphical subdivisions (e.g. stages). The quality of the fossil record is thus interpreted as more or less uniform when families are used as OTUs and the stratigraphical column is scaled to stages. Therefore, it is unlikely that discoveries of new members of well-characterized Palaeozoic tetrapod clades will have any impact upon the branching sequence and chronology of key events in tetrapod history (although they may cast new light on the intrinsic relationships of the groups to which they belong). Nevertheless, certain discoveries are crucial, as in the case of fossils displaying mosaics of features previously considered diagnostic of higher level, distinct clades (Clack 2001; Ruta *et al.* 2001). Moreover, the methodology employed by Benton and Hitchin (1996) and Benton *et al.* (2000) treats phylogenetic reconstruction as independent of sampling order, even though sampling intensity (the probability that a taxon is sampled per given unit time) affects phylogenetic accuracy (Wagner 2000, and references therein).

Large gaps in the early tetrapod record, most notably the Tournaisian, persist. Sample quality from this time interval is thus extremely poor compared with more recent deposits (Benton 1999). In fact, most discoveries of early tetrapods have resulted from prolonged, concentrated collecting efforts in a limited number of stratigraphical horizons (e.g. Wood *et al.* 1985; Rolfe *et al.* 1994), although fortuitous finds remain an occasional source of important new data (Clack and Finney 1997; Paton *et al.* 1999). Consequently, certain key fossil sites have a disproportionate influence, most particularly East Kirkton in the Scottish late Viséan (Rolfe *et al.* 1994). Key East Kirkton taxa responsible for pegging divergence dates on the tree include the putative stem-lissamphibians *Balanerpeton* and *Eucritta*, and the stem-amniote *Westlothiana* (Figure 11.1). There is nothing unique to East Kirkton and early tetrapod phylogeny in this respect; such site effects are applicable to the vast majority of fossil-based estimates of evolutionary timing.

Phylogenetic reconstructions cannot be regarded as finished works, because the discovery of just one new fossil may overturn previous hypotheses about character distribution and polarity. Therefore, fossil-based estimates of major evolutionary events are not necessarily in conflict with, or challenged by, existing molecular estimates. However, we point out that this is true only if molecular estimates exceed those implied by morphology. If fossil estimates exceed molecular estimates, then it appears to us that a real conflict exists. As suggested by Stauffer *et al.* (2001), one of the best uses for molecular clock time trees is their ability to provide a framework to evaluate (and, possibly, constrain) palaeontological hypotheses of divergence.Therefore, in agreement with Hedges and Maxson (1997), molecular and palaeontological data are best used as complementary approaches to dating phylogenetic events.

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Appendix 11.1

Ahlberg and Clack's (1998) matrix of lower jaw characters is reproduced below. For convenience, characters are divided into groups of five separated by a space. For a description of characters 1–50 (upper row), the reader is referred to their publication. Eleven new characters (51–61; lower row), typed in bold, are added. *Caerorhachis* (Holmes and Carroll 1977; Ruta *et al.* 2001) is included. As in the original analysis, question marks denote missing or inapplicable characters. Character 48 (postsplenial pit line) was changed from 1 (absent) to ? (inapplicable) in *Diploceraspis*, *Sauropleura*, *Eocaptorhinus*, and *Ophiacodon* (Ruta *et al.* 2001). The new characters are as follows:

51. Rearmost extension of mesial lamina of splenial closer to anterior margin of adductor fossa (0) than to anterior end of lower jaw (1).
52. Lateral exposure of dentary smaller (0) or greater (1) than lateral exposure of angular.
53. Absence (0) or presence (1) of at least one Meckelian foramen comparable in length with the adductor fossa.
54. Absence (0) or presence (1) of small posterior Meckelian foramen between prearticular and angular.
55. Absence (0) or presence (1) of small posterior Meckelian foramen between prearticular, postsplenial, and angular.
56. Absence (0) or presence (1) of intermediate Meckelian foramen between prearticular ad postsplenial.
57. Absence (0) or presence (1) of condition: maximum depth of mesial lamina of splenial comparable with maximum depth of prearticular when both are measured at the level of the mid-length of the adductor fossa.
58. Absence (0) or presence (1) of retroarticular process.
59. Absence (0) or presence (1) of condition: posterior coronoid exposed in lateral view.
60. Absence (0) or presence (1) of condition: mesial lamina of angular deeper than prearticular when both are measured at the level of the anterior margin of the adductor fossa.
61. Absence (0) or presence (1) of condition: mesial margin of posterior coronoid shorter than that of mid-coronoid and up to about two-thirds as long as the latter.

Panderichthys
00000 00000 00000 0000? 00000 00000 00000 00000 00000 00000 000?0 0000? 0

Elginerpeton
??00? 0?000 01111 00100 01010 00111 11000 ?1??0 01??0 0001? ?00?0 0000? ?

Obruchevichthys
????? 0?00? 0?0?? 00101 01??? ?0111 11??? ????0 ??0?0 1??1? ????0 0???? ?

Ichthyostega
00001 00001 11111 ??001 01000 00011 ??000 01000 1?000 00010 100?? ?000? 0

Ventastega
00001 00001 11001 11001 01000 00111 10000 01000 01000 00010 ?00?? ?000? 0

Metaxygnathus
10000 00001 ?1010 11001 0101? 00?11 11000 00000 01000 10?10 000?? ?000? ?

Acanthostega
10000 00000 11111 11001 01101 00010 11000 01000 01000 10110 000?? ?000? 0

Whatcheeria
?0?0? ?0001 1111? 00001 01?01 00001 100?? ?10?? ????0 2011? ?00?? ??00? ?

Tulerpeton
?00?? ??000 ?1?1? ?0?01 0???? ????? ????? ????? ????0 30?1? ????? ????? ?

Crassigyrinus
00100 00131 11111 10011 01101 00?01 01000 1??00 0?100 30110 1000? ?0000 0

Greererpeton
00111 00121 11011 00001 01101 10001 01000 ?0000 1?100 20110 1000? ?0000 0

Megalocephalus
00101 10031 11111 00011 01102 00001 01011 10010 1?100 30111 10000 00000 0

Pholiderpeton
00101 11131 11111 00001 01101 10001 00010 ?1110 1?110 30111 10101 01011 0

Cochleosaurus
00101 11131 11111 00001 01101 1100? ??011 20010 1?111 ??111 000?? ?00?0 ?

Phonerpeton
00101 11131 11111 00001 01101 0100? ??011 ?0111 1?111 ??111 00000 00010 0

Eoherpeton
00101 1?111 11111 00001 ?1101 0???? ??010 ?01?0 0?111 ??111 10001 10000 1

Proterogyrinus
001?1 ?0131 11111 00001 01101 1???? ??0?0 ?11?? 1?111 ??111 1010? ?1001 0

Gephyrostegus
00101 11111 11??1 00001 01101 1100? ??000 201?0 1?111 ??111 1010? ?1010 0

Balanerpeton
00101 0?131 11111 00001 01102 0100? ??011 ?0001 1?101 ??111 00000 00000 0

Platyrhinops
0?101 01131 11111 00001 01101 0100? ??011 ?0??1 1?101 ??111 ??0?? ?00?0 ?

Microbrachis
01101 01131 11111 00001 01101 0100? ??011 ?0000 1?110 31111 10010 00000 0

Discosauriscus
01101 11131 11111 00001 11101 0100? ??011 ?01?0 1?110 31111 11010 00010 0

Eocaptorhinus
0112? ?1031 ????1 00001 11101 0100? ??1?? ?0000 1?111 ???11 1100? ?10?1 ?

Diploceraspis
0112? ?00?1 11111 00001 11101 0100? ??1?? ?0000 1?111 ???01 1001? ?0100 ?

Sauropleura
011?? ????? ????? 00001 11101 11??? ??1?? ?0000 01111 ???11 1010? ?0101 ?

Ophiacodon
00111 ?1031 1?1?1 00001 11101 0100? ??1?? ?0100 1?111 ????1 1100? ?100? ?

Caerorhachis
01101 01131 11111 ???11 01101 00001 01010 ?0010 00111 ???01 1?001 10000 1

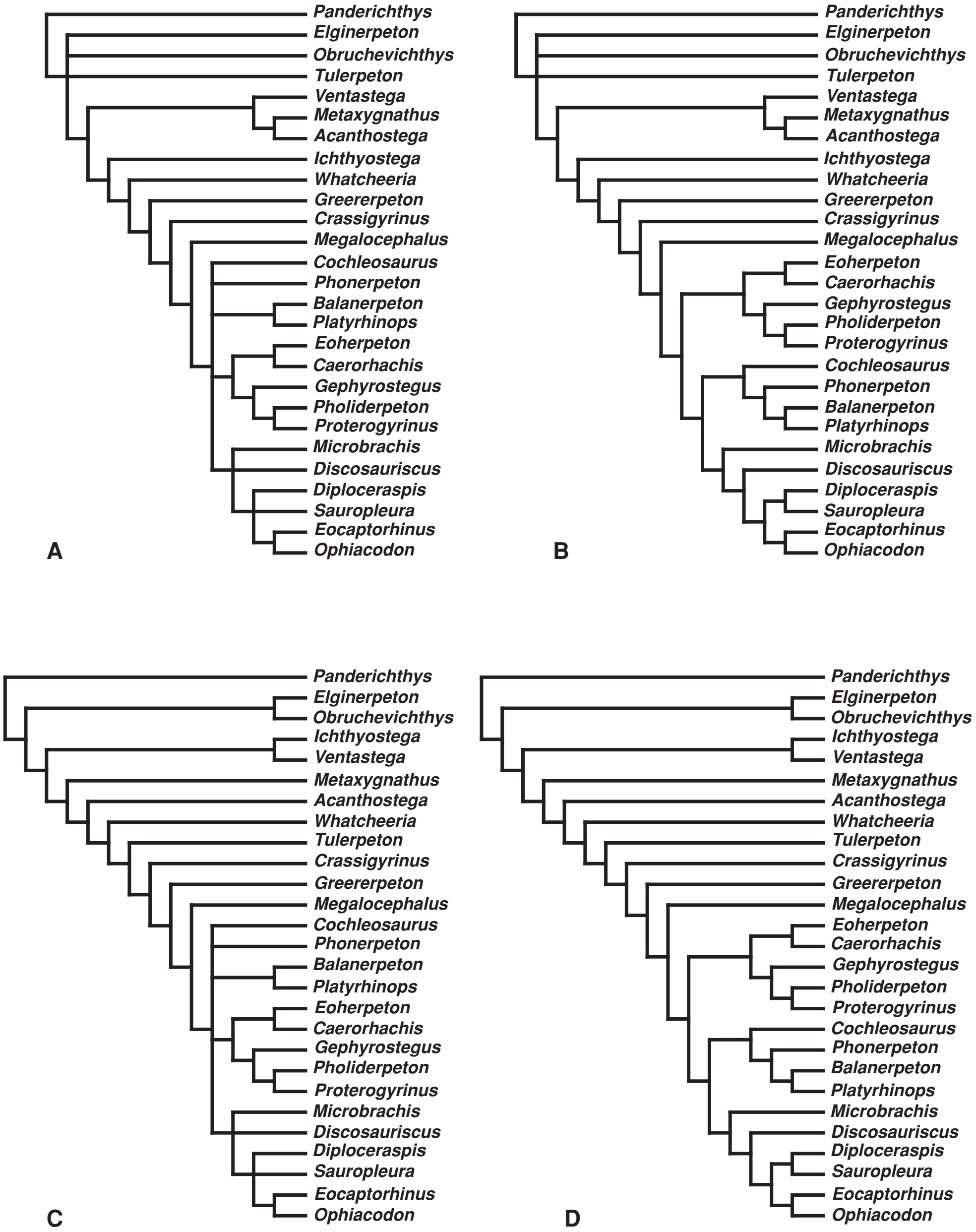

Figure 11.11 A strict consensus of 25 fundamental trees derived from the analysis of an expanded version of Ahlberg and Clack's (1998) dataset with all characters unweighted and unordered; B, strict consensus of five fundamental trees obtained after reweighting characters by their rescaled consistency indices values (best fit); C, strict consensus of five fundamental trees obtained when characters 36 and 46 of Ahlberg and Clack (1998) were ordered, but leaving all characters unweighted; D, single tree found after reweighting characters by their rescaled consistency indices values (best fit), with characters 36 and 46 ordered.

The data matrix was processed with PAUP*4.0b10 under the following search settings: 1000 random stepwise additions with one tree held in memory at any one time (MAXTREES = 1), followed by TBR branch-swapping (MAXTREES = unlimited) on trees in memory. The initial run, with all characters unordered and equally weighted, yielded 25 equally parsimonious trees at 139 steps (CI = 0.4779; RI = 0.694; RC = 0.3395), a strict consensus of which is shown in Figure 11.11A. Reweighting characters by the maximum value of their rescaled consistency indices gives five trees (CI = 0.6722; RI = 0.849; RC = 0.5884). The strict consensus of these (Figure 11.11B) has been used to construct Figure 11.4.

If characters 36 (position of centre of radiation on prearticular) and 46 (enclosure of mandibular canal) are ordered as in Ahlberg and Clack's (1998) analysis, then a PAUP* run with all characters equally weighted gives five most parsimonious trees at 140 steps (CI = 0.4745; RI = 0.7025; RC = 0.3412), the strict consensus of which is illustrated in Figure 11.11C. If characters are reweighted by the maximum value of their rescaled consistency indices, then a single tree is obtained (Figure 11.11D; CI = 0.6772; RI = 0.8641; RC = 0.603).