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Early tetrapod relationships revisited

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ABSTRACT

In an attempt to investigate differences between the most widely discussed hypotheses of early tetrapod relationships, we assembled a new data matrix including 90 taxa coded for 319 cranial and postcranial characters. We have incorporated, where possible, original observations of numerous taxa spread throughout the major tetrapod clades. A stem-based (total-group) definition of Tetrapoda is preferred over apomorphy- and node-based (crown-group) definitions. This definition is operational, since it is based on a formal character analysis. A PAUP* search using a recently implemented version of the parsimony ratchet method yields 64 shortest trees. Differences between these trees concern: (1) the internal relationships of aïstopods, the three selected species of which form a trichotomy; (2) the internal relationships of embolomeres, with *Archeria crassidisca* and *Pholiderpeton scutigerum* collapsed in a trichotomy with a clade formed by *Anthracosaurus russelli* and *Pholiderpeton attheyi*; (3) the internal relationships of derived dissorophoids, with four amphibamid species forming an unresolved node with a clade consisting of micromelerpetontids and branchiosaurids and a clade consisting of albanerpetontids plus basal crown-group lissamphibians; (4) the position of albenerpetontids and *Eocaecilia micropoda*, which form an unresolved node with a trichotomy subtending *Karaurus sharovi*, *Valdotriton gracilis* and *Triadobatrachus massinoti*; (5) the branching pattern of derived diplocaulid nectrideans, with *Batrachiderpeton reticulatum* and *Diceratosaurus brevirostris* collapsed in a trichotomy with a clade formed by *Diplocaulus magnicornis* and *Diploceraspis burkei*. The results of the original parsimony run – as well as those retrieved from several other treatments of the data set (e.g. exclusion of postcranial and lower jaw data; character reweighting; reverse weighting) – indicate a deep split of early tetrapods between lissamphibian- and amniote-related taxa. Colosteids, *Crassigyrinus*, *Whatcheeria* and baphetids are progressively more crownward stem-tetrapods. *Caerorhachis*, embolomeres, gephyrostegids, *Solenodonsaurus* and seymouriamorphs are progressively more crownward stem-amniotes. *Eucritta* is basal to temnospondyls, with crown-lissamphibians nested within dissorophoids. *Westlothiana* is basal to Lepospondyli, but evidence for the monophyletic status of the latter is weak. *Westlothiana* and Lepospondyli form the sister group to diadectomorphs and crown-group amniotes. Tuditanomorph and microbrachomorph microsaurs are successively more closely related to a clade including proximodistally: (1) lysorophids; (2) *Acherontiscus* as sister taxon to adelospondyls; (3) scincosaurids plus diplocaulids; (4) urocordylids plus aïstopods. A data set employing cranial characters only places microsaurs on the amniote stem, but forces remaining lepospondyls to appear as sister group to colosteids on the tetrapod stem in several trees. This arrangement is not significantly worse than the tree topology obtained from the analysis of the complete data set. The pattern of sister group relationships in the crownward part of the temnospondyl-lissamphibian tree re-emphasizes the important role of dissorophoids in the lissamphibian origin debate. However, no specific dissorophoid can be identified as the immediate sister taxon to crown-group lissamphibians. The branching sequence of various stem-group amniotes reveals a coherent set of internested character-state changes related to the acquisition of progressively more terrestrial habits in several Permo-Carboniferous forms.

Key words: amniotes, characters, congruence, lissamphibians, parsimony ratchet, taxon exemplar, tetrapods, total-group.

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CONTENTS

I. INTRODUCTION

This paper presents a new, detailed cladistic analysis of early tetrapods as part of an ongoing project aiming to discover sources of conflict between the most widely discussed, published tetrapod phylogenies and to search for correlated character transformations in early tetrapod evolution. A long-term goal of our investigation is to generate and test new hypotheses of relationships using, as far as possible, exhaustive taxon and character combinations not considered in previous studies. Primitive tetrapod interrelationships are a topic of considerable palaeontological and biological interest. Our knowledge of this subject has improved considerably during the last two decades (see Sections II and III). Significant fossil discoveries have cast new light on the pattern of anatomical transformations that occurred at the vertebrate transition from water to land (e.g. Jarvik, 1980, 1996; Clack, 1989, 1994*a*, *b*, 1998*b*; Coates & Clack, 1990, 1991, 1995; Ahlberg, 1991, 1995, 1998; Ahlberg, Luksevics & Lebedev, 1994; Daeschler *et al.*, 1994; Lebedev, 1984; Clack & Coates, 1995; Lebedev & Coates, 1995; Coates, 1996; Ahlberg & Clack, 1998; Ahlberg, Luksevics & Mark-Kurik, 2000; Daeschler, 2000; Shubin & Daeschler, 2001). Revised interpretations of palaeontological and comparative anatomical data have clarified the intrinsic and extrinsic relationships of numerous extinct groups (e.g. Panchen, 1985; Smithson, 1985; Panchen & Smithson, 1987, 1988, 1990; Clack, 1996), and descriptions of several new taxa are beginning to bridge the morphological and/or stratigraphical gap between Devonian and Carboniferous faunas (e.g. Clack, 1998*a*, *c*, 2001, 2002; Lombard & Bolt, 1995; Thulborn *et al.*, 1996; Clack & Finney, 1997; Paton, Smithson & Clack, 1999; see also Bolt & Lombard, 2000; Clack & Carroll, 2000, and Ruta, Milner & Coates, 2001, for a review). As in the case of other areas of palaeobiology, early tetrapod studies have benefitted from interactions between classical morphology and modern embryology at the interface between evolution and development (e.g. Shubin & Alberch, 1986; Coates, 1991, 1995, 1996; Thorogood, 1991; Duboule, 1994; Shubin, 1995; Sordino & Duboule, 1995; Sordino, van der Hoeven & Duboule, 1995; Tickle, 1995; Cohn *et al.*, 1997; Shubin, Tabin & Carroll, 1997; Coates & Cohn, 1998; Jeffery, 2001). Recently, much interest has centered on comparisons between morphological and molecular analyses, on fossil-based calibrations of molecular clocks, and on the timing of such key events as the phylogenetic split between lissamphibians and amniotes (e.g. Feller & Hedges, 1998; Kumar & Hedges, 1998; Hedges, 2001; Van Tuinen, Porder & Hadly, 2001; Ruta & Coates, in press). Reconstructing the branching sequence of early tetrapods is a necessary prerequisite to inform a wide range of questions, such as: (1) understanding the anatomical, physiological and ecological modifications that accompanied the transition from fish ancestors to four-legged vertebrates; (2) establishing the sequence of character acquisitions that shaped the early evolutionary history of lissamphibians and amniotes, from their phylogenetic separation to the diversification of their respective crown-groups; (3) reconstructing the changes in developmental pathways that resulted in new morphologies; (4) formulating and testing hypotheses concerning tempo and mode of evolutionary processes through analysis of character change and degree of character correlation; (5) assessing taxon diversity and morphological disparity through time, as inferred from the shape of cladograms; and (6) providing a framework for comparing and contrasting morphology-based and molecular chronologies of key events in vertebrate evolution. In addition, early tetrapod studies contribute an invaluable source of data for elucidating palaeobiogeographical and palaeoecological patterns in primitive terrestrial biota.

The earliest diversification of lissamphibians and amniotes is the main focus of this review. In addition, conflicting hypotheses of tetrapod interrelationships are compared, with emphasis on the lissamphibian origin debate, on the pattern of character acquisition in the amniote stem-group, and on the status and affinities of various groups of lepospondyls. There is no well-supported, let alone stable, hypothesis of early tetrapod phylogeny. The skepticism expressed by Coates, Ruta & Milner (2000), although questioned by Laurin (2002), remains justifiable. Throughout, we make extensive use of the concepts of stem-group, crown-group and total-group, first introduced by Hennig (1965, 1966, 1969) and elaborated upon by various subsequent workers (e.g. Jefferies, 1979; Craske & Jefferies, 1989; Patterson, 1981, 1993*a*, *b*, 1994). The voluminous literature dealing with the relationships of several living and extinct groups, as well as the large number of papers discussing the theory and practice of cladistic analysis, made us assume that it would be unnecessary to clarify the use of basic cladistic jargon. However, a random browse through the palaeontological literature revealed that the stem-group, crown-group and total-group concepts are still misinterpreted and, often, used incorrectly. We can add little to the exhaustive discussion of cladistic terminology in the existing literature (e.g. Jefferies, 1979; Craske & Jefferies, 1989; Smith, 1994; Budd, 2001). Therefore, only succinct definitions are appropriate here. Thus, let A and L be two monophyletic groups of extant organisms (e.g. Amniota and Lissamphibia), and let A and L be sister groups. The group including the latest common ancestor of all extant members of A (or L) plus all of its descendants, both living and extinct, is the crown-group of A (or L). All those extinct organisms which are more closely related to the extant members of A (or L) than to those of L (or A), but which do not belong in the crown group of A (or L), are part of the stem-group of A (or L). The point of latest common ancestry of A and L marks the separation between the total-group of A and the total-group of L. Any fossil organism that belongs in the total-group of A (or L) shares a more recent common ancestor with some or all of the extant members of A (or L) than it does with any extant member of L (or A). If the organism in question is more closely related, in equal measure, to all extant members of A (or L) than to those of L (or A), then it is a member of the stem-group of A (or L), i.e. it branches from the total-group of A (or L) before the basal node marking the beginning of the crown-group radiation. If it is more closely related to some (but not all) extant members of A (or L) than to others, then it is a member of the crown-group of A (or L). The stem-group is an extinct and paraphyletic assemblage by definition.

Crown-group definitions (sometimes referred to as node-based definitions) represent a particular case of nodal or apomorphy-based definitions (in this case, the node subtends the crown-group; Forey, 2001). Apomorphy-based definitions refer to the crown-group and to the portion of the stem-group subtended by the relevant apomorphy. Such a broader monophyletic assemblage corresponds to Craske & Jefferies's (1989) *scion*. Finally, stem-based definitions are simply total-group definitions (they encompass both the entire stem-group and the crown-group). As clearly stated by Donoghue, Forey & Aldridge (2000: p. 237), '… Although crown and total groups can be given separate names (deQueiroz & Gauthier, 1992), this approach results in an unnecessarily expanded classification scheme and in one of the two groups (stem-group) being paraphyletic (unless that group is represented by one species only, in which case the need for a higher group name is unnecessary). Generally, only the total group is recognized by formal Linnean rank (Patterson, 1993*b*; Smith, 1994). Thus, conodonts belong to the Gnathostomata; they are gnathostomes, albeit without jaws'. Following Donoghue *et al.*'s (2000) example, *Eusthenopteron* is a tetrapod (more precisely, a stem-group tetrapod), albeit without limbs.

Stem-groups are divided into plesions, which '… could be inserted anywhere within the classification without altering the Linnean rank of the crown group' (Smith, 1994: p. 96). Our use of the plesion concept [a totally extinct monophyletic group; see also Smith (1994)] conforms exclusively to that of Patterson & Rosen (1977), but differs from that of Craske & Jefferies (1989), for whom plesions are in principle paraphyletic assemblages. While Patterson & Rosen's (1977) concept is based upon the pattern of character acquisition along the stem-group, Craske & Jefferies's (1989) concept is formulated within the framework of a more idealistic interpretation of the shape of cladograms, whereby segments of the stem-lineage are also incorporated into the plesions. The distinction between the two plesion concepts revolves around the interpretation of cladograms as (almost) strict representations of phylogenetic trees in Craske & Jefferies (1989) and as formulations of hypotheses of character distributions in Patterson & Rosen (1977).

II. CONFLICTING CLADOGRAM TOPOLOGIES

Published cladistic analyses of early tetrapods show a congruent phylogenetic signal for some groups, such as colosteids and most Devonian forms (Carroll, 1995; Coates, 1996; Laurin & Reisz, 1997, 1999; Ahlberg & Clack, 1998; Clack, 1998*a*, *c*, 2001; Laurin 1998*a–c*; Paton *et al.*, 1999; Anderson, 2001). However, little consensus has emerged for the relationships and affinities of many other groups [e.g. lepospondyls; see Carroll (1995), Carroll & Chorn (1995), Laurin & Reisz (1997, 1999), Laurin (1998*a–c*), Paton *et al.* (1999) and Anderson (2001)], despite the discoveries of new data and the introduction of more powerful analytical techniques. This conflict triggered the present work. Visual inspection of current phylogenies reveals two distinct sets of tree topologies (see also Ruta *et al.*, 2001). The first set consists of trees which place most fossil tetrapods either in the stem-lissamphibians (e.g. temnospondyls) or in the stem-amniotes (e.g. embolomeres) (Panchen & Smithson, 1987, 1988; Panchen, 1991; Ahlberg & Milner, 1994; Coates, 1996; Clack, 1998*a*, *c*, 2001; Paton *et al.*, 1999). In these short-stemmed trees, operational taxonomic units (OTUs) are arranged mostly dichotomously (Fig. 1A, B). The second set of trees reflects the hypothesis that a greater number of fossil tetrapods traditionally allied to lissamphibians or amniotes show no special relationships to either group (e.g. Laurin & Reisz, 1997, 1999; Ahlberg & Clack, 1998; Laurin, 1998*a–c*; Anderson, 2001). In these long-stemmed trees (Fig. 1C, D), OTUs form a largely pectinate pattern (unbalanced trees; Smith, 1994). Twelve major groups of early tetrapods are usually recognized (see also below): adelospondyls; aïstopods; baphetids; colosteids; diadectomorphs; embolomeres; gephyrostegids; lysorophids; microsaurs; nectrideans; seymouriamorphs; temnospondyls. Fig. 2 shows the percentage distributions of such groups in the tetrapod, lissamphibian and amniote stem-groups, according to various recent studies. For simplicity, these distributions do not take into account several Devonian and Carboniferous genus- and species-level OTUs. The percentage distributions highlight remarkable differences in the number of groups assigned to the lissamphibian and amniote stem-groups. This is especially evident in a comparison of Carroll's (1995) and our own analyses, in which eight/nine different groups are placed within stem-amniotes, with the Laurin & Reisz (1999) and Anderson's (2001) analyses, in which most groups are almost equally distributed between the tetrapod stem-group and the lissamphibian stem-group.

Evaluation of conflicting results of published phylogenies is complicated by the use of very different taxon and/or character samples. In several studies, only a small number of OTUs has been considered. These are sometimes represented by supraspecific terminals (e.g. Carroll, 1995), and/or by few genera or species for each major group (e.g. Coates, 1996; Clack, 1998*a*, *c*, 2001; Paton *et al.*, 1999). The size of a matrix also depends upon the focus of a particular phylogenetic analysis (e.g. Laurin & Reisz, 1997, 1999; Clack, 1998*a*, *c*, 2001; 1999; Ahlberg & Clack, 1998; Laurin, 1998*a–c*; Anderson, 2001). Several theoretical considerations suggest that taxon exemplars should be as diverse as possible (e.g. Nixon & Davis, 1991; deBraga & Rieppel, 1997; Anderson, 2001; Prendini, 2001; see also discussion below). Importantly, a recent study based on simulations of true phylogenies (Salisbury & Kim, 2001) indicates that dense and random taxon sampling increases the probability of retrieving correctly the plesiomorphic condition of characters as well as the ancestral state near the tree root. Furthermore, Salisbury & Kim's (2001) simulations show that in the analysis of small clades, estimates of ancestral states are strongly affected by cladogram topology and by the number of descendent branches in progressively more distal internal nodes.

Increasing the number of taxa (as well as the number of characters) poses additional problems, e.g. (1) poor resolution caused by the amount and distribution of missing entries (Wilkinson, 1995; Kearney, 1998, 2002); (2) computation time required by large and complex data sets (Farris *et al.*, 1996; Goloboff, 1999; Nixon, 1999; Quicke, Taylor & Purvis, 2001, and references therein); (3) accuracy in the search for optimal trees; and (4) high levels of homoplasy. The number of characters is obviously a function of the number of taxa and of the degree of morphological variation both within and between examined groups. In addition, the extent to which observed morphologies are 'atomised' even for the same taxon sample varies considerably from author to author, as does the perceived importance, or 'weight', assigned to particular structures.

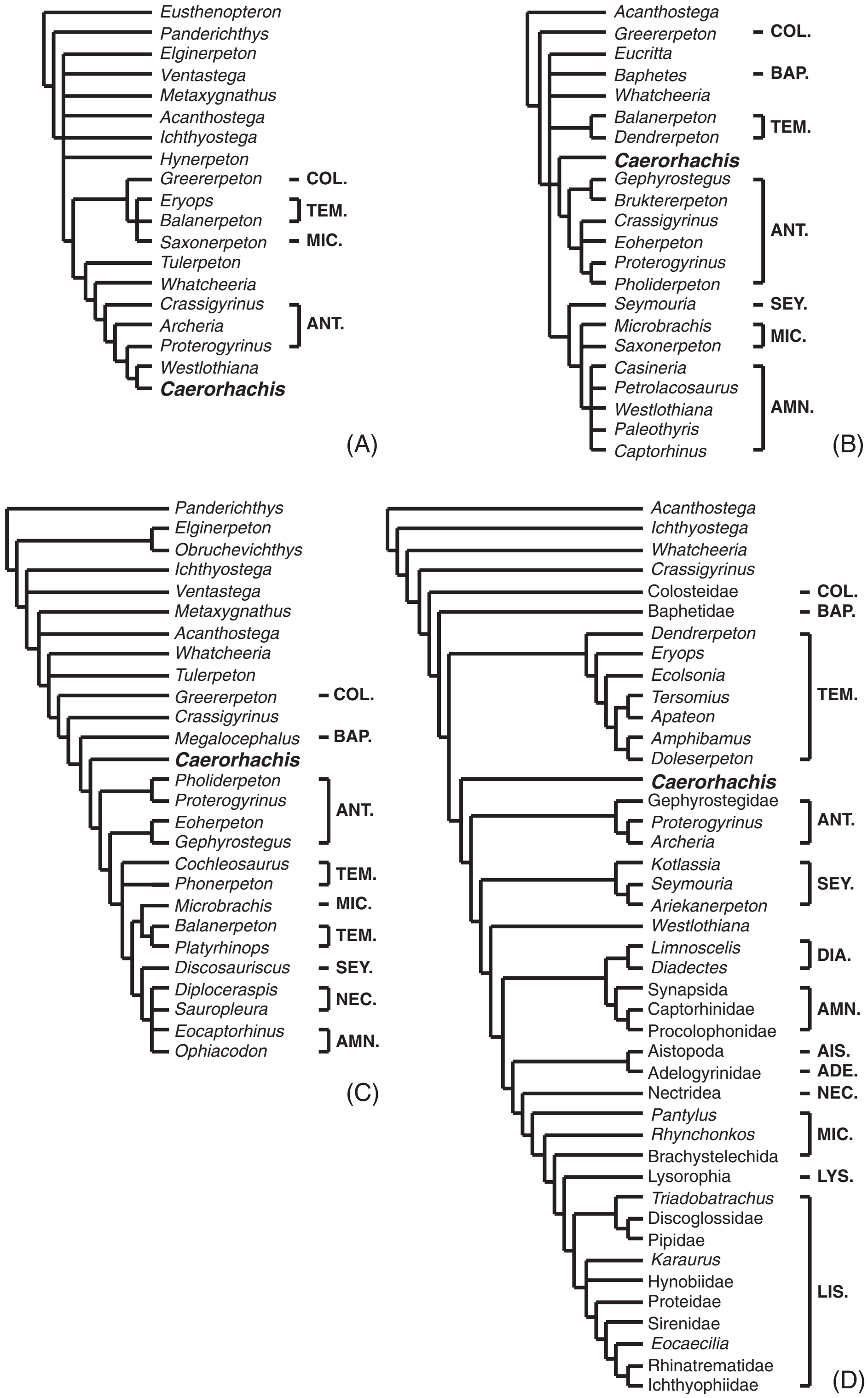

Fig. 1. Phylogenies of early tetrapods, redrawn and modified from Ruta *et al.* (2001), after inclusion of *Caerorhachis bairdi*. (A) Coates' (1996) analysis; (B) Paton *et al.*'s (1999) analysis; (C) Ahlberg & Clack's (1998) analysis; (D) Laurin's (1998 *b*) analysis. Abbreviations as follows: ADE., Adelospondyli; AIS., Aïstopoda; AMN., crown-group Amniota; ANT., Anthracosauria (including Embolomeri and Gephyrostegidae); BAP., Baphetidae; COL., Colosteidae; DIA., Diadectomorpha; LIS., crown-group Lissamphibia; LYS., Lysorophia; MIC., Microsauria; NEC., Nectridea; SEY., Seymouriamorpha; TEM., Temnospondyli.

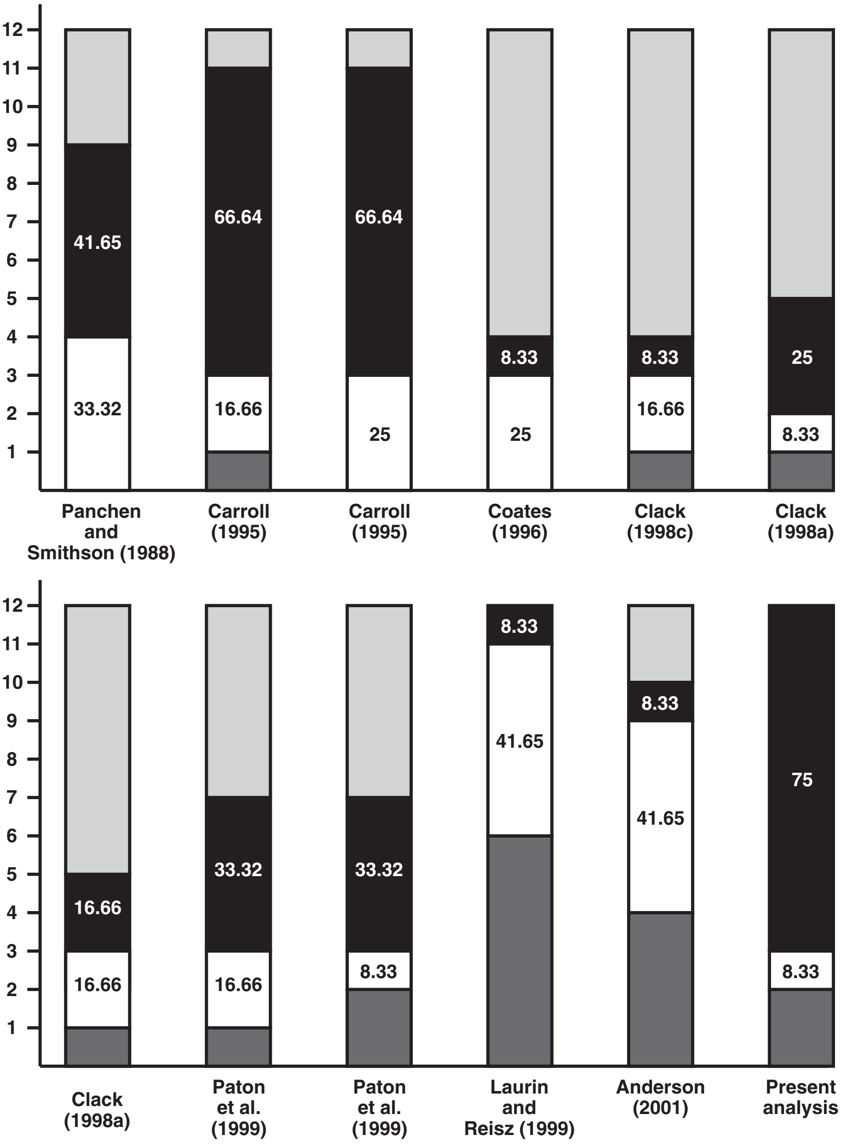

Fig. 2. Distribution of primitive tetrapod groups in recently published cladistic analyses, based on their assignment to stem-tetrapods (dark grey), stem-lissamphibians (white) or stem-amniotes (black). The vertical axis represents the total number of groups (embolomeres and gephyrostegids are treated as separate groups). Numbers inside bar diagrams indicate their percentage distributions. Light grey areas refer to groups that have not been examined. If an analysis yields different topologies, group distributions are plotted separately for each topology. The diagrams do not consider several Devonian and Carboniferous genera/species.

Clearly, characters should be targeted at the diversity displayed by the memberships of very large exemplars. Finally, inclusion/exclusion of taxa and/or characters may affect the outcome of an analysis in unpredictable ways (e.g. Clack, 1998*a*, *c*, 2001; Paton *et al*., 1999; Ruta *et al*., 2001). However, various theoretical approaches to character inclusion/exclusion often have been misguided by the lack of an adequate conceptual framework [see Grandcolas *et al*.'s (2001) discussion of the 'precise primary homologies' approach]. Also, taxon removal because of incomplete preservation and missing character scores may be undesirable, because such taxa may have a positive effect on cladogram resolution (Novacek, 1992; Wilkinson, 1995; Kearney, 1998, 2002; Anderson, 2001).

III. HISTORICAL BACKGROUND

Lack of space prevents an exhaustive treatment of the history behind phylogenetic studies of early terrestrial vertebrates. Therefore, only a brief summary is given in this section [see also Laurin (1998*b*), Carroll (2001) and Ruta *et al.* (2001)]. Among the first attempts at producing synapomorphy schemes used to reconstruct the broad pattern of relationships between major Palaeozoic tetrapod groups are those by Heaton (1979, 1980), Gardiner (1982, 1983), Holmes (1984), Smithson (1985), Gauthier, Kluge & Rowe (1988*a*, *b*), Panchen & Smithson (1987, 1988) and Godfrey (1989). Panchen & Smithson (1988) proposed a deep phylogenetic split between 'reptiliomorphs' (amniote-related groups) and 'batrachomorphs' (lissamphibian-related groups). In Panchen & Smithson's (1988) scheme, ichthyostegids, nectrideans, colosteids and microsaurs are successively more closely related to a temnospondyl-lissamphibian clade, whereas baphetids (loxommatids), anthracosauroids, seymouriamorphs (the latter two groups sometimes thought to be each other's closest relatives) and diadectomorphs are successive plesions on the amniote stem-group. The problematic *Crassigyrinus* was considered to be either a plesion between baphetids and a clade of anthracosauroids plus seymouriamorphs, or the sister taxon to anthracosauroids. Lepospondyl monophyly is explicitly rejected in Panchen & Smithson's (1988) cladogram. Subsequent studies (e.g. Lombard & Sumida, 1992; Lee & Spencer, 1997) have corroborated to a large extent the scheme of 'reptiliomorph' relationships proposed by Panchen & Smithson (1988) and Gauthier *et al.* (1988*b*).

A series of new studies on Devonian and primitive Carboniferous forms during the mid and late 1990s (Ahlberg, 1991, 1995, 1998; Coates, 1991, 1995, 1996; Ahlberg *et al.*, 1994; Daeschler *et al.*, 1994; Clack & Coates, 1995; Coates & Clack, 1995; Lebedev & Coates, 1995; Lombard & Bolt, 1995; Jarvik, 1996; Clack, 1998*b*; Milner & Lindsay, 1998), and the publication of the first, large-scale, computer-assisted cladistic analysis of Palaeozoic tetrapods by Carroll (1995), gave new impetus to early tetrapod research. In Carroll's (1995) study, the hypothesis of a chronologically deep phylogenetic event leading to the separation between lissamphibians and amniotes is implicit, although no members of the lissamphibian crown-group were included. In addition, lepospondyls form a clade on the amniote stem-group. Following the description of the postcranium of *Acanthostega*, Coates' (1996) analysis [an elaborated version of Lebedev & Coates's (1995) work] followed previous authors' suggestions that the lissamphibian/amniote split was a deep phylogenetic event. It also corroborated Lebedev & Coates's (1995) conclusion that such a split can be traced back to the late Devonian, based on Lebedev & Coates's (1995) and Coates' (1996) interpretation of *Tulerpeton* as a primitive 'reptiliomorph'. Other studies supporting a fundamental dichotomy between Palaeozoic tetrapods, based on different subsets of anatomical characters, are those by Sumida & Lombard (1991), Berman, Sumida & Lombard (1992), Sumida, Lombard & Berman (1992), Lee & Spencer (1997), Sumida (1997) and Berman (2000).

Clack (1998*a*, *c*, 2001) and Paton *et al.* (1999) published detailed character analyses for several Palaeozoic groups with an aim to assess the relationships of such problematic forms as *Crassigyrinus*, *Whatcheeria*, *Eucritta* and *Casineria*. These works paved the way to further scrutiny of problematic regions of the tetrapod tree. Examples include the lissamphibian-amniote split, the pattern of character acquisition in the crownward part of the tetrapod stem-group and in the basal portions of the lissamphibian and amniote stem-groups, and the placement of 'difficult' taxa, such as baphetids.

Significantly, the results of Laurin & Reisz's (1997, 1999) and Laurin's (1998*a–c*) analyses departed radically from those of previous studies. In these works, the tetrapod stem-group became much longer, because a series of groups (e.g. embolomeres, temnospondyls) were removed from amniote or lissamphibian ancestry. As a result, the established pattern of character-state changes along the amniote and lissamphibian stem-groups collapsed. Some of the characters generally considered to be diagnostic of basal 'reptiliomorphs' and 'batrachomorphs' now informed the order of cladogenetic events preceding the crown-tetrapod radiation. Lepospondyls now formed a paraphyletic array of stem-group lissamphibians, whereas diadectomorphs [as well as *Solenodonsaurus* in Laurin & Reisz's (1999) analysis] became the only plausible stem-group amniotes. Some of the conclusions reached by Laurin & Reisz (1997, 1999) and Laurin (1998*a–c*) were corroborated by Ahlberg & Clack's (1998) analysis of lower jaw characters, especially with regards to the stem-tetrapod affinities of *Crassigyrinus*, *Tulerpeton*, *Whatcheeria*, colosteids and baphetids. Ahlberg & Clack's (1998) analysis incorporated isolated material into a wider taxon set, and detected patterns of jaw character transformation across the fish–tetrapod transition and the crownward part of the stem-group. However, they also found that lower jaw data are apparently insufficient to retrieve a single origin for several long-accepted Palaeozoic groups, which appear, instead, as para- or polyphyletic assemblages [but see Ruta & Coates (in press)].

The most recent cladistic analyses of early tetrapods are those by Anderson (2001) and Clack (2002). Although few taxa were considered outside lepospondyls, Anderson's (2001) work generally agrees with Laurin & Reisz's (1997, 1999) and Laurin's (1998*a–c*) results by placing lepospondyls on the lissamphibian stem, and seymouriamorphs, embolomeres and temnospondyls on the tetrapod stem. Clack's (2002) analysis encompasses a diverse range of early tetrapod groups, and offers a rather unconventional branching pattern. Whatcheeriids, *Crassigyrinus*, *Eoherpeton*, embolomeres and gephyrostegids are successively more closely related to a diverse group including, on the one hand, *Westlothiana* as sister taxon to lepospondyls, and on the other, seymouriamorphs and temnospondyls as successive sister groups to a clade of colosteids plus *Caerorhachis* paired with *Eucritta* plus baphetids. Evaluation of the results of Anderson's (2001) and Clack's (2002) studies is beyond the scope of the present review.

Persistent conflict indicates that the resolution of several phylogenetic problems must await comprehensive treatment of the expanding tetrapod data base, as well as input from smaller-scale studies targeted at the specific relationships within various groups. As noted by Carroll (2001: p. 1212), 'We have a great deal of knowledge of the anatomy of a vast array of Paleozoic tetrapods (Heatwole & Carroll, 2000), but the specific interrelationships of the major taxa and their affinities with the modern orders remain impossible to establish with assurance without much more knowledge of fossils from the Lower Carboniferous and from the period between the Lower Permian and the Jurassic'. Carroll's (2001) statement identifies the problem of discovering unambiguous phylogenetic signal behind the broad spectrum of primitive tetrapod morphologies. This review is intended to resolve some of the current problems, not only by presenting a new hypothesis of relationships, but also by identifying the limits and difficulties of the ongoing debate. Unlike Carroll (2001), we argue that lack of critical fossils from crucial periods of tetrapod history may be less significant than a detailed scrutiny of the evidence available, at least in some regions of the tetrapod tree.

IV. TAXONOMIC DEFINITIONS

Two issues of taxonomic nomenclature are addressed here. The first relates to the definition and taxonomic content of Tetrapoda, and the second concerns the introduction of '… new [taxonomic] names and altered meanings for old names' (Greene, 2001: p. 738), and their use in phylogenetic systematics.

Several definitions of Tetrapoda have been proposed. Laurin & Reisz (1997, 1999), Laurin (1998*a–c*) and Laurin, Girondot & deRicqlès (2000*a*, *b*) adopt a node-based definition, referring the Tetrapoda exclusively to the crown-group. In several important respects, this resembles Gaffney's (1979: p.103) explicitly nodal definition of the Neotetrapoda (*contra* Laurin, 2002). All of these definitions have been established with clear reference to taxon naming within a phylogenetic framework (e.g. deQueiroz & Gauthier, 1990, 1992, 1994; Cantino *et al.*, 1999; Bryant & Cantino, 2002, and references therein). According to Laurin *et al.* (2000*b*), the '… [phylogenetic nomenclatural] system clarifies the taxonomy … because there is only one valid phylogenetic definition (the first published one) for each taxon name'. We note that this definition prunes the content of the Tetrapoda, relative to previous uses of this term (Coates, 1996; Benton, 2000; Coates *et al.*, 2000; Forey, 2001; see also below). However, as pointed out by Coates *et al.* (2000: p. 327), not only the biological community, but '… the world at large has a say about what is, or is not, a tetrapod'.

Tetrapods have long been identified on the basis of limbs with digits, i.e. synonymous with dactyly, but it is now clear that digit presence extends beyond the crown clade. Within Laurin's (1998*b*) and Laurin & Reisz's (1999) preferred tree topologies, several Upper Devonian to Upper Permian dactylous groups, crownward of *Panderichthys*, are excluded from the Tetrapoda. Instead, these clades now rank among a heterogeneous stem assemblage of 'non-tetrapod stegocephalians'. The Tetrapoda, *sensu* Laurin (1998*b*), is poorly informative in evolutionary as well as general biological discussions of dactylous vertebrates as a whole, although this has been one of the most easily recognized of all vertebrate groups (Goodrich, 1930; Romer, 1966; Gaffney, 1979; Panchen & Smithson, 1987, 1988; Benton, 1988, 2001; Carroll, 1988; Schultze & Trueb, 1991). As an alternative, we advocate the use of a total-group (stem-based) definition of the Tetrapoda.

Objections to a stem-based definition have been raised by Ahlberg (1998) and Ahlberg & Clack (1998) (see also Clack, 1998*c*, 2001). Their arguments can be summarized as follows: (1) there is as yet no consensus on the identity of the Recent sister group of living tetrapods (Forey, 1998; Zardoya & Meyer, 2001); (2) the taxonomic content of the 'fish-like' portion of the tetrapod stem-group is not agreed upon [see Zhu & Schultze (2001) and Johanson & Ahlberg (2001) for summary hypotheses]; and (3) digits cannot be used to characterize the basal 'fish-like' part of the tetrapod stem-group. Furthermore, although limb bone fragments have been attributed to various Devonian stem-tetrapods (e.g. Ahlberg, 1991, 1998; Ahlberg *et al.*, 1994), the occurrence of digits in such forms is unknown. For these reasons, Ahlberg (1998) and

Ahlberg & Clack (1998) propose an apomorphy-based definition, but acknowledge that this represents only a temporary solution (see also Clack, 1998*c*). Specifically, dactyly is chosen as the key derived character for Tetrapoda – again, in agreement with traditional definitions (see comments in Anderson, 2001). This clade encompasses all taxa crownward of Elpistostegalia (the group including *Panderichthys* and allied forms). However, once again, the exclusion of various basal groups from Tetrapoda (e.g. the paraphyletic array of 'osteolepiform fishes' ; Ahlberg & Johanson, 1998) limits the information content discovered in cladistic analysis, although less so than Laurin's and Laurin & Reisz's node-based definition. Such basal groups are named, rather clumsily, 'non-tetrapod tetrapodomorphs' (e.g. Cloutier & Ahlberg, 1996; Ahlberg & Johanson, 1998).

Operationally, the adoption of a total-group definition (e.g. Jefferies, 1979; Craske & Jefferies, 1989; Budd, 2001; Jeffery, 2001) solves some of the above-mentioned nomenclatural problems (see also discussion in Coates, 1996). Thus, the tetrapod stem-group includes any fossil taxon that can be shown, based on a formal character analysis, to be more closely related to lissamphibians and amniotes than to any other living group. This holds true regardless of the presence/absence of key apomorphic features (such as digits), and the identity of the tetrapods' extant sister taxon (e.g. Jeffery, 2001). If a fossil is more closely related to either extant lissamphibians or extant amniotes, it is a member of the crown-group by definition (see above). Uncertainty in the placement of extinct forms in the basal part of the crown-group or in the crownward part of the stem-group is irrelevant, because the membership of a total-group only concerns closeness of relationship of any fossil to one particular extant clade (Patterson & Rosen, 1977; Jefferies, 1979; Craske & Jefferies, 1989; Forey, 1993; Patterson, 1993*a*, *b*, 1994; Smith, 1994; Nixon & Carpenter, 2000; Budd, 2001; but see also Brochu & Sumrall, 2001). The approach advocated here is not new. For example, the 'stem-modified node-based definition' employed by Meng *et al.* (1994) and Wyss & Meng (1996) is much the same in its formulation [see comments in Sereno (1998, 1999) and Bryant & Cantino (2002)]. Importantly, a total-group definition can accommodate a node-based phylogenetic definition without sacrificing cladistic information, whereas the converse is not true. From a purely operational perspective, stability in taxonomic content and degree of corroboration of clades (Lee & Spencer, 1997) may become secondary issues. Also, Lee & Spencer (1997) and Sereno (1998, 1999) showed that adoption of crown-clade definitions does not necessarily lead to increased taxonomic stability. Furthermore, we leave aside the issues of naming cladogram nodes within extinct monophyla, and the widespread misuse of plesions [*sensu* Patterson & Rosen, 1977; see Craske & Jefferies's (1989) approach to plesion subdivision].

Several examples from the literature show that the often heated debates on assignments of taxonomic names to specific cladogram nodes (e.g. Aves, Mammalia, Tetrapoda) may be ill-conceived. These debates could be avoided by adopting total-group definitions, which are only marginally affected by reshuffling of extinct taxa, or by changes in the fossil membership of crown-groups. Thus, referring to *Eusthenopteron* as a stem-tetrapod should not be more puzzling or counter-intuitive than regarding ceratopian dinosaurs (e.g. *Triceratops*) as stem-birds, sail-back pelycosaurs (e.g. *Dimetrodon*) as stem-mammals, or *Australopithecus* as a stem-human. In all cases, an explicit hypothesis of relationship with a living monophylum is provided, and '… the name and rank given to the clade formed by the modern phena is extended to include all stem group members of that taxon' (Smith, 1994: p. 97). Sereno (1998, 1999) notes that the interpretation of fossils always relies upon identification of one or more key features shared with a Recent taxon, even if such fossils fall outside the crown-group. Thus, using an appropriate name modifier might be suitable in dealing with crown-clades (e.g. living or Recent Mammalia; living or Recent Aves) instead of restricting a well-known name to the crown-clade exclusively.

Apomorphy-based names are problematic in at least two respects. First, a taxon for which a character cannot be coded (e.g. because of unknown or inapplicable information) may fall inside or outside a group defined upon the possession of the character in question. Its inclusion or exclusion from the group depends upon alternative character state optimizations (e.g. accelerated or delayed transformations). Likewise, if a taxon does not show a certain character, but its position in a cladogram is nested between groups that display that character, then optimization implies either parallel acquisitions (delayed transformation), or a single origin followed by secondary loss in the taxon in question (accelerated transformation). Second, key apomorphy definitions can be problematic. Various conditions of particular structures may occur at different stem-group nodes (e.g. integumentary structures preceding true feathers in several theropods; e.g. Xing, Zhong-He & Prum, 2001).

Anderson's (2001) definition of Tetrapoda uses Elpistotegalia and crown-tetrapods as 'anchor' taxa, and is argued to be consistent with traditional usage as well as phylogenetic nomenclature. We acknowledge the rationale behind Anderson's (2001) usage, but the exclusion of taxa less crownward than Elpistostegalia is somewhat arbitrary. Moreover, the monophyly of Elpistostegalia is questionable, and there is always the potential that incompletely known fossils, such as *Elpistostege* (Schultze & Arsenault, 1985), could turn out to be more closely related to alternative groups, the consequences of which would depart radically from Anderson's stated intention.

A further nomenclatural issue concerns the application of historically laden names to novel phylogenetic definitions (see also Anderson, 2001). Laurin's (1998*a–c*) Anthracosauria is a prime example, because it includes none of the taxa traditionally placed within 'anthracosaurs', such as embolomeres, gephyrostegids and, more questionably, seymouriamorphs (Heaton, 1980; Smithson, 1985; Panchen & Smithson, 1987, 1988; Gauthier *et al.*, 1988*b*; Forey, 2001). Instead, the new definition refers to a clade encompassing *Solenodonsaurus*, diadectomorphs and crown-amniotes. Consequently, *Anthracosaurus russelli* Huxley, 1863 is neither an anthracosaur nor a tetrapod, whereas T. H. Huxley himself would be classified as a cotylosaurian anthracosaur. Such long-abandoned terms as Cotylosauria and Stegocephali, traditionally referring to archaic grade-groups, are now re-introduced with a novel content. Thus, Cotylosauria includes Anthracosauria minus *Solenodonsaurus* (i.e. diadectomorphs plus crown-amniotes), whereas Stegocephali includes all taxa with digits, i.e. tetrapods in the traditional sense (Goodrich, 1930; Gaffney, 1979; Coates, 1996; Ahlberg, 1998; Ahlberg & Clack, 1998; Anderson, 2001). This resurrectionist approach is currently the subject of intense debate [for conflicting views, see Benton (2000), Nixon & Carpenter (2000), Cantino (2000), Coates *et al.* (2000), Forey (2001), Brochu & Sumrall (2001), Bryant & Cantino (2002), and references therein].

V. TAXON EXEMPLARS

The limits and content of several early tetrapod groups are widely agreed upon and, with few exceptions (e.g. anthracosaurs, microsaurs, temnospondyls), their monophyly has not been disputed (Säve-Söderbergh, 1934; Carroll, 1970; Heaton, 1980; Smithson, 1985, 1986, 1994, 2000; Gauthier *et al.*, 1988*b*; Clack, 1994*c*, 1998*a*, *c*; Smithson *et al.*, 1994; Lombard & Bolt, 1995; Coates, 1996; Laurin & Reisz, 1997, 1999; Laurin, 1998*a–c*; Ahlberg & Clack, 1998; Paton *et al.*, 1999; Berman, 2000; Bolt & Lombard, 2000; Anderson, 2001; Ruta *et al.*, 2001). Ninety species are included in the present work (see Appendix 1 for a list of the specimens examined). OTUs are chosen according to three criteria: (1) sample of maximally diverse taxon exemplars (Nixon & Davis, 1991; Anderson, 2001; Prendini, 2001); (2) inclusion of the majority of taxa considered in previous studies; (3) use of species as terminals (e.g. Bininda-Emonds, Gittleman & Purvis, 1999; Anderson, 2001). Justification for the exclusion of some species is provided in the relevant taxonomic sections below. The plesiomorphic conditions of various tetrapod groups remain untested in several analyses. Therefore, large exemplars are used when hypotheses of relationships within a particular group are unavailable, or are based on a limited character/taxon sample. Diverse exemplars may also prevent spurious pairing of taxa resulting either from long branch attraction or from a host of convergent characters. For instance, a cluster of 'absence' features may discriminate against sister group relationships based on a smaller number of 'good' apomorphies. Finally, if members of a group display conflicting character distributions, exemplars should encompass such distributions.

Few basal crown-lissamphibians and crown-amniotes are considered here. Recent supraspecific OTUs are omitted, since large-scale interrelationships of primitive tetrapods are our main focus. Laurin & Reisz's (1997, 1999) and Laurin's (1998*a–c*) analyses include several families from each of the three lissamphibian orders. However, comparisons between Palaeozoic and Recent faunas demand a proper evaluation of the primitive condition for several extant groups, and may be impractical, given the aims of this study. As an alternative approach, primitive members of various modern clades could be included to document crown-tetrapod diversity in the Mesozoic and Caenozoic. The utility of such a comprehensive data set is nontheless dubious, since convergent features are likely to be widespread. Also, the size of the resulting matrix and the abundant missing entries may introduce severe computation problems.

(1) Devonian and Lower Carboniferous taxa

(*a*) *Taxonomic sample*

Acanthostega gunnari Jarvik, 1952.
Ichthyostega stensioei Säve-Söderbergh, 1932.
Tulerpeton curtum Lebedev, 1984.
Ventastega curonica Ahlberg, Luksevics & Lebedev, 1994.
Caerorhachis bairdi Holmes & Carroll, 1977.
Crassigyrinus scoticus Watson, 1929.
Eucritta melanolimnetes Clack, 1998*a*.

Westlothiana lizziae Smithson & Rolfe, 1990.
Whatcheeria deltae Lombard & Bolt, 1995.

(*b*) *Remarks*

The four Devonian species considered here have been the subjects of intense recent scrutiny. Work on the first discovered Devonian tetrapod, *Ichthyostega* (Jarvik, 1980, 1996; see notes and references therein for comments on species status), has been followed by detailed investigations of exceptionally well preserved and abundant material of *Acanthostega*, including descriptions of the snout and palate (Clack, 1994*a*), braincase (Clack, 1994*a*, 1998*b*), stapes (Clack, 1989, 1994*b*), skeletal gill apparatus (Coates & Clack, 1991), limbs (Coates, 1991, 1995, 1996; Clack & Coates, 1995; Coates & Clack, 1990, 1995) and postcranium (Coates, 1996). The branching sequence of the majority of Devonian tetrapods is generally agreed upon [but see Lebedev & Coates (1995), Coates (1996), Ahlberg & Clack (1998), Laurin (1998*a–c*) and Laurin & Reisz (1997, 1999)]. The following taxa, known mainly from lower jaw rami and/or incomplete postcranial remains, are omitted: *Metaxygnathus denticulus* Campbell & Bell, 1977, *Obruchevichthys gracilis* Vorobyeva, 1977, *Elginerpeton pancheni* Ahlberg, 1995 [see also Ahlberg (1991, 1998)], *Hynerpeton bassetti* Daeschler, Shubin, Thomson & Amaral, 1994, *Livoniana multidentata* Ahlberg, Lukseviks & Mark-Kurik, 2000 and *Densignathus rowei* Daeschler, 2000.

Crassigyrinus scoticus and *Whatcheeria deltae* are among the most problematic of early Carboniferous tetrapods [reviews in Clack & Carroll (2000) and Bolt & Lombard (2000)]. Traditionally, they have been regarded as having ‘reptiliomorph’ affinities (e.g. Panchen, 1973, 1985; Panchen & Smithson, 1987, 1988; Lebedev & Coates, 1995; Lombard & Bolt, 1995; Coates, 1996; Clack, 1998*a*, *c*, 2001; Paton *et al*., 1999; Bolt & Lombard, 2000), but evidence in support of their placement among basal stem-amniotes has been challenged repeatedly (e.g. Laurin & Reisz, 1997, 1999; Ahlberg & Clack, 1998; Laurin, 1998*a–c*; Clack & Carroll, 2000; Clack, 2002). *Westlothiana* from the uppermost Viséan of East Kirkton is usually considered to be one of the most primitive stem-amniotes (Smithson & Rolfe, 1990; Smithson *et al*., 1994). However, Laurin & Reisz (1999) placed *Westlothiana* as the closest outgroup to the tetrapod crown-clade. *Caerorhachis*, probably from the lowermost Serpukhovian of Scotland (Holmes & Carroll, 1977), was originally described as a basal temnospondyl [see Milner & Sequeira (1994) and Coates (1996) for an alternative view], but has been reinterpreted as a primitive ‘reptiliomorph’ by Ruta *et al*. (2001). More recently, Clack (2002) has placed this tetrapod as sister group to colosteids. Finally, *Eucritta* from East Kirkton displays a unique array of baphetid, temnospondyl and ‘anthracosaur’ features (Clack, 1998*a*, 2001) that account for the instability of the basal part of the tetrapod crown-group (but see comments in Thorley & Wilkinson, 1999).

(2) **Acherontiscidae**

(*a*) *Taxonomic sample*

Acherontiscidae: *Acherontiscus caledoniae* Carroll, 1969*b*.

(*b*) *Remarks*

Re-examination of the single known specimen of *Acherontiscus* (lowermost Serpukhovian of Scotland) indicates that it is probably an immature or pedomorphic adelospondyl (M. Ruta, personal observations). Vertebral construction is light; ribs are weakly ossified; skull roof, cheek bones, arrangement of circumnarial bones and mandibular shape are consistent with this interpretation. Discussion of the anatomy and relationships of this poorly known form will be presented in a future publication.

(3) **Adelospondyli**

(*a*) *Taxonomic sample*

Adelogyrinidae: *Adelospondylus watsoni* Carroll, 1967; *Adelogyrinus simorhynchus* Watson, 1929; *Dolichopareias disjectus* Watson, 1929.

(*b*) *Remarks*

Adelospondyls, ranging from the upper Viséan to the lowermost Serpukhovian, have been reviewed by Andrews & Carroll (1991), Carroll *et al*. (1998) and Carroll (2000). Details of the skull roof are known in most species and, in the case of *Adelospondylus*, a partially preserved palate is also observed. Lower jaws and partial postcranial remains are associated with *Adelogyrinus* and *Adelospondylus*. A fourth species, *Palaeomolgophis scoticus* Brough & Brough, 1967, known from a postcranium and associated partial skull roof, incomplete palate and lower jaws, will be discussed in conjunction with the planned revision of *Acherontiscus caledoniae*. Adelospondyls display a highly specialized skull roof (e.g. reduction and/or loss of several bones; presence of a squamosotabular element), heavily ossified gill arches, and apparent absence of endochondral shoulder girdle and limbs. Conversely, the dermal portion of the shoulder girdle is robust. Limb absence may well be a preservational artifact, especially because of the very few specimens known. No pelvic girdle has been observed. Some details of the snout and elongate skull roof and cheek bones resemble those in colosteids (Smithson, 1982; Schultze & Bolt, 1996; Panchen & Smithson, 1987). Similarities with colosteids are also evident in the general morphology and flange-like processes of the ribs. By contrast, the vertebrae are gastrocentrous, like those of microsaurs and lysorophids (see below).

(4) Aïstopoda

(*a*) *Taxonomic sample*

Lethiscidae: *Lethiscus stocki* Wellstead, 1982.
Ophiderpetontidae: *Oestocephalus amphiuminum* Cope, 1868.
Phlegethontiidae: *Phlegethontia linearis* Cope, 1871.

(*b*) *Remarks*

Aïstopods, ranging from the mid Viséan to the upper part of the Lower Permian, are limbless, snake-like tetrapods characterized by a broad postorbital emargination of the cheek, covered by a sheet of integument with embedded ossicles. The suspensorial configuration led Lund (1978) to suggest the occurrence of a snake-like skull kinetism in *Phlegethontia*, but Anderson's (in press) review of phlegethontiid crania indicates that this is incorrect, although limited kinesis near the snout tip may have occurred. The highly specialized nature of aïstopods poses problems for a correct assessment of their affinities [Carroll, 1998; see Anderson (2001) for ongoing anatomical and systematic revision of this clade]. *Lethiscus* is usually regarded as the most basal known aïstopod, based on its skull roof pattern (see also Milner, 1994). According to Anderson, Carroll & Rowe (2001), *Lethiscus* shows similarities with ophiderpetontids, which are paraphyletic relative to other aïstopods. *Oestocephalus* and *Phlegethontia* are the best known genera within ophiderpetontid and phlegethontiid aïstopods, respectively (review in Carroll *et al*., 1998). The cranial anatomy of *Oestocephalus* has been recently redescribed by Carroll (1998). McGinnis' (1967) and Lund's (1978) classical papers on *Phlegethontia* are now superseded by Anderson's (in press) revision of this genus. Several cranial and postcranial characters of aïstopods (especially the morphology of the vertebrae in some taxa) indicate possible affinities with nectrideans, in agreement with Thomson & Bossy's (1970) Holospondyli (= aïstopods plus nectrideans) hypothesis.

(5) Baphetidae

(*a*) *Taxonomic sample*

Baphetidae: *Baphetes kirkbyi* Watson, 1929; *Megalocephalus pachycephalus* (Barkas, 1873).

(*b*) *Remarks*

The interrelationships of baphetids, an uppermost Viséan to uppermost Moscovian group of tetrapods with keyhole-shaped orbits and a closed palate, remain unclear. Unequivocal association of cranial and postcranial material can be established only for *Baphetes* cf. *kirkbyi* (Milner & Lindsay, 1998). The lower jaw mesial surface is known in detail only in *Megalocephalus* (Beaumont, 1977; Ahlberg & Clack, 1998). The aberrant *Spathicephalus* Watson, 1929 (Beaumont & Smithson, 1998) is morphologically very divergent from remaining baphetids, although it is likely to be the sister taxon to these (Beaumont & Smithson, 1998). *Loxomma* Huxley, 1862 is in several respects intermediate morphologically between *Baphetes* and *Megalocephalus*, but its exclusion from the data set has no impact on the outcome of the analysis. Baphetids have been variously regarded as derived stem-tetrapods, basal stem-lissamphibians, or even basal 'reptiliomorphs'. Evidence in support of each of these hypotheses is problematic (Beaumont, 1977; Panchen, 1980; Panchen & Smithson, 1987, 1988; Ahlberg & Milner, 1994; Carroll, 1995; Laurin & Reisz, 1997, 1999; Beaumont & Smithson, 1998; Clack, 1998*a*, *c*, 2001; Laurin, 1998*a–c*; Milner & Lindsay, 1998). Various cranial and postcranial features (e.g. supratemporal–postparietal contact; fang pairs on palatal bones; shape of the humerus) indicate the primitive nature of this group, and contrast with such autapomorphic features as keyhole-shaped orbits, drop-shaped choanae and small temporal notches bordered anteriorly by the supratemporal (e.g. Clack, 1998*a*, 2001).

(6) Colosteidae

(*a*) *Taxonomic sample*

Colosteidae: *Colosteus scutellatus* (Newberry, 1856); *Greererpeton burkemorani* Romer, 1969.

(*b*) *Remarks*

Colosteids range from the upper Viséan to the uppermost Moscovian. *Colosteus* and *Greererpeton* are the best known members of the group (Smithson, 1982; Hook, 1983; Godfrey, 1989), but only the latter has been considered in most recent analyses of early tetrapod interrelationships. New data on the skull and lower jaw of *Greererpeton* (Bolt, 1996; Schultze & Bolt, 1996; Ahlberg & Clack, 1998; Bolt & Lombard, 2001) have confirmed previous hypotheses about the primitive status of the group [but see Hook (1983), Holmes (2000) and Carroll (2001) for alternative conclusions]. Plesiomorphic characters (e.g. trunk elongation; rhachitomous vertebrae; L-shaped humerus; anteriorly expanded clavicles) are associated with a unique pattern of circumnarial bones and a notch in the anterior extremity of the dentary. Coates (1996) demonstrated the presence of a five-digited manus in *Greererpeton*. The occurrence of a four-digited manus in *Colosteus* is based on data from Hook (1983), although the limb material of this genus is less well preserved than that of *Greererpeton*. Superficially, colosteids resemble certain temnospondyls [e.g. eobrachyopids (= saurerpetontids)], but similarities between the two groups are usually assumed to be convergent. Various skull roof features (e.g. elongate frontals and parietals) resemble those of certain lepospondyls (e.g. adelospondyls, nectrideans) and may indicate a close relationship (e.g. Panchen & Smithson, 1987; Milner, 1993; see also discussion of cranial data analysis below).

(7) Diadectomorpha

(*a*) *Taxonomic sample*

Diadectidae: *Diadectes absitus* Berman, Sumida & Martens, 1998.
Limnoscelidae: *Limnoscelis paludis* Williston, 1911.

(*b*) *Remarks*

Diadectomorphs range from the upper Bashkirian to the upper part of the Lower Permian, and are usually regarded as the closest relatives of crown-amniotes (e.g. Lee & Spencer, 1997), based on cranial and postcranial characters (Laurin & Reisz, 1997, 1999; Laurin, 1998*a–c*), morphology of the occiput (Berman, 2000), and atlas–axis complex (Sumida & Lombard, 1991; Berman *et al.*, 1992; Sumida *et al.*, 1992). According to Berman *et al.* (1992) and Berman (2000), the highly autapomorphic nature of *Diadectes* makes this taxon unsuitable for polarising characters at the base of the amniote tree. For this reason, and in agreement with previous studies (e.g. Laurin & Reisz, 1997, 1999; Laurin, 1998*a–c*), a second diadectomorph – *Limnoscelis paludis* – is included in this work (Williston, 1912; Romer, 1946; Fracasso, 1987; Berman & Sumida, 1990; Berman *et al.*, 1992; Berman, 2000). Pending a detailed redescription of *Tseajaia campi* Vaughn, 1964, this taxon is excluded from the data matrix (Moss, 1972; Walliser, 1998, 1999). The arrangement of bones in the posterior and posterolateral portions of the skull table of diadectomorphs is reminiscent of those in several primitive crown-amniotes (e.g. Berman *et al.*, 1998; Berman, 2000). This is especially evident in the enlargement of the parietals and in the expansion of the supraoccipital. A series of recent papers (Sumida & Lombard, 1991; Berman *et al.*, 1992, 1998; Sumida *et al.*, 1992; Berman, 2000) have clarified several poorly understood aspects of diadectomorph osteology, but the origin and diversification of this group remain problematic.

The Pennsylvanian *Solenodonsaurus janenschi* Broili, 1924 has been generally allied to 'reptiliomorphs' (Pearson, 1924; Brough & Brough, 1967; Carroll, 1970; Gauthier *et al.*, 1988*b*; Laurin & Reisz, 1999), based on its skull table morphology, gastrocentrous vertebrae and curved ribs. It is included in the present work because of its combination of features found in different 'reptiliomorphs', such as gephyrostegids, seymouriamorphs, diadectomorphs and basal crown-amniotes. According to Laurin & Reisz (1999), *Solenodonsaurus* is the sister taxon to a clade encompassing diadectomorphs and crown-amniotes (but see Lee & Spencer, 1997).

(8) Embolomeri and Eoherpetontidae

(*a*) *Taxonomic sample*

Anthracosauridae: *Anthracosaurus russelli* Huxley, 1863.
Archeriidae: *Archeria crassidisca* (Cope, 1884).
Eogyrinidae: *Pholiderpeton attheyi* (Watson, 1926); *Pholiderpeton scutigerum* Huxley, 1869.
Eoherpetontidae: *Eoherpeton watsoni* Panchen, 1975.
Proterogyrinidae: *Proterogyrinus scheelei* Romer, 1970.

(*b*) *Remarks*

Embolomeres and eoherpetontids [uppermost Viséan to lowermost Upper Permian; review in Panchen (1980)] include some of the best known Coal Measures 'anthracosaurs' (*sensu* Smithson, 1985, 1986, and Panchen & Smithson, 1987, 1988; see also Clack, 1994*c*). Several authors interpret 'anthracosaurs' as a basal radiation of aquatic or semiaquatic, long-bodied and amniote-like taxa (e.g. Panchen & Smithson, 1988; Coates, 1996; Lee & Spencer, 1997; Clack, 1998*a*, *c*, 2001; Paton *et al.*, 1999). However, their phylogenetic position relative to amniotes has been questioned (Laurin & Reisz, 1997, 1999; Laurin, 1998*a–c*), and the possibility that they fall outside the tetrapod crown-group cannot be ruled out (Dr J. A. Clack, personal communication to M. Ruta, 2001; see also Clack, 2002). Although embolomere anatomy is known in great detail (e.g. Romer, 1957; Panchen 1964, 1970, 1972, 1973, 1977, 1980; Holmes, 1980, 1984, 1989; Smithson, 1985; Clack, 1987*a*, *b*; Clack & Holmes, 1988), surveys of character distribution have not resulted in a consensus over their intrinsic relationships (e.g. Holmes, 1984, 1989; Smithson, 1985; Clack, 1987*a*). *Silvanerpeton miripedes* Clack, 1994*c* and *Eldeceeon rolfei* Smithson, 1994, both from the uppermost Viséan site of east Kirkton, are two of the earliest known 'anthracosauroids'. Several postcranial features (e.g. U-shaped intercentra and pleurocentra; low neural spines; small tabular horns) suggest that they are less derived than embolomeres.

(9) Gephyrostegidae

(*a*) *Taxonomic sample*

Gephyrostegidae: *Bruktererpeton fiebigi* Boy & Bandel, 1973; *Gephyostegus bohemicus* Jaekel, 1902.

(*b*) *Remarks*

The monophyly of gephyrostegids (lower Bashkirian to uppermost Moscovian) is supported by some recent studies (Paton *et al.*, 1999), and implicitly assumed in others (e.g. Laurin & Reisz, 1997, 1999; Laurin, 1998*a–c*). Gephyrostegids have long been considered to share characteristics with 'anthracosaurs' and higher 'reptiliomorphs' (e.g. Carroll, 1970, 1986, 1991*b*; Heaton, 1980; Smithson, 1985). Several cranial features resemble conditions in embolomeres, seymouriamorphs and various basal crown-amniotes (e.g. protorothyridids and captorhinids). Similarities with primitive amniotes are also evident in palatal bone proportions and in the morphology of the parasphenoid (e.g. Lee & Spencer, 1997). However, they lack a toothed transverse pterygoid flange, long regarded as a key amniote apomorphy (discussions in Carroll, 1970, 1991*b*). Likewise, their lower jaws (Ahlberg & Clack, 1998) include a mixture of features otherwise found in embolomeres and basal amniotes. Finally, the postcranium combines primitive features (e.g. U-shaped intercentra and pleurocentra) with several derived ones (e.g. reduced dorsal iliac blade; scapulocoracoid extending posteroventrally with respect to the posterior glenoid margin; L-shaped tarsal intermedium). Although morphological evidence is not strong (e.g. Carroll, 1991*b*), gephyrostegids may lie closer to early amniotes than embolomeres (see also Lee & Spencer, 1997).

(10) Lysorophia

(*a*) *Taxonomic sample*

Cocytinidae: *Brachydectes elongatus* Wellstead, 1991; *Brachydectes newberryi* Cope, 1868.

(*b*) *Remarks*

Lysorophids (upper Bashkirian to upper part of Lower Permian) are among the most enigmatic of all lepospondyls. The most recent account of the group is by Wellstead (1991). Their highly specialized and elongate skulls are characterized by a bar-like, anteroventrally sloping suspensorium and by a large fenestration in the cheek region that becomes confluent with the orbit anteriorly (Bolt & Wassersug, 1975). Other noteworthy features are the extreme reduction and poor ossification of limbs and girdles, the presence of vertebral keels, the occurrence of sutures between neural arches and vertebral bodies and the extreme elongation of the trunk region. As in the case of microsaurs, the occiput of lysorophids is strap-shaped. In addition, lysorophids share various cranial and mandibular characters with one or more microsaur families. For example, the configuration of the mandible and the shape and proportions of the premaxillae are reminiscent of those of brachystelechids (see also Wellstead, 1991). Laurin & Reisz (1997, 1999) and Laurin (1998*a–c*) place lysorophids as the nearest relatives of crown-lissamphibians. However, most of the characters supporting this position appear to be secondary losses (e.g. those related to certain cranial and palatal bones; see also Carroll & Bolt, 2001). Furthermore, some supposed synapomorphies are dubious. An example is represented by the occurrence of a cheek emargination, which is only superficially similar to that of certain primitive crown-lissamphibians and dissorophoids (Carroll, 2001). In these groups, the maxillary arcade is often incomplete posteriorly and the palatal bones are reduced to slender rods or struts. Conversely, the maxillary arcade of lysorophids is extensively sutured medially with broad palatal bones. Anderson (2001) considers lysorophids to be allied to aïstopods – both groups being nested within nectrideans (Fig. 3). *Brachydectes* is here treated as a composite genus, with anatomical information based on both *B. elongatus* and *B. newberryi* (see also Anderson, 2001).

(11) Microsauria

(*a*) *Taxonomic sample*

Brachystelechidae: *Batropetes fritschia* (Geinitz & Deichmüller, 1882).

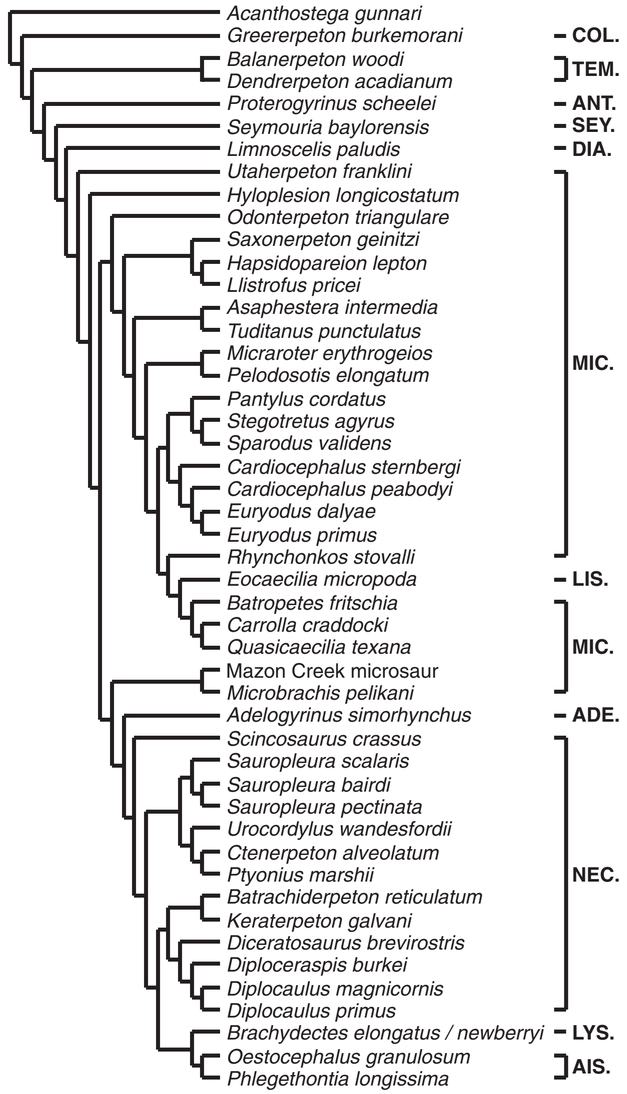

Fig. 3. Anderson's (2001) cladogram of lepospondyls. Abbreviations as in Fig. 1.

Hapsidopareiontidae: *Hapsidopareion lepton* Daly, 1973; *Saxonerpeton geinitzi* (Credner, 1890).

Goniorhynchidae: *Rhynchonkos stovalli* (Olson, 1970).

Gymnarthridae: *Cardiocephalus sternbergi* Broili, 1904*a*; *Euryodus primus* Olson, 1939.

Hyloplesiontidae: *Hyloplesion longicostatum* Fritsch, 1876.

Microbrachidae: *Microbrachis pelikani* Fritsch, 1876.

Odonterpetontidae: *Odonterpeton triangulare* Moodie, 1909.

Ostodolepidae: specimen BPI 3839 [possibly belonging to *Micraroter erythrogeios* Daly, 1973; see Carroll & Gaskill (1978)]; *Pelodosotis elongatum* Carroll & Gaskill, 1978.

Pantylidae: *Pantylus cordatus* Cope, 1871; *Stegotretus agyrus* Berman, Eberth & Brinkman, 1988.

Tuditanidae: *Asaphestera intermedia* (Dawson, 1894); *Tuditanus punctulatus* Cope, 1874.

(*b*) *Remarks*

Microsaurs range from the uppermost Serpukhovian/lowermost Bashkirian to the upper part of the Lower Permian and are the most diverse of all lepospondyl groups. Carroll & Gaskill (1978, and references therein) monographed the entire group. Gregory, Peabody & Price (1956) is a standard reference for gymnarthrids. Fifteen of the 21 genera examined by Anderson (2001; Fig. 3) are included in the present work. The following taxa, however, are omitted: (1) the brachystelechids *Carrolla* Langston & Olson, 1986 and *Quasicaecilia* Carroll, 1990; (2) one species from each of the two genera *Cardiocephalus* and *Euryodus* (Gymnarthridae); (3) the hapsidopareiontid *Llistrofus* Carroll & Gaskill, 1978; (4) the pantylid (*fide* Anderson, 2001) *Sparodus* Fritsch, 1876; (5) *Utaherpeton* Carroll, Bybee & Tidwell, 1991; and (6) an unnamed microsaur from Mazon Creek. A recently described, unnamed microsaur from Goreville, Illinois (Lombard & Bolt, 1999) is also excluded because of incomplete preservation.

Differences in the arrangement of skull roof bones are the most distinctive features of microbrachomorph and tuditanomorph microsaurs (Carroll & Gaskill, 1978). Few characters are shared by these two groups, the most important of which is the strap-shaped configuration of the exoccipitals and basioccipital, which is observed also in lysorophids (see above). Microbrachomorphs and tuditanomorphs possess a single bone in the position usually occupied by the intertemporal, supratemporal and tabular in several early tetrapods. In agreement with previous works (e.g. Carroll & Gaskill, 1978), the bone in question is interpreted as a tabular, based upon topological similarity. We note that this conjectural homology assessment affects further character scores that depend upon the morphology and spatial relationships of the tabular.

The extrinsic relationships of microsaurs are debated [see Milner (1993) for a summary]. Panchen & Smithson (1988) and Milner (1993) regard the presence of a 'waisted', propellor-blade like humerus as a synapomorphy of microsaurs and temnospondyls. However, humerus shape varies considerably both among temnospondyls and, to a lesser extent, among microsaurs. The hypothesis that caecilians evolved from long-bodied, presumably burrowing lepospondyls (Carroll & Currie, 1975; Carroll, 2000) has received support in certain recent analyses (e.g. Laurin & Reisz, 1997, 1999; Laurin, 1998*a*–*c*; Anderson, 2001). In particular, Anderson's (2001) study points to brachystelechids as the nearest relatives of caecilians.

Few phylogenetic analyses of microsaurs are available in the literature. Gymnarthrid interrelationships and a family-level analysis of tuditanomorphs are detailed by Schultze & Foreman (1981; see also Milner, 1993), whereas pantylids are discussed by Berman *et al.* (1988). Laurin & Reisz (1997, 1999) and Laurin (1998*a–c*) dispute the monophyletic status of microsaurs. In their analyses, *Pantylus*, *Rhynchonkos and* Brachystelechidae are progressively more closely related to lysorophids plus crown-lissamphibians, implying *ipso facto* the paraphyletic status of tuditanomorphs. However, their taxon sample does not represent adequately microsaur diversity, and is biased towards inclusion of taxa with presumed gymnophionan (*Rhynchonkos*) or generalized lissamphibian similarities (Brachystelechidae) (Carroll & Currie, 1975; Carroll, 2000; Anderson, 2001). In Anderson's (2001) cladogram, tuditanomorph microsaurs include, in proximo-distal sequence, hapsidopareiontids (monophyletic), tuditanids (monophyletic), ostodolepids (monophyletic), and a clade of pantylids plus gymnarthrids placed as sister group to a clade of rhynchonkids, brachystelechids and *Eocaecilia*. In the same study, microbrachomorphs are distributed as follows: (1) *Utaherpeton* and *Hyloplesion* are basal to all remaining lepospondyls; (2) *Odonterpeton* is basal to hapsidopareiontids and more derived tuditanomorphs; (3) *Microbrachis* and the unnamed microsaur from Mazon Creek form the monophyletic sister group to all other (non-microsaur) lepospondyls.

(12) Nectridea

(*a*) *Taxonomic sample*

Diplocaulidae: *Batrachiderpeton reticulatum* (Hancock & Atthey, 1869); *Diceratosaurus brevirostris* (Cope, 1875); *Diplocaulus magnicornis* Cope, 1882; *Diploceraspis burkei* Romer, 1952; *Keraterpeton galvani* Wright & Huxley, 1866.

Scincosauridae: *Scincosaurus crassus* Fritsch, 1876.

Urocordylidae: *Ptyonius marshii* Cope, 1875; *Sauropleura* Cope, 1868 [treated as a composite genus with data from two species, *S. pectinata* Cope, 1868 and *S. scalaris* (Fritsch, 1883)]; *Urocordylus wandesfordii* Wright & Huxley, 1866.

(*b*) *Remarks*

Nectrideans are known from the upper Bashkirian to the lowermost Upper Permian, and are usually divided into urocordylids, scincosaurids and diplocaulids. The present work encompasses 75% of the taxa examined by Anderson (2001; Fig. 3). The genus *Ctenerpeton* Cope, 1897 and some species of *Diplocaulus* and *Sauropleura* are excluded. Diagnostic characters of nectrideans are observed almost exclusively in the postcranial skeleton (A. C. Milner, 1980) and relate to vertebral morphology (e.g. configuration of neural and haemal arches; extra-articulations above zygapophyses). Some of these characters are shared with at least some aïstopods (Bossy & Milner, 1998; Anderson, in press). A striking aspect of the anatomy of all nectrideans is the extreme elongation of the tail. Hardly any character of the skull roof and palate can be identified as a shared derived feature of the three families. However, there is agreement on the derived status of diplocaulids relative to other nectrideans. Various analyses (A. C. Milner, 1980; Milner, 1993; Bossy & Milner, 1998) place scincosaurids as the sister taxon to diplocaulids, based upon such unique features as the quadrate-bracing internal shelf of the squamosal. According to Panchen & Smithson (1988), nectrideans are just crownward of ichthyostegids on the lissamphibian stem, based largely on the presence of a four-digited manus. Milner's (1993) scheme of relationships agrees mostly with that of Panchen & Smithson (1988), except that nectrideans and colosteids appear as sister taxa. Three characters of the skull table are used by Milner (1993) to unite nectrideans with colosteids. Two of these – skull table elongation; broad postorbital-parietal contact – are also present (each one separately or both together) in other lepospondyl taxa (e.g. *Acherontiscus*; adelospondyls), and their conditions reverse within derived nectrideans. The third character (prefrontal bordering external naris and excluding nasal from naris margin) is problematic. Although the prefrontal enters the nostril in many nectrideans, the nasal does contribute to the nostril in several genera. Nectrideans are similar in several respects to aïstopods (e.g. Thomson & Bossy, 1970; Anderson, in press), but no support for a nectridean-aïstopod clade has been found in recent studies (Carroll, 1995; Laurin & Reisz, 1997, 1999; Laurin, 1998*a–c*; Anderson, 2001). In Anderson's (2001) cladogram, aïstopods and lysorophids form the sister group to diplocaulids, with urocordylids and scincosaurids as progressively more outlying clades. These results are in agreement with the observation that hardly any cranial feature of nectrideans is uniquely shared by all members of this group (Beerbower, 1963; A. C. Milner, 1980; Milner, 1993; Bossy & Milner, 1998), and that similarities with representatives of other clades are widespread (Anderson, in press).

(13) Seymouriamorpha

(*a*) *Taxonomic sample*

Discosauriscidae: *Discosauriscus austriacus* (Makowsky, 1876).
Kotlassiidae: *Kotlassia prima* Amalitsky, 1921.
Seymouriidae: *Seymouria baylorensis* Broili, 1904*b*; *S. sanjuanensis* Vaughn, 1966.

(*b*) *Remarks*

The phylogenetic position of seymouriamorphs (Pennsylvanian/Permian boundary to late Upper Permian) has been debated for almost a century. Characters of the lower jaw (e.g. rearward extension of splenial; anterior mandibular foramen), skull roof (e.g. suture between parietal and tabular), palate (e.g. transverse pterygoid flange bearing no teeth) and vertebral column (e.g. gastrocentrous vertebrae with cylindrical pleurocentra; swollen neural arches) indicate possible amniote affinities (Gauthier *et al.*, 1988*a*, *b*; Sumida & Lombard, 1991; Sumida *et al.*, 1992; Klembara, 1997; Lee & Spencer, 1997; Sumida, 1997; Ahlberg & Clack, 1998; Berman *et al.*, 2000; Klembara & Bartík, 2000, and references therein). However, the construction of the palate and occiput reveal several primitive traits (White, 1939; Laurin, 1995, 1996*b*; Berman, 2000). Soft tissue and osteological markers indicate the presence of gill filaments and electroreceptors in certain forms (Ivakhnenko, 1981; Kuznetsov & Ivakhnenko, 1981; Klembara, 1994, 1995). Various features of the limbs (especially the femur) and pelvic girdle (e.g. shape of the ilium and development of iliac shelf) resemble closely those of diadectomorphs. Among the characters supporting seymouriamorph monophyly are a broad, transverse *lamina ascendens* of the pterygoid (but this character may be more widely distributed among early tetrapods), small posttemporal fenestrae, otic tubes and slender stapes [summary in Laurin (1998*b*, 2000); see also Klembara (1997) and Klembara & Bartík (2000)].

In the present work, *Seymouria* is treated as a composite genus. Anatomical information is based on the works of White (1939), Berman & Martens (1993), Laurin (1995, 1996*b*), Berman *et al.* (2000) and Klembara, Martens & Bartík (2001). *Seymouria baylorensis* and *S. sanjuanensis* differ in details of the skull roof and postcranium, but a comparative study of these species must await an exhaustive redecription of *S. sanjuanensis* (Dr J. Klembara, personal communication to M. Ruta, 2001; but see also Berman *et al.*, 2000). The cranial and postcranial anatomy of *Discosauriscus* have been thoroughly restudied by Klembara (1997, and references therein) and Klembara & Bartík (2000, and references therein). *Kotlassia* has been re-examined by Bystrow (1944). Unfortunately, several osteological details of the latter form are very poorly known and need adequate redescription. Pending a reassessment of several eastern European and western Asian seymouriamorphs [see Ivakhnenko (1981), Kuznetsov & Ivakhnenko (1981), Zhang, Li & Wan (1984), Laurin (1996*a*, *c*, 1998*a*–*c*) and Laurin & Reisz (1997, 1999)], these are not considered further here, but the reader should refer to Ivakhnenko (1987) and Novikov, Shishkin & Golubev (2000) for reviews.

(14) Temnospondyli

(*a*) *Taxonomic sample*

Amphibamidae: *Amphibamus grandiceps* Cope, 1865; *Doleserpeton annectens* Bolt, 1969; *Eoscopus lockardi* Daly, 1994; *Platyrhinops lyelli* (Wyman, 1858).
Branchiosauridae: *Apateon pedestris* Meyer, 1844; *Leptorophus tener* (Schönfeld, 1911); *Schoenfelderpeton prescheri* Boy, 1986.
Cochleosauridae: *Chenoprosopus lewisi* Hook, 1993; *Cochleosaurus florensis* Rieppel, 1980.
Dendrerpetontidae: *Dendrerpeton acadianum* Owen, 1853.
Dissorophidae: *Broiliellus brevis* Carroll, 1964; *Ecolsonia cutlerensis* Vaughn, 1969.
Edopidae: *Edops craigi* Romer, 1935.
Eobrachyopidae: *Isodectes obtusus* (Cope, 1868).
Eryopidae: *Eryops megacephalus* Cope, 1877.
Micromelerpetontidae: *Micromelerpeton credneri* Bulman and Whittard, 1926.
Trematopidae: *Acheloma cumminsi* Cope, 1882; *Phonerpeton pricei* (Olson, 1941).
Trimerorhachidae: *Neldasaurus wrightae* Chase, 1965; *Trimerorhachis* cfr. *insignis* Case, 1935.
Family *incertae sedis*: *Balanerpeton woodi* Milner & Sequeira, 1994.

(*b*) *Remarks*

The nature and status of temnospondyls (uppermost Viséan to Albian), the most abundant and diverse of all groups of early tetrapods, are intensely debated. Temnospondyls have long played a pivotal role in our understanding of lissamphibian origins (e.g. Bolt, 1969, 1977, 1979, 1991; Milner, 1988, 1990, 1993, 2000; Trueb & Cloutier, 1991; Rocek & Rage, 2000*a*; Gardner, 2001). However, some recent analyses have questioned their lissamphibian affinities (Laurin & Reisz, 1997, 1999; Laurin, 1998*a*–*c*). The most distinctive character of temnospondyls is the occurrence of interpterygoid vacuities at least half as wide as the skull and bordered by triradiate pterygoids (Milner, 1988, 1990, 1993; Milner & Sequeira, 1994; Holmes, 2000). Although palatal vacuities are known in several other groups, those present in the vast majority of temnospondyls have a strongly concave perimeter, including the anteriormost extremity (*Edops* being one notable exception). These features occur in at least one microsaur and in some nectrideans (Carroll & Gaskill, 1978; A. C. Milner, 1980; Milner, 1993; Bossy & Milner, 1998; Ruta *et al.*, 2001). However, Anderson (2001) has demonstrated recently that regressions of estimated areas of the interpterygoid vacuities over skull lengths in several temnospondyls and microsaurs are significantly different, and that the vacuities of microsaurs are absolutely smaller than those of temnospondyls. Cochleosaurid edopoids possess plectrum- or teardrop-shaped vacuities in the posterior half of the palate, somewhat intermediate between those of *Edops* and higher temnospondyls (Milner & Sequeira, 1998). We follow Milner & Sequeira (1994, 1998) in considering edopoids as the most basal temnospondyl clade. The large-scale interrelationships of post-edopoid temnospondyls remain poorly understood, despite much recent progress (e.g. Schoch & Milner, 2000; Yates & Warren, 2000; Damiani, 2001). In Milner's (1990) phylogenetic scheme, post-edopoid temnospondyls are divided, in order of increasing affinities with crown-lissamphibians, into a trimerorhachoid complex, a stereospondyl complex (a derived and diverse clade within archegosauroids), an eryopoid complex and a dissorophoid complex (Holmes, 2000; Schoch & Milner, 2000). Eryopoids are variously regarded as a paraphyletic group relative to stereospondyls, or to stereospondyls plus dissorophoids (Milner, 1990; Milner & Sequeira, 1998). Yates & Warren (2000) group trimerorhachoids (their Dvinosauria) with stereospondyls, and place this broader clade (termed the Limnarchia) as sister taxon to an eryopoid–dissorophoid clade (their Euskelia).

An exhaustive treatment of temnospondyls is beyond the scope of the present work. Certain studies have explored the interrelationships of several temnospondyl subgroups (e.g. Schoch & Milner, 2000; Yates & Warren, 2000; Damiani, 2001; Steyer, 2002), although a large-scale computerized phylogeny of the whole clade has not been attempted (but see Milner, 1990). For this reason, we use mostly those genera that have been included in previous small-scale analyses (e.g. Berman, Reisz & Eberth, 1985; Dilkes, 1990; Trueb & Cloutier, 1991; Daly, 1994; Milner & Sequeira, 1994, 1998; Godfrey & Holmes, 1995; Godfrey, Fiorillo & Carroll, 1987; Holmes, Carroll & Reisz, 1998; Laurin, 1998*a–c*; Holmes, 2000).

Taxon sample is necessarily limited. It does, however, encompass members of most major temnospondyl groups. The content and limit of some of these groups are still poorly understood. *Eryops* appears to be a generalized eryopoid (Holmes, 2000), and is undoubtedly one of the best known Palaeozoic tetrapods (Romer, 1922, 1947; Miner, 1925; Sawin, 1941; Moulton, 1974). Trimerorhachoids are the subject of ongoing investigation (see Sequeira, 1998). Finally, dissorophoid interrelationships are still in a state of flux, despite the amount of morphological information available for several families (e.g. Watson, 1940; Carroll, 1964; Boy, 1972, 1974, 1978, 1985, 1986, 1987, 1995; Bolt, 1979, 1991; Milner, 1988, 1990, 1993; Dilkes, 1990; Trueb & Cloutier, 1991; Schoch, 1992; Daly, 1994; Boy & Sues, 2000, and references therein). One of the dissorophoids examined by Laurin & Reisz (1997, 1999) and Laurin (1998*a–c*) – the genus *Tersomius* Case, 1910 – is excluded from the present study. Specimens attributed to *Tersomius* consist of assorted skulls some of which probably belong to immature dissorophids and to various amphibamids (Bolt, 1977; Dr A. R. Milner, personal communication to M. Ruta, 2001).

(15) Crown-group Lissamphibia

Numerous recent discoveries (e.g. Jenkins & Walsh, 1993; Shubin & Jenkins, 1995; Jenkins & Shubin, 1998; Evans & Sigogneau-Russell, 2001; Gao & Shubin, 2001) add to our knowledge of primitive lissamphibian diversity [reviews in Báez & Basso (1996), Carroll (2000), Milner (2000) and Rocek (2000), and references therein]. Small-scale analyses of early salientians, caudates and gymnophionans (e.g. Báez & Basso, 1996; Evans & Sigogneau-Russell, 2001; Gao & Shubin, 2001; Gao & Wang, 2001) provide a framework for the choice of exemplars. Only certain fossil representatives of the three modern lissamphibian clades are considered here: the Early Jurassic stem-gymnophionan *Eocaecilia micropoda* Jenkins & Walsh, 1993 (review in Carroll, 2000); the Early Triassic stem-salientian *Triadobatrachus massinoti* (Piveteau, 1936) (Watson, 1940; Hecht, 1960, 1962; Kuhn, 1962; Estes & Reig, 1973; Rage & Rocek, 1986, 1989; Rocek & Rage, 2000*b*); the Late Jurassic stem-caudate *Karaurus sharovi* Ivakhnenko, 1978 (review in Milner, 2000). The Early Cretaceous caudate *Valdotriton gracilis* Evans & Milner, 1996, is also included in the analysis. Additional primitive lissamphibians will be considered in an expanded version of our data set. Published schemes of character distribution [summaries in Estes (1981) and Milner (1988)] support the basal position of

Triadobatrachus, *Karaurus* and *Eocaecilia* relative to other fossil salientians, caudates and gymnophionans, respectively. The family Albanerpetontidae, briefly reviewed by Milner (2000), consists of problematic salamander-like forms variously regarded as caudate relatives or as derived stem-lissamphibians (see also McGowan & Evans, 1995). In a recent paper, Gardner (2001, and references therein) placed albanerpetontids on the stem of the caudate-salientian group [but see also Trueb & Cloutier (1991) and Milner (2000)]. Coding for albanerpetontids is based on information from two of the best preserved species, *Albanerpeton inexpectatum* Estes & Hoffstetter, 1976 (Gardner, 1999) and *Celtedens ibericus* McGowan & Evans, 1995. Pending a re-assessment of such problematic groups as batrachosauroidids and scapherpetontids (review in Milner, 2000), these are excluded from the present study.

(16) Crown-group Amniota

Only three stem-diapsid taxa are considered – the captorhinid *Captorhinus aguti* Cope, 1882 (Fox & Bowman, 1966; Modesto, 1998); the protorothyridid *Paleothyris acadiana* Carroll, 1969*a* (Carroll, 1970, 1991*b*; Clark & Carroll, 1973); the araeoscelidian *Petrolacosaurus kansensis* Lane, 1945 (Peabody, 1952; Reisz, 1977, 1981). These appear to be generalized basal crown-amniotes, and their anatomy is known in sufficient detail (Carroll & Baird, 1972). Additional species from the basal portions of the synapsid and reptile branches of the amniote crown-group will be considered in an expanded version of our data set (see also Gauthier *et al.*, 1988*b*). The diversification of primitive amniotes has been the subject of intense revision over the last ten years (e.g. Carroll & Currie, 1991). The fundamental split of amniotes into Synapsida (mammals and their extinct relatives) and Reptilia (turtles, lizards, snakes, birds, crocodiles and their extinct relatives) is widely accepted (Reisz, 1986; Hopson, 1991). However, the branching pattern in the basal part of crown-Reptilia has not reached a satisfactory consensus. The core of the problem revolves around the position of turtles and the placement of several Permo-Carboniferous and Triassic groups (e.g. Ivakhnenko, 1987; Gauthier *et al.*, 1988*a*, *b*; Reisz & Laurin, 1991; Lee, 1993, 1995, 1996; Laurin & Reisz, 1995; Rieppel & deBraga, 1996; deBraga & Rieppel, 1997; Rieppel & Reisz, 1999).

Paton *et al.* (1999) interpreted the Scottish upper Viséan tetrapod *Casineria kiddi* as the earliest known amniote, and placed it in a polytomy with *Westlothiana*, *Captorhinus*, *Petrolacosaurus* and *Paleothyris*. In Paton *et al.*'s (1999: p. 512) words, although the results of their phylogenetic analysis '… are not very robust, [they] nonetheless appear to place *Casineria* not only on the amniote stem but also among the true amniotes of the Late Carboniferous … It could thus be an amniote, predating not only the earliest true amniotes from the Westphalian, but also the earliest previously known stem-amniote, *Westlothiana*, from East Kirkton'.

(17) Outgroups

Recent comprehensive analyses (Cloutier & Ahlberg, 1996; Ahlberg & Johanson, 1998; Zhu & Schultze, 2001; Johanson & Ahlberg, 2001) have repeatedly and consistently found panderichthyids and tristichopterids to be successively more outlying sister groups to the limbed tetrapods. In agreement with these studies, and *contra* Rosen *et al.*'s (1981) hypothesis (for a detailed and comprehensive analytical criticism, see Panchen & Smithson, 1987), the tristichopterid *Eusthenopteron foordi* Whiteaves, 1881 (Andrews & Westoll, 1970; Jarvik, 1980, and references therein) and the panderichthyid *Panderichthys rhombolepis* (Gross, 1930) (Vorobyeva, 1977, 1992, 2000; Vorobyeva & Schultze, 1991; Ahlberg, Clack & Luksevics, 1996; Ahlberg & Clack, 1998, and references therein) are used to polarize characters.

VI. CHARACTERS

We are in the process of compiling a new, expanded matrix for early tetrapods based upon the data set presented here, and including a detailed character discussion. To aid cross-reference between elements of the present and future matrices, each character, as stated in Appendix 2, is preceded by a bold number identifying its position in the current data matrix (see Appendix 3), and by an italicized, abbreviated name and number for the osteological feature to which it refers (this second number will remain in future versions). A key feature of subsequent data sets will be to provide detailed treatments of each aspect of the anatomy of primitive tetrapods. Work in this direction has already begun (e.g. Lombard & Bolt, 1999; Bolt & Chatterjee, 2000; Bolt & Lombard, 2001).

VII. ANALYSIS

(1) Character coding

The theoretical and practical problems associated with different regimes of character coding are intensely debated topics (e.g. Scotland & Pennington, 2000). In the present work, most characters are binary and refer to the presence or absence of a structure (or condition of a structure). Multistate characters are coded as unordered (non-additive) in all analyses. All characters are equally weighted and optimized using ACCTRAN. A discussion of the results implied by different coding methods (cf. Pleijel, 1995) is outside the aims of this work, and will be detailed elsewhere. The data matrix includes unknown scores for inapplicable characters. In this respect, the coding regime is similar to Forey & Kitching's (2000) contingent method. Optimization of state changes (available upon request from the authors) often leads to undesirable results, as in the case of inapplicable scores. For example, an unknown score for the condition of a certain bone (e.g. suture pattern between intertemporal and cheek region in a taxon that lacks an intertemporal; e.g. *Solenodonsaurus*) may be fully optimized on a branch that subtends a taxon in which the bone in question is absent.

(2) The parsimony 'ratchet'

A data matrix consisting of 90 taxa coded for 319 osteological characters (224 cranial and 95 postcranial) was built in MacClade 3.0.5 (Maddison & Maddison, 1992), which was also used to manipulate trees in experiments of taxon pruning and regrafting, in the analysis of suboptimal cladograms, and in comparisons between conflicting positions for various taxa. Cladistic analyses were performed on a PowerMac G4 computer using PAUP* 4.0b10 (Swofford, 1998). Because PAUP* only supports MINSTEPS, tree lengths reported treat all polytomies as soft.

The widespread occurrences of missing entries and the moderately large size of the complete data matrix made it likely *a priori* that finding the optimum tree(s) under parsimony optimality criteria would be difficult. Therefore, we employed a range of tree searching strategies to maximize our chances of finding optimal islands. In order to cover a wide range of tree space in a practical length of time (days) we carried out 40000 random stepwise additions followed by TBR (tree bisection-reconnection) branch-swapping searching, but holding only one tree in memory at any one time (i.e. MAXTREES = 1) (Quicke *et al.*, 2001). These searches hit trees of the shortest length recovered over 150 times. Searching on each tree with unlimited MAXTREES recovered the same island of trees. No shorter trees were recovered by employing the iterative re-weighting strategy proposed by Quicke *et al.* (2001). Searching on subsets of characters (e.g. see below for a discussion of cranial character analysis, removal of lower jaw characters and reverse weighting tree search strategy) was essentially the same from a methodological point of view, except that only 5000 random stepwise additions were used.

(3) Results

A parsimony analysis with all characters unordered and equally weighted yielded 64 equally parsimonious trees, constituting a single island, with a length of 1375 steps [ensemble consistency index (CI) excluding uninformative characters = 0.2392; ensemble retention index (RI) = 0.6727; ensemble rescaled consistency index (RC) = 0.1654]. A strict consensus (Fig. 4) shows the following unresolved relationships: (1) the node subtending all included species of aïstopods; (2) an internal node within the embolomeres, with a trichotomy subtending *Archeria crassidisca*, *Pholiderpeton scutigerum* and a clade formed by *Anthracosaurus russelli* and *Pholiderpeton attheyi*; (3) the node subtending derived dissorophoids, with four amphibamid species collapsed in a polytomy with a clade including micromelerpetontids and branchiosaurids and a clade encompassing albanerpetontids and basal crown-group lissamphibians; (4) the node leading to albanerpetontids and *Eocaecilia micropoda*, both forming an unresolved trichotomy with a collapsed clade including *Karaurus sharovi*, *Valdotriton gracilis* and *Triadobatrachus massinoti*; and (5) an internal node within diplocaulid nectrideans, with *Batrachiderpeton reticulatum* and *Diceratosaurus brevirostris* collapsed in a polytomy with a clade formed by *Diplocaulus magnicornis* and *Diploceraspis burkei*.

One of the 64 fundamental trees (Fig. 5, also shown as circular cladogram in Fig. 6) was chosen to discuss character distribution at selected nodes (character-state distribution for all trees is available upon request from the authors). Overall tree topology is fairly balanced, as evidenced by the Colless index, $I_c = 0.357$, which is closer to the value of a fully dichotomous cladogram (0) than to that of a completely pectinate cladogram (1) (Heard, 1992; Colless, 1995). This contrasts with rather higher I_c values obtained from other recent tetrapod phylogenies, such as those of Carroll (1995; $I_c = 0.83$ or 0.75, depending upon tree topology), Coates (1996; $I_c = 0.7$), Laurin & Reisz (1999; $I_c = 0.49$), Paton *et al.* (1999; $I_c = 0.46$, 0.44 or 0.42, depending upon tree topology) and Anderson (2001; $I_c = 0.42$). For brevity, only ACCTRAN-optimized characters are taken into account in the remainder of the paper (unless otherwise specified).

We used two simple methods to evaluate the amount of phylogenetic signal present in the matrix. The first method is based on comparisons between the

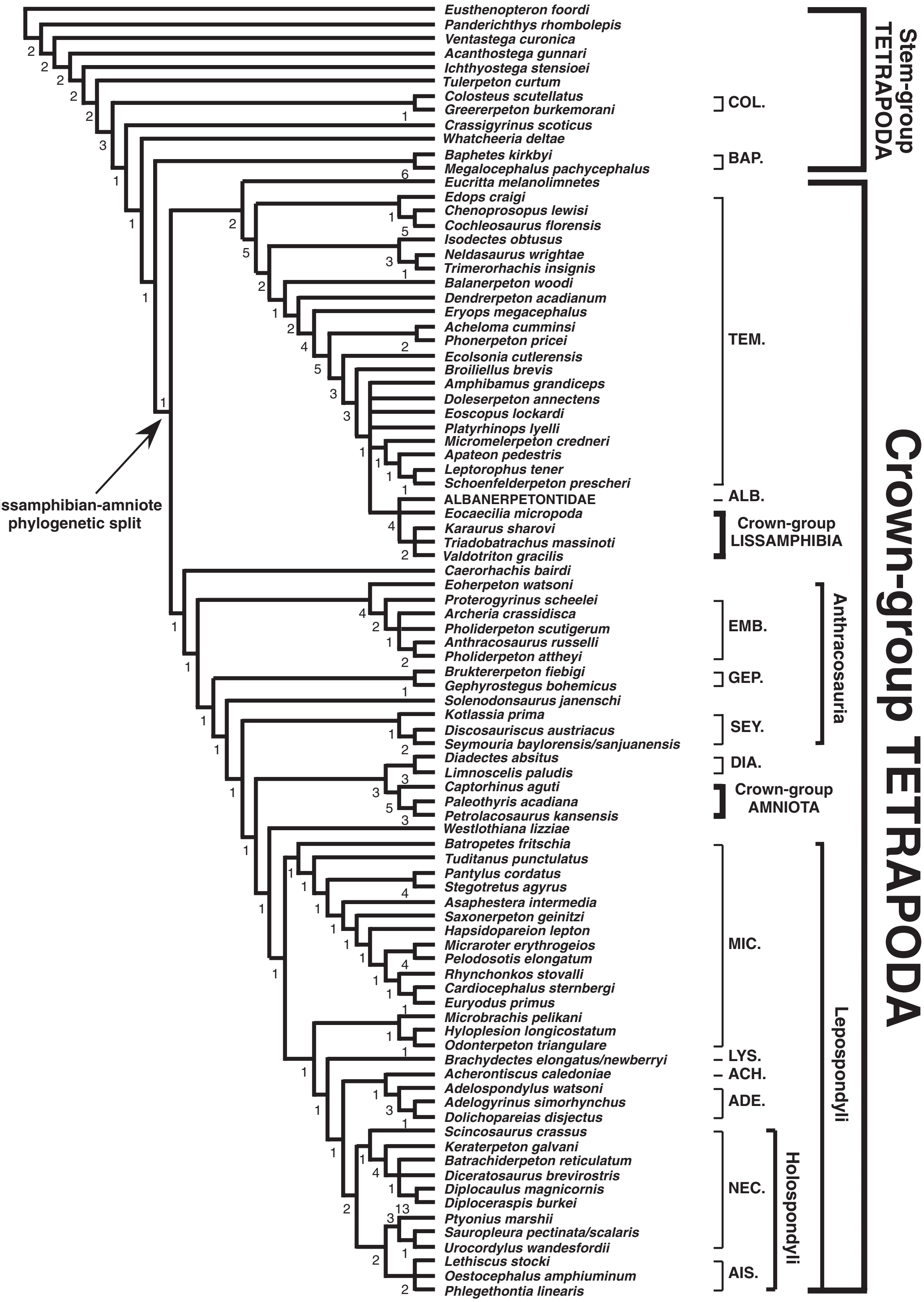

Fig. 4. Strict consensus of 64 equally parsimonious trees deriving from the total data set. Numbers at nodes represent decay index values. Abbreviations as in Fig. 1 with the following additions: ACH., Acherontiscidae; ALB., Albanerpetontidae; EMB., Embolomeri; GEP., Gephyrostegidae.

Fig. 5. One of the fundamental trees deriving from the original parsimony run. Numbers at nodes refer to bootstrap percentage values for clades with bootstrap support greater than 50%. Remaining, unlabelled nodes are collapsed in a bootstrap 50% majority-rule consensus tree.

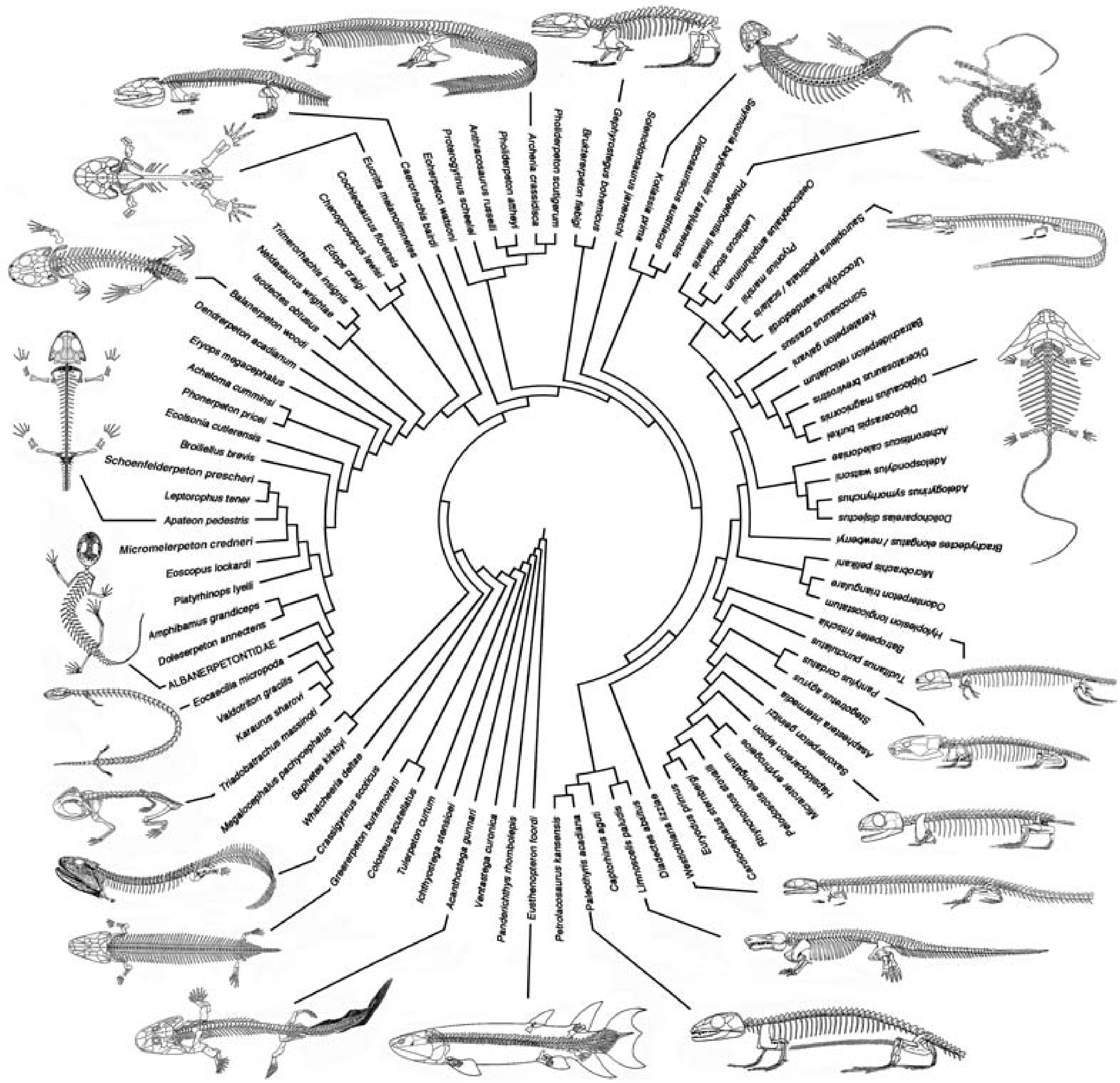

Fig. 6. Circular dendrogram of tetrapod interrelationships using the branching sequence shown in Fig. 5. Selected taxa illustrated as indicators of morphological diversity (figures not drawn to the same scale).

CI value associated with the real data set, and the expected CI value for an ideal data set of the same size (Sanderson & Donoghue, 1989). The latter value, referred to as $\mathrm{CI}_{\mathrm{expected}}$, is related to the number of taxa (n) through the following simple equation:

$$\mathrm{CI}_{\mathrm{expected}} = 0.9 - 0.022n + 0.000213n^2. \qquad (1)$$

The above formula presents some theoretical problems. A graph of the above equation, with $\mathrm{CI}_{\mathrm{expected}}$ plotted as a function of the number of taxa, shows that the former decreases continuously for n comprised between 0 and approximately 51. A continuous increase in $\mathrm{CI}_{\mathrm{expected}}$ values is found for n comprised between approximately 51 and approximately 107 taxa. Thus, the equation represents increasing levels of homoplasy in a data set only within a restricted taxon number interval, with $\mathrm{CI}_{\mathrm{expected}}$ reaching its minimum theoretical value when only 51 taxa are considered. Homoplasy levels decrease for n greater than 51. Obviously, the equation is not valid for n greater than 107, because $\mathrm{CI}_{\mathrm{expected}}$ would be greater than 1. For 90 taxa, $\mathrm{CI}_{\mathrm{expected}} = 0.645$. The fact that the CI obtained from our data set is considerably lower than the expected CI value may not necessarily imply low levels of phylogenetic information. It does, however, suggest that 'noise' is pervasive.

The second method used to measure the amount of 'noise' in the data is based on the index of Klassen, Mooi & Locke (1991), which compares the CI of a real data set with that of a random matrix of the same size. The index, referred to as $\mathrm{CI}_{\mathrm{random}}$, is calculated as follows:

$$\mathrm{CI}_{\mathrm{random}} = 2.937n^{-\mathbf{0.9339}}. \qquad (2)$$

Briefly, $\mathrm{CI}_{\mathrm{random}}$ values that are lower than CI values associated with a real data set imply the presence of phylogenetic signal in the latter. For 90 taxa, $\mathrm{CI}_{\mathrm{random}} = 0.044$. This value is considerably lower than 0.239 retrieved in the original analysis, suggesting that despite the broad range of fossil taxa included, non-random matrix structure exceeds the level of background noise.

Most cladogram nodes are collapsed in a bootstrap 50% majority-rule consensus tree based on 10000 replicates employing the fast stepwise addition option of PAUP*. Bootstrap percentage values greater than 50% are plotted on the selected tree (Fig. 5). Decay index values (Bremer support values) are indicated on the strict consensus tree in Fig. 4. As expected, there is, usually, a good match between bootstrap percentage and decay index. Bremer supports were estimated by running up to 10000 random additions holding no more than one tree for TBR swapping at any one time. Searches were terminated either when they reached the MPT (most parsimonious tree) length of +1 (i.e. Bremer support = 1) or when the length of the shortest tree found had been hit at least 40 times.

(*a*) *The tetrapod stem-group*

The branching order of post-panderichthyid Devonian taxa (Fig. 5; see also lower left sector of Fig. 6) is in broad agreement with the results of several previous works (but see Ahlberg & Clack, 1998). A sister group relationship between *Acanthostega* and *Ichthyostega* (e.g. Laurin & Reisz, 1999) can be obtained at the cost of three additional steps. Several authors (Lombard & Bolt, 1995; Lebedev & Coates, 1995; Coates, 1996; Clack, 1998*a*, *c*; Paton *et al.*, 1999) have considered *Tulerpeton*, *Crassigyrinus*, *Whatcheeria* and baphetids to be amniote relatives. However, as the morphological and taxonomical data base for early tetrapods expands, the systematic affinities of these tetrapods are changing (e.g. Clack, 2002). The stem-group topology recovered by the present analysis agrees with Ahlberg & Clack's (1998), Laurin & Reisz's (1997, 1999) and Laurin's (1998*a–c*) results, although the position of the above-mentioned taxa is very weakly supported (Panchen, 1973, 1985, 1991; Panchen & Smithson, 1987, 1988; Lombard & Bolt, 1995; Clack, 1996, 1998*a*, *c*, 2001, 2002; Bolt & Lombard, 2000; Clack & Carroll, 2000). Thus, if baphetids are placed on the amniote stem as sister group to *Caerorhachis* plus more derived stem-amniotes, then tree length increases by five steps only. With four extra steps, baphetids can be grafted to the lissamphibian stem as sister group to *Eucritta* plus temnospondyls. Only two additional steps are required to place a clade consisting of *Eucritta* and baphetids on the lissamphibian stem as sister group to temnospondyls, and five to place the same clade on the amniote stem as sister group to *Caerorhachis* plus more derived stem-amniotes. However, tree length increases by as many as 32 steps if we impose Clack's (2001) tree topology, wherein *Whatcheeria* and *Gephyrostegus* are successive sister taxa to *Crassigyrinus* and embolomeres, and the *Eucritta*-baphetid clade is placed as sister taxon to all of these groups.

Tulerpeton and baphetids are known from incomplete material [but see Lebedev & Coates (1995) and Milner & Lindsay (1998)]. The position of *Tulerpeton* as a primitive stem-amniote in Lebedev & Coates's (1995) and Coates' (1996) cladograms implies that the lissamphibian-amniote phylogenetic split had occurred by the late Devonian (Famennian; see also discussion below). Conversely, the present study favours a stem-tetrapod placement for *Tulerpeton*. Thus far, all studies of *Tulerpeton* have assumed the coherent nature of the contributory material, ranging from the near-articulated postcranium to isolated palatal and lower jaw fragments (Lebedev, 1984; Lebedev & Clack, 1993; Lebedev & Coates, 1995). We were interested to test the placement and coherence of *Tulerpeton* as a natural taxon. For this purpose, we built a data matrix in which *Tulerpeton* was divided into two taxa, *Tulerpeton1* consisting of cranial and lower jaw data (with postcranial data coded as unknown), and *Tulerpeton2*, consisting of postcranial data (with cranial and lower jaw data coded as unknown). The strict consensus of the resulting 256 equally parsimonious trees at 1403 steps (CI = 0.2545; RI = 0.6727; RC = 0.1755) resembles that recovered from the original analysis, but places *Tulerpeton1*, *Tulerpeton2*, *Crassigyrinus* and colosteids in a polytomous node between *Ichthyostega* and *Whatcheeria*. Inspection of an Adams consensus and of an agreement subtree [i.e. a taxonomically 'pruned' cladogram showing the largest subset of taxa for which all fundamental trees agree upon relationships (Swofford, 1998)] reveals that *Tulerpeton1* is a rogue taxon, but that *Tulerpeton2* is unequivocally placed between *Ichthyostega* and colosteids. Therefore, despite the unstable position of *Tulerpeton1*, we conclude that both this taxon and *Tulerpeton2* fall in the tetrapod stem-group. These results provide insufficient evidence to warrant the treatment of the cranial and postcranial data as belonging to separate OTUs, although conclusive evidence can only come from more complete *Tulerpeton* material.

The tetrapod crown-group is supported by the following character-state changes (character consistency index expressed as c.i.), none of which represent unambiguous synapomorphies: 51 (c.i. = 0.2; 0 → 1), presence of postparietal-exoccipital suture; 78 (c.i. = 0.125; 0 ⇒ 1), postorbital broadly crescentic, narrowing posteriorly to a point; 93 (c.i. = 0.333; 1 ⇒ 0), jugal without deep, V-shaped indentation along its dorsal margin; 115 (c.i. = 0.286; 3 → 4), absence of lateral line system on skull roof; 116 (c.i. = 0.286; 3 ⇒ 4), absence of mandibular canal; 208 (c.i. = 0.25; 1 → 0), mid coronoid with denticles; 212 (c.i. = 0.2; 1 ⇒ 0), posterior coronoid with denticles; 214 (c.i. = 0.25; 0 ⇒ 1), posterior coronoid with posterodorsal process; 238 (c.i. = 0.167; 0 → 1), latissimus dorsi process aligned with ectepicondyle; 240 (c.i. = 0.5; 0 → 1), absence of ventral humeral ridge.

Eucritta and *Caerorhachis* bracket the base of the tetrapod crown-group (Fig. 5; see also upper left sector of Fig. 6), thus corroborating previous interpretations of their primitive nature (Clack, 1998*a*, 2001; Ruta *et al.*, 2001). The mosaic of characters that both taxa share with such diverse groups as baphetids, 'anthracosaurs' and temnospondyls indicates strongly that they may be phylogenetically close to the divergence of lissamphibian and amniote clades (Clack, 1998*a*, 2001; Ruta *et al.*, 2001). Consistent with this interpretation, only two steps are added to tree length if *Eucritta* is placed in any of the following positions (locations of other taxa being unchanged): sister taxon to baphetids; crownward of baphetids on the tetrapod stem; sister taxon to *Caerorhachis* plus more crownward stem-amniotes. With three extra steps, *Eucritta* can be placed between *Caerorhachis* and embolomeres. With four extra steps, it can be paired with *Caerorhachis*. Tree length increases by four steps if *Caerorhachis* is placed either crownward of baphetids on the tetrapod stem or as sister taxon to *Eucritta* plus more crownward temnospondyls. Alternative placements for *Eucritta* and *Caerorhachis* (further away from the crown-group basal node) involve additional steps.

This deep split between lissamphibian- and amniote-related taxa has interesting implications for the distribution of certain characters long regarded as 'reptiliomorph' or 'anthracosauroid' apomorphies (Lombard & Bolt, 1995; Clack, 1998*a*, *c*; Paton *et al.*, 1999; Bolt & Lombard, 2000). Several of these may in fact represent tetrapod plesiomorphies at a post-colosteid level, that persist in basal crown-group members. Here, we focus on four such characters: orbit shape, skull roof suture patterns, vertebral body construction and the number of manus digits.

Orbits with an irregularly shaped outline (i.e. neither round nor elliptical) are widespread among early tetrapods. A plausible functional explanation for these shapes has not been found (Clack, 1987*b*), although several alternatives for the marked antorbital vacuities of baphetids have been offered (Beaumont, 1977; Bjerring, 1986; Milner & Lindsay, 1998), including development of broad insertion areas for jaw musculature; presence of salt glands; and presence of electrosensory organs. Irregular orbits are also present in *Crassigyrinus*, *Whatcheeria*, *Eucritta* and, among embolomeres, *Anthracosaurus*, *Carbonoherpeton*, *Eoherpeton* and *Pholiderpeton attheyi* (Panchen, 1972, 1975, 1977, 1980, 1985; Beaumont, 1977; Klembara, 1985; Clack, 1987*a*, *b*, 1998*a*, *c*, 2001; Beaumont & Smithson, 1998; Milner & Lindsay, 1998). According to Clack (1998*a*), the antorbital vacuities of baphetids may represent exaggerated (possibly peramorphic) versions of the small anteroventral orbital embayments of *Eucritta* (see also Clack, 2001). A similar embayment is also observed in the embolomere *Palaeoherpeton* (Panchen, 1964, 1980). In *Crassigyrinus*, the orbit outline is near rhomboidal (Panchen, 1985; Clack, 1998*c*), and includes a small but distinct anteroventral corner or embayment. A less pronounced version of such rhomboidal orbits is found in *Eoherpeton* (Smithson, 1985). In baphetids, the dorsal (orbital) margin of the jugal includes a characteristic, deep notch (Beaumont, 1977). However, jugal notches are also present in *Anthracosaurus*, *Carbonoherpeton*, *Pholiderpeton attheyi* and *Whatcheeria* (Panchen, 1964, 1972, 1977, 1980; Klembara, 1985; Clack, 1987*a*, *b*, 1998*b*, *c*; Lombard & Bolt, 1995). According to our analysis, angular orbits are a transitory condition, since they occur in a series of stem-tetrapods, some basal stem-amniotes and one stem-lissamphibian. They are not an unambiguous shared derived feature of discrete monophyletic groups. One of the orbit characters employed by Clack (1998*c*, 2001) relates to the occurrence of an anteroventral orbit corner (our character 105), observed in *Crassigyrinus*, *Eucritta* and *Whatcheeria*. Under ACCTRAN optimization, this character appears to be transitional in the portion of the stem-group comprised between colosteids and baphetids (i.e. nodes leading to *Crassigyrinus* and *Whatcheeria*) and is acquired in parallel by *Eucritta*. However, if DELTRAN is used, then *Crassigyrinus*, *Eucritta* and *Whatcheeria* are shown to have acquired an anteroventral orbit corner three times independently.

The distribution of characters describing skull table suture patterns corroborates earlier hypotheses that alternative configurations, including mutually exclusive contacts between supratemporal and postparietal, and between parietal and tabular, have diagnostic value for lissamphibian and amniote relatives (Panchen, 1980; Panchen & Smithson, 1988). Leaving aside the question of bone homologies in the skull table of several lepospondyls, we note that a supratemporal-postparietal suture (complement arrangement of bones as expressed in character 39, related to the parietal-tabular contact), is conserved as a primitive character (under ACCTRAN and DELTRAN) in the temnospondyl-lissamphibian clade (but see Boy, 1986). On the amniote branch (with the possible exclusion of *Caerorhachis*; Holmes & Carroll, 1977; Ruta *et al.*, 2001), a parietal-tabular contact is observed in all taxa in which these bones are recognisable as separate ossifications (but see Smithson, 1986), including some lepospondyls (e.g. the urocordylid nectridean *Sauropleura*).

Several models have been proposed to explain the derivation of different vertebral centra from one another or from hypothetical archetypes. Study of primitive tetrapods has clarified the polarity of this character complex (e.g. Coates, 1996). A rhachitomous pattern (or derivations thereof) is ubiquitous in stem-tetrapods and among most temnospondyls. The unusual vertebral construction observed in some specimens of *Whatcheeria* (Lombard & Bolt, 1995) appears to be a simple modification (although not necessarily in a strict phylogenetic sense) of the multipartite centrum of such taxa as colosteids and several temnospondyls (Godfrey, 1989). The morphology of the poorly preserved centra of *Tulerpeton* (Lebedev & Coates, 1995) and baphetids (Milner & Lindsay, 1998) is also consistent with a rhachitomous model, despite little information on their postcranial skeletons. A gastrocentrous pattern dominates among amniote-like taxa (as well as some derived temnospondyls, e.g. Bolt, 1991; Holmes, 2000; Boy & Sues, 2000). This ranges from the simple construction of *Caerorhachis* (Holmes & Carroll, 1977; Ruta *et al.*, 2001) and several basal 'anthracosaurs' (small intercentra and U-shaped pleurocentra, e.g. *Silvanerpeton* and *Eldeceeon*; Clack, 1994*b*; Smithson, 1994), to the massive, disc-like intercentra and pleurocentra of various embolomeres (e.g. *Archeria*; Holmes, 1989), and the pleurocentrum-dominated vertebrae of several lepospondyls, seymouriamorphs, diadectomorphs and crown-amniotes (White, 1939; Romer, 1956, 1966; Carroll & Gaskill, 1978; Sumida, 1997; Carroll, 1988; Carroll *et al.*, 1998; Benton, 2000; Klembara & Bartík, 2000).

In our original data set, conditions describing the number of digits in the manus were treated as independent characters, thus imposing no linkage between them. However, we also explored the effects of multistate coding for digit number. The highest number of digits (eight in *Acanthostega*) was given state 0 whereas the lowest (three in microbrachomorphs) was given state 5. The character was treated as unordered, thus allowing free transformations between different conditions. A PAUP* run gave 384 equally parsimonious trees at 1400 steps (CI = 0.2558; RI = 0.6723; RC = 0.1762). A strict consensus is almost identical to that obtained from the original analysis, except for a considerable loss of resolution among microbrachomorph and some tuditanomorph microsaurs. Reconstruction of the character-state changes relative to the number of digits on a selected cladogram shows that character optimization is equivocal (under both ACCTRAN and DELTRAN) in the post-panderichthyid part of the tetrapod stem-group. This is not unexpected given the unavailability of data in several stem-tetrapod taxa (*Ichthyostega*, *Crassigyrinus*, *Whatcheeria*, baphetids), and the conflicting distribution of states among colosteids (Hook, 1983; Coates, 1996). Among crown-tetrapods, the presence of a manus with no more than four digits is acquired in parallel in the temnospondyl-lissamphibian clade and in the *Westlothiana*-lepospondyl clade. Within lepospondyls, digit number decreases further in microbrachomorphs. Therefore, a five-digited manus does not identify any particular clade. Rather, this condition appears to be transitional among several basal stem-amniotes and primitive crown-amniotes.

(*b*) *The lissamphibian stem-group*

The basal node of the temnospondyl-lissamphibian clade (including *Eucritta*) is supported by several homoplastic features, some of which relate to optimizations of missing character scores: 144 (c.i. = 0.083; 0→1), pterygoid with posterolateral flange; 178 (c.i. = 0.5; 0→1), absence of parasymphysial plate; 188 (c.i. = 0.2; 1→0), rearmost extension of mesial lamina of splenial closer to anterior end of lower jaw than to adductor fossa; 215 (c.i. = 0.167; 0→1), posterior coronoid exposed in lateral view; 229 (c.i. = 0.2; 1→0), posterior margin of interclavicle not drawn out into parasternal process; 230 (c.i. = 0.2; 1→0), parasternal process not elongate and parallel-sided; 257 (c.i. = 0.154; 2⇒1), radius approximately as long as ulna; 280 (c.i. = 0.143; 1⇒0), ribs mostly straight in at least part of the trunk; 314 (c.i. = 0.25; 0→1), presence of no more than four digits in manus. The shortest path leading from the base of the tetrapod crown-group to the node subtending crown-group lissamphibians includes 115 character-state changes over 12 internodes with an average of 9.6 changes for each internode. Comparisons between crownward stem-tetrapods and temnospondyls reveal the conservative morphology of various skeletal characters in the latter (e.g. skull roof suture pattern; vertebral construction). Unfortunately, the Mississippian record of temnospondyls is sparse (worse than that of stem-group amniotes), presumably as a result of palaeoecological factors. The significance of the near-complete material of *Balanerpeton* is thus emphasised as a unique glimpse of conditions in the earliest members of the group.

Crownward of *Eucritta*, the branching pattern of the basal part of the temnospondyl tree (Fig. 5; see also upper and middle left sectors in Fig. 6) conforms mostly to the results of several alternative recent analyses (Milner, 1990; Milner & Sequeira, 1994, 1998; Holmes *et al.*, 1998; Holmes, 2000). The Permo-Carboniferous edopoids are a basal clade of long-snouted forms known mostly from cranial material. Several derived edopoids (e.g. *Cochleosaurus* and *Chenoprosopus*) are characterized by broad dorsomesial extensions of the premaxillae, teardrop-shaped choanae, and elongation of the pre- and interchoanal regions (Milner & Sequeira, 1998). The anteriorly sutured pterygoids and the absence of premaxillary alary processes represent possible plesiomorphic characters. Various features of the skull and palate of the recently described *Adamanterpeton ohioensis* indicate the primitive condition from which more derived edopoids might have arisen (Milner & Sequeira, 1998). For example, its rather narrow palatal vacuities are proportioned similarly to those of *Eucritta* and *Caerorhachis* (Holmes & Carroll, 1977; Holmes, 2000; Ruta *et al.*, 2001).

The phylogenetic position of *Balanerpeton* and *Dendrerpeton* has been debated (Milner, 1980; Milner & Sequeira, 1994; Holmes *et al.*, 1998; Holmes, 2000). Only two extra steps are required to pair *Dendrerpeton* with *Balanerpeton*, as in Holmes *et al.*'s (1998) phylogeny, or to place them as successively more closely related taxa to eryopoids plus higher temnospondyls. With three extra steps, *Dendrerpeton* and *Balanerpeton* can be placed, in that order, as successively more closely related taxa to trimerorhachoids and higher temnospondyls, as in Milner & Sequeira's (1994) cladogram. If *Balanerpeton* is paired with trimerorhachoids or inserted between edopoids and trimerorhachoids, then only one extra step is added to tree length. If these latter rearrangements are applied to *Dendrerpeton*, then tree length increases by two and three steps, respectively. *Dendrerpeton* is sister taxon to a clade encompassing eryopoids, dissorophoids and crown-lissamphibians. In the light of recent work on *D. acadianum* (Holmes *et al.*, 1998), the position of this taxon sheds new light on the early diversification of eryopoids and dissorophoids. In particular, it calls for a reassessment of the distribution of such key dissorophoid/salientian features as the occurrence of a posterodorsal process of the quadrate (Lombard & Bolt, 1979; Bolt & Lombard, 1985; Milner, 1988, 1990; Bolt, 1991; Daly, 1994).

The interrelationships of dissorophoids depart significantly from those of previous studies (e.g. Milner, 1990, 1993; Trueb & Cloutier, 1991; Daly, 1994). Dissorophids emerge as paraphyletic and branch from the lissamphibian stem between trematopids (monophyletic) and a poorly resolved clade consisting of amphibamids, micromelerpetontids, branchiosaurids, albanerpetontids and crown-lissamphibians. The position of *Ecolsonia* – crownward of trematopids – agrees with one of the two alternative hypotheses of relationship of this taxon postulated by Berman *et al.* (1985), but contrasts with its relatively derived position in Daly's (1994) analysis. The most surprising results concern the derived portion of the lissamphibian stem. Thus, amphibamids are paraphyletic with respect to a micromelerpetontid-branchiosaurid clade. Together, these taxa are paired with albanerpetontids plus crown-lissamphibians (Fig. 6, mid-lower left sector). Inspection of an agreement subtree reveals that the only unequivocal pattern of sister group relationships among derived dissorophoids consists of *Leptorophus* and *Schoenfelderpeton* as sister groups, with *Apateon*, *Micromelerpeton* and *Eoscopus* as progressively more 'outlying' taxa. This broader clade joins albanerpetontids as sister taxon to *Karaurus* plus *Triadobatrachus* in the agreement subtree. This result may reflect a genuine pattern of relationships, or may be due to lack of additional characters. As pointed out by Milner (1993), conflicting character distributions suggest that several dissorophoid lineages approached the condition of basal crown-lissamphibians independently and to varying degrees.

The amount of character convergence in crownward stem-lissamphibians might explain why our analysis fails to retrieve a sister group relationship between one or few specific dissorophoids and crown taxa in some of the most parsimonious solutions. In others, however, including the tree used for character discussion, crown-lissamphibians plus albanerpetontids are paired with a clade consisting of *Amphibamus* plus *Doleserpeton* (e.g. Bolt, 1969, 1979, 1991; Trueb & Cloutier, 1991; Milner, 1993). The sequence of cladogenetic events in the crownward part of the temnospondyl tree re-emphasizes the importance of dissorophoids in the lissamphibian origin debate [but see Laurin & Reisz (1997, 1999) and Laurin (1998*a–c*) for a contrasting opinion]. The node subtending derived dissorophoids plus crown-lissamphibians is supported by the following character-state changes: 29 (c.i. = 0.1; 0⇒1), maxilla entering orbit margin; 73 (c.i. = 0.077; 0⇒1), parietal–parietal width greater than distance between the posterior margin of the skull table and the posterior margin of the orbits, measured along the midline; 104 (c.i. = 0.105; 2→1), minimum interorbital distance smaller than maximum orbit diameter; 126 (c.i. = 0.2; 0→1), presence of distinct posterolateral process of the vomer bordering more than half of the posterior margin of the choana; 150 (c.i. = 0.333; 0→1), quadrate ramus of pterygoid straight, rod-like and gently tapering distally; 249 (c.i. = 0.25; 0⇒1), slender and elongate humerus, the length of which is more than three times the width of its distal end; 252 (c.i. = 0.125; 0⇒1), width of entepicondyle less than half the length of the humerus; 283 (c.i. = 1; 0⇒1), longest trunk ribs poorly ossified, slender rods, the length of which is smaller than the length of three mid-trunk vertebrae.

Laurin & Reisz's (1997, 1999) and Laurin's (1998*a–c*; Fig. 1d) analyses deserve further comment. These authors consider only a limited sample of putative shared derived characters linking dissorophoids to lissamphibians. Despite the inclusion of such key taxa as *Doleserpeton*, their temnospondyl exemplar does not adequately encompass internested sets of lissamphibian apomorphies identified in previous studies (e.g. Milner, 1988, 1990, 1993; Bolt, 1991; Trueb & Cloutier, 1991; Daly, 1994; Gardner, 2001). Laurin's (1998*a–c*) and Laurin & Reisz's (1997, 1999) lepospondyl-lissamphibian clade is mostly supported by 'absence' characters (e.g. losses of certain cranial and mandibular bones). 'Absence' data pose special problems in phylogenetic reconstructions (Poe & Wiens, 2000). It is difficult to assess, *a priori*, whether they contain true phylogenetic signal. Clusters of 'absence' features may bias the results of an analysis in favour of sister group relationships between taxa that display few, if any, derived characters, by means of swamping any signal derived from alternative character sets. In the case of lissamphibians and lysorophids, Laurin's (1998*a–c*) and Laurin & Reisz's (1997, 1999) analyses place emphasis on the simplification of the skull roofing pattern (e.g. bone reduction and/or loss). In fact, examples of such simplification occur repeatedly throughout osteichthyan clades, and often show distinct phylogenetic trends (e.g. synapsids; Sidor, 2001, and further examples therein). Although putative temnospondyl-lissamphibian synapomorphies (e.g. dental features) are also included in Laurin's (1998*a–c*) and Laurin & Reisz's (1997, 1999) analyses, several other characters used in previous studies (e.g. configuration of various palatal elements) are omitted (e.g. Milner, 1988, 1990, 1993; Bolt, 1991; Trueb & Cloutier, 1991; Daly, 1994). This may be significant.

We decided to assess the impact of 'absence' characters against a larger set of putative temnospondyl-lissamphibian synapomorphies than that used by Laurin (1998*a–c*) and Laurin & Reisz (1997, 1999). Milner (1993) found that in four genera of Amphibamidae, he could discern as few as one (in *Platyrhinops*) and as many as six (in *Doleserpeton*) synapomorphies with crown-lissamphibians. When crown-lissamphibians were placed as sister taxon to *Doleserpeton*, Milner (1993) found that four characters related to dentition, palate and vertebrae originated only once within dissorophoids. In the present analysis, at least some of the fundamental trees (including that in Fig. 4) show that as many as nine characters support a sister group relationship between a clade including *Amphibamus* plus *Doleserpeton*, and a clade including albanerpetontids plus crown-lissamphibians: 32 (c.i. = 0.5; 0⇒1), maxillary facial process shaped like a rectangular flange; 127 (c.i. = 0.167; 0⇒1), palatine without fangs; 133 (c.i. = 0.333; 0→1), palatine poorly ossified, slender and strut-like; 134 (c.i. = 0.167; 0→1), absence of ectopterygoid; 183 (c.i. = 0.1; 0⇒1), dentary without anterior pair of fangs; 218 (c.i. = 0.5; 0→1), presence of pedicely on marginal teeth; 258 (c.i. = 0.091; 1⇒0), absence of olecranon process on ulna; 293 (c.i. = 0.333; 0→1), trunk pleurocentra fused midventrally; 296 (c.i. = 0.125; 0→1), neural spines of trunk vertebrae fused to centra. Placing albanerpetontids plus crown-lissamphibians as sister group to *Doleserpeton* requires only one extra step, as does Gardner's (2001) preferred tree topology (albanerpetontids on the common stem-group of salientians and caudates, with caecilians as sister group to remaining lissamphibians). Based on Gardner's (2001) branching scheme, the following characters unite crown-lissamphibians with *Doleserpeton* (with or without implied reversals within crown-group lissamphibians): vomer with transverse patch of small teeth posteromesial to choana (125); absence of ectopterygoid (134); pterygoid sutured with maxilla (146); trunk pleurocentra fused midventrally (293); trunk pleurocentra fused middorsally (294); neural spines of trunk vertebrae fused to centra (296).

We performed further tests to evaluate the significance of alternative taxon arrangements in the crownward part of the temnospondyl branch. In particular, Carroll & Bolt's (2001) hypothesis of separate origins of caudates and salientians from among dissorophoids postulates that *Doleserpeton* and *Apateon* are the most crownward plesions on the salientian and caudate stem-groups, respectively. For simplicity, dissorophoid relationships were left unchanged. We constrained *Triadobatrachus* to appear as sister taxon to *Doleserpeton*, and caudates plus caecilians (with albanerpetontids as a more outlying group) as sister taxon to *Apateon*. This arrangement entails 18 extra steps, but represents a considerably worse fit for the total data than the shortest trees overall (Templeton test: $P = 0.0027$; Kishino–Hasegawa test: $P = 0.0026$; Winning-sites test: $P = 0.0046$). Forcing *Eocaecilia* to appear as sister taxon to the microsaur *Rhynchonkos* [see Carroll & Currie (1975), Carroll (2000) and references therein], but leaving the rest of the ingroup topology unchanged, entails 29 extra steps. Again, such a topology represents a considerably worse fit for the total data than the most parsimonious trees (Templeton test: $P = 0.0001$; Kishino–Hasegawa test: $P = 0.0001$; Winning-sites test: $P = 0.0002$). Similar results (Templeton test: $P < 0.0001$; Kishino–Hasegawa test: $P < 0.0001$; Winning-sites test: $P = 0.0001$) are obtained if a *Rhynchonkos-Eocaecilia* clade is created with *Triadobatrachus* as sister taxon to *Doleserpeton* and caudates plus albanerpetontids as sister goup to *Apateon* (tree length increases by 42 steps). Tests of Laurin's (1998*a–c*) and Laurin & Reisz's (1997, 1999) hypothesized sister group relationship between lysorophids and crown-group lissamphibians are described below (Section VII.3*h*).

A final remark concerns the position of albanerpetontids and caudates. In the present analysis, albanerpetontids appear to be the most crownward plesion on the lissamphibian stem [but see Trueb & Cloutier (1991) and Gardner (2001)]. However, only one extra step is required to place albanerpetontids as sister taxon to *Eocaecilia*, or as a stem-group member of the salientian-caudate clade. Pairing albanerpetontids with either *Triadobatrachus* or caudates increases tree length by four steps. At six, seven and eight extra steps, albanerpetontids can be placed as sister taxon to *Valdotriton*, *Karaurus* or *Triadobatrachus*, respectively. A caecilian-caudate clade requires three extra steps. Although this clade has not been retrieved in several traditional, morphology-based schemes of lissamphibian relationships (e.g. Estes, 1981; Duellmann & Trueb, 1986; Milner, 1988), it is nonetheless found in some morphological studies [discussion in Milner (1988), and references therein], as well as in some recent molecular analyses (e.g. Feller & Hedges, 1998, and references therein).

Feller & Hedges (1998) erected the clade Procera for the monophyletic group including salamanders plus caecilians, and listed some osteological and soft anatomical features in support of it. However, evaluation of the osteological evidence must await a redescription of *Eocaecilia* (but see Carroll, 2000) as well as a reexamination of several early salamander-like taxa (e.g. batrachosauroidids; scapherpetontids; the problematic *Ramonellus* Nevo & Estes, 1969; review in Milner, 2000). The Procera hypothesis has some interesting implications for the assessment of character distribution among primitive crown-group lissamphibians. For instance, Laurin (1998*b*) reasoned that the presence of a tympanum, deduced to have existed in at least some temnospondyls, cannot be used as a valid argument to support derivation of lissamphibians from temnospondyls. Because the tympanum is present only in salientians (frogs), the conventional phylogenetic arrangement of salientians as sister taxon to caudates (with caecilians as sister taxon to the remaining two orders) would entail unparsimonious independent losses of a tympanum in caecilians and salamanders (which could nevertheless have happened), or its loss at the base of the lissamphibian crown-group followed by reacquisition in frogs, depending upon character optimization. However, if salamanders and caecilians are indeed sister groups, only a single loss event at the base of the Procera is required under all character optimizations. Furthermore, Milner (1988; quoting Smirnov, 1986) points out the fundamental similarities between the early developmental stages of the salientian and caudate ears and the fact that the adult ear of frogs may represent the likely primitive condition for both groups, the caudate ear being secondarily reduced.

(*c*) *The amniote stem-group*

Eleven character-state changes support the basal node of the amniote stem-group. Once again, none of these synapomorphies is unambiguous. These changes include: 5 (c.i. = 0.2; 0→1), premaxillae less than two-thirds the width of the skull; 66 (c.i. = 0.1; 1→0), supratemoral contact with squamosal smooth; 68 (c.i. = 0.2; 0→1), tabulars with subdermal blade-like postero-lateral horns; 107 (c.i. = 0.125; 0⇒2), pineal foramen situated anterior to interparietal suture mid length; 117 (c.i. = 0.333; 0→1), ventral, exposed surface of vomers narrow, elongate and strip-like, without extensions anterolateral or posterolateral to choana and two and a half to three times longer than wide; 234 (c.i. = 0.125; 0→1), scapulocoracoid extending ventral to posteroventral margin of glenoid; 253 (c.i. = 0.125; 0→1), length of humeral shaft portion proximal to entepicondyle greater than the width of humeral head; 261 (c.i. = 0.2; 0⇒1), ilium with transverse pelvic ridge; 276 (c.i. = 0.25; 0⇒1), tarsus with L-shaped proximal element; 293 (c.i. = 0.333; 0⇒1), pleurocentra fused midventrally; 315 (c.i. = 0.25; 0→1), presence of no more than five digits in manus. The shortest path leading from the base of the tetrapod crown-group to the node subtending crown-group amniotes includes 72 character-state changes over eight internodes with an average of nine changes for each internode. The branching sequence of taxa in the proximal half of the amniote stem (Fig. 5) reflects the conventional view that embolomeres are an early offshoot of (perhaps secondarily) aquatic, long-bodied amniotes, and that gephyrostegids are more crownward, and presumably more terrestrial forms (Fig. 6, uppermost sector). See Laurin & Reisz (1997, 1999) and Laurin (1998*a–c*) for alternative views. Likewise, the pattern of sister group relationships in the crownward part of the amniote tree is in partial agreement with several previous hypotheses (e.g. Gauthier *et al.*, 1988*b*; Sumida & Lombard, 1991; Berman *et al.*, 1992; Sumida *et al.*, 1992; Laurin & Reisz, 1997, 1999; Laurin, 1998*a–c*; Berman, 2000).

The position of seymouriamorphs reflects traditional theories of primitive amniote relationships (e.g. Heaton, 1980; Gauthier *et al.*, 1988*b*; Sumida & Lombard, 1991; Berman *et al.*, 1992; Sumida *et al.*, 1992; Lee & Spencer, 1997; Berman, 2000), and emphasizes the key role of this group in understanding the evolution of several amniote characters. Among the internested changes leading to the condition of several crown-amniotes are: rearward shift and reduction/loss of posterior bones of skull table; widening of parietals; enlargement of the transverse pterygoid flanges; 'swollen' neural arches; consolidation of the atlas-axis complex; reduction and loss of intercentra; rearward position of neural arches relative to the position of pre- and post-zygapophyses; development of an iliac shelf; progressive reduction of entepicondylar length and width relative to humeral shaft; modifications of humeral and femoral processes (Sumida & Lombard, 1991; Berman *et al.*, 1992; Sumida *et al.*, 1992; Sumida, 1997; Berman *et al.*, 1998; Berman, 2000). In this context, it is interesting to note that *Solenodonsaurus* appears in a less crownward position than that retrieved by some recent analyses (notably, Laurin & Reisz, 1999). The present position reflects in part the 'transitional' nature of this tetrapod (Carroll, 1970; Gauthier *et al.*, 1988*b*; see above). However, it also conflicts, in part, with the distribution of certain cranial (e.g. absence of intertemporal) and trunk features (e.g. long, curved ribs) occurring in the crownward part of the amniote tree (although some of these characters are already found in some embolomeres).

Character-state changes at the node subtending *Solenodonsaurus* and more crownward amniotes are as follows: 40 (c.i. = 0.167; 0→1), presence of suture between parietal and postorbital; 60 (c.i. = 0.167; 0→1), intertemporal absent as separate ossification; 61 (c.i. = 0.167; 0→1), intertemporal interdigitating with cheek (it is noteworthy that the occurrence of this character-state change provides no phylogenetic information for this branch whatsoever, since it derives from optimization of a morphological condition that is linked to a more generalized character; such an optimization exemplifies problems deriving from missing entries to signify inapplicable characters, and introduces a bias in the computation of branch length); 66 (c.i. = 0.1; 0→1), interdigitating contact between supratemporal and squamosal; 68 (c.i. = 0.2; 1→0), tabulars without subdermal blade-like postero-lateral horns; 89 (c.i. = 0.083; 0⇒1), jugal entering ventral margin of skull roof; 104 (c.i. = 0.105; 1⇒0), interorbital distance greater than maximum orbit diameter; 118 (c.i. = 0.125; 0→1), vomer without fang pair; 127 (c.i. = 0.167; 0→1), palatine without fang pair; 197 (c.i. = 0.25; 0→1), angular reaching posterior end of lower jaw; 216 (c.i. = 0.25; 0→1), posterodorsal process of posterior coronoid contributing to highest point of lateral margin of adductor fossa; 231 (c.i. = 0.143; 0⇒1), interclavicle wider than long; 239 (c.i. = 0.111; 0→1), humerus with distinct supinator process projecting anteriorly; 247 (c.i. = 0.2; 0⇒1), humerus with expanded proximal and distal ends; 294 (c.i. = 0.25; 0⇒1), trunk pleurocentra fused middorsally; 296 (c.i. = 0.125; 0⇒1), trunk neural spines fused to centra.

Several recently described 'reptiliomorph' taxa from the Mississippian deserve additional comment. *Eldeceeon* (Smithson, 1994) and *Silvanerpeton* (Clack, 1994*c*), both from the uppermost Viséan of Scotland, are similar to stratigraphically younger embolomeres, and may indeed be the latter's plesiomorphic sister taxa. Further preparation of the *Eldeceeon* and *Silvanerpeton* material is likely to illuminate character distribution patterns at the base of the 'reptiliomorph' radiation. A third Mississippian tetrapod, *Casineria* (Paton *et al.*, 1999) from the upper Viséan of Scotland, might represent a more derived amniote than *Eldeceeon* and *Silvanerpeton*. *Casineria* was initially excluded from our data set because the large number of missing entries (86.5% of total number of characters) indicated that it would behave as a 'rogue' taxon. This was confirmed by a parsimony run of the original data set after inclusion of *Casineria*. The resulting 2208 most parsimonious trees at 1407 steps yield a mostly unresolved strict consensus, although the temnospondyl–lissamphibian relationships are the same as those in the original analysis (including the branching sequence of temnospondyl taxa and the position of *Eucritta* at the base of the lissamphibian stem-group). Conversely, all stem-group tetrapods crownward of *Tulerpeton*, and several plesions in the amniote stem-group are collapsed into a large polytomy. Inspection of the Adams consensus reveals a far less dramatic pattern of sister group relationships by relocating '… taxa in conflicting positions … to the most inclusive node that they have in common among the fundamental cladograms' (Kitching *et al.*, 1998: p. 199). Such relocations affect, among others, *Acherontiscus* (joining colosteids in an unresolved node between *Tulerpeton* and *Crassigyrinus*) and, unsurprisingly, *Casineria*. Loss of resolution also affects, in part, microsaurs. In the Adams consensus, *Casineria* forms a polytomy with a clade of diadectomorphs plus crown-amniotes and a clade of *Westlothiana* plus lepospondyls. Random scanning through different samples of trees from the pool of 2208 fundamental topologies shows *Casineria* in one or the other of four possible positions: (1) sister taxon to *Westlothiana* plus lepospondyls; (2) sister taxon of lepospondyls (this arrangement is retrieved in 77% of the fundamental trees, as shown by a 50% majority-rule consensus); (3) nested within crown-amniotes (e.g. as sister taxon to *Captorhinus* in some trees); (4) nested within microsaurs (in several alternative positions within tuditanomorphs and microbrachomorphs). Paton *et al.*'s (1999) conclusions regarding the affinities of *Casineria* are partly supported by the present study. Both analyses fail to resolve the position of *Casineria* relative to such diverse taxa as basal crown-amniotes, *Westlothiana* and (in the present study) microsaurs. Clearly, a more precise phylogenetic assessment of this tetrapod is not possible in the absence of cranial and more complete postcranial material. Available evidence from limb proportions, shape of the ilium, configuration of the vertebral centra and ribs suggest that *Casineria* should be regarded as a 'reptiliomorph' of uncertain phylogenetic affinities.

(*d*) *The affinities of* Westlothiana

Westlothiana (Fig. 6, lower right sector) is prominent because it combines generalized amniote-like features with lepospondyl characters. The two current interpretations of the phylogenetic position of *Westlothiana*, regarded either as a primitive amniote (Smithson, 1989; Smithson & Rolfe, 1990; Smithson *et al.*, 1994) or as the most crownward plesion in the tetrapod stem-group (Laurin & Reisz, 1999), are contrasted with the hypothesis of relationships presented here (Fig. 5; see also Clack, 2002). According to Smithson *et al.* (1994), *Westlothiana* branches from the amniote stem between seymouriamorphs and diadectomorphs. Smithson *et al.*'s (1994) hypothesis is compatible with our results, except for the fact that *Westlothiana* is basal to a lepospondyl clade. Tree branch manipulation within MacClade shows that relocating *Westlothiana* between seymouriamorphs and the clade including diadectomorphs plus crown-amniotes requires fewest additional steps (four) compared with alternatives. The position of *Westlothiana* in the shortest trees is supported by 14 character-state changes. Most of these are, however, homoplastic and/or based on optimization of missing or inapplicable entries: 27 (c.i. = 0.2; 0→1), portion of lacrimal lying anteroventral to orbit abbreviated; 49 (c.i. = 0.125; 1→0), total width of postparietal smaller than four times its length; 82 (c.i. = 0.333; 0⇒1), presence of kink in anteromedial margin of postorbital; 116 (c.i. = 0.286; 4→0), mandibular canal totally enclosed; 141 (c.i. = 0.5; 1⇒0), absence of transverse flange of pterygoid; 163 (c.i. = 0.5; 0→1), exoccipitals forming with basioccipital a concave, continuous and strap-shaped articular surface; 170 (c.i. = 0.25; 1⇒0), absence of posterolaterally directed, ridge-like thickenings (ridges ending in basal tubera) on basal plate of parasphenoid; 215 (c.i. = 0.167; 1→0), posterior coronoid not exposed in lateral view; 235 (c.i. = 0.25; 0→1), absence of glenoid foramen on scapulocoracoid; 255 (c.i. = 0.167; 1→0), length of humerus greater than that of two and a half mid trunk vertebrae; 267 (c.i. = 0.143; 1⇒0), absence of a distinct rugose area on the fourth trocanter; 312 (c.i. = 0.25; 0⇒1), height of neural arch in midtrunk vertebrae smaller than the length between pre- and postzygapophyses; 314 (c.i. = 0.25; 0→1), presence of no more than four digits in manus; 315 (c.i. = 0.333; 1→0), absence of five digits in manus.

In Anderson's (2001) analysis, the microsaur *Utaherpeton* is identified as the most basal lepospondyl. Aside from considerations of the status of microsaurs (discussed further below), it is noteworthy that *Utaherpeton* and *Westlothiana* are similar in several respects. Comparisons between these two taxa are necessarily limited by their poor preservation. However, they resemble each other in the shape and relative proportions of the bones in the preorbital region of the skull, in the morphology of the mandible, in the vertebral construction, and in the shape of the puboischiadic plate (especially with regards to the ischium/pubis length ratio). Some of these features are also found in several microsaur taxa, especially primitive tuditanomorphs. Major differences between *Utaherpeton* and *Westlothiana* (e.g. in the morphology and proportions of limb elements) may reflect in part the immature condition of *Utaherpeton*

(Carroll *et al.*, 1991; Carroll & Chorn, 1995). The amniote affinities of microsaurs [e.g. Olson, 1962; Vaughn, 1962; Brough & Brough, 1967; but see also Romer (1950), Carroll & Baird (1968), Carroll & Gaskill (1978), and references therein] are also supported by Paton *et al.*'s (1999) analysis, although the latter includes only a limited sample of microsaurs.

Taken together, these observations offer an alternative perspective on the significance of *Westlothiana* for our understanding of the evolutionary history of primitive amniotes. The conjectured amniote or microsaur affinities of *Westlothiana* are no longer mutually exclusive. In fact, *Westlothiana* now appears as something of a keystone taxon, contributing to a more inclusive and explanatory hypothesis of early amniote diversity. It seems that, early in amniote history, certain terrestrial forms became elongate (although not necessarily small, *contra* Carroll, 1996) and displayed skink-like overall body proportions, similar to those of certain later microsaurs (e.g. rhynchonkids, ostodolepids and, possibly, gymnarthrids). Such proportions might be interpreted as adaptations to a burrowing life-style, at least in some of the above-mentioned taxa.

(*e*) *The status of microsaurs*

Our scheme of relationships supports microsaur paraphyly (Fig. 5; see also lower mid-right sector in Fig. 6), but differs from Anderson's (2001) analysis in the branching order of the tuditanomorph families as well as in the fact that microbrachomorphs other than brachystelechids form a clade. This clade (admittedly a poorly supported one) is the sister taxon to remaining lepospondyls. Brachystelechids are paired with a monophyletic tuditanomorph assemblage. The arrangement of tuditanomorphs mostly agrees with Schultze & Foreman's (1981) and Milner's (1993) hypotheses. There are, however, some differences between those studies and the present result. First, we found no evidence for a monophyletic Tuditanidae as defined by Carroll & Gaskill (1978), although this may be due, in part, to limited character choice and poor preservation of *Tuditanus* (Carroll & Baird, 1968). *Tuditanus*, Pantylidae and *Asaphestera* are progressively more closely related to other tuditanomorphs. Second, Hapsidopareiontidae are paraphyletic, with *Saxonerpeton* and *Hapsidopareion* as successive sister taxa to a clade including ostodolepids, rhynchonkids and gymnarthrids. Hapsidopareiontids, ostodolepids and gymnarthrids have emarginated cheeks (character 112). The greater or lesser degree of emargination in hapsidopareiontids and ostodolepids, respectively, may represent a trend towards acquisition of a secondarily closed and solid cheek, like that observed in the rhynchonkid-gymnarthrid clade [possibly adaptated to a burrowing life-style (Carroll & Gaskill, 1978; Milner, 1993)]. Among gymnarthrids, *Cardiocephalus* shows a rather shallow emargination, the presence of which was disputed by Carroll & Gaskill (1978). The configuration of the cheek region of *Cardiocephalus* is comparable to that of ostodolepids. ACCTRAN optimization shows that the emargination of *Cardiocephalus* is convergent with that of hapsidopareiontids and ostodolepids. Cheek morphology varies in gymnarthrids. Thus, *Euryodus* and *Sparodus* display a conventional cheek with a straight ventral margin, whereas *Pariotichus* and *Cardiocephalus* show a shallow cheek embayment (Carroll & Gaskill, 1978; Schultze & Foreman, 1981; Carroll *et al.*, 1998).

(*f*) *The aïstopod-nectridean clade*

The present analysis retrieves a scincosaurid-diplocaulid clade (Fig. 5; see also upper mid-right sector in Fig. 6) – in agreement with A. C. Milner's (1980) and Milner's (1993) hypotheses – and an aïstopod-urocordylid clade. Only two extra steps are required to reconstruct a monophyletic Nectridea or to place aïstopods as sister taxon to diplocaulids. Tree length increases by 11 steps when the nectridean genera are arranged as in Anderson's (2001) analysis (constraining nectrideans to be monophyletic but without changing the position of lysorophids and aïstopods), and by 17 steps when lysorophids and aïstopods are sister group to diplocaulids [Anderson's (2001) topology]. The present work supports in part Thomson & Bossy's (1970) concept of Holospondyli, but forces us to explore further characters that may re-establish nectridean monophyly. An emended diagnosis of nectrideans that takes into account the position of aïstopods does not seem to be warranted. However, the possibility that aïstopod ancestry is rooted into basal nectrideans cannot be entirely ruled out. If a tree topology is reconstructed that matches Anderson's (2001; Fig. 3) arrangement of lepospondyl taxa down to genus level (including the position of caecilians among derived tuditanomorphs), then tree length increases by 55 steps, and the tree is a significantly worse fit for the data than the most parsimonious trees ($P < 0.0001$ for Templeton, Kishino–Hasegawa and Winning-sites tests). Similar statistical test results are obtained if a further constraint is imposed on Anderson's (2001) topology by maintaining his arrangement of lepospondyls but forcing lissamphibian monophyly at a deeper level (i.e. with caecilians' ancestry rooted into lepospondyls, and salientians' and caudates' ancestry rooted into dissorophoid temnospondyls; see also discussion in Milner, 1988, 1993). The new constraint entails 85 extra steps.

The aïstopod-nectridean clade is supported by the following character-state changes (several of which represent optimized missing entries): 16 (c.i. = 0.067; 1→0), prefrontal less than three times as long as wide; 136 (c.i. = 0.091; 1→0), ectopterygoid without denticles; 138 (c.i. = 0.125; 1→0), ectopterygoid with tooth row; 282 (c.i. = 0.333; 1→0), absence of elongate posterodorsal flange in most trunk ribs; 286 (c.i. = 0.5; 0⇒1), presence of extra articulations above zygapophyses in at least some trunk and caudal vertebrae; 287 (c.i. = 1; 0⇒1), neural and haemal spines rectangular to fan-shaped in lateral view; 288 (c.i. = 1; 0⇒1), neural and haemal spines facing each other dorsoventrally; 289 (c.i. = 0.5; 0⇒1), haemal spines fused to caudal centra; 296 (c.i. = 0.125; 0⇒1), neural spines of trunk vertebrae fused to centra; 311 (c.i. = 0.5; 1⇒0), absence of capitular facets on posterior rim of vertebral midtrunk centra.

The sister group relationship between aïstopods and urocordylids is based on five character-state changes (again, several reversals and optimized missing entries are implied within the clade): 63 (c.i. = 0.25; 1⇒0), presence of supratemporal; 104 (c.i. = 0.105; 0⇒1), interorbital distance smaller than maximum orbit diameter; 137 (c.i. = 0.2; 1→0), ectopterygoid longer than palatine; 267 (c.i. = 0.143; 0→1), presence of distinct rugose area on fourth trochanter; 290 (c.i. = 1; 0→1), presence of extra articulations on haemal spines.

(*g*) Acherontiscus *is an adelospondyl*

As many as 14 characters indicate a sister group relationship between *Acherontiscus* and adelospondyls: 13 (c.i. = 0.143; 0⇒1), nasal length less than one-third the frontal length; 38 (c.i. = 0.143; 0→1), anterior margin of frontal deeply wedged between posterolateral margins of nasals; 67 (c.i. = 0.25; 0→1), absence of tabular as separate ossification; 77 (c.i. = 0.333; 0⇒1), postorbital excluded from margin of orbit; 86 (c.i. = 1; 0→1), single squamosotabular in the position of squamosal and tabular; 104 (c.i. = 0.105; 0→2), interorbital distance subequal to maximum orbit diameter; 107 (c.i. = 0.125; 2→0), position of pineal foramen behind interparietal suture mid point; 115 (c.i. = 0.286; 4⇒1), lateral line system on skull roof mostly enclosed, with short sections in grooves; 116 (c.i. = 0.286; 4→3), mandibular canal entirely in grooves; 128 (c.i. = 0.067; 0→1), palatine with denticles; 151 (c.i. = 0.25; 0→1), distinct anterior digitiform process of palatal ramus of pterygoids; 167 (c.i. = 0.5; 0→1), basioccipital circular and recessed; 191 (c.i. = 0.143; 1→0), presence of postsplenial; 281 (c.i. = 0.5; 0→1), presence of spur-like posterodorsal processes in at least some trunk ribs. Additional characters from the mandible and postcranial skeleton are currently being examined in conjunction with a revision of *Acherontiscus*. We found a remarkable array of similarities (proportions of several skull roof bones; vertebral and rib morphology) between *Acherontiscus* and adelospondyls, on one side, and colosteids, on the other. We were, therefore, interested to discover that only five additional steps are required to shift the *Acherontiscus*-adelospondyl clade retrieved in the original parsimony run to a stem-tetrapod position, as sister taxon to colosteids. This topology does not represent a significantly worse fit of the data than the fundamental trees (Templeton test: $P=0.3532$; Winning-site test: $P=0.4583$; Kishino–Hasegawa test: $P=0.354$; the results are based on comparisons between the first tree obtained from the original analysis and a constrained tree in which the clade *Acherontiscus* plus adelospondyls is sister group to colosteids; comparisons with additional selected trees [10, 20, 30, 40, 50, 60] also imply values of $P \gg 0.05$). In the light of such findings, we are exploring the significance of additional characters in evaluating the question of lepospondyl monophyly and the affinities of adelospondyls (see also below). If independently corroborated by other characters, such a hypothesis of relationships suggests that tendency towards body elongation and limb reduction/loss occurred early in the evolutionary history of tetrapods, and was acquired convergently in several crown-group lineages (e.g. microsaurs; embolomeres; urocordylids; aïstopods).

(*h*) *The position of lysorophids*

The highly specialized lysorophids share characters with one or more representatives of various lepospondyl groups, although they are generally considered to be closely related to microsaurs (Wellstead, 1991; Carroll *et al.*, 1998). Several cranial characters of *Brachydectes* resemble those of *Batropetes* (Carroll & Gaskill, 1978; Carroll, 1991*a*). However, placing *Batropetes* as sister taxon to *Brachydectes* requires nine steps. This topology is only slightly worse than the most parsimonious trees, although the level of significance is not high (Templeton test: $P=0.0389$; Winning-sites test: $P=0.0636$; Kishino–Hasegawa test: $P=0.0388$). Nine steps are also required to place lysorophids as sister taxon to aïstopods as in Anderson's (2001) analysis (again, with a low level of significance).

We were interested to compare our tree topology (Fig. 4), with particular reference to the position of lysorophids, with Laurin & Reisz's (1997, 1999) and Laurin's (1998*a–c*) preferred topology (Fig. 1D), in which lysorophids are the closest relatives of crown-group lissamphibians. To this purpose, we carried out three separate exercises, in which taxa were rearranged in order to match as closely as possible Laurin & Reisz's (1997, 1999) and Laurin's (1998*a–c*) cladogram. For simplicity, tests were performed using Laurin & Reisz's (1999) tree, since their study supersedes those of Laurin & Reisz (1997) and Laurin (1998*a–c*).

In the first exercise, we kept intrinsic relationships within major groups mostly unaltered, but rearranged such groups according to the branching sequence favoured by Laurin & Reisz (1999). In particular, *Rhynchonkos*, *Batropetes* and *Brachydectes* were placed as a series of progressively more crownward plesions on the lissamphibian stem-group. The new arrangement entails 74 additional steps and is a considerably worse fit for the whole character set than the most parsimonious trees ($P < 0.0001$ for Templeton, Winning-sites and Kishino–Hasegawa tests).

In the second exercise, our taxon sample was stripped down to resemble Laurin & Reisz's (1997, 1999) and Laurin's (1998*a–c*) taxon matrix (except for the exclusion of living groups and of the genus *Tersomius*; see above). All taxa belonging to a given group were kept in the analysis if such a group was represented by a supraspecific OTU in Laurin & Reisz's (1999) dataset (e.g. Gephyrostegidae; Aïstopoda; Nectridea). The reduced matrix yielded 24 equally parsimonious trees at 985 steps ($CI = 0.3326$; $RI = 0.648$; $RC = 0.2296$) supporting a derivation of lissamphibians from dissorophoids. Nine of these trees were compared with Laurin & Reisz's (1999) topology. In all cases examined, their favoured branching pattern represents a considerably worse fit for the total data than the topology retrieved from the original parsimony run (significance at $P < 0.0001$ for Templeton, Winning-sites and Kishino–Hasegawa tests). The strict consensus of the 24 fundamental trees resembles that of the original analysis (Fig. 4), except in the following features: (1) embolomeres and gephyrostegids are sister groups, as in Laurin & Reisz (1999); (2) seymouriamorphs are paraphyletic, with *Seymouria* and *Kotlassia* as successive plesions on the amniote stem-group; and (3) *Westlothiana*, *Batropetes*, *Rhynchonkos*, *Pantylus* and *Brachydectes* are successively more closely related to a clade including, proximodistally, *Scincosaurus*, diplocaulids, urocordylids and a monophyletic adelospondyl-aïstopod group.

In the third exercise, we constrained crown-lissamphibians (without albanerpetontids) to appear as sister group to lysorophids without changing the relationships of the other taxa. When we compared the resulting tree (at 22 extra steps) with the fundamental cladograms, we found significant differences (Templeton test: $P = 0.0008$; Winning-sites test: $P = 0.0013$; Kishino–Hasegawa test: $P = 0.0007$). However, it is important to note that if albanerpetontids are grouped with crown-lissamphibians, and this clade is placed as sister group to lysorophids, then tree length increases by only 10 steps, and the new topology is not fundamentally different from the shortest cladograms overall (Templeton test: $P = 0.1736$; Winning-sites test: $P = 0.2207$; Kishino–Hasegawa test: $P = 0.174$). As explained below (see Section VII.7), this result depends upon the unstable 'balance' beween different character sets that support alternative, conflicting, positions for crown-lissamphibians. Specifically, the character signal supporting the lissamphibian-dissorophoid relationship is diluted by the pervasive noise associated with a host of reversals and 'absence' features (especially cranial features). In fact, albanerpetontid crania, like lysorophid examples, include unusually few bones, and, despite gross morphological differences, we argue that it is the apparent shared pattern of simplification that forces these taxa together.

(4) **Reweighted analysis**

Reweighting characters by their consistency index values (best fit) yields one tree ($CI = 0.4068$; $RI = 0.7666$; $RC = 0.3279$; Fig. 7) which differs from the fundamental trees (consensus in Fig. 4) in two main respects. First, *Crassigyrinus* and *Whatcheeria* are sister taxa and branch from the tetrapod stem between *Tulerpeton* and colosteids. We strongly suspect that this reweighting procedure reveals a likely new clade of stem-tetrapods. *Crassigyrinus* has long been considered as a 'peculiar aberrant form' (Milner *et al.*, 1986: p. 4), but at least some of these peculiarities are now emerging as possible synapomorphies for a discrete, *Whatcheeria*-like assemblage of archaic Mississippian forms with a plausible Late Devonian origin (see also Clack, 2002). Second, baphetids and *Eucritta* are sister taxa (cf. Clack, 2001) and form the most crownward stem-tetrapod plesion. With *Eucritta* snapped to the baphetids, edopoids assume the most basal position on the lissamphibian stem, thereby emphasizing the extreme patchiness of the early lissamphibian record (Milner & Sequeira, 1998). It is also noteworthy that the reweighted analysis resolves the branching pattern of derived temnospondyls in favour of a sister group relationship between a clade encompassing *Amphibamus* plus *Doleserpeton* and a clade of branchiosaurids with

Fig. 7. Single tree deriving from reweighting characters by their consistency index (c.i.) values (best fit).

Leptorophus as sister taxon to *Apateon* plus *Schoenfelderpeton*. This broader group is paired with albanerpetontids plus crown-lissamphibians. Progressively less crownward taxa include *Micromelerpeton*, *Eoscopus* and *Platyrhinops*.

(5) Cranial data

The results of a PAUP* analysis applied to cranial and mandibular characters were examined in order to assess the influence of different character partitions on tree topology. However, the postcranial character set could not be processed successfully, due to time- and memory-consuming computer requirements.

The all-cranial version of the data set produced 1188 fundamental trees at 1022 steps (CI = 0.2485; RI = 0.6787; RC = 0.1707). Despite the extremely poor resolution of a strict consensus, the monophyletic status of several groups is corroborated, although the arrangement of several taxa departs significantly from that of the original analysis. An Adams consensus (Fig. 8) reveals the instability of taxa including *Acherontiscus*, *Caerorhachis*, *Whatcheeria*, adelospondyls, aïstopods, lysorophids and urocordylids. Also noteworthy is the unstable position of various 'reptiliomorphs' (e.g. *Gephyrostegus*, *Seymouria*, *Solenodonsaurus*, *Kotlassia* and *Limnoscelis*). On the lissamphibian stem, the relationships of the most crownward temnospondyls differ from those of the original parsimony run in that *Broiliellus* is sister taxon to crown-lissamphibians. Progressively less crownward taxa include: (1) a clade formed by *Amphibamus* and *Doleserpeton*; (2) *Platyrhinops*; (3) a clade formed by *Eoscopus* and *Micromelerpeton* as successive sister taxa to branchiosaurids. As in the reweighted analysis (using the complete character set; Fig. 7), the cranial data support the polyphyly of amphibamids.

The most striking result of the cranial analysis is the identification of two distinct monophyletic groups of lepospondyls in several trees. The first group consists of microsaurs, placed as sister taxon to *Westlothiana* on the amniote stem, in agreement with the original parsimony run. The second group consists of a heterogeneous assemblage of aïstopods, lysorophids, adelospondyls and nectrideans, forming the sister group to colosteids in at least some trees.

In the first group, pantylids are paired with gymnarthrids, as in Anderson's (2001) cladogram, whereas *Odonterpeton* and *Batropetes* form a clade between *Saxonerpeton* and *Hapsidopareion*. The pantylid–gymnarthrid sister group relationship is supported by their similar tooth morphology and by their general skull proportions. The match between the cladogenetic event sequence and the stratigraphical appearance of microsaur families is better than that obtained when using the total data set. The pairing of *Odonterpeton* and *Batropetes* is rather unexpected. However, characters in common to both genera are the robust aspect of the mandible and the sloping of the posterior cheek margin. The material of *Odonterpeton* is imperfectly known and requires thorough redescription.

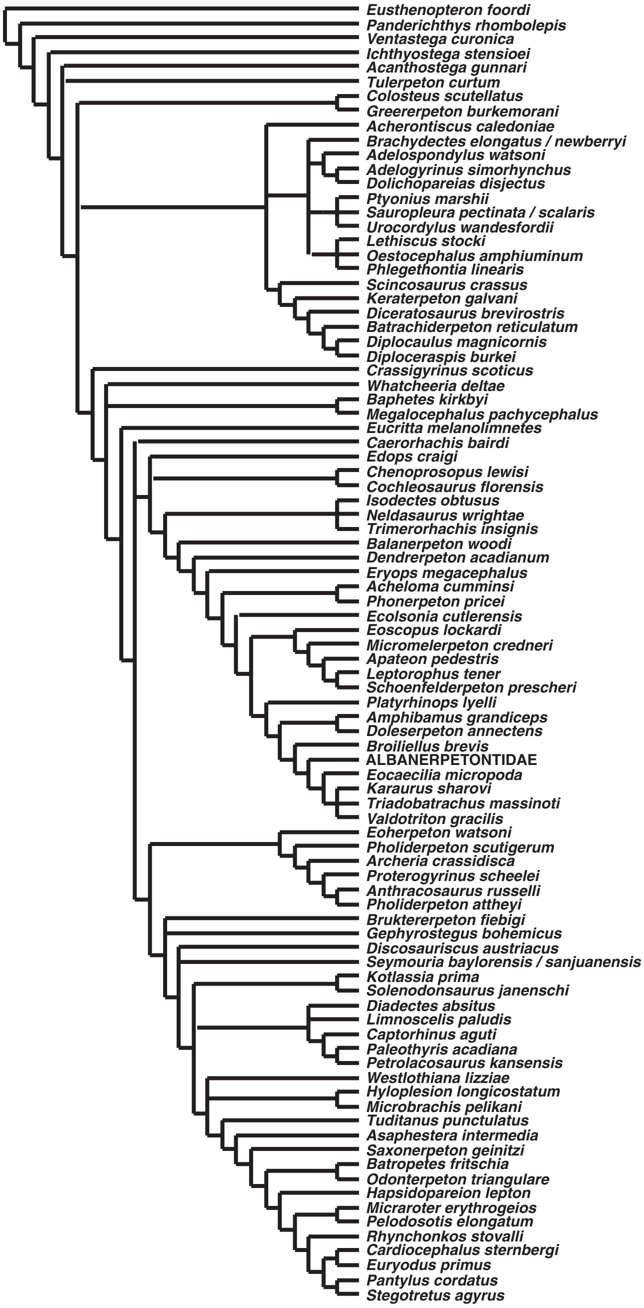

Fig. 8. Adams consensus of 1188 equally parsimonious trees obtained after removal of postcranial characters.

A stem-tetrapod position for various lepospondyls, such as those within the second group, has been proposed by Milner (1993), who speculated that nectrideans might be progenetically dwarf relatives of colosteids. The large size of certain long-horned diplocaulids would, we assume, result from subsequent peramorphosis. Body elongation, increase in vertebral count and morphological uniformity, and limb reduction/loss are often associated with swimming and/or burrowing lifestyles. Aïstopods may represent the very nadir of these morphological trends.

We explored further the effects of placing lepospondyls other than microsaurs in a stem-tetrapod position (see also above for a discussion of adelospondyls). If the adelospondyls-nectrideans-aïstopods clade deriving from the original parsimony run (i.e. using the complete set of characters) is grafted to colosteids in order to match the results of the all-cranial analysis, the resulting tree topology is found to be only a slightly worse fit for the data than the most parsimonious cladograms overall (Templeton test: $P = 0.0197$; Winning-sites test: $P = 0.01$; Kishino–Hasegawa test: $P = 0.0224$; the results are based on comparisons between all trees obtained from the original analysis and a constrained tree forcing lepospondyls other than microsaurs into a stem-tetrapod position). The hypothesis that some lepospondyl lineages diversified early in tetrapod history, before the lissamphibian-amniote split, cannot be entirely ruled out. However, this hypothesis requires independent testing using several new characters, and will be dealt with elsewhere.

(6) Deletion of lower jaw characters

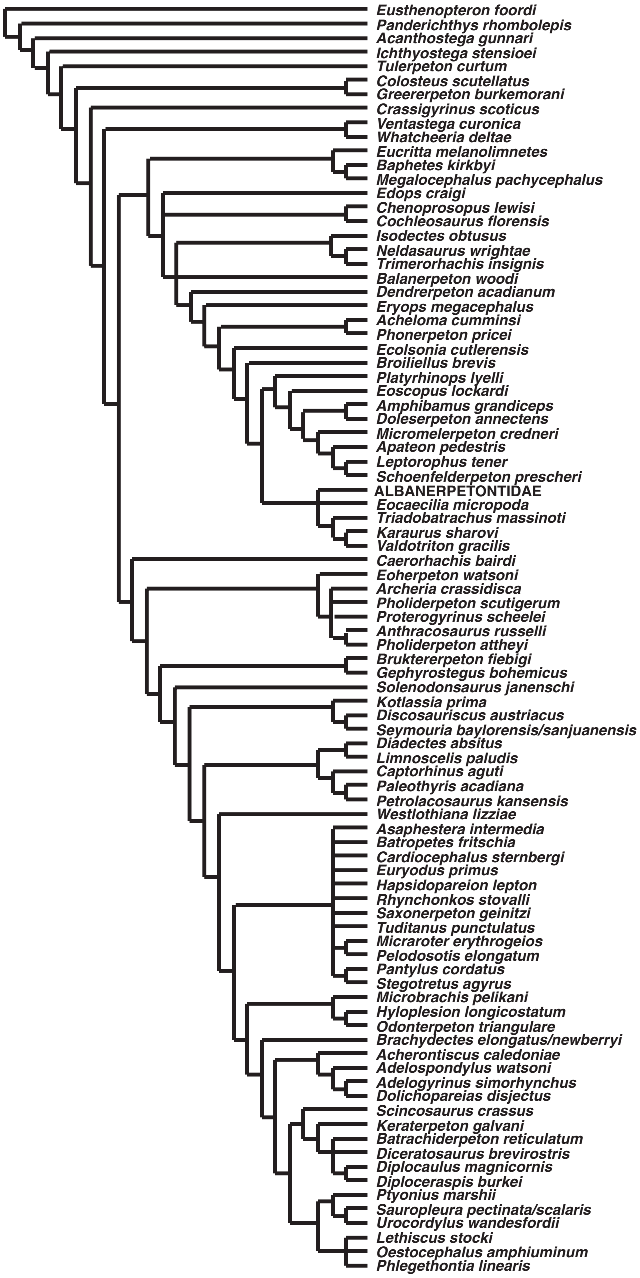

Fig. 9. Strict consensus of 2160 equally parsimonious trees obtained after removal of lower jaw characters.

To assess the impact of lower jaw morphology on cladogram topology, we ran a cladistic analysis excluding mandibular characters. The strict consensus of 2160 trees at 1220 steps (CI = 0.2322; RI = 0.6737; RC = 0.1607; Fig. 9) is only slightly less resolved than that based on the total data set. It differs from the latter in the following respects: (1) *Ventastega* and *Whatcheeria* are sister taxa and form the most crownward plesion on the tetrapod stem-group; (2) *Eucritta* plus baphetids form the most basal clade in the lissamphibian stem-group; (3) *Edops* and cochleosaurids form an unresolved node with higher temnospondyls; (4) *Balanerpeton* and trimerorhachoids likewise form an unresolved node with higher temnospondyls; (5) crown-lissamphibians are more deeply nested into the derived portion of the temnospondyl tree, and form the sister group to a fully resolved clade in which amphibamids are a paraphyetic assemblage relative to a micromelerpetontid-branchiosaurid clade; (6) within crown-lissamphibians, relationships are resolved in favour of a salientian-caudate clade, with *Karaurus* and *Valdotriton* as sister taxa; however, albenerpetontids and *Eocaecilia* are collapsed in a polytomy with the remaining lissamphibians; and (7) most tuditanomorphs are collapsed in a large polytomy, except for ostodolepids and pantylids; loss of resolution among tuditanomorphs is due to the unstable positions of *Batropetes*, *Hapsidopareion*, *Rhynchonkos* and *Tuditanus*.

Ahlberg & Clack (1998) have recently discussed the results of a cladistic analysis of early tetrapods based on lower jaw features (see also Daeschler, 2000). The relationships of several taxa in their work differ substantially from those of previous analyses. One of the most unexpected results is the fact that such traditional groups as temnospondyls and 'anthracosaurs' appear as polyphyletic arrays of taxa. The conflict between the phylogenetic signal provided by the lower jaw and the cladogenetic pattern based on other data may be rooted into the paucity of mandibular characters (see also comments in Ruta *et al.*, 2001). Although it is possible to identify, as Ahlberg & Clack (1998) did, a series of morphological trends affecting the evolution of lower jaws in passing from stem-tetrapods to basal crown-tetrapods, the degree of character resolution may be insufficient to yield hypotheses of relationships (both between and within groups) that match those based on other skeletal features. Thus, while a host of cranial and postcranial features support a single origin for temnospondyls, their lower jaws change little within various lineages in this group. Differences between such lineages are most prominent in the relative size and position of Meckelian foramina, and in the proportions of infradentaries and coronoids [see Schoch & Milner (2000), Yates & Warren (2000) and Damiani (2001)]. The observation that certain primitive characters (e.g. parasymphysial plate) are retained in a variety of otherwise very distinctive groups (e.g. baphetids, colosteids, some embolomeres) suggests that the lower jaw underwent modifications at a slower rate than other parts of the skeleton. Interestingly, such modifications appear to be largely decoupled from changes that affected the skull roof, palate and postcranium both in taxa spanning the fish–tetrapod transition and in some basal members of the crown-group. At higher levels of the tetrapod hierarchy, and especially among amniote-related taxa, important modifications are clustered consistently around specific cladogram nodes (e.g. number and proportions of coronoids; extensions of mesial laminae of infradentary bones; enlargement and reduction in number of Meckelian foramina; decrease in the curvature of the posterior two-thirds of the lower margin). As Ahlberg & Clack (1998: p. 42) pointed out, '... it is curious to observe that the trends towards reduction of the coronoids and the endoskeletal components of the jaw continue in the synapsids, but not the other amniote lineages. A modern lizard or crocodile jaw is still in most respects comparable to that of the Early Permian *Eocaptorhinus*'. On the lissamphibian stem, on the other hand, modifications were less drastic than in the amniote stem – hence the overall similarities between the lower jaws of various basal and derived temnospondyls (regardless of absolute size). Furthermore, although the lower jaws of several crown-lissamphibians are highly derived relative to those of their Palaeozoic counterparts (Ahlberg & Clack, 1998), Schoch (1998) has shown that identification of homologous features is possible when embryological data are combined with sequences of growth stages recovered from the fossil record. Intriguingly, Schoch's (1992) analysis of morphological changes in the development of two different species of *Apateon* reveals striking similarities between this dissorophoid and certain primitive salamanders, e.g. at the level of the parasphenoid, quadrate ramus of pterygoid and vomer.

(7) Reverse weighting

Trueman's (1998) reverse weighting procedure assists searches for conflicting signals within data sets. The method is based on successive removals of unambiguous synapomorphies (i.e. characters with c.i. = 1) following parsimony runs. Synapomorphy stripping should reveal residual or masked phylogenetic signal within the remaining character set. We note that PAUP* calculates c.i. values on the basis of each individual tree, and not on performance of characters across the entire tree set (providing that several trees are found). It is thus possible that characters with a c.i. of 1 may support nodes that do not occur in a strict consensus. Therefore, we propose that such characters should be retained for subsequent rounds of reverse weighting. While these characters perform as if signal-consistent within a particular tree, they exhibit homoplastic distribution across the entire tree set. Consequently, they remain a source of alternative phylogenetic patterns, and any list of characters with a c.i. of 1 should be plotted on a strict consensus of the entire tree set (including the particular tree from which the c.i.'s were obtained). This seems to be a more discriminatory procedure than that applied by other workers (see Rieppel, 2000).

Fifty-five characters identified as unambiguous synapomorphies at the end of the original parsimony run were excluded (1, 4, 8, 19, 22, 26, 31, 52, 54, 55, 65, 72, 76, 86, 87, 92, 99, 108, 111, 152, 157, 161, 162, 164, 166, 185, 199, 211, 217, 223, 225, 226, 227, 236, 241, 260, 263, 264, 271, 274, 275, 277, 278, 283, 287, 288, 290, 291, 305, 307, 308, 309, 310, 316, 318). The new, reduced data set yielded 1608 trees at 1341 steps (CI = 0.2266; RI = 0.6543; RC = 0.1512), a strict consensus of which is very poorly resolved. The most important feature of these trees is the fact that crown-lissamphibians and albanerpetontids now appear to be nested within lepospondyls. Remaining portions of the tree, however, remain largely unchanged. A selected tree shows that the position of lissamphibians is accounted for by reversals as well as by optimizations of missing characters. An agreement subtree shows that albanerpetontids plus crown-lissamphibians maintain the same relationships with adelospondyls in all trees, with urocordylids, diplocaulids, *Scincosaurus*, pantylids and a heterogeneous microsaur clade (with microbrachomorphs nested within remaining tuditanomorphs) as progressively more distantly related taxa. Also evident in the agreement subtree is the paraphyletic status of gephyrostegids, seymouriamorphs and diadectomorphs, and the fact that edopoids branch from the temnospondyl tree between *Balanerpeton* and eryopoids. A further five characters (167, 210, 301, 302, 303) were identified as unambiguous synapomorphies in a selected tree obtained from the reduced data set, but no further analysis was carried out due to computation time (the further five characters are unambiguous synapomorphies in some distal portions of the cladogram, and their removal is likely to produce further decrease in the resolution of a strict consensus). Deep nodes in the strict consensus appear to be entirely supported by homoplastic changes.

Character reversals and optimized missing entries have a profound effect on the analysis. They introduce diffused 'noise' which accumulates when sets of 'presence' characters, such as certain lissamphibian-temnospondyl synapomorphies, are removed. These results show that evidence for a lissamphibian-dissorophoid clade, based on the whole data set, is consistently stronger than the alternative hypothesis of a sister group relationship between lissamphibians and lepospondyls.

(8) Chronology

A minimum hypothesis of the timing of the principal events in tetrapod phylogeny, as implied by the cladogram in Figs 5 and 6, is shown in Fig. 10. The date of the crown-group node is effectively pegged by the occurrence of the earliest known aïstopod *Lethiscus* (Wellstead, 1982). This material is slightly older than the late Viséan East Kirkton locality (Rolfe, Clarkson & Panchen, 1994), and thus in excess of 338 million years before present. A quick inspection of Fig. 10 shows a proliferation of taxa during the Viséan, but this pattern results from, on the one hand, the problematic nature of the few known scattered remains of Tournaisian tetrapods (Clack & Carroll, 2000), and on the other, the disproportionate influence of key faunas, such as East Kirkton (Rolfe *et al.*, 1994). It is noteworthy that all recent phylogenetic analyses identify basal crown taxa within the diversity of mid-Viséan tetrapods, and it therefore appears that the proposed date for the crown-node (on the basis of morphological data) is unusually robust. Subsequent changes appear more likely to result from new fossil discoveries than from new or alternative phylogenies (cf. Laurin, 1998*b*; Paton *et al.*, 1999). The inferred timing of the lissamphibian-amniote split falls some 20 million years short of the estimate derived from molecular data (Hedges, 2001); the significance or otherwise of this is dicussed in greater detail elsewhere (Ruta & Coates, in press).

VIII. FUTURE RESEARCH

Despite the increase in early tetrapod data, numerous aspects of their evolutionary history remain obscure. The earliest phases of diversification of several groups, including those with an extensive fossil record (e.g. temnospondyls), are poorly understood. Furthermore, the earliest known members of various taxa display almost complete arrays of apomorphies found in later representatives (e.g. microsaurs; nectrideans; Carroll & Gaskill, 1978; A. C. Milner, 1980; Milner, 1993; Carroll *et al.*, 1998), thus providing little information on their ancestry and sister taxon relationships. Some tetrapods show puzzling combinations of characters shared with members of two or more different groups (e.g. *Caeorhachis*; *Crassigyrinus*; *Eucritta*; *Whatcheeria*; Lombard & Bolt, 1995; Clack, 1996, 1998*a*, *c*, 2001; Bolt & Lombard, 2000; Ruta *et al.*, 2001). Still others are extremely specialized from their first appearance in the fossil record (e.g. adelospondyls; aïstopods; lysorophids; Wellstead, 1982, 1991; Carroll, 1998; Carroll *et al.*, 1998). All of these observations, coupled with the vagaries of fossil preservation, suggest no imminent, unequivocal, solution to the problem of evaluating the phylogenetic position of several crucial taxa.

Recent research is beginning to shed new light on the anatomy and relationships of rare and problematic forms, such as lepospondyls (Carroll, 1998; Carroll *et al.*, 1998; Anderson, 2001, in press; Anderson *et al.*, 2001). Several issues related to lepospondyl interrelationships are likely to undergo extensive revision in the near future. Published analyses of lepospondyls reveal a disconcerting lack of agreement, to the point that almost any pattern of relationships has been proposed (Smithson, 1985; Panchen & Smithson, 1987; Milner, 1993; Carroll, 1995; Carroll & Chorn, 1995; Laurin & Reisz, 1997, 1999; Laurin, 1998*a–c*; Anderson, 2001). The most challenging task posed by lepospondyl studies consists of identifying good symapomorphies with other major groups. Comparisons between the results generated by different character set partitions (see above) show that much work is still needed to unravel the confounding signal produced by convergence. However, these comparisons already suggest that at least some of

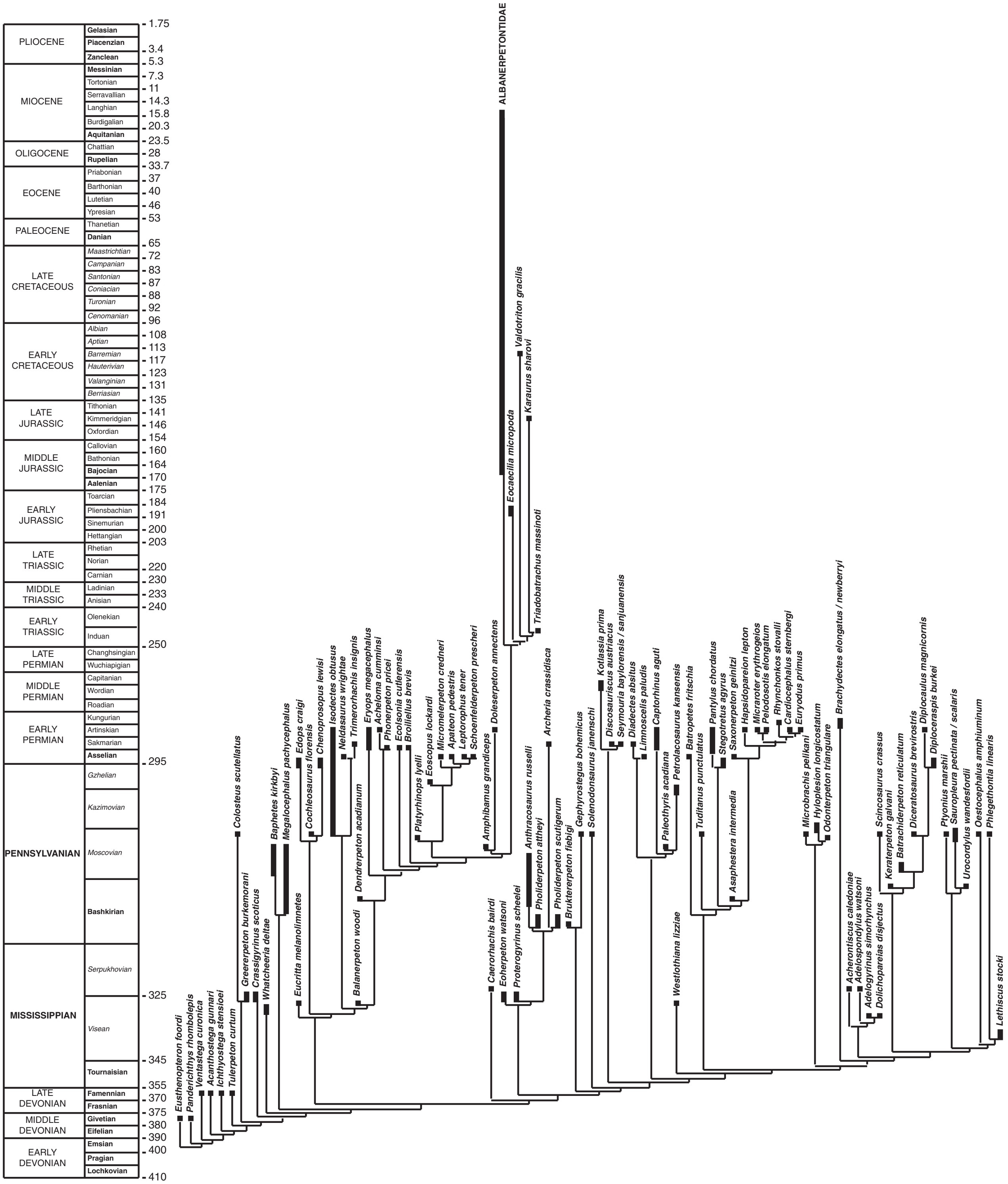

Fig. 10. The selected tree shown in Fig. 5 plotted on a stratigraphic timescale, modified from Ruta & Coates (in press).

the hypothesized sister group relationships may be correct (e.g. Thomson & Bossy, 1970; Wellstead, 1991).

Commonly held assumptions about the polarity of several characters in the most crownward part of the tetrapod stem-group are challenged by new discoveries (Clack & Finney, 1997; Clack, 2002). Future work on the earliest known Carboniferous faunas (Thulborn *et al.*, 1996; Clack & Carroll, 2000) may provide further insight into the pattern of character distribution near the base of the crown-group.

Theories of lissamphibian origin, or origins, continue to be the source of considerable conflict. As Carroll & Bolt (2001: p.38A) have noted, the problem with certain recently published phylogenetic hypotheses (e.g. Laurin & Reisz, 1997, 1999; Laurin, 1998*a–c*) is that they '… support a monophyletic origin of the modern [lissamphibian] orders, but imply a large number of biologically improbable character reversals and an immediate common ancestor with very few characters shared with any of the derived orders' (see also Carroll, 2001). Investigations of patterns of skeletal ossification in several derived temnospondyls (notably, dissorophoids), and comparisons with developmental data from modern as well as extinct lissamphibians (e.g. Schoch, 1992, 1995, 1998; Carroll, Kunst & Albright, 1999; Boy & Sues, 2000; Carroll, 2001; Carroll & Bolt, 2001; Chipman & Tchernov, 2002) provide a large amount of new morphological information that is likely to be incorporated in comprehensive, morphology-based cladistic analyses. Particularly challenging topics include the single or multiple origins of lissamphibians from among dissorophoids (Bolt, 1969, 1977, 1979, 1991; Lombard & Bolt, 1979; Bolt & Lombard, 1985; Milner, 1988, 1993; Trueb & Cloutier, 1991; Carroll, 2001; Carroll & Bolt, 2001; Dr A. R. Milner, personal communication to M. Ruta, 2001), and the ancestry of caecilians (review in Carroll, 2000).

Interrelationships of various putative stem-amniote groups remain controversial. The impact on phylogenetic reconstruction of several Permian and late Carboniferous forms (e.g. chroniosuchids; kotlassiids; nycteroleterids) cannot be properly evaluated without a detailed revision of their osteology. The morphological gap between diadectomorphs and primitive crown-amniotes is puzzling, despite the fact that several characters of the former foreshadow the condition of basal crown-amniotes (Berman & Sumida, 1990; Sumida & Lombard, 1991; Berman *et al.*, 1992, 1998; Sumida *et al.*, 1992; Sumida, 1997; Berman, 2000). Future research targeted at the most primitive 'anthracosauroids' (e.g. Clack, 1994*c*; Smithson, 1994) may yield new data on the early radiation of 'reptiliomorphs', with particular emphasis on the skeletal modifications that accompanied the transition from semiaquatic/aquatic (e.g. embolomeres) to more fully terrestrial forms (e.g. gephyrostegids; *Solenodonsaurus*). The position of seymouriamorphs is interesting in this context. Although some of their characters appear to be more primitive than those observed in certain early terrestrial 'reptiliomorphs', this may simply reflect the paedomorphic or juvenile condition of some forms (e.g. discosauriscids). On balance, similarites between diadectomorphs and seymouriamorphs are striking, and point to a more derived placement of the latter on the amniote stem relative to embolomeres and gephyrostegids.

IX. CONCLUSIONS

(1) In an attempt to investigate conflicts between the most widely discussed hypotheses of early tetrapod relationships, we assembled a large data matrix encompassing character sets from each published study. This has not been a literature-based exercise. We have incorporated, where possible, original observations of numerous taxa spread throughout the major clades, as well as data from the redescriptions of *Tulerpeton* (Lebedev & Coates, 1995), *Acanthostega* (Coates, 1996) and *Caerorhachis* (Ruta *et al.*, 2001). The results of our new analysis indicate a deep phylogenetic split between lissamphibian- and amniote-related groups. A series of Lower Carboniferous early tetrapods branch from the tetrapod stem. These include colosteids, *Crassigyrinus*, *Whatcheeria* and baphetids, in order of increasing proximity to the crown-group. Some of these taxa (notably *Crassigyrinus*, *Whatcheeria* and baphetids) have been allied to amniotes in certain analyses, but their 'reptiliomorph' characters are now emerging as generalized tetrapod features (see also Clack, 2002). The tetrapod crown-group is bracketed at its base by *Eucritta* and *Caerorhachis*, notorious for their debated affinities (Holmes & Carroll, 1977; Milner & Sequeira, 1994; Coates, 1996; Clack, 1998*a*; Holmes, 2000) and for their curious mixture of features otherwise regarded as unique to mutually exclusive groups, such as baphetids, embolomeres and temnospondyls (Clack, 2001; Ruta *et al.*, 2001).

(2) Despite the large number of 'absence' features seemingly shared by crown-lissamphibians and certain lepospondyls (notably, lysorophids), a sister group relationship between lissamphibians and dissorophoid temnospondyls best accounts for the distribution of putative synapomorphies in these two groups. Several alternative hypotheses of lissamphibian ancestry imply a worse fit of the total data. However, no specific dissorophoid can be identified as the nearest relative of crown-lissamphibians. Rather, these are paired with a heterogeneous clade including amphibamids, micromelerpetontids and branchiosaurids. Such an arrangement probably results from the fact that different lineages of dissorophoids approached the condition of basal lissamphibians independently (Milner, 1993). The pattern of sister group relationships in the crownward part of the temnospondyl branch re-emphasizes

the importance of dissorophoids in the debate about lissamphibian origin. The evolutionary implications of these results have yet to be explored in depth. Initially recognized patterns include the morphological conservatism of stem-lissamphibians relative to the diversity of stem-amniotes. Comparisons between dissorophoids and various living and extinct caudates show that the latter appear as generalized in their postcranial and cranial features as their supposed ancestors from among derived temnospondyls (Bolt, 1969, 1977, 1979, 1991; Milner, 1988, 1990, 1993, 2000; Trueb & Cloutier, 1991; Schoch, 1992, 1995, 1998; Carroll, 2001). Most importantly, we have tried to show that comprehensive treatments of the available evidence from the fossil record, rather than the use of just some key characters, can overturn hypotheses of relationships based on clusters of 'absence' features. Alternative patterns of relationships, based on a large proportion of such features (e.g. Laurin & Reisz, 1997, 1999; Laurin, 1998*a–c*), appear to be less informative with regards to the ancestry of some or all of the lissamphibian orders. As explained by Carroll (2001, p. 1207), Laurin & Reisz's (1997, 1999) and Laurin's (1998*a–c*) hypothesized sister group relationship between lysorophids and crown-lissamphibians relies upon some characters that lysorophids share '… with each of the three groups [of lissamphibians]: greatly elongate body with much reduced limbs in common with the earliest known caecilian, a fenestrate skull, vaguely comparable with those of frogs and salamanders, and loss of many similar skull bones, but the total configuration is that of a chimaera that has no unique derived characters in common with any of the individual orders'.

(3) The branching sequence of stem-group amniotes reveals a coherent series of internested character-state changes leading up to the condition of basal crown-amniotes. In particular, changes in body proportions account for a progressive tendency towards the acquisition of terrestrial habits (e.g. gephyrostegids; some seymouriamorphs; diadectomorphs). The interrelationships of primitive amniotes are largely in agreement with the conventional view that 'anthracosaurs' (i.e. embolomeres and gephyrostegids), seymouriamorphs and diadectomorphs are successively more closely related to crown-amniotes. However, the analysis also shows *Westlothiana* and lepospondyls to be amniote relatives, although support for lepospondyl monophyly is weak.

(4) Cranial data are in conflict with total data with regard to the position of lepospondyls other than microsaurs. The placement of microsaurs on the amniote stem persists even when postcranial data are omitted. The relationships of remaining lepospondyls change significantly under these conditions, since they are relocated on the tetrapod stem, as sister group to colosteids. Such an arrangement is not significantly worse than the topology based on the whole character suite. Importantly, it emphasizes similarities between colosteids and various lepospondyls (notably adelospondyls). Additional characters may identify some of the lepospondyls as stem-tetrapod offshoots.

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XII. APPENDIX 1. LIST OF SPECIMENS EXAMINED (FOR INSTITUTIONAL ABBREVIATIONS SEE THE RELEVANT LITERATURE)

Acanthostega gunnari: several specimens as listed by Clack (1989, 1994*a*, *b*, 1998*b*), Coates & Clack (1990, 1991), Coates (1996) and Ahlberg & Clack (1998). *Acherontiscus caledoniae*: RSM 1967/13/1 (Carroll, 1969*b*). *Adelogyrinus simorhynchus*: NMS G 1895/63/7, 1889/101/17 (Andrews & Carroll, 1991). *Adelospondylus watsoni*: NMS G 1885/57/51 (Andrews & Carroll, 1991). *Balanerpeton woodi*: BMNH R. 10952-5, 12014-6; NMS G 1985/4/1-2, 6, 1987/7/32-33, 35-36, 1990/79/1, 3-4, 1991/47/2, 1992/14/2, 1992/48/1-2 (Milner & Sequeira, 1994). *Baphetes* cf. *B. kirkbyi*: BMNH R. 9663 (Milner & Lindsay, 1998). *Batrachiderpeton reticulatum*: HM G25-28/30 (Bossy & Milner, 1998). *Brachydectes newberryi*: BMNH R. 2544 (Wellstead, 1991). *Caerorhachis bairdi*: cast of MCZ 2271 (Holmes & Carroll, 1977). *Colosteus scutellatus*: BMNH R. 2547, 2548, 2660, 2664, 9949 (Hook, 1983). *Crassigyrinus scoticus*: RSM 1859.33.104, BMNH R. 10000 (Clack, 1998*c*). *Dendrerpeton acadianum*: BMNH R. 436, 439, 4158, 4163-4165, 4167, 4553, 4555 (Milner, 1980). *Discosauriscus austriacus*: many of the specimens in the collection of the Zoological Institute, Faculty of Natural Sciences, Comenius University, Bratislava (Klembara, 1997; Klembara & Bartík, 2000). *Dolichopareias disjectus*: NMS G 1950/56/7, 1881/43/37 (Andrews & Carroll, 1991). *Greererpeton burkemorani*: CMNH 10931, 10939, 11034, 11036, 11068-70, 11072, 11073, 11079, 11082, 11090, 11092, 11093, 11095, 11113, 11129-33, 11219, 11220, 11231-4, 11238, 11240, 11241, 11319, 11320, 11073 (Smithson, 1982; Godfrey, 1989). *Hyloplesion longicostatum*: RSM 1899.32.3 plus several galvanotypes in the collections of the Grant Museum of Zoology, University College London, UK (Carroll & Gaskill, 1978). *Megalocephalus pachycephalus*: BMNH R. 2363, 2366 (Beaumont, 1977). *Microbrachis pelikani*: RSM 1898.105.26 plus several galvanotypes in the collections of the Grant Museum of Zoology, University College London, UK and latex peels in the collections of the Department of Ecology, Comenius University, Bratislava, Slovakian Republic (Carroll & Gaskill, 1978). *Oestocephalus amphiuminum*: BMNH 2657a, 2673 (Carroll, 1998). *Pantylus cordatus*: plaster cast of skull of MCZ 2040 in the collections of the Grant Museum of Zoology, University College London, UK (Carroll & Gaskill, 1978). *Phlegethontia linearis*, *Ptyonius marshii*, *Sauropleura pectinata*, *Scincosaurus crassus*, *Urocordylus wandesfordii*: several galvanotypes in the collections of the Grant Museum of Zoology, University College London, UK. *Proterogyrinus scheelei*: CMNH 10938, 10950, 11035, 11067, 11091, 11111, 11112 (Holmes, 1984). *Tulerpeton curtum*: PIN 2921/7a-f, 16-30, 63, 135, 448, 865, 866 (Lebedev & Coates, 1995). *Westlothiana lizziae*: NMS G 1990/72/1; 1991/47/1 (Smithson *et al.*, 1994).

XIII. APPENDIX 2. CHARACTER LIST

(1) Cranial skeleton

(*a*) *Skull table*

Premaxilla

1. *PREMAX* 1. *Absence* (0) *or presence* (1) *of alary process.* This and the following two characters describe conditions of the backward-pointing, triangular to digitiform processes of the posterodorsal margins of the premaxillae. These processes are found in many derived temnospondyls (e.g. some trimerorhachoids, eryopoids; dissorophoids) as well as in several living and fossil lissamphibians (Milner, 1990; Milner & Sequeira, 1994, 1998; Holmes *et al.*, 1998). They either overlap the nasals (the latter often show impressions for the alary processes), as in several temnospondyls and lissamphibians, or form a butt joint with these, as in albanerpetontids (Gardner, 2001). The alary processes are here considered to be distinct from the posterodorsal nasal rami of the premaxillae, which appear remarkably well developed in several taxa, including lysorophids (Bolt & Wassersug, 1975) and captorhinids (Modesto, 1998), and conjoined along the dorsal skull midline. Ontogenetic shifts of the nasal rami in a mesial direction (and resulting obliteration of the interpremaxillary space) has been documented in *Discosauriscus austriacus* (Klembara, 1997).

2. *PREMAX* 2. *Alary process shorter than wide* (0) *or as long as/longer than wide* (1). See character 1 above. In some temnospondyls (e.g. *Doleserpeton*, *Micromelerpeton*) and primitive lissamphibians (e.g. *Karaurus*, *Valdotriton*), the alary processes are shaped like equilateral or isosceles triangles (Bolt, 1969; Ivakhnenko, 1978; Boy, 1995; Evans & Milner, 1996), whereas in others (e.g. *Dendrerpeton*), the processes are less well developed and extend backward only for a short distance (Holmes *et al.*, 1998).

3. *PREMAX* 3. *Alary process less than* (0) *or at least one-third as wide as premaxillae* (1). See character 1 above. The alary processes can be rather small relative to the width of the premaxillae (e.g. *Eryops*; Sawin, 1941), or broad and only slightly less wide than the premaxillae (e.g. *Apateon*; Schoch, 1992).

4. *PREMAX* 4. *Premaxillae without* (0) *or with* (1) *flat, expanded anteromedial dorsal surface and marginal elongation.* This is one of the characters used by Milner & Sequeira (1994, 1998) to characterize edopoids (see also Godfrey & Holmes, 1995). In edopoids, the anteromedial portion of the premaxillae is a broad, flat sheet of bone, and the bones show an elongate lateral margin bordering the snout.

5. *PREMAX* 7. *Premaxillae more* (0) *or less than* (1) *two-thirds as wide as skull.* This is a modified version of one of Gauthier *et al.*'s (1988*b*) characters, found ubiquitously among 'reptiliomorphs', and which characterizes also several lepospondyls and some primitive lissamphibians (e.g. *Eocaecilia*; Carroll, 2000). Narrow premaxillae, even in stem-amniotes showing broad and spade-shaped snouts (e.g. *Discosauriscus*; Klembara, 1997), contrast with the broad premaxillae of temnospondyls and several stem-tetrapods.

6. *PREMAX* 8. *Mouth subterminal so that anteriormost surface of premaxilla faces ventrally: absent* (0) *or present* (1). This character refers to the distinctly oblique anteroventral surface of the premaxillae in several microsaurs (e.g. *Batropetes*; *Cardiocephalus*; *Euryodus*; *Micraroter*; *Pantylus*; *Pelodosotis*; *Rhynchonkos*; Carroll & Gaskill, 1978; Carroll, 1991*a*), some diadectomorphs (e.g. *Limnoscelis*; Williston, 1911; Romer, 1946; Heaton, 1980) and captorhinomorphs (e.g. *Captorhinus*; Fox & Bowman, 1966; Heaton, 1979). It confers a pointed aspect to the tip of the snout, as described by Laurin (1998*b*), and may be related to burrowing habits, at least in some taxa.

7. *PREMAX* 9. *Absence* (0) *or presence* (1) *of shelf-like premaxilla-maxilla contact mesial to tooth row on palate.* In *Ichthyostega* (Jarvik, 1980, 1996), *Crassigyrinus* (Clack, 1996, 1998*c*) and *Greererpeton* (Smithson, 1982), the ventral surfaces of premaxilla and maxilla form a mesially projecting surface and the two bones contact each other in a mesial position relative to the marginal dentition. The distribution of this character conforms to that of recent cladistic analyses by Clack (1998*c*, 2001).

Anterior tectal

8. *TEC* 1. *Presence* (0) *or absence* (1) *of anterior tectal.* As pointed out by Clack (1998*c*), the distinction between the anterior tectal and the septomaxilla is disputed. When the two elements are scored as equivalent, following Clack's (1998*b*) example, the results of a PAUP* analysis are identical to those of the original run. The scoring of both elements conforms to Clack's (1998*c*, 2001) analyses, with *Acanthostega* and *Ichthyostega* scored as possessing an anterior tectal, but lacking a septomaxilla.

Lateral rostral

9. *LAT ROS* 1. *Presence* (0) *or absence* (1) *of lateral rostral.* As in the case of the anterior tectal (see character 8 above), we follow Clack (1998*c*, 2001) in coding for the presence of a lateral rostral in *Ichthyostega* [see also Jarvik (1980, 1996) and Carroll (1995)].

Septomaxilla

10. *SPTMAX* 1. *Absence* (0) *or presence* (1) *of septomaxilla.* As explained under character 8 above, the septomaxilla and anterior tectal are here treated as separate elements (Clack, 1998*c*, 2001), with *Acanthostega* and *Ichthyostega* scored as lacking a septomaxilla.

11. *SPTMAX* 2. *Septomaxilla not a detached ossification inside nostril* (0) *or a detached ossification* (1). The occurrence of a detached septomaxilla inside the nostril (i.e. this element is not part of the dermal skull roof) characterizes several derived temnospondyls and certain stem-amniotes (e.g. *Discosauriscus*, *Limnoscelis*, *Seymouria*) (White, 1939; Romer, 1946; Milner & Sequeira, 1994; Laurin, 1995, 1996*b*; Klembara, 1997)

Nasal

12. *NAS* 1. *Absence* (0) *or presence* (1) *of paired dorsal nasals.* At a post-panderichthyid level of organization, paired nasals are widespread in tetrapods (Panchen & Smithson, 1988; Carroll, 1995; Coates, 1996; Ahlberg, 1998; Clack, 1998*c*, 2001), except in those taxa (e.g. derived diplocaulid nectrideans) in which only one element is found in the position usually occupied by paired nasals in most other tetrapods (A. C. Milner, 1980; Bossy & Milner, 1998).

13. *NAS* 2. *Nasals more* (0) *or less than* (1) *one-third as long as frontals.* This is one of several characters describing patterns of elongation in the preorbital region of the skull roof. Its distribution in the taxa surveyed in this study is rather irregular. In adelospondyls, aïstopods, colosteids, some microsaurs and certain urocordylids, the nasals are greatly reduced in size relative to the frontals. This is especially evident in adelospondyls, aïstopods and colosteids.

14. *NAS* 5. *Absence* (0) *or presence* (1) *of condition: nasals broad plates delimiting most of the posterodorsal and mesial margins of nostrils and with lateral margins diverging abruptly anteriorly.* As defined here, this character describes the snout morphology in several dissorophoids and *Karaurus* (Boy, 1972, 1974, 1978, 1985, 1986, 1987, 1995; Bolt, 1969, 1977, 1979, 1991; Ivakhnenko, 1978; Schoch, 1992), in which the nasals are not simply expanded and flat sheets of bones, but contribute to most of the posterodorsal and mesial margins of the nostrils. In addition, the anterior part of their lateral margins diverges markedly anterolaterally, so that the nasals increase abruptly in width anteriorly.

15. *NAS* 6. *Parietal/nasal length ratio less than* (0) *or greater than* 1.45 (1). This character refers to a pattern of skull roof bone proportions that matches in part the distribution of character 13 above, although its derived condition occurs sporadically in some lepospondyl groups and temnospondyls. It also represents one of the distinguishing features of adelospondyls and colosteids (Smithson, 1982; Hook, 1983; Andrews & Carroll, 1991).

Prefrontal

16. *PREFRO* 2. *Prefrontal less than* (0) *or more than* (1) *three times longer than wide.* Together with the previous character, the elongation of the prefrontals characterizes adelospondyls and colosteids (Smithson, 1982; Hook, 1983; Andrews & Carroll, 1991; Milner, 1993), but is found also in some representatives of other groups (e.g. aïstopods, baphetids; embolomeres; temnospondyls; lysorophids; microsaurs; albanerpetontids).

17. *PREFRO* 3. *Absence* (0) *or presence* (1) *of condition: antorbital portion of prefrontal expanded to form a near-equilateral triangular lamina.* The presence of a short and broadly triangular preorbital portion of the prefrontal, such as is observed in dissorophoids and *Karaurus* (Boy, 1972, 1974, 1978, 1985, 1986, 1987, 1995; Bolt, 1969, 1977, 1979, 1991; Ivakhnenko, 1978; Schoch, 1992) is not related simply to paedomorphic shortening of the preorbital skull region. Several short-snouted taxa (e.g. *Discosauriscus*; Klembara, 1997) do not show the derived condition of this character.

18. *PREFRO* 6. *Prefrontal not sutured with premaxilla* (0) *or sutured* (1). *Acherontiscus*, colosteids and albanerpetontids show the derived condition of this feature (Carroll, 1969*b*; Smithson, 1982; Hook, 1983). Although the snout of *Acherontiscus* is poorly preserved, a prefrontal–premaxilla contact is deduced to have existed, based on the position and morphology of the anteriormost part of the prefrontal, which sends an anteroventral flange lying immediately in front of the lacrimal.

19. *PREFRO* 7. *Prefrontal without* (0) *or with* (1) *stout, lateral outgrowth.* The outgrowth in question is a stout process marking the posteromesial boundary of the antorbital vacuity in baphetids other than *Spathicephalus* (Beaumont, 1977; Beaumont & Smithson, 1998), and is introduced here as a distinct character to distinguish between several kinds of irregular orbit outlines (i.e. neither elliptical nor circular) among Palaeozoic tetrapods (see also Clack, 1987*b*, 1998*a*, *c*, 2001).

20. *PREFRO* 8. *Absence* (0) *or presence* (1) *of condition: prefrontal entering nostril margin.* The derived state of this character occurs, among others, in some primitive lissamphibians, certain derived temnospondyls, *Greererpeton*, and some microsaurs, lysorophids, nectrideans and aïstopods (Smithson, 1982; Carroll, 1995; Bossy & Milner, 1998; Laurin, 1998*b*). We code for this character separately instead of as a state in a multistate treatment of the relationships between nostril and surrounding bones, as Carroll (1995) did. This is to prevent the introduction of constraints in the derivation of different bone arrangements in the snout from one another.

21. *PREFRO* 9. *Prefrontal not sutured with maxilla* (0) *or sutured* (1). Some nectrideans and adelospondyls, as well as colosteids and certain primitive lissamphibians, exhibit a lateral contact between prefrontal and maxilla (Smithson, 1982; Carroll, 1995; Bossy & Milner, 1998). As in the case of the previous character, the mutual relationships between these bones are treated separately from the conditions of other elements of the snout. This is also one of the conditions described by Clack (1998*c*, 2001) regarding the lacrimal contribution (or lack thereof) to the margin of the nostril.

22. *PREFRO* 10. *Prefrontal contributes to more* (0) *or less than* (1) *half of anteromesial orbit margin.* The derived condition of this character is observed in various derived temnospondyls and primitive lissamphibians (Boy, 1972, 1974, 1978, 1985, 1986, 1987, 1995; Bolt, 1969, 1977, 1979, 1991; Ivakhnenko, 1978; Schoch, 1992).

Lacrimal

23. *LAC* 1. *Presence* (0) *or absence* (1) *of lacrimal. Phlegethontia* (Anderson, in press) and *Valdotriton* (Evans & Milner, 1996) lack a lacrimal as a separately ossified element.

24. *LAC* 2. *Lacrimal not allowing* (0) *or allowing* (1) *contact between prefrontal and jugal.* The prefrontal-jugal contact excludes the lacrimal from the orbit margin, as in *Acanthostega* (Clack, 1994*a*), *Archeria* (Holmes, 1989), *Chenoprosopus* (Hook, 1993; Milner & Sequeira, 1994, 1998), *Cochleosaurus* (Rieppel, 1980; Milner & Sequeira, 1994, 1998), *Crassigyrinus* (Panchen, 1985; Clack, 1998*c*), *Diplocaulus* (A. C. Milner, 1980), *Edops*

(Romer & Witter, 1942), *Eoherpeton* (Panchen, 1975; Smithson, 1985), *Eryops* (Sawin, 1941), *Ichthyostega* (Jarvik, 1980, 1996), *Micromelerpeton* (Boy, 1995), *Pholiderpeton attheyi* and *P. scutigeum* (Panchen, 1972; Clack, 1987*a*), *Ventastega* (Ahlberg *et al.*, 1994). However, in *Isodectes* (Sequeira, 1998) the lacrimal separates the prefrontal from the jugal but it fails to contact the orbit margin due to an intervening exposure of the palatine.

25. *LAC* 4. *Lacrimal without* (0) *or with* (1) *dorsomesial digitiform process.* A dorsomesial digitiform process of the lacrimal is observed in *Brachydectes* (Wellstead, 1991), such tuditanomorphs as *Cardiocephalus*, *Euryodus*, some specimens of *Micraroter* and *Tuditanus* (Carroll & Gaskill, 1978), and in urocordylid nectrideans (A. C. Milner, 1980; Bossy & Milner, 1998).

26. *LAC* 5. *Lacrimal without* (0) *or with* (1) *V-shaped emargination along its posterior margin.* Together with character 19, a deep V-shaped notch of the lacrimal characterizes the anterior portion of the antorbital vacuity of various baphetids (Beaumont, 1977; Beaumont & Smithson, 1998).

27. *LAC* 6. *Absence* (0) *or presence* (1) *of condition: portion of lacrimal lying anteroventral to orbit abbreviated* (1). As in the case of character 17, an abbreviated preorbital region of the lacrimal is found in several dissorophoids. However, the derived state of this character is also found in urocordylid and diplocaulid nectrideans, *Batropetes*, *Oestocephalus* and adelospondyls. Not all short-snouted tetrapods exhibit such a state, as demonstrated by *Discosauriscus* (Klembara, 1997).

Maxilla

28. *MAX* 3. *Maxilla extending behind level of posterior margin of orbit* (0) *or terminates anterior to it* (1). A rearward extension of the maxilla is a widespread feature of several early tetrapods, and contrasts with the situation of some diplocaulid nectrideans, several microsaurs, embolomeres, primitive crown-amniotes and such stem-amniote groups as gephyrostegids, seymouriamorphs and diadectomorphs (Carroll & Gaskill, 1978; Gauthier *et al.*, 1988*b*; Carroll, 1991*b*; Klembara, 1997; Lee & Spencer, 1997; Bossy & Milner, 1998).

29. *MAX* 5. *Maxilla not entering* (0) *or entering* (1) *orbit margin.* The derived condition of this character is widespread among early tetrapods, and occurs in some adelospondyls (Andrews & Carroll, 1991), some dissorophoids and primitive lissamphibians (Boy, 1972, 1974, 1978, 1985, 1986, 1987, 1995; Bolt, 1969, 1977, 1979, 1991; Ivakhnenko, 1978; Schoch, 1992; Evans & Milner, 1996; Carroll, 2000), aïstopods (Wellstead, 1982; Carroll, 1998; Anderson, in press), some urocordylids and diplocaulids (Bossy & Milner, 1998). It is not directly related to small size of the skull and presence of large orbits, as shown by some amphibamids and seymouriamorphs (e.g. Bolt, 1969; Laurin, 1996*a*, *c*; Klembara, 1997).

30. *MAX* 6. *Maxillary arcade closed* (0) *or open* (1) *posteriorly.* A gap between the maxilla and the jugal occurs in primitive caudates (Ivakhnenko, 1978; Evans & Milner, 1996) and branchiosaurids (Boy, 1986). The maxillary arcade is closed in albanerpetontids, as demonstrated by Gardner (1999, 2001). The skull emargination of lysorophids (Wellstead, 1991) is of a different pattern, as explained in the text (see also Carroll, 2001).

31. *MAX* 7. *Dorsal maxillary margin not forming* (0) *or forming* (1) *distinct dorsal 'step'.* In pantylids (Carroll & Gaskill, 1978; Berman *et al.*, 1988), the pronounced facial process is separated from the posterior part of the dorsal margin of the maxilla by a sharp dorsal bend.

32. *Max* 8. *Absence* (0) *or presence* (1) *of condition: maxillary facial process shaped like a rectangular flange.* A (sub)-rectangular facial process of the maxilla occurs in primitive lissamphibians and several dissorophoids (Boy, 1972, 1974, 1978, 1985, 1986, 1987, 1995; Bolt, 1969, 1977, 1979, 1991; Ivakhnenko, 1978; Rage & Rocek, 1986, 1989; Schoch, 1992; Evans & Milner, 1996; Carroll, 2000; Rocek & Rage, 2000*b*).

33. *Max* 9. *Posterior end of maxilla not lying* (0) *or lying level with* (1) *posterior end of vomers.* The derived condition of this character is one of the synapomorphies uniting scincosaurids and diplocaulids (A. C. Milner, 1980; Bossy & Milner, 1998).

Frontal

34. *FRO* 1. *Frontal unpaired* (0) *or paired* (1). Paired frontals occur commonly among early tetrapods including panderichthyids (Carroll, 1995; Laurin, 1998*b*), except in derived diplocaulids, albanerpetontids, *Phlegethontia* and *Sauropleura* (A. C. Milner, 1980; Bossy & Milner, 1998; Gardner, 1999, 2001; Anderson, in press).

35. *FRO* 2. *Frontal shorter than* (0), *longer than* (1), *or subequal to* (2) *parietals.* This is one of several characters describing the relative proportions of the bones in the skull roof and the pattern of elongation of its inter-, pre- and postorbital regions (see also Milner, 1993).

36. *FRO* 4. *Frontal excluded from* (0) *or contributing to* (1) *margin of orbit.* The coding for this character follows mainly Laurin (1998*b*). The derived condition is acquired in parallel in several dissorophoids and primitive lissamphibians, as well as in gephyrostegids, crown-amniotes, derived diplocaulid nectrideans and some microsaurs.

37. *FRO* 5. *Frontals and parietals not co-ossified as fronto-parietal* (0) *or co-ossified* (1). The derived state characterizes salientians only (review in Milner, 1988).

38. *FRO* 6. *Absence* (0) *or presence* (1) *of condition: anterior margin of frontals deeply wedged between posterolateral margins of nasals.* In its derived state, this character occurs in adelospondyls, colosteids, *Gephyrostegus*, urocordylid nectrideans and *Whatcheeria* (Carroll, 1970; A. C. Milner, 1980; Smithson, 1982; Hook, 1983; Andrews & Carroll, 1991; Lombard & Bolt, 1995; Bossy & Milner, 1998). In these taxa, the posteror margins of the nasals are more or less deeply excavated to accommodate the anteriormost part of the frontals.

Parietal

39. *PAR* 1. *Absence* (0) *or presence* (1) *of parietal/tabular suture.* Panchen & Smithson (1987, 1988), Gauthier *et al.* (1988*b*) and most subsequent authors have placed emphasis on the mutual spatial relationships of the bones in the posterior and posterolateral parts of the skull table, and have considered them to be indicators of a deep dichotomy among primitive tetrapods. A parietal-tabular suture appears on the tetrapod stem and is maintained in crown-amniotes in Laurin's (1998*b*) analysis. Conversely, our study shows that the contact between these two bones characterizes a large portion of the 'reptiliomorph' branch of the tetrapod tree (see discussion above).

40. *PAR* 2. *Absence* (0) *or presence* (1) *of parietal/postorbital suture.* The derived state of this character appears as a transitional stem-tetrapod feature, and is also acquired in a large assemblage of stem-amniotes (with reversals among most tuditanomorphs, seymouriamorphs and *Scincosaurus* (Carroll & Gaskill, 1978; A. C. Milner, 1980; Laurin, 1995, 1996*b*; Klembara, 1997; Bossy & Milner, 1998).

41. *PAR* 4. *Anterior margin of parietal lying in front of* (0), *level with* (1), *or behind* (2) *orbit midlength.* Together with character 35, this character relates the proportions of various skull elements to each other. Its distribution is less random than that of character 35. The derived state 1 is found in some Devonian tetrapods, *Whatcheeria* and *Kotlassia*. The derived state 2 is found in some stem-tetrapods (*Tulerpeton*, colosteids, *Crassigyrinus* and baphetids) as well as in almost all crown-tetrapods.

42. *PAR* 5. *Anteriormost third of parietals not wider than frontals* (0) *or at least marginally wider* (1). With the exception of *Eusthenopteron*, *Panderichthys*, *Platyrhinops*, *Eocaecilia* and *Triadobatrachus*, all other taxa show the derived condition of this feature.

43. *PAR* 6. *Parietals more than two and a half times as long as wide* (0) *or less* (1). *Eusthenopteron*, *Panderichthys*, colosteids, trimerorhachoids, lysorophids, adelospondyls, aïstopods and urocordylids show the plesiomorphic state for this character (see also characters 35 and 41 above).

44. *PAR* 7. *Absence* (0) *or presence* (1) *of parietal/squamosal suture on skull roof.* Crown-lissamphibians, crown-amniotes, *Batropetes*, microbrachomorphs and diplocaulids display the derived condition of this character. This is one of several characters describing the contact between the skull table and the cheek (Carroll, 1995; Coates, 1996; Clack, 1998*c*, 2001; Laurin, 1998*b*).

45. *PAR* 8. *Parietal-frontal suture not strongly interdigitating* (0) *or strongly interdigitating* (1). The derived state of this character is not a simple function of the size or degree of ossification of the skull roof bones, and its distribution is rather discontinuous (e.g. most lepospondyls; some 'reptiliomorphs', some temnospondyls, colosteids).

46. *PAR* 9. *Parietal-postparietal suture not strongly interdigitating* (0) *or strongly interdigitating* (1). The occurrences of the derived condition of this character match closely those of the previous character.

Postparietal

47. *POSPAR* 1. *Presence* (0) *or absence* (1) *of postparietals.* Salientians, caudates, *Batropetes*, *Scincosaurus* and *Phlegethontia* all lack ossified postparietals (A. C. Milner, 1980; Milner, 1988, 2000; Carroll, 1991*a*; Bossy & Milner, 1998; Rocek & Rage, 2000*b*; Anderson, in press).

48. *POSPAR* 2. *Postparietals paired* (0) *or unpaired* (1). The derived condition is found only in *Ichthyostega* (Jarvik, 1980, 1996), diadectomorphs (Romer, 1946; Berman *et al.*, 1998; Berman, 2000) and *Odonterpeton* (*fide* Carroll & Gaskill, 1978).

49. *POSPAR* 3. *Postparietal less than* (0) *or more than* (1) *four times wider than long.* In its derived state, this character is observed in several post-embolomere 'reptiliomorphs', in *Microbrachis* and *Hyloplesion* and in several of the temnospondyls that lie crownward of *Balanerpeton* [see Milner (1990) and Yates & Warren (2000) for analysis of this character in temnospondyls].

50. *POSPAR* 4. *Postparietals without* (0) *or with* (1) *median lappets.* The median posterior lappets of the postparietals occur in *Crassigyrinus*, *Whatcheeria*, embolomeres and *Ptyonius*. The distribution of this character follows Clack (1998*c*), except for the coding of *Dendrerpeton* (see Holmes *et al.*, 1998).

51. *POSPAR* 5. *Absence* (0) *or presence* (1) *of postparietal/exoccipital suture.* The relationships between the occiput and the skull table have been dealt with extensively in the literature on early tetrapods (e.g. Smithson, 1985; Panchen & Smithson, 1987, 1988) Carroll (1995) recognized no fewer than 12 states describing the nature of the skull table-occiput contact. Berman's (2000) analysis of occipital characters is followed in part here, since it simplifies to a greater degree the known spatial relationships of the otic capsules and supraoccipital (where present). The derived condition of character 51 is found among most lepospondyls, temnospondyls, a few 'reptiliomorphs' and colosteids.

52. *POSPAR* 6. *Postparietals not entirely on occipital surface* (0) *or entirely on this surface* (1). The derived state of this character is shared by diadectomorphs and crown-amniotes (Berman, 2000).

53. *POSPAR* 7. *Postparietals without* (0) *or with* (1) *posteroventrally sloping occipital exposure.* A gently sloping surface at the back of the postparietals characterizes some tuditanomorphs and lysorophids (Carroll & Gaskill, 1978; Wellstead, 1991).

54. *POSPAR* 8. *Postparietals without* (0) *or with* (1) *sinuous posterior ridge.* A sinuous ridge runs across the posterior part of the postparietals in ostodolepids (Carroll & Gaskill, 1978).

55. *POSPAR* 9. *Postparietals without* (0) *or with* (1) *broad, concave posterior emargination.* This character is taken from A. C. Milner's (1980) analysis of nectridean interrelationships and is shared by some diplocaulids.

56. *POSPAR* 10. *Nasals not smaller than postparietals* (0) *or smaller* (1). Nasals which are comparatively much smaller than the postparietals occur in colosteids, aïstopods, nectrideans (except urocordylids) and adelospondyls (A. C. Milner, 1980; Wellstead, 1982; Andrews & Carroll, 1991; Bossy & Milner, 1998; Carroll, 1998; Anderson, in press).

Postfrontal

57. *POSFRO* 1. *Presence* (0) *or absence* (1) *of postfrontal.* Albanerpetontids (Gardner, 2001), salientians (Rocek & Rage, 2000*b*), caudates (Evans & Milner, 1996; Milner, 2000) and lysorophids all lack ossified postfrontals.

58. *POSFRO* 3. *Postfrontal not contacting tabular* (0) *or contacting it* (1). The derived condition of this character describes the dermal skull roof configuration of tuditanomorph microsaurs (Carroll & Gaskill, 1978), and is acquired in parallel by *Scincosaurus* (A. C. Milner, 1980; Bossy & Milner, 1998).

59. *POSFRO* 4. *Absence* (0) *or presence* (1) *of condition: posterior margin of postfrontal lying flush with posterior jugal margin.* The posterior margins of the postfrontal and jugal lie approximately at the same transverse level in *Leptorophus* (Boy, 1972), *Paleothyris* and *Petrolacosaurus* (Clark & Carroll, 1973; Reisz, 1977, 1981), *Diplocaulus* (A. C. Milner, 1980; Bossy & Milner, 1998), *Phlegethontia* (Anderson, in press), as well as in ostodolepid, gymnarthrid and rhynchonkid microsaurs (Gregory *et al.*, 1956; Carroll & Gaskill, 1978).

Intertemporal

60. *INTEMP* 1. *Intertemporal present* (0) *or absent* (1) *as a separate ossification.* The distribution of the intertemporal is problematic, as recognized by Clack (1998*c*). Intertemporal presence has been considered to be primitive for tetrapods, because it has been homologized with the intertemporal of 'osteolepiforms'. *Panderichthys* (Vorobyeva & Schultze, 1991) and *Greererpeton* (Smithson, 1982) have been coded as polymorphic for this character. Under ACCTRAN and, partially, under DELTRAN optimizations, intertemporal absence appears as a transitional feature encompassing a series of crownward stem-tetrapods (*Acanthostega*, *Ichthyostega* and *Colosteus*; Clack, 1994*a*; Jarvik, 1980, 1996; Hook, 1983). An intertemporal is present in the apical part of the tetrapod stem-group, as well as the basal portions of the lissamphibian and amniote stem-groups. However, we note that *Megalocephalus* lacks an intertemporal (Beaumont, 1977). The bone is lost again in the clade including crown-lissamphibians and temnospondyls more derived than *Dendrerpeton* (Milner, 1988, 1990). It disappears also in *Solenodonsaurus* (Carroll, 1970; Laurin & Reisz, 1999), diadectomorphs (Romer, 1946; Berman *et al.*, 1998), crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981), *Westlothiana* (Smithson *et al.*, 1994) and lepospondyls (Carroll & Gaskill, 1978; A. C. Milner, 1980; Andrews & Carroll, 1991; Wellstead, 1991; Bossy & Milner, 1998). Carroll & Gaskill (1978) discussed the possibility that the intertemporal may have been incorporated in surrounding skull roof bones in the ancestry of the two major groups of microsaurs. Putative differing fusion patterns provide the basis for the distinction between tuditanomorphs (intertemporal-postfrontal fusion) and microbrachomorphs (intertemporal-parietal fusion). We question the homology of the intertemporals of limbed tetrapods, which seem to be anamestic, and the canal-bearing intertemporals which are widespread among basal osteichthyans. Discrete coding for these alternative conditions is likely to provide a more informative signal.

61. *INTEMP* 2. *Intertemporal not interdigitating with cheek* (0) *or interdigitating* (1). The plesiomorphic condition, as found in *Crassigyrinus* (Clack, 1998*c*, 2001; Paton *et al.*, 1999), is acquired in parallel in *Trimerorhachis* (Case, 1935), some embolomeres (Holmes, 1984, 1989; Smithson, 1985; Clack, 1987*a*), gephyrostegids (Carroll, 1970; Boy & Bandel, 1973) and at least one seymouriamorph (Klembara, 1997).

62. *INTEMP* 3. *Intertemporal not contacting squamosal* (0) *or contacting it* (1). *Whatcheeria* (Lombard & Bolt, 1995) and seymouriamorphs (White, 1939; Bystrow, 1944;

Laurin, 1996*b*; Klembara, 1997) show the derived condition of an intertemporal-squamosal suture.

Supratemporal

63. *SUTEMP* 1. *Presence* (0) *or absence* (1) *of supratemporal.* A separately ossified supratemporal is missing in crown-lissamphibians (Carroll, 2000; Milner, 2000; Rocek & Rage, 2000*a*), as well as in microsaurs (Carroll & Gaskill, 1978), lysorophids (Wellstead, 1991), adelospondyls (Andrews & Carroll, 1991), scincosaurids and diplocaulids (A. C. Milner, 1980; Bossy & Milner, 1998), and *Phlegethontia* (Anderson, in press).

64. *SUTEMP* 2. *Absence* (0) *or presence* (1) *of condition: supratemoral forming anterior edge of temporal notch.* This character is considered by Clack (1998*a*, 2001) as a potential synapomorphy of *Eucritta* and baphetids [see also Beaumont (1977), Beaumont & Smithson (1998) and Milner & Lindsay (1998)].

65. *SUTEMP* 3. *Absence* (0) *or presence* (1) *of condition: supratemoral narrow and strap-like, at least three times as long as wide.* The derived configuration of the supratemporal is observed in some aïstopods (Wellstead, 1982; Carroll, 1998) and urocordylids (A. C. Milner, 1980; Bossy & Milner, 1998).

66. *SUTEMP* 4. *Supratemoral contact with squamosal smooth* (0) *or interdigitating* (1). This is one of several characters describing the nature of the contact between the skull table and the cheek (Clack, 1998*c*, 2001; Paton *et al.*, 1999). The derived state appears in the tetrapod stem-group (Beaumont, 1977; Smithson, 1982; Hook, 1983; Jarvik, 1980, 1996; Clack, 1994*a*; Lombard & Bolt, 1995), although *Crassigyrinus* shows a reversal to the primitive state, and is maintained in most temnospondyls; exceptions are *Isodectes* (Sequeira, 1998), *Broiliellus* (Carroll, 1964), and some amphibamids (Watson, 1940; Bolt, 1969, 1991). On the amniote branch, the derived state appears in *Anthracosaurus* (Panchen, 1977; Clack, 1987*b*), *Solenodonsaurus* (Carroll, 1970; Laurin & Reisz, 1999) and some seymouriamorphs (White, 1939; Bystrow, 1944; Laurin, 1996*a*).

Tabular

67. *TAB* 1. *Tabular present* (0) *or absent* (1) *as separate ossification.* A separately ossified tabular is absent in crown-lissamphibians (except perhaps *Eocaecilia*; Evans & Milner, 1996; Carroll, 2000; Milner, 2000; Rocek & Rage, 2000*b*), *Captorhinus* (Fox & Bowman, 1966), *Odonterpeton* (Carroll & Gaskill, 1978) and adelospondyls (Andrews & Carroll, 1991). In the latter group, a 'squamosotabular' ossification is present in the position normally occupied by the squamosal and tabular in other tetrapods (see also character 86 below).

68. *TAB* 2. *Absence* (0) *or presence* (1) *of subdermal, blade-like postero-lateral horn of tabular.* As defined here [see also Smithson (1985), Clack (1987*a*, 1998*c*, 2001) and Paton *et al.* (1999)], a subdermal, blade-like posterolateral tabular horn characterizes *Acanthostega* (Clack, 1994*a*), *Crassigyrinus* (Clack, 1998*c*), *Whatcheeria* (Lombard & Bolt, 1995), *Caerorhachis* (Holmes & Carroll, 1977; Ruta *et al.*, 2001), embolomeres (Panchen, 1972, 1977; Holmes, 1984, 1989; Smithson, 1985; Clack, 1987*a*, 1998*c*, 2001) and gephyrostegids (Carroll, 1970; Boy & Bandel, 1973). See also Klembara (1997) for a discussion of this character.

69. *TAB* 3. *Absence* (0) *or presence* (1) *of rounded, subdermal, button-like posterior process of tabular.* This character is found in colosteids (Smithson, 1982), baphetids (Beaumont, 1977; Beaumont & Smithson, 1998), *Edops* (Romer & Witter, 1942) and, possibly, *Dendrerpeton* (Holmes *et al.*, 1998).

70. *TAB* 4. *Tabular contacts squamosal on dorsal surface of skull table* (0) *or not* (1). In its derived state, this character is found in stem-tetrapods more derived than colosteids (Beaumont, 1977; Lombard & Bolt, 1995; Clack, 1998*c*), *Eucritta* (Clack, 2001), various temnospondyls (except some trimerorhachoids, *Broiliellus*, *Ecolsonia* and *Doleserpeton*; Chase, 1965; Carroll, 1964; Bolt, 1969, 1991; Berman *et al.*, 1985; Sequeira, 1998), *Eocaecilia* (Carroll, 2001), embolomeres (Panchen, 1972, 1977; Holmes, 1984, 1989; Smithson, 1985; Clack, 1987*a*, 1998*c*, 2001), gephyrostegids (Carroll, 1970), seymouriamorphs (White, 1939; Bystrow, 1944; Laurin, 1996*b*; Klembara, 1997), diadectomorphs (Romer, 1946; Berman *et al.*, 1998), *Paleothyris* and *Petrolacosaurus* (Clark & Carroll, 1973; Reisz, 1977, 1981), and *Westlothiana* (Smithson *et al.*, 1994). It is present also in *Ptyonius* (A. C. Milner, 1980; Bossy & Milner, 1998).

71. *TAB* 5. *Tabular contact with squamosal smooth* (0) *or interdigitating* (1). This is one of the characters describing the nature of the contact between the cheek and the skull table (Clack, 1998*c*, 2001; Paton *et al.*, 1999). An interdigitating tabular-squamosal suture occurs in *Ichthyostega* (Jarvik, 1980, 1996), *Greererpeton* (Smithson, 1982), *Neldasaurus* (Chase, 1965), *Ecolsonia* (Berman *et al.*, 1985), *Pantylus* and ostodolepids (Carroll & Gaskill, 1978).

72. *TAB* 6. *Absence* (0) *or presence* (1) *of condition: tabular elongate posteriorly or posterolaterally in the form of massive horn.* This character is a shared derived feature of diplocaulid nectrideans (Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998).

73. *TAB* 7. *Parietal-parietal width smaller than* (0) *or greater than* (1) *distance between posterior margin of skull table and posterior margin of orbits measured along the skull midline.* The apomorphic condition of this character shows no simple distribution among crown-tetrapods. It is recorded in several dissorophoids and crown-lissamphibians (Bolt, 1969, 1991; Schoch, 1992; Daly, 1994; Milner, 2000; Rocek & Rage, 2000*a*), as well as seymouriamorphs (White, 1939; Bystrow, 1944; Laurin, 1996*b*; Klembara, 1997), diadectomorphs (Romer, 1946; Berman *et al.*, 1998), *Paleothyris* and *Petrolacosaurus* (Clark & Carroll, 1973; Reisz, 1977, 1981), *Westlothiana* (Smithson *et al.*, 1994), various tuditanomorphs, some microbrachomorphs (Carrol & Gaskill, 1978) and some diplocaulids (Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998).

74. *TAB* 8. *Tabular without* (0) *or with* (1) *posteroventrally sloping occipital exposure.* The posterior region of the tabulars of *Stegotretus* (Berman *et al.*, 1988), ostodolepids, rhynchonkids and gymnarthrids (Gregory *et al.*, 1956; Carroll & Gaskill, 1978) slopes obliquely posteroventrally and is distinctly separated from its anterior region.

Postorbital

75. *POSORB* 1. *Postorbital present* (0) *or absent* (1) *as a separate ossification.* Absence of separately ossified postorbitals is shared by crown-lisamphibians (Carroll, 2000; Milner, 2000; Rocek & Rage, 2000*b*), lysorophids (Wellstead, 1991), *Adelospondylus* (Andrews & Carroll, 1991) and the aïstopods *Oestocephalus* and *Phlegethontia* (Carroll, 1998; Anderson, in press).

76. *POSORB* 2. *Postorbital without* (0) *or with* (1) *ventrolateral digitiform process fitting into deep vertical jugal groove.* The presence of a distinct, ventrolateral digitiform process of the postorbital is a shared derived feature of urocordylid nectrideans (A. C. Milner, 1980; Bossy & Milner, 1998).

77. *POSORB* 3. *Postorbital contributing to* (0) *or excluded from* (1) *margin of orbit.* The postorbital is excluded from the orbit margin in *Colosteus* (Hook, 1983), *Acherontiscus* (Carroll, 1969*b*), *Adelogyrinus* and *Dolichopareias* (Andrews & Carroll, 1991) and the diplocaulids *Diplocaulus* and *Diploceraspis* (Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998).

78. *POSORB* 4. *Postorbital irregularly polygonal* (0) *or broadly crescentic and narrowing to a posterior point* (1). The derived state of this character is recorded in *Eucritta* (Clack, 1998*a*, 2001), most temnospondyls (*Chenoprosopus*, *Trimerorhachis* and *Phonerpeton* are exceptions; Hook, 1993; Case, 1935; Dilkes, 1990), several stem-amniotes (except the embolomere *Anthracosaurus*; Panchen, 1977), *Paleothyris* (Clark & Carroll, 1973) and *Westlothiana* (Smithson *et al.*, 1994).

79. *POSORB* 5. *Postorbital not contacting tabular* (0) *or contacting it* (1). A postorbital-tabular suture occurs in *Scincosaurus* (A. C. Milner, 1980; Bossy & Milner, 1998) and tuditanomorphs (except *Hapsidopareion*; Carroll & Gaskill, 1978).

80. *POSORB* 6. *Postorbital not wider than orbit* (0) *or wider* (1). Under ACCTRAN, the apomorphic condition of this character is acquired in parallel by *Acanthostega* (Clack, 1994*a*), colosteids (Smithson, 1982; Hook, 1983), *Edops* (Romer & Witter, 1942), *Trimerorhachis* (Case, 1935), *Pantylus* (Carroll & Gaskill, 1978), and a diverse assemblage consisting of adelospondyls (except *Adelogyrinus*; Andrews & Carroll, 1991), *Lethiscus* (Wellstead, 1982) and nectrideans (except *Keraterpeton* and *Diploceraspis*; Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998).

81. *POSORB* 7. *Absence* (0) *or presence* (1) *of condition: postorbital at least one-fourth the width of the skull table at the same transverse level.* The distribution of this character is almost identical to that of the previous character, except that all temnospondyls exhibit the plesiomorphic state which is also observed, among nectrideans, in *Scincosaurus* and *Diploceraspis*.

82. *POSORB* 8. *Anteriormost part of dorsal margin of postorbital with sigmoid profile absent* (0) *or present* (1). Characteristic 'kink' is observed in the anteromedial margin of the postorbital in most microsaurs (ostodolepids are a notable exception; Carroll & Gaskill, 1978).

Squamosal

83. *SQU* 1. *Anterior part of squamosal lying behind* (0) *or in front* (1) *of parietal midlength.* The derived condition is found in almost all tetrapods more derived than *Ichthyostega*. Exceptions are *Greererpeton* (Smithson, 1982), *Eucritta* (Clack, 2001), *Trimerorhachis* (Case, 1935), some crown-lissamphibians (Evans & Milner, 1996; Milner, 2000), such microsaurs as *Batropetes* (Carroll, 1991*a*), *Tuditanus*, *Asaphestera*, hapsidopareiontids and ostodolepids (Carroll & Gaskill, 1978) and aïstopods (Wellstead, 1982; Carroll, 1998).

84. *SQU* 2. *Absence* (0) *or presence* (1) *of condition: posterior margin of squamosal sloping anteroventrally.* Despite similarities in the suspensorium configuration, an anteroventrally sloping squamosal does not identify a clade. The character appears to have been developed in albanerpetontids (Gardner, 2001), *Batropetes* (Carroll, 1991*a*), *Cardiocephalus*, *Odonterpeton* (Carroll & Gaskill, 1978) and lysorophids (Wellstead, 1991).

85. *SQU* 3. *Squamosal without* (0) *or with* (1) *broad, concave semicircular embayment.* A squamosal embayment is observed in *Adelospondylus* (Andrews & Carroll, 1991), some seymouriamorphs (Bystrow, 1944; Klembara, 1997), most temnospondyls (*Isodectes* is an exception; Sequeira, 1998) and *Triadobatrachus* (Rocek & Rage, 2000*b*).

86. *SQU* 4. *Absence* (0) *or presence* (1) *of single 'squamosotabular' in the position of squamosal and tabular.* This is one of the features employed by Andrews & Carroll (1991) to diagnose adelospondyls.

87. *SQU* 5. *Squamosal without* (0) *or with* (1) *internal shelf bracing quadrate from behind.* The derived configuration of the squamosal is shared by scincosaurid and diplocaulid nectrideans (Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998).

Jugal

88. *JUG* 1. *Presence* (0) *or absence* (1) *of jugal.* A separately ossified jugal is absent in salientians, caudates and lysorophids (Wellstead, 1991; Evans & Milner, 1996; Milner, 2000; Rocek & Rage, 2000*b*).

89. *JUG* 2. *Jugal not contributing* (0) *or contributing* (1) *to ventral margin of skull roof.* The jugal enters the ventral skull roof margin in *Baphetes* (Beaumont, 1977), cochleosaurid edopoids (Rieppel, 1980; Hook, 1993; Godfrey & Holmes, 1995; Milner & Sequeira, 1998), some trimerorhachoids (Chase, 1965; Sequeira, 1998), *Schoenfelderpeton* (Boy, 1972), albanerpetontids (Gardner, 2001), *Eocaecilia* (Carroll, 2000), several embolomeres (Panchen, 1972; Holmes, 1984, 1989) and all amniotes more derived than gephyrostegids. Among lepospondyls, the plesiomorphic state is observed in *Oestocephalus* (Carroll, 1998) and the urocordylids *Sauropleura* and, possibly, *Urocordylus* (A. C. Milner, 1980; Bossy & Milner, 1998).

90. *JUG* 3. *Jugal not contacting* (0) *or contacting* (1) *pterygoid.* A jugal-pterygoid suture is found in *Megalocephalus* (Beaumont, 1977), cochleosaurid edopoids (Rieppel, 1980; Hook, 1993; Godfrey & Holmes, 1995; Milner & Sequeira, 1998), some embolomeres (Holmes, 1984, 1989; Clack, 1987*a*) and *Captorhinus* (Fox & Bowman, 1966).

91. *JUG* 4. *Jugal depth below orbit greater* (0) *or smaller* (1) *than half orbit diameter.* Primitively, the jugal forms a broad area ventral to the orbit (*Whatcheeria* is an exception among stem-tetrapods; Lombard & Bolt, 1995). Among crown-tetrapods, the plesiomorphic state is observed in edopoids (Milner & Sequeira, 1998), *Eryops* (Sawin, 1941), *Pholiderpeton scutigerum* (Clack, 1987*a*) and *Diplocaulus* (A. C. Milner, 1980; Bossy & Milner, 1998).

92. *JUG* 6. *Absence* (0) *or presence* (1) *of condition: jugal ventrally expanded to form flange overlapping posterior end of maxilla.* This particular configuration of the jugal is a synapomorphy of pantylids (Carrol & Gaskill, 1978; Berman *et al.*, 1988).

93. *JUG* 7. *Jugal without* (0) *or with* (1) V*-shaped indentation of dorsal margin.* A dorsal indentation of the jugal occurs in *Crassigyrinus* (Clack, 1998*c*), *Whatcheeria* (Lombard & Bolt, 1995), baphetids (Beaumont, 1977), and a clade comprising *Anthracosaurus* (Panchen, 1977; Clack, 1987*b*) and *Pholiderpeton attheyi* (Panchen, 1972). This is one of the characters describing irregular orbit outlines in early tetrapods, and appears as a transitional stem-tetrapod feature under both ACCTRAN and DELTRAN.

94. *JUG* 8. *Jugal not extending* (0) *or extending* (1) *anterior to anterior orbit margin.* The jugal extends anterior to the anterior orbit margin in *Acanthostega* (Clack, 1994*a*), edopoids (Milner & Sequeira, 1998), *Eryops* (Sawin, 1941), most embolomeres (Panchen, 1972, 1977; Holmes, 1989; Smithson, 1985), *Seymouria* (White, 1939; Laurin, 1996*b*), *Captorhinus* (Fox & Bowman, 1966), *Pantylus* (Carroll & Gaskill, 1978), *Scincosaurus* and derived diplocaulids (Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998).

Quadratojugal

95. *QUAJUG* 1. *Presence* (0) *or absence* (1) *of quadratojugal. Valdotriton* (Evans & Milner, 1996) and lysorophids (Wellstead, 1991) do not show an ossified quadratojugal.

96. *QUAJUG* 2. *Absence* (0) *or presence* (1) *of condition: quadratojugal much smaller than squamosal.* The derived condition of this character occurs in *Karaurus* (Milner, 2000), and several microsaurs, such as *Odonterpeton* and a clade composed of *Asaphestera*, hapsidopareiontids, ostodolepids, rhynchonkids and gymnarthrids (Carroll & Gaskill, 1978).

97. *QUAJUG* 3. *Absence* (0) *or presence* (1) *of condition: quadratojugal an anteroposteriorly elongate and dorsoventrally narrow splinter of bone.* The distribution of the derived condition of this character overlaps that of the preceding character, except for its absence in *Asaphestera*.

Quadrate

98. *QUA* 1. *Quadrate without* (0) *or with* (1) *dorsal process.* The dorsal process of the quadrate was discussed by Bolt (1969, 1991), Bolt & Lombard (1985) and Milner (1988, 1993). It is regarded as the homologue of the tympanic annulus which suspends the tympanum in several salientians. It occurs in *Dendrerpeton* (Holmes *et al.*, 1998), trematopids (Olson, 1941; Dilkes, 1990), dissorophids and amphibamids (Bolt, 1969, 1991; Daly, 1994). A similar process has been documented in other taxa, such as certain seymouriamorphs (White, 1939; Bystrow, 1944; Laurin, 1996*b*; Klembara, 1997) and diadectomorphs (Romer, 1946; Berman *et al.*, 1998), but it is not certain whether it had the same function.

Preopercular

99. *PREOPE* 1. *Absence* (1) *or presence* (0) *of preopercular.* A preopercular is lost in all tetrapods more derived than

Ichthyostega (Clack, 1998*c*, 2001; see also discussion in Panchen, 1991).

Nostrils

100. *NOS* 3. *Absence* (0) *or presence* (1) *of condition: nostrils elongate and key-hole shaped. Acheloma*, *Phonerpeton* and *Ecolsonia* share the derived state (Olson, 1941; Berman *et al.*, 1985; Dilkes, 1990). See also Dilkes (1990) and Daly (1994) for a discussion of this character.

101. *NOS* 4. *Absence* (0) *or presence* (1) *of condition: nostrils elliptical, with greater axis oriented obliquely in anteromedial to posterolateral direction, and at least* 70% *the length of the internasal suture.* The derived condition of the nostril is found in branchiosaurids (Boy, 1972; Schoch, 1992; Boy & Sues, 2000), some amphibamids (Watson, 1940; Bolt, 1969, 1977, 1979, 1991) and certain crown-lissamphibians (Evans & Milner, 1996; Milner, 2000).

Internarial fenestra

102. *INT FEN* 1. *Absence* (0) *or presence* (1) *of internarial fenestra.* The presence of an internarial fenestra (see Clack, 1998*c*, 2001) characterizes *Acanthostega* (Clack, 1994*a*), *Ichthyostega* (Jarvik, 1980, 1996), *Greererpeton* (Smithson, 1982), *Crassigyrinus* (Clack, 1996, 1998*c*), baphetids (Beaumont, 1977), some dissorophoids (Olson, 1941; Bolt, 1969, 1991; Boy, 1972, 1987, 1995; Dilkes, 1990; Schoch, 1992; Daly, 1994) and *Karaurus* (Milner, 2000).

Orbits

103. *ORB* 1. *Interorbital distance greater than* (0), *smaller than* (1), *or subequal to* (2) *half skull table width.* The plesiomorphic state is found in *Eocaecilia* (Carroll, 2000), most tuditanomorphs and one microbrachomorph (Carroll & Gaskill, 1978) and in *Batrachiderpeton* (A. C. Milner, 1980; Bossy & Milner, 1998). State 2 appears sporadically on the tree, in *Colosteus* (Hook, 1983), *Chenoprosopus* (Hook, 1993; Milner & Sequeira, 1998), *Eoherpeton* (Smithson, 1985), some seymouriamorphs (White, 1939; Bystrow, 1944; Laurin, 1996*b*), *Diadectes* (Berman *et al.*, 1998), *Westlothiana* (Smithson *et al.*, 1994), *Batropetes*, *Tuditanus*, *Microbrachis* and *Hyloplesion* (Carroll & Gaskill, 1978; Carroll, 1991*a*), *Scincosaurus*, some diplocaulids (A. C. Milner, 1980; Bossy & Milner, 1998) and *Oestocephalus* (Carroll, 1998).

104. *ORB* 2. *Interorbital distance greater than* (0), *smaller than* (1) *or subequal to* (2) *maximum orbit diameter.* The different states of this character show a more complicated distribution than those of the preceding character. State 1, found in *Acanthostega* (Clack, 1994*a*), *Crassigyrinus* (Clack, 1998*c*) and *Whatcheeria* (Lombard & Bolt, 1995), is widespread among crown-tetrapods. It is observed in *Eucritta* (Clack, 2001), *Trimerorhachis* (Case, 1935), *Balanerpeton* (Milner & Sequeira, 1994), and most dissorophoids and crown-lissamphibians (Bolt, 1969, 1991; Boy, 1972, 1987, 1995; Schoch, 1992; Daly, 1994; Evans & Milner, 1996; Milner, 2000; Rocek & Rage, 2000*b*). It is also found in many embolomeres (Panchen, 1972, 1977; Holmes, 1984, 1989; Clack, 1987*a*), gephyrostegids (Carroll, 1970), *Discosauriscus* (Klembara, 1997), basal crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981) and a clade of aïstopods plus urocordylids (Wellstead, 1982; A. C. Milner, 1980; Bossy & Milner, 1998; Carroll, 1998; Anderson, in press). State 2 characterizes baphetids (Beaumont, 1977), such dissorophoids as *Ecolsonia* and *Broiliellus* (Carroll, 1964; Berman *et al.*, 1985), *Batropetes* (Carroll, 1991*a*), adelospondyls (Andrews & Carroll, 1991) and derived diplocaulids (Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998). The plesiomorphic condition, exhibited by *Ichthyostega* (Jarvik, 1980, 1996) and colosteids (Smithson, 1982; Hook, 1983), occurs also in edopoids (Milner & Sequeira, 1998), some trimerorhachoids (Chase, 1965; Sequeira, 1998), *Dendrerpeton* (Holmes *et al.*, 1998), *Eryops* (Sawin, 1941), *Platyrhinops* (Milner, 2000), *Eocaecilia* (Carroll, 2000), *Eoherpeton* (Smithson, 1985), *Solenodonsaurus* (Laurin & Reisz, 1999), some seymouriamorphs (White, 1939; Bystrow, 1944; Laurin, 1996*b*), diadectomorphs (Romer, 1946; Berman *et al.*, 1998), most microsaurs (Carroll & Gaskill, 1978) scincosaurids and several diplocaulids (A. C. Milner, 1980; Bossy & Milner, 1998).

105. *ORB* 3. *Absence* (0) *or presence* (1) *of angle at anteroventral orbit corner.* The derived state of this character (coding follows Clack, 1998*c*, 2001) is observed in *Crassigyrinus* (Clack, 1998*c*), *Whatcheeria* (Lombard & Bolt, 1995) and *Eucritta* (Clack, 2001). It appears as a transitional feature of stem-tetrapods under ACCTRAN, but is developed independently in *Crassigyrinus* and *Whatcheeria* under DELTRAN.

Pineal foramen

106. *PIN FOR* 1. *Presence* (0) *or absence* (1) *of pineal foramen.* A pineal foramen is absent in cochleosaurid edopoids (Milner & Sequeira, 1998), *Pantylus*, ostodolepids (Carroll & Gaskill, 1978), lysorophids (Wellstead, 1991), albanerpetontids and most crown-lissamphibians (Evans & Milner, 1996; Carroll, 2000; Milner, 2000; Gardner, 2001). Milner & Sequeira (1998) discussed in detail the occurrence of this character in cochleosaurids. Several species show progressive obliteration of the foramen during growth. As a general condition, closure of the foramen is a diagnostic feature of cochleosaurids with a skull length of 120 mm or more.

107. *PIN FOR* 2. *Position of pineal foramen behind* (0), *at the level of* (1) *or anterior to* (2) *interparietal suture mid length.* The plesiomorphic state of this character occurs in stem-tetrapods (Beaumont, 1977; Jarvik, 1980, 1996; Smithson, 1982; Hook, 1983; Clack, 1994*a*, 1998*c*; Lombard & Bolt, 1995), as well as *Eucritta* (Clack, 2001) and temnospondyls (Milner & Sequeira, 1998). Reversal to this condition occurs sporadically, in some temnospondyls (*Trimerorhachis*; *Eryops*; Case, 1935; Sawin 1941), stem-amniotes (*Pholiderpeton scutigerum*; Clack, 1987*a*), crown-amniotes (*Paleothyris*; Clark & Carroll, 1973), microsaurs (*Asaphestera*; Carroll & Gaskill, 1978), adelospondyls (*Adelogyrinus*; *Dolichopareias*; Andrews & Carroll, 1991) and aïstopods (*Oestocephalus*; Carroll, 1998). State 1 is observed in *Kotlassia*, *Diplocaulus*, *Diploceraspis*, *Stegotretus*, *Ecolsonia*, *Adelospondylus*, *Isodectes* (Bystrow, 1944; Beerbower, 1963; A. C. Milner, 1980; Berman *et al.*, 1988; Andrews & Carroll, 1991; Bossy & Milner, 1998; Sequeira, 1998). State 2 is found in most crown-tetrapods.

Central, elongate and lightly sculptured area of skull table

108. *L SC SKU* 1. *Absence* (0) *or presence* (1) *of lightly sculptured area.* Milner & Sequeira (1998, p. 279) describe 'Depressed areas with subdued sculpture between parallel anteroposterior sculpture ridges on either side of the skull table' as a shared derived feature of cochleosaurid edopoids (see also Godfrey & Holmes, 1995). Accordingly, the derived state of this character is assigned to *Cochleosaurus* and *Chenoprosopus*.

Posttemporal fossae

109. *PTF* 1. *Fossa at dorsolateral corner of occiput, not bordered laterally, roofed over by skull table and floored by dorsolateral extension of opisthotic* (0)*; fossa near dorsolateral corner of occiput, roofed over by occipital flanges of tabular and postparietal and bordered laterally and ventrally by dorsolateral extension of opisthotic meeting ventromedial flange of tabular* (1)*; small fossa near ventrolateral corner of occiput bordered laterally by ventromedial flange of tabular, roofed over by dorsal portion of lateral margin of supraoccipital–opisthotic complex and floored by lateral extension of opisthotic* (2)*; absence of fossa* (3). The different conditions of the posttemporal fossae and associated codings are based on Berman's (2000) recent study of the occipital region in early tetrapods. State 3 is acquired in parallel in *Ichthyostega* (Jarvik, 1980, 1996) and embolomeres (Panchen, 1977; Holmes, 1984, 1989; Smithson, 1985; Clack, 1987*a*). State 2 characterizes diadectomorphs and crown-amniotes (Romer, 1946; Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981; Berman *et al.*, 1998). State 1 is widespread among derived stem-tetrapods (Beaumont, 1977; Smithson, 1982, 1985).

Proportions of skull table

110. *SKU TAB* 1. *Absence* (0) *or presence* (1) *of condition: postorbital region of skull roof abbreviated.* Although shortening of the postorbital skull roof region occurs in various degrees, several crown-group taxa are distinctly different from the outgroup and from stem-tetrapods in that their skull roof is usually wider than long, regardless of the morphology and proportions of its various constituent bones. Several temnospondyls more crownward than trimerorhachoids (Carroll, 1964; Bolt, 1969, 1991; Boy, 1972, 1987, 1995; Berman *et al.*, 1985; Schoch, 1992; Daly, 1994; Milner & Sequeira, 1994) and crown-lissamphibians (Carroll, 2000; Milner, 2000; Rocek & Rage, 2000*b*) have acquired the derived state of this character independent of several basal and crown-amniotes, *Westlothiana*, microsaurs, *Scincosaurus* and derived diplocaulids (White, 1939; Bystrow, 1944; Romer, 1946; Beerbower, 1963; Fox & Bowman, 1966; Carroll, 1970; Boy & Bandel, 1973; Panchen, 1977; Reisz, 1977, 1981; A. C. Milner, 1980; Smithson *et al.*, 1994; Laurin, 1996*b*; Klembara, 1997; Berman *et al.*, 1998; Bossy & Milner, 1998).

Temporal fenestra

111. *TEM FEN* 1. *Absence* (0) *or presence* (1) *of broad postorbital opening* (*aïstopod pattern*). In all aïstopods, a large temporal fenestra, not confluent with the orbit, occupies more than half of the skull length (Wellstead, 1982; Carroll, 1998; Anderson, in press). Repatterning of the postorbital region of the skull involves loss of some bones.

Cheek emargination

112. *CHE EMA* 1. *Absence* (0) *or presence* (1) *of ventral cheek emargination* (*pattern of certain tuditanomorph microsaurs*). In hapsidopareiontids, ostodolepids and some gymnarthrids (Gregory *et al.*, 1956; Carroll & Gaskill, 1978), the ventral cheek margin is excavated to various degrees without involving loss of cheek bones. This excavation, particularly evident in hapsidopareiontids and ostodolepids, confers a strongly arched profile to the posteroventral part of the skull table.

Interfrontonasal

113. *IFN* 1. *Absence* (0) *or presence* (1) *of interfrontonasal.* An interfrontonasal appears to be diagnostic of *Eryops* (Sawin, 1941), and is present in other eryopoids, such as *Clamorosaurus* Gubin, 1983.

Suspensorium

114. *SUS* 1. *Absence* (0) *or presence* (1) *of anteroposteriorly narrow, bar-like squamosal.* The derived condition of the squamosal results in a shortened, oblique configuration of the posterior, external surface of the suspensorium in lysorophids (Wellstead, 1991), aïstopods (Wellstead, 1982; Carroll, 1998; Anderson, in press), as well as in the microsaurs *Batropetes* (Carroll, 1991*a*), *Hapsidopareion* and, possibly, *Cardiocephalus* (Carroll & Gaskill, 1978).

Sensory canals

115. *SC* 1. *Lateral line system on skull roof totally enclosed* (0), *mostly enclosed with short sections in grooves* (1), *mostly in grooves with short sections enclosed* (2), *entirely in grooves* (3), *absent* (4). The codings for this and the following character are based on data collated from analyses by Clack (1998*c*, 2001), Ahlberg & Clack (1998) and Paton *et al.* (1999). Inspection of the data set reveals that, in the case of both characters, state 4 is widespread in the crown-group, and that states 1, 2 and 3 are acquired independently (and, often, coexist) in different clades.

116. *SC* 2. *Mandibular canal totally enclosed* (0), *mostly enclosed with short sections in grooves* (1), *mostly in grooves with short sections enclosed* (2), *entirely in grooves* (3), *absent* (4). See character 115 above.

(*b*) *Palate*

Vomer

117. *VOM* 1. *Absence* (0) *or presence* (1) *of condition: ventral, exposed surface of vomers narrow, elongate and strip-like, without extensions anterolateral or posterolateral to choana and two and a half to three times longer than wide.* The derived state of this character is widespread on the amniote branch of the tetrapod tree (Gauthier *et al.*, 1988*b*; Lee & Spencer, 1997). Importantly, its occurrence does not depend upon the overall morphology of the preorbital skull region. It is found in broad-snouted stem-amniotes, such as *Discosauriscus* (Klembara, 1997), as well as in long-snouted forms, such as embolomeres (Panchen 1977; Holmes, 1984, 1989; Smithson, 1985; Clack, 1987*a*), gephyrostegids (Carroll, 1970), diadectomorphs (Romer, 1946; Fracasso, 1987; Berman *et al.*, 1998), crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981) and *Westlothiana* (Smithson *et al.*, 1994). Microsaurs (Carroll & Gaskill, 1978), lysorophids (Wellstead, 1991), *Sauropleura* and *Urocordylus* (Bossy & Milner, 1998) also show elongate vomers. The plesiomorphic condition of this character is widespread in stem-tetrapods and in the temnospondyl-lissamphibian clade, regardless of the degree of elongation of the snout (several longirostrine temnospondyls represent an exception; Schoch & Milner, 2000).

118. *VOM* 3. *Vomer with* (0) *or without* (1) *fang pair.* The coding of this character follows Gauthier *et al.* (1988*b*), Clack (1998*c*, 2001) and Laurin (1998*b*). Vomerine fangs are absent in *Ichthyostega* (Jarvik, 1980, 1996), certain dissorophoids and crown-lissamphibians (Watson, 1940; Carroll, 1964, 2000; Bolt, 1969, 1977, 1979, 1991; Boy, 1972; Evans & Milner, 1996; Milner, 2000), *Pholiderpeton attheyi* (Panchen, 1972), *Kotlassia* (Bystrow, 1944), diadectomorphs (Romer, 1946; Fracasso, 1987; Berman *et al.*, 1998), crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981), and all lepospondyls in which the palate is visible (*Euryodus* is, however, an exception, since fang pairs are present; also, *Micraroter* is polymorphic for this character; Carroll & Gaskill, 1978).

119. *VOM* 4. *Vomer without* (0) *or with* (1) *denticles.* The presence of a denticle shagreen patch on the vomer shows a rather uneven distribution. Among stem-tetrapods, it is observed in *Tulerpeton* (Lebedev & Clack, 1993), *Whatcheeria* (Lombard & Bolt, 1995) and baphetids (Beaumont, 1977). Among crown-tetrapods, it is found in *Eucritta* (Clack, 2001), several temnospondyls (Sawin, 1941; Romer & Witter, 1942; Carroll, 1964; Bolt, 1969, 1991; Berman *et al.*, 1985; Milner & Sequeira, 1994, 1998; Holmes *et al.*, 1998; Dilkes, 1990; Daly, 1994), *Caerorhachis* (Holmes & Carroll, 1977; Ruta *et al.*, 2001), gephyrostegids (Carroll, 1970), *Discosauriscus* (Klembara, 1997), *Seymouria* (White, 1939; Laurin, 1996*b*), *Petrolacosaurus* (Reisz, 1977, 1981), some tuditanomorphs (e.g. *Saxonerpeton*; *Micraroter*; *Euryodus*) and all microbrachomorphs (Carroll & Gaskill, 1978).

120. *VOM* 5. *Vomer excluded from* (0) *or contributing to* (1) *interpterygoid vacuities.* The vomers enter the margins of the palatal vacuities in post-edopoid temnospondyls, albanerpetontids and crown-lissamphibians (Milner, 1988, 1990, 2000; Carroll, 2000; Rocek & Rage, 2000*b*; Gardner, 2001), as well as in *Hyloplesion* (Carroll & Gaskill, 1978) and derived diplocaulids (Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998).

121. *VOM* 7. *Vomer not forming* (0) *or forming* (1) *suture with maxilla anterior to choana.* The derived condition of this character is found in *Ichthyostega* (Jarvik, 1980, 1996), *Crassigyrinus* (Clack, 1996, 1998*c*), *Cochleosaurus* (Godfrey & Holmes, 1995; Milner & Sequeira, 1998), certain trimerorhachoids (Case, 1935; Chase, 1965), *Eoscopus* (Daly, 1994) and primitive crown-lissamphibians, where observed (Evans & Milner, 1996; Carroll, 2001).

122. *VOM* 8. *Vomer with* (0) *or without* (1) *toothed lateral crest.* With the exception of *Crassigyrinus* (Clack, 1998*c*) and *Eoscopus* (Daly, 1994), all tetrapods more derived than *Tulerpeton* lack a lateral crest on the ventral surface of the vomer (for descriptions, see Lebedev & Clack, 1993).

123. *VOM* 9. *Vomer with* (0) *or without* (1) *anterior crest.* The distribution of this character is almost identical to that of the previous character, except that the derived condition is also present in *Ichthyostega*

(Jarvik, 1980, 1996) and *Tulerpeton* (Lebedev & Clack, 1993).

124. *VOM* 10. *Vomer in contact with anterior ramus of pterygoid* (0) *or not* (1). Absence of a vomer-pterygoid contact is found in *Isodectes* (Sequeira, 1998), all temnospondyls more derived than *Ecolsonia* (Milner, 1988, 1990), crown-lissamphibians (Evans & Milner, 1996; Carroll, 2000; Milner, 2000; Rocek & Rage, 2000*b*) and derived diplocaulids (Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998).

125. *VOM* 11. *Vomer without* (0) *or with* (1) *transverse patch of small teeth posteromesial to choana.* Several crown-lissamphibians share the derived condition of this feature with *Doleserpeton* (Bolt, 1969, 1977, 1979, 1991; Milner, 1988, 1990, 1993, 2000).

126. *VOM* 12. *Absence* (0) *or presence* (1) *of distinct posterolateral vomer process bordering more than half of posterior margin of choana.* The derived state of this character occurs in some amphibamids and branchiosaurids (Bolt, 1969, 1977, 1979, 1991; Boy, 1972; Milner, 1988, 1990, 1993, 2000; Schoch, 1992), as well as in *Karaurus* (Milner, 2000).

Palatines

127. *PAL* 1. *Palatine with* (0) *or without* (1) *fangs.* Loss of palatine fangs occurs independently in *Ichthyostega* (Jarvik, 1980, 1996), some branchiosaurids (Boy, 1972), some amphibamids and crown-lissamphibians (Bolt, 1969, 1977, 1979, 1991; Milner, 1988, 1990, 1993, 2000; Carroll, 2000; Rocek & Rage, 2000*b*), and in a large portion of the amniote tree including *Kotlassia* (Bystrow, 1944), diadectomorphs (Romer, 1946; Berman *et al.*, 1998), crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981) and most lepospondyls except pantylids (Beerbower, 1963; Carroll & Gaskill, 1978; A. C. Milner, 1980; Berman *et al.*, 1988; Wellstead, 1991; Bossy & Milner, 1998).

128. *PAL* 2. *Palatine without* (0) *or with* (1) *denticles.* Presence of a denticle shagreen patch on the palatines is recorded in *Whatcheeria* (Lombard & Bolt, 1995), baphetids (Beaumont, 1977), *Eucritta* (Clack, 2001), some temnospondyls (Watson, 1940; Sawin, 1941; Romer & Witter, 1942; Berman *et al.*, 1985; Milner & Sequeira, 1994, 1998; Godfrey & Holmes, 1995; Holmes *et al.*, 1998), *Caerorhachis* (Holmes & Carroll, 1977; Ruta *et al.*, 2001), gephyrostegids (Carroll, 1970), some seymouriamorphs (White, 1939; Laurin, 1996*b*; Klembara, 1997), certain crown-amniotes (Clark & Carroll, 1973; Reisz, 1977, 1981), *Westlothiana* (Smithson *et al.*, 1994), microbrachomorphs, some tuditanomorphs (Carroll & Gaskill, 1978), at least one adelospondyl (*Adelospondylus*; Andrews & Carroll, 1991) and one nectridean (*Scincosaurus*; A. C. Milner, 1980; Bossy & Milner, 1998).

129. *PAL* 3. *Palatine excluded from* (0) *or contributing to* (1) *interpterygoid vacuities.* The derived state of this character is shared by scincosaurids and diplocaulids (Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998), as well as by derived dissorophoids and crown-lissamphibians (Carroll, 1964; Bolt, 1969, 1977, 1979, 1991; Boy, 1972, 1987, 1995; Milner, 1988, 1990, 1993, 2000; Carroll, 2000; Rocek & Rage, 2000*b*). It is also documented in *Isodectes* (Sequeira, 1998).

130. *PAL* 4. *Palatine with* (0) *or without* (1) *tooth row* (3+). A palatine tooth row is present in all stem-tetrapods less derived than baphetids (Clack, 1998*c*, 2001; Paton *et al.*, 1999), as well as in trimerorhachoids (Case, 1935; Chase, 1965), some dissorophoids and *Eocaecilia* (Bolt, 1969, 1977, 1979, 1991; Boy, 1972, 1987, 1995; Milner, 1988, 1990, 1993, 2000; Schoch, 1992; Carroll, 2000; Rocek & Rage, 2000*b*), *Kotlassia* (Bystrow, 1944), some tuditanomorphs and microbrachomorphs (Carroll & Gaskill, 1978) and nectrideans other than *Scincosaurus* (Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998).

131. *PAL* 5. *Palatine without* (0) *or with* (1) *lateral exposure in anteroventral orbit margin.* Among the taxa included in the present analysis, a lateral exposure of the palatine contributing to the orbit margin is present in *Isodectes* (Sequeira, 1998); *Ecolsonia* (Berman *et al.*, 1985), *Micromelerpeton* (Boy, 1995) and *Doleserpeton* (Bolt, 1969, 1977, 1979, 1991).

132. *PAL* 6. *Absence* (0) *or presence* (1) *of condition: palatine articulates with maxilla only at its anterior end. Apateon* (Schoch, 1992), *Leptorophus* and *Schoenfelderpeton* (Boy, 1972) share the derived condition (Milner, 1990, 1993; Trueb & Cloutier, 1991). This is also present in *Petrolacosaurus* (Reisz, 1977, 1981).

133. *PAL* 7. *Palatine not reduced* (0) *or reduced* (1) *to slender, strut-like bone.* As described by Milner (1990, 1993), this condition is found in micromelerpetontids, branchiosaurids, some amphibamids and some crown-lissamphibians (Boy, 1972, 1987, 1995; Bolt, 1969, 1977, 1979, 1991; Milner, 1990, 1993; Rocek & Rage, 2000*b*).

Ectopterygoids

134. *ECT* 1. *Presence* (0) *or absence* (1) *of ectopterygoid.* The ectopterygoid is absent in *Doleserpeton* (Bolt, 1969, 1977, 1979, 1991), crown-lissamphibians (Evans & Milner, 1996; Carroll, 2000; Milner, 2000; Rocek & Rage, 2000*b*), *Captorhinus* (Fox & Bowman, 1966; Laurin, 1998*b*), pantylids (Carroll & Gaskill, 1978; Berman *et al.*, 1988), lysorophids (Wellstead, 1991), scincosaurids and diplocaulids (A. C. Milner, 1980; Bossy & Milner, 1998).

135. *ECT* 2. *Ectopterygoid with* (0) *or without* (1) *fangs.* Ectopterygoid fangs [see coding in Clack (1998*c*, 2001) and Paton *et al.* (1999)] are absent in *Acanthostega* (Clack, 1994*a*), *Ichthyostega* (Jarvik, 1980, 1996), *Trimerorhachis* (Case, 1935), micromelerpetontids, branchiosaurids (Boy, 1972, 1987, 1995; Milner, 1990, 1993; Schoch, 1992), *Brukterpeton* (Boy & Bandel, 1973), seymouriamorphs and all more crownward stem-amniotes, as well as crown-amniotes (White, 1939; Bystrow, 1944; Romer, 1946; Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981; Smithson *et al.*, 1994; Laurin, 1996*b*; Klembara, 1997; Berman *et al.*, 1998), as well as several lepospondyls (Carroll & Gaskill, 1978; A. C. Milner, 1980; Wellstead, 1991; Bossy & Milner, 1998).

136. *ECT* 3. *Ectopterygoid without* (0) *or with* (1) *denticles.* A denticle shagreen patch on the ectopterygoid is observed in *Whatcheeria* (Lombard & Bolt, 1995), baphetids (Beaumont, 1977), some temnospondyls (Sawin, 1941; Romer & Witter, 1942; Milner & Sequeira, 1994, 1998; Godfrey & Holmes, 1995; Holmes *et al.*, 1998), *Caerorhachis* (Holmes & Carroll, 1977; Ruta *et al.*, 2001), *Proterogyrinus* (Holmes, 1984), gephyrostegids (Carroll, 1970; Boy & Bandel, 1973), some seymouriamorphs (White, 1939; Laurin, 1996*b*; Klembara, 1997), *Westlothiana* (Smithson *et al.*, 1994), some microbrachomorphs, few tuditanomorphs (Carroll & Gaskill, 1978) and at least one adelospondyl (*Adelospondylus*; Andrews & Carroll, 1991).

137. *ECT* 4. *Ectopterygoid longer than/as long as palatines* (0) *or not* (1). Primitively, the ectopterygoid is an elongate and subrectangular bone, as found in the tetrapod stem-group, in temnospondyls up to the level of trematopids (e.g. Olson, 1941; Sawin, 1941; Romer & Witter, 1942; Milner & Sequeira, 1994, 1998; Godfrey & Holmes, 1995; Holmes *et al.*, 1998), in *Caerorhachis* and embolomeres (Panchen, 1972, 1977; Holmes & Carroll, 1977; Smithson, 1985; Clack, 1987*a*; Ruta et al., 2001). A reversal to the plesiomorphic state is documented in *Ptyonius* (A. C. Milner, 1980; Bossy & Milner, 1998) and some seymouriamorphs (Bystrow, 1944; Klembara, 1997).

138. *ECT* 5. *Ectopterygoid with* (0) *or without* (1) *tooth row* (3+). Absence of an ectopterygoid tooth row [see coding in Clack (1998*c*, 2001) and Paton *et al.* (1999)] is a shared derived feature of baphetids and crown-tetrapods, but reversals to the primitive state are widespread. Such reversals are documented in trimerorhachoids (Case, 1935; Chase, 1965), micromelerpetontids and branchiosaurids (Boy, 1972, 1987, 1995; Milner, 1990, 1993; Schoch, 1992), embolomeres (Panchen, 1972, 1977; Holmes, 1984, 1989; Smithson, 1985; Clack, 1987*a*), *Kotlassia* (Bystrow, 1944), ostodolepid, gymnarthrid and rhynchonkid tuditanomorphs (Gregory *et al.*, 1956; Carroll & Gaskill, 1978) and *Ptyonius* (A. C. Milner, 1980; Bossy & Milner, 1998; optimized as present in remaining nectrideans under ACCTRAN).

139. *ECT* 6. *Ectopterygoid contacting maxilla* (0) *or not* (1). A separation between ectopterygoid and maxilla is found in micromelerpetontids and branchiosaurids (Boy, 1972, 1987, 1995; Milner, 1990, 1993; Schoch, 1992), in *Petrolacosaurus* (Reisz, 1977, 1981) and in the microbrachomorphs *Hyloplesion* and *Odonterpeton* (Carroll & Gaskill, 1978).

140. *ECT* 7. *Absence* (0) *or presence* (1) *of condition: ectopterygoid narrowly wedged between palatine and pterygoid.* The derived state is shared by *Hyloplesion* (in which it is more pronounced) and *Odonterpeton* (Carroll & Gaskill, 1978).

Pterygoids

141. *PTE* 3. *Absence* (0) *or presence* (1) *of pterygoid flange oriented transversely.* There is as yet no consensus on what counts as a transverse pterygoid flange, although this is one of the most widely discussed apomorphies of amniotes (Heaton, 1980; Gauthier *et al.*, 1988*b*; Carroll, 1991*b*; Lee & Spencer, 1997). As pointed out by Laurin (1998*b*), this character is more widespread among tetrapods than previously assumed, and is certainy present in some temnospondyls (Yates & Warren, 2000). However, we point out that the flanges of *Eryops*, *Amphibamus* and *Ecolsonia* (Watson, 1940; Sawin, 1941; Berman *et al.*, 1985) are neither as developed as, nor conform to the pattern (e.g. transverse orientation) of, those of gephyrostegids (Carroll, 1970), seymouriamorphs (White, 1939; Bystrow, 1944; Laurin, 1996*a*; Klembara, 1997), diadectomorphs (Romer, 1946; Berman *et al.*, 1998) and crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981). This character should be read in conjunction with character 144 below. It refers to the presence of a transverse, ventrally directed thickening of the posterior margin of the pterygoid region lying immediately posterolateral to the recess for the basipterygoid process. It may coexist with a posterolateral flange (character 144 below), as in seymouriamorphs.

142. *PTE* 4. *Absence* (0) *or presence* (1) *of teeth on transverse pterygoid flange. Limnoscelis* shares the presence of pterygoid teeth on the transverse flange with *Paleothyris* and *Petrolacosaurus* (Romer, 1946; Clark & Carroll, 1973; Reisz, 1977, 1981).

143. *PTE* 7. *Absence* (0) *or presence* (1) *of condition: quadrate ramus of pterygoid laterally oriented.* In caudates, the laterally directed quadrate ramus of the pterygoid extends almost perpendicularly to the anteroposterior axis (Evans & Milner, 1996; Milner, 2000).

144. *PTE* 9. *Pterygoid without* (0) *or with* (1) *posterolateral flange.* A posterolateral flange (not transversely oriented) is found in several primitive and derived temnospondyls (Olson, 1941; Sawin, 1941; Romer & Witter, 1942; Carroll, 1964; Chase, 1965; Bolt, 1969, 1977, 1979, 1991; Berman *et al.*, 1985; Dilkes, 1990; Daly, 1994; Milner & Sequeira, 1994, 1998; Godfrey & Holmes, 1995; Holmes *et al.*, 1998; Carroll, 2000; Milner, 2000), as well as seymouriamorphs (see also character 141 above), *Limnoscelis* (Romer, 1946; the situation of *Diadectes* is unclear), some tuditanomorphs and few microbrachomorphs (Carroll & Gaskill, 1978).

145. *PTE* 10. *Pterygoids not sutured with each other* (0) *or sutured* (1). Pterygoids that fail to meet in the midline are documented in temnospondyls (except *Edops*; Romer & Witter, 1942; Milner & Sequeira, 1998) and crown-lissamphibians, as well as *Kotlassia* (Bystrow, 1944), *Pelodosotis*, *Rhynchonkos* and *Hyloplesion* (Carroll & Gaskill, 1978), lysorophids (Wellstead, 1991) and *Scincosaurus* (A. C. Milner, 1980; Bossy & Milner, 1998).

146. *PTE* 11. *Pterygoid not sutured with maxilla* (0) *or sutured* (1). A maxilla-pterygoid contact is documented in *Doleserpeton* (Bolt, 1969, 1991), *Valdotriton* (Evans & Milner, 1996) and *Triadobatrachus* (Rocek & Rage 2000*b*).

147. *PTE* 12. *Pterygoid not sutured with posterior end of palatine* (0) *or sutured* (1). *Platyrhinops* (Milner, 2000), *Doleserpeton* (Bolt, 1969, 1991) and *Eocaecilia* (Carroll, 2000) share the derived condition of this character.

148. *PTE* 13. *Pterygoid without* (0) *or with* (1) *distinct, mesially directed process for the basipterygoid recess.* The derived condition characterizes several temnospondyls and some crown-lissamphibians (Olson, 1941; Sawin, 1941; Carroll, 1964; Bolt, 1969, 1977, 1979, 1991; Boy, 1972, 1987, 1995; Berman *et al.*, 1985; Holmes *et al.*, 1998; Schoch, 1992; Daly, 1994; Boy & Sues, 2000; Milner, 2000; Rocek & Rage, 2000*b*).

149. *PTE* 14. *Absence* (0) *or presence* (1) *of condition: quadrate ramus of pterygoid robust, indistinctly merging into basal and palatal processes.* A quadrate ramus merging indistinctly into the posterior part of the palatal ramus is observed in micromelerpetontids, branchiosaurids and crown-lissamphibians (Boy, 1972, 1987, 1995; Schoch, 1992; Boy & Sues, 2000; Carroll, 2000; Milner, 2000; Rocek & Rage, 2000*b*).

150. *PTE* 15. *Absence* (0) *or presence* (1) *of condition: quadrate ramus of pterygoid straight, rod-like and gently tapering distally.* The derived condition occurs in micromelerpetontids, branchiosaurids, some amphibamids and *Eocaecilia* (Bolt, 1969, 1977, 1979, 1991; Boy, 1972, 1987, 1995; Schoch, 1992; Boy & Sues, 2000; Carroll, 2000; Milner, 2000).

151. *PTE* 16. *Palatal ramus of pterygoid without* (0) *or with* (1) *distinct, anterior, unornamented digitiform process.* The process in question, at the anterior end of the palatal ramus of the pterygoid, is visible in colosteids (Smithson, 1982; Hook, 1983), *Euryodus* and *Microbrachis* (Carroll & Gaskill, 1978) and in *Adelospondylus* (Andrews & Carroll, 1991).

152. *PTE* 17. *Basal region of pterygoid immediately anterior to quadrate ramus without* (0) *or with* (1) *sharply defined, elongate longitudinal groove.* An anteroposteriorly elongate sulcus, marking a deflection between two parts of the basal region of the pterygoid is found in hapsidopareiontids, ostodolepids, rhynchonkids and gymnarthrids (Carroll & Gaskill, 1978).

Interpterygoid vacuities

153. *INT VAC* 1. *Presence* (0) *or absence* (1) *of interpterygoid vacuities.* Regardless of their outline and extension, vacuities are widespread among tetrapods. Entirely closed ('sealed off') palates are documented in baphetids (Beaumont, 1977), *Eucritta* (Clack, 2001), *Discosauriscus* (discussion in Klembara, 1997), *Diadectes* (Berman *et al.*, 1998), lysorophids (Wellstead, 1991) and *Batrachiderpeton* (A. C. Milner, 1980; Bossy & Milner, 1998).

154. *INT VAC* 2. *Absence* (0) *or presence* (1) *of condition: interpterygoid vacuities occupying at least half of palatal width.* The derived state of this character occurs in most temnospondyls (*Edops* is a notable exception; Romer & Witter, 1942; Milner & Sequeira, 1994, 1998; Holmes, 2000; Ruta *et al.*, 2001), crown-lissamphibians (Carroll, 2000; Milner, 2000; Rocek & Rage, 2000*b*), *Ptyonius* and several derived diplocaulids (Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998). See also discussion in Anderson (2001).

155. *INT VAC* 3. *Absence* (0) *or presence* (1) *of condition: interpterygoid vacuities concave along their whole margins.* Except for *Ptyonius*, the distribution of this character is identical to that of the previous character (see also Ruta *et al.*, 2001).

156. *INT VAC* 4. *Absence* (0) *or presence* (1) *of condition: interpterygoid vacuities together broader than long.* The distribution of this character is identical to that of character 155, except for *Eocaecilia* (Carroll, 2000), *Chenoprosopus* (Hook, 1993; Milner & Sequeira, 1998), trimerorhachoids (Case, 1935; Chase, 1965; Sequeira, 1998), *Balanerpeton* (Milner & Sequeira, 1994), *Dendrerpeton* (Holmes *et al.*, 1998), *Eryops* (Sawin, 1941) and dissorophids (Olson, 1941; Dilkes, 1990).

Choanae

157. *CHO* 1. *Absence* (0) *or presence* (1) *of condition: choanae wider anteriorly than posteriorly.* The derived condition is shared by *Chenoprosopus* and *Cochleosaurus* (Hook, 1993; Godfrey & Holmes, 1995; Milner & Sequeira, 1998).

Anterior palatal vacuity

158. *ANT VAC* 1. *Presence* (0) *or absence* (1) *of anterior palatal vacuity*. Absence of an anterior palatal vacuity characterizes all tetrapods more crownward than *Crassigyrinus* (*Megalocephalus*, however, is an exception; Beaumont, 1977). A reversal to the plesiomorphic condition is documented in trimerorhachoids (Case, 1935; Chase, 1965; Sequeira, 1998), *Acheloma* (Olson, 1941) and *Micromelerpeton* (Boy, 1995).

159. *ANT VAC* 2. *Anterior palatal vacuity single* (0) *or double* (1). A double palatal vacuity occurs in *Acanthostega* (Clack, 1994*a*), *Greererpeton* (Smithson, 1982), *Crassigyrinus* (Clack, 1996, 1998*c*) and trimerorhachoids (Case, 1935; Chase, 1965; Sequeira, 1998).

(*c*) *Occiput and braincase*

Supraoccipital

160. *SUPOCC* 1. *Supraoccipital absent* (0) *or present* (1) *as separate ossification*. The derived state of this character is found in *Limnoscelis* (Berman *et al.*, 1992; Berman, 2000), basal crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981), *Westlothiana* (Smithson *et al.*, 1994), lysorophids and microsaurs (Carroll & Gaskill, 1978; Wellstead, 1991). However, Berman (2000) postulated that the microsaur supraoccipital is not homologous with that of amniotes. Our treatment of this element is more conservative, but we acknowledge several merits in Beman's (2000) proposal (see also discussion of *Cardiocephalus* therein). According to Berman (2000), the bone conventionally referred to as a supraoccipital in many microsaurs and lysorophids derives from the tectum posterius, and not from the tectum synoticum as in other taxa. Recoding the occurrence of a supraoccipital according to Berman's (2000) suggestion (and imposing an unknown condition for *Westlothiana*) does not affect the results of the analysis, but restricts the presence of a separately ossified supraoccipital to crown-amniotes and *Limnoscelis* only.

Exoccipitals

161. *EXOCC* 2. *Absence* (0) *or presence* (1) *of condition: exoccipitals enlarged to form flattened, widely spaced double occipital condyles*. This character is treated separately from characters 162 and 164 below. It is observed in scincosaurids and diplocaulids (Beerbower, 1963; A. C. Milner, 1980; Bossy & Milner, 1998), in which the condylar surfaces are transversely expanded and extremely flattened dorsoventrally.

162. *EXOCC* 3. *Absence* (0) *or presence* (1) *of condition: exoccipitals enlarged, about as broad as high and forming stout, double occipital condyles*. Enlarged exoccipital condyles (although not necessarily appressed and obliterating the basioccipital; see character 164 below) are observed in *Dendrerpeton* and more derived temnospondyls (Olson, 1941; Bolt, 1969, 1991; Berman *et al.*, 1985; Milner, 1988, 1990, 1993, 2000; Dilkes, 1990; Holmes *et al.*, 1998; Carroll, 2000; Rocek & Rage, 2000*b*; Gardner, 2001).

163. *EXOCC* 4. *Absence* (0) *or presence* (1) *of condition: exoccipitals forming continuous, concave, strap-shaped articular surfaces with basioccipital*. A strap-shaped, transversely concave articular surface of the occiput is found exclusively in microsaurs and lysorophids (Carroll & Gaskill, 1978; Wellstead, 1991).

164. *EXOCC* 5. *Absence* (0) *or presence* (1) *of condition: exoccipitals expanded and appressed to each other, so as to obliterate basioccipital posterior surface*. The derived condition characterizes a more restricted set of taxa than that implied by character 162 above, including dissorophoids, albanerpetontids and crown-lissamphibians.

Basioccipital

165. *BASOCC* 1. *Basioccipital notochordal* (0) *or not* (1). Following Clack (1998*c*, 2001), a notochordal basioccipital is primitively preset in *Acanthostega*, *Ichthyostega* and *Crassigyrinus*. Under DELTRAN, the plesiomorphic condition appears to be a transitional feature of stem-tetrapods, implying parallel acquisitions of the derived state in *Greererpeton* (Smithson, 1982) and in a clade consisting of baphetids plus crown-tetrapods. Under ACCTRAN, the plesiomorphic state of *Crassigyrinus* appears as a reversal.

166. *BASOCC* 5. *Articular surface of basioccipital not convex* (0) *or convex* (1). A convex basioccipital is usually considered to be a shared derived character of crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981), but a less pronounced version of their 'bulbous' basioccipital articular surface is present in diadectomorphs (Romer, 1946; Fracasso, 1987; Berman *et al.*, 1998; Berman, 2000) [see also Gauthier *et al.* (1988*b*) and Carroll (1991*b*)].

167. *BASOCC* 6. *Absence* (0) *or presence* (1) *of condition: basioccipital circular and recessed*. Although usually regarded as an aïstopod synapomorphy (Carroll, 1998; see also Anderson (in press)), a basioccipital with a recessed posterior surface for a condylar process of the first cervical vertebra is also reported in *Adelogyrinus* (Andrews & Carroll, 1991).

Opisthotic

168. *OPI* 2. *Absence* (0) *or presence* (1) *of condition: opisthotic forming thick plate with supraoccipital, separating exoccipitals* *from skull table*. Based on Berman's (2000) recent investigation, the derived condition of the character in question is found in baphetids (Beaumont, 1977), embolomeres (Panchen, 1977; Holmes, 1984, 1989; Smithson, 1985; Clack, 1987*a*), diadectomorphs (Romer, 1946; Berman *et al.*, 1998; Berman, 2000) and basal crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981).

Parasphenoid

169. *PASPHE* 1. *Parasphenoid without* (0) *or with* (1) *elongate, strut-like cultriform process.* A parallel-sided, strut-like cultriform process is a temnospondyl feature (Milner, 1988, 1990, 1993, 2000), although its presence is also recorded in colosteids (Smithson, 1982; Hook, 1983), *Microbrachis* (Carroll & Gaskill, 1978) and *Ptyonius* (Bossy & Milner, 1998).

170. *PASPHE* 3. *Parasphenoid without* (0) *or with* (1) *posterolaterally directed, ventral thickenings* (*ridges ending in basal tubera*). The occurrence of elongate ridges on the parasphenoid is documented in *Crassigyrinus* (Clack, 1998*c*), *Eucritta* (Clack, 2001), embolomeres (Panchen, 1972, 1977; Holmes, 1984, 1989; Smithson, 1985; Clack, 1987*a*), seymouriamorphs (White, 1939; Bystrow, 1944; Laurin, 1996*b*; Klembara, 1997), diadectomorphs (Romer, 1946; Fracasso, 1987; Berman *et al.*, 1998) and crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981).

171. *PASPHE* 6. *Parasphenoid without* (0) *or with* (1) *single median depression.* A shallow depressed area occupies a subcentral position in the posterior plate of the parasphenoid of *Crassigyrinus* (Clack, 1998*c*, 2001), *Whatcheeria* (Lombard & Bolt, 1995), *Eucritta* (Clack, 2001) and several stem-amniotes, including *Caerorhachis* (Holmes & Carrol, 1977; Ruta *et al.*, 2001), embolomeres (Panchen, 1972, 1977; Holmes, 1984, 1989; Smithson, 1985; Clack, 1987*a*), *Kotlassia* (Bystrow, 1944), *Diadectes* (Berman *et al.*, 1998), basal crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981) and *Westlothiana* (Smithson *et al.*, 1994).

172. *PASPHE* 7. *Parasphenoid without* (0) *or with* (1) *paired lateral depressions.* In *Greererpeton* (Smithson, 1982), baphetids (Beaumont, 1977), *Cochleosaurus* (Godfrey & Holmes, 1995) and *Micraroter* (Carroll & Gaskill, 1978), the posterior plate of the parasphenoid shows two shallow, anteroposteriorly elongate depressions (Coates, 1996; Clack, 1998*c*, 2001).

173. *PASPHE* 9. *Ventral cranial fissure not sutured* (0), *sutured but traceable* (1), *or eliminated* (2). Coding of this character follows Clack (1998*c*, 2001). Among ingroup taxa, *Ichthyostega* shows the plesiomorphic condition, whereas state 1 occurs in *Acanthostega* and *Crassigyrinus*.

174. *PASPHE* 11. *Parasphenoid without* (0) *or with* (1) *anterolateral wings projecting anterior to cultriform insertion.* In *Apateon* (Schoch, 1992), *Amphibamus* (Watson, 1940), *Doleserpeton* (Bolt, 1969), *Karaurus* (Milner, 2000) and *Triadobatrachus* (Rocek & Rage, 2000*b*), the basipterygoid processes extend considerably laterally and slightly anterior to the proximal insertion of the cultriform process, so that the anterior margin of the parabasisphenoid appears shallowly concave.

175. *PASPHE* 12. *Parasphenoid without* (0) *or with* (1) *triangular denticle patch with raised margins at base of cultriform process.* A triangular patch of denticles with distinct, raised margins is observed in *Cochleosaurus* (Godfrey & Holmes, 1995), *Dendrerpeton* (Holmes *et al.*, 1998), *Eoscopus* (Daly, 1994) and *Doleserpeton* (Bolt, 1969).

176. *PASPHE* 13. *Absence* (0) *or presence* (1) *of condition: parasphenoid much wider than long immediately behind basal articulation.* The derived condition of this feature is shared by derived dissorophoids (Bolt, 1969, 1977, 1979, 1991; Boy, 1972, 1986, 1995), albanerpetontids (Gardner, 2001) and crown-lissamphibians (Schoch, 1992, 1995, 1998; Carroll, 2000; Milner, 2000; Rocek and Rage, 2000*b*), but it is found also in *Isodectes* (Sequeira, 1998) and *Batropetes* (Carroll, 1991*a*). In all these taxa, the posterior plate of the parasphenoid is at least 25% wider than long and subrectangular or subtrapezoidal in outline.

(*d*) *Lower jaw*

Jaw articulation

177. *JAWART* 1. *Jaw articulation lying behind* (0), *level with* (1) *or anterior to* (2) *occiput.* No coherent set of internested state changes can be detected for this character. The plesiomorphic state, related or not to the presence of an elongate suspensorium, is widespread among stem-group taxa and several temnospondyls, but the two derived states occur among trimerorhachoids and some dissorophoids. State 2 is found in several primitive crown-lissamphibians, as well as in diplocaulids, some aïstopods, lysorophids, various tuditanomorphs and few microbrachomorphs. The plesiomorphic condition characterizes also the basal portion of the amniote stem-group, few tuditanomorphs and some urocordylids. State 1 occurs in seymouriamorphs, diadectomorphs, crown-amniotes, *Westlothiana* and some lepospondyls. Coding follows Clack (1998*c*, 2001), Paton *et al.* (1999) and Laurin (1998*b*).

Parasymphysial plate

178. *PSYM* 1. *Presence* (0) *or absence* (1) *of parasymphysial plate.* A parasymphysial plate is ubiquitous among stem-tetrapods, such as *Ventastega* (Ahlberg *et al.*, 1994), *Acanthostega* (Ahlberg & Clack, 1998), *Ichthyostega* (Jarvik, 1980, 1996), *Greererpeton* (Bolt & Lombard, 2001), *Crassigyrinus* (Ahlberg & Clack, 1998), *Whatcheeria* (Lombard & Bolt, 1995) and baphetids (Beaumont, 1977; Ahlberg & Clack, 1998). It is also present in the basal part of the amniote stem-group, in *Caerorhachis* (Holmes & Carroll, 1977; Ruta *et al.*, 2001), *Archeria* (Holmes, 1989) and *Pholiderpeton scutigerum* (Clack, 1987*a*). Some mandibular fragments of *Proterogyrinus*, originally figured by Holmes (1984), show a disrupted, denticle-covered area of bone near the symphysis; the latter may represent a parasymphysial plate, although evidence is ambiguous. Whether a parasymphysial plate is present in *Anthracosaurus* is uncertain (Panchen, 1977).

179. *PSYM* 2. *Parasymphysial plate without* (0) *or with* (1) *paired fangs.* Parasymphysial plate fangs occur in *Acanthostega* (Ahlberg & Clack, 1998), *Ichthyostega* (Jarvik, 1980, 1996), *Greererpeton* (Bolt & Lombard, 2001), *Crassigyrinus* (Ahlberg & Clack, 1998), baphetids (Beaumont, 1977; Ahlberg & Clack, 1998) and, possibly, *Caerorhachis* (Holmes & Carroll, 1977; Ruta *et al.*, 2001).

180. *PSYM* 3. *Parasymphysial plate without* (0) *or with* (1) *tooth row.* A tooth row on the parasymphysial plate is observed in *Ventastega* (Ahlberg *et al.*, 1994), *Acanthostega* (Ahlberg & Clack, 1998) and *Whatcheeria* (Lombard & Bolt, 1995).

181. *PSYM* 4. *Parasymphysial plate with* (0) *or without* (1) *denticles.* Among the ingroup taxa, clusters of denticles on the parasymphysial plate are observed in *Acanthostega* (Ahlberg & Clack, 1998) and, possibly, *Caerorhachis* (Holmes & Carroll, 1977; Ruta *et al.*, 2001).

Dentary

182. *DEN* 1. *Dentary with* (0) *or without* (1) *accessory tooth row.* Within the crown-group, acces sory tooth rows are recorded in *Pantylus* and *Captorhinus* (Fox & Bowman, 1966; Carroll & Gaskill, 1978).

183. *DEN* 2. *Dentary with* (0) *or without* (1) *anterior fang pair.* The loss of anterior dentary fangs is observed in *Acheloma* (Olson, 1941), some derived amphibamids (Bolt, 1969), albanerpetontids (Gardner, 2001), crown-lissamphibians (Carroll, 2000; Milner, 2000), several embolomeres such as *Anthracosaurus* (Panchen, 1977), *Pholiderpeton attheyi* (Panchen, 1972) and *Archeria* (Holmes, 1989), gephyrostegids (Carroll, 1970), seymouriamorphs (White, 1939; Bystrow, 1944; Laurin, 1996*b*; Klembara, 1997), *Diadectes* (Romer, 1946; Berman *et al.*, 1998), *Paleothyris* and *Petrolacosaurus* (Clark & Carroll, 1973; Reisz, 1977, 1981), *Westlothiana* (Smithson *et al.*, 1994) and the majority of lepospondyls, except pantylids, *Microbrachis* and, possibly, *Acherontiscus* (Carroll, 1969*b*; Carroll & Gaskill, 1978; Berman *et al.*, 1988).

184. *DEN* 3. *Dentary with* (1) *or without* (0) *chamfered ventral margin.* A chamfered ventral margin of the dentary has been documented only in *Metaxygnathus* (not included in our analysis), *Ventastega* and *Acanthostega* (Ahlberg *et al.*, 1994; Ahlberg & Clack, 1998).

185. *DEN* 4. *Dentary without* (0) *or with* (1) *U-shaped notch for premaxillary tusks.* The occurrence of a deep, smooth-surfaced notch near the anterior end of the lateral surface of the dentary is an apomorphy of colosteids (Smithson, 1982; Godfrey, 1989; Bolt & Lombard, 2001).

186. *DEN* 7. *Dentary toothed* (0) *or toothless* (1). A toothless dentary is autapomorphic for salientians (Milner, 1988; Rocek & Rage, 2000*b*).

187. *DEN* 8. *Dentary length greater* (0) *or smaller* (1) *than half the length between snout and occiput.* The derived condition of an abbreviated, stout dentary is found in White, 1939; Batropetes (Carroll, 1991*a*) and *Brachydectes* (Wellstead, 1991).

Splenial

188. *SPL* 2. *Absence* (0) *or presence* (1) *of condition: rearmost extension of mesial lamina of splenial closer to anterior margin of adductor fossa than to anterior end of jaw.* The derived state of this character (see also Ruta *et al.*, 2001) is widespread in the amniote branch of the tetrapod tree [notable exceptions are *Phlegethontia* (Anderson, in press), *Pholiderpeton attheyi* (Panchen, 1972) and *Rhynchonkos* (Carroll & Gaskill, 1978)]. It is also observed in *Greererpeton* (Bolt & Lombard, 2001), *Crassigyrinus* (Ahlberg & Clack, 1998) and *Megalocephalus* (Beaumont, 1977; Ahlberg & Clack, 1998).

189. *SPL* 3. *Absence* (0) *or presence* (1) *of suture between splenial and anterior coronoid.* The plesiomorphic state of this character, as found in the outgroups, is also present in *Acanthostega* and *Crassigyrinus* (see Ahlberg & Clack, 1998).

190. *SPL* 4. *Absence* (0) *or presence* (1) *of suture between splenial and middle coronoid.* The contact between the splenial and the middle coronoid occurs, under ACCTRAN optimization, in edopoids (Godfrey & Holmes, 1995), trimerorhachoids (Case, 1935), *Phonerpeton* (Dilkes, 1990), embolomeres other than *Anthracosaurus* (Panchen, 1972, 1977; Holmes, 1984, 1989; Smithson, 1985; Clack, 1987*a*), *Gephyrostegus* (Carroll, 1970; Ahlberg & Clack, 1998), *Discosauriscus* (Klembara, 1997), *Seymouria* (White, 1939; Laurin, 1996*b*) and *Rhynchonkos* (Carroll & Gaskill, 1978).

Postsplenial

191. *POSPL* 1. *Presence* (0) *or absence* (1) *of postsplenial.* A separately ossified postsplenial is absent in albanerpetontids (Gardner, 2001), crown-lissamphibians (Schoch, 1998; Carroll, 2000; Milner, 2000; Rocek &

Rage, 2000*b*), diadectomorphs (Romer, 1946; Berman *et al.*, 1998), crown-amniotes except *Petrolacosaurus* (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981), *Hapsidopareion*, *Euryodus* (Carroll & Gaskill, 1978), lysorophids (Wellstead, 1991), aïstopods (Carroll, 1998; Anderson, in press) and nectrideans (Beerbower, 1963; Bossy & Milner, 1998).

192. *POSPL* 2. *Postsplenial without* (0) *or with* (1) *mesial lamina.* Under ACCTRAN, a mesial lamina of the postsplenial is recorded in all tetrapods more crownward than *Crassigyrinus* (Ahlberg & Clack, 1998), although a reversal to the plesiomorphic condition characterizes *Gephyrostegus* (Carroll, 1970) as well as lepospondyls other than microsaurs.

193. *POSPL* 3. *Postsplenial with* (0) *or without* (1) *pit line.* Following Ahlberg *et al.* (1994) and Ahlberg & Clack (1998), absence of a postsplenial pit line is recorded in all tetrapods more crownward than *Ventastega* (however, *Ichthyostega* is an exception; Jarvik, 1980, 1996).

Angular

194. *ANG* 1. *Presence* (0) *or absence* (1) *of angular.* A separately ossified angular is absent in *Phlegethontia* (Anderson, in press), and crown-lissamphibians except *Karaurus* (Milner, 1988, 2000).

195. *ANG* 2. *Angular without* (0) *or with* (1) *mesial lamina.* Following Ahlberg & Clack (1998), the occurrence of an angular mesial lamina characterizes all tetrapods more crownward than *Tulerpeton*, although *Gephyrostegus* (Carroll, 1970) shows a reversal to the plesiomorphic condition.

196. *ANG* 3. *Angular contacting prearticular* (0) *or not* (1). The derived feature of this character is apparently autapomorphic for *Acanthostega* (Ahlberg & Clack, 1998).

197. *ANG* 4. *Angular not reaching* (0) *or reaching* (1) *posterior end of lower jaw.* The posteriormost part of the external surface of the angular reaches the rear end of the lower jaw in *Isodectes* (Sequeira, 1998), dissorophoids (Olson, 1941; Boy, 1972, 1987, 1995; Berman *et al.*, 1985; Dilkes, 1990; Boy & Sues, 2000), *Discosauriscus* (Klembara, 1997), *Seymouria* (White, 1939; Laurin, 1996*b*), diadectomorphs (Romer, 1946; Berman *et al.*, 1998), crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981), *Westlothiana* (Smithson *et al.*, 1994) and lepospondyls (Carroll & Gaskill, 1978; Andrews & Carroll, 1991; Wellstead, 1991; Bossy & Milner, 1998; Carroll, 1998).

Surangular

198. *SURANG* 1. *Presence* (0) *or absence* (1) *of surangular.* Absence of a separately ossified surangular is recorded in albanerpetontids (Gardner, 2001), crown-lissamphibians (Carroll, 2000; Milner, 2000; Rocek & Rage, 2000*b*) and *Phlegethontia* (Anderson, in press).

199. *SURANG* 3. *Surangular with* (0) *or without* (1) *pit line.* Following Ahlberg & Clack (1998), absence of a surangular pit line is recorded in all tetrapods more crownward than *Ventastega* (see also Ahlberg *et al.*, 1994).

200. *SURANG* 5. *Absence* (0) *or presence* (1) *of condition: lateral exposure of the surangular smaller than that of the angular.* In the tuditanomorphs *Hapsidopareion*, *Cardiocephalus* and *Euryodus* (Gregory *et al.*, 1956; Carroll & Gaskill, 1978), the lateral surface of the surangular is a slender, dorsoventrally narrow, elongate and oblique splinter of bone situated at the posterodorsal corner of the angular.

Prearticular

201. *PREART* 5. *Prearticular sutured with splenial* (0) *or not* (1). In post-edopoid temnospondyls, *Anthracosaurus* and *Pholiderpeton attheyi* (Panchen, 1972, 1977), the prearticular fails to contact the splenial (Ahlberg & Clack, 1998).

Anterior coronoid

202. *ANT COR* 1. *Anterior coronoid present* (0) *or absent* (1). The anterior coronoid is either absent as a separate ossification or of questionable identification in albanerpetontids (Gardner, 2001), crown-lissamphibians (Schoch, 1998; Carroll, 2000; Milner, 2000; Rocek & Rage, 2000*b*), *Diadectes* (Berman *et al.*, 1998), crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981), *Pantylus*, *Rhynchonkos* (Carroll & Gaskill, 1978), lysorophids (Wellstead, 1991), *Batrachiderpeton*, *Diploceraspis* (Beerbower, 1963; Bossy & Milner, 1998) and *Phlegethontia* (Anderson, in press).

203. *ANT COR* 2. *Anterior coronoid with* (0) *or without* (1) *fangs.* Absence of fangs on the anterior coronoid is a character of all tetrapods more derived than *Ventastega* (Ahlberg & Clack, 1998); exceptions are *Greererpeton* (Bolt & Lombard, 2001) and *Gephyrostegus* (Carroll, 1970).

204. *ANT COR* 3. *Anterior coronoid with* (0) *or without* (1) *denticles.* A patch of denticles on the anterior coronoid is documented in *Crassigyrinus*, *Whatcheeria* and crown-tetrapods (where observed) (Ahlberg & Clack, 1998).

205. *ANT COR* 4. *Anterior coronoid with* (0) *or without* (1) *tooth row.* All tetrapods more crownward than colosteids (except *Whatcheeria*; Lombard & Bolt, 1995) lack a tooth row on the anterior coronoid (Ahlberg & Clack, 1998).

Middle coronoid

206. *MID COR* 1. *Middle coronoid present* (0) *or absent* (1). The middle coronoid is either absent as a separate ossification or cannot be identified unambiguously in albanerpetontids (Gardner, 2001), crown-lissamphibians (Schoch, 1998; Carroll, 2000; Milner, 2000;

Rocek & Rage, 2000*b*), *Diadectes* (see Berman *et al*., 1998), crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981), *Pantylus* (Carroll & Gaskill, 1978), lysorophids (Wellstead, 1991), *Batrachiderpeton*, *Diploceraspis* (Beerbower, 1963; Bossy & Milner, 1998) and *Phlegethontia* (Anderson, in press).

207. *MID COR* 2. *Middle coronoid with* (0) *or without* (1) *fangs*. Middle coronoid fangs are absent in all tetrapods more derived than *Ventastega* (Ahlberg & Clack, 1998), but *Gephyrostegus* shows a reversal to the plesiomorphic condition (Carroll, 1970).

208. *MID COR* 3. *Middle coronoid with* (0) *or without* (1) *denticles*. A denticle patch on the middle coronoid characterizes most Devonian taxa, *Whatcheeria*, baphetids and tuditanomorphs (although only *Rhynchonkos* can be scored for this character) (Beaumont, 1977; Carroll & Gaskill, 1978; Jarvik, 1980, 1996; Ahlberg *et al*., 1994; Lombard & Bolt, 1995; Ahlberg & Clack, 1998).

209. *MID COR* 4. *Middle coronoid with* (0) *or without* (1) *marginal tooth row*. *Ventastega* (Ahlberg *et al*., 1994), *Acanthostega* (Ahlberg & Clack, 1998), *Ichthyostega* (Jarvik, 1980, 1996), *Whatcheeria* (Lombard & Bolt, 1995), *Trimerorhachis* (Case, 1935) and *Rhynchonkos* (as well as remaining tuditanomorphs under A) show a tooth row on the middle coronoid (Carroll & Gaskill, 1978; Ahlberg & Clack, 1998).

Posterior coronoid

210. *POST COR* 1. *Posterior coronoid present* (0) *or absent* (1). The posterior coronoid is absent as a separate ossification, or cannot be identified unambiguously, in lysorophids (*fide* Wellstead, 1991), *Sauropleura* (Bossy & Milner, 1998), *Phlegethontia* (Anderson, in press), albanerpetontids (Gardner, 2001) and crown-lissamphibians (Carroll, 2000; Milner, 2000; Rocek & Rage, 2000*b*). However, we do point out recent contributions by Schoch (1998) bearing on the issue of identification of the caudate coronoid as the posterior coronoid.

211. *POST COR* 2. *Posterior coronoid with* (0) *or without* (1) *fangs*. Following Ahlberg & Clack (1998), absence of fangs on the posterior coronoid characterizes all post-panderichthyid tetrapods.

212. *POST COR* 3. *Posterior coronoid with* (0) *or without* (1) *denticles*. A patch of denticles occurs in colosteids, all temnospondyls in which the third coronoid is observed, most stem-amniotes and several lepospondyls (it is absent, however, in *Pantylus* and *Diploceraspis*; Beerbower, 1963; Carroll & Gaskill, 1978). *Panderichthys*, Devonian tetrapods, *Whatcheeria*, baphetids and crown-amniotes exhibit a denticle-less posterior coronoid (Ahlberg & Clack, 1998).

213. *POST COR* 4. *Posterior coronoid with* (0) *or without* (1) *tooth row*. A tooth row is primitively present in several Devonian taxa, such as *Ventastega* (Ahlberg *et al*., 1994), *Acanthostega* (Ahlberg & Clack, 1998) and *Ichthyostega* (Jarvik, 1980, 1996), but is also documented in *Whatcheeria* (Lombard & Bolt, 1995), *Trimerorhachis* (Case, 1935), *Diploceraspis* (Beerbower, 1963) and *Anthracosaurus* (Panchen, 1977).

214. *POST COR* 5. *Posterior coronoid without* (0) *or with* (1) *posterodorsal process*. In its derived condition, this character is present in the majority of crown-tetrapods (Ahlberg & Clack, 1998), except in the diplocaulid *Batrachiderpeton* (Bossy & Milner, 1998) and in the embolomeres *Anthracosaurus* (Panchen, 1977), *Pholiderpeton attheyi* (Panchen, 1972) and *Proterogyrinus* (Holmes, 1984).

215. *POST COR* 6. *Posterior coronoid not exposed* (0) *or exposed* (1) *in lateral view*. The posterior coronoid is visible in lateral aspect, immediately posterodorsal to the rearmost end of the dentary, in *Greererpeton* (Bolt & Lombard, 2001), *Whatcheeria* (Lombard & Bolt, 1995), some temnospondyls (e.g. *Isodectes*, *Eryops*, *Micromelerpeton*, *Leptorophus*, *Schoenfelderpeton*; Sawin, 1941; Boy, 1972, 1987, 1995; Sequeira, 1998; Boy & Sues, 2000), such embolomeres as *Archeria* (Holmes, 1989) and *Pholiderpeton scutigerum* (Clack, 1987*a*; Ahlberg & Clack, 1998), gephyrostegids (Carroll, 1970), seymouriamorphs (White, 1939; Bystrow, 1944; Laurin, 1996*b*; Klembara, 1997; Ahlberg & Clack, 1998), diadectomorphs (Berman *et al*., 1998) and primitive crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981).

216. *POST COR* 7. *Posterodorsal process of posterior coronoid not contributing* (0) *or contributing* (1) *to tallest point of lateral margin of adductor fossa* (*'surangular' crest*). Where present, the posterodorsal process of the posterior coronoid may extend rearward and dorsalward to the point of maximum elevation of the 'surangular' crest. Under ACCTRAN, the derived state of this character is found in temnospondyls more derived than trimerorachoids (Sawin, 1941; Boy, 1972, 1987, 1995; Dilkes, 1990; Boy & Sues, 2000), in stem-amniotes more derived than gephyrostegids (White, 1939; Bystrow, 1944; Laurin, 1996*b*; Klembara, 1997; Ahlberg & Clack, 1998; Berman *et al*., 1998), and in some basal crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973), although not in *Petrolacosaurus* (Reisz, 1977, 1981). It is also recorded in *Microbrachis* and *Pantylus*, although the situation of other microsaurs is uncertain (Carroll & Gaskill, 1978).

Adductor fossa

217. *ADD FOS* 1. *Adductor fossa facing dorsally* (0) *or mesially* (1). A mesially facing adductor fossa occurs in baphetids and all crown-tetrapods in which the posterior part of the mesial surface of the lower jaw is observed. Coding for this character follows Ahlberg & Clack (1998).

(*e*) *Teeth*

218. *TEETH* 1. *Absence* (0) *or presence* (1) *of pedicely on marginal teeth.* The derived condition of this character is present in *Amphibamus* and *Doleserpeton* (Bolt, 1969, 1977, 1979, 1991; Milner, 1988, 1990, 1993, 2000; Trueb & Cloutier, 1991), and is shared with crown-lissamphibians, although only *Eocaecilia* (Carroll, 2000) and *Valdotriton* (Evans & Milner, 1996) could be scored for the presence of pedicely.

219. *TEETH* 2. *Marginal teeth monocuspid* (0) *or multicuspid* (1). Multicuspid teeth characterize different tetrapod groups, but the position and number of the cusps vary (Carroll, 1991*a*; Gardner, 1999, 2001). For this reason, we coded for the 'multicuspid' condition separately from the condition 'two cuspules labiolingually arranged', detailed in the following character. We also note that in several Permo-Carboniferous and Triassic stem-amniotes, the marginal teeth show several cusps (Ivakhnenko, 1987). Laurin (1998*b*) did not distinguish between the mesiolateral cusps shown by brachystelechids and the labiolingual cusps of dissorophoids/lissamphibians, thus conflating under the same state (multicuspid) different morphological patterns.

220. *TEETH* 3. *Marginal teeth without* (0) *or with* (1) *two cuspules labiolingually arranged.* This character is present in some dissorophoids, notably *Amphibamus* and *Doleserpeton* (Bolt, 1969, 1977, 1979, 1991; Milner, 1988, 1990, 1993, 2000; Trueb & Cloutier, 1991), and is shared with crown-lissamphibians, although only *Eocaecilia* could be scored for this condition (Carroll, 2000).

221. *TEETH* 5. *Dentary teeth not larger* (0) *or larger* (1) *than maxillary teeth.* Dentary teeth are distinctly larger than maxillary teeth in colosteids (Smithson, 1982; Hook, 1983), but this condition is achieved in parallel by the temnospondyls *Isodectes* (Sequeira, 1998) and *Balanerpeton* (Milner & Sequeira, 1994).

222. *TEETH* 6. *Marginal tooth crowns not chisel-tipped* (0) *or chisel-tipped* (1). The crown tips of the marginal teeth are chisel-shaped in adelospondyls (Andrews & Carroll, 1991), as well as in some embolomeres, notably *Proterogyrinus* (Holmes, 1984), *Pholiderpeton attheyi* (Panchen, 1972, 1980), *P. scutigerum* (Clack, 1987*a*) and *Archeria* (Holmes, 1989).

223. *TEETH* 7. *Marginal tooth crowns without* (0) *or with* (1) *dimple.* According to Andrews & Carroll (1991), the presence of an anteroposteriorly elongate depression, or dimple, on the proximal half of the labial and lingual surfaces of the tooth crowns is regarded as a diagnostic feature of adelospondyls (see also character 222).

224. *TEETH* 8. *Absence* (0) *or presence* (1) *of condition: marginal tooth crowns robust, conical structures.* Pantylid and gymnarthrid microsaurs possess blunt and massive tooth crowns the height of which is only slightly greater than or as great as their basal width (Gregory *et al.*, 1956; Carroll & Gaskill, 1978).

(2) Postcranial skeleton

(*a*) *Pectoral girdle*

Cleithrum

225. *CLE* 1. *Absence* (0) *or presence* (1) *of T-shaped dorsal expansion of cleithrum.* A robust, T-shaped expansion of the dorsal portion of the cleithrum is an apomorphy of diplocaulid nectrideans (A. C. Milner, 1980; Bossy & Milner, 1998).

226. *CLE* 2. *Cleithrum with* (0) *or without* (1) *postbranchial lamina.* As discussed by Coates (1996), a postbranchial lamina is primitively retained in Devonian taxa (*Acanthostega*, *Ichthyostega*) and *Greererpeton*, and may be present also in *Whatcheeria* [but see Coates (1996), Lombard & Bolt (1995) and Bolt & Lombard (2000)].

227. *CLE* 3. *Cleithrum co-ossified with* (0) *or separate from* (1) *scapulocoracoid.* The derived state of this character [coding based on Carroll (1995), Coates (1996), Clack (1998*c*, 2001) and Laurin (1998*b*)] is found in *Tulerpeton* and all post-Devonian tetrapods (Lebedev & Coates, 1995).

Clavicle

228. *CLA* 3. *Clavicles meet anteriorly* (0) *or not* (1). The condition of anteriorly separated clavicles is widespread among early tetrapods; it is found in *Acanthostega*, *Ichthyostega*, baphetids, most temnospondyls and the vast majority of 'reptiliomorphs', except seymouriamorphs (White, 1939; Bystrow, 1944; Laurin, 1995, 1996*b*; Klembara & Bartík, 2000), some tuditanomorphs (Carroll & Gaskill, 1978), *Scincosaurus* and diplocaulid nectrideans (A. C. Milner, 1980; Bossy & Milner, 1998). The present character has been scored as unknown in *Crassigyrinus* (but see Clack, 1998*c*, 2001).

Interclavicle

229. *INTCLA* 1. *Absence* (0) *or presence* (1) *of condition: posterior margin of interclavicle drawn out into parasternal process.* This character is widespread among stem-tetrapods (*Acanthostega*, *Ichthyostega*, *Tulerpeton*, *Crassigyrinus*, *Whatcheeria*) and several 'reptiliomorphs' (except for lepospondyls other than microsaurs) (White, 1939; Bystrow, 1944; Carroll & Gaskill, 1978; Jarvik, 1980, 1996; Carroll, 1995; Laurin, 1995, 1996*b*; Lebedev &

Coates, 1995; Lombard & Bolt, 1995; Coates, 1996; Klembara & Bartík, 2000; Smithson, 2000).

230. *INTCLA* 2. *Absence* (0) *or presence* (1) *of condition: parasternal process elongate and parallel-sided for most of its length. Ichthyostega*, *Whatcheeria* and the vast majority of stem- and crown-amniotes display an elongate parasternal process (White, 1939; Bystrow, 1944; Carroll & Gaskill, 1978; Jarvik, 1980, 1996; Carroll, 1995; Laurin, 1995, 1996*b*; Lombard & Bolt, 1995; Klembara & Bartík, 2000; Smithson, 2000).

231. *INTCLA* 3. *Absence* (0) *or presence* (1) *of condition: interclavicle wider than long.* This is one of several characters (e.g. see Clack, 1998*c*, 2001) describing the overall shape of the interclavicle. The occurrence of the derived state matches that of the previous character to a large extent; however, it is not found in the majority of lepospondyls, basal 'reptiliomorphs' (embolomeres and gephyrostegids) and most temnospondyls (*Ecolsonia*, *Apateon* and *Schoenfelderpeton* are notable exceptions).

232. *INTCLA* 4. *Interclavicle rhomboidal with posterior half longer* (0) *or shorter* (1) *than anterior half.* See also Clack (1998*c*, 2001). The derived state is shown by colosteids, some trimerorhachoids and lepospondyls other than microsaurs and lysorophids.

Scapulocoracoid

233. *SCACOR* 1. *Absence* (0) *or presence* (1) *of separate scapular ossifications.* Based on Carroll (1995), Lebedev & Coates (1995), Coates (1996), Clack (1998*c*) and Laurin (1998*c*), the derived state of this character is found sporadically among tetrapods, and does not identify monophyletic groups with the exception of the clade encompassing *Discosauriscus* and *Seymouria*.

234. *SCACOR* 2. *Glenoid subterminal* (0) *or not* (1) (*scapulocoracoid extending ventral to posteroventral margin of glenoid*). Reisz (1981) noted this feature in several basal crown-amniotes, but its occurrence is more widespread (e.g. *Ichthyostega*, *Tulerpeton*, several lepospondyls, derived temnospondyls).

235. *SCACOR* 3. *Presence* (0) *or absence* (1) *of enlarged glenoid foramen.* The derived condition of this character is found in *Acanthostega*, derived temnospondyls and most lepospondyls (Carroll & Gaskill, 1978; Coates, 1996).

236. *SCACOR* 4. *Absence* (0) *or presence* (1) *of ventromesially extended infraglenoid buttress.* The derived state (where observed) is found in all tetrapods more derived than *Acanthostega* (Lebedev & Coates, 1995; Coates, 1996).

Anocleithrum

237. *ANOCLE* 1. *Presence* (0) *or absence* (1) *of anocleithrum.* The distribution of the anocleithrum among early tetrapods is rather sparse. Among Devonian post-panderichthyid tetrapods, it is found in *Acanthostega* and *Tulerpeton* (Lebedev & Coates, 1995; Coates, 1996), whereas among post-Devonian taxa, it has been recorded so far in *Pholiderpeton scutigerum* (Clack, 1987*b*) and *Discosauriscus austriacus* (Klembara & Bartík, 2000). J. Klembara and M. Ruta (personal observations) have identified a possible anocleithrum in a small specimen of the Upper Carboniferous-Lower Permian seymouriamorph *Utegenia*.

(*b*) *Forelimb*

Humerus

238. *HUM* 1. *Latissimus dorsi process offset anteriorly* (0) *or aligned with ectepicondyle* (1). Coding for this character is based on Coates (1996; see also Clack, 1998*c*, 2001). The primitive condition is found in *Acanthostega* (Coates, 1996), *Whatcheeria* (Lombard & Bolt, 1995), baphetids (Milner & Lindsay, 1998), *Discosauriscus* [Klembara, 1997; but see also Klembara *et al.* (2001) for an alternative interpretation of this process in *Seymouria*], *Pantylus* (Carroll & Gaskill, 1978) and diadectomorphs (Heaton, 1980; Berman & Sumida, 1990; Sumida, 1997; Berman *et al.*, 1998).

239. *HUM* 2. *Absence* (0) *or presence* (1) *of distinct supinator process projecting anteriorly.* A distinct, robust and anteriorly projecting supinator process occurs in some temnospondyls (especially heavily built and terrestrial forms), some seymouriamorphs, diadectomorphs, several primitive crown-amniotes and some nectrideans (Miner, 1925; Olson, 1941; Bystrow, 1944; Heaton, 1980; Reisz, 1977, 1981; Sumida, 1997; Berman *et al.*, 1998; Bossy & Milner, 1998).

240. *HUM* 3. *Presence* (0) *or absence* (1) *of ventral humeral ridge.* Embolomeres are the only group among crown-tetrapods that retain such a ridge, which is otherwise found in some stem-tetrapods (Jarvik, 1980, 1996; Panchen, 1985; Godfrey, 1989; Lebedev & Coates, 1995; Coates, 1996; Milner & Lindsay, 1998).

241. *HUM* 4. *Latissimus dorsi process confluent with* (0) *or distinct from* (1) *deltopectoral crest.* The description of this character is based on data from Lebedev & Coates (1995) and Coates (1996). The derived state is observed in all tetrapods more derived than *Tulerpeton*.

242. *HUM* 5. *Presence* (0) *or absence* (1) *of entepicondylar foramen.* See Carroll (1995), Lebedev & Coates (1995), Coates (1996), Clack (2001) and Laurin (1998*b*) for an analysis of the distribution of this character. The entepicondylar foramen is absent in some tuditanomorphs, most nectrideans and most temnospondyls [for exceptions, see Carroll & Gaskill (1978), A. C. Milner

(1980), Milner (1988, 1990, 1993) and Bossy & Milner (1998)].

243. *HUM* 6. *Presence* (0) *or absence* (1) *of ectepicondylar foramen.* The ectepicondylar foramen is absent in crown-tetrapods as well as in *Tulerpeton* (Lebedev & Coates, 1995), *Greererpeton* (Godfrey, 1989), *Whatcheeria* (Lonbard & Bolt, 1995) and baphetids (Milner & Lindsay, 1998).

244. *HUM* 7. *Presence* (0) *or absence* (1) *of distinct ectepicondyle.* This character is slightly modified from Laurin (1998*b*). Absence of a distinct ectepicondyle characterizes several derived temnospondyls, crown-lissamphibians, certain tuditanomorphs, microbrachomorphs and lysorophids (Boy, 1972, 1974, 1978, 1985, 1986, 1987, 1995; Bolt, 1969, 1977, 1979, 1991; Carroll & Gaskill, 1978; Ivakhnenko, 1978; Wellstead, 1991; Schoch, 1992; Evans & Milner, 1996; Gardner, 1999, 2001; Rocek & Rage, 2000*b*).

245. *HUM* 8. *Absence* (0) *or presence* (1) *of condition: ectepicondylar ridge extending distally to reach distal humeral end.* The derived state of this character is found in panderichthyids and all more crownward tetrapods (Vorobyeva, 1977, 1992, 2000; Vorobyeva & Schultze, 1991).

246. *HUM* 9. *Distal extremity of ectepicondylar ridge aligned with ulnar condyle* (0), *between ulnar and radial condyles* (1), *or aligned with radial condyle* (2). *Tulerpeton* (Lebedev & Coates, 1995), colosteids (Godfrey, 1989), *Whatcheeria* (Lombard & Bolt, 1995) and *Eoherpeton* (Smithson, 1985) possess state 1. State 2 characterizes most crown-tetrapods.

247. *HUM* 10. *Humerus without* (0) *or with* (1) *expanded extremities* (*waisted*). Regardless of the degree of torsion along the axis of the shaft, expansion of the humeral head and humeral condylar extremity occurs in temnospondyls, crown-lissamphibians, several 'reptiliomorphs' (but not embolomeres and gephyrostegids), crown-amniotes, most microsaurs (except *Microbrachis*), lysorophids and *Scincosaurus* (Wellstead, 1991; Coates, 1996; Bossy & Milner, 1998; Clack, 1998*c*, 2001).

248. *HUM* 11. *Radial condyle terminal* (0) *or ventral* (1). Except for *Ichthyostega* (Jarvik, 1980, 1996), stem-tetrapods show a terminal radial condyle, as do some temnospondyls and basal 'reptiliomorphs'.

249. *HUM* 12. *Humerus slender and elongate, with length less* (0) *or more* (1) *than three times the diameter of its distal end.* The derived state of this character applies to several derived dissorophoids and crown-lissamphibians (Milner, 1988, 1990, 1993), but it is known also in some crown-amniotes (Clark & Carroll, 1973; Reisz, 1977, 1981; Carroll, 1991*b*).

250. *HUM* 13. *Posterolateral margin of entepicondyle lying distal with respect to plane of radial-ulnar facets* (0) *or not* (1). The primitive condition of the entepicondyle is found in the outgroups (Andrews & Westoll, 1970; Vorobyeva, 1977, 1992, 2000), but occurs also in some temnospondyls, such as *Eryops* and trematopids (Miner, 1925; Olson, 1941).

251. *HUM* 14. *Posterolateral margin of entepicondyle markedly concave* (0) *or not* (1). The derived state is found in *Eusthenopteron* and *Acheloma* only (Andrews & Westoll, 1970; Olson, 1941).

252. *HUM* 15. *Width of entepicondyle greater* (0) *or smaller* (1) *than half humeral length.* In its derived state, this character is acquired in parallel by the clade encompassing derived dissorophoids plus crown-lissamphibians (Milner, 1988, 1990, 1993; Boy & Sues, 2000), *Pholiderpeton scutigerum* (Clack, 1987*a*) among embolomeres, crown-amniotes, most lepospondyls, except pantylid and ostodolepid tuditanomorphs, diplocaulids and *Urocordylus* (Carroll & Gaskill, 1978; A. C. Milner, 1980; Bossy & Milner, 1998).

253. *HUM* 16. *Portion of humeral shaft length proximal to entepicondyle smaller* (0) *or greater* (1) *than humeral head width.* The derived condition relates to elongation of the humerus in various stem-amniotes (exceptions are *Proterogyrinus*, seymouriamorphs and diadectomorphs), crown-amniotes and most lepospondyls other than diplocaulids and *Urocordylus* (White, 1939; Bystrow, 1944; Fox & Bowman, 1966; Reisz, 1977, 1981; Heaton, 1980; A. C. Milner, 1980; Holmes, 1984; Laurin, 1995, 1996*b*; Sumida, 1997; Bossy & Milner, 1998; Klembara & Bartík, 2000). It is also known in trimerorhachoids, dissorophoids and crown-lissamphibians.

254. *HUM* 17. *Presence* (0) *or absence* (1) *of accessory foramina on humerus.* Following Lebedev & Coates (1995), Coates (1996) and Clack (1998*c*, 2001), the primitive state of this character is observed in all tetrapods more derived than *Tulerpeton*. *Crassigyrinus* is, however, a notable exception (Panchen, 1985).

255. *HUM* 18. *Humerus length greater* (0) *or smaller* (1) *than the length of two and a half mid-trunk vertebrae. Tulerpeton*, colosteids and *Crassigyrinus* exhibit the plesiomorphic condition, which also appears as a reversal in *Westlothiana* and lepospondyls (except for tuditanomorphs) (Hook, 1983; Godfrey, 1989; Smithson *et al.*, 1994; Lebedev & Coates, 1995; Coates, 1996).

Radius

256. *RAD* 1. *Radius longer* (0) *or shorter* (1) *than humerus.* Most post-panderichthyid tetrapods exhibit the derived condition (Coates, 1996). The plesiomorphic state appears in some diplocaulids (A. C. Milner, 1980; Bossy & Milner, 1998).

257. *RAD* 2. *Radius longer than* (0), *as long as* (1), *or shorter than* (2) *ulna.* The derived conditions expressed by states 1 and 2 overlap each other in several regions of the tree, including the lissamphibian stem (state 1 occurs in crown-lisamphibians and some dissorophoids as well as among basal temnospondyls) and the lepospondyl branch (in some microbrachomorphs and most nectrideans).

Ulna

258. *ULNA* 1. *Absence* (0) *or presence* (1) *of olecranon process.* An olecranon process [see coding in Coates (1996), Clack (1998*c*, 2001) and Laurin (1998*b*)] occurs in some Devonian and most post-Devonian taxa. It is absent in some tetrapods that possess poorly developed and/or miniaturized limbs.

(*c*) *Pelvic girdle*

Ilium

259. *ILI* 3. *Absence* (0) *or presence* (1) *of dorsal iliac process.* Following Lebedev & Coates (1995), Coates (1996), Clack (1998*c*, 2001) and Laurin (1998*b*), the presence of a dorsal iliac process is primitive for tetrapods (Devonian and various basal Carboniferous forms). Its loss or drastical reduction is documented in temnospondyls, crown-amniotes and most lepospondyls (some microsaurs represent exceptions; Carroll & Gaskill, 1978).

260. *ILI* 6. *Supraacetabular iliac buttress less* (0) *or more* (1) *prominent than postacetabular buttress.* The coding for this character derives from Coates (1996). Its derived state characterizes all tetrapods more derived than *Acanthostega.*

261. *ILI* 7. *Absence* (0) *or presence* (1) *of transverse pelvic ridge.* A transverse pelvic ridge appears in some temnospondyls (notably *Eryops* and *Dendrerpeton*; Romer, 1947; Holmes *et al.*, 1998). It also represents a transient feature of basal stem-amniotes, in agreement with the conclusions of Coates (1996) and Ruta *et al.* (2001). For a discussion of the nature of the ridge and its possible homology with the iliac shelf of seymouriamorphs and diadectomorphs, see Sumida (1997) and Klembara & Bartík (2000).

262. *ILI* 9. *Absence* (0) *or presence* (1) *of condition: ilium an elongate rod directed anteriorly.* This character applies exclusively to salientians (Milner, 1988; Rage & Rocek, 2000*b*).

263. *ILI* 10. *Acetabulum directed posteriorly* (0) *or laterally* (1). The coding for this character is from Coates (1996) and characterizes all post-*Eusthenopteron* tetrapods (Andrews & Westoll, 1970; Vorobyeva, 1977, 1992, 2000).

Ischium

264. *ISC* 1. *Ischium not contributing* (0) *or contributing* (1) *to pelvic symphysis.* The distribution of this character is identical to that of the previous character.

(*d*) *Hindlimb*

Femur

265. *FEM* 1. *Absence* (0) *or presence* (1) *of condition: internal trocanter with a distinct process. Whatcheeria*, some primitive crown-lissamphibians, certain embolomeres, *Seymouria* and *Limnoscelis* display the plesiomorphic condition (White, 1939; Romer, 1946; Panchen, 1972; Lombard & Bolt, 1995).

266. *FEM* 2. *Absence* (0) *or presence* (1) *of condition: internal trocanter separated from femur by distinct trough-like space.* This character is based on data from Coates (1996). It appears in its derived state in certain dissorophoids and microsaurs, some 'reptiliomorphs' (e.g. *Caerorhachis*, *Kotlassia* and *Westlothiana*; Bystrow, 1944; Holmes & Carroll, 1977; Smithson *et al.*, 1994; Ruta *et al.*, 2001) and several stem-tetrapods, including *Acanthostega*, *Tulerpeton*, *Crassigyrinus*, *Whatcheeria* and colosteids (Panchen, 1985; Godfrey, 1989; Lebedev & Coates, 1995; Lombard & Bolt, 1995).

267. *FEM* 3. *Absence* (0) *or presence* (1) *of condition: fourth trocanter with a distinct rugose area.* The character appears in stem-tetrapods and is maintained in the basal part of the stem-lissamphibian and stem-amniote trees. It is found also in some primitive crown-amniotes, such as *Captorhinus* (Fox & Bowman, 1966). It is lost in most lepospondyls, some seymouriamorphs, gephyrostegids and various primitive crown-amniotes.

268. *FEM* 4. *Proximal end of adductor crest of femur not reaching* (0) *or reaching* (1) *midshaft length.* Coates (1996) examined patterns of proximal displacement of several processes of the femur in several lineages within the tetrapod crown-group. *Whatcheeria*, some seymouriamorphs (White, 1939; Klembara & Bartík, 2000), diadectomorphs (Romer, 1946; Berman & Sumida, 1990) and *Balanerpeton* (Milner & Sequeira, 1994) appear to reverse to the plesiomorphic state, whereas *Greererpeton* (Godfrey, 1989) and *Crassigyrinus* (Panchen, 1985) show the derived condition.

269. *FEM* 5. *Femur shorter than* (0), *as long as* (1), *or longer than humerus* (2). *Acanthostega* (Coates, 1996), trimerorhachoids (Case, 1935), *Ecolsonia* (Berman *et al.*, 1985) and pantylids (Berman *et al.*, 1988) exhibit state 1, whereas state 2 is ubiquitous among remaining tetrapods. We coded *Ichthyostega* as unknown, pending redescription of postcranial material showing association of anterior and posterior limbs.

Tibia

270. *TIB* 7. *Without* (0) *or with* (1) *flange on posterior edge.* The coding for this character follows Lebedev & Coates (1995) and Coates (1996). The derived condition is shown by *Tulerpeton*, *Whatcheeria* and *Westlothiana*

(Smithson *et al.*, 1994; Lebedev & Coates, 1995; Lombard & Bolt, 1995).

Fibula

271. *FIB* 1. *Fibula not waisted* (0) *or waisted* (1). Based on Lebedev & Coates (1995), Coates (1996) and Clack (1998*c*, 2001), a waisted fibula occurs in all tetrapods more crownward than *Ichthyostega*.

272. *FIB* 3. *Absence* (0) *or presence* (1) *of ridge near posterior edge of flexor surface of fibula*. This and the following characters describe conditions of the flexor surface of the fibula [see Lebedev & Coates (1995) and Coates (1996)]. Character 272 shows its derived state in *Acanthostega*, *Crassigyrinus*, *Baphetes*, *Eryops*, embolomeres, *Gephyrostegus*, *Seymouria* and *Limnoscelis* (White, 1939; Romer, 1946, 1947; Carroll, 1970; Panchen, 1980, 1985; Holmes, 1984, 1989; Smithson, 1985; Milner & Lindsay, 1998).

273. *FIB* 4. *Absence* (0) *or presence* (1) *of rows of tubercles near posterior edge of flexor surface of fibula*. The derived condition is present only in *Tulerpeton* (Lebedev & Coates, 1995) and *Whatcheeria* (Lombard & Bolt, 1995).

Tarsus

274. *TAR* 1. *Absence* (0) *or presence* (1) *of ossified tarsus*. All post-panderichthyid tetrapods show ossified elements in the tarsus (discussion in Coates, 1996).

275. *TAR* 2. *Absence* (0) *or presence* (1) *of one proximal tarsal ossification, or presence of more than two ossifications* (2). Proximal tarsal elements are observed in *Acanthostega* and all more derived tetrapods (Jarvik, 1980, 1996; Lebedev & Coates, 1995; Coates, 1996).

276. *TAR* 3. *Tarsus without* (0) *or with* (1) *L-shaped proximal tarsal element*. A proximal tarsal element with an indentation along its proximal margin (Lebedev & Coates, 1995; Coates, 1996) is found in *Tulerpeton* (Lebedev & Coates, 1995), several basal stem-amniotes including embolomeres and gephyrostegids (but not seymouriamorphs; White, 1939; Carroll, 1970; Boy & Bandel, 1973; Holmes, 1984, 1989; Sumida, 1997; Berman *et al.*, 2000; Ruta *et al.*, 2001), *Westlothiana* (Smithson *et al.*, 1994), *Diadectes* (Heaton, 1980; Sumida, 1997) and several primitive crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981).

277. *TAR* 4. *Absence* (0) *or presence* (1) *of distal tarsals between fibulare and digits*. The derived condition of this character is found in *Tulerpeton* and all more crownward Letrapods [data from Lebedev & Coates (1995) and Coates (1996)].

278. *TAR* 5. *Absence* (0) *or presence* (1) *of distal tarsals between tibiale and digits*. The distribution of this character is identical to that of the previous character.

(*e*) *Axial skeleton*

Ribs

279. *RIB* 2. *Cervical ribs with* (0) *or without* (1) *flattened distal ends*. The coding for this character follows in part Clack (1998*c*, 2001). The primitive state appears to be widespread among tetrapods. The derived condition is optimized as transitional for at least part of the tetrapod stem-group (from *Ichthyostega* to *Whatcheeria*) under ACCTRAN.

280. *RIB* 3. *Ribs mostly straight* (0) *or ventrally curved* (1) *in at least part of the trunk*. Markedly curved trunk ribs (curvature extending from proximal head to distal tip of the ribs) are found in stem-tetrapods more derived than *Acanthostega* [implying reversal in colosteids under ACCTRAN (see Godfrey, 1989)], as well as on the amniote branch of the tetrapod tree, including the vast majority of lepospondyls. Poorly pronounced curvature characterizes the ribs of *Discosauriscus* and *Seymouria* (White, 1939; Klembara & Bartík, 2000), derived diplocaulids (Bossy & Milner, 1998) and aïstopods (McGinnis, 1967; Wellstead, 1982; Carroll, 1998; Anderson, in press). As noted by A. R. Milner (1990), a slight curvature is observed in some of the largest temnospondyls (see also Schoch & Milner, 2000).

281. *RIB* 5. *Absence* (0) *or presence* (1) *of triangular spur-like posterodorsal process in at least some trunk ribs*. Such a process is found uniquely in the ribs of colosteids and adelospondyls (Godfrey, 1989; Andrews & Carroll, 1991). It differs from the slender, needle-like process of certain aïstopods (McGinnis, 1967).

282. *RIB* 6. *Absence* (0) *or presence* (1) *of condition: elongate posterodorsal flange in midtrunk ribs*. The distribution of this character overlaps that of the previous character, but it is not identical to the latter. It describes the occurrence of a sheet-like flange stretching along part of the posterodorsal margin of at least some trunk ribs, and is observed in lysorophids (Wellstead, 1991) as well as colosteids and adelospondyls (Godfrey, 1989; Andrews & Carroll, 1991).

283. *RIB* 7. *Absence* (0) *or presence* (1) *of condition: longest trunk ribs poorly ossified, slender rods, the length of which is smaller than the length of three trunk vertebrae*. This is one of the characters used by Milner (1988, 1990, 1993, 2000) to unite derived dissorophoids with crown-lissamphibians (see also Boy & Sues, 2000).

Cervical vertebrae

284. *CER VER* 1. *Atlas neural arch halves unfused* (0) *or fused* (1). Albanerpetontids (Gardner, 1999, 2001), crown-lissamphibians (Bolt, 1991), pantylids, *Rhynchonkos* (Carroll & Gaskill, 1978), *Scincosaurus* and diplocaulids (Bossy & Milner, 1998) display the derived condition of this feature [data from Sumida & Lombard (1991), Sumida *et al.* (1992), Carroll (1995) and Laurin (1998*b*)].

285. *CER VER* 3. *Axial arch not fused* (0) *or fused* (1) *to axial* (*pleuro*)*centrum*. Fusion between axial arch and centrum occurs in crown-lissamphibians, crown-amniotes, diadectomorphs, *Westlothiana* and most lepospondyls [data from Carroll & Gaskill (1978), Sumida & Lombard (1991), Sumida *et al.* (1992), Smithson *et al.* (1994), Carroll (1995) and Laurin (1998*b*)].

Trunk and tail vertebrae

286. *TRU VER* 1. *Absence* (0) *or presence* (1) *of extra articulations above zygapophyses in at least some trunk and caudal vertebrae*. The derived condition of this character unites nectrideans and aïstopods, although it may not be present in all members of the latter group (A. C. Milner, 1980; Wellstead, 1982; Milner, 1993; Bossy & Milner, 1998; Carroll, 1998; Anderson, in press).

287. *TRU VER* 2. *Absence* (0) *or presence* (1) *of condition: neural and haemal spines rectangular to fan-shaped in lateral view*. This and the following two characters were used by A. C. Milner (1980), Milner (1993) and Bossy & Milner (1998) to characterize nectrideans.

288. *TRU VER* 3. *Absence* (0) *or presence* (1) *of condition: neural and haemal spines facing each other dorsoventrally*. See character 287 above.

289. *TRU VER* 4. *Haemal spines not fused* (0) *or fused* (1) *to caudal centra*. See character 287 above. The derived state is present also in *Valdotriton* (Evans & Milner, 1996).

290. *TRU VER* 5. *Absence* (0) *or presence* (1) *of extra articulations on haemal spines*. The derived condition is a shared feature of urocordylids [data from A. C. Milner (1980), Milner (1993) and Bossy & Milner (1998)].

291. *TRU VER* 6. *Absence* (0) *or presence* (1) *of long, distally bifurcated transverse processes on trunk centra*. The derived condition is a shared feature of *Diplocaulus* and *Diploceraspis* [data from A. C. Milner (1980), Milner (1993) and Bossy & Milner (1998)]. See also character 297 below.

292. *TRU VER* 7. *Absence* (0) *or presence* (1) *of ossified pleurocentra*. Absence of ossified pleurocentra is only documented in *Panderichthys* (Vorobyeva, 1992; Vorobyeva & Schultze, 1991) and *Crassigyrinus* (Panchen, 1985).

293. *TRU VER* 8. *Trunk pleurocentra not fused midventrally* (0) *or fused* (1). The derived condition characterizes *Doleserpeton* (Bolt, 1969; Daly, 1994), albanerpetontids (Gardner, 1999, 2001), crown-lissamphibians (Bolt, 1991) and the entire amniote branch of the tetrapod tree.

294. *TRU VER* 9. *Trunk pleurocentra not fused middorsally* (0) *or fused* (1). Dorsal fusion of pleurocentra has been documented by Lombard & Bolt (1995) in some specimens of *Whatcheeria*, and is also found in albanerpetontids (Gardner, 1999, 2001), crown-lissamphibians (Bolt, 1991), some embolomeres (Panchen, 1972; Clack, 1987*a*; Holmes, 1989), *Solenodonsaurus* (Laurin & Reisz, 1999), seymouriamorphs (White, 1939; Bystrow, 1944; Klembara & Bartík, 2000), diadectomorphs (Heaton, 1980; Sumida, 1997; Berman *et al.*, 1998), crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981; Carroll, 1991*b*), *Westlothiana* (Smithson *et al.*, 1994) and lepospondyls (Carroll, 1999).

295. *TRU VER* 10. *Neural spines without* (0) *or with* (1) *distinct convex lateral surfaces*. 'Swollen' neural arches are present in seymouriamorphs (White, 1939; Bystrow, 1944; Klembara & Bartík, 2000), diadectomorphs (Heaton, 1980; Sumida, 1997; Berman *et al.*, 1998), various basal amniotes (the condition is polymorphic for *Petrolacosaurus*; Reisz, 1977, 1981) and *Westlothiana* (Smithson *et al.*, 1994).

296. *TRU VER* 11. *Neural spines of trunk vertebrae not fused to centra* (0) *or fused* (1). This character has a non-homogeneous distribution. It is observed in *Doleserpeton* (Bolt, 1969; Daly, 1994), albanerpetontids (Gardner, 1999, 2001), crown-lissamphibians (Bolt, 1991), *Solenodonsaurus* (Laurin & Reisz, 1999), some seymouriamorphs (White, 1939; Bystrow, 1944), diadectomorphs (Heaton, 1980; Sumida, 1997; Berman *et al.*, 1998), crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981; Carroll, 1991*b*), *Westlothiana* (Smithson *et al.*, 1994), microsaurs (except pantylids, *Pelodosotis* and microbrachomorphs; Carroll & Gaskill, 1978), nectrideans (A. C. Milner, 1980; Bossy & Milner, 1998) and aïstopods (McGinnis, 1967; Wellstead, 1982; Carroll, 1998, 1999; Anderson, in press).

297. *TRU VER* 12. *Absence* (0) *or presence* (1) *of bicipital rib bearers on trunk centra*. Caudates and derived diplocaulids possess this character (A. C. Milner, 1980; Milner, 1988; Evans & Milner, 1996; Bossy & Milner, 1998). A specialized condition of rib bearers is detailed under character 291 above.

298. *TRU VER* 13. *Presence* (0) *or absence* (1) *of trunk intercentra*. Loss of ossified intercentra characterizes albanerpetontids (Gardner, 1999, 2001) and several lepospondyls (Carroll & Gaskill, 1978; A. C. Milner, 1980; Bossy & Milner, 1998; Andrews & Carroll, 1991; Carroll, 1998, 1999), except some tuditanomorphs, microbrachomorphs and *Acherontiscus* (*fide* Carroll, 1969*b*).

299. *TRU VER* 14. *Trunk intercentra not fused middorsally* (0) *or fused* (1). The derived condition occurs in some embolomeres (Panchen, 1972; Clack, 1987*a*; Holmes, 1989).

300. *TRU VER* 15. *Absence* (0) *or presence* (1) *of lateral and ventral carinae on trunk centra.* Lateral and ventral elongate keels are present in the centra of lysorophids and adelospondyls (Andrews & Carroll, 1991; Wellstead, 1991).

301. *TRU VER* 16. *Absence* (0) *or presence* (1) *of strong proximal emargination in haemal spines of posterior tail vertebrae.* This character describes the proximal constriction of posterior haemal spines in the diplocaulids *Keraterpeton*, *Diceratosaurus*, *Diplocaulus* and *Diploceraspis* (A. C. Milner, 1980; Bossy & Milner, 1998).

302. *TRU VER* 17. *Absence* (0) *or presence* (1) *of strong proximal emargination in haemal spines of anterior tail vertebrae.* See also preceding character. The proximal constriction of anterior haemal spines is found in *Diceratosaurus*, *Diplocaulus* and *Diploceraspis* (A. C. Milner, 1980; Bossy & Milner, 1998).

303. *TRU VER* 18. *Absence* (0) *or presence* (1) *of striate ornament on vertebral centra.* As described by A. C. Milner (1980) and Bossy & Milner (1998), striations are present on the vertebral centra of *Diceratosaurus*, *Diplocaulus* and *Diploceraspis*.

304. *TRU VER* 19. *Absence* (0) *or presence* (1) *of condition: tallest ossified part of neural arch in posterior trunk vertebrae lying above posterior half of vertebral centrum.* As described here, this feature occurs in *Doleserpeton* (Bolt, 1991; Daly, 1994), some seymouriamorphs (White, 1939; Bystrow, 1944; Sumida, 1997), *Limnoscelis* (Romer, 1946), primitive crown-amniotes (Fox & Bowman, 1966; Clark & Carroll, 1973; Reisz, 1977, 1981; Carroll, 1991*b*), *Westlothiana* (Smithson *et al.*, 1994), microsaurs (Carroll & Gaskill, 1978) and lysorophids (Wellstead, 1991).

305. *TRU VER* 20. *Absence* (0) *or presence* (1) *of prezygapophyses on trunk vertebrae.* The derived condition of this character occurs in all post-panderichthyid tetrapods (Coates, 1996).

306. *TRU VER* 21. *Absence* (0) *or presence* (1) *of postzygapophyses on trunk vertebrae.* The distribution of this character overlaps that of the preceding character (Coates, 1996), except for the occurrence of the plesiomorphic state in *Crassigyrinus* (Panchen, 1985) and, possibly, *Trimerorhachis* (Case, 1935).

307. *TRU VER* 22. *Absence* (0) *or presence* (1) *of prezygapophyses on proximal tail vertebrae.* The distribution of this character overlaps that of character 305 above (Coates, 1996).

308. *TRU VER* 23. *Absence* (0) *or presence* (1) *of postzygapophyses on proximal tail vertebrae.* The distribution of this character overlaps that of character 305 above (Coates, 1996).

309. *TRU VER* 24. *Absence* (0) *or presence* (1) *of prezygapophyses on distal tail vertebrae.* The derived state of this character is found in *Tulerpeton* and all more derived tetrapods (Lebedev & Coates, 1995; Coates, 1996).

310. *TRU VER* 25. *Absence* (0) *or presence* (1) *of postzygapophyses on distal tail vertebrae.* The distribution of this character overlaps that of character 309 above (Coates, 1996).

311. *TRU VER* 26. *Absence* (0) *or presence* (1) *of capitular facets on posterior rim of vertebral midtrunk centra.* A capitular facet on the posterior rim of vertebral midtrunk centra is found in some tuditanomorphs, microbrachomorphs, lysorophids and adelospondyls (Carroll & Gaskill, 1978; Carroll, 1991*a*; Andrews & Carroll, 1991; Wellstead, 1991).

312. *TRU VER* 27. *Height of neural arch in midtrunk vertebrae greater* (0) *or smaller* (1) *than distance between pre- and postzygapophyses.* The derived state is present in microsaurs (Carroll & Gaskill, 1978; Carroll, 1991*a*), lysorophids (Wellstead, 1991), *Westlothiana* (Smithson *et al.*, 1994), *Kotlassia* (Bystrow, 1944) and *Captorhinus* (Fox & Bowman, 1966).

(*f*) *Digits*

313. *DIG* 1. *Absence* (0) *or presence* (1) *of digits.* Dactyly (Coates, 1996) is a feature of all post-panderichthyid tetrapods, except where secondary loss of limbs occurs (aïstopods).

314. *DIG* 2. *Absence* (0) *or presence* (1) *of no more than four digits in manus.* A tetradactyl manus characterizes *Colosteus* (*fide* Hook, 1983), the temnospondyl-lissamphbian clade (Milner, 1988) and lepospondyls other than microbrachomorphs (Carroll *et al.*, 1998).

315. *DIG* 3. *Absence* (0) *or presence* (1) *of no more than five digits in manus.* A pentadactyl manus characterizes *Greererpeton* (Coates, 1996) and the 'reptiliomorph' branch of the tetrapod tree (excluding lepospondyls).

316. *DIG* 4. *Absence* (0) *or presence* (1) *of no more than three digits in manus.* A tridactyl manus is observed in microbrachomorphs (Carroll & Gaskill, 1978).

(*g*) *Fins*

317. *DOR FIN* 1. *Presence* (0) *or absence* (1) *of dorsal fin.* A dorsal fin is lost in *Panderichthys* and all more crownward tetrapods (Jarvik, 1980, 1996; Lebedev & Coates, 1995; Cloutier & Ahlberg, 1996; Coates, 1996; Ahlberg & Johanson, 1998).

318. *CAU FIN* 1. *Presence* (0) *or absence* (1) *of caudal fin.* A caudal fin is lost in *Tulerpeton* (under ACCTRAN optimization) and all more crownward tetrapods (Jarvik, 1980, 1996; Lebedev & Coates, 1995; Cloutier & Ahlberg, 1996; Coates, 1996; Ahlberg & Johanson, 1998).

319. *BAS SCU* 1. *Presence* (0) *or absence* (1) *of basal scutes.* Basal fin scutes are lost in *Panderichthys* and all more crownward tetrapods (Cloutier & Ahlberg, 1996; Ahlberg & Johanson, 1998).

XIV. APPENDIX 3. DATA MATRIX

Characters are divided into groups of five, arranged in horizontal rows and numbered from left to right; bold numbers refer to characters in the leftmost position in each row; parentheses ( ) indicate polymorphism, whereas braces { } indicate partial uncertainty; question marks denote unknown or inapplicable characters.

Acanthostega gunnari

```
  1  0??00 00010 ?1000 00000 00010 00000 00012 00001 11100 00000
 51  00000 00001 ??000 10100 00000 00001 10000 00000 00010 00000
101  01110 00000 00001 10000 00000 00000 00001 00000 0?001 00000
151  00000 00010 00000 00000 00100 00011 01010 00000 00100 10010
201  00110 01100 11000 ?0000 00000 00110 00001 00000 00001 00001
251  10001 10010 00111 11010 01010 00000 00000 00000 01000 00000
301  00001 11100 00100 0101
```

Acherontiscus caledoniae

```
  1  ????? ??11? ?1101 1010? ?0000 01000 00?1? 00??1 ????? ?????
 51  ????? ????? ????? ????? ????0 010?1 10?00 ??0?? 1?00? ???1?
101  0???0 ??0?0 0000{12} ????? ????? ????? 0???? ????? ????? ?????
151  ????? ????? ????? ????? ????? ?1??? ??000 00??? ???0? ?1???
201  ????? ????? ????? ??000 ?000? ???0? 01??? ????? ????? ?????
251  ????? ????? ????? ????? ????? ????1 ??0?? 00000 01110 00010
301  000?? ????? ????? ?11?
```

Adelogyrinus simorhynchus

```
  1  0??00 0?11? ?1101 0000? 100?0 01010 00?1? ?01?1 ?10?1 10000
 51  ?0000 10?01 ??1?? ?1??? ??0?0 010?0 00?00 1?0?? 10000 0001?
101  0?120 00??0 0000? 3???? ????? ????? 0???? ????? ????? ?????
151  ????? ????? 00001 01??? ????? ?1??? ??100 00??? 0010? ?1010
201  ????? ????? ????? ??000 01100 11?0? 01??? ?1??? ????? ?????
251  ????? ????? ????? ????? ????? ????1 1100? 0???? 0111? 001?1
301  ????1 1???? 10??? ?1??
```

Adelospondylus watsoni

```
  1  ????? ????? ?11?1 1000? 00000 010?0 00012 001?? 210?1 10000
 51  ?0000 10?01 ??1?? ?1??? ??0?1 ????? ???01 10010 10000 0001?
101  ???20 01?10 0000{12} 3???? ????? ??10? 00001 11100 0?00? 00000
151  10000 0???? ????? ???0? ??2?? ?1??? ??100 00??? 0??0? ?1010
201  ????? ????? ????? ??000 0110? ???0? ????? ????? ????? ?????
251  ????? ????? ????? ????? ????? ????1 110?? 0???? 01110 001?1
301  ????1 1???? 1???? ????
```

ALBANERPETONTIDAE

```
  1  11100 0?11? ?1101 10101 01000 00?10 01?02 1000? ?1100 ?????
 51  ????? ?1??? ????? ????? ????? ????? ??110 0?01? ???0? ??010
101  001?0 1?0?1 0000? ????? ????? ????? ????? ????? ????? ?????
151  ????? ????? 01011 00??? ????? ??1?? ?1100 000?? 1??01 ??1??
201  ?1??? 1???1 ????? ?1010 0000? ????? ????? ???0? ?111? ?1111
251  11111 120?? ???1? ???2? 1???? ???00 00110 00000 01110 ?01?0
301  0000? ????? 00110 0111
```

Amphibamus grandiceps

```
  1  11000 0?11? ?1010 01000 01000 00010 01011 00000 21100 00010
 51  ?0000 00001 ??000 00??? ?0100 00100 00101 00000 10000 00110
101  10110 020?1 0000? ?0111 01110 11111 ?0100 01100 0?000 00101
151  00011 101?? 01011 00?10 00210 10??? ???00 00??? 0??0? ??010
201  ?0??? 0???0 ????? ?1111 00000 1110? 000?? 11?01 ?111? ?1?11
251  11111 1??01 0011? ???20 100?? ???00 001?0 00000 01000 00000
301  00001 11111 00110 0111
```

Anthracosaurus russelli

```
  1  0??01 0011? ?1000 10000 00000 00?00 00011 00010 21100 00001
 51  00000 00000 10000 10101 ?0100 00000 00100 00000 10110 00010
101  00110 02031 0000{12} 3100? 01100 00001 00000 00000 0?00? 00000
151  00000 001?0 00001 00101 10200 00??? ?1100 00?10 01101 0?010
201  101?? 01010 10000 ??000 0000? ????? ????? ????? ????? ?????
251  ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
301  ????? ????? ????? ????
```

Apateon pedestris

```
  1  10100 0011? ?1011 01000 01000 00010 01011 10000 21100 00010
 51  ?0000 00001 ??000 100?1 ?0100 00100 00101 00000 10000 00?10
101  11110 02011 0000? ?0001 01110 10010 01101 01010 0?000 00111
151  00011 101?? ????? ???10 00210 11??? ???00 00??? 0??0? ??010
201  ????? ????? ????? ?1?00 00000 1110? 100?? 11?01 ???1? ?1?11
251  11111 1100? 0011? ???20 1???? ???00 001?? 00000 0???0 ?0000
301  000?1 11111 00110 0111
```

Archeria crassidisca

```
  1  0??01 00110 ?1000 10000 00010 00100 00011 00010 21100 10001
 51  00000 00000 00000 00101 ?0000 00100 00100 00011 10010 00010
101  00110 02030 0000{23} ????0 ????0 ???0? 0?00? 0?000 0?001 00000
151  00000 0???0 00001 00101 10200 00000 11100 00111 01101 00010
201  00101 01010 10111 01000 01000 11111 00000 11100 10101 20001
251  10111 12111 10111 01120 11012 11101 ??000 00000 01110 00010
301  00001 11111 00101 0111
```

Asaphestera intermedia

```
  1  0??01 0011? ?1000 00000 00000 00100 00011 ?0010 21100 00000
 51  10000 00101 ??1?? ?0??0 00100 00010 01000 00010 10000 10?10
101  00000 00011 00004 {01}???? ????? ??100 000?? ????? 0?0?? 00000
151  00000 0???1 00101 000?? ????? ????? ??100 00??? ???0? ?1010
201  ????? ????? ????? ??000 0000? ??110 10011 1??0? ?0101 21?0?
251  ???11 ???1? 0011? ???{12}? ????? ????1 000?? 00??? 0???0 10??0
301  ???11 1???? ?11?? ?1?1
```

Balanerpeton woodi

```
  1  10100 0011? ?1010 00000 00000 00000 00011 00000 2110(01) (01)0000
 51  ?0000 00000 10000 10001 ?0000 00100 00101 00000 10000 00010
101  00110 020?1 00004 40011 01100 00101 00000 10100 0?010 00000
151  00011 101?? 00001 00?10 00200 001?? ?1000 00010 01101 00010
201  10101 01010 101?? ?1000 10000 1110? 000?? ?1?01 ?011? ?1001
251  10011 11101 00111 1?020 10012 01100 00000 00000 01000 00000
301  00001 111?? 00110 0111
```

Baphetes kirkbyi

```
  1  0??00 00111 01000 00010 00000 10000 00011 00000 2110? ?0000
 51  00000 00000 10010 10011 ?0000 00000 00100 00010 00100 00010
101  01120 00010 00003 ?0010 01100 00101 00000 10100 0?001 00000
151  001?? ?01?0 0000? 00100 01200 00010 1??00 00??? 0?1?? ?????
201  ????? ????? ????? ??000 0000? ????? ????? ??000 10101 20001
251  1001? ???11 0011? ????0 110?? ????? ????? 00000 0???? ??00?
301  000?? ????? ????? ???1
```

Batrachiderpeton reticulatum

```
  1  0??00 00110 ?1001 00000 00000 01110 00010 00011 21111 00000
 51  10001 10001 ??1?? ?0000 01100 00001 10100 01010 10000 00010
101  00000 020?0 00004 40100 ?1100 010?0 0001? ????? 0?001 00000
151  001?? ?01?? 10001 00?00 00200 021?? ?1100 001?? 1??01 01010
201  01??? 1???0 10100 ??000 00001 1100? 01??? ????? ????? ?????
251  ????? ????? ???1? ????? ????? ????? ????? 11110 0???0 ????0
301  00001 11111 00110 0???
```

Batropetes fritschia

```
  1  0??01 1011? ?1000 00001 00000 01100 00?12 10011 21110 ?1???
 51  ????? ?0001 ??1?? ?0000 00100 00010 0?010 0001? 1000? ??010
101  00220 020?1 00011 ????? ????? ????? ????? ????? 0?0?? ??000
151  000?? ????1 00101 00000 00200 12??? ?1100 01??? ???0? ?????
201  ????? ????? ????? ??010 00000 ?1111 10011 11?01 ?01?? ?1101
251  11111 121?? 001?1 101(12)0 1001? 01?01 000?? 000(01)0 0111? (01)01?0
301  00011 11111 11110 0111
```

Brachydectes elongatus / newberryi

```
  1  0??00 00110 ?1000 10001 00001 01?10 00110 0001? ?1001 10000
 51  10100 01??1 ??1?? ?0000 00?01 ????? ??110 001?? ????1 ??010
101  00??0 1?010 00014 4110? 01100 010?1 ?001? ????? 0?000 00000
151  001?? ?01?1 00101 00000 00200 021?? ?1100 01??? 1??01 0101?
201  ?1??? 1???1 ????? ??000 00000 1110? 101?? ?1?0? ?111? ?1?01
251  11110 1100? 00111 00120 1???? ???11 0100? 00000 0???0 00??1
301  00011 111?? 111?? 0111
```

Broiliellus brevis

```
  1  ???00 0?11? ?1000 01000 01000 00000 0?012 10000 21100 00000
 51  ?0000 00001 ??000 00000 ?0000 00100 00101 00000 10000 00?10
101  00120 020?1 0000? ?01?1 01110 00?1? 000?? ????? 0?010 00100
151  00011 101?? ????? ???10 00200 10??? ???00 00??? ???0? ?1???
201  ????? ????? ????? ?1011 00000 11??? ??0?? ?1?0? ?111? ?1?01
251  10111 ????1 00111 0???? ????? ????0 000?? 00000 0???0 0?000
301  000?1 1???? ?0??? ?111
```

Bruktererpeton fiebigi

```
  1  0???? ??11? ?1000 ?00?0 000?? ?0??0 00011 10010 21100 00010
 51  ?0000 0???0 0?000 001?? ?000? ????? ????? 00??? ????? ????0
101  00??? 02??1 ?00?? ??0?? ????? ?0?0? ??001 1??00 ????1 ?0???
151  ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
201  ????? ????? ????? ??000 ?000? 11??? ??1?0 1?101 10101 20101
251  10111 121?? ????1 10120 10012 1??01 000?? 00000 01100 00000
301  00001 11111 001?? ?111
```

Caerorhachis bairdi

```
  1  0???? ????? ?1000 ????? ????? ??0?0 0001? ?0000 21101 10000
 51  ?0000 000?0 1?000 ?0100 ?0000 00100 00100 00??0 ????0 00?1?
101  00??? 0{12}0?0 0000? ??010 ?1100 00101 ?0000 10100 0?001 00000
151  00000 001?? 0000? ????0 10200 00010 01000 00110 01?01 00010
201  00101 01010 10110 01000 0000? ????? ????? ????? ????? ?????
251  ????? ??111 10111 1?1?0 1??12 11101 000?0 00000 01100 00000
301  00001 11111 001?? ?111
```

Captorhinus aguti

```
  1  0??01 10111 01000 00000 00000 00100 00011 100?1 21110 00010
 51  01000 00?01 ??000 01??? ??0?0 000?0 00100 00011 10010 00010
101  00110 02020 00004 41100 01100 01001 0001? ????? 10001 00000
151  00000 001?1 00001 10101 10200 011?? ?0000 00??? 1??01 01010
201  01??? 1???0 11111 11000 0000? ??111 10010 11101 10101 21101
251  11111 12101 ?0111 11120 1??12 11101 00001 00000 01111 10000
301  00011 11111 01101 0111
```

Cardiocephalus sternbergi

```
  1  0??01 10111 01000 10000 00001 00110 00010 00010 21100 00000
 51  10100 00111 ??1?? ?0000 00010 00010 01?1? 00010 1000? ??010
101  00000 020?1 01014 {01}1100 01100 01000 00001 01000 0?001 00000
151  01000 0?1?0 00101 00000 00200 02??? ?1100 001?? 01101 ?1011
201  ????? ????? ????? ?1000 0001? ????? ????? ????? ????? ?????
251  ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
301  ????? ????? ????? ????
```

Chenoprosopus lewisi

```
  1  0??10 00111 01000 10000 00010 00000 00011 00000 21100 00000
 51  ?0000 00000 10000 100?1 ?0000 00000 00101 00011 00010 00010
101  00200 1?1?0 00004 400?0 01100 00?01 00000 ?0100 0?010 00000
151  00011 011?? 00001 00?10 0?200 00??? ???00 ?0??? 0?101 ??010
201  ?0??? 0???0 ????? ??000 0000? ????? ????? ????? ????? ?????
251  ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
301  ????? ????? ????? ????
```

Cochleosaurus florensis

```
  1  ???10 00111 01000 00000 00010 00100 00011 00000 21100 00000
 51  ?0000 00000 10000 100?1 ?0000 00100 00101 00011 00010 00010
101  00100 1?1?0 00004 40010 11100 00101 00000 10100 0?010 00100
151  00011 111?? ????? ???10 01201 001?? ?1000 00011 01101 00010
201  00101 01010 1011? ?1000 0000? ????? ????? ????? ????? ?????
251  ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
301  ????? ????? ????? ????
```

Colosteus scutellatus

```
  1  0??00 0?110 ?1101 10100 1?000 00000 00011 00101 21001 (01)0000
 51  ?0000 10001 ??000 100?0 00000 01001 10100 000?? 00000 00?10
101  0?200 000?0 00002 2???? ????? ?0?00 00000 ??000 ??00? 00000
151  10000 00??? ????? ???1? ??2?? ?0??? ?1001 00??? ????? ?????
201  ?0110 0???0 10100 ??000 1000? ??000 01??? ????? ????? ?????
251  ????0 1???? ????? ????? ????? ????? ????? 00000 01000 0?000
301  00001 1???? ??110 0???
```

Crassigyrinus scoticus

```
  1  0??00 01111 11000 00001 00010 00000 00011 00000 2110? ?0001
 51  ?0000 00000 0?000 00101 ?0000 00000 00100 00000 00100 00010
101  01111 000?0 00001 30000 10000 00000 00000 00000 0?001 ?0000
151  00?00 0001? ????0 00?01 10100 00010 11000 00100 00101 00010
201  00101 01010 ????? ?0000 00000 ?1?10 00??? ??100 10001 {12}0001
251  10000 1001? 00111 11121 110?? ????1 0000? 00000 00??0 ?0000
301  000?1 0???? 001?? ?1?1
```

Dendrerpeton acadianum

```
  1  10000 00111 11000 00000 00000 00000 00010 00000 21101 10010
 51  ?0000 00000 10000 10011 ?0000 00100 00101 00000 100(01)0 00110
101  00200 020?0 00004 ?0011 ?1100 00101 00000 10100 0?010 00100
151  00011 001?? 01001 00?10 00201 00??? ???00 00??? 01101 00010
201  ?0??? 0???0 ????? ?1000 00000 1110? 00000 11?01 ?0101 21001
251  10011 11101 10111 1?120 1??12 01100 000?? 00000 01000 00000
301  00001 1???? 00110 0111
```

Diadectes absitus

```
  1  0??01 00111 01000 00000 00000 00100 00011 00011 21100 00110
 51  01000 00001 ??000 00001 ?0100 00100 00100 00010 10000 00110
101  00200 02021 00004 41100 01100 01001 00001 01100 100?1 00000
151  001?? ?01?? 00001 10101 10200 011?? ?1100 001?? 1??01 01010
201  01??? 1???0 1?111 11000 00000 11111 10110 11011 10101 21101
251  10011 12111 10111 01020 1001{12} 11?01 00001 00000 01111 10000
301  00001 11111 00101 0111
```

Diceratosaurus brevirostris

```
  1  0??00 0?110 ?1001 10001 00000 01110 00?12 00011 21111 00000
 51  ?0001 100?1 ??1?? ?00?0 01000 00001 10100 0101? 10000 00?10
101  00200 020?0 00004 4???? ????? ????? 0???? ????? 0?00? 0?000
151  00011 1???? ????? ???0? ????? ????? ??100 00??? ????? ?????
201  ????? ????? ????? ??000 ?0001 1100? 01??? ?1?0? ?11?? ???01
251  10010 0110? 0011? ???20 1???? ????1 000?1 11110 0???0 10??0
301  11101 11111 00110 0111
```

Diplocaulus magnicornis

```
  1  0??01 00110 ?0??? 00000 10010 01100 00101 10?11 21110 00000
 51  10001 ?0011 ??1?? ?0000 01100 01001 10100 01010 00010 00010
101  ?0120 010?1 00004 40101 01110 01010 000?? ????? 0?001 00000
151  00011 101?? 10001 00?00 00200 02??? ??100 00??? ????? ?????
201  ????? ????? ????? ??000 00001 1100? 01??? ?1?0? ?1101 ?0?01
251  10010 110?? ???1? ???20 1???? ???00 000?1 11110 1???0 11??0
301  11101 11111 00110 0111
```

Diploceraspis burkei

```
  1  0??01 00110 ?0??? ????? ????? ??100 00101 10?11 21110 00000
 51  10001 ?0001 ??1?? ?0000 01100 01000 00100 01010 10010 00010
101  ?0120 01011 00004 40101 01110 01010 000?? ?1??? 0?001 01000
151  00011 101?0 10001 00000 00200 021?? ?1100 001?? 1??01 01010
201  01??? 1???0 11010 01000 0000? ??00? 01??? ?1??? ????? ?????
251  ????? ????? ????? ????? ????? ????? ???11 11110 1???0 11??0
301  11101 11111 00110 011?
```

Discosauriscus austriacus

```
  1  0??01 00111 11000 00000 00000 00100 00012 00010 21100 00010
 51  ?0000 00000 01000 00001 ?0100 00100 00101 00010 10000 00110
101  00110 02011 00003 31010 01100 00101 00001 10100 10011 00000
151  001?? ?01?? 0000? 00?01 00200 011?? ?1100 00111 01101 01010
201  00101 01010 10111 11000 00000 11011 10100 10001 10101 21001
251  10011 1101? 10111 00020 100?? ???00 00000 00000 01111 00000
301  00001 11111 00101 01?1
```

Doleserpeton annectens

```
  1  11000 0011? ?1010 01000 01000 00000 01011 10000 21100 00010
 51  ?0000 00001 ??000 00000 ?0100 00100 00101 00000 10000 00110
101  11110 020?1 00004 40111 01111 11010 1011? ????? 0?010 11101
151  00011 101?? 01011 00?10 00211 101?? ?1100 00??? 0??0? ?1010
201  ?0??? 0???0 ????? ??111 0000? ?1??? ??0?? ?1??? ?111? ?1?11
251  1111? ??00? ?01?1 1?1?? ????? ????0 0010? 00000 011(01)0 10000
301  00011 11111 00110 0??1
```

Dolichopareias disjectus

```
  1  0??00 0?110 ?1101 10001 10000 010?0 00?10 001?1 210?1 10000
 51  ?0?00 10001 ??1?? ?1??? ??0?0 010?1 10?0? 1?0?? 1000? ???10
101  00??0 000?0 00001 ????? ????? ????? ????? ????? ????? ?????
151  ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
201  ????? ????? ????? ??000 ?110? ????? ????? ????? ????? ?????
251  ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
301  ????? ????? ????? ????
```

Ecolsonia cutlerensis

```
  1  11000 0?111 11000 00001 01000 00000 00012 10000 21101 00010
 51  10000 00001 ??000 10000 10000 00100 00101 00000 10000 00011
101  00120 01011 00004 ?0011 ?1100 0010? 10000 01?00 0?010 00100
151  00011 10??0 01011 00010 0020? 101?? ?1?00 00010 01?01 01010
201  10101 01010 101?? ?1000 00000 1110? 10010 11111 11101 21101
251  1??1? ??101 00111 0?1?? 1001{12} 0???0 000?? 00000 01000 00000
301  00001 11111 00??? ???1
```

Edops craigi

```
  1  0??10 00111 01000 00000 00010 00000 00011 00000 21100 00000
 51  10000 00000 10000 10011 ?0000 00101 00101 00000 00010 00010
101  00100 00010 00004 40010 01100 00101 00000 10100 0?011 00000
151  00000 001?0 00001 00010 00200 001?? ?1000 0001? 01101 00010
201  ?0101 01010 1011? 01000 0000? ????? ????? ???11 ?1101 21101
251  1001? ????? ????? ????? ????? ????? ????? 00??? 01000 00000
301  ????1 1???? ?0??? ????
```

Eocaecilia micropoda

```
  1  11101 00111 ?1000 0000? 01000 00?10 01010 000?? 20110 00000
 51  ?0000 00001 ??1?? ?0000 00001 ????? ??100 0001? 10000 00?10
101  00000 1?0?1 00004 40101 11110 01010 0001? ????? 0?010 01011
151  00011 001?? 01011 00?00 00200 121?? ?1100 000?? 1??1? ??1??
201  ?1??? 1???1 ????? ??111 0000? ????? ??0?? ?1??? ?11?? ?1?11
251  11111 1{12}??? ????1 00110 1???? ???10 0011? 00000 01110 ?0000
301  00001 11111 ?01?? ?111
```

Pholiderpeton (= *Eogyrinus*) *attheyi*

```
  1  0??01 0011? ?1000 00000 00010 00000 00011 00010 21100 00001
 51  ?0000 00000 10000 00101 ?0000 00100 00100 00010 10110 00010
101  00110 020?0 00002 3?100 01100 00001 00000 00000 0?001 00000
151  00000 001?? ????? ???01 10200 00??? ?1100 00011 01101 00010
201  10101 01010 10100 ?1000 0100? ????? ????? ????? ????? ?????
251  ????? ????? ????0 ?11?? ????? ????1 000?? 00000 01110 00010
301  00001 111?? ?0??? ????
```

Eoherpeton watsoni
1 0??01 00110 ?1000 00000 00010 00100 00011 00010 21100 00000
51 ?0000 00000 0?000 00101 ?0000 00?00 00?00 00000 10010 00?10
101 0020? 02030 00004 41??? ????? ?000? 00000 ?0000 0?00? ?0000
151 00?00 0???? ????? ??1?1 10200 ????? ?1?00 00111 01101 00010
201 00101 01010 101?0 ?1000 0000? ?1??? ??010 1?100 10101 10001
251 1011? ???11 1011? ??1?0 110?? ????1 0000? 00000 01100 00000
301 00001 111?? 00??? ???1

Eoscopus lockardi
1 11100 0011? ?1000 01000 01000 00010 00012 10000 21100 10010
51 ?0000 00001 ??000 1000? ?0100 00100 00101 00000 10000 00110
101 01110 020?1 00004 ??011 10010 10?11 00000 ?1100 0?010 00101
151 00011 101?0 ????? ???1? ???01 ??1?? ???00 00??? 01101 0????
201 ?0?0? 0?0?0 ?0??? ??000 0000? ?110? 000?1 ???0? ?111? ?1?1?
251 ???11 12101 00111 101?0 10012 01100 00100 00000 010(01)0 00000
301 00001 11111 00110 0111

Eryops megacephalus
1 11000 00111 11000 00000 00010 00100 00011 00000 21100 00010
51 10000 00001 ??000 10001 ?0000 00100 00101 00000 00010 00010
101 00100 00011 00104 40011 01100 00101 00000 10100 0?010 00100
151 00011 001?0 01001 00010 00200 001?? ?1000 00010 01101 00010
201 10101 01010 10111 11000 00000 1110? 00000 11111 11101 21100
251 10011 12101 101?1 01120 11012 01100 000(01)0 00000 01000 00000
301 00001 11111 00110 0111

Eucritta melanolimnetes
1 0??00 0?11? ?1000 00000 00000 00000 00012 00000 21100 000?0
51 ?0000 00000 10010 100?1 ?0000 00100 00000 000?? 10000 00?10
101 00111 000?0 0000? ??010 0110? ?0101 00000 ??000 0?0?1 ?0000
151 001?? ????? ????? ???01 10200 00??? ???00 00??? ????? ?????
201 ????? ????? ????? ??000 00000 ?11(01)(01) 000?? ?1?0? ?0101 ?0001
251 1001? 1111? ?011? ???20 1??1? ???00 000?? ????? ????? ?????
301 ????? ????? ??1?? ???1

Euryodus primus
1 0??01 10111 01000 00000 00001 00000 00010 00010 21100 00000
51 10100 00111 ??1?? ?0000 00010 00010 01?00 00010 10000 11010
101 00000 020?1 00004 {01}101? 01100 01100 00001 11000 0?01? 00000
151 11000 0?1?? 00101 00000 00200 02??? ?1100 001?? 1??01 01011
201 0???? ????? ????? ?1000 0001? ?1?11 1001? 1?101 11101 21101
251 11111 ??1?1 ?0111 10120 1001{12} ????? ???01 00??? 01110 10000
301 ???11 1???? 011?? ???1

Eusthenopteron foordi
1 0??00 00000 ?0??? 00000 00000 00000 00000 00?00 00000 00000
51 00000 ?0010 00000 00000 00000 00001 00000 00000 00000 00000
101 ?0000 02000 00?00 00000 00000 00000 00000 00000 0?000 00000
151 00000 00000 00000 00000 00000 01000 0?000 00000 00000 00000
201 00010 00100 0?0?? ?0000 00000 0000? 00000 00?00 00000 00000
251 00000 00000 00000 ?0000 0000? ????0 000?0 00000 01000 00000
301 00000 00000 000?? ?000

Gephyrostegus bohemicus

```
  1  0??01 0011? ?1000 00000 00000 00100 00011 10110 21100 00010
 51  ?0000 00000 0?000 001?1 ?0000 00100 00100 00000 10000 00010
101  00110 020?1 00004 41010 0???? 00101 00000 11100 1?001 00000
151  00000 001?? 0000? 00?0? ??20? ??1?? ?1100 00111 00100 00010
201  00001 00010 10111 01000 00000 11111 00010 11101 10101 20101
251  10111 12111 1011? ?0120 11012 11101 00000 00000 01100 00000
301  00001 1???? ?0101 0111
```

Rhynchonkos (= *Goniorhynchus*) *stovalli*

```
  1  0??01 10111 01000 00000 00000 001?0 00012 00010 21100 00000
 51  10100 00111 ??1?? ?0000 00010 00010 01100 00010 1000? ??010
101  00000 0(12)0?1 00004 4?100 01100 01000 00001 01000 0?000 00000
151  01000 001?1 00101 00000 00200 021?? ?1100 000?1 01101 01010
201  01??? 01100 1???? ?1000 0000? ????? ????? ???01 ?111? ?1101
251  11111 12101 00111 00120 10012 ?1111 00011 00??? 01110 10000
301  ???11 111?? 011?? ?111
```

Greererpeton burkemorani

```
  1  0??00 01110 ?1101 10101 10000 00000 00011 00101 21001 10000
 51  10000 1000(01) ??000 10010 10000 00001 10000 00000 00000 00010
101  01100 00010 00002 20000 01100 00000 00000 00000 0?001 00000
151  10000 00010 00001 00010 01200 00010 11001 00110 00101 00010
201  00010 01010 10101 ?0000 10000 0100? 01000 11100 10101 10001
251  10010 12101 00111 11120 10012 0?110 11000 00000 01000 00000
301  00001 111?? 00101 01?1
```

Hapsidopareion lepton

```
  1  0??01 00111 01000 00000 00000 00100 00011 00010 21100 00000
 51  10100 00101 ??1?? ?0000 00100 00000 01000 00010 10000 11010
101  00000 020?1 01014 {01}1100 ?1100 01000 00001 01100 0?01? 00000
151  01000 0???1 00101 00000 00200 02??? ?1100 001?? 1??01 01011
201  0???? ????? ????? ??000 0000? ????? ????? ????? ????? ?????
251  ????? ????? ????? ????? ????? ???0? ???00 ????? ????? ?????
301  ????? ????? ????? ????
```

Hyloplesion longicostatum

```
  1  0??01 0011? ?1101 00000 00000 001?0 00010 00011 21111 10010
 51  ?0000 00001 ??1?? ?0000 00100 00?00 01100 00010 10000 00010
101  00200 020?1 00004 {01}1?11 0??0? 01101 00001 11111 0?000 00000
151  00000 001?? ??1?? ??00 00200 01??? ??100 00??? 0?10? ?1???
201  ????? ????? ????? ??000 00000 11??? ??01? ???01 ??11? ?1?01
251  11110 12101 00111 00120 10012 01101 000?? 00??? 0???0 ?0??0
301  ???11 111?? ?1100 11?1
```

Ichthyostega stensioei

```
  1  0??00 01000 ?1000 00000 00010 00000 00012 00001 11100 001?0
 51  ?0000 00001 ??000 10000 10000 00000 00000 00000 00000 00000
101  01100 00030 00000 00100 10100 01000 00001 00000 0?001 00000
151  00000 0000? 00000 00000 00000 00010 11000 00010 00000 00010
201  00110 01100 11000 ?0000 00000 00111 10010 1?100 00001 00101
251  10001 12111 00111 010?0 00011 00011 000?? 00000 01000 00000
301  00001 11100 001?? ?101
```

Isodectes obtusus
```
  1  10000 00111 01001 00000 00000 00000 00010 00000 21000 100(01)0
 51  10000 00000 10000 00000 00000 00100 00100 00011 10000 00010
101  00100 010?0 00001 10001 01110 00?1? 1000? ???0? 0?000 0?000
151  00011 00010 00001 00010 00200 12??? ??000 00??? 0?10? ?1010
201  ????? ????0 10111 ?1000 1000? ???10 00??? ????? ????? ??0??
251  ???1? ????? ????? ????? ????? ????? ????? ????? ????? ?????
301  ????? ????? ????? ????
```

Karaurus sharovi
```
  1  11100 0011? ?1010 01001 110?0 00?11 01012 100?? {12}1110 ?1???
 51  ????? ?1??1 ??1?? ?1??? ??1?1 ????? ??000 001?? ????0 11?10
101  11110 1?0?1 00004 ?0101 ?1111 1???? ???1? ????? 0?100 0?110
151  00011 101?? 01011 00?00 00210 12??? ??1?? 000?? 1??01 ??1??
201  ?1??? 1???1 ????? ????? ????? ?1??? ??0?? ?1?01 ?111? ?1?1?
251  ???11 1110? ?01?? ???2? 1???? ???00 0011? 00000 0???0 11??0
301  00001 11111 00110 01?1
```

Keraterpeton galvani
```
  1  0??00 0?110 ?1001 00001 00000 01100 00?10 00011 21111 10000
 51  ?0000 10001 ??1?? ?00?0 01000 00000 10100 0101? 10000 00?10
101  00200 020?0 00004 4???? ????? ????? 0???? ????? 0?00? 0?000
151  00?00 0???? ????? ????? ????? ????? ??100 00??? ???0? ?1010
201  ????? ????? ????? ??000 ?0001 1100? 01??? ?1?0? ?11?? ?0?01
251  10010 0110? 001?? ???20 1???? ????1 000?1 11110 0???0 10??0
301  10001 11111 001?? ?111
```

Kotlassia prima
```
  1  0??01 0011? ?1000 00000 00000 00100 00010 00010 11101 10000
 51  10000 00000 11000 10001 ?0100 00100 00101 000?0 10000 00010
101  00200 01011 00004 41100 01100 01000 00001 00000 10010 00000
151  00000 001?0 00001 00001 10200 011?? ?1100 00110 01101 00010
201  00101 01010 10111 11000 00000 11011 10000 11?11 ?1101 21?01
251  10011 ??111 ?01?1 11120 1001? 0?101 0000? 00000 01111 10000
301  00011 11111 011?? ?111
```

Leptorophus tener
```
  1  1?100 0011? ?1011 01000 01000 00010 01011 10000 21101 ?00??
 51  ?0000 00011 ??000 10??1 ?0000 00100 00101 00000 10000 00?10
101  11110 020?1 00004 40101 01110 01010 ?1101 01010 0?000 00111
151  00011 101?? ????? ???10 00200 101?? ?1??? 00010 01101 01010
201  10101 01010 10111 11011 0000? ???0? 00??? ???0? ?111? ?1?1?
251  ???1? 110?? ????? ????? ????? ????? ????? 00000 ????0 00??0
301  000?1 1???? ?01?? ???1
```

Lethiscus stocki
```
  1  0??00 ??11? ?1101 00000 00000 00010 00?1? ?0??1 21001 10?00
 51  ?0000 1000? ??001 000?? ?00?0 00001 10000 0???? ??000 ???10
101  00110 02??0 10014 ????? ????? ????? ????? ????? ????? ?????
151  ????? ????? ????? ????? ????? ????? ??1?? 00??? ????? ?????
201  ????? ????? ????? ????? ???0? ????? ????? ?1??? ????? ?????
251  ????? ????? ????? ????? ????? ????0 ????1 0???? 0???0 101?0
301  ???01 11111 000?? ?11?
```

Limnoscelis paludis

```
  1  0??01 10111 11000 00000 00000 00100 00011 00111 21101 001?0
 51  01000 00001 ??000 00001 ?0100 00100 00100 0001? 10000 00110
101  00000 02021 00004 411?? 011?0 01?0? 00001 0??00 1101? 00000
151  00000 001?1 00001 10101 00200 01??? ?1000 00??? 1??01 01010
201  0???? 01010 10??? ?1000 00000 11??? ??010 1?011 10101 21101
251  10011 12111 10110 ?1010 1101? ???01 00001 00000 01111 10000
301  00011 11111 00101 0111
```

Megalocephalus pachycephalus

```
  1  0??00 00111 01000 10010 00000 10000 00011 00000 21100 00000
 51  00000 00001 ??010 1001? ?0000 00000 00100 00001 00100 00010
101  01120 00010 00003 30010 01100 00101 00000 10100 0?001 00000
151  001?? ?0000 00001 00100 01200 00010 11000 00111 01101 00010
201  00111 01110 11100 ?1000 0000? ????? ????? ????? ????? ?????
251  ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
301  ????? ????? ????? ????
```

Micraroter erythrogeios

```
  1  0??01 10111 01000 0000? 0000(01) 001?0 00012 00010 21100 00000
 51  10110 00111 ??1?? ?0000 10110 00010 00?00 000?? 10000 11010
101  00000 1?011 01004 ?1(01)10 01100 01100 00001 11000 0?001 ?0000
151  01000 001?1 00101 00000 01200 02??? ?1100 001?? 01101 01010
201  0???? ????? ????? ?1000 00000 11011 101?? 11??? ????? ?????
251  ????? ???01 00111 001?? ????? ???01 00001 00000 01110 10000
301  00011 11111 011?? ?111
```

Microbrachis pelikani

```
  1  0??01 0011? ?1101 00000 00000 01100 00010 00011 211?1 00010
 51  10000 00001 ??1?? ?0000 00100 000?0 01100 00010 10000 00010
101  00200 020?1 0000{23} 31110 01100 01101 00001 11100 0?01? 00000
151  10000 001?? 00101 00010 00200 011?? ?1000 00110 01101 01010
201  00101 01010 10110 11000 00000 11111 101?? ???01 ?01?? ?0101
251  11110 11011 00111 00120 1001? ???01 00001 00000 01110 001?0
301  00011 11111 11100 1111
```

Micromelerpeton credneri

```
  1  11100 00111 11000 01000 01010 00000 00010 100(01)0 21100 00010
 51  ?0000 00001 ??000 100?1 ?0000 00100 00101 00000 10000 00?10
101  01110 020?1 00001 {23}0001 01110 00010 10101 01000 0?000 00111
151  00011 1000? ????? ???10 00200 111?? ?1000 00010 01101 01010
201  10??? 01010 10111 11000 0000? ??10? 00??? ???0? ?111? ?1?0?
251  ???11 1100? ?01?? ???2? 1???? ???00 001?? 00??? 01000 00000
301  ???01 11111 00110 0111
```

Neldasaurus wrightae

```
  1  ???00 0011? ?1000 10000 00000 00000 00012 00000 21000 00000
 51  10000 00000 10000 10000 10000 00100 00101 00010 100?0 00?10
101  00100 02010 0000{23} ?00?1 11100 00?00 00000 ??000 0?010 00000
151  00011 00010 00001 00010 00200 00??? ??000 00??? 01101 00010
201  ????? ????? ????? ?1000 0000? ??00? 010?0 ?110? 11101 21001
251  10111 1210? 001?1 0?1?? ????? ????0 000?? 00000 01000 00000
301  00001 1???? 00110 01?1
```

Odonterpeton triangulare

```
  1  0??01 0011? ?1101 00000 00000 00000 00012 100?1 21110 00100
 51  ?0000 00?01 ??1?? ?1??? ??0?0 000?0 0?110 00010 10000 11010
101  00000 020?1 00004 ?1110 01100 01100 00001 01111 0?001 00000
151  00000 001?? ????? ???00 00200 02??? ?1100 0???? 0??0? ?????
201  ????? ????? ????? ??000 00000 11??? ????? ?1?0? ????? ?1?01
251  11110 110?? ????? ????? ????? ???01 000?? 00??? 0???0 00??0
301  ????1 1???? 11100 11?1
```

Oestocephalus amphiuminum

```
  1  0??01 0011? ?1101 10001 00000 01010 00010 0000? 21001 10000
 51  10000 10001 ??001 00000 00001 ????? ??000 00000 10000 00010
101  0?210 00010 10014 4???? ???0? ?1000 000?? ????? 0?00? 00000
151  0000? 0???0 00001 01000 00200 01??? ?1?00 00??? 1??01 01010
201  0???? ????? ????? ??000 0(01)000 11??? ????? ?1??? ????? ?????
251  ????? ????? ????? ????? ????? ???00 000?1 1???? 0???0 101?0
301  ??001 11111 000?? ?11?
```

Paleothyris acadiana

```
  1  0??01 00111 01000 00000 00000 00100 00011 10011 21111 00010
 51  01000 00011 ??000 00001 ?0100 00100 00100 00010 10000 00010
101  00110 00021 00004 41100 01100 01101 000?? ????? 11001 00000
151  00000 001?1 00001 10101 10200 01??? ?1100 001?? 1??01 01010
201  0???? ????0 11111 11000 00000 11111 10010 1?111 10101 21111
251  1???1 12101 00111 00120 10012 11111 00001 00000 01110 10000
301  00011 111?? 00101 0111
```

Panderichthys rhombolepis

```
  1  0??00 00000 ?0??? 00000 00000 00000 00010 00?00 00000 10000
 51  ?0000 ?000(01) ??000 00000 00000 00001 00000 00000 00000 00000
101  ?0100 000?0 00?00 00000 00000 00000 00000 0?000 ??0?0 00000
151  00000 0000? 00000 00?00 00000 00000 0(01)000 00000 00000 00000
201  00010 00100 01000 ?0000 00000 0000? 00000 00?00 00001 00000
251  ???00 000?? ????? ????0 ???0? ????0 0000? 00000 00??0 ?0000
301  000?0 00000 000?? ?101
```

Pantylus cordatus

```
  1  0??01 10111 01101 00000 00000 00100 10011 00010 21101 10000
 51  10000 00101 ??1?? ?0000 10000 00011 01100 00010 11010 00010
101  00000 1?011 00004 ?1100 01100 00001 0001? ????? 0?001 00000
151  00000 001?1 00101 00000 00200 011?? ?0000 001?? 01101 01010
201  01??? 1???0 1111? 11000 00010 11011 10000 11001 10101 21101
251  10111 12101 00111 001?0 ???1{12} 01101 00011 00000 01110 001?0
301  00011 11111 11110 01?1
```

Pelodosotis elongatum

```
  1  0??01 1011? ?1000 00000 00000 00100 00012 00010 21100 00000
 51  ?0110 00111 ??1?? ?0000 10110 00010 00000 0001? 10000 11010
101  00000 1?0?1 01004 ??1?0 ?1100 01?00 000?? ????? 0?000 ?0000
151  01000 0?1?1 00101 00?00 00200 02??? ???00 00??? ???0? ?1010
201  ????? ????? ????? ??000 00000 11111 100?1 ?1?01 ?0101 21101
251  10111 1210? ?0111 00120 100?? ???01 0000? 00??? 01110 00000
301  ???11 1???? ?11?? ?1?1
```

Petrolacosaurus kansensis
1 0??01 00111 ?1000 00000 00000 00100 00011 10011 21110 00010
51 01000 00011 ??000 00001 ?0100 00000 00100 00010 10000 00010
101 00110 02021 00004 41110 01100 01101 01001 01110 11001 00000
151 00000 001?1 00001 10101 10200 011?? ?1100 001?? 01101 01010
201 01??? 1???0 11111 01000 00000 11111 10010 11111 10101 21111
251 11111 12101 00111 00120 10012 11101 00001 00000 0111(01) 10000
301 00011 11111 00101 01?1

Phlegethontia linearis
1 0??00 00110 ?1100 00000 ?01?? ??110 00?0? ?0??? 21??1 ?1???
51 ????? ?0011 ??1?? ????? ??0?1 ????? ???00 00010 1000? ??010
101 00110 020?0 10014 4???? ????? ????? 0???? ????? ????? ?????
151 ??00? 0???0 00001 01??? ????? ?21?? ?1100 000?? 1??1? ??1??
201 ?1??? 1???1 ????? ??000 00000 11??? ????? ?1??? ????? ?????
251 ????? ????? ????? ????? ????? ???00 00001 ????? 0???0 101?0
301 ??001 11111 000?? ?11?

Pholiderpeton scutigerum
1 0??01 00110 ?1000 00?00 ?0010 0010? 00011 00?1? ?110? ?0001
51 00000 00000 0?000 00101 ?0?00 00?00 00?00 00001 00000 00010
101 00110 00?30 00003 31000 01100 0000? ?0000 00000 0?001 ?0000
151 00000 001?0 00001 00101 10200 00000 11000 00111 01101 00010
201 00101 01010 10111 01000 01000 11?1? ??000 10??0 ?0?01 {12}??01
251 1111? 121?? ????? ????? ????? ???01 0000? 00000 01110 00010
301 00001 1???? ?01?? ???1

Phonerpeton pricei
1 11000 00??? ?1000 00001 01000 01000 00011 10000 21100 00010
51 10000 00001 ??000 1000? ?0000 00000 00101 00000 10000 00111
101 01110 02011 00004 40011 01100 0010? (01)000? 10?00 0?010 00000
151 00011 001?0 01011 00010 00200 0?1?? ?1000 00011 01101 01010
201 10101 01010 1011? 11000 00000 11??? ????0 1?111 1?101 2110?
251 ????? ??1?? ????? ????? ????? ????0 000?? 00000 01000 00000
301 00001 11111 ?0??? ???1

Platyrhinops lyelli
1 11100 0011? ?1010 01000 01000 00010 00012 00000 20100 00010
51 ?0000 00001 ??000 100?1 ?0100 00100 00101 00000 10000 00110
101 ?0100 020?1 00004 400?1 01110 10?11 ?0000 ?1100 0?010 01100
151 00011 1?1?0 ????? ???10 00200 101?? ?1?00 00010 01101 0?010
201 10??? 01010 1011? ?1011 00000 11?0? 00??? ???0? ?110? ?1?11
251 11111 121?? ????1 0012? ????? ???00 001?? 00000 01000 ?0000
301 00001 11111 00??? ?1??

Proterogyrinus scheelei
1 0??01 00110 ?1000 10000 000?0 00000 00011 00010 21100 00001
51 00000 00000 00000 00101 ?0000 00100 00100 00011 100?0 00010
101 00110 02030 0000{12} 41??0 ???0? ?0001 00000 1?000 0?001 00000
151 00000 0???0 00001 00101 10200 00??? ?1000 0011? 0?101 00010
201 ?0?0? 01010 1010? ?1000 01000 11110 00000 11100 10101 20101
251 10011 11111 10111 01120 11012 11101 00000 00000 01100 00000
301 00001 11111 00101 0111

Ptyonius marshii

```
  1  0??00 00110 ?1000 00001 00001 01000 00011 00111 21001 10001
 51  00000 00001 ??001 000?1 ?0000 10001 10100 00010 10000 00?10
101  00110 020?0 00004 40100 ?1100 01000 00001 00000 0?001 00000
151  00010 001?? 00?01 00?10 00200 01??? ??100 00??? ???0? ?1010
201  ????? ????? ????? ??000 00000 1110? 010?? 11?0? ?11?? ?0101
251  11110 1110? 0011? ???20 1???? ????1 000?1 11111 0???0 10??0
301  00001 11111 00110 0111
```

Sauropleura pectinata/scalaris

```
  1  0??00 00110 ?1(01)0(01) 10001 00001 01010 00001 00111 21001 10000
 51  ?0000 00001 ??001 000?0 00000 10001 10100 00000 10000 00010
101  00110 02010 00004 4110? 01100 01000 000?? ????? 0?00? 00000
151  00000 001?? 00001 00?00 00200 001?? ?1100 001?? 1??0? 01010
201  0???? ????1 ????? ?1000 00000 1110? 010?? 11?1? ?11?? ?0101
251  11110 1110? 0011? ???20 1??1? 0?1?1 00001 11111 0???0 10??0
301  00001 11111 00110 0111
```

Saxonerpeton geinitzi

```
  1  0??01 0011? ?1000 00000 00000 001?0 00012 ?0010 21100 00000
 51  ?0000 00101 ??1?? ?0000 00100 00010 0?000 00010 10000 11?10
101  00000 020?1 0000? {01}111? 01100 0110? 000?? ????? 0?01? 00000
151  00000 001?? ????? ???00 00200 01??? ??100 00??? ???0? ?1???
201  ????? ????? ????? ??000 00000 11111 1001? ?1?01 ?011? ?1101
251  11111 12101 00111 001(12)0 10012 01101 000?? 00??? 0???0 ?0??0
301  ???11 1???? 11110 01?1
```

Schoenfelderpeton prescheri

```
  1  1?100 0011? ?1011 01000 01000 00?11 01010 00000 21101 10010
 51  ?0000 00001 ??000 ?0??1 ?0000 00100 00101 00010 10000 00?10
101  11110 020?1 00004 40101 01110 11010 ?1101 01010 0?000 00111
151  00011 101?? ????? ???10 00200 12??? ?1?00 000?? 01101 01010
201  ????? ????0 ???11 11?00 0000? ???0? 10??? ???0? ?111? ?1?0?
251  ???1? 1101? ?01?? ????? ????? ????? ????? 00??? ????? ????0
301  ????1 1???? ?0110 0??1
```

Scincosaurus crassus

```
  1  0??00 00110 ?1001 00001 00000 01100 00110 00010 21101 ?1???
 51  ????? ?0101 ??1?? ?00?0 00?00 00011 00100 01010 10010 00010
101  00200 020?1 00004 401?? ?11?0 01111 0001? ????? 0?000 00000
151  00000 001?? 10001 00?00 00200 01??? ????? ????? ????? ?????
201  ????? ????? ????? ??000 ?0000 1100? 000?1 11?11 ?0??? ?1101
251  11110 1210? 00111 00120 1??1? ????1 000?1 11110 01110 101?0
301  00001 11111 001?? ?111
```

Seymouria baylorensis/sanjuanensis

```
  1  0??01 00111 11000 00000 00000 00100 00011 00010 21100 000(01)0
 51  10000 00000 11000 10001 ?0100 00100 00100 00010 10010 00110
101  00200 02011 00004 41010 01100 00101 00001 1110? 10011 00000
151  00000 001?0 00001 00001 00200 011?? ?1100 00111 01101 01010
201  00101 01010 10111 11000 00000 11011 ?0110 11111 10101 21101
251  10011 12111 10110 ?1020 11012 01100 00000 00000 01111 10000
301  00011 11111 00101 0111
```

Solenodonsaurus janenschi

```
  1  ????1 ??11? ?1000 ??000 00000 00100 00?11 00111 21101 100??
 51  ?0000 00001 ??000 10??? ?0000 00100 00100 0?01? 10000 00?1?
101  0?100 020?1 00004 ????? ????? ????? ????? ????0 ????? ?????
151  ????? ????? ????? ????? ????? ?0??? ????? ?0??? ???0? ??010
201  ????? ????? ????? ??000 ?0000 11?11 100?? ????1 ?0101 21?01
251  10?11 120?? ????? ????? ????? ???01 000?? 00000 01110 100?0
301  00001 1???? 001?? ?1?1
```

Stegotretus agyrus

```
  1  0??01 10111 01000 00000 00000 00000 10012 00010 21100 00000
 51  10100 00101 ??1?? ?0000 ?0010 00010 01?00 00010 11000 00010
101  00000 010?1 00004 ?1100 01100 00001 0001? ????? 0?001 ?0000
151  00000 001?1 00101 00000 00200 02??? ??000 00??? ???0? ?1010
201  ????? ????? ????? ?1000 0001? ???1? 1000? 11??? ?1??? ?1?0?
251  ????1 1211? ?0111 10110 ????? ????? ????? 00000 01110 001?0
301  00011 1???? 111?? ?1?1
```

Acheloma cumminsi (= *Trematops milleri*)

```
  1  11000 0011? ?1000 00001 01000 01000 00011 10000 21100 00010
 51  10000 00001 ??000 ?0001 ?0000 00100 00101 00000 10000 00111
101  01110 02011 0000? ????1 ???0? ?0?01 000?? ????? 0?010 ?0100
151  00011 00000 01011 00010 00200 00??? ?1100 00??? ???0? ?1010
201  ????? ????? ????? ?1000 00000 11??? ??010 1111? 11101 21100
251  0011? ??101 00111 001?0 1??12 011?0 000?? 00000 01000 00000
301  00001 1???? 001?? ???1
```

Triadobatrachus massinoti

```
  1  ????? ????? ?1??? ???0? ?1??? ???1? 01??? 11??? ?011? ?1???
 51  ????? ?1??1 ??1?? ?1??? ??1?1 ????? ???01 001?? ????? ???1?
101  ??11? 0?0?1 0000? ????? ???1? ?1011 ??11? ????? 0?000 10110
151  00011 1???? 01011 00?00 00210 10??? ????? 10??? 1??1? ??1??
201  ?1??? 1???1 ????? ????? ????0 11??? ??1?? ?1?01 ?111? ?1?11
251  11111 1110? ?1110 ?0?20 1001{12} 0??00 0011? 00000 0???0 10??0
301  00001 11111 001?? ?111
```

Trimerorhachis insignis

```
  1  10000 00111 ?1000 00000 00000 00000 00010 00000 21000 00000
 51  10000 00000 00000 1000(01) 00000 00001 00001 00000 10000 00010
101  00110 00010 0000{23} ??001 11100 00000 00001 00000 0?000 00000
151  00011 00010 00001 00010 00200 011?? ?1000 00011 01101 00010
201  101?? 01000 10010 01000 0000? ??10? 011?0 ?1?0? ?1101 21001
251  10111 11101 0011? ???10 100?? ???01 000?? 00000 010?0 00000
301  00001 0???? 00110 0111
```

Tuditanus punctulatus

```
  1  ????? ??11? ?1000 0000? 00001 001?0 00?11 00010 21100 00???
 51  ?0??? 001?1 ??1?? ?0??0 001?0 00010 01000 0001? 10000 00?10
101  ?0200 0?0?1 0000? ????? ????? ????? 0???? ????? 0?00? ??000
151  ?0000 0???? 00101 00?00 00200 00??? ??00 00??? ???0? ?1010
201  ????? ????? ????? ??000 00000 11111 10??? ???0? ?01?? ?1001
251  11111 1{12}?11 00111 001?0 1001{12} {01}1?11 000?? 00??? 0???0 10??0
301  ???11 11??? ?1110 0111
```

Tulerpeton curtum

```
  1   ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
 51   ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
101   ????? ????? ????? 3?01? ?01?0 ????? ????? ????? ????? ?????
151   ????? ??00? ????? ????? ????? ????? ?1000 0???? ???00 ?0???
201   ????? ????? ????? ??000 ?0000 ?101? 00010 10100 00101 10001
251   1000? 111?? ????1 11021 10112 111?? ????? ????? 0100? ?0000
301   ????? ????? ??100 0???
```

Urocordylus wandesfordii

```
  1   0??00 0?1?? ????? ????? ??001 01000 00??? ????? ????? ?????
 51   ????? ????? ????? ?00?0 00??0 100?1 10?00 00000 10?00 00?1?
101   ????0 ????0 00?0? ????? ????? ?1?00 ?00?? ????? ??0?? ?0?00
151   ??000 0???? ????? ????? ????? ????? ?1100 00??? ???0? ?1010
201   ????? ????? ????? ??000 ?0000 1110? 010?? ?1?0? ?01?? ?0101
251   10010 1110? 0?111 01120 1??1? ????1 000?1 11111 0???0 101?0
301   00001 11111 00110 0111
```

Valdotriton gracilis

```
  1   11100 0011? ?1001 01001 111?? ???11 01010 100?? 011?0 ?1???
 51   ????? ?1??1 ??1?? ?1??? ????1 ????? ??000 001?? ????1 ???10
101   10110 1?0?1 00004 ?0101 11111 0???? ???1? ????? 0?100 1?010
151   00011 1?1?0 01011 00?00 00200 121?? ?1100 00??? 1??1? ??1??
201   ?1??? 1???1 ????? ??1?? 0000? ?1??? ??011 11?01 ?111? ?1?11
251   11111 1100? ?0111 0?120 100?? ???00 001?1 00010 0???0 11??0
301   00001 11111 00110 0111
```

Ventastega curonica

```
  1   0???? ????? ????? ????? ??010 00000 00??? ????? ????? ?????
 51   ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
101   ????0 ????? ????0 ????? ????? ????? ????? ????? ????? ?????
151   ????? ????? ????? ????? ????? ??001 11010 00010 00000 00000
201   00010 00100 11000 ?0000 0000? ??0?? ????? ????? ????? ?????
251   ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
301   ????? ????? ????? ????
```

Westlothiana lizziae

```
  1   0??01 00111 01100 ?000? 000?? 0?1?? 00?11 00011 21100 00000
 51   ?0000 000?1 ??000 00??1 ?0100 00100 01?00 000?? 10000 00010
101   002?0 020?1 0000? ????? ????? ??101 ?0001 1?100 0?00? ?0000
151   00000 0???1 ????? ???00 10200 01??? ??100 00??? ???0? ?1010
201   ????? ????? ????? ??000 0000? ?1??? ??0?? ??111 10101 21?01
251   11110 12111 00111 10121 10012 111?1 000?? 00000 01111 10000
301   00011 11111 011?? ?111
```