DATES, NODES AND CHARACTER CONFLICT: ADDRESSING THE LISSAMPHIBIAN ORIGIN PROBLEM

Marcello Ruta*

Department of Geology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago,
IL 60605-2496, USA

Michael I. Coates

Department of Organismal Biology and Anatomy, University of Chicago, 1027 East 57th Street, Chicago,
IL 60637-1508, USA

SYNOPSIS Extant amphibians consist of Salientia (frogs), Caudata (salamanders), and Gymnophiona (caecilians). The mutual relationships of these groups are controversial, with either Batrachia (Salientia + Caudata) or Procera (Gymnophiona + Caudata) as emerging clades in recent molecular and morphological analyses. The monophyly of amphibians as a whole is supported by independent data, but their origins and affinities with early tetrapods are debated. A new cladistic analysis of early tetrapods retrieves Temnospondyli (the most species-rich group of early tetrapods) as the closest relatives of crown group amphibians. One temnospondyl group, the Dissorophoidea, forms a series of consecutive outgroups to crown amphibians. In particular, the Lower Permian amphibamid *Doleserpeton* is the most derived plesion on the amphibian stem. The Albanerpetontidae, a group of salamander-like tetrapods ranging from the Jurassic to the Pliocene, are placed as stem Gymnophiona. The shortest trees support the Batrachia hypothesis. However, the Procera hypothesis is not a significantly worse fit for the whole character set. Exhaustive treatment of characters and taxa is the most appropriate way to disentangle contrasting phylogenetic signals in large matrices. Tests of different crown topologies show that placement of amphibians within lepospondyls (e.g. as sister taxon to Lysorophia) is not a significantly worse fit for the whole character set than a close temnospondyl–lissamphibian relationship. However, the latter phylogenetic hypothesis best captures the most coherent assembly of derived lissamphibian apomorphies.

KEY WORDS Tetrapoda, Lissamphibia, Batrachia, Procera, Temnospondyli, Lepospondyli

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* Current address: Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, B58 IRJ, UK.

Introduction

Extant amphibians, including frogs, toads, salamanders, newts and caecilians (a small and poorly understood clade of limbless, secretive and burrowing animals superficially similar to earthworms) include nearly 20% of all tetrapods. Their study informs numerous fields in both the general and applied life sciences and they are used extensively as 'model' organisms to illustrate basic concepts of vertebrate anatomy and physiology. Renewed interest in amphibian biology is timely in an age in which preservation of natural habitats, and the retrieval or rescuing of species of medical and/or general zoological interest, are top priorities on bioconservation agendas worldwide (Fanning *et al.* 1982; Williams *et al.* 1997; Biju & Bossuyt 2003). Research networks and collaborative programmes devoted to several aspects of amphibian biology can be found at the following web links: http://amphibiatree.org and http://www.amphibiaweb.org. Both of these aim to provide an extensive database as well as iconographic material encompassing all currently recognised species (more than 6100).

In this paper, we present a new phylogeny for early tetrapods and examine its bearings on the issue of caecilian origins and crown amphibian interordinal relationships. The results from the new analysis are also used to evaluate statistical support for alternative hypotheses of amphibian ancestry and the implications that such hypotheses have for a chronology of the major evolutionary episodes in the group's history. We argue that the current debate on the phylogenetic context of amphibian origins deserves a fresh look, considering both the rapid advances in our knowledge of the diversity and morphology of Palaeozoic tetrapods and the initial results from analyses based upon large taxon/character matrices. A scrutiny of these matrices, and a synthesis of all the available data for Palaeozoic tetrapods, remain major tasks for future investigations in this area of vertebrate phylogeny (Ruta *et al.* 2003; Schoch & Milner 2004; Clack & Finney 2005

and comments therein). However, before discussing our new analysis, we set out to provide a brief summary of the results from recent morphological and molecular studies of crown amphibian relationships, review the earliest fossil record of the three major amphibian orders and introduce some of the key issues in current, fossil-based theories of amphibian ancestry.

A 'modern' systematic concept of amphibians did not become fully established until the second half of the last century (e.g. Parsons & Williams 1963; Milner 1988). Remarkably, in certain classifications, they continued to appear as either a paraphyletic or a polyphyletic group until the mid 1980s (e.g. Jarvik 1980; Løvtrup 1985). However, numerous molecular and anatomical (both hard and soft tissue) data now provide compelling evidence in support of the monophyly of amphibians as a group (Milner 1988; Duellman & Trueb 1994; Pough *et al.* 2001). Much of the controversy currently centres on the mutual relationships of their three orders, as well as on their affinities with Palaeozoic tetrapods. As regards amphibians' putative early fossil relatives, two vexing questions characterise the debate on amphibian origins: (1) was their ancestry rooted into one or several Palaeozoic groups of tetrapods? (2) what are these groups? (Milner 1988, 1993; Laurin 1998; Laurin & Reisz 1999; Anderson 2001; Ruta *et al.* 2003; Vallin & Laurin 2004; Schoch & Milner 2004). A related issue concerns the ancestry of caecilians, because these are morphologically quite distinct from frogs and salamanders (see Schoch & Milner 2004 for discussions and see comments below).

Answers to these questions should provide insights into the origin and early radiation of a major, extant tetrapod clade and permit a more precise characterisation of the biological consequences of the fish-to-tetrapod transition. These questions have a direct bearing upon issues such as rates of morphological change, palaeobiogeography and palaeoecology, in short, the ensemble of conditions that led to the establishment of the early land vertebrate communities

(see also Laurin 2004 for a discussion of related topics in early amniote evolution). In addition, clarifying amphibian phylogeny (both within their crown and within their stem) offers an unprecedented opportunity to explore the use of well-dated amphibian fossils as calibration points for refining current molecular time scales of major events in vertebrate evolution (Kumar & Hedges 1998; Dyke & Van Tuinen 2004; Van Tuinen & Dyke 2004; Van Tuinen & Hadly 2004; Van Tuinen & Hedges 2004). A further step in this direction consists of integrating data from fossil taxa belonging to more ancient and/or more basal evolutionary lineages that precede the crown group radiation (for recent discussions of this subject, see Roelants & Bossuyt 2005; San Mauro *et al.* 2005; for additional information, see Reisz & Müller 2004; Evans *et al.* 2005).

AIMS

The aims of the present work are to evaluate contributions of palaeontological data to early amphibian phylogeny, outline the potentials and limitations of such data, provide a convenient summary of the probable minimum time scale of events in amphibian phylogeny and indicate directions for future research. New and revised data (both characters and taxa) have been added to Ruta *et al.*'s (2003) recent matrix. The results from the present study are used to survey character distribution among the early members of the three extant groups of amphibians, as well as within clades that lie immediately beyond the boundaries of the crown group radiation (specifically, several amphibamid temnospondyls, see below).

NAMES, NOTATIONS AND GROUP BOUNDARIES

The boundaries of an extant monophylum are based upon conventions first introduced by Hennig (1966) and modified by numerous subsequent authors. The crown group of an extant monophylum includes its latest common ancestor and all descendants from the latter, both extant and extinct. The total group of an extant monophylum includes the crown group and all those fossils (collectively referred to as the stem group) that do not belong in the crown, but which are closer to extant crown species than to other extant species (see Craske & Jefferies 1989; Kitching *et al.* 1998; Budd 2001). Each stem group consists of fossil monophyla, termed plesions (Patterson & Rosen 1977; Patterson 1981, 1993; see Craske & Jefferies 1989 for a different concept of plesion and its delimitations). Preferences for a total group definition have been discussed elsewhere (Ruta *et al.* 2003), but alternative treatments of clade terminology are available (e.g. see Laurin & Anderson 2004 on the use and meaning of the term 'Tetrapoda'). Regardless of the size of a totally extinct clade, or parts thereof, it is its proximity to a living monophylum that matters in an operational definition (cf. Patterson 1981, 1993), not the subdivisions and naming of its constituent subclades (see Craske & Jefferies 1989 for treatments of plesion subgroups).

Extant amphibians include three orders: Salientia, Caudata and Gymnophiona. These terms identify the frog, salamander and caecilian total groups, respectively. Anura, Urodela and Apoda refer to their respective crown groups

(Milner 1988; Evans & Milner 1996; Evans & Sigogneau-Russell 2001). As an example, any extant species of frog could be equally said to be a member of the Anura, or a member of the crown Salientia. Any extinct frog that falls outside the crown group belongs to stem Salientia, i.e. it is not a member of Anura.

'Batrachia' applies to the (Caudata + Salientia) clade. 'Procera' applies to the (Caudata + Gymnophiona) clade (Milner 1988; Feller & Hedges 1998). However, no term has yet been coined for the (Salientia + Gymnophiona) clade, for which, however, there is little or no cladistic support (Milner 1988; Schoch & Milner 2004; but see also Zhang *et al.* 2003).

The term 'Lissamphibia' is usually applied to the amphibian crown group (Milner 1988). References to Palaeozoic 'amphibians', mostly as a grade group term, are widespread both in the palaeontological and in some of the zoological literature, regardless of whether any of these Palaeozoic taxa are phylogenetically closer to the amphibian crown (Lissamphibia) than to the amniote crown (see also conflicting results in Ruta *et al.*'s 2003 and Vallin & Laurin's 2004 studies). To avoid any confusion, we opt to use 'Amphibia' exclusively as a total group term throughout this article.

Parenthetical notations are used to indicate clade structure. Thus, if two taxa, B and C, are more closely related to each other than either is to a third taxon, A, then the relationships of A, B and C can be written as (A + (B + C)). If A, B and C are collapsed in an unresolved node (or polytomy), then their relationships can be written as (A B C).

The geological ages of all the relevant fossils discussed in this paper are based upon the most recent International Stratigraphic Chart prepared by the International Commission on Stratigraphy (http://www.stratigraphy.org/chus.pdf).

LISSAMPHIBIAN RELATIONSHIPS

Morphological phylogenies

Classic examples of specialised morphological characters that unite most or all of the extant amphibians include: bicuspid and pedicellate teeth; a sensory area in the inner ear called the *papilla amphibiorum*; a *levator bulbi* eye muscle; absence of numerous skull and lower jaw bones (unlike the condition in several groups of early tetrapods); mucous and granular skin glands; paired occipital condyles; absence of palatal fangs; straight and short ribs; absence or reduction of dermal bones in the shoulder girdle, and others. See Milner 1988, Duellman & Trueb 1994, Evans & Sigogneau-Russell 2001, Pough *et al.* 2001 and Schoch & Milner 2004 (especially p. 363, table 1) for a more exhaustive treatment of such characters.

Morphological analyses of amphibian interordinal relationships are underrepresented in the literature and usually based upon small taxon samples from a few families. In most of them, Batrachia emerges as a monophyletic group. Characters in support of this clade have been discussed extensively (Bolt & Lombard 1985; Milner 1988, 1993; Bolt 1991; Trueb & Cloutier 1991; Trueb 1993; Gardner 2001; McGowan 2002). However, some fossil-based analyses (Laurin 1998; Laurin & Reisz 1999; Vallin & Laurin 2004) have found Caudata to be paraphyletic relative to Gymnophiona. In this, they agree at least in part with the results from a number of molecular works that support Procera (Feller & Hedges
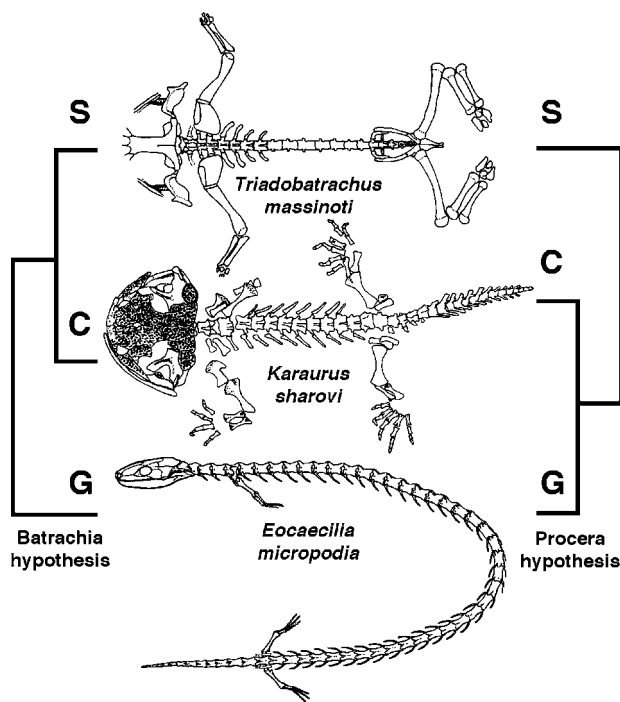
Figure 1 The two main hypotheses of amphibian interordinal relationships. Capital letters S, C and G indicate, respectively, total group Salientia, Caudata and Gymnophiona. These three orders are illustrated by their most plesiomorphic representatives. *Triadobatrachus* and *Karaurus* are after Milner (1994). *Eocaecilia* is after Carroll (2000b). Drawings are not to scale.

1998; Zhang *et al*. 2003). A test of the robustness of Procera requires the inclusion of additional taxa from a broader range of living and fossil families (Schoch & Milner 2004; Evans *et al*. 2005), as well as replacement of supraspecific taxa with species in the relevant data sets (see Prendini 2001 for a protocol outlining the choice of taxonomic exemplars). Both the Procera and the Batrachia hypothesis are shown in Fig. 1, in the form of simplified cladograms. Salientia, Caudata and Gymnophiona are illustrated by their most primitive fossil members (and see below).

Thus far, no study has attempted a review of crown amphibian interrelationships using a comprehensive sample of taxa from the basal portions of stem Salientia, stem Caudata and stem Gymnophiona. Moreover, recent fossil discoveries (e.g. Evans & Sigogneau-Russell 2001) are likely to exert a significant influence upon the results of morphological analyses. Further sources of currently under-utilised phylogenetic signal are also available, including soft tissue anatomy and diversity in developmental patterns (e.g. Rocek 2003; Rose 2003; Wake 2003). Despite a number of theoretical objections (e.g. Schulmeister & Wheeler 2004), it is worth emphasising that developmental variation is receptive to a cladistic treatment, when characterised as differences in the sequences of ontogenetic events (Jeffery *et al*. 2002a, b, 2005).

Molecular phylogenies

Four recent molecular analyses addressing, in detail, interordinal relationships of amphibians have found these to cohere

as a clade. However, these analyses have yielded irreconcilable patterns within the crown group. Thus, they supported either Batrachia (Zardoya & Meyer 2001; San Mauro *et al*. 2004) or Procera (Feller & Hedges 1998; Zhang *et al*. 2003). These studies are not open to easy comparisons, as they share little taxonomic overlap (Table 1) and the molecular data employed, as well as the analytical methods, differ. For example, Feller & Hedges (1998) reported anomalies (also cited by Zhang *et al*. 2003) in a particular gene sequence of *Xenopus laevis* (the African clawed frog; also included by Zardoya & Meyer 2001) and used a novel sequence instead. But whether different sequences and/or methods of analysis are alone sufficient and causal for conflicting results is a moot point (see Schoch & Milner 2004 for additional comments and a review of molecular phylogenies).

Recently, an overarching analysis by San Mauro *et al*. (2005), inclusive of 25 anurans, 12 urodeles and seven apodans (plus eight outgroups), was used as the basis for a revised molecular time scale of key episodes in amphibian evolution. We comment on some of the major conclusions from that study below, especially the estimated time of origin of crown amphibians. The study in question retrieved a Batrachia clade, although with low statistical support for Bayesian inference, minimum evolution and maximum parsimony.

It would be valuable to assess the sensitivity of these analyses to random inclusions and exclusions of taxa, different outgroup samples, alternative optimisations and inclusion of additional sequences. For instance, a maximum parsimony analysis performed by Zhang *et al*. (2003) on their data set retrieved a (Gymnophiona + Salientia) clade, although with very low statistical support. This noteworthy result, however, lacks any support whatsoever from morphological data (e.g. Milner 1988; Schoch & Milner 2004).

Earliest crown amphibians

Salientia

Triadobatrachus massinoti from the Early Triassic of Madagascar (Piveteau 1936; Fig. 1) is the most basal representative of the Salientia. The list of synapomorphies it shares with other Salientia includes, among other features, a toothless dentary, a rod-like and anteriorly directed ilium and fused frontals and parietals (Rage & Rocek 1989; Rocek & Rage 2000a, b). Incomplete remains of a second, only slightly younger and more derived stem Salientia, *Czatkobatrachus polonicus*, are known (Evans & Borsuk-Bialynicka 1998). *Eodiscoglossus oxoniensis*, from the Middle Jurassic of England (Evans *et al*. 1990), is the earliest true frog, i.e. the oldest member of the crown clade Anura. This 165 million year old fossil belongs to the family Discoglossidae, which includes the extant midwife toads and painted frogs. It postdates *Triadobatrachus* by approximately 85 million years. Over the last decade, the Mesozoic record of Salientia has been enriched by several significant discoveries as well as a reinterpretation of several previous finds (Báez & Basso 1996; Rocek 2000). One of the most interesting taxa, *Prosalirus bitis*, represents the earliest Jurassic Salientia, but it may not belong within the Anura (Shubin & Jenkins 1995; Jenkins & Shubin 1998; Gao & Wang 2001). It is nearly 30 million years older than *Eodiscoglossus oxoniensis* and throws light

Table 1 Comparisons among the taxonomic samples used in four recent molecular analyses of amphibian relationships.

	Feller & Hedges 1998	Zardoya & Meyer 2001	Zhang *et al.* 2003	San Mauro *et al.* 2004
Alligator mississippiensis	–	+	–	–
Balaenoptera musculus	–	+	–	–
Carassius auratus	–	–	+	–
Chrysemis picta	–	+	–	–
Cyprinus carpio	–	–	+	–
Didelphys virginiana	–	+	–	–
Eumeces egregius	–	+	–	–
Gallus gallus	+	+	+	–
Homo sapiens	+	+	+	–
Latimeria chalumnae	–	+	+	+
Oncorhynchus mykiss	–	+	+	–
Protopterus dolloi	–	+	+	+
Salmo salar	–	–	+	–
Trachemys scripta	+	–	–	–
Eleutherodactylus cuneatus	+	–	–	–
Rana nigromaculata	–	–	+	+
Rana pipiens	+	–	–	–
Xenopus laevis	+	+	–	+
Ambystoma mexicanum	+	–	–	–
Mertensiella luschani	–	+	+	+
Plethodon yonahlossee	+	–	–	–
Ranodon sibiricus	–	–	–	+
Siren intermedia	+	–	–	–
Epicrionops sp.	+	–	–	–
Gegeneophis ramaswamii	–	–	–	+
Ichthyophis bannanicus	+	–	–	–
Ichthyophis glutinosus	–	–	–	+
Rhinatrema bivittatum	–	–	–	+
Scolecomorphus vittatus	–	–	–	+
Typhlonectes natans	+	+	+	+
Uraeotyphlus cf. oxyurus	–	–	–	+

For each species, the 'plus' and 'minus' signs indicate whether that species has, or has not, been included in a given analysis. Species are divided into four blocks including, from top to bottom, outgroups, Anura, Urodela and Apoda.

on the earliest skeletal changes associated with the evolution of jumping adaptations in the frog skeleton.

Caudata

Karaurus sharovi, found in the Late Jurassic of Kazakhstan, is about 152 million years old and is the most complete and most primitive representative of Caudata (Ivakhnenko 1978; Milner 2000; Fig. 1). With more derived Caudata, it shares a foreshortened palatal ramus of the pterygoid, a forked basal hyoid element and bicipital rib-bearing processes. It postdates slightly the earliest known crown group salamanders (Urodela), which have been described as dating from the Middle Jurassic of England and China (see also Evans *et al.* 1988; Evans & Milner 1994; Milner 2000; Gao & Shubin 2001, 2003). However, we draw attention to the fact that the supposed Jurassic age of the earliest known members of the salamander crown group from China (Gao & Shubin 2001, 2003) has come under closer scrutiny and been challenged in recent works (e.g. Evans *et al.* 2005). The stem caudate *Kokartus honorarius* from the Middle Jurassic of Kirghizistan (Nessov *et al.* 1996) is 13 million years older

than *Karaurus* and regarded as a paedomorphic relative of the latter (Milner 2000). For analysis of character distribution in the basal parts of the caudate stem group, see Evans *et al.* (1988, 2005). *Triassurus sixtelae* (Late Triassic of Uzbekistan: Ivakhnenko 1978; Milner 2000) is a problematic fossil sharing only two features with Caudata, namely a strut-like squamosal-pterygoid support for the quadrate as well as an open cheek. Although poorly preserved, it may provide tantalising glimpses of the only known, putative pre-Jurassic Caudata. Small size and poor degree of ossification are possible larval features of *Triassurus* (Evans *et al.* 2005).

Gymnophiona

Eocaecilia micropodia from the Early Jurassic of North America is the most primitive and most complete member of the stem Gymnophiona (Jenkins & Walsh 1993; Carroll 2000b), predating the only other known stem member by approximately 50 million years (Evans & Sigogneau-Russell 2001; see below) and the earliest crown member (Apoda) by nearly 100 million years (Evans *et al.* 1996). This lengthy

stem reflects the extreme inadequacy of the caecilian fossil record and is unlikely to deliver significant data about a late radiation of Apoda relative to the timing of origination of the other two orders of crown amphibians (see Feller & Hedges 1998 and San Mauro *et al*. 2005 for a discussion of the biogeography and timing of lissamphibian divergence, as well as additional remarks by Schoch & Milner 2004). Unlike Apoda, *Eocaecilia* retains a tail and reduced pectoral and pelvic girdles and limbs. It also possesses a femur with a flat, triangular trochanteric crest, as well as an atlas vertebra with an anterior and peg-like *tuberculum interglenoideum*, or odontoid process. Both these features are much like those in basal Caudata. The *tuberculum interglenoideum* is flanked in Caudata by two cotyles for the articulation with the occiput and is present in Albanerpetontidae (see below) and in certain members of the Palaeozoic lepospondyls (see below). The gymnophionan identity of *Eocaecilia* is manifest in numerous features of the skull table, palate, braincase, lower jaw and vertebral column, including: the presence of a tentacular groove anteroventral to the orbit; a mesial (i.e. internal) set of teeth in the lower jaw and in the palate, each set forming a row parallel to the marginal lower and upper teeth, respectively; a robust and conical process projecting internally from the mesial side of the lower jaw; and fused posterior braincase units (for additional features, see also Jenkins & Walsh 1993; Carroll 2000*b*; Fig. 1). Evans & Sigogneau-Russell (2001) have described a second stem group Gymnophiona, *Rubricacaecilia monbaroni*, from the Early Cretaceous of Morocco. This animal is more derived than *Eocaecilia* (although much less complete) in that it shows a sharp, mid-ventral keel on the postatlantal vertebrae and a reduced number of teeth on the pseudodentary (the bone carrying marginal teeth in the caecilian lower jaw). However, it is more primitive than all extant gymnophionans in that it retains a *tuberculum interglenoideum* and does not possess elongate, anteroventral basapophyseal processes on the trunk vertebrae. Interestingly, incomplete remains of a femur have also been attributed, albeit tentatively, to *Rubricacaecilia* (Evans & Sigogneau-Russell 2001).

Albanerpetontidae

Our review of early crown amphibian groups would be incomplete without reference to a small, but geologically long-ranging, clade of salamander-like tetrapods known as the Albanerpetontidae (Fig. 2A), because these have been variously assigned to stem Caudata, stem Batrachia, or stem Amphibia (Milner 1988; Gardner 2001; McGowan 2002; Ruta *et al*. 2003). Albanerpetontids are known from the Middle Jurassic to the early Pliocene (i.e. about 170 to 5 million years ago: Venczel & Gardner 2003) and have played a substantial role in the current debate on amphibian origins over the last few years (see McGowan & Evans 1995; Gardner 2001; McGowan 2002). Their skeletal specialisations include tricuspid and chisel-like teeth and an interdigitating joint between the lower jaw halves. Despite their overall salamander-like appearance, these fossils are problematic. They have poorly developed basapophyses as well as a *tuberculum interglenoideum*, also documented in some Gymnophiona and basal Caudata (see also Milner 1988; Trueb 1993; Gardner 2001; McGowan 2002; Wake 2003). These characters might provide the basis for a division of crown amphibians into frogs, on the one hand, and albanerpetont-

ids, salamanders and caecilians, on the other. As ever, new data are needed to test this hypothesis (Evans *et al*. 2005).

Here, we offer an alternative, albeit tenuous, solution to the albanerpetontid conundrum, the significance of which is discussed in conjunction with the problem of caecilian/proceran ancestry.

PALAEONTOLOGICAL THEORIES OF LISSAMPHIBIAN ORIGINS

The most controversial chapter in the biology of amphibians concerns the identification of their closest relatives from among the increasing variety of Palaeozoic tetrapods. Different and conflicting hypotheses have resulted from analyses of data sets published over the last 10 years, encompassing various taxonomic exemplars from most or all of the Palaeozoic tetrapod clades. For discussions of conflicting phylogenies focussing on the amphibian–amniote divergence and, in general, for an overview of the affinities of various Palaeozoic groups, see Panchen & Smithson (1987, 1988), Laurin (1998), Laurin & Reisz (1999), Anderson (2001), Clack (2002*a*), Ruta *et al*. (2003), Schoch & Milner (2004), Vallin & Laurin (2004) and Clack & Finney (2005).

Elsewhere, the amphibian origin problem has been addressed from a 'top-to-bottom' perspective, through comparisons between selected extant and extinct taxa (Carroll 2000*a*, *b*, 2001, 2004; Carroll *et al*. 1999). Detailed surveys of similarities between particular genera or species of Palaeozoic tetrapods and chosen exemplars of Recent amphibian orders are valuable in formulating primary homologies (*sensu* de Pinna 1991). However, this approach cannot offer a stringent test of alternative hypotheses of lissamphibian origins, because neither character sets nor taxon samples are sufficiently large to include the full range of known morphological variation. Note also that none of the studies cited above has included a formal cladistic analysis. Consequently, evolutionary scenarios such as those presented by Carroll *et al*. (1999) and Carroll (2000*a*, *b*, 2001, 2004) are not amenable to test without a data set and a suitable taxonomic sample.

Two groups of fossil tetrapods – the temnospondyls and the lepospondyls – continue to play pivotal (although conflicting) roles in the amphibian origin debate (Milner 1988, 1993; Schoch & Milner 2004). The roles of these clades will be summarised in the following sections.

Temnospondyl theories

The temnospondyl theory (or theories) of amphibian origins (Moodie 1916; Watson 1919, 1926, 1940) has been developed and elaborated upon by numerous authors (e.g. Bolt 1969, 1977, 1979, 1991; Milner 1988, 1990, 1993, 1994, 2000; Trueb & Cloutier 1991; Gardner 2001; and references therein). With over 160 genera, temnospondyls represent the longest-ranging and most species-rich group of early tetrapods. Their fossil record spans about 210 million years, from the Early Carboniferous to the late Early Cretaceous. Large openings in the palate, the presence of four digits in the manus and the possession of short and straight ribs distinguish them from other groups of early tetrapods. Dissorophoid temnospondyls have received a considerable amount of interest, because of their proposed phylogenetic proximity to
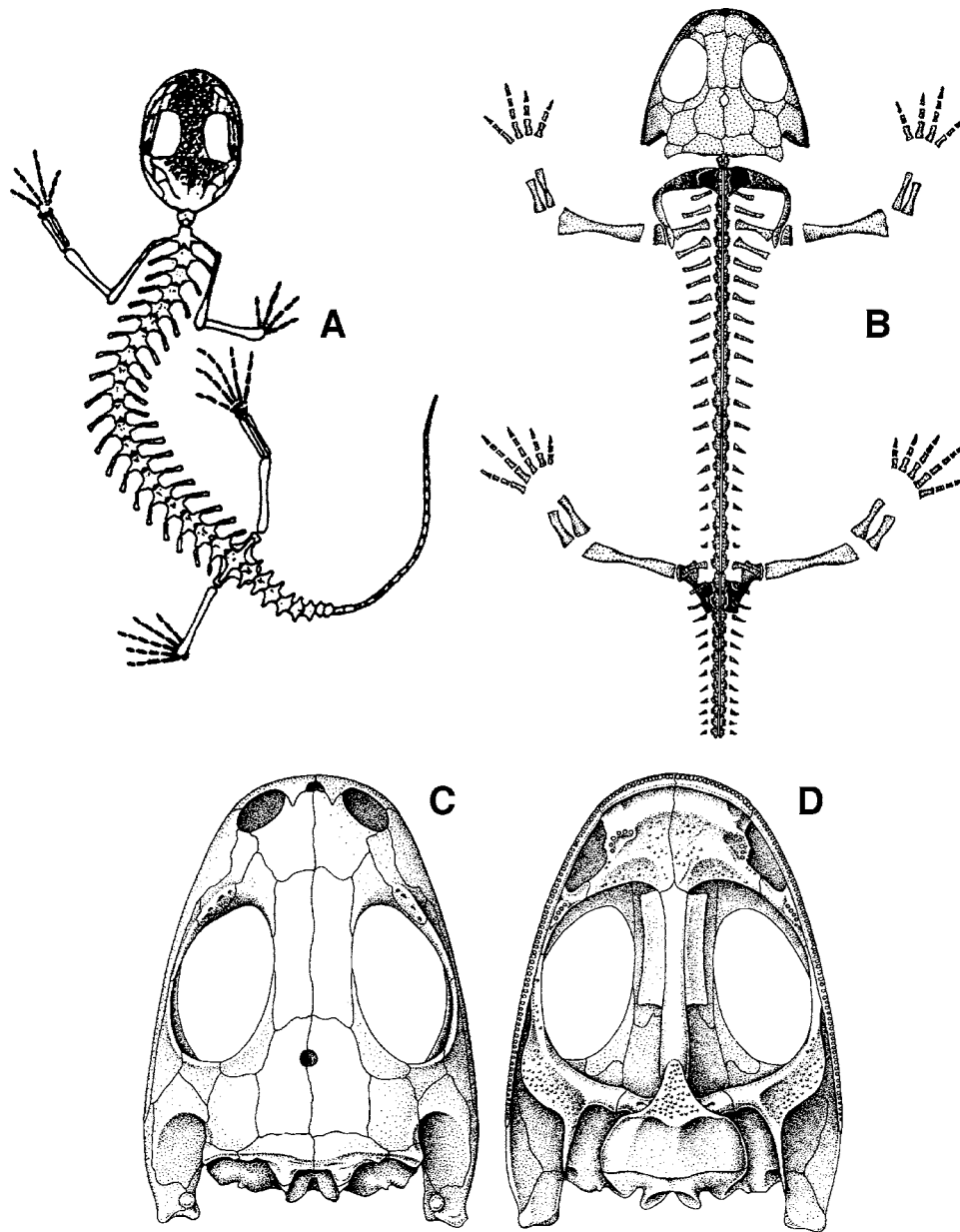
Figure 2 Dissorophoids and albanerpetontids. (**A**) Dorsal skeletal reconstruction of *Celtedens ibericus* (Albanerpetontidae; after McGowan & Evans 1995). (**B**) Dorsal skeletal reconstruction of *Apateon pedestris* (Branchiosauridae; after Boy 1972). (**C, D**) Dorsal and ventral skull reconstructions of *Doleserpeton annectens* (Amphibamidae; after Bolt 1969). Drawings are not to scale.

Lissamphibia (Schoch & Milner 2004). Recently, Carroll (2004) has suggested that some of their derived members might represent a grade group of species belonging in the stems of frogs and salamanders (see below).

Two dissorophoid families, Branchiosauridae (Fig. 2B) and Amphibamidae (Figs 2C & D), are especially similar to some extant and fossil Batrachia. Much attention has been paid to features of their dentition, as the bicuspid crowns and pedicellate tooth bases of numerous amphibamids are strikingly batrachian-like, as are the clumps of vomerine denticles at the front of the palates in certain species. Similarities with anurans include: a broad squamosal embayment at the rear of the cheek; a wide, flat parabasisphenoid plate with anterolateral, wing-like basipterygoid processes; the slender and almost splinter-like morphology of some palatal bones; large

orbits and reduced size of several circumorbital bones; abbreviated and stumpy ribs (these characters do not always co-occur and a number of them are observed in other lissamphibians as well; see also Milner 1988, 1993; Bolt 1991; Holmes 2000; Schoch & Milner 2004; and references therein).

Yet further support for the temnospondyl hypothesis has been claimed from comparisons between the cranial ontogeny in some basal salamanders and inferred ossification patterns in a very abundant and extraordinarily well-preserved branchiosaurid, *Apateon* (Schoch 1992, 1995, 1998, 2002*a, b*; Schoch & Carroll 2003; Fig. 2B). Striking similarities in their ossification sequences have provided a framework for reconstructing the origin and evolution of certain features related to salamander feeding adaptations (Schoch & Carroll 2003). However, such data alone cannot be used to establish

unambiguously close affinities between dissorophoids and lissamphibians, because outgroup comparisons are simply not available. It is quite possible that these similarities are no more than symplesiomorphic conditions for tetrapods.

Other authors have used patterns of skeletal ontogeny in dissorophoids and Batrachia to theorise that the lissamphibian (or a large portion thereof) origin is linked to heterochronic shifts responsible for skull remodelling via miniaturisation (Bolt 1991; Milner 1993). The open, lightly built skulls of Salientia and Caudata, in which homologues of several bones present in early tetrapods fail to ossify, offer examples of such remodelling effects (for more detailed discussions, see Bolt 1991; Milner 1993; Schoch 1995, 1998, 2002a, b; Rocek 2000). However, Gymnophiona pose problems for this scenario, as their skulls are heavily built and closed. The necessary implication, under the temnospondyl theory, is that their robust crania result from secondary adaptations, presumably to a burrowing life-style (Evans & Sigogneau-Russell 2001; Wake 2003) and that ancestral forms possessed skulls much like those in the majority of Salientia and Caudata (also see discussion below). However, other researchers have supported an independent origin of these amphibians from a different group of Palaeozoic tetrapods, notably microsaur lepospondyls (e.g. Carroll 2000b; Anderson 2001).

In recent papers, we have found temnospondyls to be paraphyletic relative to Lissamphibia as a whole (Ruta & Coates 2003; Ruta et al. 2003). These results have also shown that, in the derived portion of the amphibian stem, cladogram nodes exhibit a considerable degree of homoplasy. This could be due to acquisition of convergent traits in small, paedomorphic tetrapods. However, the problem with these kinds of scenarios is that their malleability is sufficient to support almost any transformation. Thus, it is also noteworthy that the position of caecilians in these analyses is not strongly supported and that alternative phylogenetic placements, such as from among lepospondyl groups (Carroll 2000b; Anderson 2001), do not entail statistically significant differences from the shortest trees.

Recently, however, Schoch & Milner (2004) have argued in favour of temnospondyls as the most plausible candidates for the ancestry of all amphibians, based upon morphological, developmental and biostratigraphical arguments, and have discussed in great detail the set of osteological data in support of this hypothesis. They emphasise the impact on tree shape of conflicting phylogenetic signals associated with different character subsets within a single matrix. This is important given the influence that multiple 'absence' characters may have on taxon grouping (see discussion in Ruta et al. 2003). 'Absence' data should be treated with caution, as different causal factors might be associated with the loss of osteological structures and, in some instances, the probability of homoplastic absence (i.e. loss) is very likely to exceed that of homoplastic presence (i.e. multiple morphological originations).

Lepospondyl theories

Temnospondyl theories have been scrutinised and rejected in several recent papers (Laurin 1998; Laurin & Reisz 1999; Vallin & Laurin 2004) in which temnospondyls have been placed on the tetrapod stem and lepospondyls have been substituted for amphibian stem-group membership. Lepospondyls include five Palaeozoic groups: Microsauria, Lysorophia, Nectridea, Aïstopoda and Adelospondyli (Carroll et al. 1998; Carroll 2000a; Anderson 2001; Anderson et al. 2003). Most are characterised by the presence of spool-like vertebrae and elongate trunks, as well as a series of 'absence' features (although variation occurs within them), including lack of some skull table bones and (often) palatal fangs, absence of a labyrinth-like pattern in tooth histology, absence of a posterior embayment in the cheek and reduced or absent limbs and girdles. Other features are shared by a few of these groups only, including a tuberculum interglenoideum of the atlas and intravertebral spinal nerve foramina (see Anderson 2001). The majority of these features have been often cited in support of a single origin for lepospondyls. In fact, it is still unclear whether the latter constitute a monophyletic radiation, or whether each of the five major groups is more closely related to a separate clade of non-lepospondyl tetrapods, or whether only some of the lepospondyls should be grouped together (see Panchen & Smithson 1987, 1988; Milner 1988, 1993; Carroll et al. 1998; Anderson 2001; Ruta et al. 2003; Schoch & Milner 2004; Vallin & Laurin 2004; and references therein).

Certain species within each lepospondyl group share a few osteological characters with a number of amphibians, but the distribution of these characters does not present a coherent, inter-nested set directed towards the amphibian crown radiation (see Milner 1988). In some analyses (Laurin 1998; Laurin & Reisz 1999; Vallin & Laurin, 2004), lepospondyls form a grade group relative to crown amphibians and one particular group, the Lysorophia (Figs 3A–C), forms the most derived stem amphibian plesion (Fig. 4A). The long-bodied Lysorophia are characterised by large orbitotemporal openings, short and deep lower jaw rami, robust and conical teeth, an enlarged braincase floor and small girdles and limbs. However, apart from 'absence' features, hardly any osteological character is shared with one or more of the three orders of amphibians. We note that lysorophians share a broad parabasisphenoid plate with salamanders and caecilians. However, this character is hard to quantify and the outline of the plate is highly variable within these two groups.

An alternative set of lepospondyl–amphibian evolutionary hypotheses places Microsauria as paraphyletic relative to (Eocaecilia + Gymnophiona) (Anderson, 2001; Carroll 2000a, b; McGowan, 2002). However, it is noteworthy that these studies retrieved different microsaur families or genera as near-ancestral gymnophionans. Thus, in one example, Carroll (2000a, b) regarded Rhynchonkos (Figs 3D–F) as being close to the morphotype of caecilians' Palaeozoic ancestors (Fig. 4B) and resemblances are indeed intriguing (see Anderson 2001). However, the postulated affinity of Gymnophiona (or indeed, of all amphibians in some studies) with lepospondyls has been questioned repeatedly (see Milner 1993; Schoch & Milner 2004) and putative synapomorphies uniting Eocaecilia and Rhynchonkos have been interpreted as homoplastic, reflecting convergent adaptations to a burrowing life-style rather than shared common ancestry. Schoch & Milner (2004: 354) argued that several of these similarities are '... part of the clique of character-states associated with all burrowing lower tetrapods', including amphisbaenian squamates, and contrasted them with such dissorophoid features of Eocaecilia as '... rudimentary pterygoid flange, broad vomers, rounded interpterygoid vacuities and palatines broadly exposed in the vacuity
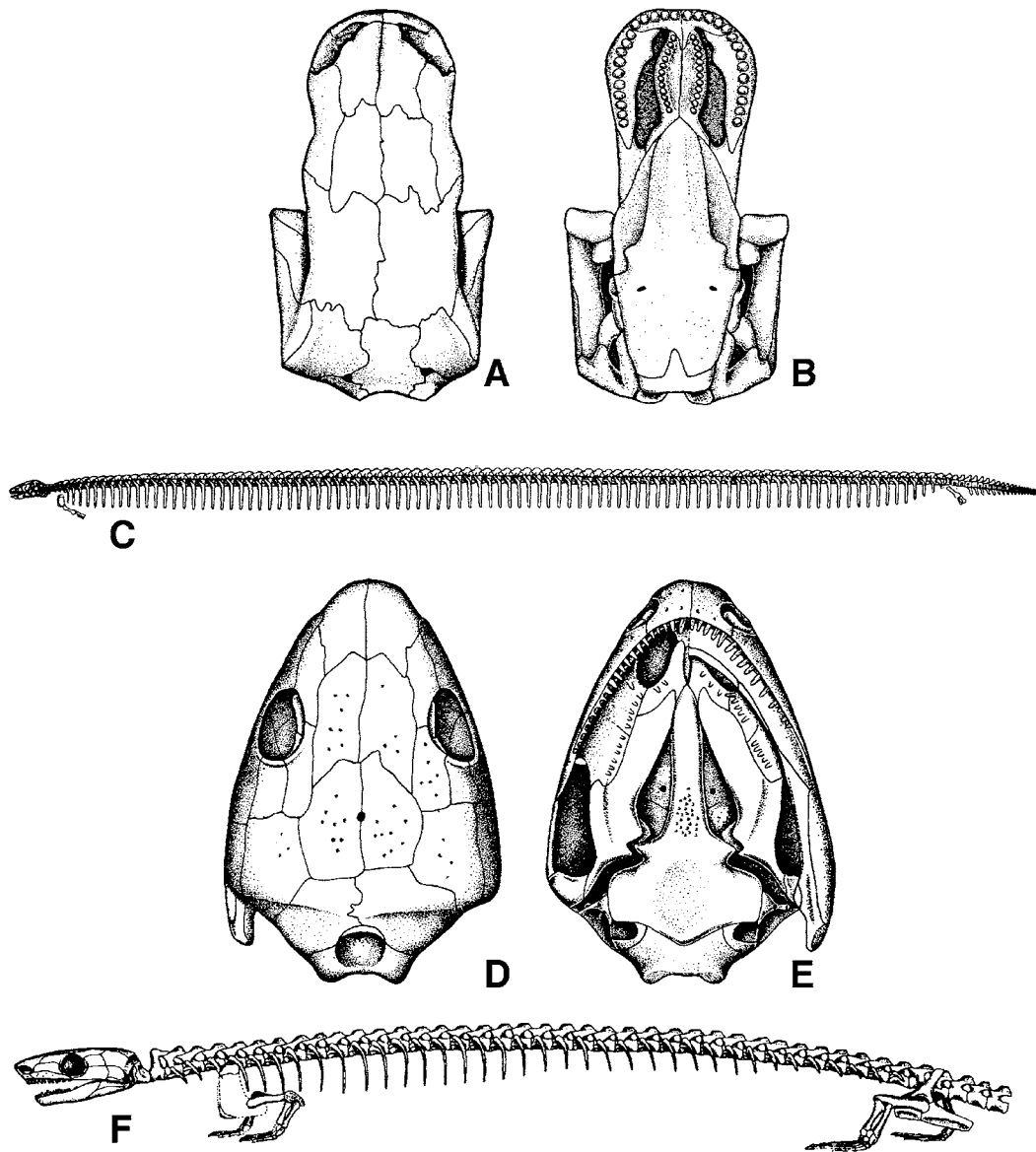
Figure 3 Lepospondyls. (**A–C**) Dorsal and ventral skull reconstructions and left lateral aspect of *Brachydectes elongatus* (Lysorophia; after Wellstead 1991). (**D–F**) Dorsal and ventral skull reconstructions and left lateral aspect of *Rhynchonkos stovalli* (Microsauria; after Carroll & Gaskill 1978). Drawings are not to scale.

margins'. Thus, despite undeniable similarities between *Eocaecilia* and *Rhynchonkos*, the former shares certain cranial as well as postcranial traits with some derived temnospondyls that are not observed in the latter.

Other theories

Among other works that have addressed the amphibian origin problem, McGowan's (2002) analysis departs considerably from remaining studies and, for this reason, it is dealt with in a brief separate section. McGowan's (2002) data included Gymnophiona, Salientia, Caudata, Albanerpetontidae and seven microsaur families as supraspecific taxa, plus eight species of dissorophoid temnospondyls. The latter were found to be paraphyletic relative to the crown amphibians. Within the latter, Albanerpetontidae emerged as stem Batrachia and this clade formed the sister group to Gymnophiona plus Microsauria (the latter formed a paraphyletic array in the gymnophionan stem: Fig. 4C).

A REVISED PHYLOGENY FOR EARLY TETRAPODS

General remarks

To investigate the causes that underlie competing theories of lissamphibian origin, we returned to our recent, large-scale cladistic analysis of Palaeozoic tetrapods (Ruta *et al.* 2003). The rationale behind this analysis was to encompass different taxonomic ranges of previous hypotheses and ensure that characters and taxa should reflect the greatest feasible range of observed variation (cf. Poe & Wiens 2000; Prendini 2001). The utility of a large taxon sample in
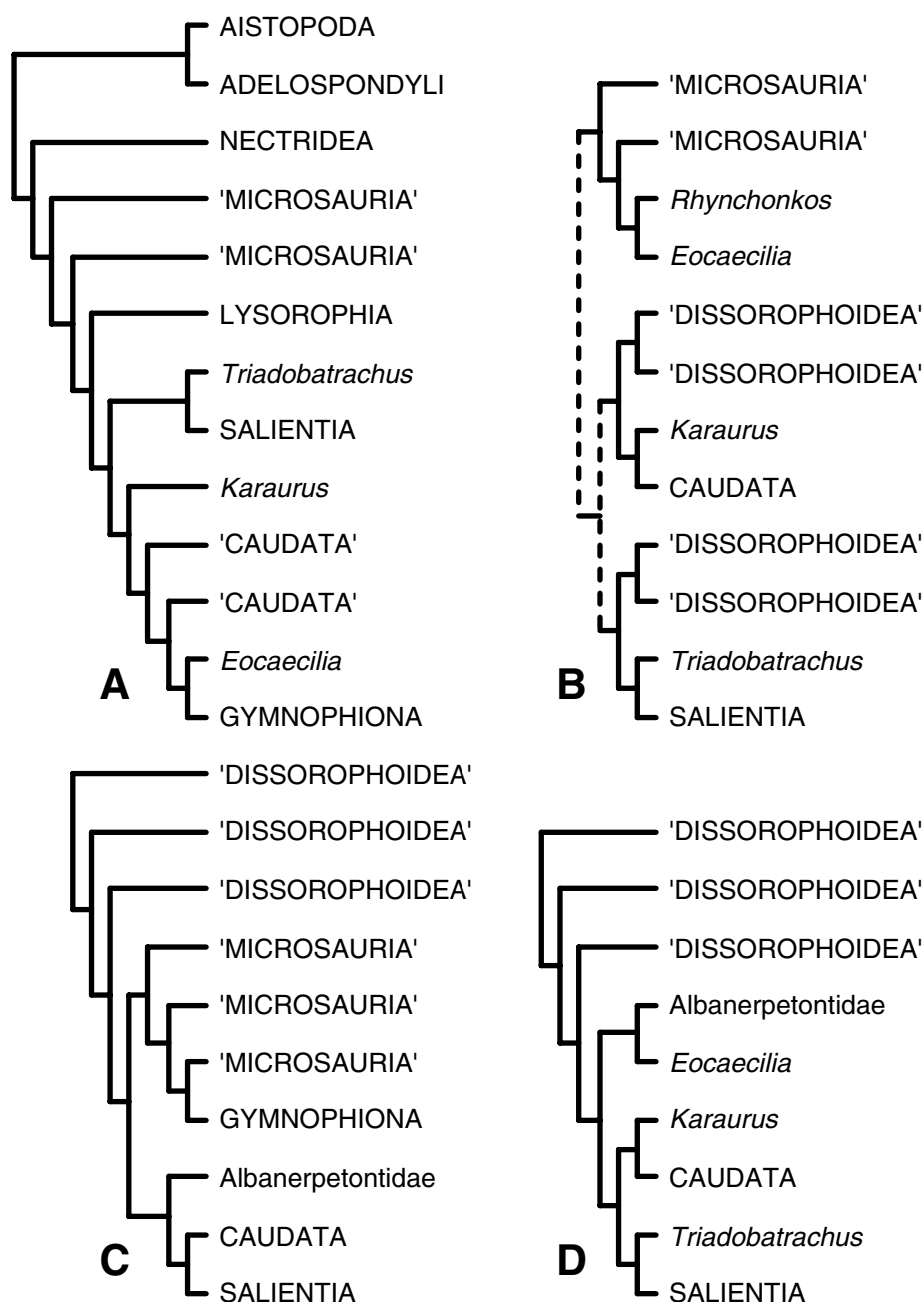
Figure 4 Simplified cladograms illustrating some current hypotheses of lissamphibian relationships with early tetrapods. (**A**) Laurin's (1998) hypothesis: lepospondyls form a paraphyletic group relative to crown amphibians, with Lysorophia as their immediate sister group. (**B**) Carroll's (2001, 2004) hypothesis: Salientia and Caudata are placed as sister groups to amphibamid and branchiosaurid dissorophoids, respectively; see the text for details), while Gymnophiona are nested within microsaurs, as sister group of *Rhynchonkos*. (**C**) McGowan's (2002) hypothesis: Batrachia are sister group to a clade including Microsauria plus Gymnophiona; Dissorophoidea are paraphyletic relative to this broader group. (**D**) the hypothesis preferred here (see the text for details): Dissorophoidea form a paraphyletic group relative to crown amphibians.

inferring character-state conditions near the tree root has been detailed extensively (see Salisbury & Kim 2001; Flynn *et al*. 2005). To cope with the problem of analysing large data sets, search strategies were used that allow coverage of a wide range of tree space within a practical length of time (Quicke *et al*. 2001), using standard computer software (PAUP* 4.0b10: Swofford 2003).

The results of Ruta *et al*.'s (2003) analysis (schematically illustrated in Fig. 4D) provide only partial resolution

in the derived portion of the amphibian stem group. Here, matrix size is increased to a total of 102 taxa and 339 characters (see Appendix 1). The character list and data matrix are given in Appendixes 2 and 3, respectively. Appendix 2 also lists amendments to the coding originally presented by Ruta *et al*. (2003).

All tree searches follow the protocol outlined previously by Ruta *et al*. (2003). More specifically, we carried out 2000 random stepwise addition sequences followed by tree
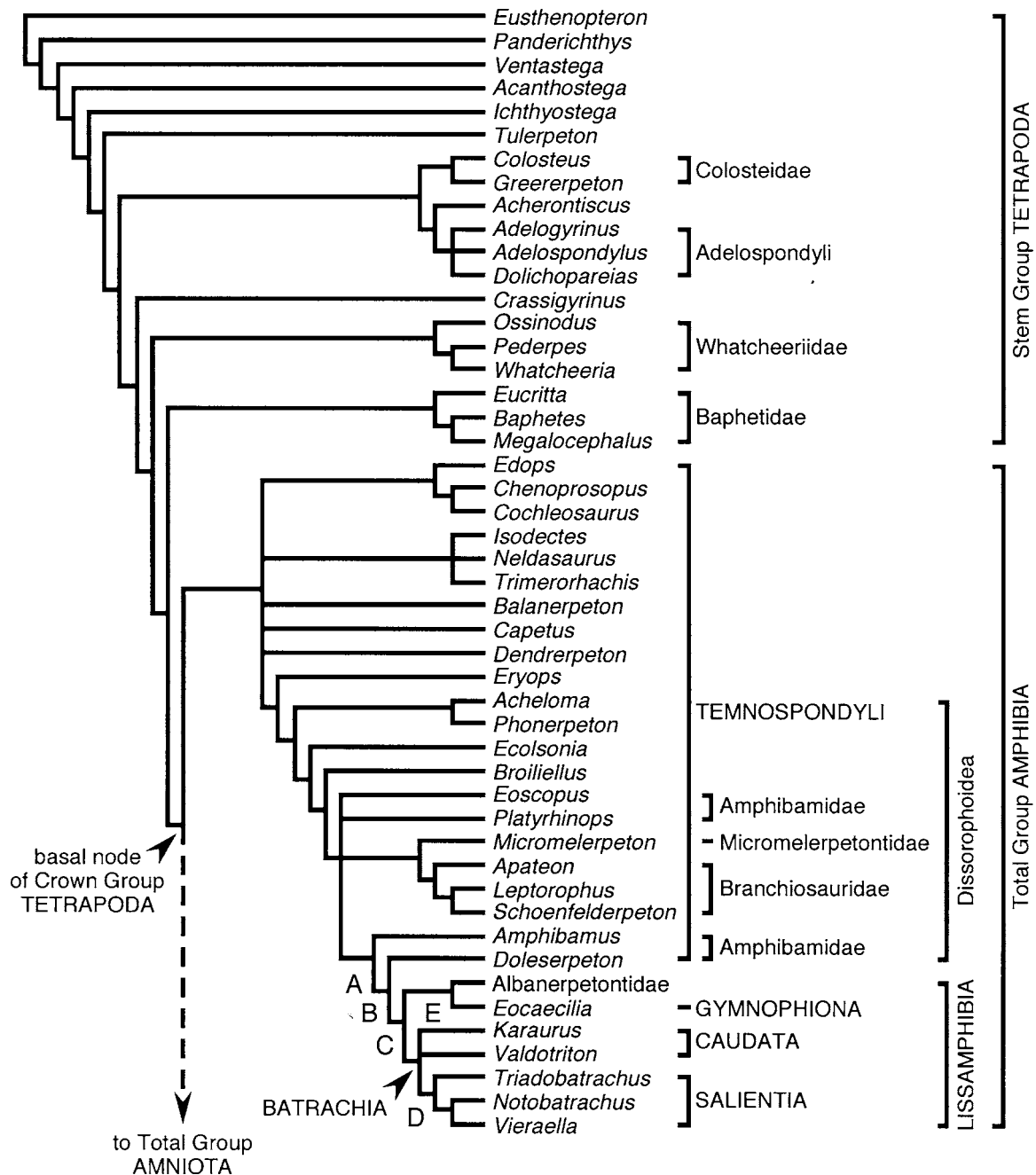
Figure 5 The strict consensus of 324 most parsimonious trees from a parsimony analysis (see the text for details). The relationships of stem tetrapods and total group amphibians are illustrated.

bisection–reconnection (TBR) branch-swapping searching, but holding only one tree in memory at any one time (i.e. the MAXTREES command in PAUP* was set to 1: Quicke *et al.*, 2001). Searching on each tree with unlimited MAX-TREES recovered the same island of trees. No shorter trees were found by employing the iterative re-weighting strategy proposed by Quicke *et al.* (2001).

Results

A maximum parsimony analysis in PAUP* v. 4.0b10 (Swofford 2003) resulted in 324 trees, 1584 steps long, with

Consistency Index (CI) = 0.22 (excluding six uninformative characters), Retention Index (RI) = 0.67 and Rescaled Consistency Index (RC) = 0.15. The strict consensus of these trees is well resolved (Figs 5 & 6). The Colless Index of tree imbalance (Colless 1995), based on the first PAUP* tree, is 0.318218 and was calculated using MeSA v.1.9.15, by Paul-Michael Agapow (http://www.agapow.net/software/mesa/). The agreement subtree (a pruned cladogram including the largest subset of taxa for which all shortest trees agree upon relationships; not shown here) consists of 94 taxa (subtree size = 92.16%). Pruned taxa include: five temnospondyls, namely *Balanerpeton*, *Capetus*, *Trimerorhachis*, *Eoscopus*

to Total Group
AMPHIBIA
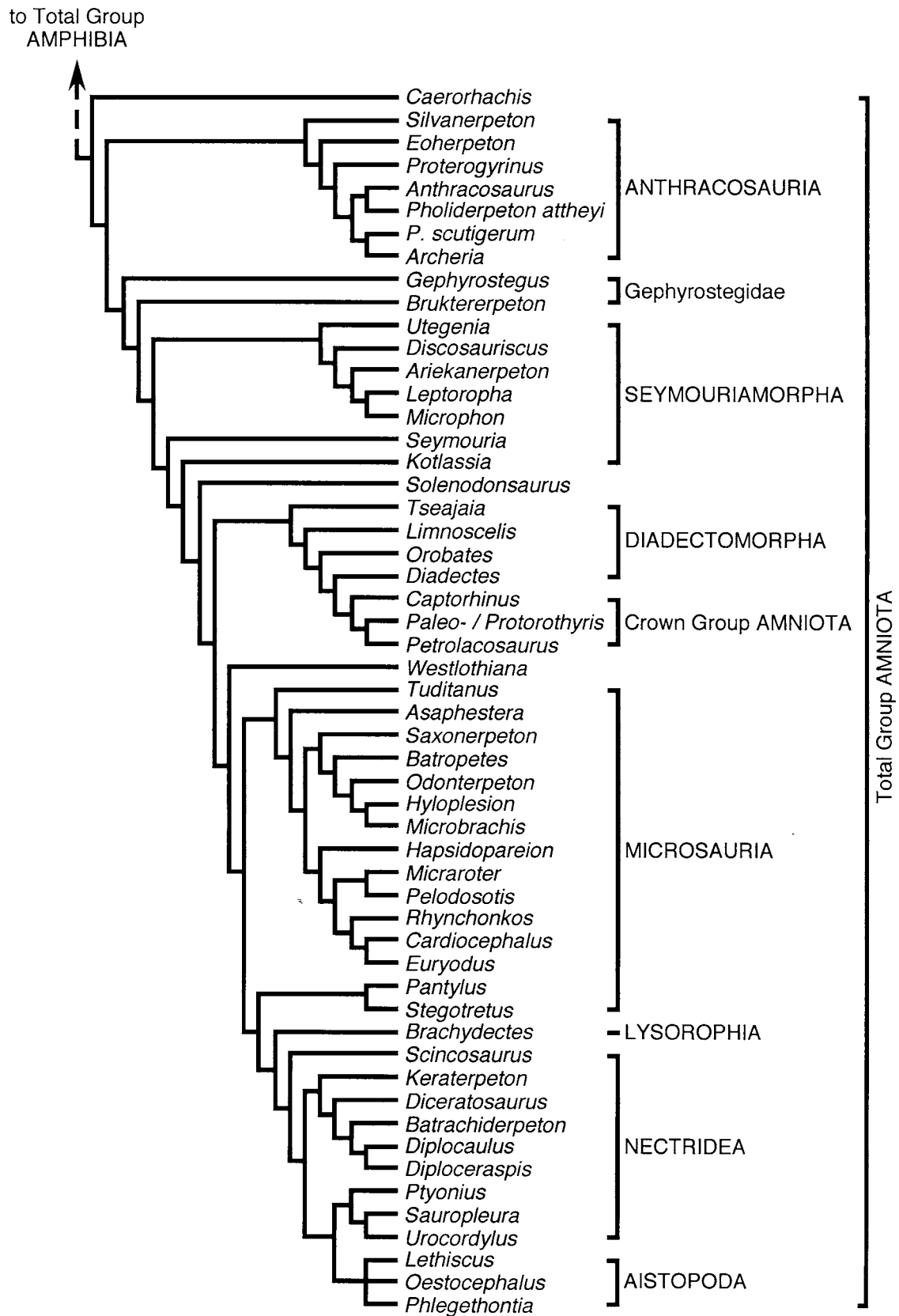
Figure 6 The strict consensus of 324 most parsimonious trees from a parsimony analysis (see the text for details). The relationships of total group amniotes are illustrated.

and *Platyrhinops*; the aïstopod *Phlegethontia*; the adelospondyl *Dolichopareias*; and the caudate *Valdotriton*. Figure 5 indicates nodes discussed in the text and in Appendix 4. Most of these are resolved in the strict consensus (Caudata is the only exception and character discussion of this clade is based only on those trees that show a resolved Caudata) and, therefore, character distribution is identical in all minimal trees.

Our results differ from those of Ruta *et al.* (2003) in that the interrelationships of basal temnospondyl are poorly resolved. In a strict consensus, the following temnospondyl taxa form a polytomy: *Balanerpeton*; *Capetus*; *Dendrerpeton*; a fully resolved clade of edopoids (*Edops* + (*Chenoprosopus* + *Cochleosaurus*)); an unresolved clade of dvinosaurs (*Isodectes* + *Neldasaurus* + *Trimerorhachis*). However, most remaining temnospondyls, namely eryopoids and dissorophoids, form a series of progressively more derived plesions on the amphibian stem. In particular, the two amphibamid dissorophoids, *Amphibamus* and *Doleserpeton*, are adjacent plesions to the Lissamphibia (e.g. Milner 1993). We also note that a single origin for amphibamids (also including *Eoscopus* and *Platyrhinops*) is retrieved in a subset of the shortest trees. In the strict consensus, *Eoscopus* and *Platyrhinops* are in a polytomy with a fully resolved micromelerpetontid–branchiosaurid clade (*Micromelerpeton* + (*Apateon* + (*Leptorophus* + *Schoenfelderpeton*))). Thus, the new analysis provides better resolution for amphibamids than Ruta *et al.*'s (2003). Finally, within Lissamphibia, the Albanerpetontidae are placed as stem Gymnophiona.

Further differences between Ruta *et al.*'s (2003) and the present analysis are as follows. *Eucritta* is removed from its former key position at the base of the amphibian stem group and emerges as the sister taxon to the baphetid clade (*Baphetes* + *Megalocephalus*) (Clack 2002*a*, *b*; Warren & Turner 2004; but see also Sequeira 2004). The baphetids form the most derived stem tetrapod plesion. On the amniote stem, gephyrostegids, seymouriamorphs and diadectomorphs form a sequence of increasingly crownward grades (but see Bulanov 2003; Berman *et al.* 2004; Klembara & Ruta 2004*a*, *b*). *Solenodonsaurus* occurs immediately crownward of seymouriamorphs (Laurin & Reisz 1999). Except for aïstopods, lepospondyls are fully resolved, but there are important differences between the present study and Ruta *et al.*'s (2003): (1) the nectridean *Scincosaurus* is the sister taxon to the clade that includes all remaining nectrideans plus aïstopods; (2) *Tuditanus* and *Asaphestera* are successive sister taxa, in that order, to the majority of remaining microsaurs; the latter consist of a clade in which *Saxonerpeton* and *Batropetes* are successively more closely related to (*Odonterpeton* + (*Hyloplesion* + *Microbrachis*)) and a clade in which *Hapsidopareion* joins ((*Micraroter* + *Pelodosotis*) + (*Rhynchonkos* + (*Cardiocephalus* + *Euryodus*))); finally, the (*Pantylus* + *Stegotretus*) clade and the lysorophids (*Brachydectes*) form successive sister groups to the nectridean–aïstopod clade; (3) adelospondyls (including the problematic *Acherontiscus*) are removed from their position among the stem amniotes and appear as the sister group to the colosteids (*Colosteus* + *Greererpeton*); however, the strict consensus provides no resolution for the adelospondyls *Adelogyrinus*, *Adelospondylus* and *Dolichopareias*.

These results are of particular interest, as they provide the only support for lepospondyl polyphyly based on a character analysis and are consistent with previous finds (Ruta *et al.* 2003) that a relocation of the adelospondyls from the amniote stem to the tetrapod stem does not entail significant redistribution of character-states. However, additional data are necessary to provide a better characterisation of the adelospondyl–colosteid grouping.

When all characters are reweighted by the maximum value of their rescaled consistency indices, nine most parsimonious trees are found (CI = 0.47, excluding six uninformative characters; RI = 0.82; RC = 0.4). In this reweighted analysis (Fig. 7), the sequence of basal temnospondyls includes: a resolved edopoid clade; *Capetus*; *Balanerpeton* as sister taxon to a resolved clade of dvinosaurs; *Dendrerpeton*. In the derived region of the amphibian stem, the amphibamids *Eoscopus*, *Platyrhinops*, *Amphibamus* and *Doleserpeton* form successive sister taxa, in that order, to crown amphibians. Within the latter, the monophyly of caudates emerges unambiguously. A major rearrangement of taxa occurs in the tetrapod stem, where *Ossinodus*, *Tulerpeton*, (*Pederpes* + *Whatcheeria*) and *Crassigyrinus* branch, in that order, as a series of plesions between *Ichthyostega* and the colosteid–adelospondyl clade. Another major difference between the original and reweighted analyses is the branching sequence of some microsaurs, with (*Odonterpeton* + (*Hyloplesion* + *Microbrachis*)) and *Batropetes* as successive sister taxa to all remaining lepospondyls.

Interrelationships of derived dissorophoids and Lissamphibia

The amphibian crown group includes no Palaeozoic taxa and nests within the dissorophoid-grade temnospondyls. Distribution of character-states among both derived dissorophoids and basal lissamphibians is shown in Appendix 4 and refers to some selected nodes in the derived portion of the amphibian total group (such nodes are highlighted in Fig. 5). Alternative trees, however, do not involve major differences in character-state changes at those nodes. Also, regardless of the various placements of *Eoscopus* and *Platyrhinops*, all trees show *Amphibamus* and *Doleserpeton* as successive outgroups, in that order, to lissamphibians.

Our new data do not deliver results that are consistent either with a stepwise acquisition of lissamphibian features *in a single family of dissorophoids*, or with separate derivations of lissamphibian orders from different dissorophoid families (for further discussion of this point, see Carroll 2004). The two nodes A and B (Fig. 5) subtending the (*Amphibamus* + (*Doleserpeton* + Lissamphibia)) and the (*Doleserpeton* + Lissamphibia) clades, respectively, are supported by the largest number of putative, derived lissamphibian–dissorophoid features, despite the amount of homoplasy. Examples include: distribution of the palatal denticles; the shape, proportions and mutual positions of numerous palatal bones; the general proportions of the parabasisphenoid plate; patterns of ossification of the trunk vertebrae. Interestingly, many of these features are also observed in *Eocaecilia* (see comments in Schoch & Milner 2004), despite the fact that both skull shape and proportions in this fossil (as well as in extant caecilians) differ remarkably from those of Salientia, Caudata and most temnospondyls (including derived dissorophoids; additional data are reported in Appendix 4). Several homoplastic state changes in the crownward part of the amphibian stem are also observed in other
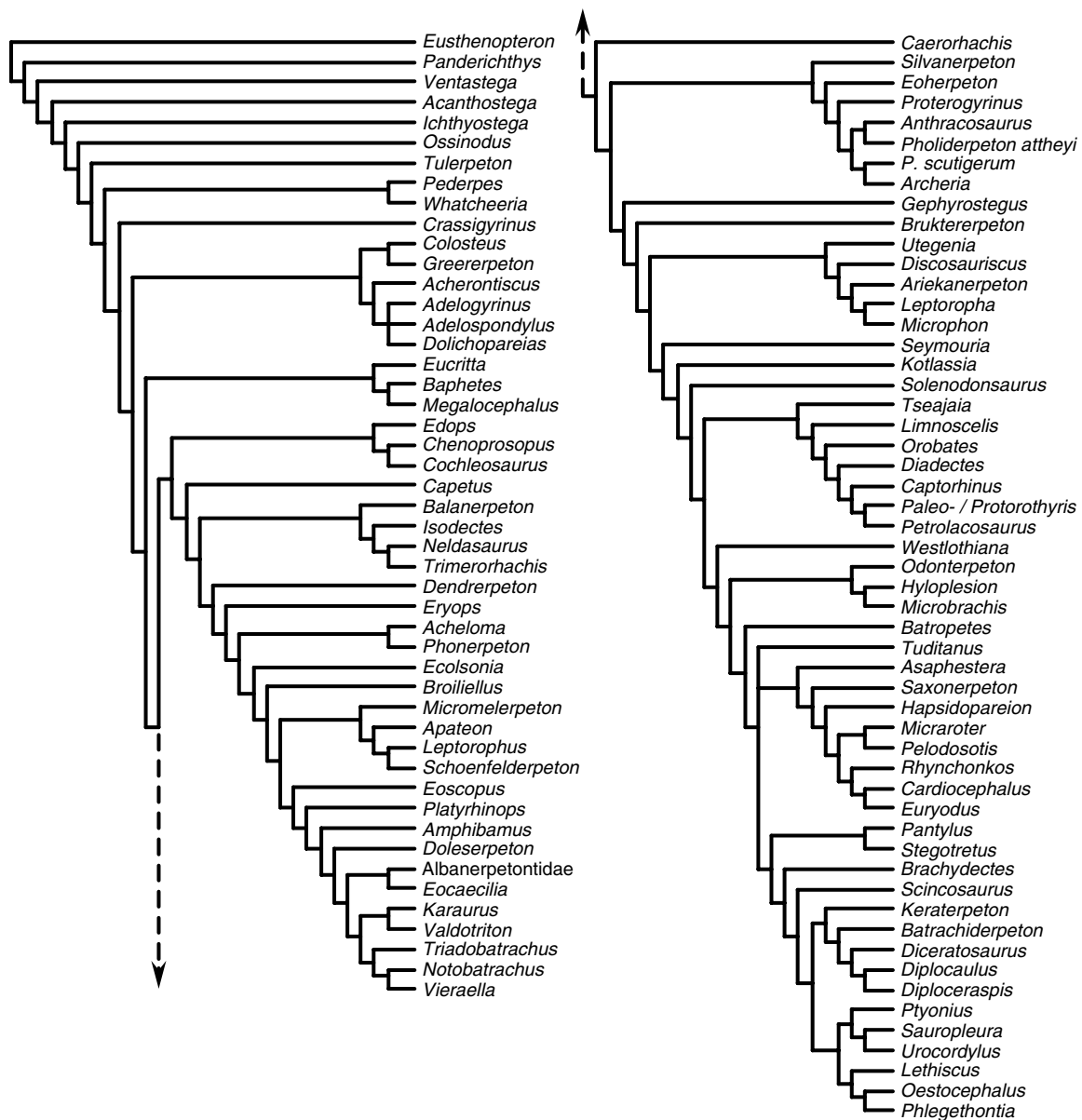
Figure 7   The strict consensus of nine most parsimonious trees from a reweighted analysis (see the text for details).

regions of the tree, but they appear to be rarely documented among temnospondyls more basal than dissorophoids.

The significance of alternative patterns of dissorophoid–lissamphibian relationships was assessed via a series of simple statistical tests in PAUP*. For example, certain members of both the Branchiosauridae and the Amphibamidae compete for a crownward placement on the amphibian stem (e.g. Milner 1993). If we constrain lissamphibians and branchiosaurids to group together, then 162 shortest suboptimal trees are found to be compatible with this enforced topology (length = 1595 steps; CI = 0.22; RI = 0.67; RC = 0.15). These do not entail a statistically significant difference in character-state redistribution relative to the shortest trees ($P > 0.05$, based upon Templeton, Kishino-Hasegawa and Winning-sites tests) and are just 11 steps longer than the latter. A strict consensus of the 162 trees places a resolved Lissamphibia (with support for Batrachia) in a polytomy with the branchiosaurs *Apateon*, *Leptorophus* and *Schoenfelderpeton*. Albanerpetontids, micromelerpetontids and amphibamids are placed as successively more distal taxa to this branchiosaur–lissamphibian clade.

It might be argued that it is the presence of just one, or few, basal crown amphibians that 'forces' remaining crown taxa to cluster with dissorophoids. In particular, given the overall similarities between *Doleserpeton* and several basal batrachians and the peculiar skull construction of caecilians, we were interested to see how taxon exclusion might impact tree shape in the derived part of the amphibian total group, especially as far as the position of caecilians is concerned. To this end, we deleted Caudata (*Karaurus* and *Valdotriton*) and Salientia (*Triadobatrachus*, *Notobatrachus* and *Vieraella*).

PAUP* found a clade of (Gymnophiona + Albanerpetontidae) nested within derived dissorophoids. Also, the clade (Micromelerpetontidae + Branchiosauridae) and the Amphibamidae appear as two successive sister groups, in that order, to the (Gymnophiona + Albanerpetontidae) clade in a strict consensus of 54 most parsimonious trees at 1506 steps (CI = 0.22; RI = 0.66; RC = 0.15).

It is not difficult to envisage a series of anatomical transformations that might have taken place at a post-dissorophoid level of amphibian evolution, leading to crown amphibians. A number of these hypothesised transformations were discussed by Milner (2000) and Rocek & Rage (2000*a*) for the dissorophoid-to-Caudata and dissorophoid-to-Salientia transitions, respectively. However, although a number of caecilian features can be compared fairly directly with those of derived dissorophoids (tooth morphology being an example), others can only be explained in terms of reversals or losses. A few instances of these are discussed below (see Schoch & Milner 2004 for further examples).

The spatial relationships between palatine and palatal ramus of the pterygoid, which are observed in several dissorophoids and in *Eocaecilia* (whereby the anterior extremity of the palatal ramus of the pterygoid abuts against the palatine posterior margin, thus producing a continuous sheet of bone), are absent in both Caudata and Salientia. The conditions of these two groups are derived, given the topology of our most parsimonious trees (supporting the Batrachia) and optimisation of missing entries due to character inapplicability (e.g. absence of a palatine in the Caudata).

The palatal openings of *Eocaecilia* appear to be narrower than in many temnospondyls, but as in the latter, they are broadly rounded along their anterior margins, unlike those of most microsaurs, including *Rhynchonkos*. Similarly broad and rounded palatal openings are also seen in many basal and derived Salientia and Caudata (morphometric characterisation of the proportions of the palatal openings was provided by Anderson 2001 for several early tetrapods).

Both Caudata and Gymnophiona exhibit very broad parabasisphenoid plates, instead of the 'winged' plates found in dissorophoids and Salientia. Such broad plates continue nearly indistinctly into a wide cultriform process. However, in *Eocaecilia* this process resembles a slightly more robust version of the strut-like, parallel-sided process found in dissorophoids and in salientians. In the Procera scenario of crown amphibian interordinal relationships, a broad parabasisphenoid is uniquely shared by caecilians and salamanders.

Caudates and gymnophionans do not have a squamosal notch. This could be attributed to an independent loss of the tympanum (see Ruta *et al.* 2003; *contra* Laurin 1998) in the two groups when the Batrachia topology of crown amphibian relationships is considered. The fundamental similarities in the development of the ear of Salientia and Caudata suggest that, in the latter, the ear appears to be secondarily reduced. The ear of Gymnophiona may have undergone an even more drastic reduction, perhaps as a result of burrowing habits (see also Milner 1988 for discussion). As an alternative interpretation and under a Procera scenario of crown amphibian evolution, different stages of ear reduction took place in the common ancestry of salamanders and caecilians.

All three amphibian orders share with dissorophoids abbreviated, straight ribs, although these have been lost in some crown amphibians. This is one of the few characters that have been maintained almost unchanged at the dissorophoid–lissamphibian transition, regardless of the batrachian or proceran hypotheses.

The mapping of some of these characters on alternative cladogram topologies shows that the acquisition or loss of various morphological conditions may not have followed a simple pattern and the states of terminal taxa may be subject to different evolutionary explanations depending upon the preferred crown group topology.

Albanerpetontidae as stem Gymnophiona

The placement of Albanerpetontidae as close relatives of Gymnophiona is a new feature of the present analysis. It is, however, also one of the most problematic. The data presented in Appendix 4 reveal that the majority of characters supporting this clade are optimisations of inapplicable scores, reversals of conditions found in other lissamphibians and losses. It is also important to note that several characters have uncertain polarity (Gardner 2001; Evans & Sigogneau-Russell 2001; Schoch & Milner 2004; Evans *et al.* 2005). The forthcoming redescription of *Eocaecilia* (see also Carroll 2000*a*, *b*; Evans & Sigogneau-Russell 2001) will be invaluable in testing this novel hypothesis.

In our recent cladistic analysis (Ruta *et al.* 2003), we failed to place albanerpetontids in an unambiguous position: they were either collapsed in a trichotomy with Batrachia and Gymnophiona, or descended to a stem amphibian position after a reweighted character analysis. Alternatively, Gardner (2001) assigned albanerpetontids to the common stem of Salientia plus Caudata and provided an exhaustive discussion of their positions relative to the major amphibian orders in several suboptimal tree topologies. Based upon our matrix, a stem batrachian position for albanerpetontids does not entail significant differences relative to the shortest trees ($P \gg 0.05$ for Templeton, Kishino-Hasegawa and Winning-sites tests).

If dissorophoids are accepted as immediate outgroups to lissamphibians as a whole, then transitional stages leading from a dissorophoid-like ancestor to *Eocaecilia* must necessarily have entailed acquisition of a solid, well-ossified skull table, reduced eyes and a broad and robust parabasisphenoid complex. These characters might have been acquired in a small and/or presumably fossorial ancestor (for a discussion of these characters in today's blindsnakes and worm lizards, see Trueb 1993; Wake 2003; Kearney 2003; Kley & Kearney 2006).

The results from our cladistic analysis bridge, in part, the morphological gulf between *Eocaecilia* and dissorophoids, although they call for additional character scrutiny and new fossil species. Albanerpetontids were almost certainly not directly ancestral to Gymnophiona. However, the combination of features that they share with certain basal Gymnophiona and Caudata (Evans & Sigogneau-Russell 2001) attests either to an extraordinary amount of convergence, or to a retention of features acquired near the base of the crown amphibian radiation and lost secondarily in Salientia (see also McGowan & Evans 1995; Schoch & Milner 2004; Evans *et al.* 2005; and tests of the statistical significance of the Procera topology, below).

Alternatively, under a Procera scenario of crown amphibian evolution, many of the features in question
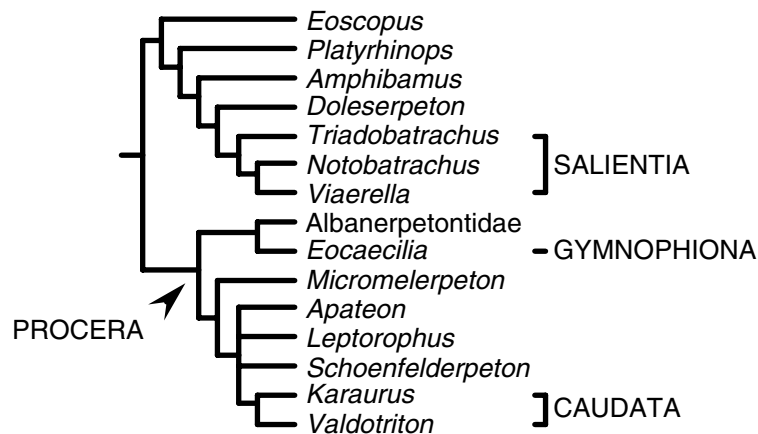
Figure 8 Portion of a strict consensus of 378 trees that are compatible with Carroll's (2004) hypothesis of separate origins of Salientia and Caudata from among dissorophoids (see the text for details).

might provide support for an albanerpetontid–caecilian–salamander clade.

EVALUATION OF ALTERNATIVE SCENARIOS OF AMPHIBIAN ORIGINS

Separate origins for the three amphibian orders

The hypothesis that Salientia, Caudata and Gymnophiona originated from different groups of early tetrapods has been discussed repeatedly (see Carroll *et al*. 1999; Carroll 2000*a*, *b*, 2001, 2004; Carroll & Bolt, 2001; Schoch & Carroll 2003). The central issue concerns the taxonomic membership of the amphibian crown group (i.e. the identity of fossil groups that fall in the crown). In some works, the issue of separate origins has been conflated with the concept of amphibian 'polyphyly'. However, this would be correct only if the origins of amphibians could *not* be traced to a single common ancestor, thereby implying that one or more of the three extant orders is phylogenetically closer to amniotes (e.g. Holmgren 1949; Jarvik, 1980; Løvtrup 1985) than to other lissamphibians. However, the latter evolutionary hypothesis appears implausible, as lissamphibian monophyly is now supported by multiple data sources, as explained above (Parsons & Williams 1963; Milner 1988; Trueb 1993; Duellman & Trueb 1994; Feller & Hedges 1998; Zardoya & Meyer 2001; Meyer & Zardoya 2003; Schoch & Milner 2004; San Mauro *et al*. 2005).

A separate origin for Caudata and Salientia was proposed by Carroll & Bolt (2001) and has been discussed in greater detail by Carroll (2004). Specifically, a derivation of Caudata from Branchiosauridae was based upon similarities between cranial ossification sequences in *Apateon* and some extant salamanders. As explained earlier, it is difficult to establish the polarity of these sequences without information on growth series from other fossil groups, as these arguments rest upon two-taxon statements. Recently, Carroll (2004) examined data on postcranial ossification sequences, and proposed a close relationship between Salientia and Amphibamidae (see also Bolt 1991). We note, however, that the similar-

ities between *Apateon* and some basal and derived Caudata are not confined exclusively to chronological sequences of ossification onsets. They also include shapes and proportions, as well as the spatial relationships of various bones, regardless of their ossification stages (Schoch 1995, 1998). These observations might provide an ontogeny-independent test of the affinities of at least certain dissorophoids with some Batrachia.

Carroll's (2004) hypothesis presents broad implications for the chronology of key events in tetrapod evolution, as discussed in greater detail below. Therefore, we were interested to see if our data set could accommodate this hypothesis without significant differences in the character-state distribution. To this purpose, we constrained Salientia plus Amphibamidae, on the one hand, and Caudata plus Branchiosauridae, on the other, to cluster together. The relationships between taxa within each of these two constrained clades were left unresolved, in order to allow PAUP* to choose between alternative trees. Also, no topology was imposed for the amphibian crown (i.e. Batrachia *versus* Procera) and *Eocaecilia* and Albanerpetontidae were left in a polytomy with all remaining tetrapods.

PAUP* retrieved 378 minimal trees at 1611 steps, with CI = 0.22, RI = 0.66 and RC = 0.15. The derived part of the amphibian stem appears well resolved in their strict consensus. The amphibamids *Eoscopus*, *Platyrhinops*, *Amphibamus* and *Doleserpeton* are successive plesions to a fully resolved Salientia. A fully resolved Caudata is collapsed in a polytomy with the three branchiosaurs *Apateon*, *Leptorophus* and *Schoenfelderpeton*. The micromelerpetontid *Micromelerpeton* and the (*Eocaecilia* + Albanerpetontidae) clade form successive sister groups, in that order, to the caudate–branchiosaur clade. Albanerpetontidae and Branchiosauridae, therefore, are nested within the crown group Procera (Fig. 8).

These suboptimal trees imply a significant rearrangement of character-states despite the addition of a mere 27 steps to the shortest tree length overall and they represent a worse fit for the whole data set than the most parsimonious trees from the original analysis (*P* < 0.05 under Templeton, Kishino-Hasegawa and Winning-sites tests). Within the confines of our taxon and character sets, these results show that a

single origin of all lissamphibians from among dissorophoids (with *Amphibamus* and *Doleserpeton* as the phylogenetically closest relatives of the crown group) is better supported than a scenario involving separate origins from two dissorophoid families. Furthermore, differences between the shortest trees overall and those that support independent origins of the three lissamphibian orders become more significant when *Eocaecilia* is constrained to group with the microsaur *Rhynchonkos* (Carroll 2000*a*). A strict consensus (not illustrated here) of the resulting suboptimal trees is poorly resolved for the majority of Permo–Carboniferous tetrapods.

Although Carroll's (2004) hypothesis is not favoured by our data, it is worth examining further, as it presents two major and interesting implications: (1) it places amphibamids and branchiosaurids within the crown Batrachia; (2) it assigns a much older age to the origin of crown Batrachia than that based upon *Triadobatrachus* in the single origin scenario, about 308 million years ago. This earlier age approximates that of another widely cited standard marker, i.e. the bird–mammal separation around 318 million years ago. This latter marker is usually reported as dating to 310 million years ago (revised data are based upon the latest version of the International Stratigraphic Chart). This 10 million year time interval between the minimum estimated ages for the origin of crown batrachians and crown amniotes would thus bracket the advent of most of the extant tetrapod biodiversity, i.e. the origin of modern batrachian and amniote radiations (for further discussions, see also Kumar & Hedges 1998; Ruta & Coates 2003; Graur & Martin 2004; Hedges & Kumar 2004; Reisz & Müller 2004).

Batrachia versus Procera

To test the significance of differences in character-state distribution between the Batrachia and Procera hypotheses of crown amphibian interrelationships, we constrained *Eocaecilia*, *Karaurus* and *Valdotriton* to cluster together in an unresolved polytomy. PAUP* retrieved 162 trees at 1587 steps (CI = 0.23; RI = 0.67; RC = 0.15). Their strict consensus is poorly resolved in the derived part of the amphibian total group, where all amphibamids are collapsed in a polytomy together with a micromelerpetontid–branchiosaurid clade and with crown amphibians. Both Procera and Salientia are completely resolved, but they join Albanerpetontidae in a polytomy. Templeton, Kishino-Hasegawa and Winning-sites tests show that these trees do not differ significantly from the shortest trees overall ($P \gg 0.05$). In agreement with the conclusions of our previous work (Ruta *et al*. 2003), the data do not appear to be decisive in choosing between the Batrachia and Procera scenarios of crown group amphibian interrelationships, although they favour slightly the former (see also comments in Schoch & Milner 2004).

Lysorophia as sister group to Lissamphibia

If Laurin's (1998; see also Laurin & Reisz 1999 and Vallin & Laurin 2004) hypothesis of a close relationship between crown amphibians and Lysorophia (*Brachydectes*) is enforced as a topological constraint, then PAUP* finds 60 suboptimal trees (1593 steps; CI = 0.23; RI = 0.66; RC = 0.16). Their strict consensus (not shown here) is well resolved and similar to that obtained from the original run. The lysorophian–lissamphibian clade (with a batrachian topology) joins albanerpetontids and this broader group forms the sister taxon to a nectridean–aïstopod clade. Temnospondyl relationships are well resolved, with *Capetus* as sister taxon to edopoids. *Balanerpeton* and an unresolved clade of dvinosaurs join all other temnospondyls (represented by a fully resolved *Dendrerpeton–Eryops*–dissorophoid clade) in a polytomy. Differences between the suboptimal trees that agree with Laurin's (1998) topology and those found in the original analysis are not statistically significant ($P \gg 0.05$ under Templeton, Kishino-Hasegawa and Winning-sites tests) and imply the addition of a mere nine steps. This highlights the extraordinary amount of character conflict in data matrices in which both temnospondyls and lepospondyls compete for their placement as the closest relatives of crown amphibians. The degree of phenetic (overall) similarities between some groups of lepospondyls and some lissamphibians is conspicuous, as discussed below, and results, to a considerable extent, from the plethora of 'absence' features in common to them.

McGowan's 2002 analysis

An experiment that employs a reduced number of taxa from our data matrix was devised to assess the effects of taxon deletion on tree shape. We were interested to see how sensitive McGowan's (2002) data is to a wider sampling of characters than the one he used. The vast majority of groups were excluded from our data except temnospondyls, albanerpetontids, lissamphibians and microsaurs. In order to match McGowan's (2002) taxon coverage as closely as possible, the temnospondyl sample included only the genera used by McGowan (2002), except *Branchiosaurus* and *Tersomius*. These were excluded because they require (and, in the case of *Tersomius*, are undergoing) redescription. Also, microsaur species were included instead of families, so as to maximise the morphological diversity of their sample.

A PAUP* analysis rooted on an all-zero hypothetical outgroup delivers 27 shortest trees, each 543 steps long (CI = 0.41; RI = 0.68; RC = 0.34) in which temnospondyls form the monophyletic sister group to (Albanerpetontidae + Lissamphibia). McGowan's (2002) preferred topology is a much worse fit for the data ($P \ll 0.05$) than the shortest trees from the reduced data set, under Templeton, Kishino-Hasegawa and Winning-sites tests. If this topology is enforced as a constraint, then PAUP* yields one tree at 581 steps, compatible with a microsaur–caecilian clade (CI = 0.38; RI = 0.64; RC = 0.29).

A CLOSER LOOK AT CONFLICTING SIGNALS

Different phylogenetic signals might be associated with different portions of a data matrix. When the strengths of these signals appear to be nearly balanced, they are likely to yield a set of conflicting tree topologies as well as a poorly resolved consensus. The effects produced by these conflicting signals have not been sufficiently explored insofar as they affect analyses of early tetrapod relationships. Large data sets, by virtue of their wide-ranging character and taxon coverage, might provide an opportunity to explore such conflicts.

As discussed above, the outstanding conflict between various hypotheses of early tetrapod phylogeny centres on

the temnospondyl versus lepospondyl theories of lissamphibian stem group membership. Laurin (1998) has provided the only cladistic hypothesis in support of a lysorophian–lissamphibian sister group relationship. With regard to the current discussion, tests performed on his data matrix yielded three important results. First, using his data set, a temnospondyl–lissamphibian clade was shown to be a statistically worse fit for the whole character set than the topology of his shortest trees (see also Vallin & Laurin 2004). Secondly, removal of lissamphibian orders from his data set, either each one separately or two at once, failed to cause remaining order(s) to group with temnospondyls. Thirdly, each of his lepospondyl groups clusters with lissamphibians even in the absence of all remaining lepospondyls. Clearly, even the most drastic experiments of taxon deletion fail to break the strong signal that links lepospondyls to lissamphibians in Laurin's (1998) data.

Using our own data, the 720 suboptimal trees placing lissamphibians with lepospondyls are 15 steps longer than the most parsimonious trees from the original analysis. Batrachia is sister group to Gymnophiona (i.e. no Palaeozoic taxa belong in the crown amphibians) and this lissamphibian clade is sister group to a clade of aïstopods plus nectrideans. More distal outgroups to this broader groups include lysorophians and pantylid microsaurs (*Pantylus* + *Stegotretus*). Despite relocation of lissamphibians to lepospondyls, the topology of the 720 suboptimal trees is not significantly different from the shortest trees for Kishino-Hasegawa, Templeton and Winning-sites tests, although in the case of some of these suboptimal trees, *P* values appear to be only slightly larger than 0.05. Thus, we conclude that data supporting a temnospondyl–lissamphibian relationship carry only a slightly stronger signal than those supporting a lepospondyl–lissamphibian relationship. These two data sets appear, therefore, to be nearly balanced, but it is easy to see that the majority of characters favouring lysorophians as amphibians' closest relatives (as in Laurin's 1998 cladogram) consist mostly of reversals and absence features (Schoch & Milner 2004; see also Ruta *et al*. 2003).

TIME SCALES OF AMPHIBIAN EVOLUTION

Temporal extensions of ghost lineages

The early fossil record of lissamphibians is poor, as one might expect at the base of a crown group. Therefore, it can only support heavily qualified estimates of clade divergence dates. Fossils such as *Karaurus*, *Eocaecilia* and *Triadobatrachus* share multiple apomorphies with more derived representatives of their respective orders, suggesting that the separation of these from each other, and from various groups of early tetrapods, must have been well under way during the Palaeozoic. However, despite the vagaries of the fossil record, we point out that different phylogenetic hypotheses (e.g. Batrachia *versus* Procera; single *versus* separate origins of Salientia and Caudata from among dissorophoids; lepospondyl *versus* temnospondyl theory) make different predictions about the extensions of ghost lineages. These predictions can be tested in the light of future fossil discoveries, as well as compared with those based upon molecular estimates of divergence dates. Schoch & Milner (2004) have recently discussed the plausibility of ghost lineage durations implied by different theories of lissamphibian ancestry. Their argument revolves around a consideration of the geographical and chronological distributions of Palaeozoic tetrapods, as well as the implied temporal extensions of putative stem groups of the amphibian orders into the Palaeozoic. In their view, the derivation of some of the lissamphibian orders from temnospondyls, as well as the hypothesised phylogenetic proximity of caecilians to the microsaur *Rhynchonkos*, are consistent with the presence of a wide range of tetrapod groups in the Permo–Carboniferous assemblages of equatorial Laurasia, some of which at least show inter-nested sets of features in common with crown amphibians. Conversely, in Laurin's (1998) and Laurin & Reisz's (1999) phylogenies, a lissamphibian–lysorophian relationship assumes that the stem group of the lissamphibians '... would have to exist as a ghost-lineage at least throughout the Late Carboniferous and Permian and be entirely unrepresented in the amphibian-rich limnic and lacustrine assemblages of equatorial Laurasia' (Schoch & Milner 2004: 367).

In our preferred hypothesis, the amphibamid *Doleserpeton* and the basal stem salientian *Triadobatrachus* are separated by a time interval of about 30 million years (Ruta & Coates 2003). However, a small number of stratigraphically younger dissorophoid temnospondyls are known, such as *Tungussogyrinus* (Permo–Triassic boundary of Siberia) and *Micropholis* (Early Triassic of South Africa) (Milner 1990; Shishkin 1998; Holmes 2000; Schoch & Rubidge 2005). It is uncertain whether these genera will turn out to occupy a more derived position than *Doleserpeton* on the amphibian stem group. Nevertheless, their occurrences demonstrate stratigraphical continuity between the latest known dissorophoids and the earliest known crown amphibians (*contra* Laurin 1998 and Laurin *et al*. 2000; also comments in Ruta & Coates 2003 on the timing of key evolutionary episodes in early tetrapod history).

Amphibian crown group divergence under different models

Here, we employ minimum estimated dates for the divergence of the lissamphibian crown (Fig. 9) to quantify the extension of ghost lineages under conservative as well as 'relaxed' models. Under conservative models, the divergence between two sister clades is minimally dated to the earliest record of the older clade, or slightly before it (see discussion in Smith 1994). Under relaxed models, the total group of each clade is extended back in time, thus resulting in older divergence dates than those in the conservative model. As an example, in Fig. 9A, the Procera scenarios of divergence for the total group Salientia (S), Caudata (C) and Gymnophiona (G) are shown under conservative (left), much relaxed (middle) and slightly relaxed (right) models. In the conservative model, Procera diverged from Salientia at the very latest during the Early Triassic. Another implication of this model is that both total group Caudata and total group Gymnophiona started in the Jurassic. In the middle diagram of the Procera scenario, dashed lines drawn below the earliest occurrences of all total groups imply that the history of these started in pre-Mesozoic times. However, a 'compromise' scenario is shown in the right hand diagram, where only a part of the Procera stem extends into pre-Triassic times.
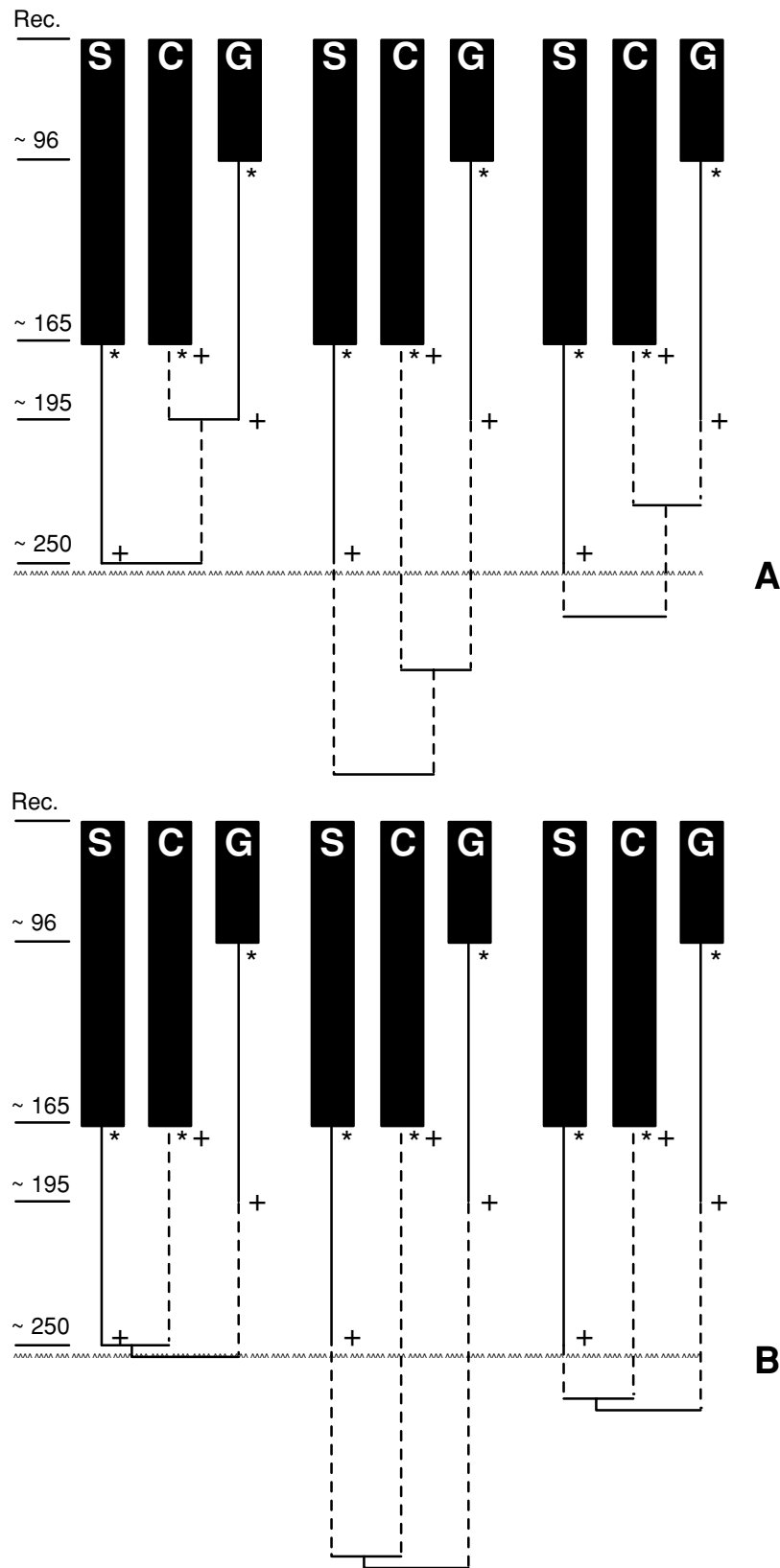
Figure 9 (**A**) Scenarios of divergence for the Salientia (S), Caudata (C) and Gymnophiona (G) total groups, under a conservative (left), much relaxed (middle) and slightly relaxed (right) divergence model in the Procera hypothesis (see the text for details). (**B**) Scenarios of divergence for the three orders, and under the same models, in the Batrachia hypothesis. In all figures: dashed vertical lines are ghost lineage extensions; solid vertical lines mark stem group extensions; the black rectangular areas indicate crown group extensions. The earliest occurrences of stem members of each amphibian order are indicated by a 'plus' sign, while earliest crown members are denoted by an asterisk. A time scale in millions of years is on the left side of each figure. The horizontal zig-zag line marks the approximate position of the Permo-Triassic boundary.

Figure 9B refers to the Batrachia scenario. Once again, diagrams from left to right show a conservative, a much relaxed and a slightly relaxed divergence model. Note that in this scenario, even a conservative divergence model requires an extension of ghost lineages for both the Caudata and the Gymnophiona total groups. It also predicts the existence of Triassic stem representatives for both these orders. In the much relaxed model (central diagram), ghost lineage extensions are also more conspicuous than in the analogous divergence model applied to the Procera scenario (this holds true in the case of the slightly relaxed model as well, in the right hand diagram).

These divergence models omit *Triassurus*, a putative Late Triassic stem caudate (Milner 2000; see above). If this fossil was included in Fig. 9 then a Late Triassic divergence for total group Gymnophiona would be implied in the conservative model of the Procera scenario. However, we note that it has a negligible impact on the Batrachia scenario and does not affect our major conclusions concerning the extension of ghost lineages.

The accuracy of these models in either scenario can only be confirmed or challenged by new palaeontological discoveries. In addition, the models do not take into account any rates of morphological change and rely upon an almost literal (and certainly incomplete) reading of the fossil record. However, when only minimum age estimates based upon known fossil occurrences are taken into account, it emerges that the Procera scenario entails many fewer assumptions about ghost lineage extensions than the Batrachia scenario.

Results from molecular studies on the divergence of amphibian clades provide an additional tool to place time constraints on each model. As an example, in a recent work on the origin of crown frogs (Anura), Roelants & Bossuyt (2005) proposed that the emergence of this clade dates back to the Upper Triassic. The earliest known Anura would thus predate by almost 55 million years the earliest known Jurassic stem salientians, such as *Prosalirus*, *Vieraella* and *Notobatrachus*. However, their conclusions are congruent with the known occurrences of Triassic stem salientians (*Triadobatrachus*, *Czatkobatrachus*) and point to an as yet unrecorded history of diversification of some of the basalmost lineages among the extant anuran clades.

Recent contributions to the time scale of amphibian evolution

San Mauro *et al.* (2005) produced a large-scale molecular analysis of lissamphibians based upon the nuclear gene RAG1 and used its results to construct a time scale of major events in crown amphibian evolution. The most intriguing conclusion from their investigation is that the origin of the lissamphibian crown group (i.e. the initial separation of the three extant amphibian orders) took place considerably earlier than previously hypothesised, around 367 million years ago (Upper Devonian). The 95% confidence interval placed on this event ranges from 417 million years ago (i.e. in the proximity of the Silurian–Devonian boundary) to 328 million years ago (middle part of the Mississippian). According to San Mauro *et al.* (2005), the separation between caudates and salientians occurred 357 million years ago (lowermost part of the Mississippian), with a 95% confidence interval of

from 405 million years ago (upper part of the Lower Devonian) to 317 million years ago (base of the Pennsylvanian).

San Mauro *et al.* (2005) did not rule out the possibility that some of their proposed divergence dates might have been overestimated. They further discussed biases towards age overestimation that are inherent to conventional molecular dating and presented a suite of approaches/techniques directed at minimising such biases, including the choice of genes that show an appropriate rate of change, diverse taxonomic sampling, inclusion of multiple calibration constraints and a relaxation of molecular clocks. San Mauro *et al.*'s (2005) conclusions call for comments and, in the following, we highlight and discuss some of the implications of their finds.

(1) Phylogenetic proximity of Palaeozoic groups to lissamphibians.

Remarks: According to San Mauro *et al.* (2005), the rapid, early diversification of crown amphibians explains both the lack of fossil sister groups that appear morphologically close to them and the lack of plausible ancestors. Thus, their results imply that none of the groups of Palaeozoic tetrapods, altogether spanning a period of more than 100 million years, is a suitable candidate for the ancestry of extant amphibians (see also Schoch & Milner 2004 for a rebuttal of this argument based upon a consideration of ghost range extensions).

Comments: Aside from the fact that fossil ancestors are usually difficult to recognise (Smith 1994), we disagree with San Mauro *et al.*'s (2005) conclusions regarding the lack of fossil sister groups that are morphologically close to amphibians. Much of the discussion in the present paper (see also results above) targets precisely this issue. Furthermore, they omit any reference to the most recent palaeontological contributions to the lissamphibian origin controversy and this sets up something of a 'straw man'. Available analyses of early tetrapod relationships have found some, or even the majority, of Palaeozoic tetrapod clades to belong in the tetrapod crown and have assigned such clades to either the amphibian or the amniote stem group.

(2) Character acquisition.

Remarks: For San Mauro *et al.* (2005: 592), the '... separation of the three orders of modern amphibians in the Paleozoic occurred almost immediately (in evolutionary terms) after the "jump to land" of sarcopterygian fishes ... and in parallel with the diversification of extinct lineages of amphibians (e.g. *Acanthostega* or *Ichthyostega*)'.

Comments: The use of the term 'amphibians' for Devonian taxa is informal and implies generic reference to Palaeozoic clades. However, the initial diversification of amphibians that San Mauro *et al.* (2005) discuss implies a reference to their crown. The estimated Upper Devonian origin for the latter would imply that any suitable stem representative of lissamphibians ought to be sought from within a group of pre-Famennian, limbed tetrapods. However, there is no necessary conflict with the more recent, upper bound end of their date-range estimate for crown amphibian origins (328 million years ago), especially if a derivation of the extant orders from

among separate lineages of dissorophoids is accepted (see above). Incidentally, this upper bound age coincides with the earliest fossil record of the amphibian total group (see below), based upon our preferred phylogeny. We also point out that San Mauro *et al.*'s (2005) hypothesis requires an extraordinary burst of morphological evolution, i.e. rapid accumulation of character change over a short time span. A major difficulty with this scenario is that several recent palaeontological finds are slowly but steadily beginning to bridge morphological gaps among Lower Carboniferous groups and point to a stepwise acquisition of derived traits in the tetrapod stem as well as in the basal portions of the amphibian and amniote stems.

(3) Ghost lineage extensions.

Remarks: San Mauro *et al.*'s (2005) hypothesised Upper Devonian origin for the modern amphibian radiation requires that the origin of the amniote total group be also pushed back in time.

Comments: Once again, if the focus of attention is moved away from the mean of the 95% confidence interval proposed by San Mauro *et al.* (2005), then there appears to be little conflict between their finds and the palaeontological evidence. An upper date of 328 million years ago is not too far off from the existing minimum age estimate for the crown amniote divergence of between 311 and 317 million years ago. However, the earliest putative stem amniotes date from the lower or middle part of the Mississippian (Ruta *et al.* 2003) and there is growing evidence that tends to support the acquisition of progressively more derived amniote traits in Permo–Carboniferous clades that precede the advent of the crown amniote radiation.

As a concluding note, recent updates of the International Stratigraphic Chart allow us to revise date estimates for the major phylogenetic events in the early evolutionary history of tetrapods (modified from Ruta & Coates 2003). Based upon our preferred phylogeny (Figs 5 & 6), the earliest crown tetrapods are about 335 million years old: the aïstopod *Lethiscus* is from the middle Viséan, in the Mississippian (Carroll *et al.* 1998; Carroll 2000a; Anderson 2001; Ruta & Coates 2003; Ruta *et al.* 2003; but see also Baird 1964; Wellstead 1982; Anderson *et al.* 2003). However, we speculate that the separation between amphibian and amniote total groups is either a latest Famennian or an earliest Tournaisian event, 360–355 million years ago. The earliest record of the amphibian total group dates back to the latest Viséan, around 328 million years ago (earliest known temnospondyls: Milner & Sequeira 1994). During the following 210 million years, the amphibian stem, represented exclusively by Temnospondyli in our scheme of relationships, diversified extensively giving rise to several major clades, including the Dissorophoidea (Milner 1990; Holmes 2000; Warren 2000; Yates & Warren 2000). Temnospondyls coexisted with lissamphibians for more than 130 million years during the Mesozoic. A gap of about 85 million years intervenes between the earliest known crown amphibians and the earliest known crown Salientia and Caudata. A further 69 million years separate the latter two groups from the earliest known crown Gymnophiona (Fig. 9).

Future research

Information from the amphibian fossil record highlights the need for multiple and extensive collecting efforts from critical stratigraphic intervals and investigations of microvertebrate remains continue to show the potential yield of this kind of study (e.g. Gardner *et al.* 2003). Integration of data from recently discovered fossils into large-scale cladistic analyses will hopefully provide greater stability for progressively larger portions of the tetrapod tree and, ultimately, a resolution of the conflict that the most recent studies have engendered (e.g. see Laurin & Reisz 1999; Anderson 2001; Ruta *et al.* 2003; Clack & Finney 2005). At the core of this conflict are the affinities of several early groups with one or the other of the two major tetrapod clades, the amphibians and the amniotes.

Regarding amphibians, future studies that incorporate the most primitive as well as some of the more derived representatives of the three orders are likely to yield more circumspect assessments of the polarities of several features and arbitrate between the Procera and the Batrachia scenarios of lissamphibian evolution. Molecular analyses performed on a larger taxonomic sample (including basal members from all or the majority of living families) will also inform this issue in total evidence approaches to amphibian interrelationships. A most vexing problem, namely caecilian ancestry, will ultimately rely upon a better knowledge of the fossil record. More complete material of the enigmatic albanerpetontids will prove to be crucial in this respect, as these organisms share numerous features with basalmost caudates and gymnophionans. Furthermore, a fine-scale (species-level) resolution of the interrelationships of dissorophoid temnospondyls will inform, to a larger extent, distribution of character-states in the derived part of the amphibian stem.

With a more robust phylogenetic framework in place, it will be possible to employ fossil (internal) calibration points from a wider range of lissamphibian clades in future molecular time scales of tetrapod divergence. A fine scatter of these points is likely to include both the oldest members of extant families and plesions at different levels of inclusiveness, e.g. from the amphibian stem.

Finally, we hope that this review will initiate constructive debates and offer a platform for further discussions of amphibian (in particular) and tetrapod (in general) evolution.

Acknowledgements

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APPENDIX 1: TAXA ADDED TO RUTA *ET AL*.'S (2003) DATA

Consulted literature for each of the newly added species is reported in brackets. Asterisks indicate taxa for which either original specimens or casts were examined by the authors.

Ariekanerpeton sigalovi *, *Leptoropha talonophora*, *Microphon exiguus* (Bulanov 2003).

Capetus palustris (Sequeira & Milner 1993).

Notobatrachus degiustoi, *Vieraella herbsti* (Báez & Basso 1996; Rocek 2000).

Orobates pabsti (Berman *et al*. 2004).

Ossinodus pueri* (Warren & Turner 2004).

Pederpes finneyae* (Clack 2002b; Clack & Finney 2005).

Silvanerpeton miripedes* (Clack 1994).

Tseajaia campi (Moss 1972; Berman *et al*. 1992).

Utegenia shpinari* (Bulanov 2003; Klembara & Ruta 2004*a, b*).

APPENDIX 2: CHARACTER LIST

To facilitate cross-reference among different versions of our matrix, we have adopted a convention established in Ruta *et al*.'s (2003) paper: each character is preceded by a bold number that identifies its position in the current matrix (Appendix 3) and by an acronym plus number which provide a reference to the same character in all versions of the data matrix. The acronym and number are followed by a character description. New characters added to Ruta *et al*.'s (2003) data matrix are denoted by an asterisk. Remarks are provided as explanatory notes for the purpose of clarity in the description of several skeletal features, or wherever a change in the coding of Ruta *et al*. (2003) has been introduced.

1. PREMAX 1. *Premaxilla alary process: absent (0); present (1)*. The alary process is a subtriangular bony lappet that detaches from the posterior margin of the dorsal ramus of the premaxilla and extends posteriorly overlapping the nasal. We have recoded this feature for both Albanerpetontidae and *Eocaecilia* as being absent (*contra* Ruta *et al*. 2003), as in these taxa there is no clear separation of the lappet from the posterior margin of the dorsal ramus of the premaxilla. However, the coding for *Eocaecilia* might change in future analyses, pending a thorough redescription of this fossil (Carroll 2000*b*). Ruta *et al*.'s (2003) coding for Albanerpetontidae (Gardner 2001) was due to a misinterpretation of data in Gardner (2001; pers. comm. 2004).

2. PREMAX 2. *Premaxilla alary process shorter than wide (0) or as long as/longer than wide (1)*. Length and width of the alary process are measured as the distance between its posterior apex and the posterior margin of the dorsal ramus of the premaxilla and as the distance between the two points where the posterior margin of the dorsal ramus turns abruptly posteriorly to form the alary process.

3. PREMAX 3. *Premaxilla alary process less than (0) or at least one-third as wide as premaxilla (1)*. The width of the premaxilla is the transverse distance between the medialmost point of its dorsal ramus and the lateralmost point of its posterior ramus, measured in dorsal aspect.

4. PREMAX 4. *Premaxilla with flat, expanded anteromedial dorsal surface and elongated along its lateral margin but not along its medial margin, when observed in dorsal aspect: absent (0); present (1)*. This is one of the characters used by Milner & Sequeira (1998) and modified by Sequeira (2004), as a synapomorphy of edopoid temnospondyls. In these, the premaxilla shows a conspicuous elongation along its lateral margin, from its lateralmost extremity, in contact with the maxilla, to its anterior point (anterior extremity of interpremaxillary suture). The bone increases uniformly in width anteromedially, but the interpremaxillary suture is less than half as long as its lateral margin.

5. PREMAX 7. *Premaxillae more (0) or less than (1) two-thirds as wide as skull table*. The total width of the conjoined premaxillae is measured as the distance between their lateralmost extremities; the total skull table width is between the lateral extremities of the suspensoria.

6. PREMAX 8. *Anteriormost surface of premaxilla orientated obliquely, so that mouth opens subterminally: absent (0); present (1)*. The derived condition of this feature refers to the oblique anteroventral surface of the premaxillae, which results in a distinct slope in some taxa and a subterminal mouth opening.

7. PREMAX 9. *Shelf-like contact between premaxilla and maxilla occuring mesial to marginal tooth row on palate and extending mesially for at least twice the width of such a row: absent (0); present (1)*. In some taxa, both the premaxilla and maxilla send a bony 'shelf' projecting mesial to the marginal dentition.

8. TEC 1. *Anterior tectal: present (0); absent (1)*. We have coded this and the following two characters

following Clack (2002*b*). The anterior tectal is a small bone that borders the external nostril dorsally and is found in the basal tetrapods *Acanthostega* and *Ichthyostega*, as well as in the piscine ancestors of limbed tetrapods.

9. SPTMAX 2. *Septomaxilla a detached ossification inside nostril: no (0); yes (1)*. Unlike in Ruta *et al.* (2003), we have eliminated two characters, one related to the presence of a lateral rostral and one related to the presence of a septomaxilla. Homology between these two bones has been generally accepted, although we opted to treat them as separate bones in our former review. However, the occurrence of a septomaxilla cannot always be shown in the available material of several taxa and we are no longer confident that it can be treated as a simple presence/absence character. Therefore, we have scored as unknown those instances in which a septomaxilla is not observed and have coded for its position relative to the nostril margin (i.e. as part of the skull roof or as an internal bone).

10. NAS 1. *Paired nasals: absent (0); present (1)*. Derived keraterpetontid nectrideans show a reversal to the condition exhibited by the outgroups.

11. NAS 2. *Nasals more (0) or less than (1) one-third as long as frontals*. The metric cut-off points used to discriminate states were selected following a series of ratio measurements in different groups. The derived state is particularly evident in assorted lepospondyls and in colosteids. The length of each bone was measured along the greatest distance between its anterior and posterior extremities. Paired bones appear to be often comparable in size. However, in those cases in which a bone differs slightly from its antimere, the largest of the two antimeres is chosen for measurements.

12. NAS 5. *Nasals broad plates delimiting most of the posterodorsal and mesial margins of nostrils and with lateral margins diverging abruptly in their anterior portions: absent (0); present (1)*. The morphology of the nasals, combined with their contributions to the nostrils, characterises some temnospondyls and lissamphibians.

13. NAS 6. *Parietal/nasal length ratio less than (0) or greater than 1.45 (1)*. The metric cut-off points was chosen on the basis of the condition shown by certain lepospondyls (notably, adelospondyls) and colosteids, although the derived state is seen also in some other tetrapods (e.g. some temnospondyls and lissamphibians).

*14. PREFRO 1. *Separately ossified prefrontal: present (0); absent (1)*. The prefrontal is absent in Salientia (Milner 1988; Trueb 1993), but the condition in *Triadobatrachus* is uncertain (Rage & Rocek 1989; Rocek & Rage 2000*b*).

15. PREFRO 2. *Prefrontal less than (0) or more than (1) three times longer than wide*. The prefrontal length is calculated, in dorsal aspect, as the distance between the anterior and posterior extremities of the bone, between the rearmost point of its posterior ramus and the anteriormost point of its dorsomesial surface. The derived state occurs in lepospondyls (notably, adelospondyls) colosteids, as well as some temnospondyls.

16. PREFRO 3. *Antorbital portion of prefrontal forming near-equilateral triangular lamina: absent (0); present (1)*. In derived dissorophoids and in some basal lissamphibians, the portion of the prefrontal bone that lies immediately anterior to the anterior orbit margin appears to be foreshortened and is shaped like a small triangular flange. As in the case of other cranial bones, it exhibits a considerable degree of size reduction relative to the situation in other temnospondyls.

17. PREFRO 6. *Prefrontal/premaxilla suture: absent (0); present (1)*. The distribution of the derived state of this character is extremely patchy and it characterises colosteids, albanerpetontids and *Acherontiscus*.

18. PREFRO 7. *Prefrontal without (0) or with (1) stout, lateral outgrowth*. In most baphetids, the keyhole-shaped orbits reveal a constriction between the orbit proper and the antorbital vacuity. This constriction is delimited laterally by a stout process that is observed on the lateral margin of the prefrontal. However, such baphetids as *Spathicephalus* (not included in our data set), do not reveal a constriction and their orbits possess an elongate, subelliptical and smooth outline (see also Beaumont & Smithson 1998).

19. PREFRO 8. *Prefrontal entering nostril margin: no (0); yes (1)*. A contribution of the prefrontal to the margin of the external nostril is seen in a variety of tetrapods, but it shows no clear phylogenetic pattern.

20. PREFRO 9. *Prefrontal/maxilla suture: absent (0); present (1)*. As in the case of the suture between the prefrontal and the premaxilla (see also above), the distribution of this character is very patchy.

21. PREFRO 10. *Prefrontal contributes to more (0) or less than (1) half of orbit anteromesial margin*. This is one of the characters that relate to size reduction of circumorbital bones in several dissorophoids and some lissamphibians. In dorsal aspect, and imagining the orbit divided into four quadrants, the derived state of this character refers to the contribution of the orbital margin of the prefrontal to the anteromesial quadrant.

22. LAC 1. *Separately ossified lacrimal: present (0); absent (1)*. The lacrimal is absent in Salientia (Milner 1988; Trueb 1993). The condition in *Triadobatrachus* is uncertain (Rage & Rocek 1989; Rocek & Rage 2000*b*). The aïstopod *Phlegethontia* also lacks this bone (Anderson 2002).

23. LAC 2. *Lacrimal allowing contact between prefrontal and jugal: no (0); yes (1)*. A suture between the prefrontal and the jugal is observed in some lepospondyls, temnospondyls, anthracosaurs and some stem tetrapods.

24. LAC 4. *Lacrimal without (0) or with (1) dorsomesial digitiform process*. The process in question appears as a slender projection of the posterodorsal corner of the preorbital portion of the lacrimal. It is especially evident in a number of microsaurs and in urocordylid nectrideans.

25. LAC 5. *Lacrimal without (0) or with (1) anteriorly directed, V-shaped emargination along its posterior margin*. This is one of the characters associated with the presence of a keyhole-shaped orbit in some (but not all) baphetids. The antorbital vacuity of such taxa as *Baphetes* and *Megalocephalus* has an acute, triangular

anterior apex excavated in the posterior margin of the lacrimal.

26. LAC 6. *Portion of lacrimal lying anteroventral to orbit abbreviated: absent (0); present (1).* In several lepospondyls (as well as in some temnospondyls), the antorbital part of the lacrimal is considerably foreshortened, regardless of relative snout proportions and barely extends for one fourth of its total length anteroventral to the orbit.

27. MAX 3. *Posterior extremity of maxilla extending behind level of orbit posterior margin (0) or lying anterior to this margin (1).* The derived state of this character is observed in several stem and basal crown amniotes, but occurs sporadically in some temnospondyls and basal lissamphibians as well.

28. MAX 5. *Maxilla contributing to orbit margin: no (0); yes (1).* In some lepospondyls, temnospondyls and basal lissamphibians, the maxilla forms part of the ventral margin of the orbit.

29. MAX 6. *Maxillary arcade closed (0) or open (1) posteriorly.* The derived state refers to the presence of a gap along the posterior half of the ventral margin of the skull table, where the posterior extremity of the maxilla fails to contact the ventral margin of the suspensorium. This condition is observed in certain basal lissamphibians and in the dissorophoid *Schoenfelderpeton*. In the latter taxon, the open maxillary arcade is assumed to represent a derived feature. However, such a feature is documented as an ontogenetic stage during the skull growth of several temnospondyls (notably, branchiosaurs).

30. MAX 7. *Dorsal margin of maxilla forming distinct dorsal 'step': no (0); yes (1).* In the microsaurs *Pantylus* and *Stegotretus*, the dorsal margin of the maxilla rises abruptly and almost vertically, contributing to the formation of a tall, 'step'-like facial process.

31. MAX 8. *Maxillary facial process shaped like an approximately rectangular flange: absent (0); present (1).* The derived state of this character, found among certain dissorophoids and basal lissamphibians, refers to the presence of a subrectangular facial process, detaching as a flange-like structure from the dorsal margin of the maxilla.

32. MAX 9. *Posterior extremity of maxilla not lying (0) or lying (1) at level of posterior extremity of vomers.* Foreshortened maxillae are observed in lysorophians as well as in scincosaurid and derived keraterpetontid nectrideans.

33. FRO 1. *Frontal unpaired (0) or paired (1).* The plesiomorphic condition, seen in *Eusthenopteron*, reverses sporadically in a number of crown tetrapod taxa.

34. FRO 2. *Frontals shorter than (0), longer than (1), or approximately equal in length (2) to parietals.* The length of each bone was measured along the greatest distance between its anterior and posterior extremities. Paired bones appear to be often comparable in size. However, in those cases in which a bone differs slightly from its antimere, the largest of the two antimeres is chosen for measurements. The distribution of character-states does not appear to be congruent either between or within groups.

35. FRO 4. *Frontal excluded from (0) or contributing to (1) orbit margin.* The frontal enters the orbit in various crown tetrapods, both within the amniote and within the lissamphibian total groups. Although frontals and parietals are co-ossified in Salientia (see next character), there is no doubt that the anterior (frontal) component of their frontoparietal contributes to the margin of the orbit.

36. FRO 5. *Co-ossified frontal and parietal (frontoparietal bone): absent (0); present (1).* Co-ossified frontals and parietals are a shared derived feature of Salientia. In the most primitive salientian, *Triadobatrachus*, a suture between the two antimeres of the frontoparietal complex is still traceable.

37. FRO 6. *Frontal anterior margin deeply wedged between nasal posterolateral margins: absent (0); present (1).* In colosteids and some lepospondyls, among other taxa, the anteriormost portion of the frontals is inserted between the nasals for at least one-third of the length of the latter.

38. PAR 1. *Parietal/tabular suture: absent (0); present (1).* This is one of the most frequently cited, putative shared derived features of total group amniotes.

39. PAR 2. *Parietal/postorbital suture: absent (0); present (1).* A parietal/postorbital suture occurs in certain lepospondyls, colosteids, some Devonian tetrapods, diadectomorphs and basal crown amniotes.

40. PAR 4. *Anterior margin of parietal lying in front of (0), level with (1), or behind (2) orbit midlength.* State 2 is the most widespread derived condition for this character, whereas state 1 is recorded only sporadically, e.g. in *Acanthostega*, *Ichthyostega* and *Whatcheeria*. The midlength of the orbit is measured along its greatest anteroposterior diameter, in dorsal aspect.

41. PAR 5. *Anteriormost third of parietals not wider (0) or at least marginally wider (1) than frontals.* The derived state occurs almost ubiquitously in the study group. In dorsal aspect, the anterior portions of the parietals are, together, wider than the maximum width of the frontals. Reversals to the primitive condition are observed in some basal crown amniotes and crown lissamphibians.

42. PAR 6. *Parietals more (0) or less (1) than two and a half times as long as wide.* The metric cut-off points used to discriminate between the two states are based upon the pattern of parietal elongation in the outgroups. Certain lepospondyls as well as colosteids show a reversal to the plesiomorphic condition.

43. PAR 7. *Parietal/squamosal suture extending in part onto the dorsal surface of skull table: no (0); yes (1).* The derived condition of this character describes a dorsalward position for the parietal/squamosal suture, i.e. the contact between these two bones is not confined to the dorsal portions of the suspensorium (cheek region, i.e. lateral surface of the skull table immediately posterior to the orbit and including squamosal, quadratojugal and jugal).

44. PAR 8. *Parietal/frontal suture strongly interdigitating: no (0); yes (1).* The strong interdigitations of the sutural seam are characteristically shaped like a series of interlocking, finger-like projections, resulting in a wavy and irregularly sinuous profile. The distribution

of the derived state is irregular, as is also that of the following character.

45. PAR 9. *Parietal/postparietal suture strongly interdigitating: no (0); yes (1).* There appears to be no clear phylogenetic signal associated with this character.

46. POSPAR 1. *Separately ossified postparietal: present (0); absent (1).* Absence of postparietals is documented in very few taxa, including the microsaur *Batropetes*, the aïstopod *Phlegethontia*, the nectridean *Scincosaurus* and most primitive crown lissamphibians (except *Eocaecilia*).

47. POSPAR 2. *Postparietals paired (0) or unpaired (1).* In several diadectomorphs, in the microsaur *Odonterpeton* and in the Devonian tetrapod *Ichthyostega*, a single postparietal ossification is observed.

48. POSPAR 3. *Postparietal less than (0) or more than (1) four times wider than long.* The metric cut-off point used to discriminate the derived state takes into account the anteroposteriorly abbreviated ornamented surface of the postparietals in (mostly) stem amniotes (e.g. certain seymouriamorphs) and various dissorophoid temnospondyls.

49. POSPAR 4. *Postparietals without (0) or with (1) median lappets.* In some anthracosaurs, in the nectridean *Ptyonius* and in *Crassigyrinus* and *Whatcheeria*, the posteromesial corner of the ornamented surface of the postparietal extends into a small process, which adjoins its antimere forming a posteriorly directed lappet.

50. POSPAR 5. *Postparietal/exoccipital suture: absent (0); present (1).* A direct contact between exoccipitals and postparietals is observed, in particular, in some lepospondyls and temnospondyls.

51. POSPAR 6. *Postparietals entirely on occipital surface: no (0); yes (1).* In diadectomorphs and basal crown amniotes, the postparietal provides no contribution to the dorsal surface of the skull table and appears to be confined to the occiput.

52. POSPAR 7. *Postparietals without (0) or with (1) posteroventrally sloping occipital exposure.* In lysorophians and some microsaurs, the ornamented surface of the postparietals bends abruptly posteroventrally, thus exhibiting a slope that continues onto the occipital surface of the skull.

53. POSPAR 8. *Postparietals without (0) or with (1) sinuous posterior ridge.* In some microsaurs, the boundary between the ornamented and unornamented surfaces of the postparietals is marked by a bilaterally symmetrical, sinuous ridge.

54. POSPAR 9. *Postparietals without (0) or with (1) broad, concave posterior emargination.* The derived state of this character is found in some keraterpetontid nectrideans, in which the posterior margin of the horn-like extensions of the tabulars and the central part of the posterior edge of the skull table, together, form a broadly parabolic outline.

55. POSPAR 10. *Nasals not smaller (0) or smaller (1) than postparietals.* In dorsal aspect, the extension of the ornamented surface of both nasals is smaller than that of the postparietals in such taxa as adelospondyls, colosteids, some aïstopods and some keraterpetontid nectrideans.

56. POSFRO 1. *Separately ossified postfrontal: present (0); absent (1).* Lack of an ossified postfrontal is recorded in albanerpetontids, lysorophians and most basal crown lissamphibians (except *Eocaecilia*).

57. POSFRO 3. *Postfrontal/tabular suture: absent (0); present (1).* The derived state of this character is observed in tuditanomorph microsaurs.

58. POSFRO 4. *Postfrontal posterior margin lying flush with jugal posterior margin: no (0); yes (1).* The distribution of the derived state of this character appears to be incongruent, as it is observed in a handful of aïstopods, microsaurs, nectrideans and basal crown amniotes. In these taxa, the rearmost part of the ornamented surfaces of the postfrontal and jugal lie at the same transverse level in a dorsal or lateral view of the skull table.

59. INTEMP 1. *Separately ossified intertemporal: present (0); absent (1).* Absence of an ossified intertemporal occurs in the majority of crown tetrapod taxa (it is, however, present in the basal portions of both stem lissamphibians and stem amniotes) as well as in several stem tetrapods.

60. INTEMP 2. *Intertemporal not interdigitating (0) or interdigitating (1) with cheek (see above for definition of cheek).* There appears to be no signal associated with the derived state of this character, which refers to the occurrence of strong interdigitations (see above for a definition) in the sutural seam between the lateral margin of the intertemporal and the dorsal margin of the cheek.

61. INTEMP 3. *Intertemporal/squamosal suture: absent (0); present (1).* An intertemporal/squamosal contact is documented in most seymouriamorphs and in whatcheeriids.

*62. INTEMP 4. *Intertemporal shaped like a small, subquadrangular bone, less than half as broad as the supratemporal: absent (0); present (1).* In our data set, a diminutive intertemporal characterises baphetids (*Eucritta* and *Baphetes*; the bone is absent in *Megalocephalus*) and the temnospondyls *Balanerpeton*, *Isodectes* and *Trimerorhachis* (Milner & Sequeira 1994; Clack 2002*b*). The ornamented surface of the intertemporal is approximately square and can be 'contained' within the supratemporal in the derived condition of the character.

63. SUTEMP 1. *Separately ossified supratemporal: present (0); absent (1).* A supratemporal is absent in several lepospondyls and crown lissamphibians.

64. SUTEMP 2. *Supratemoral forming entire edge of dorsalmost part (in lateral aspect) of temporal notch: no (0); yes (1).* In baphetids (as well as in the whatcheeriid *Pederpes*), the supratemporal borders the whole temporal notch. When the skull table is observed in dorsal aspect, the notch occupies the mesialmost portion of the temporal embayment (free posterior margin of suspensorium in lateral aspect).

65. SUTEMP 3. *Supratemporal narrow and strap-like, at least three times as long as wide: absent (0); present (1).* The derived condition of this character is based on metric cut-off points seen mostly in aïstopods and some nectrideans.

66. SUTEMP 4. *Supratemporal/squamosal suture: smooth (0); interdigitating (1).* A strongly interlocking suture (see above for a definition) between the lateral margin of the supratemporal and the dorsal margin of the squamosal is observed in taxa from very

different groups, but no clear signal is associated with the distribution of the derived state.

67. TAB 1. *Separately ossified tabular: present (0); absent (1).* Absence of a tabular is documented in most basal crown lissamphibians, in adelospondyls, as well as in *Captorhinus*, *Odonterpeton* and *Phlegethontia*.

68. TAB 2. *Blade-like, posterolateral horn of tabular lying ventral to tabular ornamented surface: absent (0); present (1).* Under the definition of a tabular 'horn', we include processes of the subdermal part of the bone, which in anthracosaurs has also a separate dermal component.

69. TAB 3. *Rounded, button-like posterior process of tabular lying ventral to tabular ornamented surface: absent (0); present (1).* In baphetids and colosteids, the process in question is a small conical extension of the posterior surface of the tabular. A similar smaller process is found in *Whatcheeria*, but it lies in a more lateral position and is almost confluent with the ornamented surface.

70. TAB 4. *Tabular/squamosal suture extending onto skull table dorsal surface: present (0); absent (1).* The distribution of this character is mostly incongruent. In several taxa, the suture between these two bones extends onto the dorsal surface of the skull table.

71. TAB 5. *Tabular/squamosal suture: smooth (0); interdigitating (1).* The nature of the squamosal–tabular suture has no simple relationship with skull size and (inferred) degree of maturity. The derived state is found, among others, in some temsonpondyls, microsaurs and colosteids.

72. TAB 6. *Tabular (including its ornamented surface) elongate posterolaterally or posteriorly in the form of a massive, horn-like process, conferring a boomerang-like shape to skull outline in plan view: absent (0); present (1).* The derived state is found in keraterpetontid nectrideans.

73. TAB 7. *Parietal–parietal width smaller than (0) or greater than (1) distance between skull table posterior margin and orbit posterior margin, measured along skull midline.* The greatest width of the articulated parietals is measured between the most lateral projections of their lateral margins. The posterior margin of the skull table is the rearmost point of its sculptured surface, in dorsal aspect (it coincides in most taxa with the rearmost part of the tabulars).

74. TAB 8. *Tabular without (0) or with (1) posteroventrally sloping occipital exposure.* In some taxa (e.g. some gymnarthrid microsaurs), the lateral profile of the tabular slopes posteroventrally.

*75. TAB 9. *Dorsoventrally flattened, posteriorly directed, subhorizontal outgrowth from posterolateral ventral surface of tabular: absent (0); present (1).* Klembara & Ruta (2004*a*) described a flat process projecting rearward from the subdermal (unsculptured) portion of the tabular as a feature uniting several Eurasiatic seymouriamorphs and variable in shape from mesially curved and blade-like to almost rectangular.

*76. TAB 10. *Tabulars entirely on occipital surface: no (0); yes (1).* The derived state of this character is observed in some diadectomorphs and in several basal crown amniotes (data from Laurin 1998; Laurin & Reisz 1999; Vallin & Laurin 2004). In these taxa, the tabular provides no contribution to the posterolateral corners of the skull roof.

77. POSORB 1. *Separately ossified postorbital: present (0); absent (1).* Apart from some aïstopods, lysorophians and adelospondyls, lack of an ossified postorbital also characterises crown lissamphibians.

78. POSORB 2. *Postorbital without (0) or with (1) ventrolateral digitiform process fitting into deep, vertical groove along jugal lateral surface.* The digitiform process in question is observed in urocordylid nectrideans.

79. POSORB 3. *Postorbital contributing to (0) or excluded from (1) orbit margin.* In *Colosteus*, adelospondyls and derived keraterpetontid nectrideans, there is no contribution of the postorbital to the orbit margin.

80. POSORB 4. *Postorbital irregularly polygonal (0) or broadly crescentic and narrowing to a posterior point (1).* The shape of the postorbital ornamented surface may appear extremely irregular, especially among stem tetrapods. In several temnospondyls and many stem amniotes, the overall outline of the bone is triangular (and more or less elongate anteroposteriorly) and terminates in an acute posterior extremity.

81. POSORB 5. *Postorbital/tabular suture: absent (0); present (1).* In most microsaurs and in the nectridean *Scincosaurus*, the postorbital forms a suture with the tabular.

82. POSORB 6. *Postorbital not wider (0) or wider (1) than orbit.* The width of the postorbital is measured, in dorsal aspect, as the distance between the extremities of its anteroventral (lateral) and anterodorsal (mesial) processes, whereas the orbit width is its maximum transverse diameter (in dorsal view). The derived state of this character occurs sporadically among stem tetrapods and in some lepospondyls (e.g. most nectrideans, among others).

83. POSORB 7. *Postorbital at least one-fourth of the width of the skull roof at the same transverse level: absent (0); present (1).* In the derived condition of this character, the maximum width of the postorbital is compared with that of the skull roof, i.e. the portion of the skull table posterior to the orbits and encompassing the bones of the lateral temporal series.

84. POSORB 8. *Anteriormost part of postorbital mesial margin with sigmoid profile in dorsal or lateral aspect: absent (0); present (1).* This is a feature of the majority of microsaurs and refers to the presence of a sudden twist along the course of the mesial margin of the postorbital, resulting in a S-shaped profile of such a margin.

85. SQU 1. *Anterior part of squamosal lying posterior to (0) or anterior to (1) parietal midlength.* In the majority of ingroup taxa, the anteriormost part of the ornamented surface of the squamosal lies well in front of the midlength of the parietals (calculated with a good approximation along the interparietal suture).

86. SQU 2. *Posterior margin of squamosal sloping posterodorsally to anteroventrally in lateral aspect: absent (0); present (1).* This is a feature of albenerpetontids, lysorophians and a handful of microsaurs. In all these taxa, the free edge of the squamosal (rear margin of its ornamented surface) is orientated obliquely.

87. SQU 3. *Squamosal without (0) or with (1) broad, concave embayment.* An embayment is widespread

among early tetrapods, a deeply incised squamosal notch is seen only in some stem amniotes and, conspicuously, in temnospondyls and salientians.

88. SQU 4. *A single 'squamosotabular' bone in the position of squamosal and tabular: absent (0); present (1).* This is a synapomorphy of adelospondyls, in which an enlarged bone appears in the position normally occupied by the squamosal, on the posteriormost part of the cheek, and the tabular, on the posterolateral corner of the skull roof.

89. SQU 5. *Squamosal without (0) or with (1) internal shelf bracing quadrate from behind.* In scincosaurid and keraterpetontid nectrideans, the ventral side of the squamosal sends a bony sheet, or strut, which provides support and buttressing for the quadrate.

90. JUG 1. *Separately ossified jugal: present (0); absent (1).* Lack of an ossified jugal occurs in salientians and lysorophians.

91. JUG 2. *Jugal not contributing (0) or contributing (1) to skull table ventral margin.* In the derived condition of this character, exhibited by most total group amniotes and by some temnospondyls, baphetids, albanerpetontids as well as primitive caecilians, the ventral margin of the jugal forms part of the skull table and intervenes between the lacrimal and the quadratojugal (if present).

92. JUG 3. *Jugal/pterygoid contact: absent (0); present (1).* In taxa as diverse as certain embolomeres, baphetids, temnospondyls and basal crown amniotes, the jugal and/or the pterygoid send a stout process that contributes to the anterior margin of the subtemporal fossa.

93. JUG 4. *Depth of jugal ventral to orbit greater (0) or smaller (1) than half of anteroposterior orbit diameter.* In the majority of the ingroup taxa, the maximum dorsoventral extension of the jugal (from the margin of the orbit to its ventral edge) is smaller than 50% of the maximum diameter of the orbit (measured parallel to the skull longitudinal axis in dorsal view).

94. JUG 6. *Jugal ventrally expanded, forming flange overlapping posterior end of maxilla: absent (0); present (1).* In the microsaurs *Pantylus* and *Stegotretus*, the ventral margin of the jugal shows a sinuous profile and a sudden increase in depth; as a result, the bone appears to form an extensive vertical flange lying immediately posterior to its suborbital ramus; such a flange covers the rear extremity of the maxilla in lateral aspect.

95. JUG 7. *Jugal without (0) or with (1) V-shaped indentation of its orbital margin.* In *Crassigyrinus*, *Whatcheeria*, some baphetids and certain embolomeres, the dorsal (orbital) margin of the jugal has a deep, V-shaped profile, which accounts for a distinctly angular shape of the ventral half of the orbit.

96. JUG 8. *Jugal not extending (0) or extending (1) anterior to orbit anterior margin.* The derived state of this character refers to the anterior extension of the anterior margin of the jugal relative to that of the orbit, when the skull is observed in lateral view.

97. QUAJUG 1. *Separately ossified quadratojugal: present (0); absent (1).* The lack of an ossified quadratojugal characterises lysorophians, the caudate *Valdotriton* and the salientian *Notobatrachus*.

98. QUAJUG 2. *Quadratojugal depth less than one-fourth of squamosal depth: absent (0); present (1).* The depth of both bones is measured, in lateral aspect, between their ventral edge and the dorsalmost part of their external surface. Aside from *Karaurus*, some microsaurs show the derived condition of this character.

99. QUAJUG 3. *Quadratojugal anteroposteriorly elongate and bar-like: no (0); yes (1).* The distribution of the derived state of this character is almost co-extensive with that of the previous character, except for the microsaur *Asaphestera*, where the derived state for the present character is not observed.

100. QUA 1. *Quadrate without (0) or with (1) dorsal process.* The process in question is recorded mostly in dissorophoids and is hypothesised to have supported a cartilaginous tympanum in life.

101. PREOPE 1. *Preopercular: absent (0); present (1).* Except for *Pederpes*, all taxa more derived than *Ichthyostega* lack an operculum on the posterior region of the dorsal surface of the suspensorium.

*102. NOS 1. *Nostrils posterolaterally expanded: absent (0); present (1).* This is a feature of branchiosaurid dissorophoids, in which the external nostril outline widens in its posterolateral portion (Boy & Sues 2000).

103. NOS 3. *Nostrils key-hole shaped: absent (0); present (1).* In the basal dissorophoids *Acheloma*, *Ecolsonia* and *Phonerpeton*, the nostril is expanded anteroposteriorly, with substantial contributions from the nasal and the maxilla (or lacrimal) and smaller contributions from the prefrontal and the premaxilla.

104. NOS 4. *Nostrils elliptical, with greater axis orientated obliquely in anteromedial to posterolateral direction and at least 70% of the length of the internasal suture: absent (0); present (1).* The derived state of this feature encompasses both the outline and the proportions of the nostrils relative to the suture between the nasal bones. It is found in some derived dissorophoids and some basal crown lissamphibians.

105. INT FEN 1. *Internarial fenestra: absent (0); present (1).* A partial separation between paired elements (usually nasals and premaxillae) in the anterior part of the skull table, either covered by a bone or exposed, occurs in some stem tetrapods and in certain temnospondyls, among others.

106. ORB 1. *Interorbital distance greater than (0), smaller than (1), or subequal to (2) half of skull table width.* The interorbital distance is the minimum distance separating the mesial (in dorsal aspect) margins of the orbits. While state 1 is widespread among stem tetrapods and total group amphibians, states 0 and 1 are more widely distributed in total group amniotes.

107. ORB 2. *Interorbital distance greater than (0), smaller than (1), or subequal to (2) maximum orbit diameter.* The alternative states of this character do not show a congruent distribution. In the majority of total group amniotes, state 0 is predominant in the derived half of their tree, whereas state 1 is more widespread in the basal part of their tree. The reverse is the case among total group amphibians and stem tetrapods. State 2 is rarely observed.

108. ORB 3. *Angle at orbit anteroventral corner: absent (0); present (1).* In *Whatcheria*, *Eucritta* and

Crassigyrinus, the orbit exhibits a distinct 'corner' in its anteroventral part, forming an 'angular' junction between its anterior and ventral margins.

*109. ORB 4. *Orbit deeper than long: no (0); yes (1).* In *Whatcheeria* (Lombard & Bolt 1995) and *Pederpes* (Clack 2002*b*; Clack & Finney 2005), the depth of the orbit (i.e. the maximum distance between its dorsal and ventral margins in lateral aspect) is greater than its maximum anteroposterior length.

*110. ORB 5. *Orbit anteroposterior diameter shorter (0), longer (1), or subequal to (2) distance between orbit posterior margin and suspensorium anterodorsal margin.* The distribution of the different states of this character is extremely irregular and shows several instances of parallel developments and reversals (see also Clack 2002*b*; Ruta *et al.* 2003).

111. PIN FOR 2. *Pineal foramen occurring posterior to (0), at the level of (1), or anterior to (2) interparietal suture mid length, or absent (3).* A pineal foramen is absent in lysorophians, some temnospondyls and microsaurs, as well as most basal crown lissamphibians (except *Triadobatrachus*). State 0 is seen in stem tetrapods, but occurs rarely among crown tetrapods. State 2 is seen in the majority of total group amniotes and amphibians. State 1 occurs sporadically in crown tetrapods.

112. L SC SKU 1. *Lightly sculptured area (subdued dermal ornament) adjacent to skull roof midline: absent (0); present (1).* This character (see discussion in Sequeira 2004) occurs in derived edopoids.

113. PTF 1. *Posttemporal fossa occurring at occiput dorsolateral corner, delimited dorsally by skull table, not bordered laterally and floored by dorsolateral extension of opisthotic (0); fossa present near occiput dorsolateral corner, delimited dorsally by occipital flanges of tabular and postparietal and bordered laterally as well as ventrally by dorsolateral extension of opisthotic meeting tabular ventromedial flange (1); small fossa present near occiput ventrolateral corner, bordered laterally by tabular ventromedial flange, delimited dorsally by dorsal portion of the lateral margin of the supraoccipital–opisthotic complex and floored by lateral extension of opisthotic (2); absence of fossa (3).* State 1 is the most widespread condition in our study group, whereas states 2 and 3 apply to diadectomorphs plus crown amniotes and to anthracosaurs, respectively. State 0 characterises less derived stem tetrapods, whereas more derived stem tetrapods exhibit state 1.

114. SKU TAB 1. *Postorbital region of skull table abbreviated and at least one-third wider than long: absent (0); present (1).* The derived state is acquired in parallel by total group amniotes and amphibians (except the most basal taxa of both groups).

*115. FONT 1. *Dorsal exposure of frontoparietal fontanelle: absent (0); present (1).* The frontoparietal fontanelle is exposed in the salientians *Notobatrachus* and *Vieraella* (Báez & Basso 1996).

116. TEM FEN 1. *Broad opening in skull postorbital region (aïstopod pattern): absent (0); present (1).* In aïstopods, a large temporal opening lies posterior to the orbit, from which it is separated by a continuous, slender bar of bone. This pattern differs from that shown by lysorophians, in which a single orbitotemporal opening (temporal opening confluent with orbit) is present.

117. CHE EMA 1. *Ventral emargination of cheek (pattern of certain tuditanomorph microsaurs): absent (0); present (1).* In lateral aspect, the ventral edge of the cheek of such microsaurs as *Micraroter*, *Pelodosotis*, *Cardiocephalus* and *Hapsidopareion* shows a variously developed, broadly concave emargination.

118. IFN 1. *Interfrontonasal: absent (0); present (1).* Although uninformative (presence of derived state in *Eryops*), this character is kept here for future references to expanded versions of our matrix.

119. SUS 1. *Anteroposteriorly narrow, bar-like squamosal: absent (0); present (1).* An elongate, bar-shaped squamosal is found in some microsaurs, lysorophians and aïstopods.

120. SC 1. *Lateral line system on skull table 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).* Except in the stem tetrapod portion of the tree, the distribution of character states matches that of the next character.

121. 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 preceding character.

122. VOM 1. *Ventral, exposed surface of vomers (i.e. excluding areas of overlap with surrounding bones) narrow, elongate and strip-like, without extensions anterolateral and posterolateral to the choana, and two and a half to three times longer than wide: absent (0); present (1).* The derived condition of this character is a shared feature of most total group amniotes and was determined to be diagnostic based on comparisons and measurements across all ingroup taxa. We note that the qualifying statement about proportions and extension of the vomers relative to the choana should be read as a single condition.

123. VOM 3. *Vomer with (0) or without (1) fangs comparable in size to, or larger than, marginal teeth (premaxillary or maxillary).* The lack of fangs (whether a cluster or a pair) characterises many dissorophoids, *Ichthyostega* and basal crown lissamphibians, as well as some anthracosaurs and most other stem and crown amniotes.

124. VOM 4. *Vomer without (0) or with (1) small teeth (denticles) forming continuous shagreen or discrete, patches, the basal diameter and/or height of which is less than 30% of that of adjacent marginal teeth (premaxillary or maxillary) and remaining vomer teeth (if present).* The derived state occurs in some stem tetrapods as well as in a number of stem amniotes and amphibians.

125. VOM 5. *Vomer excluded from (0) or contributing to (1) interpterygoid vacuities.* Vomers participate in the outline of the vacuities in several temnospondyls and basal lissamphibians, as well as in a handful of lepospondyls and diadectomorphs.

126. VOM 7. *Vomer/maxilla suture anterior to the choana: absent (0); present (1).* In some stem tetrapods, in a handful of temnospondyls and in basal caecilians and caudates, the vomer–maxilla suture lies anterior to the choana in palatal view.

127. VOM 8. *Vomer with (0) or without (1) toothed lateral crest.* In several stem tetrapods as well as in a handful of crown tetrapods, the ventral surface of the vomer carries a raised ridge, or crest, with irregularly distributed, small teeth.

128. VOM 9. *Vomer with (0) or without (1) transversely orientated, anterior crest.* The distribution of the derived state of this character is almost co-extensive with that of the preceding character.

129. VOM 10. *Vomer contact with pterygoid palatal ramus: present (0); absent (1).* In several derived temnospondyls and lissamphibians, as well as scincosaurid and some keraterpetontid nectrideans, the palatal ramus of the pterygoid fails to contact the vomer.

130. VOM 11. *Vomer without (0) or with (1) nearly transverse patch of small teeth (denticles) lying posteromesial to choana.* The derived condition of this character is found in *Doleserpeton* and some basal salientians.

131. VOM 12. *Distinct posterolateral process of vomer bordering more than half of choana posterior margin: absent (0); present (1).* In amphibamids, some branchiosaurids and *Karaurus*, the posterolateral region of the vomer forms a robust process, delimiting more than 50% of the posterior margin of the choana (such a margin is the portion of the choanal border delimited by two lines running parallel to the skull's longitudinal axis and passing through the lateralmost and medialmost points of such a border).

132. VOM 13. *Vomers shaped like broad and flat plates of bone, approximately as long as wide: absent (0); present (1).* In amphibamids and some basal crown lissamphibians the vomers are square in outline and resemble flat plates.

133. PAL 1. *Palatine with (0) or without (1) fangs comparable in size to or larger than marginal teeth (premaxillary or maxillary).* The lack of fangs (whether a cluster or a pair) characterises many dissorophoids, basal crown lissamphibians, and *Ichthyostega*, as well as derived stem amniotes and crown amniotes.

134. PAL 2. *Palatine without (0) or with (1) small teeth (denticles) forming continuous shagreen or discrete patches, the basal diameter and/or height of which is less than 30% of that of adjacent marginal teeth (maxillary) and remaining vomer teeth (if present).* Denticles occur in some stem tetrapods, many basal and derived temnospondyls and several stem and crown amniotes (although without a congruent distribution in the latter two groups).

135. PAL 4. *Palatine with (0) or without (1) row of teeth (3+) comparable in size to, or greater than marginal teeth (maxillary) and parallel to these.* A palatine tooth row is primitively present in the majority of stem tetrapods, as well as in some primitive and derived temnospondyls, *Eocaecilia* and assorted groups of stem amniotes (notably several microsaurs and nectrideans)

136. PAL 5. *Palatine without (0) or with (1) lateral exposure in anteroventral margin of orbit.* A dorsal, sculptured surface of the palatine contributes to the anteroventral angle of the orbit in some dissorophoids and *Isodectes*.

137. PAL 6. *Palatine articulates with maxilla only at anterior extremity of the former: absent (0); present (1).* In branchiosaurids (as well as in the basal crown amniote *Petrolacosaurus*), only a small anterior part of the lateral margin of the palatine contacts the maxilla, whereas the rest of the palatine is separated by a gap from the mesial side of the maxilla.

138. PAL 7. *Palatine shaped like a slender, strut-like bone: absent (0); present (1).* In most dissorophoids and basal crown lissamphibians, the ventral surface of the palatine is a narrow, lightly built and rod-like structure.

*139. PAL 8. *Separately ossified palatine: present (0); absent (1).* Absence of a palatine is a feature of some Lissamphibia (Milner 1988). Separate palatine ossifications are not present in the two Mesozoic Salientia, *Notobatrachus* and *Vieraella*, considered here. Báez & Basso (1996) suggested tentatively that palatine and vomer were coalescent in *Vieraella* (see also Rocek 2000).

140. ECT 1. *Separately ossified ectopterygoid: present (0); absent (1).* Basal crown lissamphibians and the amphibamid *Doleserpeton* lack separately ossified ectopterygoids, as do the microsaurs *Pantylus* and *Stegotretus*, the basal crown amniote *Captorhinus*, lysorophians and some derived nectrideans.

141. ECT 2. *Ectopterygoid with (0) or without (1) fangs comparable in size to or larger than marginal teeth (premaxillary or maxillary) and remaining ectopterygoid teeth (if present).* The absence of ectopterygoid fangs shows an incongruent distribution, e.g. in the Devonian tetrapods *Acanthostega* and *Ichthyostega*, certain temnospondyls, as well as most stem and crown amniotes.

142. ECT 3. *Ectopterygoid without (0) or with (1) small teeth (denticles) forming continuous shagreen or discrete patches, the basal diameter and/or height of which is less than 30% of that of adjacent marginal teeth (premaxillary or maxillary) and remaining ectopterygoid teeth (if present).* Denticles are present in some stem tetrapods, some temnospondyls and assorted groups of stem tetrapods.

143. ECT 4. *Ectopterygoid longer than/as long as (0) or shorter than (1) palatine.* The derived state of this character is observed in several temnospondyls as well as numerous stem and crown amniotes. The length of both palatal bones is measured along their axis of greater elongation, parallel to the adjacent ventral edge of the skull table.

144. ECT 5. *Ectopterygoid with (0) or without (1) row of teeth (3+) comparable in size to, or greater than, marginal teeth (maxillary) and parallel to these.* Baphetids and the vast majority of crown tetrapods exhibit the derived condition of this character.

145. ECT 6. *Ectopterygoid/maxilla contact: present (0); absent (1).* The ectopterygoid fails to contact the maxilla in branchiosaurids, in the basal crown amniote *Petrolacosaurus* and in the microsaurs *Odonterpeton* and *Hyloplesion*.

146. ECT 7. *Ectopterygoid narrowly wedged between palatine and pterygoid: no (0); yes (1).* In the microsaurs *Odonterpeton* and *Hyloplesion*, the anterior portion of the ectopterygoid is deeply inserted between the

posterior extremities of the palatine and of the palatal ramus of the pterygoid.

147. PTE 3. *Transverse flange of pterygoid absent (0), present without transverse tooth row (1), or present and carrying transverse tooth row.* In several stem and basal crown amniotes, the lateral portion of the area of the pterygoid corresponding to the junction between the palatal and the quadrate rami shows a transversely orientated, ventrally directed flange, sometimes lined with a transverse row of robust teeth.

148. PTE 7. *Pterygoid quadrate ramus orientated mostly laterally in ventral aspect: absent (0); present (1).* The derived condition of this character is observed among several primitive and derived caudates. In these, the quadrate ramus is often a stout structure, detaching at a nearly right angle from the rest of the pterygoid bone and running transversely to the quadrate.

149. PTE 9. *Pterygoid without (0) or with (1) a posterolateral flange.* In ventral aspect, the portion of the pterygoid lateral margin lying just anterior to the quadrate ramus forms a more or less distinct flange with a sinuous course in several temnospondyls and some stem amniotes.

150. PTE 10. *Pterygoids sutured with each other: no (0); yes (1).* In some stem tetrapods and many total group amniotes (where observed), the palatal rami of the pterygoids are in contact. The nature of this contact, however, is often difficult to reconstruct. Furthermore, pterygoids might come in contact during ontogeny.

151. PTE 11. *Pterygoid/maxilla contact: absent (0); present (1).* The derived state of this feature occurs in *Doleserpeton* and some basal crown lissamphibians.

152. PTE 12. *Pterygoid sutured with posterior extremity of palatine: absent (0); present (1).* In *Doleserpeton, Eocaecilia* and *Diploceraspis*, the anterior extremity of the pterygoid palatal ramus abuts against the posterior margin of the palatine, so as to form a continuous sheet of bone.

153. PTE 13. *Pterygoid without (0) or with (1) distinct, mesially directed process for basipterygoid articulation.* In several temnospondyls and some basal crown lissamphibians, the process is a stout, tubular structure, with parallel-sided or nearly parallel-sided anterior and posterior surfaces.

154. PTE 14. *Pterygoid quadrate ramus a robust structure, indistinctly merging into basal and palatal processes: absent (0); present (1).* In basal crown lissamphibians and certain dissorophoids, the quadrate ramus is a stout structure, slightly longer than wide and without a neat separation from the rest of the bone.

155. PTE 15. *Pterygoid quadrate ramus straight, rod-like and gently tapering distally in ventral aspect: absent (0); present (1).* In some dissorophoids and *Eocaecilia*, the ventral surface of the quadrate ramus is parallel-sided for most of its length and narrows smoothly in its rearmost part.

156. PTE 16. *Pterygoid palatal ramus without (0) or with (1) distinct, anterior and unornamented digitiform process.* In some microsaurs and adelospondyls, as well as in colosteids, the anterior end of the palatal ramus narrows abruptly and forms a relatively smooth, finger-like structure that is clearly separated from the rest of the ramus ventral surface.

157. PTE 17. *Basal region of pterygoid immediately anterior to quadrate ramus without (0) or with (1) sharply defined, elongate longitudinal groove.* An anteroposteriorly orientated, narrow and shallow depression is found in some microsaurs, where it runs for a short distance anteriorly from the point where the basal region and the quadrate ramus merge into each other.

*158. PTE 18. *Pterygoid palatal ramus a robust, abbreviated, flange-like to digitiform structure, as long as or barely longer than combined length of quadrate ramus plus basicranial articulation: absent (0); present (1).* This character is found in several basal and derived Caudata (Milner 2000).

*159. PTE 19. *Robust, strut-like, pterygoid–squamosal process providing support for quadrate: absent (0); present (1).* In Caudata (see Trueb 1993; Milner 2000), the pterygoid quadrate ramus and the squamosal 'clasp' the quadrate at the level of their lateral extremities. Together, the latter form a robust, strut-like element.

160. INT VAC 1. *Interpterygoid vacuities: present (0); absent (1).* In the majority of the taxa considered here, vacuities are present between the medial margins of the palatal bones and the lateral margins of the parasphenoid. In a number of ingroup taxa, such as baphetids, the palatal vacuities are sealed off. There are ontogenetic arguments to support the hypothesis that in some taxa (e.g. *Discosauriscus*), the vacuities became closed during growth.

161. INT VAC 2. *Interpterygoid vacuities occupy at least half of palatal width: absent (0); present (1).* In several temnospondyls and basal crown lissamphibians (as well as in certain nectrideans), the palatal vacuities are together at least half as wide as the whole palate at the same transverse level as their maximum width.

162. INT VAC 3. *Interpterygoid vacuities concave along their whole margins: absent (0); present (1).* The derived state of this character is almost co-extensive with that of the previous character and refers to the continuous curvature of their profile in ventral aspect.

163. INT VAC 4. *Interpterygoid vacuities together broader than long: absent (0); present (1).* Width and length refer to the maximum transverse width of both vacuities and to the distance from their anteriormost margin to the basicranial region, respectively.

164. CHO 1. *Choana wider in its anterior half than in its posterior half: no (0); yes (1).* In some basal temnospondyls, the outline of the choana is vaguely triangular, with an expanded anterior half and a tapering posterior half.

165. CHO 2. *Choana expanded transversely along its medial margin: absent (0); present (1).* In amphibamids and batrachians, the choanae are comparatively more expanded medially than in other groups (see Schoch & Milner 2004 for discussion of this feature).

166. ANT VAC 2. *Anterior palatal vacuity present and single (0), present and double (1), or absent (2).* In several stem tetrapods and some temnospondyls, either a single or two anterior openings are visible on the palate.

167. SUPOCC 1. *Separately ossified supraoccipital: absent (0); present (1).* A supraoccipital is present as a

separately ossified bone in many stem and basal crown amniotes.

168. EXOCC 2. *Exoccipitals enlarged to form flattened, widely spaced occipital condyles: absent (0); present (1).* In several nectrideans, especially keraterpetontids, the occipital condyles are very flat, but not appressed.

169. EXOCC 3. *Exoccipitals enlarged, about as broad as high and forming stout occipital condyles: absent (0); present (1).* In several derived temnospondyls, the posterior processes of the exoccipitals are robust and and their articular facets are isodimensional.

170. EXOCC 4. *Exoccipitals forming continuous, concave, strap-shaped articular surfaces with basioccipital: absent (0); present (1).* The derived state is found in microsaurs, where the articulation surface is wider than high and forms a semitoroidal facet.

171. EXOCC 5. *Exoccipitals appressed to each other and transversely expanded, so as to obliterate basioccipital posterior surface: absent (0); present (1).* In the derived condition of this character, the basioccipital is either partially or fully obliterated by the medial expansions of the posterior articulation facets of both exoccipitals.

172. BASOCC 1. *Basioccipital notochordal: yes (0); no (1).* Primitively, a basioccipital forming a thin ring of bone surrounding the notochord is seen in *Acanthostega*, *Ichthyostega* and *Crassigyrinus*, in contrast to the more derived condition of an ossified, subcylindrical body.

173. BASOCC 5. *Basioccipital articulation convex: no (0); yes (1).* In most diadectomorphs and in basal crown amniotes, the posterior, articulation surface of the basioccipital is approximately hemispherical.

174. BASOCC 6. *Articulation surface of the basioccipital circular and recessed: absent (0); present (1).* In aïstopods and adelospondyls, the basioccipital has a circular outline and carries a funnel-like excavation.

175. OPI 2. *Opisthotic forming a thickened plate together with the supraoccipital, preventing the exoccipitals from contacting the skull table: absent (0); present (1).* An opisthotic–supraoccipital complex is observed in several anthracosaurs, diadectomorphs, basal crown amniotes, *Greererpeton* and baphetids.

176. PASPHE 1. *Parasphenoid without (0) or with (1) elongate, strut-like cultriform process.* A parallel-sided, bar-shaped cultriform process characterises, mostly, colosteids and the majority of temnospondyls.

*177. PASPHE 2. *Anterior, triangular, wedge-like, more or less distinct process immediately anterior to level of basipterygoid processes: absent (0); present (1).* A description of this character was provided by Klembara & Ruta (2004*a*). It is found in Eurasiatic seymouriamorphs, but its occurrence in *Seymouria* is dubious (see also comments on different *Seymouria* species in Klembara & Ruta 2004*a*). The process occurs at the boundary between the posteriormost part of the parasphenoid stem and the anterior part of the parasphenoid plate (transverse level of the basipterygoid processes).

178. PASPHE 3. *Parasphenoid without (0) or with (1) a pair of posterolaterally orientated, ventral thickenings (ridges ending in basal tubera).* In some stem tetrapods and in several stem and basal crown amniotes, the ventral plate of the parasphenoid carries a pair of elongate, blunt- to sharp-topped and obliquely directed ridges diverging slightly posterolaterally.

*179. PASPHE 4. *Parasphenoid without elongate, broad posterolateral processes (0), or with processes that are less than (1), or at least half as wide as (2) parasphenoid plate.* This character refers to the degree of elongation of the posterolateral corners of the parasphenoid plate. The width of the latter is measured as the distance between two hypothetical, parallel lines that are drawn posteriorly from the basipterygoid processes. Wing-like and elongate processes have been observed in seymouriamorphs as well as in some microsaurs and diadectomorphs, where they form subtriangular and flat projections (see Klembara & Ruta 2004*a, b*)

180. PASPHE 6. *Parasphenoid without (0) or with (1) single median depression.* A subcentral, more or less distinct depressed area is visible on the ventral surface of the parasphenoid plate in a handful of stem tetrapods and in assorted stem as well as basal crown amniotes.

181. PASPHE 7. *Parasphenoid without (0) or with (1) paired lateral depressions.* This character is kept separate from the preceding one, as there is uncertainty about the homology of paired depressions with the single shallow area of other taxa. A pair of depressions characterises very few stem tetrapods, some temnospondyls and at least one microsaur.

182. PASPHE 9. *Ventral cranial fissure not sutured (0), or sutured but traceable (1), or not traceable (2).* This character is left unordered, although state 1 represents an intermediate stage between 0 and 2. The latter characterises most taxa. State 1 does not identify a clade and occurs only in a small number of stem tetrapods. In the primitive state, the two halves of the braincase are visibly separated and a conspicuous fissure intervenes between them. In the derived states, either a suture is observed, or the two braincase halves are fused.

183. PASPHE 11. *Basipterygoid processes of the basisphenoid shaped like anterolaterally directed stalks, subtriangular or rectangular in ventral view and projecting anterior to the insertion of the cultriform process: absent (0); present (1).* In certain derived dissorophoids and in basal salientians and caudatans, the wing-like basipterygoid processes project markedly laterally and occur slightly anterior to the proximal insertion of the cultriform process, so that the latter appears to be 'sunken' in the shallowly concave, anterior margin of the parabasisphenoid plate.

184. PASPHE 12. *Parasphenoid without (0) or with (1) patch of denticles sitting on raised triangular area near cultriform process posterior extremity.* This feature occurs in a handful of temnospondyls.

185. PASPHE 13. *Parasphenoid much wider than long immediately posterior to level of basal articulation: absent (0); present (1).* In dissorophoids and basal crown lissamphibians, the posterior ventral plate of the parasphenoid is at least twice as wide as long immediately posterior to the level of the proximal insertions of the basipterygoid processes.

186. PASPHE 14. *Outline of posterior ventral plate of parasphenoid subrectangular: absent (0); present (1).* The derived state of this character is observed in dissorophoids and basal crown lissamphibians.

187. JAW ART 1. *Jaw articulation lying posterior to (0), level with (1), or anterior to (2) occiput.* There appears to be no clear signal associated with the distribution of different character-states, even within the same clade. In the majority of cases, the posterior level of the occiput lies only slightly posterior to the posterior margin of the skull roof, so the latter can be used as a landmark in those cases in which the occiput is not preserved.

188. PSYM 1. *Parasymphysial plate: present (0); absent (1).* The parasymphysial plate, occurring anterior to the coronoid series on the mesial surface of the lower jaw, is absent in temnospondyls, in the majority of stem amniotes and in crown lissamphibians and amniotes.

189. PSYM 2. *Parasymphysial plate without (0) or with (1) paired fangs, comparable in size with or greater than dentary teeth.* Parasymphysial fangs are present in some stem tetrapods, such as *Acanthostega*, *Greererpeton*, *Megalocephalus*, *Baphetes* and *Crassigyrinus* (Ahlberg & Clack 1998).

190. PSYM 3. *Parasymphysial plate without (0) or with (1) anteroposterior tooth row orientated subparallel to marginal dentary teeth and the basal diameter and/or height of which is 30% or greater than that of marginal teeth and twice or more that of denticles, if present.* A parasymphysial tooth row occurs, in our data, in *Ventastega*, *Acanthostega* and *Whatcheeria*.

191. PSYM 4. *Parasymphysial plate with (0) or without (1) small teeth (denticles) forming continuous shagreen or discrete patches and the basal diameter and/or height of which is less than 30% of that of adjacent marginal dentary teeth.* Denticles are absent in most stem tetrapods as well as in certain anthracosaurs.

192. *DEN 1. Dentary with (0) or without (1) accessory tooth rows.* The basal crown amniote *Captorhinus* and the microsaur *Pantylus* have accessory tooth rows on the dentary. We point out that this is a slightly modified version of one of Ahlberg & Clack's (1998) characters, which they report in the Devonian stem tetrapod *Elginerpeton* (not included in our data matrix). We have coded for the presence of tooth rows other than the marginal row in two clearly unrelated taxa. However, this character is kept here for future references to expanded versions of our data set.

193. DEN 2. *Dentary with (0) or without (1) anterior fangs generally comparable in size with, or greater than, other dentary teeth and lying close to symphysial region and usually mesial to marginal dentary teeth.* The distribution of this character is not congruent. Dentary fangs are not present in the derived part of the amphibian total group and among the majority of total group amniotes.

194. DEN 3. *Dentary with (1) or without (0) 'chamfered' ventral margin.* A bevelled and relatively smooth ventral margin of the dentary is documented exclusively in the two Devonian taxa *Ventastega* and *Acanthostega*.

195. DEN 4. *Dentary without (0) or with (1)* U-*shaped notch for premaxillary tusks.* The notch in question occupies the anterior part of the dentary lateral surface in colosteids, and appears as a deep U-shaped excavation.

196. DEN 7. *Dentary toothed (0) or toothless (1).* Absence of dentary teeth is a salientian synapomorphy.

197. DEN 8. *Dentary length greater (0) or smaller (1) than half of distance between snout and occiput.* In *Batropetes* and *Brachydectes* the dentary is anteroposteriorly abbreviated and stout in aspect.

198. SPL 2. *Posteriormost extension of splenial mesial lamina closer to anterior margin of adductor fossa than to anterior extremity of jaw, when the lower jaw ramus is observed in mesial aspect and in anatomical connection (i.e. symphysial region orientated towards the observer): absent (0); present (1).* With a few exceptions, the derived condition occurs in total group amniotes, but it is also documented in *Greererpeton*, *Megalocephalus* and *Crassigyrinus*.

199. SPL 3. *Splenial/anterior coronoid suture: absent (0); present (1).* Aside from the outgroups, *Acanthostega* and *Crassigyrinus* are the only ingroup taxa in which the mesial lamina of the splenial fails to meet the anterior coronoid.

200. SPL 4. *Splenial/middle coronoid suture: absent (0); present (1).* The derived condition of this character occurs in some anthracosaurs as well as seymouriamorphs and among basal temnospondyls, but it shows no clear phylogenetic pattern.

201. POSPL 1. *Separately ossified postsplenial: present (0); absent (1).* The derived condition of this feature is a synapomorphy of crown lissamphibians, but it is found also in diadectomorphs and most basal crown amniotes, as well as in some lepospondyls.

202. POSPL 2. *Postsplenial without (0) or with (1) mesial lamina.* A mesially exposed extension of the angular is a widespread feature of tetrapods more derived than whatcheeriids.

203. POSPL 3. *Postsplenial with (0) or without (1) pit line.* Among Devonian tetrapods, *Ventastega* and *Ichthyostega* show a pit line on the postsplenial (Ahlberg & Clack 1998).

204. ANG 1. *Separately ossified angular: present (0); absent (1).* The derived condition of this feature is a synapomorphy of crown lissamphibians (but the bone is present as a separate ossification in the caudate *Karaurus*).

205. ANG 2. *Angular without (0) or with (1) mesial lamina.* A mesially exposed extension of the angular is a widespread feature of tetrapods more derived than *Tulerpeton* (*Pederpes* and *Gephyrostegus* are notable exceptions).

206. ANG 3. *Angular/prearticular suture: present (0); absent (1).* In the present data set, the derived condition of this character is observed only in *Acanthostega*. We nevertheless retain this feature for future, expanded versions of our matrix. Ahlberg & Clack (1998) also code for the derived state in *Metaxygnathus*, which is not included in the current data.

207. ANG 4. *Angular not reaching (0) or reaching (1) lower jaw posterior end.* The derived condition of

this character, found in the derived portions of both the amniote and the lissamphibian total groups, refers to the dorsalward extension of the rearmost part of the angular external surface. In lateral aspect, the sutural seam of the angular dorsal margin lies well dorsal to the posteroventral 'angle' of the jaw profile.

208. SURANG 1. *Separately ossified surangular: present (0); absent (1)*. The derived condition of this feature is a synapomorphy of crown lissamphibians.

209. SURANG 3. *Surangular with (0) or without (1) pit line*. In tetrapods more derived than *Ventastega* a sensory pit line is absent (Ahlberg & Clack 1998).

210. SURANG 5. *Surangular lateral exposure much smaller than angular lateral exposure: no (0); yes (1)*. In the diadectomorph *Orobates* and, especially, the microsaurs *Hapsidopareion*, *Cardiocephalus* and *Euryodus*, the external surface of the surangular is reduced to a slender splinter of bone, the extension of which is less than one-third of that of the angular.

211. PREART 5. *Prearticular/splenial suture: present (0); absent (1)*. The prearticular fails to contact the splenial on the mesial side of the lower jaw ramus in temnospondyls more derived than edopoids, as well as in *Anthracosaurus* and *Pholiderpeton attheyi*.

212. ANT COR 1. *Separately ossified anterior coronoid: present (0); absent (1)*. The absence of a differentiated anterior coronoid characterises the lissamphibian crown group, some diadectomorphs and crown amniotes, as well as most lepospondyls.

213. ANT COR 2. *Anterior coronoid with (0) or without (1) fangs comparable in size to or larger than marginal dentary teeth*. In tetrapods more derived than *Ventastega*, fangs are generally absent from the anterior coronoid (*Gephyrostegus* and *Greererpeton* are notable exceptions).

214. ANT COR 3. *Anterior coronoid with (0) or without (1) small teeth (denticles) forming continuous shagreen or discrete patches and the basal diameter and/or height of which is less than 30% of that of adjacent marginal dentary teeth*. Denticles occur in the majority of crown group taxa.

215. ANT COR 4. *Anterior coronoid with (0) or without (1) anteroposterior tooth row orientated subparallel to marginal dentary teeth and the basal diameter and/or height of which is 30% or greater than that of marginal teeth and twice or more that of denticles, if present*. The derived state is seen in all tetrapods more derived than colosteids (with the notable exception of *Whatcheeria*).

216. MID COR 1. *Separately ossified middle coronoid: present (0); absent (1)*. The absence of a differentiated middle coronoid characterises the lissamphibian crown group, some diadectomorphs and crown amniotes, as well as some lepospondyls.

217. MID COR 2. *Middle coronoid with (0) or without (1) fangs comparable in size to or larger than marginal dentary teeth*. Except in the case of *Pederpes* and *Gephyrostegus*, no middle coronoid fangs are present in tetrapods more crownward than *Ventastega*.

218. MID COR 3. *Middle coronoid with (0) or without (1) small teeth (denticles) forming continuous shagreen or discrete patches and the basal diameter and/or height of which is less than 30% of that of adjacent marginal dentary teeth*. Denticles occur in the majority of crown group taxa.

219. MID COR 4. *Middle coronoid with (0) or without (1) anteroposterior tooth row orientated subparallel to marginal dentary teeth and the basal diameter and/or height of which is 30% or greater than that of marginal teeth and twice or more that of denticles, if present*. Several outgroup and a handful of ingroup taxa display a marginal tooth row on the middle coronoid.

220. POST COR 1. *Separately ossified posterior coronoid: present (0); absent (1)*. The absence of a differentiated posterior coronoid characterises the lissamphibian crown group, as well as such taxa as *Phlegethontia*, *Sauropleura* and *Brachydectes*.

221. POST COR 2. *Posterior coronoid with (0) or without (1) fangs comparable in size to or larger than marginal dentary teeth*. The occurrence of posterior coronoid fangs characterises the outgroups.

222. POST COR *3. Posterior coronoid with (0) or without (1) small teeth (denticles) forming continuous shagreen or discrete patches and the basal diameter and/or height of which is less than 30% of that of adjacent marginal dentary teeth*. Denticles occur in the majority of crown group taxa.

223. POST COR 4. *Posterior coronoid with (0) or without (1) anteroposterior tooth row orientated subparallel to the marginal dentary teeth and the basal diameter and/or height of which is 30% or greater than that of marginal teeth and twice or more that of denticles, if present*. The plesiomorphic condition of this character is widespread among stem group tetrapods, but is very rarely observed in crown tetrapods.

224. POST COR 5. *Posterior coronoid without (0) or with (1) posterodorsal process*. The posterior coronoid often sends a backward process detaching immediately posterolateral to its main dentigerous part and contributing in various degrees to the anterolateral portion of the adductor fossa.

225. POST COR 6. *Posterior coronoid exposed in lateral view: no (0); yes (1)*. In some taxa, the posterior coronoid is visible when the jaw ramus is orientated in lateral view and appears as either a sliver or a more substantial lappet of bone tightly appressed against the surangular and posterodorsal to the posterior ramus of the dentary.

226. POST COR 7. *Posterodorsal process of posterior coronoid contributing to tallest point of lateral margin of adductor fossa: no (0); yes (1)*. This character refers to the extension, backward and dorsalward, of the process. In some taxa, the latter forms part of the tallest point of the lateral margin of the adductor fossa, regardless of the presence or absence, in the surangular, of a 'crest' (that is, a peak in the profile of the dorsal margin of the surangular).

227. ADD FOS 1. *Adductor fossa facing dorsally (0) or mesially (1)*. The coding of this character follows Ahlberg & Clack (1998). A mesially facing adductor fossa of the lower jaw results basically from the fact that its mesial and lateral margins lie at different levels relative to one another.

228. TEETH 1. *Marginal tooth pedicely: absent (0); present (1)*. Tooth pedicely is a feature of certain dissorophoids and lissamphibians and one of the most frequently discussed, putative dissorophoid–lissamphibian synapomorphies (see Bolt 1991; Milner 1993; Schoch & Milner 2004). In these taxa, the teeth bear a base, or pedicel, upon which the apical portion of the tooth crown sits.

229. TEETH 3. *Marginal teeth without (0) or with (1) two cuspules labiolingually arranged.* Unlike in Ruta *et al.* (2003), we have not coded for the monocuspid *versus* multicuspid condition of teeth, to avoid duplication. The multicuspid teeth of such tetrapods as the microsaur *Batropetes* or the albanerpetontids cannot be treated as an alternative state, as they are not readily comparable, despite the fact that their cusps are not labiolingually arranged (*contra* Laurin 1998 and a more recent version of his matrix). Two labiolingual cusps characterise some dissorophoids and lissamphibians (for discussions of this feature, see Bolt 1991; Milner 1993; Schoch & Milner 2004).

*230. TEETH 4. *Conspicuous peak involving one or more anterior maxillary teeth: absent (0); present (1)*. A maxillary peak is a widespread but irregularly distributed feature and occurs in several unrelated taxa. The coding for this character largely follows Clack (2002*b*). It is most evident in *Ichthyostega* and whatcheeriids, as well as in certain temnospondyls, in *Seymouria* and in some microsaurs. A less conspicuous peak appears in diadectomorphs and several basal crown amniotes.

231. TEETH 5. *Dentary teeth larger than maxillary teeth: no (0); yes (1)*. This character occurs sporadically (e.g. some temnospondyls; colosteids) among stem and crown tetrapod taxa.

232. TEETH 6. *Marginal tooth crowns chisel-tipped: no (0); yes (1)*. In labial or lingual view, the marginal tooth crowns of some taxa reveal a chisel-like, asymmetrical extremity. This feature occurs in taxa as diverse as adelospondyls as well as some embolomeres, among others.

233. TEETH 7. *Marginal tooth crowns without (0) or with (1) 'dimple'*. In adelospondyls, the marginal teeth display a small, shallow depression or pit.

234. TEETH 8. *Marginal tooth crowns robust and conical: absent (0); present (1)*. In some microsaurs (notably, pantylids and gymnarthrids), the crowns of several marginal teeth appear as stout, low, conical structures, presumably adapted for a crushing action.

*235. TEETH 9. *Number of maxillary teeth greater than 40 (0), between 30 and 40 (1), smaller than 30 (2)*. The coding for this character follows largely Clack (2002*b*). There appears to be little phylogenetic signal associated with the distribution of the different states.

236. CLE 1. T-*shaped dorsal expansion of cleithrum: absent (0); present (1)*. This feature characterises keraterpetontid nectrideans. In lateral aspect, the dorsal portion of the cleithrum is enlarged and sends a robust pair of processes, orientated in a T-shaped fashion.

237. CLE 2. *Cleithrum with (0) or without (1) postbranchial lamina*. Postbranchial laminae are primitively retained in a number of Carboniferous and Devonian tetrapods, e.g. *Acanthostega*, *Ichthyostega*, *Greererpeton* and *Whatcheeria*. The lamina is a narrow sheet of bone projecting from the anterior edge of the cleithrum.

238. CLE 3. *Cleithrum co-ossified with scapulocoracoid: yes (0); no (1)*. Separately ossified scapulocoracoid and cleithrum occur in all tetrapods more derived than *Ichthyostega*.

239. CLA 3. *Clavicles meet anteriorly: yes (0); no (1)*. In the derived condition, the anteroventral plates of the clavicles fail to contact each other and a strip of the ventral side of the interclavicle is interposed between them. On both sides of this strip, the impressions of the clavicular plates are discernible and their morphology provides clues to the degree of separation between them.

240. INTCLA 1. *Interclavicle posterior margin not drawn out into parasternal process (0), with parasternal process that is not parallel-sided (1), or with elongate, slender process that is parallel-sided for most of its length (2)*. The derived condition represented by state 2 occurs among some Devonian and Carboniferous taxa, as well as among many stem and basal crown amniotes.

241. INTCLA 3. *Interclavicle wider than long (excluding parasternal process, if present): absent (0); present (1)*. In those taxa in which a parasternal process is present, the length of the interclavicle is measured from its anterior extremity to the point where its posterolateral margins are deflected and continue into the lateral margins of the process.

242. INTCLA 4. *Interclavicle rhomboidal with posterior part longer (0) or shorter (1) than anterior part*. The boundary between the anterior and posterior parts of the interclavicle is a transverse line running through its lateral corners.

*243. INTCLA 5. *Transversely elongate grooves and ridges on central part of interclavicle ventral surface: absent (0); present (1)*. In *Pederpes* (Clack 2002b; Clack & Finney 2005) and *Ossinodus* (Warren & Turner 2004), sharp-edged and often coalescent ridges separated by grooves produce a characteristic pattern on the ventral surface of the interclavicle, where they are mostly orientated transversely and subparallel to each other.

244. SCACOR 1. *Separate scapular ossification: absent (0); present (1)*. In those taxa in which a scapulocoracoid complex is observed, it is often possible to assess the presence of either separate ossifications or a single ossification. Relating these two conditions to ontogenetic stages is challenging, as comparative material is not always abundant and there appears to be no direct link with overall size or degree of ossification in remaining portions of the skeleton.

245. SCACOR 2. *Glenoid subterminal: yes (0); no (1)*. In the derived state of this character, the scapulocoracoid extends ventral and slightly posterior to the posteroventral margin of the glenoid, thus forming a distinct 'wall' of bone, visible in lateral aspect.

246. SCACOR 3. *Enlarged glenoid foramen: absent (0); present (1)*. Loss of an enlarged glenoid foramen

occurs sporadically and does not show any clear phylogenetic signal.

247. SCACOR 4. *Ventromesially extended infraglenoid buttress: absent (0); present (1).* This feature, observed in tetrapods more derived than *Acanthostega*, is described as a thickening jutting out on the visceral (internal) side of the scapular blade, occurring posterior to the subscapular fossa and sweeping mesioventrally towards the floor of the coracoid region of the scapulocoracoid (Coates 1996).

248. ANOCLE 1. *Anocleithrum: present (0); absent (1).* An ossified anocleithrum occurs in a few taxa only, but its distribution shows no obvious phylogenetic signal.

249. HUM 1. *Latissimus dorsi process offset anteriorly relative to the ectepicondyle (0) or aligned with the latter (1).* When the greater axis of the ectepicondyle is extended proximally, it is aligned with the latissimus dorsi process in the derived condition of this character, in those taxa where both structures are readily distinguishable.

250. HUM 2. *Distinct supinator process projecting anteriorly: absent (0); present (1).* The supinator attachment area may be represented by faint rugosities. However, in some taxa it bears a conspicuous blunt process detaching from the distal part of the anterior surface of the humerus.

251. HUM 3. *Sharp-edged, ventral humeral ridge: present (0); absent (1).* The ridge in question has a sporadic occurrence in primitive tetrapods, but it is an outstanding feature of 'osteolepiform' humeri.

252. HUM 4. *Latissimus dorsi process confluent with (0) or distinct from (1) deltopectoral crest.* The primitive condition, best seen in *Acanthostega* (see Coates 1996), shows the latissimus dorsi process in continuity with the deltopectoral crest, the two structures being bridged by a thin sheet of bone. In other taxa, the two structures are well separated, although in *Pederpes* (Clack & Finney 2005) a thin ridge detaches from the latissimus dorsi process and runs anteriorly, stopping just short of the anterior margin of the humerus.

253. HUM 5. *Entepicondyle foramen: present (0); absent (1).* Absence of this foramen occurs in a variety of groups within crown tetrapods.

254. HUM 6. *Ectepicondyle foramen: present (0); absent (1).* This is one of the two major foramina visible on the majority of tetrapod humeri (see also preceding character) and lies in close proximity to the ectepicondyle. It is seen in *Acanthostega*, *Ichthyostega* and *Crassigyrinus*.

255. HUM 7. *Distinct ectepicondyle ridge: present (0); absent (1).* The ectepicondyle ridge runs on the extensor surface of the humerus and resembles in most cases a thick, raised keel, but variation in shape and proportions, especially among stem tetrapods, are known (for discussions, see Coates 1996; Clack & Finney 2005).

256. HUM 8. *Ectepicondyle ridge reaching distal humeral end: no (0); yes (1).* Where present, the ectepicondylar ridge is often observed to approach closely or even extend slightly beyond the periosteal lining of the distal extremity of the humerus.

257. HUM 9. *Distal extremity of ectepicondyle ridge aligned with ulnar condyle (0), between ulnar and radial condyles (1), or aligned with radial condyle (2).* We have not imposed any order on the transformation between character-states, but we point out that the distribution of the three states shows a good congruence with the phylogenetic pattern, in that state 1 appears in assorted basal stem tetrapods from the Devonian and Carboniferous and state 0 is found in *Acanthostega* and *Ichthyostega*.

258. HUM 10. *Humerus without (0) or with (1) waisted shaft.* The presence of a distinctly concave surface of the shaft, in extensor view, characterises most taxa in the study group, although there are exceptions, e.g. among basal tetrapods and certain stem amniotes.

259. HUM 11. *Position of radial condyle: terminal (0); ventral (1).* In the derived state, the radial condyle appears on the distal portion of the flexor surface of the humerus, rather than on the terminal surface of its distal extremity.

260. HUM 12. *Humerus slender and elongate, its length being more than three times the maximum width of its distal end: absent (0); present (1).* Metric cut-off points were selected on the basis of a survey of humerus proportions in all taxa. The derived state mainly characterises some derived dissorophoids and crown amphibians, but is observed in other taxa as well. In the derived condition, the humerus does not show the elaborate, tetrahedral shape of primitive tetrapods and resembles a 'stretched' hourglass. The distal end width is measured in the plane of its dorsoventral flattening.

261. HUM 13. *Posterolateral margin of entepicondyle lying distal relative to plane of radial and ulnar facets: yes (0); no (1).* The primitive condition of this character is observed sporadically. The derived condition refers to a distal extension of the entepicondyle relative to the distal articular area.

262. HUM 14. *Posterolateral margin of the entepicondyle markedly concave: yes (0); no (1).* In the outgroup *Eusthenopteron*, the posterolateral margin of the entepicondyle is recurved in dorsal aspect, a condition also found in some other 'osteolepiforms'.

263. HUM 15. *Width of entepicondyle greater (0) or smaller (1) than half humerus length.* The entepicondyle width is measured in the plane of the entepicondyle flattening, as the distance between its free margin and a line parallel to the humerus greater axis and passing through the point of attachment of the entepicondyle posterior margin into the general surface of the bone. The humerus length is the maximum distance between its proximal and distal extremities.

264. HUM 16. *Portion of humerus shaft length proximal to entepicondyle smaller (0) or greater (1) than humerus head width.* The humerus head width is the maximum distance that occurs between its anterior and posterior margins when it rests in the plane of its dorsoventral flattening. The shaft length is measured from the point of attachment of the entepicondyle posterior margin into the general surface of the bone to a plane passing immediately distal to the humerus deltopectoral crest. While in some taxa these points appear to be weakly defined, they are nevertheless identifiable.

265. HUM 17. *Accessory foramina on humerus: present (0); absent (1).* In 'osteolepiforms' and some stem

tetrapods, the humerus is pierced by numerous foramina (particularly evident on the flexor surface), but the number of these decreases in more derived taxa, so that only a few conspicuous foramina remain.

266. HUM 18. *Humerus length greater (0) or smaller (1) than combined length of two and a half mid-trunk vertebrae.* Survey of taxa shows the derived condition to have an incongruent distribution being present, usually, in small and/or supposedly immature forms. The metric cut-off points were selected based on these forms and through comparisons with their larger counterparts.

*267. HUM 19. *Process '2' on humerus: absent (0); present (1).* This character is based upon Coates (1996) and refers to the presence of a small, acuminate distal process along the posterior margin of the proximal (relative to the entepicondyle) part of the humerus. Such a process is observed in *Acanthostega* and in *Whatcheeria*, but occurs also in some of the more derived taxa, e.g. the anthracosaurs *Eoherpeton*, *Proterogyrinus*, and *Archeria*. Its presence in *Tulerpeton* is uncertain.

268. RAD 1. *Radius longer (0) or shorter (1) than humerus.* Primitively, the radius is at least slightly longer than the humerus, although this condition occurs also in some keraterpetontid nectrideans. The lengths of each bone take into account the longest distance measured between their proximal and distal extremities.

269. RAD 2. *Radius longer than (0), as long as (1), or shorter than (2) ulna.* Primitively the radius appears to be slightly longer than the ulna. Although there are no instances of a radius longer than an ulna showing an olecranon process, we have kept the present character separate from the coding of this process (see below), as future finds might document a broader range of variation in the proportions of these two bones.

*270. RAD 3. *Compound radio-ulna: absent (0); present (1).* A compound bone deriving from the fusion of the radius and ulna constitutes a shared derived feature of all Salientia more derived than *Triadobatrachus* (Milner 1988; Rage & Rocek 1989; Rocek 2000; Rocek & Rage 2000*a*, *b*).

271. ULNA 1. *Olecranon process: absent (0); present (1).* A digitiform or hook-like process projecting from the proximal extremity of the ulna occurs in the majority of tetrapods more derived than *Acanthostega*, but its absence in some taxa (e.g. certain seymouriamorphs, see also Klembara & Ruta 2004*a*, *b*) might be due to immaturity or paedomorphic development. For simplicity, we have adopted a typological approach to the coding of this character.

272. ILI 3. *Dorsal iliac process: absent (0); present (1).* Primitively, tetrapods exhibit a double-headed ilium. However, the plesiomorphic condition of a simple iliac process is observed in 'osteolepiforms'. For consistency with the coding of other characters, we have therefore assigned the derived state to a double-headed ilium.

*273. ILI 4. *Posterior iliac process subhorizontal, stout, abbreviated posteriorly and tapering rearward in lateral aspect: absent (0); present (1).* A robust, rearward-pointing, posterior iliac process is found in seymouriamorphs and diadectomorphs (Sumida 1997; see also

Klembara & Ruta 2004*b*). In these taxa, the dorsal profile of the ilium is smoothly rounded in lateral aspect and continues gradually into the dorsal edge of the posterior process. The latter is only slightly longer than deep and strongly built.

274. ILI 6. *Supraacetabular iliac buttress less (0) or more (1) prominent than postacetabular buttress.* In all tetrapods more derived than *Acanthostega*, the supraacetabular buttress is strongly developed and forms a robust shelf that is slightly larger than the postacetabular buttress.

275. ILI 7. *Transverse pelvic ridge: absent (0); present (1).* A transverse ridge sweeping from a point immediately dorsal to the acetabulum and running obliquely in a posterodorsal direction is found in taxa as diverse as certain temnospondyls and many stem and basal crown amniotes.

276. ILI 9. *Ilium shaped like an elongate rod directed anteriorly/anterodorsally: absent (0); present (1).* This is a character of all Salientia. However, it might be possible to identify, in the morphology of the ilia of several dissorophoid temnospondyls, conditions that appear to anticipate the shape of the frog ilium. The ontogeny of certain dissorophoids might offer clues to the development of an anteriorly or anterodorsally directed, rod-like ilium in the salientian total group (Ralf Werneburg, pers. comm. 2005).

277. ILI 10. *Acetabulum directed posteriorly/posterolaterally (0) or laterally (1).* In the ingroup taxa, the iliac acetabular surface faces distinctly laterally, rather than slightly posterolaterally. Although uninformative, this character is kept here as a useful reference in future, higher-level tetrapod phylogenies that encompass multiple outgroups from among 'osteolepiform' fishes.

278. ISC 1. *Ischium contributing to pelvic symphysis: no (0); yes (1).* The derived condition of this character is found in the ingroup (see also Coates 1996 for a discussion). This character is uninformative (see also preceding character).

*279. PUB 1. *Number of pubic obturator foramina: multiple (0), single (1), or absent (2).* This character (see also Coates 1996; Clack 2002*b*) can be coded in very few taxa, as the pubic bones are rarely ossified in many groups. Multiple foramina have been observed in Devonian taxa and *Whatcheeria*.

280. FEM 1. *Internal trochanter raised as a distinct protuberance: absent (0); present (1).* The internal trochanter may appear either as a weakly developed, indistinct area, or as a conspicuous, blunt or digitiform protuberance.

281. FEM 2. *Internal trochanter separated from the general surface of the femur shaft by a distinct, trough-like space: absent (0); present (1).* In some taxa, the internal trochanter and the part of the femur shaft from which it detaches are separated by a deeply notched web of bone, but it is difficult to relate the presence of the latter to any particular growth stage and its distribution is incongruent.

282. FEM 3. *Fourth trochanter of femur with distinct rugose area: no (0); yes (1).* The presence of a rough-textured and/or striated area on the fourth trochanter has a very patchy distribution in our data set and does

not always appear to be related to the overall size of the taxa.

283. FEM 4. *Proximal end of femur adductor crest reaching midshaft length: no (0); yes (1).* This character has been discussed at length by Coates (1996) and refers to the extension, proximally, of the proximal extremity of the adductor crest, on the flexor surface of the femur.

284. FEM 5. *Femur shorter than (0), as long as (1), or longer than humerus (2).* Bone lengths are measured along the greatest distance between the ossified portions of their proximal and distal extremities.

*285. FEM 6. *Internal trochanter of femur shaped like a flat, triangular, acuminate process: absent (0); present (1).* In several Caudata and *Eocaecilia*, the internal trochanter of the femur is shaped like a triangular, distally pointed and flat process, which is often spike-like (Jenkins & Walsh 1993; Evans & Milner 1996; Milner 2000; see discussion in Evans & Sigogneau-Russell 2001). However, the condition of *Karaurus* is unknown.

*286. TIB 6. *Outline of tibia medial margin shaped like a distinct, subsemicircular embayment contributing to interepipodial space and the diameter of which is less than one-third of bone length: absent (0); present (1).* The derived state of this character is seen in *Whatcheeria* (Lombard & Bolt 1995) and *Pederpes* (Clack 2002b; Clack & Finney 2005), both of which exhibit a massively built and stout tibia with flared proximal and distal extremities. The length of the tibia is measured, in extensor or flexor aspect, along the greatest distance between the ossified portions of the proximal and distal ends.

287. TIB 7. *Tibia without (0) or with (1) flange along its posterior edge.* This character has been described by Coates (1996).

288. FIB 1. *Fibula waisted: no (0); yes (1).* As in the case of other limb bones, a waisted shaft implies the presence of a distinct constriction of the shaft.

289. FIB 3. *Ridge near posterior edge of fibula flexor surface: absent (0); present (1).* A description of this ridge has been provided by Coates (1996) and has been further discussed by Clack & Finney (2005).

290. FIB 4. *Rows of tubercles near posterior edge of fibula flexor surface: absent (0); present (1).* This character is kept separate from the preceding character, although such rows of tubercles might be homologous with the continuous ridge seen in an almost identical position on the fibula of certain taxa.

291. TAR 2. *Proximal tarsal ossifications: absent (0); presence of single ossification (1); presence of more than two ossifications (2).* This and the following three characters describe different conditions of tarsal elements and their derived states are contrasted with the lack of an ossified tarsus, which is the condition observed in the outgroups. This was treated as an alternative character by Ruta *et al.* (2003), but it is deleted from the present data set to avoid redundancy with other characters describing the tarsus.

292. TAR 3. L-*shaped proximal tarsal element: absent (0); present (1).* In several stem and crown amniotes, the proximal tarsal element in question (an intermedium

or modifications thereof through fusion with adjacent bones) carries a shallow proximal notch or excavation. Sometimes this is pronounced, distinctly angular and confers a vaguely L-shaped outline to this tarsal element.

293. TAR 4. *Distal tarsal ossifications between fibulare and digits: absent (0); present (1).* The derived condition, in which tarsal ossifications occur between the fibulare and the digits, is seen in taxa more derived than *Ichthyostega*.

294. TAR 5. *Distal tarsal ossifications between tibiale and digits: absent (0); present (1).* The distribution of the derived state of this character matches that of the previous character.

295. RIB 1. *Ribs* K-*shaped in at least some part of the trunk: absent (0); present (1).* A K-shaped rib morphology is found in aïstopods and results from the presence of spike-like projections of the shaft joined by a thin web of bone. A lucid discussion of this morphology has been presented by Anderson (2003).

296. RIB 2. *Cervical ribs with (0) or without (1) flattened distal ends.* In several tetrapods, the distal extremity of the cervical ribs is dorsoventrally flat or carries a terminal triangular flange (for discussion of these structures, see Coates 1996; Clack & Finney 2005).

297. RIB 3. *Ribs mostly straight (0) or ventrally curved (1) in at least part of the trunk.* A strong curvature of the trunk ribs is almost ubiquitous among stem and crown amniotes, but it is present in other tetrapods as well. However, whether this morphology accounted for similar functions in different groups is not certain (Clack & Finney 2005). In basal crown amniotes and their putative stem group relatives, curved ribs might have been associated with active rib cage movements during ventilation. In certain stem taxa, such as *Ichthyostega*, the robust ribs (and perhaps their associated flanges) might have helped stabilise the trunk region during movement and prevent its lateral flexion (Clack & Finney 2005).

298. RIB 4. *Broad rectangular flanges in at least some trunk ribs: absent (0); present (1).* This character describes broad (at least twice as wide as the rib proximal shaft), often overlapping, laminar sheets of bone that occupy a considerable portion of the rib length in the mid part of the trunk. Considerable variation occurs, as revealed by *Eryops* and *Pederpes* (for an overview, see Clack & Finney 2005) and the distribution of this character is highly incongruent.

299. RIB 5. *Triangular spur-like posterodorsal process in at least some trunk ribs: absent (0); present (1).* Colosteids and adelospondyls show a proximal spur-like to plectrum-shaped process in the posterior third of most trunk ribs.

300. RIB 6. *Elongate posterodorsal triangular flange in the midtrunk ribs: absent (0); present (1).* Colosteids, adelospondyls and lysorophians show a distally tapering, triangular flange in the posterior third of most trunk ribs (see also preceding character).

301. RIB 7. *Longest trunk ribs poorly ossified, slender rods, the length of which is smaller than the length of three trunk vertebrae: absent (0); present (1).* A survey of rib morphology and their general proportions relative

to vertebrae allowed us to identify the chosen metric cut-off points as the derived state for several derived dissorophoids and crown amphibians.

302. CER VER 1. *Halves of atlas neural arch unfused (0) or fused (1)*. Where observed, this character shows a rather incongruent distribution, even within the same group.

303. CER VER 3. *Axis arch not fused (0) or fused (1) to axis (pleuro)centrum*. Fusion between the arch and the body of the second vertebra shows incongruent distributions, its derived state being present in crown and stem amniotes, as well as in some crown amphibians.

304. CER VER 4. *Odontoid process, or tuberculum interglenoideum, on anterior surface of atlas body: absent (0); present (1)*. We follow Anderson (2001) in the coding of this character, which describes an anteriorly protruding, stout process of the atlas body fitting into a variously deep recess or pit in the occiput. Its presence is not ubiquitous among lepospondyls and no evidence of it was found in preserved atlases of adelospondyls (M.R., pers. obs. 2001). For simplicity, we have not considered morphological variations of this structure in all taxa that show it. Schoch & Milner (2004) have addressed, in some detail, this feature and have shown that its mere absence or presence is not as clear-cut as previously surmised. A protruding structure comparable with an odontoid process is even found in some temnospondyls, as well as in certain extant anurans.

305. TRU VER 1. *Extra articulations above zygapophyses in at least some trunk and caudal vertebrae: absent (0); present (1)*. This is one of several vertebral characters that diagnose nectrideans and some aïstopods. It refers to interdigitating projections of the neural arches situated dorsal to the zygapophyses and resembling the latter in modalities of articulation.

306. TRU VER 2. *Neural and haemal spines rectangular to fan-shaped in lateral view: no (0); yes (1)*. In nectrideans, the neural and haemal spines are almost a mirror image of one another and are characteristically flattened laterally while fanning out distally to various degrees.

307. TRU VER 3. *Neural and haemal spines aligned dorsoventrally: absent (0); present (1)*. The neural and haemal spines of nectrideans face directly opposite each other dorsoventrally and are nearly identical in overall proportions (see preceding character).

308. TRU VER 4. *Haemal spines not fused (0) or fused (1) to caudal centra*. Fusion between caudal centra and haemal spines, presumably associated with a membrane bone modality of vertebral development (Milner 1988), is observed almost exclusively in nectrideans.

309. TRU VER 5. *Extra articulations on haemal spines: absent (0); present (1)*. Urocordylid nectrideans display the derived condition of this character, with the haemal spines forming loosely interdigitating contacts.

310. TRU VER 7. *Ossified pleurocentra: absent (0); present (1)*. As in the case of the intercentrum (see below), we have not taken into account the causes underlying the lack of ossified pleurocentra in some taxa.

311. TRU VER 8. *Trunk pleurocentra fused midventrally: no (0); yes (1)*. The derived state of this character refers to the adjoining of the ventral extremities of primitively paired pleurocentra.

312. TRU VER 9. *Trunk pleurocentra fused middorsally: no (0); yes (1)*. The derived state of this character refers to the adjoining of the dorsal extremities of primitively paired pleurocentra.

313. TRU VER 10. *Neural arches without (0) or with (1) distinct convex lateral surfaces*. In cross section, the neural arches of certain stem and basal crown amniotes are 'swollen', i.e. their lateral surfaces show a characteristically inflated or smoothly convex profile.

314. TRU VER 11. *Neural arches of trunk vertebrae fused to centra: no (0); yes (1)*. Fusion between arches and centra does not appear to be simply related to overall size, or inferred degree of specimen maturity (see Laurin 2004 for a thorough discussion of related topics concerning the evolution of body size in early tetrapods).

315. TRU VER 12. *Bicipital rib bearers on trunk centra: absent (0); present (1)*. Bicipital, rib-bearing processes characterised by a bifid distal extremity with two facets for the capitulum and tuberculum of the rib are found in caudates and some derived keraterpetontid nectrideans. In the latter, however, the whole process has a more substantial, proximal undivided portion and a distally bifurcated extremity.

316. TRU VER 13. *Trunk intercentra: present (0); absent (1)*. As in the case of other structures that are observed in some taxa but not in others, we have adopted a simple, typological approach to the coding of this feature, regardless of the causes underlying the derived 'absence' condition.

317. TRU VER 14. *Trunk intercentra fused middorsally: no (0); yes (1)*. The derived state of this character refers to the presence of a dorsally continuous intercentrum, often resembling a flat cylinder or spool and resulting from the adjoining of the dorsal extremities of a primitively crescent-like intercentrum.

318. TRU VER 15. *Anteroposteriorly elongate, lateral and ventral carinae on trunk centra: absent (0); present (1)*. Robust, blunt-edged carinae or keels occur on the centra of certain lepospondyls, including adelospondyls and lysorophians.

319. TRU VER 16. *Strong proximal emargination along anterior and posterior margins of haemal spines of tail vertebrae: absent (0); present (1)*. The anterior and posterior margins of the proximal portion of the haemal spines of some nectrideans appear to be strongly concave, thus conferring a constriction to the portion of haemal spine that lies close to the vertebral centrum in lateral projection.

320. TRU VER 18. *Striated ornament on vertebral centra: absent (0); present (1)*. A 'pleated' or unevenly striated surface sculpture characterises the neural spines of some of the more derived keraterpetontid nectrideans.

321. TRU VER 19. *Tallest ossified part of neural arch in posterior trunk vertebrae situated above (aligned vertically with) posterior half of vertebral centrum: no (0); yes (1)*. This character describes a condition in

which the tallest part of the neural arch is vertically aligned with the posterior half of the (pleuro)centrum (where observed) in the posterior region of the trunk.

322. TRU VER 20. *Prezygapophyses on trunk vertebrae: absent (0); present (1)*. This and the following five characters have been kept separated to account for the possibility that acquisition of fully developed and ossified zygapophyses occurred in a 'stepwise' fashion along the backbone (e.g. tail of certain Devonian taxa, notably *Acanthostega* and *Ichthyostega*; trunk of *Crassigyrinus* and *Trimerorhachis*)

323. TRU VER 21. *Postzygapophyses on trunk vertebrae: absent (0); present (1)*. See preceding character.

324. TRU VER 22. *Prezygapophyses on proximal tail vertebrae: absent (0); present (1)*. See character 322, above.

325. TRU VER 23. *Postzygapophyses on proximal tail vertebrae: absent (0); present (1)*. See character 322, above.

326. TRU VER 24. *Prezygapophyses on distal tail vertebrae: absent (0); present (1)*. See character 322, above.

327. TRU VER 25. *Postzygapophyses on distal tail vertebrae: absent (0); present (1)*. See character 322, above.

328. TRU VER 26. *Capitular facets situated on posterior rim of vertebral midtrunk centra: absent (0); present (1)*. The derived state of this character is found in some lepospondyls, in which the facet for the capitulum of the rib lies close to the posterior rim of the centrum, in lateral aspect.

329. TRU VER 27. *Height of the ossified portion of the neural arch in midtrunk vertebrae greater (0) or smaller (1) than the distance between pre- and postzygapophyses*. The height of the neural arch is measured from its dorsal extremity to the points of insertion of pre- and postzygapophyses in lateral aspect. The distance between pre- and postzygapophyses is measured between the anteriormost and posteriormost edges of their articulation facets in lateral aspect, respectively.

330. TRU VER 28. *Crenulations or fimbriate sculpture along dorsal margin of ossified portion of neural spines: absent (0); present (1)*. This character is presumably related to the modalities of vertebral ossification in nectrideans (Milner 1988), but it is kept separate from the preceding character as it does not fully overlap with the latter. In lateral aspect, the neural spines of all nectrideans and of some aïstopods (pers. obs.) are irregularly jagged or crenulated along their dorsal edge.

331. TRU VER 29. *Intravertebral foramina for spinal nerves in at least some trunk vertebrae: absent (0); present (1)*. Vertebral foramina are recorded in *Eocaecilia*, the caudate *Valdotriton* (condition in *Karaurus* unknown) and aïstopods.

332. TRU VER 30. *Transverse processes stout and abbreviated, the length of which is less than 30% of neural arch height: absent (0); present (1)*. The derived state is found in colosteids and adelospondyls.

333. DIG 1. *Digits: absent (0); present (1)*. Ruta *et al.* (2003) have discussed alternative codings, in particular as a multistate character, for the condition of the anterior autopod. As those Devonian taxa in which the autopod is preserved are autapomorphic relative to digit number, no separate coding has been introduced for

them. Instead, we have included the presence of digits as the general condition (a differentiated autopod; see Coates 2003), followed by further characters for the conditions of digit numbers in post-Devonian taxa. As in our 2003 work, we have not coded for the posterior autopod, as number of digits (except for some Devonian taxa) is not affected by the same degree of variation observed in the anterior autopod.

334. DIG 2. *Manus with no more than four digits: absent (0); present (1)*. The presence of only four digits in the manus characterises the amphibian total group, certain stem tetrapods and some lepospondyls.

335. DIG 3. *Manus with no more than five digits: absent (0); present (1)*. The presence of only five digits in the manus characterises certain stem tetrapods and most stem amniotes (except for several lepospondyls) and basal crown amniotes.

336. DIG 4. *Manus with no more than three digits: absent (0); present (1)*. The presence of only three digits in the manus characterises microbrachomorph microsaurs.

337. DOR FIN 1. *Ossified lepidotrichia in dorsal fin: present (0); absent (1)*. We opt to code for the presence of ossified lepidotrichia, as the mere presence of a dorsal fin fold may not always be observed directly. This character is uninformative, as it applies to *Eusthenopteron* only, but it is used as a reference for future modifications of our data set (character and/or taxon addition/deletion).

338. CAU FIN 1. *Ossified lepidotrichia in caudal fin: present (0); absent (1)*. As in the case of the previous character, the caudal fin character refers to the condition of the lepidotrichia. Therefore, any integument fold of the tail that has no ossified lepidotrichia (e.g. the tail of the branchiosaurid *Apateon*) is discounted. As defined here, this character applies to 'osteolepiforms', *Acanthostega* and *Ichthyostega*.

339. BAS SCU 1. *Basal scutes: present (0); absent (1)*. Bony scutes are present near the insertion of paired and unpaired fins in several pre-panderichthyid 'osteolepiforms'. However, our matrix includes only *Eusthenopteron* and *Panderichthys* as outgroups and, therefore, this character is uninformative. Although analysis of a combined matrix inclusive of 'osteolepiforms' and limbed tetrapods has not been constructed, we retain this character for future developments of our data.

Appendix 3: Taxon–character matrix

Characters are numbered from left to right and divided into groups of ten. Question marks indicate unknown or inapplicable characters. The notations {} and () have been assigned to uncertainty and polymorphic coding, respectively. For brevity, the following replacements have been introduced: a = {0,1}; b = {0,2}; c = {1,2}; d = {2,3}; e = {0,1,2,3}; f = (0,1); g = (1,2). In some cases, we have coded for taxa using data from closely related species in the same genus (as in the case of *Brachydectes*, *Sauropleura* and *Seymouria*), or from closely related genera (as in the case of *Paleothyris* plus *Protorothyris*, as well as Albanerpetontidae; for the latter, information relies upon *Albanerpeton inexpectatum* and *Celtedens ibericus*).

Acanthostega gunnari

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0 ? ? 0 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 0 1 0 0 0 0 0 0 0    0 0 1 2 0 0 0 0 1 1    1 1 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 1 ?
? ? 0 0 0 1 0 1 0 0    0 0 0 0 0 0 0 0 0 0    0 1 1 0 0 0 0 0 0 0    0 0 0 0 0 1 0 0 0 0    0 0 0 0 1 1 1 0 0 0    0 0 0 0 0 0 0 0 0 1
1 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    1 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 1 0 0 0 0    0 0 0 0 0 0 0 0 0 0
0 1 0 0 0 0 0 0 1 1    0 1 0 1 0 0 0 0 0 0    0 0 1 0 0 1 0 0 1 0    0 0 1 1 0 0 1 1 0 0    1 1 0 0 0 ? 0 0 0 0    0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 1 0 0 0 0    0 0 0 0 0 1 0 0 0 0    1 1 0 0 0 1 1 1 0 0    0 1 0 0 0 0 1 1 0 1    1 1 0 1 0 0 0 0 1 0    0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 1 1 1 1 0 0 0 0 0    0 0 1 0 0 0 1 0 1
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Acheloma cumminsi

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1 1 0 0 0 0 0 1 ? 1    0 0 0 0 0 0 0 0 1 0    1 0 0 0 0 1 0 0 0 0    0 0 1 1 1 0 0 0 0 2    1 1 0 0 0 0 0 1 0 1    0 0 0 0 0 0 0 1 ?
? ? 0 0 0 ? 0 0 0 1    ? 0 0 0 0 0 0 0 0 1    0 0 0 0 1 0 1 0 0 0    0 0 1 0 0 0 0 0 0 1    1 0 1 0 1 1 1 0 0 1    2 0 1 1 0 0 0 0 0 ?
? ? ? ? 1 ? ? ? 0 ?    ? 0 0 ? 1 0 0 0 0 ?    ? ? ? ? ? ? 0 0 1 0    ? 0 1 0 0 0 0 0 0    1 1 0 0 0 0 0 0 1 0    1 1 0 0 0 1 0 0 0 0
0 2 0 0 0 0 0 ? ? ?    ? 1 1 0 0 0 0 ? ? ?    ? ? ? 0 ? ? 1 0 1 0    ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? 1 0 0 0    0 0 0 0 ? 0 1 1 ? ?
? ? ? 0 1 0 1 1 1 1    ? 1 1 1 0 1 2 1 1 0    0 0 0 1 1 ? 0 ? ? 0    1 0 0 1 0 0 1 1 ? 1    0 0 1 ? 0 0 0 1 ? ?    2 0 1 1 0 ? 0 0 0 0
0 ? ? ? 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 1 1 ? ? ? ? 0 0 0    0 0 1 ? ? ? ? ? ? 1
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Acherontiscus caledoniae

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0 ? ? ? 0 0 0 0 0 1    1 1 0 0 0 0 1 0 0 0    ? ? ? ? ? ? ? ? ? 0    0 1 ? ? ? ? 1 1 ?
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Adelogyrinus simorhynchus

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0 ? ? 0 0 0 ? 1 ? 1    1 0 1 0 0 0 0 0 ? 1    0 0 ? 0 0 1 0 1 0 0    0 ? 1 ? ? 0 1 ? 1 ?    1 0 ? 1 1 0 0 0 0 ?    0 0 0 0 1 0 ? 0 1 ?
? ? 1 ? ? ? 1 ? ? ?    ? ? 0 ? ? ? 0 0 1 0    ? 0 0 0 ? 0 0 1 ? 0    ? ? 1 0 0 0 0 0 0 0    1 0 ? 0 1 2 0 0 0    0 ? ? 0 0 0 0 0 0 ?
3 ? ? ? ? ? ? ? ? ?    ? ? ? ? 0 ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 0    0 1 0 1 ? ? ? ? ? ?
? ? ? ? ? ? 1 ? ? ?    ? ? 1 0 0 0 0 ? ? ?    0 0 1 0 ? ? 1 0 1 0    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 0    0 1 1 0 1 0 1 1 ? 0
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0 0 ? 0 0 ? ? ? ? 1    1 1 ? 0 0 1 ? 1 ? ?    ? 1 1 ? ? ? ? 1 0 ?    0 1 ? ? ? ? 1 ? ?
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Adelospondylus watsoni

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? ? ? ? ? ? ? ? ? 1    1 ? 1 0 1 0 0 0 ? 0    0 0 0 0 0 1 0 ? 0 0    0 0 1 2 0 0 1 ? ? 2    1 0 ? 1 1 0 0 0 0 ?    0 0 0 0 1 0 ? 0 1 ?
? ? 1 ? ? ? 1 ? ? ?    ? ? 0 ? ? ? 1 ? ? ?    ? ? ? ? ? 0 1 1 0 0    1 0 1 0 0 0 0 0 0 0    1 ? ? ? ? ? 2 0 0 0    1 ? 1 0 0 0 0 0 0 c
3 ? ? ? ? ? ? ? ? ?    ? ? ? 1 ? 0 0 0 0 0    1 1 1 1 0 0 0 0 0 ?    0 0 0 0 0 1 0 0 0 0    0 0 0 ? ? ? ? ? ? ?    ? ? ? ? ? 0 0 ? 0 ?
? 2 ? ? ? ? 1 ? ? ?    ? ? 1 0 0 0 0 ? ? ?    0 ? ? 0 ? ? 1 0 1 0    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 ?    0 1 1 0 ? ? ? ? ? 0
? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? 0 ? 1 0 1 1
0 ? ? 0 ? ? ? ? ? 1    1 1 0 0 0 1 ? 1 ? ?    ? 1 1 ? ? ? ? 1 ? ?    0 1 ? ? ? ? ? ? ?
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ALBANERPETONTIDAE

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0 ? ? 0 0 0 ? 1 ? 1    1 0 1 0 1 0 1 0 1 0    1 0 0 0 0 0 ? 1 0 0    1 ? 0 2 1 0 0 0 ? ?    1 1 0 0 ? ? ? ? ? ?    ? ? ? ? ? 1 ? ? ? ?
? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? 1 1 0 0 ? 0    1 ? ? ? 0 ? ? ? 0    1 0 0 0 0 1 ? 0 0 ?    3 0 ? 1 0 0 0 0 0 ?
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? ? ? ? ? ? ? ? ? 0    ? ? 1 1 1 ? ? 1 1 1    1 1 1 1 1 1 0 1 2 0    0 ? ? ? ? ? 1 ? ?    ? ? ? 2 ? ? ? 1 ? ?    ? ? ? ? 0 0 0 0 0 0
1 1 0 1 0 0 0 0 0 1    1 1 0 ? 0 1 ? 0 0 0    0 ? ? ? ? ? 0 0 0    0 0 1 1 0 0 1 1 1
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Amphibamus grandiceps

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1 1 0 0 0 0 ? 1 ? 1    0 1 0 0 0 1 0 0 0 0    1 0 0 0 0 0 0 1 0 0    1 0 1 1 0 0 0 0 0 2    1 1 0 0 0 0 0 0 1 0 ?    0 0 0 0 0 0 0 0 1 ?
? ? 0 0 0 0 0 ? ? ?    ? 0 1 0 ? 0 0 0 0 1    0 0 0 0 1 0 1 0 0 0    0 0 1 0 0 0 0 0 0 1    1 0 0 1 0 1 1 0 0 1    2 0 ? 1 0 0 0 0 0 ?
? 0 1 1 1 0 1 1 1 0    1 1 1 1 0 ? 0 1 0 0    0 0 1 1 0 0 0 0 0 0    0 0 1 0 1 0 0 0 0 0    1 1 1 0 1 2 ? 0 1 0    1 1 0 0 ? 1 0 0 0 0
0 2 1 0 1 1 0 ? ? ?    ? ? ? 0 0 0 0 ? ? ?    0 ? ? 0 ? ? ? 0 1 0    ? 0 ? ? ? 0 ? ? ? 0    ? ? ? ? ? ? 1 1 1 0    0 0 0 0 0 0 1 1 1 0
0 0 0 0 ? ? 1 1 ? 0    1 ? 1 1 1 ? ? 1 ? 1    1 1 1 1 1 1 0 1 ? 0    ? 0 0 1 0 0 1 1 ? ?    ? ? ? 2 ? 0 0 1 0 0    ? ? ? ? 0 0 0 0 0 0
1 ? 0 0 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 1 1 1 1 1 1 0 0 0    0 0 1 1 0 0 1 1 1
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Anthracosaurus russelli

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0 ? ? 0 1 0 0 1 ? 1    0 0 0 0 1 0 0 0 0 0    0 0 0 0 0 0 ? 0 0 0    0 0 1 1 0 0 0 1 0 2    1 1 0 0 0 0 0 0 1 0    0 0 0 0 0 0 0 0 0 1
0 0 0 0 0 1 0 1 0 1    ? 0 1 0 0 0 0 0 0 0    0 0 0 0 1 0 0 0 0 0    0 0 1 0 1 1 0 0 0 0    1 0 0 0 0 1 1 0 0 2    2 0 3 1 0 0 0 0 0 c
3 1 1 0 ? 0 1 1 0 0    0 0 0 0 1 0 0 0 0 0    0 0 0 0 0 0 0 0 0 ?    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 2 0 0 0 0    0 1 0 0 1 0 0 1 0 1
0 2 0 0 0 0 0 ? ? ?    ? 1 1 0 0 0 0 ? 1 0    0 1 1 0 1 0 ? 0 1 0    1 0 1 ? ? 0 1 0 1 0    1 0 0 0 0 ? ? 0 0 1    0 0 0 0 2 ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?
```

Apateon pedestris

```
1 0 1 0 0 0 0 1 ? 1    0 1 1 0 0 1 0 0 0 0    1 0 0 0 0 0 0 1 0 0    1 0 1 1 1 0 0 0 0 2    1 1 0 0 0 0 0 1 0 ?    0 0 0 0 0 0 0 1 ?
? ? 0 0 0 1 0 0 ? 1    ? 0 1 0 0 0 0 0 0 1    0 0 0 0 1 0 1 0 0 0    0 0 1 0 0 0 0 0 0 ?    1 1 0 1 1 1 1 0 0 1    2 0 1 1 0 0 0 0 0 ?
? 0 0 0 1 0 1 1 1 0    1 0 0 0 0 0 1 1 0 0    1 0 1 0 1 0 0 0 0 0    0 0 1 1 1 0 0 0 0 0    1 1 1 0 0 2 ? ? ?    ? ? ? ? ? 1 0 0 0 0
0 2 1 0 1 1 1 ? ? ?    ? ? ? 0 0 0 0 ? ? ?    0 ? ? 0 ? ? ? 0 1 0    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? 1 ? 0 0    0 0 0 0 ? 0 1 1 1 0
1 0 0 0 ? ? 1 1 ? 0    1 ? ? ? 1 ? ? ? 1 ? 1    1 1 1 1 1 1 0 1 1 0    0 0 0 ? 0 0 1 1 ? ?    ? ? ? 2 ? 0 0 1 ? ?    ? ? ? ? 0 0 0 0 0 0
1 ? ? ? 0 0 0 0 0 ?    ? ? 0 ? 0 0 0 0 0 0    ? 1 1 1 1 1 1 0 0 0    0 0 1 1 0 0 1 1 1
```

Archeria crassidisca

```
0??01001?1   0000100000   0010001000   0011000102   1100100010   0000000000
0000000101   ?000000001   0000100000   1110010000   1000011001   203000000d
????0????0   ?????0?000   ?0?0000001   0000000000   000???0000   0100100101
0200000000   1110000111   0110100010   0010101010   1011101000   0100001112
0000001110   0101012000   1101111120   1101101111   0112000110   2111?01???
0000000001   1100001000   0111111000   001010111
```

Ariekanerpeton sigalovi

```
0??0100101   0000000000   0000001000   0012000102   110000010?   0000000000
1000000001   ?010100001   0010100000   101000000?   1000020002   2011000003
d101001100   0001100000   110100101?   000000000?   000002?000   0?00?01120
0200001 1??   ?110000?1?   0110101010   ?010101010   1011011000   0000201102
1001?0???0   1101012100   1100110110   0?1?1011??   ???2?0?1??   ????001000
0???000001   1f100000?0   011???? 000  001010111
```

Asaphestera intermedia

```
0??01001?1   0000000000   0000001000   0011?00102   1100000001   000000101?
??1??? 0??0   0010?00000   1001000000   101000010?   1000000002   0011000004
a?????????   ???100000?   ??????00??   0000000000   000???1001   01000?????
?????????   ??10000???   ???0??1010   ?????????   ???????000   0000 2???11
1000111??0   ??010121?0   ????110??0   010?0011??   ???c??????   ????0?1000
0??100????   ??010??0??   111??????1?  001???1?1
```

Balanerpeton woodi

```
10100001?1   0100000000   0000000000   0011000002   110ff0000?   0000000001
0100010001   ?000000001   0000101000   0010000000   1000011002   20?1000004
4001101100   0001100000   0101000010   0000000000   111002?000   0100?10000
0200000 1??   ?100000010   0110100010   1010101010   101???1000   1000001110
0000???1?0   1?011??100   1100110110   10010011?1   1?02000100   2011000000
0000000001   0000000000   01111??000   001100111
```

Baphetes kirkbyi

```
0??0000101   0000000100   0000100000   0011000002   110??00000   0000000001
0101010011   ?000000000   0000100000   1000100000   100011200c   0010000003
?001001100   0001100000   0101000001   0000000001   ???0020000   0?00100000
1200000010   1??0000???   0?1???????   ?????????   ???????000   00001?????
???????00   0101012000   11001?0???   ?10100 11??  ?????00110   ?????????
????00000?   ?????00?00   ????????0   ????????1
```

Batrachiderpeton reticulatum

```
0??00001?1   0010000000   0000011100   0010000112   1111000001   000110001?
??1???0000   0110000000   0110100010   1010000000   1000000000   20?0000004
40100?1100   0010000001   ??????0001   0000000001   ???002?100   0100?000?0
0200002 1??   ?1100001??   1??0101010   01???1??0   10100??000   0000211100
010???????   ?????????   ?????????   ???????1??   ?????????   ?????????
???011110?   ??0????000   0111111001   001100???
```

Batropetes fritschia

```
0??01101?1   0000000010   0000011000   0?12100112   1110?1????   ?????0001?
??1???0000   0010000000   100?010000   1?1000???0   1000022001   20?1000011
?????????   ?????????   ??????00??   ??00000000   ??????1001   01000000?0
0200002 ???  ?110001???   ???0??????   ?????????   ???????000   000020?112
10001111?0   1?01???110   1111110120   1?0?001?11   101g000100   ?01?001000
0??1000f01   11?f01?000   1111111110   001100111
```

Brachydectes elongatus / B. newberryi

```
0??00001?1   0000100010   000101?100   0110000 1??  1001100001   010001??1?
??1???0000   00?0001???   ????110001   ??????1??0   10000??0?1   3010000014
4110?01100   00101?0001   ??????0000   0000000001   ???0021001   0100000000
0200002 1??  ?110001???   1??010101?   ?1???1???1   ???????000   0000201110
1001???1?0   ??111??1?0   1111100110   000?0011?1   00120001??   ????011001
00?100000?   ??000??100   11111??110   001??0111
```

Broiliellus brevis

```
???000?1?1   0000010000   1000000000   ?012100002   110000000?   000000001?
??00000000   ?000000001   0000101000   001000000?   1000012001   20?100000?
?0??101110   000??0000?   ??????0010   0010000000   111002????   ?????10000
0200110???  ???0000???   ???0??1???   ?????????   ??????1000   000000011??
???0???1?0   ??111??1?0   1101110???   ??01001111   0???0?????   ????0?0000
0???00000?   ??00?00000   ?11??????00  00????111
```

Bruktererpeton fiebigi

```
0??????1?1   0000?00?00   00???0??00   0011100102   110000010?   0000???00
?000000 1??   ?00000????   ???????00?   ?????????   ?0000?????   2??10?00??
??0???????   ??0????000   11??00???1   ?0?????00?   ?????????   ?????????
?????????   ?????????   ?????????   ?????????   ??????000   ?0001?11??
???1?01?10   1101012010   1101110120   1????????1   1012000100   21??001000
0???000001   1000000000   0111111000   001???111
```

Caerorhachis bairdi

```
0???????1   000???????   ??????0?00   001??00002   110110000?   0000000?01
?0000?0100   ?000000001   000010000?   ?0?????000?   1???0?????   c0?000000?
??010?1100   00011?0000   0101000001   0000000000   000002?000   0?????0001
0200000010   0100000110   01?0100010   0010101010   1011001000   00000?????
?????????   ?????????   ????????0   11011011?1   1?1?0001??   2111001000
0?00000001   1000000000   0111111000   001???111
```

Capetus palustris

```
1110000 1?1   0000000000   1000000000   0011000002   0101 10000?   0000000000
0000000001   ?000000001   0010101000   0000010000   1000000000   00?1000004
4001??110?   0?????0000?   ??????001?   0000000000   101??2??00   ?????1????
?20?000???   ????000???   0?1010?010   ????????0   ???????001   0000a????0
000???????   ?????????   ?????????   ?????????   ?????????   ?????????
?????????   ?????????   ?????????   ?????????
```

Captorhinus aguti

```
0??0110101   0000000000   0000001000   0011100?12   1110000100   100000?01?
??00001???   ??0???0000   ?000100000   1110010000   1000011000   2020000004
4110001100   0010100001   ??????1001   0000000000   0000021000   0110100111
0200001 1??   ?000000???   1??0101010   01???1???0   1111111001   00002???12
1000101110   1101012110   1111110120   1001?01111   11120001??   2111001000
0010000001   1111000000   1111111010   001010111
```

Cardiocephalus sternbergi

```
0??0110101   0000100000   0001001100   0010000102   1100000001   010000111?
??1???0000   0001000000   1001?1?000   101000???0   1000000000   20?1001014
a110001100   0?10000000   1010000001   0000001000   000??20001   0100000020
0200002???   ?110001??   01101?1011   ?????????   ??????1001   00012?????
?????????   ?????????   ?????????   ?????????   ?????????   ?????????
?????????   ?????????   ?????????   ?????????
```

Chenoprosopus lewisi

```
0??1000101   0000100000   0010000000   0011000002   110000 00?   0000000001
00000100?1   ?000000000   0000101000   1100010000   1000020000   31?0000004
400?001100   000?100000   0?01000010   0000000000   110102?000   0100?10000
?200000???   ???00?0???   0?101??010   ?0???0??0   ??????000   00001?????
?????????   ?????????   ?????????   ?????????   ?????????   ?????????
?????????   ?????????   ?????????   ?????????
```

Cochleosaurus bohemicus

```
???1000101   0000000000   0010001000   0011000002   110000000?   0000000001
00000100?1   ?000000001   0000101000   1100010000   1000020000   31?0000004
4001011100   0001100000   0101000010   0010000000   111102????   ?????10000
120100 01??   ?110000011   0110100010   0010101010   1011??1000   00001?????
?????????   ?????????   ?????????   ?????????   ?????????   ?????????
?????????   ?????????   ?????????   ?????????
```

Colosteus scutellatus

```
0??000?1?1   1010101001   ?000000000   0011001012   1001f000?   000010001?
??000100?0   0000000010   0110100000   ??0000000?   1000?20000   00?0000002
2?????????   ?00?000000   0??000?00?   0000010000   00000?????   ?????10???
?2????0???   ?100100???   ?????????   ?01100???0   10100??000   1000???00
010???????   ?????????   ?????0?1??   ?????????   ?????????   ?????????
????000001   0000?00000   011??????0   011100???
```

Crassigyrinus scoticus

```
0??0001111   0000000010   0010000000   0011000002   110??0001?   0000000000
?000000101   ?000000000   0000100000   0000100000   1000111102   00?0000001
3000010000   0000000000   0000000001   ?000000 0?   000001????   ?000?00101
0100000010   1100000100   0010100010   0010101010   ?????0000   000010?1?1
000?????10   010001c000   1100000100   010?0011?1   1112001110   ????0?1000
00??000000   ??0?000000   ?10????000   001???1?1
```

Dendrerpeton acadianum

```
1 0 0 0 0 0 0 1 1 1   0 0 0 0 0 0 0 0 0 0   0 0 0 0 0 0 0 0 0 0   0 0 1 0 0 0 0 0 0 2   1 1 0 1 1 0 0 1 0 ?   0 0 0 0 0 0 0 0 0 1
0 0 0 0 0 1 0 0 1 1   ? 0 0 0 0 0 0 0 0 1   0 0 0 0 1 0 1 0 0 0   0 0 1 0 0 f 0 0 0 1   1 0 0 0 0 2 0 0 0 0   2 0 ? 0 0 0 0 0 0 4
? 0 0 1 1 ? 1 1 0 0   0 0 0 1 1 0 0 0 0 0   0 1 0 1 0 0 0 0 1 0   0 0 1 0 0 0 0 0 0 0   1 1 0 0 0 2 ? 0 1 0   0 1 0 0 ? 1 0 0 0 0
0 2 0 1 0 0 0 ? ? ?   ? ? ? 0 0 0 0 ? ? ?   0 1 1 0 1 0 0 0 1 0   ? 0 ? ? ? 0 ? ? ? 0   ? ? ? ? ? ? 1 0 0 0   0 0 0 0 0 0 1 1 1 0
0 0 0 0 0 0 1 1 ? 0   1 ? 0 1 0 1 2 1 0 0   1 1 0 0 1 1 0 1 1 0   1 0 0 1 1 0 1 1 1 1   1 ? 1 2 0 0 0 1 ? ?   2 0 1 1 0 0 0 0 0 0
0 ? ? ? 0 0 0 0 0 1   0 0 0 0 0 0 0 0 0 0   0 1 1 ? ? ? ? 0 0 0   0 0 1 1 0 0 1 1 1
```

Diadectes absitus

```
0 ? ? 0 1 0 0 1 0 1   0 0 0 0 0 0 0 0 0 0   0 0 0 0 0 1 0 0 0   0 0 1 1 0 0 0 1 1 2   1 1 0 0 0 0 1 1 0 0   1 0 0 0 0 0 0 0 1 ?
? ? 0 0 0 0 0 0 0 1   ? 0 1 0 0 1 0 0 0 1   0 0 0 0 1 0 0 0 0 0   1 0 1 0 0 0 0 0 0 1   1 0 0 0 0 2 0 0 0 1   2 0 2 1 0 0 0 0 0 4
4 1 1 0 0 0 1 1 0 0   0 0 1 0 1 0 0 0 0 0   1 0 1 1 0 0 1 0 ? 1   0 0 0 0 0 0 0 0 0 1   ? ? ? 0 0 2 ? 0 0 0   0 1 1 0 1 0 0 1 2 1
0 2 0 0 0 0 1 1 ? ?   ? 1 1 0 0 0 0 1 ? ?   1 ? ? 0 1 0 1 0 1 0   0 1 ? ? ? 1 ? ? ? 0   1 ? 1 1 1 1 1 0 0 1   0 0 0 0 2 0 1 1 1 2
1 0 0 1 1 0 1 1 0 1   1 1 0 1 0 1 2 1 1 0   1 1 0 0 1 0 0 1 2 0   1 1 1 1 1 0 1 1 1 1   0 1 0 2 0 0 0 1 0 0   c 1 1 ? 0 0 1 0 0 0
0 0 1 0 0 0 0 0 0 1   1 1 1 1 0 0 0 0 0 0   0 1 1 1 1 1 1 0 0 0   0 0 1 0 1 0 1 1 1
```

Diceratosaurus brevirostris

```
0 ? ? 0 0 0 ? 1 ? 1   0 0 1 0 1 0 0 0 1 0   0 0 0 0 0 1 1 1 0 0   0 ? 1 2 0 0 0 1 1 2   1 1 1 1 0 0 0 0 0 ?   0 0 0 1 1 0 0 ? 1 ?
? ? 1 ? ? ? 0 0 ? 0   0 1 0 0 0 0 0 0 0 0   0 1 1 0 1 0 0 0 1 0   1 ? 1 0 0 0 0 0 0 ?   1 0 0 0 0 2 0 0 0 0   2 0 ? 0 0 0 0 0 0 4
4 ? ? ? ? ? ? ? ? ?   ? ? ? ? ? 0 ? ? 0 ?   ? ? ? ? ? ? 0 0 0 ?   0 ? 0 0 0 0 0 0 0 0   1 1 1 ? ? ? ? ? ? ?   ? ? ? ? ? 0 ? ? ? ?
? ? ? ? ? ? ? ? ? ?   ? ? 1 0 0 0 0 ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? 0 0 ?   ? 0 0 0 ? 1 1 1 0 0
0 1 0 ? ? ? ? 1 ? 0   ? ? 1 1 ? ? ? ? ? 0   1 1 0 0 1 0 0 0 1 0   1 0 0 ? 0 0 1 1 ? ?   ? ? ? 2 ? 0 0 1 ? ?   ? ? ? ? 0 ? 1 0 0 0
0 ? 1 0 1 1 1 1 0 ?   ? ? 0 1 0 ? ? 0 1 1   0 1 1 1 1 1 1 0 0 1   0 0 1 1 0 0 1 1 1
```

Diplocaulus magnicornis

```
0 ? ? 0 1 0 0 1 ? 0   ? ? ? 0 0 0 0 0 0 1   0 0 1 0 0 1 1 0 0 0   0 1 0 1 1 0 ? 1 1 2   1 1 1 0 0 0 0 0 0 1   0 0 0 1 ? 0 0 1 1 ?
? ? 1 ? ? ? 0 0 0 0   0 1 1 0 0 0 0 0 1 0   0 1 1 0 1 0 0 0 1 0   1 0 0 0 0 1 0 0 0 0   1 0 0 ? 0 1 2 0 0 0   1 0 ? 1 0 0 0 0 0 4
4 0 1 0 1 0 1 1 1 0   0 0 1 0 0 0 0 0 0 ?   ? ? ? ? ? 0 0 0 1   0 0 0 0 0 0 0 0 0 0   1 1 1 0 0 2 ? 1 0 0   0 1 0 0 ? 0 0 0 0 0
0 2 0 0 0 0 2 ? ? ?   ? ? 1 0 0 0 0 ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? 0 0 0   0 0 0 0 2 1 1 1 0 0
0 1 0 ? ? ? ? 1 ? 0   ? ? 1 1 0 1 ? 0 ? 0   1 1 0 0 1 0 0 1 1 0   0 ? ? ? ? ? ? 1 ? ?   ? ? ? 2 ? 0 0 1 ? ?   ? ? ? ? 0 0 0 0 0 0
0 ? 1 0 1 1 1 1 0 ?   ? ? 0 1 1 ? ? 0 1 1   0 1 1 1 1 1 1 0 0 1   0 0 1 1 0 0 1 1 1
```

Diploceraspis burkei

```
0 ? ? 0 1 0 0 1 ? 0   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? 1 0 0 0   0 1 0 1 1 0 ? 1 1 2   1 1 1 0 0 0 0 0 0 1   0 0 0 1 ? 0 0 0 1 ?
? ? 1 ? ? ? 0 0 0 0   0 1 1 0 0 0 0 0 1 0   0 0 0 1 0 0 0 0 1 0   1 0 1 0 0 1 0 0 0 0   1 0 0 ? 0 1 2 0 0 0   1 0 1 1 0 0 0 0 0 4
4 0 1 0 1 0 1 1 1 0   0 0 1 0 0 0 0 0 0 ?   ? ? 1 ? ? ? 0 0 0 1   0 1 0 0 0 0 0 0 0 0   1 1 1 0 0 2 0 1 0 0   0 1 0 0 0 0 0 0 0 0
0 2 0 0 0 0 2 1 ? ?   ? 1 1 0 0 0 0 1 ? ?   1 ? ? 0 1 0 1 0 1 0   0 1 ? ? ? 1 ? ? ? 0   1 1 0 1 0 0 1 0 0 0   0 0 0 0 2 ? ? ? 0 0
0 1 0 ? ? ? ? 1 ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?
? 1 1 1 1 1 1 1 0 ?   ? ? 0 1 1 ? ? 0 1 1   0 1 1 1 1 1 1 0 0 1   0 0 1 1 0 0 1 1 ?
```

Discosauriscus austriacus

```
0 ? ? 0 1 0 0 1 0 1   0 0 0 0 0 0 0 0 0 0   0 0 0 0 0 0 1 0 0 0   0 0 1 2 0 0 0 1 0 2   1 1 0 0 0 0 0 1 0 ?   0 0 0 0 0 0 0 0 0 0
1 0 0 0 0 0 0 0 0 1   ? 0 1 0 1 0 0 0 0 1   0 0 0 0 1 0 1 0 0 0   1 0 1 0 0 0 0 0 0 1   1 0 0 0 0 1 1 0 0 2   2 0 1 1 0 0 0 0 0 3
3 1 0 1 0 0 1 1 0 0   0 0 0 1 1 0 0 0 0 0   1 1 0 1 0 0 1 0 1 1   0 0 0 0 0 0 0 0 0 1   ? ? ? 0 0 2 ? 0 0 0   0 ? 0 0 ? 0 1 1 2 0
0 2 0 0 0 0 1 1 ? ?   ? 1 1 0 0 0 0 1 1 1   0 1 1 0 1 0 1 0 1 0   0 0 1 0 1 0 1 0 1 0   1 0 1 1 1 1 1 0 0 0   0 0 0 0 2 0 1 1 0 2
1 0 0 1 0 0 1 0 0 0   1 1 0 1 0 1 2 1 0 0   1 1 0 0 1 1 0 1 1 0   0 1 1 ? 1 0 1 1 1 1   0 0 0 2 0 0 0 1 0 0   ? ? ? ? 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 1   1 1 1 0 0 0 0 0 0 0   0 1 1 1 1 1 1 0 0 0   0 0 1 0 1 0 1 ? 1
```

Doleserpeton annectens

```
1 1 0 0 0 0 0 1 ? 1   0 1 0 0 0 1 0 0 0 0   1 0 0 0 0 0 0 0 0 0   1 0 1 1 1 0 0 0 0 2   1 1 0 0 0 0 0 1 0 ?   0 0 0 0 0 0 0 0 1 ?
? ? 0 0 0 0 0 0 0 0   ? 0 1 0 0 0 0 0 0 1   0 0 0 0 1 0 1 0 0 0   0 0 1 0 0 0 0 0 0 1   1 0 0 1 1 1 1 0 0 1   2 0 ? 1 0 0 0 0 0 4
4 0 f 1 1 0 1 1 1 1   1 1 1 0 0 1 0 1 0 1   ? ? ? ? ? 0 0 1 0   1 1 1 0 1 0 0 0 0 0   1 1 1 0 1 2 ? 0 1 0   1 1 0 0 ? 1 0 0 0 0
0 2 1 1 1 1 0 1 ? ?   ? 1 1 0 0 0 0 ? ? ?   0 ? ? 0 ? ? 1 0 1 0   ? 0 ? ? ? 0 ? ? ? 0   ? ? ? ? ? ? ? 1 1 0   0 0 0 0 0 ? ? 1 ? ?
? ? ? 0 ? ? ? 1 ? ?   ? ? 1 1 1 ? ? 1 ? 1   1 1 1 1 1 ? 0 ? ? 0   0 0 0 ? 0 0 1 ? ? 1   1 ? 1 ? 0 ? ? ? ? ?   ? ? ? ? 0 ? 0 0 0 0
1 0 ? 0 0 0 0 0 0 1   1 f 0 1 0 0 0 0 0 0   1 1 1 1 1 1 1 0 0 0   0 0 1 1 0 0 ? ? 1
```

Dolichopareias disjectus

```
0 ? ? 0 0 0 ? 1 ? 1   1 0 1 0 1 0 0 0 1 1   0 0 0 0 0 1 0 ? 0 0   0 ? 1 0 0 0 1 ? 1 2   1 0 ? 1 1 0 0 0 0 ?   0 ? 0 0 1 0 0 0 1 ?
? ? 1 ? ? ? 1 ? ? ?   ? ? 0 ? ? ? 0 0 1 0   ? 1 1 0 ? 0 ? 1 ? 0   ? ? 1 0 0 0 ? ? ? ?   1 0 0 0 0 ? ? 0 0 0   0 0 ? 0 0 0 0 0 0 1
? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? 0 ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? 0 0 0   ? 1 1 0 0 ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ?
```

Ecolsonia cutlerensis

```
1 1 0 0 0 0 ? 1 1 1   0 0 0 0 0 0 0 0 1 0   1 0 0 0 0 0 0 0 0 0   0 0 1 2 1 0 0 0 0 2   1 1 0 1 0 0 0 1 0 1   0 0 0 0 0 0 0 0 1 ?
? ? 0 0 0 1 0 0 0 0   1 0 0 0 0 0 0 0 0 1   0 0 0 0 1 0 1 0 0 0   0 0 1 0 0 0 0 0 0 0   1 0 1 0 0 1 2 0 0 1   1 0 1 1 0 0 0 0 0 4
? 0 0 1 1 ? 1 1 0 0   0 0 0 1 ? 1 0 0 0 0   0 1 1 ? 0 0 0 0 1 0   0 0 1 0 0 0 0 0 0 0   1 1 1 0 0 ? 0 0 1 0   1 1 0 0 0 1 0 0 0 0
0 2 0 ? 1 1 0 1 ? ?   ? 1 ? 0 0 0 0 0 1 0   0 1 ? 0 1 0 1 0 1 0   1 0 1 0 1 0 1 0 1 0   1 0 1 ? ? ? 1 0 0 0   0 0 0 0 2 0 1 1 1 0
1 0 0 0 1 0 1 1 1 1   1 1 1 1 0 1 2 1 1 0   1 1 ? ? 1 ? 0 ? ? 0   1 0 0 1 0 0 1 1 1 1   0 ? 1 ? 0 ? ? 1 0 0   c 0 ? ? 0 ? 0 0 0 0
0 ? ? ? 0 0 0 0 0 1   0 0 0 0 0 0 0 0 0 0   0 1 1 1 1 1 1 0 0 0   0 0 ? ? ? ? ? ? 1
```

Edops craigi

```
0 ? ? 1 0 0 0 1 0 1    0 0 0 0 0 0 0 0 0 0    0 0 1 0 0 0 0 0 0 0    0 0 1 1 0 0 0 0 0 2    1 1 0 0 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 1
0 0 0 0 0 1 0 0 1 1    ? 0 0 0 0 0 0 0 0 1    0 1 0 0 1 0 1 0 0 0    0 0 0 0 0 1 0 0 0 0    1 0 0 0 0 1 0 0 0 0    0 0 1 0 0 0 0 0 0 4
4 0 0 1 0 0 1 1 0 0    0 0 0 1 1 0 0 0 0 0    0 1 0 1 0 0 0 0 1 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 2 0 0 0 0    0 1 0 0 0 1 0 0 0 0
0 2 0 0 0 0 0 1 ? ?    ? 1 0 0 0 0 0 0 1 ?    0 1 1 0 1 0 0 0 1 0    ? 0 1 0 1 0 1 0 1 0    1 0 1 1 ? 0 1 0 0 0    0 0 0 0 2 ? ? ? ? ?
? ? ? ? ? ? ? ? ? 1    1 ? 1 1 0 1 2 1 1 0    1 1 0 0 1 ? 0 ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?
? ? ? ? 0 0 ? ? ? 1    0 0 0 0 0 0 0 ? ?    ? 1 1 ? ? ? ? ? 0 ?    0 0 ? ? ? ? ? ? ?
```

Eocaecilia micropoda

```
0 ? ? 0 1 0 0 1 ? 1    0 0 0 0 0 0 0 0 ? 0    1 0 0 0 0 0 ? 1 0 0    1 0 1 0 0 0 0 ? ? 2    0 1 1 0 0 0 0 0 0 ?    0 0 0 0 0 0 0 1 ?
? ? 1 ? ? ? 0 0 0 0    0 0 0 0 0 1 ? ? ?    ? ? ? ? 1 0 0 0 0 0    1 ? 1 0 0 0 0 0 0 ?    1 0 0 0 0 0 0 0 0    3 0 ? 1 0 0 0 0 0 4
4 0 1 0 1 1 1 1 1 0    0 1 1 0 0 0 0 0 0 1    ? ? ? ? ? ? 0 0 1 0    0 1 0 1 1 0 0 0 0 0    1 1 0 0 0 2 ? 0 1 0    1 1 0 0 ? 0 0 0 0 0
0 2 0 0 1 1 2 1 ? ?    ? 1 1 0 0 0 0 0 ? ?    1 ? ? 1 ? ? ? 1 ? ?    ? 1 ? ? ? 1 ? ? ? 1    ? ? ? ? ? ? ? 1 1 0    0 0 0 0 0 ? ? ? ? ?
? ? ? 0 ? ? ? 1 ? ?    ? ? 1 1 ? ? ? 1 ? 1    1 1 1 1 1 1 0 1 C 0    ? ? ? ? ? ? ? ? ? 1    0 0 1 1 1 0 0 1 ? ?    ? ? ? ? 0 1 0 0 0 0
1 1 ? 1 0 0 0 0 0 1    1 1 0 ? 0 0 0 0 0 0    0 1 1 1 1 1 1 ? 0 0    1 0 1 ? ? ? 1 1 1
```

Eoherpeton watsoni

```
0 ? ? 0 1 0 0 1 ? 1    0 0 0 0 0 0 0 0 0 0    0 0 1 0 0 0 1 0 0 0    0 0 1 1 0 0 0 1 0 2    1 1 0 0 0 0 0 0 0 ?    0 0 0 0 0 0 0 0 0 0
? 0 0 0 0 0 0 1 0 1    ? 0 0 0 0 0 0 0 0 ?    0 0 0 0 ? 0 0 0 0 0    0 0 1 0 0 1 0 0 0 ?    1 0 0 0 0 2 0 ? 0 0    2 0 3 0 0 0 0 0 0 4
4 1 ? ? ? ? ? ? 0 ?    ? ? 0 0 ? 0 0 0 0 0    0 ? 0 0 0 0 0 0 0 ?    ? 0 0 0 0 0 0 0 0 ?    0 0 0 ? ? ? ? ? ? ?    ? ? ? ? 1 ? 0 1 0 1
0 2 0 0 ? ? ? ? ? ?    ? 1 ? 0 0 0 0 1 1 1    0 1 1 0 1 0 0 0 1 0    0 0 1 0 1 0 1 0 1 0    1 0 1 ? 0 ? 1 0 0 0    0 0 0 0 2 ? ? 1 ? ?
? ? ? 0 1 0 1 ? 1 0    0 1 0 1 0 1 1 0 0 0    1 1 0 1 1 ? 1 ? ? ?    ? 1 0 1 1 0 1 1 1 ?    ? ? 1 ? ? 0 0 1 1 0    ? ? ? ? 0 ? 1 0 0 0
0 0 ? 0 0 0 0 0 0 1    1 0 0 0 0 0 0 0 0 0    0 1 1 1 1 ? ? 0 0 0    0 0 ? ? ? ? ? ? 1
```

Eoscopus lockardi

```
1 1 1 0 0 0 0 1 ? 1    0 0 0 0 0 1 0 0 0 0    1 0 0 0 0 0 0 1 0 0    0 0 1 2 1 0 0 0 0 2    1 1 0 0 1 0 0 1 0 ?    0 0 0 0 0 0 0 0 1 ?
? ? 0 0 0 1 0 0 0 ?    ? 0 1 0 0 0 0 0 0 1    0 0 0 0 1 0 1 0 0 0    0 0 1 0 0 0 0 0 0 1    1 0 0 0 1 1 1 0 0 1    2 0 ? 1 0 0 0 0 0 4
? ? 0 1 1 1 0 0 1 0    1 1 0 ? 1 0 0 0 0 0    0 ? 1 1 0 0 0 0 1 0    0 0 1 0 1 0 0 0 0 0    1 1 1 0 1 2 0 ? ? ?    1 ? ? ? ? 1 0 ? ? ?
? ? 0 1 ? ? ? 1 ? ?    ? ? ? 0 0 0 0 ? ? ?    0 1 1 0 1 0 ? ? ? ?    ? 0 ? 0 ? 0 ? 0 ? 0    ? 0 ? ? ? ? 1 0 0 0    0 0 0 0 0 ? ? 1 1 0
0 0 0 0 ? 1 ? ? ? 0    ? ? 1 1 1 ? ? 1 ? 1    ? ? 1 ? 1 1 0 1 2 0    1 0 0 1 0 0 1 1 ? 1    1 0 1 ? 0 0 0 1 0 0    2 0 1 1 0 0 0 0 0 0
1 0 0 0 0 0 0 0 0 1    0 f 0 0 0 0 0 0 0 0    0 1 1 1 1 1 1 0 0 0    0 0 1 1 0 0 1 1 1
```

Eryops megacephalus

```
1 1 0 0 0 0 0 1 1 1    0 0 0 0 0 0 0 0 0 0    0 0 1 0 0 0 1 0 0 0    0 0 1 1 0 0 0 0 0 2    1 1 0 0 0 0 0 1 0 1    0 0 0 0 0 0 0 0 1 ?
? ? 0 0 0 1 0 0 0 1    ? 0 0 0 0 0 0 0 0 1    0 0 0 0 1 0 1 0 0 0    0 0 0 0 0 1 0 0 0 0    1 0 0 0 0 1 0 0 0 0    0 0 1 1 0 0 0 1 0 4
4 0 0 1 1 0 1 1 0 0    0 0 0 1 1 0 0 0 0 0    0 1 0 1 0 0 0 0 1 0    0 0 1 0 0 0 0 0 0 0    1 1 0 0 0 2 0 0 1 0    0 1 0 0 0 1 0 0 0 0
0 2 0 0 0 0 0 1 ? ?    ? 1 0 0 0 0 0 0 1 0    0 1 1 0 1 0 0 0 1 0    1 0 1 0 1 0 1 0 1 0    1 0 1 1 1 1 1 0 0 1    0 0 0 0 0 0 1 1 1 0
0 0 0 0 0 1 1 1 1    1 1 1 1 0 1 2 1 1 0    0 1 0 0 1 1 0 1 2 0    1 0 0 1 1 0 1 ? ? 1    0 1 1 2 0 0 0 1 1 0    2 0 1 1 0 0 0 1 0 0
0 f 0 0 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 1 1 1 1 1 1 0 0 0    0 0 1 1 0 0 1 1 1
```

Eucritta melanolimnetes

```
0 ? ? 0 0 0 ? 1 ? 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 1 0 0 0 0 0    0 0 1 2 0 0 0 0 0 2    1 1 0 0 0 0 0 ? 0 ?    0 0 0 0 0 0 0 0 0 1
0 1 0 1 0 1 0 0 ? 1    ? 0 0 0 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    ? ? 1 0 0 0 0 0 0 ?    1 0 0 0 0 1 1 1 0 1    0 0 ? 0 0 0 0 0 0 ?
? ? 0 1 0 0 1 1 0 ?    ? ? 0 1 1 0 0 0 0 0    0 ? ? 0 0 0 0 0 ? 1    ? 0 0 0 0 0 0 0 1    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? 0 0 1 0 1
0 2 0 0 0 0 0 ? ? ?    ? ? ? 0 0 0 0 ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 ?    0 0 0 0 2 0 ? 1 1 f
0 0 0 0 ? ? ? 1 ? 0    ? ? 0 1 0 1 ? 0 0 0    1 1 0 0 1 ? 0 1 1 0    1 1 0 ? ? 0 1 1 ? ?    ? ? ? 2 ? 0 0 1 ? ?    ? ? ? ? 0 0 0 0 0 0
0 ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? 1 ? ? ? ? ? 1
```

Euryodus primus

```
0 ? ? 0 1 1 0 1 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 1 0 0 0 0 0 0    0 0 1 0 0 0 0 1 0 2    1 1 0 0 0 0 0 0 0 1    0 1 0 0 0 0 1 1 1 ?
? ? 1 ? ? ? 0 0 0 0    0 0 0 1 0 0 0 0 0 0    1 0 0 1 ? 0 0 0 0 0    1 0 1 0 0 0 0 1 1 0    1 0 0 0 0 0 0 0 0 0    2 0 ? 1 0 0 0 0 0 4
a 1 0 1 ? 0 1 1 0 0    0 ? 1 1 0 0 0 0 0 0    1 1 1 0 0 0 0 0 1 ?    0 0 0 0 0 1 1 0 0 0    0 0 0 ? ? 2 ? 0 0 1    0 1 0 0 0 0 0 0 1 0
0 2 0 0 0 0 2 ? ? ?    ? 1 1 0 0 0 0 1 ? ?    1 ? ? 0 1 0 1 0 1 1    0 ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? 1 0 0 1    0 0 0 1 2 ? ? 1 ? 2
1 0 0 0 1 ? 1 ? 1 0    1 1 1 1 0 1 2 1 1 0    1 1 1 1 1 1 0 1 2 0    1 ? 0 1 ? 0 1 1 1 1    1 0 1 2 0 0 0 1 0 0    c ? ? ? ? ? ? ? ? ?
? 0 1 1 0 0 ? ? ? 1    1 1 0 1 0 0 0 0 ? ?    1 1 1 ? ? ? ? 0 1 ?    0 0 1 ? ? ? ? ? 1
```

Eusthenopteron foordi

```
0 ? ? 0 0 0 0 0 0 0    ? ? ? 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 ? 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 ? 0 0 1 0 0
0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 1 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 ? 0 0 0 0 0 0    2 0 0 0 0 0 0 ? 0 0
0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 1 0 0 0    0 ? 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 1 0 0 0 1 0 0    0 ? 0 ? ? ? 0 0 0 0    0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 ? 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 ? 0    ? 0 0 0 0 0 0 0 0 0    0 0 0 0 0 ? 0 0 0 0
0 ? 0 0 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 ? ? ? 0 0 0
```

Gephyrostegus bohemicus

```
0 ? ? 0 1 0 0 1 ? 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 1 0 0 0 0    0 0 1 1 1 0 1 1 0 2    1 1 0 0 0 0 0 1 0 ?    0 0 0 0 0 0 0 0 0 0
? 0 0 0 0 0 1 ? 1    ? 0 0 0 0 0 0 0 0 1    0 0 0 0 1 0 0 0 0 0    0 0 1 0 0 0 0 0 0 0    1 0 0 0 0 1 1 0 0 C    2 0 ? 1 0 0 0 0 0 4
4 1 0 1 0 0 ? ? ? ?    0 0 0 1 1 0 0 0 0 0    0 1 1 1 0 0 1 0 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 2 ? 0 0 0    0 ? 0 0 ? 0 0 ? ? ?
? 2 0 ? ? ? ? 1 ? ?    ? 1 1 0 0 0 0 1 1 1    0 0 1 0 0 0 0 0 1 0    0 0 0 0 1 0 0 0 1 0    1 0 1 1 1 0 1 0 0 0    0 0 0 0 0 0 1 1 1 2
0 0 0 0 1 0 1 1 1 0    1 1 0 1 0 1 2 0 1 0    1 1 0 1 1 1 0 1 2 0    1 1 0 1 1 0 1 1 1 ?    ? 0 1 2 ? 0 0 1 1 0    2 1 1 1 0 0 1 0 0 0
0 0 0 0 0 0 0 0 0 1    1 0 0 0 0 0 0 0 0 0    0 1 1 ? ? ? ? ? 0 0    0 0 1 0 1 0 1 1 1
```

Greererpeton burkemorani

```
0 ? ? 0 0 0 1 1 ? 1    1 0 1 0 1 0 1 0 1 1    0 0 0 0 0 0 0 0 0 0    0 0 1 1 0 0 1 0 1 2    1 0 0 1 1 0 0 0 0 0    0 0 0 0 1 0 0 0 f ?
? ? 0 0 0 1 0 0 1 0    1 0 0 0 0 0 0 0 0 0    0 1 1 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    1 0 0 0 1 1 0 0 0 0    0 0 1 0 0 0 0 0 0 2
2 0 0 0 0 0 1 1 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 1    0 0 0 0 0 1 0 0 0 0    0 0 0 0 0 1 0 0 0 0    0 1 0 0 1 1 0 0 0 0
1 2 0 0 0 0 0 0 1 0    1 1 0 0 1 0 0 1 1 0    0 0 1 0 1 0 0 0 1 0    0 0 0 1 0 0 1 0 1 0    1 0 1 1 1 ? 0 0 0 0    1 0 0 0 0 0 0 1 0 0
0 1 0 0 0 0 1 1 1 0    0 1 0 1 0 1 1 0 0 0    1 1 0 0 1 0 0 1 2 0    1 0 0 1 0 0 1 1 1 1    1 1 1 2 0 0 0 1 0 0    2 0 ? 1 0 1 0 0 1 1
0 0 0 0 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 1 1 1 1 ? ? 0 0 0    0 1 1 0 1 0 1 ? 1
```

Hapsidopareion lepton

```
0 ? ? 0 1 0 0 1 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 1 0 0 0    0 0 1 1 0 0 0 1 0 2    1 1 0 0 0 0 0 0 0 1    0 1 0 0 0 1 0 1 ?
? ? 1 ? ? ? 0 0 0 0    0 0 1 0 0 0 0 0 0 0    0 0 1 0 0 0 0 0 0    1 0 1 0 0 0 0 1 1 0    1 0 0 0 0 0 0 0 0 b    2 0 ? 1 0 0 1 0 1 4
a 1 1 0 0 ? 1 1 0 0    0 ? 1 0 0 0 0 0 0 0    1 0 1 1 0 0 0 0 1 ?    0 0 0 0 0 0 1 0 0 0    0 0 0 ? ? ? 1 0 0 1    0 1 0 0 0 0 0 0 2 0
0 2 0 0 0 0 2 ? ? ?    ? 1 1 0 0 0 0 1 ? ?    1 ? ? 0 1 0 1 0 1 1    0 ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 0    0 0 0 0 2 ? ? ? ? ?
? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?    ? ? ? ? ? 0 ? ? ? ?
? 0 0 1 ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?
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Hyloplesion longicostatum

```
0 ? ? 0 1 0 0 1 ? 1    1 0 1 0 0 0 0 0 0 0    0 0 0 0 0 0 1 ? 0 0    0 0 1 0 0 0 0 1 1 2    1 1 1 1 1 0 0 1 0 ?    0 0 0 0 0 0 0 0 1 ?
? ? 1 ? ? ? 0 0 0 0    0 0 1 0 0 0 0 0 0 ?    0 0 0 1 1 0 0 0 0 0    1 0 1 0 0 0 0 0 0 0    1 0 0 0 0 2 0 0 0 0    2 0 ? 1 0 0 0 0 0 4
a 1 ? 1 1 0 ? ? 0 ?    0 0 1 1 1 0 0 0 0 0    1 1 1 1 1 1 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 2 ? ? ? 1    ? ? ? ? ? 0 0 0 1 0
0 2 0 0 0 0 1 ? ? ?    ? ? 1 0 0 0 0 ? ? ?    0 ? 1 0 ? ? 1 ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 1    0 0 0 0 2 0 1 1 ? ?
? ? ? 0 1 ? ? ? ? 0    1 ? ? 1 1 ? ? 1 ? 0    1 1 1 1 1 0 0 1 2 0    1 0 0 1 0 0 1 1 ? 1    0 0 1 2 0 0 0 1 0 0    2 0 1 1 0 0 1 0 0 0
0 ? ? 1 0 0 ? ? ? ?    ? ? 0 ? 0 ? ? 0 ? ?    1 1 1 1 1 ? ? ? 1 ?    0 0 1 0 0 1 1 ? 1
```

Ichthyostega stensioei

```
0 ? ? 0 0 0 1 0 0 1    0 0 0 0 0 0 0 0 0 0    0 0 1 0 0 0 0 0 0 0    0 0 1 2 0 0 0 0 1 1    1 1 0 0 0 0 1 ? 0 ?    0 0 0 0 0 0 0 0 1 ?
? ? 0 0 0 1 0 0 0 0    1 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 1 1 0 0 0 0    0 0 3 0 0 0 0 0 0 0
0 0 1 0 0 1 0 1 0 0    0 0 1 0 0 0 0 0 0 0    1 0 0 0 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 ? 0 0 0    0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 1 0    1 1 0 0 0 0 0 0 1 0    0 0 0 0 0 0 0 0 1 0    0 0 1 1 0 0 1 1 0 0    1 1 0 0 0 ? 0 0 0 1    0 0 0 0 2 0 0 0 1 2
1 0 0 0 1 0 1 ? 1 0    0 0 0 0 0 1 0 0 1 0    1 1 0 0 0 1 0 1 2 0    1 1 0 1 0 0 1 1 0 1    0 1 0 ? 0 0 0 0 0 0    1 0 0 0 0 1 1 1 0 0
0 ? ? ? 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 1 1 1 1 0 0 0 0 0    0 0 1 ? ? ? 1 0 1
```

Isodectes obtusus

```
1 0 0 0 0 0 0 1 0 1    0 0 1 0 0 0 0 0 1 0    0 0 0 0 0 0 0 0 0 0    0 0 1 0 0 0 0 0 0 2    1 0 0 0 1 0 0 f 0 1    0 0 0 0 0 0 0 0 0 1
0 1 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 1    0 0 0 0 1 0 0 0 0 0    1 1 1 0 0 0 0 0 0 0    1 0 0 0 0 1 0 0 0 0    1 0 ? 0 0 0 0 0 0 1
1 0 0 0 1 0 1 1 1 0    0 0 0 ? ? 1 0 0 0 0    ? ? ? ? 0 ? 0 0 0 0    0 ? 0 0 0 0 0 0 0 0    1 1 0 0 0 1 0 0 0 0    0 1 0 0 0 1 0 0 0 0
0 2 0 0 0 0 2 ? ? ?    ? ? 0 0 0 0 0 ? ? ?    0 ? 1 0 ? ? 1 0 1 0    ? ? ? ? ? ? ? ? ? 0    1 0 1 1 1 ? 1 0 0 0    1 0 0 0 a ? ? ? ? 1
0 0 0 ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?
```

Karaurus sharovi

```
1 1 1 0 0 0 0 1 ? 1    0 1 0 0 0 1 0 0 1 1    1 0 ? 0 0 0 ? 1 1 0    1 0 1 2 1 0 0 ? ? c    1 1 1 0 ? 1 ? ? ? ?    ? ? ? ? ? 1 ? ? 1 ?
? ? 1 ? ? ? 1 ? ? ?    ? ? 1 ? ? ? 1 ? ? ?    ? ? ? ? 0 0 0 0 0 1    ? ? ? ? ? ? 0 1 1 ?    1 0 0 1 1 1 1 0 0 1    3 0 ? 1 0 0 0 0 0 4
? 0 1 0 1 ? 1 1 1 1    1 1 ? ? ? ? ? ? 1 1    ? ? ? ? ? ? 0 1 0 0    0 ? 1 1 0 0 0 1 1 0    1 1 1 0 1 2 ? 0 1 0    1 1 0 0 ? 0 0 0 0 0
0 2 1 0 1 1 2 ? ? ?    ? ? 1 ? ? 0 0 0 ? ?    1 ? ? 0 1 ? ? 1 ? ?    ? 1 ? ? ? 1 ? ? ? 1    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 1 ? ?
? ? ? 0 ? ? ? 1 ? 0    1 ? 1 1 1 ? ? 1 ? 1    ? ? ? ? 1 1 0 1 1 0    1 0 0 ? ? 0 1 ? ? ?    ? ? ? 2 ? ? ? 1 ? ?    ? ? ? ? 0 0 0 0 0 0
1 1 ? ? 0 0 0 0 0 ?    ? ? 0 1 1 ? ? 0 0 0    0 1 1 1 1 1 1 0 0 0    ? 0 1 1 0 0 1 ? 1
```

Keraterpeton galvani

```
0 ? ? 0 0 0 ? 1 ? 1    0 0 1 0 0 0 0 0 1 0    0 0 0 0 0 1 1 0 0 0    0 ? 1 0 0 0 0 1 1 2    1 1 1 1 1 0 0 0 0 ?    0 0 0 0 1 0 0 0 1 ?
? ? 1 ? ? ? 0 0 ? 0    0 1 0 0 0 0 0 0 0 0    0 0 1 0 1 0 0 0 1 0    1 ? 1 0 0 0 0 0 0 ?    1 0 0 0 0 2 0 0 0 0    2 0 ? 0 0 0 0 0 0 4
4 ? ? ? ? ? ? ? ? ?    ? ? ? ? ? 0 ? ? 0 ?    ? ? ? ? ? ? 0 0 0 ?    0 ? 0 0 0 0 0 0 0 ?    0 0 0 ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?    ? ? 1 0 0 0 0 ? ? ?    ? ? ? 0 ? ? 1 0 1 0    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 0    ? 0 0 0 2 1 1 1 0 0
0 1 0 ? ? ? ? 1 ? 0    ? ? 1 1 ? ? 0 ? 0    1 1 0 0 1 0 0 0 1 0    1 0 0 ? 0 0 1 ? ? ?    ? ? ? 2 ? 0 0 1 ? ?    ? ? ? ? 0 ? 1 0 0 0
0 ? 1 0 1 1 1 0 ?    ? ? 0 1 0 ? ? 0 1 0    0 1 1 1 1 1 1 0 0 1    0 0 1 ? ? ? 1 1 1
```

Kotlassia prima

```
0 ? ? 0 1 0 0 1 ? 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 1 0 0 0    0 0 1 0 0 0 0 1 0 1    1 1 0 1 1 0 0 0 0 1    0 0 0 0 0 0 0 0 0 1
1 0 0 0 0 1 0 0 0 1    ? 0 1 0 0 0 0 0 0 1    0 0 0 0 1 0 1 0 0 0    ? 0 1 0 0 0 0 0 0 0    1 0 0 0 0 2 0 0 0 0    1 0 1 1 0 0 0 0 0 4
4 1 1 0 0 0 1 1 0 0    0 0 1 0 0 0 0 0 0 0    1 0 0 0 0 0 1 0 1 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 2 0 0 0 0    0 1 0 0 0 0 ? 1 2 1
0 2 0 0 0 0 1 1 ? ?    ? 1 1 0 0 0 0 1 1 0    0 1 1 0 1 0 0 0 1 0    0 0 1 0 1 0 1 0 1 0    1 0 1 1 1 1 1 0 0 0    0 0 0 0 ? 0 1 1 0 2
1 0 0 0 0 0 1 1 ? 1    1 ? 1 1 0 1 2 1 ? 0    1 1 0 0 1 1 0 ? ? 0    1 1 1 1 ? 0 1 ? 1 1    1 1 1 2 0 0 0 1 0 0    ? 0 ? 1 0 0 1 1 0 0
0 0 ? 0 0 0 0 0 0 1    1 1 1 1 0 0 0 0 0 0    1 1 1 1 1 1 1 0 1 0    0 0 1 ? ? ? 1 1 1
```

Leptoropha talonophora

```
? ? ? ? ? ? ? ? ? 1    0 ? 0 0 0 0 ? 0 ? ?    0 ? ? ? ? ? ? 0 0 0    0 ? 1 2 0 0 0 1 0 2    1 1 0 0 0 0 0 1 0 ?    0 0 0 0 0 0 0 1 0 0
0 0 0 0 0 0 0 ? ? 0    ? 0 1 0 ? 0 0 0 0 1    0 0 1 0 1 0 0 0 0 0    ? ? 1 0 0 ? 0 0 0 ?    1 ? ? ? ? 2 0 ? 0 2    2 0 1 1 0 0 ? 0 0 d
? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? c 0 ? ?    ? ? 0 0 ? ? 0 0 0 ?    0 0 0 ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? 2 ? ? ?    ? 1 1 0 0 0 0 ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 0    0 0 0 0 ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?
```

Leptorophus tener

```
1 ? 1 0 0 0 0 1 ? 1     0 1 1 0 0 1 0 0 0 0     1 0 0 0 0 0 0 1 0 0     1 0 1 1 1 0 0 0 0 2     1 1 0 1 ? 0 0 ? ? ?     0 0 0 0 0 0 0 1 1 ?
? ? 0 0 0 1 0 ? ? 1     ? 0 0 0 ? 0 0 0 0 1     0 0 0 0 1 0 1 0 0 0     0 0 1 0 0 0 0 0 ?     1 1 0 1 1 1 1 0 0 1     2 0 ? 1 0 0 0 0 0 4
4 0 1 0 1 0 1 1 1 0     0 0 1 0 0 ? 1 1 0 0     1 0 1 0 1 0 0 0 0 0     0 0 1 1 1 0 0 0 0 0     1 1 1 0 0 2 ? ? ? ?     ? ? ? ? ? 1 0 0 0 0
0 2 0 0 1 1 0 1 ? ?     ? 1 ? ? ? 0 0 0 1 0     0 1 1 0 1 0 1 0 1 0     1 0 1 0 1 0 1 0 1 0     1 0 1 1 1 1 1 0 0 0     0 0 0 0 0 ? ? ? ? 0
0 0 0 ? ? ? ? ? ? 0     ? ? 1 1 1 ? ? 1 ? 1     ? ? ? ? 1 ? 0 1 1 0     0 ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?
? ? ? ? 0 0 0 0 0 ?     ? ? 0 0 0 ? ? 0 0 0     ? 1 1 ? ? ? ? ? 0 0     0 0 1 ? ? ? ? ? ? 1
```

Lethiscus stocki

```
0 ? ? 0 0 ? ? 1 ? 1     1 0 1 0 0 0 0 0 0 0     0 0 0 0 0 0 0 1 0 0     0 ? 1 ? ? 0 ? ? 1 2     1 0 0 1 1 0 ? 0 0 ?     0 0 0 0 1 0 0 0 ? ?
? ? 0 0 1 0 0 0 ? ?     ? 0 0 ? 0 0 0 0 0 0     0 1 1 0 0 0 0 0 ? ?     ? ? ? ? 0 0 0 ? ? ?     1 0 0 0 0 1 1 0 0 0     2 ? ? 0 0 1 0 0 1 4
? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?     ? ? 1 ? ? 0 0 ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? 0 2 ? ? ? ? ?
? ? ? ? ? ? ? 1 ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? 1 ? 0 ? ? ?
? ? 1 ? 0 ? ? ? ? ?     ? ? 0 1 0 1 ? 0 ? ?     0 1 1 1 1 1 1 0 0 ?     ? 0 0 ? ? ? 1 1 ?
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Limnoscelis paludis

```
0 ? ? 0 1 1 0 1 1 1     0 0 0 0 0 0 0 0 0 0     0 0 0 0 0 1 0 0 0     0 0 1 1 0 0 1 1 1 2     1 1 0 1 0 0 1 ? 0 0     1 0 0 0 0 0 0 0 1 ?
? ? 0 0 0 0 0 0 0 1     ? 0 1 0 0 1 0 0 0 1     0 0 0 0 1 0 0 0 0 0     1 ? 1 0 0 0 0 0 0 1     1 0 0 0 0 0 0 0 0 0     2 0 2 1 0 0 0 0 0 4
4 1 1 ? ? 0 1 1 ? 0     0 0 1 ? ? 0 0 0 0 0     1 0 ? ? 0 0 2 0 1 ?     0 0 0 0 0 0 0 0 0 0     0 0 0 0 0 2 1 0 0 0     0 1 1 0 1 0 0 1 0 0
0 2 0 0 0 0 1 ? ? ?     ? 1 0 0 0 0 0 ? ? ?     1 ? ? 0 1 0 1 0 1 0     0 ? ? ? ? 0 1 0 1 0     1 0 ? ? ? ? 1 0 0 1     0 0 0 0 2 0 1 1 ? ?
? ? ? 0 1 0 1 ? 0 1     1 1 0 1 0 1 2 1 1 0     1 1 0 0 1 1 0 1 2 0     1 1 1 1 1 0 1 1 1 0     ? 1 0 1 0 0 0 1 1 0     ? ? ? ? 0 0 1 0 0 0
0 0 1 0 0 0 0 0 0 1     1 1 1 1 0 0 0 0 0 0     1 1 1 1 1 1 1 0 0 0     0 0 1 0 1 0 1 1 1
```

Megalocephalus pachycephalus

```
0 ? ? 0 0 0 0 1 0 1     0 0 0 0 1 0 0 1 0 0     0 0 0 0 1 0 0 0 0 0     0 0 1 1 0 0 0 0 0 2     1 1 0 0 0 0 0 0 0 0     0 0 0 0 0 0 0 0 1 ?
? ? 0 1 0 1 0 0 1 ?     ? 0 0 0 0 0 0 0 0 0     0 0 0 0 1 0 0 0 0 0     0 1 0 0 1 0 0 0 0 0     1 0 0 0 1 1 2 0 0 c     0 0 1 0 0 0 0 0 0 3
3 0 0 1 0 0 1 1 0 0     0 0 0 1 1 0 0 0 0 0     0 1 0 1 0 0 0 0 0 1     0 0 0 0 0 0 0 0 0 1     ? ? ? 0 0 0 0 0 0 0     0 1 0 0 1 0 0 0 0 0
1 2 0 0 0 0 0 0 1 0     1 1 0 0 0 0 0 1 1 1     0 1 1 0 1 0 0 0 1 0     0 0 1 1 1 0 1 1 1 0     1 1 1 0 0 ? 1 0 0 0     0 0 0 0 1 ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ?
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Micraroter erythrogeios

```
0 ? ? 0 1 1 0 1 0 1     0 0 0 0 0 0 0 0 ? 0     0 0 0 f 0 0 1 ? 0 0     0 0 1 2 0 0 0 1 0 2     1 1 0 0 0 0 0 0 0 1     0 1 1 0 0 0 1 1 1 ?
? ? 1 ? ? ? 0 0 0 0     1 0 1 1 0 0 0 0 0 0     1 0 0 0 ? 0 0 0 0 0     ? ? 1 0 0 0 0 1 1 0     1 0 0 0 0 0 0 0 0 0     3 0 1 1 0 0 1 0 0 4
? 1 f 1 0 0 1 1 0 0     0 0 1 1 0 0 0 0 0 0     1 1 1 0 0 0 0 0 0 1     ? 0 0 0 0 0 1 0 0 0     0 0 0 0 0 2 1 0 0 1     0 1 0 0 0 0 0 0 1 0
1 2 0 0 0 0 2 ? ? ?     ? 1 1 0 0 0 0 1 ? ?     0 1 1 0 1 0 1 0 1 0     0 ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? 1 0 0 0     0 0 0 0 2 0 1 1 0 2
1 0 0 1 ? ? 1 1 ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? 0 0 1 0 0 1 1 1 1     0 0 1 ? 0 ? ? ? ? ?     ? ? ? ? 0 0 1 0 0 0
0 0 1 1 0 0 0 0 0 1     1 1 0 1 0 0 0 0 0 0     1 1 1 1 1 1 1 0 1 0     0 0 1 ? ? ? 1 1 1
```

Microbrachis pelikani

```
0 ? ? 0 1 0 0 1 ? 1     1 0 1 0 0 0 0 0 0 0     0 0 0 0 0 1 1 0 0 0     0 0 1 0 0 0 0 1 1 2     1 1 ? 1 0 0 0 1 0 1     0 0 0 0 0 0 0 0 1 ?
? ? 1 ? ? ? 0 0 0 0     0 0 1 0 0 0 0 0 0 0     ? 0 0 1 1 0 0 0 0 0     1 0 1 0 0 0 0 0 0 0     1 0 0 0 0 2 0 0 0 0     2 0 ? 1 0 0 0 0 0 d
3 1 1 1 0 0 1 1 0 0     0 0 1 1 0 0 0 0 0 0     1 1 1 1 0 0 0 0 1 ?     0 0 0 0 0 1 0 0 0 0     0 0 0 0 0 2 ? 0 0 1     0 1 0 0 0 1 0 0 1 0
0 2 0 0 0 0 1 1 ? ?     ? 1 0 0 0 0 0 1 1 0     0 1 1 0 1 0 1 0 1 0     0 0 1 0 1 0 1 0 1 0     1 0 1 1 0 1 1 0 0 0     0 0 0 0 2 0 1 1 1 2
1 0 0 1 ? ? ? ? ? 0     1 ? 0 1 ? ? ? 0 1 0     1 1 1 1 1 0 0 1 1 0     0 1 0 1 0 0 1 1 1 1     0 0 1 2 0 0 0 1 0 0     ? ? ? ? 0 0 1 0 0 0
0 0 1 1 0 0 0 0 0 1     1 1 0 0 0 1 ? 0 0 0     1 1 1 1 1 1 1 1 1 0     0 0 1 0 0 1 1 1 1
```

Micromelerpeton credneri

```
1 1 1 0 0 0 0 1 1 1     0 0 0 0 0 1 0 0 0 0     1 0 0 0 0 0 0 0 0 0     0 0 1 0 1 0 0 f 0 2     1 1 0 0 0 0 0 1 0 ?     0 0 0 0 0 0 0 0 1 ?
? ? 0 0 0 1 0 0 ? 1     ? 0 0 0 0 0 0 0 0 1     0 0 0 0 1 0 1 0 0 0     0 0 1 0 0 0 0 0 0 ?     1 0 0 0 1 1 1 0 0 1     2 0 ? 1 0 0 0 0 0 1
d 0 0 0 1 0 1 1 1 0     0 0 0 0 0 1 0 1 0 0     1 0 1 0 0 0 0 0 1 0     0 0 1 1 1 0 0 0 0 0     1 1 1 0 0 0 ? ? ? ?     ? ? ? ? ? 1 0 0 0 0
0 2 0 0 1 1 1 1 ? ?     ? 1 0 0 0 0 0 0 1 0     0 1 1 0 1 0 1 0 1 0     1 0 ? ? ? 0 1 0 1 0     1 0 1 1 1 1 1 0 0 ?     0 0 0 0 ? ? ? 1 0
0 0 0 ? ? ? ? ? ? 0     ? ? 1 1 1 ? ? 1 ? 0     ? ? ? ? 1 1 0 1 1 0     0 0 0 ? ? 0 1 ? ? ?     ? ? ? 2 ? ? ? 1 ? ?     ? ? ? ? 0 0 0 0 0 0
1 ? ? ? 0 0 ? ? ? 1     0 0 0 0 0 0 0 0 ? ?     0 1 1 1 1 1 1 0 0 ?     0 0 1 1 0 0 1 1 1
```

Microphon exiguus

```
0 ? ? 0 1 0 0 1 0 1     0 0 0 0 0 0 0 0 0 0     0 0 0 0 0 0 1 0 0 0     0 0 1 0 0 0 0 1 0 2     1 1 0 0 0 0 0 1 0 ?     0 0 0 0 0 0 0 0 0 0
1 0 0 0 0 0 0 0 0 0     ? 0 1 0 1 0 0 0 0 1     0 0 1 0 1 0 0 0 0 0     1 0 1 0 0 f 0 0 0 ?     1 0 0 1 0 0 0 0 0 2     2 0 1 1 0 0 0 0 0 3
d 1 1 1 0 0 0 0 0 0     0 0 1 1 1 0 0 0 0 0     1 1 0 0 0 0 1 0 1 ?     0 0 0 0 0 0 0 0 0 ?     0 0 0 0 0 2 ? ? ? ?     ? ? ? ? ? 0 ? ? ? 0
0 2 0 0 0 0 2 ? ? ?     ? 1 1 0 0 0 0 ? ? ?     0 ? 1 0 ? ? 1 0 1 0     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? 0 0 0     0 0 0 0 2 ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? ? ?
```

Neldasaurus wrightae

```
? ? ? 0 0 0 0 1 ? 1     0 0 0 0 1 0 0 0 0 0     0 0 0 0 0 0 0 0 0 0     0 0 1 2 0 0 0 0 0 2     1 0 0 0 0 0 0 0 0 1     0 0 0 0 0 0 0 0 0 1
0 0 0 0 0 1 0 0 0 0     1 0 0 0 0 0 0 0 0 1     0 0 0 0 1 0 1 0 0 0     1 0 1 0 0 ? 0 0 0 ?     1 0 0 0 0 1 0 0 0 0     2 0 1 0 0 0 0 0 0 d
? 0 0 ? 1 1 1 1 0 0     0 0 0 ? 0 0 0 0 0 0     0 ? ? 0 0 0 0 0 1 0     0 0 0 0 0 0 0 0 0 0     1 1 0 0 0 1 0 0 0 0     0 1 0 0 0 1 0 0 0 0
0 2 0 0 0 0 0 ? ? ?     ? ? 0 0 0 0 0 ? ? ?     0 1 1 0 1 0 0 0 1 0     ? ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? 1 0 0 0     0 0 0 0 0 ? ? 0 0
0 1 0 0 ? 0 ? 1 1 0     ? 1 1 1 0 1 2 1 0 0     1 1 0 1 1 1 0 1 2 0     1 0 0 ? 0 0 1 ? ? 1     0 ? 1 ? 0 ? ? ? ? ?     ? ? ? ? 0 ? 0 0 0 0
0 ? ? ? 0 0 0 0 0 1     0 0 0 0 0 0 0 0 0 0     0 1 1 ? ? ? ? 0 0 0     0 0 1 1 0 0 1 ? 1
```

Notobatrachus degiustoi

```
1 0 1 0 0 0 0 1 ? 1    ? 1 ? 1 ? ? ? ? ? ?    ? 1 ? ? ? ? 0 1 1 0    1 0 ? ? 1 1 ? ? ? ?    0 ? 0 ? ? 1 ? ? ? ?    ? ? ? ? ? 1 ? ? 1 ?
? ? 1 ? ? ? 1 ? ? ?    ? ? 1 ? ? ? 1 ? ? ?    ? ? ? ? ? 0 1 0 0 1    ? ? ? ? ? ? 1 ? ? ?    1 0 0 0 0 0 1 0 0 1    3 0 ? 1 1 0 0 0 0 ?
? 0 1 0 1 0 1 1 1 1    0 1 ? ? ? ? ? ? 1 1    ? ? ? ? ? ? 0 0 1 0    1 ? 1 1 0 0 0 0 0 0    1 1 1 0 1 ? ? 0 1 0    0 ? ? ? ? 0 0 0 0 0
0 2 1 0 1 1 2 ? ? ?    ? 1 1 0 0 1 0 ? ? ?    1 ? ? 1 ? ? ? 1 ? ?    ? 1 ? ? ? 1 ? ? ? 1    ? ? ? ? ? ? ? ? 1 0    ? 0 0 0 0 0 1 1 ? ?
? ? ? 1 0 1 1 1 ? 0    1 ? 1 1 1 0 ? 1 ? 1    1 1 1 1 1 0 0 ? ? 1    ? 0 0 ? 0 1 1 ? ? 0    ? 0 ? 2 ? ? ? ? ? ?    ? ? ? ? 0 0 0 0 1 0
1 1 1 0 0 0 ? ? ? ?    ? ? 0 1 0 1 ? 0 ? 0    1 1 1 ? ? ? ? 0 1 0    0 0 1 1 0 0 1 1 1
```

Odonterpeton triangulare

```
0 ? ? 0 1 0 0 1 ? 1    1 0 1 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 1 2 1 0 0 ? 1 2    1 1 1 0 0 0 1 0 0 ?    0 0 0 0 0 0 ? 0 1 ?
? ? 1 ? ? ? 1 ? ? ?    ? ? 0 ? ? ? 0 0 0 0    ? 0 0 ? 1 1 0 0 0 0    1 0 1 0 0 0 0 1 1 0    1 0 0 0 0 0 0 0 0 0    2 0 ? 1 0 0 0 0 0 4
? 1 1 1 0 0 1 1 0 0    0 0 1 1 0 0 0 0 0 0    1 0 1 1 1 1 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 2 ? ? ? ?    ? ? ? ? ? 0 0 0 ? 0
0 2 0 0 0 0 2 ? ? ?    ? 1 1 0 0 0 ? ? ? ?    0 ? ? 0 ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 0    0 0 0 0 2 0 1 1 ? ?
? ? ? ? ? ? ? 1 ? 0    ? ? ? ? ? ? ? 1 ? 0    1 1 1 1 1 0 0 1 1 0    0 ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? 0 0 1 0 0 0
0 ? ? ? 0 0 ? ? ? ?    ? ? 0 0 0 ? ? 0 ? ?    ? 1 1 ? ? ? ? 1 1 ?    0 0 1 0 0 1 1 ? 1
```

Oestocephalus amphiuminum

```
0 ? ? 0 1 0 0 1 ? 1    1 0 1 0 1 0 0 0 1 0    0 0 0 0 0 1 0 1 0 0    0 0 1 0 0 0 0 0 ? 2    1 0 0 1 1 0 0 0 0 1    0 0 0 0 1 0 0 0 1 ?
? ? 0 0 1 0 0 0 0 0    0 0 0 0 0 0 1 ? ? ?    ? ? ? ? 0 0 0 0 0 0    0 0 1 0 0 0 0 0 0 0    1 0 0 0 ? 2 1 0 0 0    0 0 1 0 0 1 0 0 1 4
4 ? ? ? ? ? ? ? 0 ?    ? ? 1 0 0 0 0 0 0 ?    ? ? ? ? ? ? 0 0 0 ?    0 0 0 0 0 0 0 0 0 0    0 ? 0 ? ? 0 0 0 0 0    0 1 0 1 0 0 0 0 0 0
0 2 0 0 0 0 1 ? ? ?    ? 1 ? 0 0 0 0 ? ? ?    1 ? ? 0 1 0 1 0 1 0    0 ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 0    0 f 0 0 2 0 1 1 ? ?
? ? ? ? ? ? ? 1 ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? 1 0 0 0 0 0
0 ? 1 0 1 ? ? ? ? ?    ? ? 0 1 0 1 ? 0 ? 0    0 1 1 1 1 1 1 0 0 1    1 0 0 ? ? 1 1 ?
```

Orobates pabsti

```
0 ? ? 0 1 0 ? 1 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 1 0 0 0    0 0 1 1 0 0 0 1 1 2    1 1 0 1 0 0 1 1 0 0    1 0 0 0 0 0 0 0 1 ?
? ? 0 0 1 0 0 0 ? 1    ? 0 1 0 0 1 0 0 0 1    0 0 0 0 1 0 0 0 0 0    1 ? 1 0 0 0 0 0 0 ?    1 0 0 0 0 0 0 0 0 1    0 0 ? 1 0 0 0 0 0 4
4 ? ? ? 1 ? ? ? 0 ?    ? ? 1 0 1 0 0 0 0 0    1 0 1 1 ? 0 1 0 0 ?    ? 0 0 0 0 ? 0 0 0 0    0 0 0 ? ? ? 1 0 0 0    ? ? ? ? ? 0 0 1 c 1
0 2 0 0 0 0 2 ? ? ?    ? ? 1 0 0 0 0 1 ? ?    1 ? ? 0 1 0 1 0 1 1    0 1 ? ? ? 1 ? ? ? 0    1 1 1 1 ? 1 1 0 0 1    f 0 0 0 2 0 1 1 ? ?
? ? ? ? ? ? ? 1 1 1    ? 1 0 1 0 1 2 1 ? 0    1 1 0 0 1 0 0 1 2 0    1 1 1 1 1 0 1 1 1 0    0 0 ? 2 0 0 ? 1 ? ?    2 1 1 1 0 0 1 0 0 0
0 0 ? ? 0 0 0 ? ? 1    ? ? 1 ? 0 ? ? ? ? 0    1 1 1 1 1 1 1 ? 0 0    0 0 1 0 1 0 ? 1 1
```

Ossinodus pueri

```
? ? ? ? 0 0 ? ? ? ?    ? ? ? 0 0 0 ? 0 ? ?    ? ? ? ? ? ? ? ? ? 0    0 ? 1 a ? 0 ? 0 0 ?    1 0 0 0 0 0 0 0 ? ?    0 0 0 0 ? 0 0 ? 0 ?
? ? 0 0 0 0 0 0 ? 1    ? 0 ? 0 0 0 ? ? ? ?    ? ? ? ? ? ? ? 0 ? ?    ? ? ? ? ? ? 0 ? ? 0    ? ? ? ? ? 2 ? ? ? ?    0 0 ? 0 0 0 ? ? ? ?
e ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? 0    0 0 ? 0 0 ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 1    ? 0 0 0 1 0 1 1 0 2
1 1 1 ? 0 0 1 ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? 0    ? 1 0 ? 1 0 1 ? ? 0    1 0 0 ? 0 0 1 0 1 0    ? ? ? ? 0 0 0 0 0 0
0 ? ? ? 0 ? ? ? ? ?    ? ? 0 0 0 ? ? ? ? ?    ? 1 1 ? ? ? ? ? ? ?    ? 0 1 ? ? ? ? ? ?
```

Paleothyris acadiana / Protorothyris archeri

```
0 ? ? 0 1 0 0 1 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 1 0 0 0    0 0 1 1 1 0 0 1 1 2    1 1 1 1 0 0 0 1 0 0    1 0 0 0 0 0 1 1 ?
? ? 0 0 0 0 0 0 0 1    ? 0 1 0 0 1 0 0 0 1    0 0 0 0 1 0 0 0 0 0    1 0 1 0 0 0 0 1 1 0    1 0 0 0 0 1 1 0 0 1    0 0 2 1 0 0 0 0 0 4
4 1 1 0 0 0 1 1 0 0    0 0 1 1 1 0 0 0 0 ?    ? ? ? ? ? ? 2 0 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 2 1 0 0 0    0 1 1 0 1 0 0 1 1 1
0 2 0 0 0 0 1 ? ? ?    ? 1 1 0 0 0 0 1 ? ?    1 ? ? 0 1 0 1 0 1 0    0 ? ? ? ? ? ? ? ? 0    1 1 1 1 1 1 1 0 0 1    0 0 0 0 1 0 1 1 1 2
1 0 0 0 1 0 1 ? 1 1    1 1 0 1 0 1 2 1 1 1    1 1 ? ? ? 1 0 1 2 0    1 0 0 1 0 0 1 1 1 1    0 0 1 2 0 0 0 1 0 0    2 1 1 1 0 1 1 0 0 0
0 0 1 0 0 0 0 0 0 1    1 1 0 1 0 0 0 0 0 0    1 1 1 1 1 ? ? 0 0 0    0 0 1 0 1 0 1 1 1
```

Panderichthys rhombolepis

```
0 ? ? 0 0 0 0 0 ? 0    ? ? ? 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 1 0 0 0 ? 0 0 0    0 0 0 0 1 0 0 0 0 ?    0 0 0 0 ? 0 0 0 f ?
? ? 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 1 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 ? 0 1 0 0 0 0    0 0 ? 0 0 0 0 ? 0 0
0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 ? 0 0 0 ? 0 ? 0    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 ? 0 0 0    0 0 0 0 ? 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0    0 f 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 0 0 0    0 0 0 1 0 0 0 1 0 0    0 1 0 0 0 ? 0 0 0 0    0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 ? 0    0 0 0 0 0 1 0 0 0 0    0 ? ? ? 0 0 0 0 0 0    0 ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? 0 ? 0 0 0 0
0 0 ? ? 0 0 0 0 0 0    ? ? 0 ? 0 0 0 0 0 0    ? 0 0 0 0 0 0 0 0 0    0 0 0 ? ? ? 1 0 1
```

Pantylus cordatus

```
0 ? ? 0 1 1 0 1 0 1    1 0 1 0 0 0 0 0 0 0    0 0 0 0 0 0 1 0 0 1    0 0 1 1 0 0 0 1 0 2    1 1 0 1 1 0 0 0 0 1    0 0 0 0 0 0 1 0 1 ?
? ? 1 ? ? ? 0 0 0 0    1 0 0 0 0 0 0 0 0 0    1 1 0 1 1 0 0 0 0 0    1 0 1 1 0 1 0 0 0 0    1 0 0 0 0 0 0 0 0 0    3 0 1 1 0 0 0 0 0 4
? 1 1 0 0 0 1 1 0 0    0 0 0 0 1 0 0 0 0 1    ? ? ? ? ? ? 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 2 1 0 0 1    0 1 0 0 0 0 0 0 2 0
0 2 0 0 0 0 1 1 ? ?    ? 0 0 0 0 0 0 1 ? ?    0 1 1 0 1 0 1 0 1 0    0 1 ? ? ? 1 ? ? ? 0    1 1 1 1 ? 1 1 0 0 1    0 0 0 1 2 0 1 1 0 2
1 0 0 0 0 1 1 0 0    1 1 0 1 0 1 2 1 1 0    1 1 0 1 1 1 0 1 2 0    1 0 0 1 0 0 1 1 ? 1    0 0 1 ? 0 0 0 ? ? ?    c 0 1 1 0 0 1 0 0 0
0 1 1 1 0 0 0 0 0 1    1 1 0 0 0 1 ? 0 0 0    1 1 1 1 1 1 1 1 1 0    0 0 1 1 0 0 1 ? 1
```

Pederpes finneyae

```
0 ? ? 0 ? 0 ? 1 ? 1    ? 0 ? 0 0 0 0 0 0 0    1 0 0 0 0 0 0 0 0 0    0 0 1 ? 0 ? 0 0 0 ?    ? ? ? ? 1 0 0 0 0 0    0 0 0 0 0 0 0 0 0 1
1 0 0 1 0 1 0 0 1 1    ? 0 1 0 0 0 0 0 0 0    0 0 0 0 ? 0 0 0 ? 0    ? 0 1 0 0 0 0 ? 0 ?    0 0 0 0 ? 2 1 0 1 1    ? ? ? 0 ? 0 0 ? 0 1
? 0 0 1 0 ? ? 0 0    ? ? 0 1 0 0 0 0 0 0    0 1 0 0 0 0 0 ? ? 1    0 0 0 ? ? 0 ? 0 0 0    0 0 0 ? ? 0 ? ? ? ?    ? ? ? ? ? 0 0 1 0 0
0 1 0 0 0 0 0 ? ? ?    ? ? ? ? ? 0 0 ? ? ?    ? 0 ? ? 0 ? 0 ? ? ?    ? ? ? ? ? ? 0 ? ? ?    ? ? ? ? ? 0 0 0 1    0 0 0 0 2 0 1 1 1 c
1 0 1 1 ? 0 ? ? 1 0    1 1 0 1 0 1 1 0 0 0    1 1 0 0 1 0 0 1 1 0    0 1 0 ? 0 0 ? ? ? 0    0 0 0 2 0 1 0 1 1 0    ? ? ? ? 0 0 0 1 0 0
0 ? 0 ? 0 0 0 ? ? 1    0 ? 0 0 0 0 0 0 ? 0    0 1 1 1 ? ? ? 0 0 0    0 0 1 ? ? ? 1 ? 1
```

Pelodosotis elongatum
```
0 ? ? 0 1 1 0 1 ? 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 1 0 0 0    0 0 1 2 0 0 0 1 0 2    1 1 0 0 0 0 0 0 0 ?    0 1 1 0 0 0 1 1 1 ?
? ? 1 ? ? ? 0 0 0 0    1 0 1 1 0 0 0 0 0 0    1 0 0 0 0 0 0 0 0 0    1 ? 1 0 0 0 0 1 1 0    1 0 0 0 0 0 0 0 0 0    3 0 ? 1 0 0 1 0 0 4
? ? 1 ? 0 ? 1 1 0 0    0 ? 1 ? 0 0 0 0 0 ?    ? ? ? ? ? ? 0 0 0 0    ? 0 0 0 0 1 0 0 0    0 0 0 ? ? 2 1 0 0 1    0 1 0 0 ? 0 0 0 2 0
0 2 0 0 0 0 2 ? ? ?    ? ? ? 0 0 0 0 ? ? ?    ? ? ? 0 ? ? 1 0 1 0    ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 0    0 0 0 0 2 0 1 1 1 2
1 0 0 0 ? 1 ? 1 ? 0    1 ? 0 1 0 1 2 1 1 0    1 1 0 1 1 1 0 1 2 0    1 0 0 ? ? 0 1 1 1 1    0 0 1 2 0 0 0 1 0 0    ? ? ? ? 0 0 1 0 0 0
0 0 ? ? 0 0 ? ? ? 1    1 1 0 0 0 0 0 0 ? ?    1 1 1 ? ? ? ? ? 1 ?    0 0 1 ? ? ? 1 ? 1
```

Petrolacosaurus kansensis
```
0 ? ? 0 1 0 0 1 ? 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 1 0 0 0    0 0 1 1 1 0 0 1 1 2    1 1 1 0 0 0 0 1 0 0    1 0 0 0 0 0 1 1 ?
? ? 0 0 0 0 0 0 0 1    ? 0 1 0 0 1 0 0 0 0    0 0 0 1 0 0 0 0 0    1 0 1 0 0 0 0 0 0    1 0 0 0 0 1 1 0 0 1    2 0 2 1 0 0 0 0 0 4
4 1 1 1 0 0 1 1 0 0    0 0 1 1 1 0 1 0 0 0    1 0 1 1 1 0 2 0 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 2 1 0 0 0    0 1 1 0 1 0 0 1 1 1
0 2 0 0 0 0 1 1 ? ?    ? 1 1 0 0 0 0 1 ? ?    0 1 1 0 1 0 1 0 1 0    0 1 ? ? ? 1 ? ? ? 0    1 1 1 1 1 0 1 0 0 1    0 0 0 0 1 0 1 1 1 2
1 0 0 0 1 0 1 1 1 1    1 1 0 1 0 1 2 1 1 1    1 1 1 1 1 1 0 1 2 0    1 0 0 1 0 0 1 1 1 1    0 0 1 2 0 0 0 1 0 0    2 1 1 1 0 0 1 0 0 0
0 0 1 0 0 0 0 0 0 1    1 1 f 1 0 0 0 0 0 0    1 1 1 1 1 1 0 0 0    0 0 1 0 1 0 1 ? 1
```

Phlegethontia linearis
```
0 ? ? 0 0 0 0 1 ? 1    1 0 0 0 0 0 0 0 0 ?    0 1 ? ? ? ? 1 1 0 0    0 ? 0 ? ? 0 ? ? ? 2    1 ? ? 1 ? 1 ? ? ? ?    ? ? ? ? ? 0 0 1 1 ?
? ? 1 ? ? ? 1 ? ? ?    ? ? 0 ? ? ? 1 ? ? ?    ? ? ? ? ? 0 0 0 0 0    1 0 1 0 0 0 ? ? ? 0    1 0 0 0 0 1 1 0 0 0    2 0 ? 0 0 1 0 0 1 4
4 ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? 1 ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? 0    0 ? 0 ? ? ? 0 0 0 0    0 1 0 1 ? ? ? ? ? ?
? ? ? ? ? ? 2 1 ? ?    ? 1 1 0 0 0 0 0 ? ?    1 ? ? 1 ? ? ? 1 ? ?    ? 1 ? ? ? 1 ? ? ? 1    ? ? ? ? ? ? ? 0 0 0    0 0 0 0 2 0 1 1 ? ?
? ? ? ? ? ? ? 1 ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?    ? ? ? ? 1 0 0 0 0 0
0 0 1 ? ? ? ? ? ? ?    ? ? 0 1 0 1 ? 0 ? 0    0 1 1 1 1 1 1 0 0 1    1 0 0 ? ? ? 1 1 ?
```

Pholiderpeton attheyi
```
0 ? ? 0 1 0 0 1 ? 1    0 0 0 0 0 0 0 0 0 0    0 0 1 0 0 0 0 0 0 0    0 0 1 1 0 0 0 1 0 2    1 1 0 0 0 0 0 0 1 ?    0 0 0 0 0 0 0 0 0 1
0 0 0 0 0 0 0 1 0 1    ? 0 0 0 0 0 0 0 0 1    0 0 0 0 1 0 0 0 0 0    1 0 1 0 1 1 0 0 0 0    1 0 0 0 0 1 1 0 0 0    2 0 ? 0 0 0 0 0 0 2
3 ? 1 0 0 0 1 1 0 0    0 0 0 0 1 0 0 0 0 0    0 0 0 0 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 2 ? ? ? ?    ? ? ? ? ? 0 0 1 0 1
0 2 0 0 0 0 0 ? ? ?    ? 1 1 0 0 0 0 0 1 1    0 1 1 0 1 0 0 0 1 0    1 0 1 0 1 0 1 0 1 0    1 0 1 0 0 ? 1 0 0 1    0 1 0 0 0 ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? 0    ? 1 1 ? 0 ? ? ? ? ?    ? ? ? ? 0 ? 1 0 0 0
0 ? ? ? 0 0 0 0 0 1    1 1 0 0 0 0 1 0 0 0    0 1 1 1 1 ? ? 0 0    0 0 ? ? ? ? ? ? ?
```

Pholiderpeton scutigerum
```
0 ? ? 0 1 0 0 1 ? 1    0 0 0 0 0 0 ? 0 0 ?    0 0 1 0 0 0 1 0 ? 0    0 0 1 1 0 0 ? 1 ? ?    1 1 0 ? ? 0 0 0 1 0    0 0 0 0 0 0 0 0 0 0
? 0 0 0 0 0 0 1 0 1    ? 0 ? 0 0 0 0 0 0 ?    0 0 0 0 ? 0 0 0 0 0    0 1 0 0 0 0 0 0 0 0    1 0 0 0 0 1 1 0 0 0    0 ? 3 0 0 0 0 0 0 3
3 1 1 0 0 0 1 1 0 0    0 0 0 0 ? ? 0 0 0 0    0 0 0 0 0 0 0 0 0 1    ? 0 0 0 0 0 0 0 0 0    0 0 0 0 0 2 0 0 0 0    0 1 0 0 1 0 0 1 0 1
0 2 0 0 0 0 0 0 0 0    1 1 0 0 0 0 0 1 1 1    0 1 1 0 1 0 0 0 1 0    0 0 1 0 1 0 1 0 1 0    1 0 1 1 1 0 1 0 0 0    0 1 0 0 0 0 1 1 ? c
? ? ? 0 0 0 1 0 ? ?    0 ? 0 ? 0 1 c ? ? 0    1 1 1 1 1 ? ? 1 2 0    1 ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?    ? ? ? ? 0 0 1 0 0 0
0 0 ? ? 0 0 0 0 0 1    1 1 0 0 0 0 1 0 0 0    0 1 1 ? ? ? ? ? 0 0    0 0 1 ? ? ? ? ? 1
```

Phonerpeton pricei
```
1 1 0 0 0 0 0 ? ? 1    0 0 0 0 0 0 0 0 1 0    1 0 0 0 0 1 0 0 0 0    0 0 1 1 1 0 0 0 0 2    1 1 0 0 0 0 0 1 0 1    0 0 0 0 0 0 0 1 ?
? ? 0 0 0 1 0 0 0 ?    ? 0 0 0 0 0 0 0 0 0    0 0 0 0 1 0 1 0 0 0    0 0 1 0 0 0 0 0 0 1    1 0 1 0 1 1 1 0 0 2    2 0 1 1 0 0 0 0 0 4
4 0 0 1 1 0 1 1 0 0    0 0 0 1 ? f 0 0 0 0    ? 1 0 ? 0 0 0 0 1 0    0 0 0 0 0 0 0 0 0 0    1 1 0 0 0 2 0 0 1 0    1 1 0 0 0 1 0 0 0 0
0 2 0 0 0 0 ? 1 ? ?    ? 1 0 0 0 0 0 1 1    0 1 1 0 1 0 1 0 1 0    1 0 1 0 1 0 1 0 1 0    1 0 1 1 ? 1 1 0 0 1    0 0 0 0 a 0 1 1 ? ?
? ? ? ? ? 0 1 ? 1 1    1 1 ? 1 0 1 2 1 1 0    ? ? ? ? ? ? ? ? 0    1 ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ?    ? ? ? ? 0 ? 0 0 0 0
0 ? ? ? 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 1 1 1 1 1 1 ? 0 0    0 0 ? ? ? ? ? ? 1
```

Platyrhinops lyelli
```
1 1 1 0 0 0 0 1 ? 1    0 1 0 0 0 1 0 0 0 0    1 0 0 0 0 0 0 1 0 0    0 0 1 2 0 0 0 0 0 2    0 1 0 0 0 0 0 1 0 ?    0 0 0 0 0 0 0 0 1 ?
? ? 0 0 0 1 0 0 ? 1    ? 0 1 0 0 0 0 0 0 1    0 0 0 0 1 0 1 0 0 0    0 0 1 0 0 0 0 0 0 1    1 0 0 ? 0 1 0 0 0 1    2 0 ? 1 0 0 0 0 0 4
4 0 0 ? 1 0 1 1 1 0    1 1 0 ? 1 ? 0 0 0 0    0 ? 1 1 0 0 0 0 1 0    0 0 1 0 0 0 0 0 0 0    1 1 1 0 1 2 0 ? ? ?    ? ? ? ? ? 1 0 0 0 0
0 2 0 0 1 1 0 1 ? ?    ? 1 ? 0 0 0 0 0 1 0    0 1 1 0 1 0 ? 0 1 0    1 0 ? ? 0 1 0 1 0    1 ? ? ? ? ? ? ? ? 1    0 0 0 0 0 0 1 1 ? 0
0 0 0 ? ? ? ? ? ? 0    ? ? 1 1 0 ? ? 1 ? 1    1 1 1 1 1 1 0 1 2 0    1 ? ? ? ? ? ? ? ? 1    0 0 1 2 0 ? ? ? ? ?    ? ? ? ? 0 0 0 0 0 0
1 ? ? ? 0 0 0 0 0 1    0 0 0 ? 0 0 0 0 0 0    0 1 1 1 1 1 1 0 0 0    0 0 ? ? ? ? 1 ? ?
```

Proterogyrinus scheelei
```
0 ? ? 0 1 0 0 1 ? 1    0 0 0 0 1 0 0 0 0 0    0 0 ? 0 0 0 0 0 0 0    0 0 1 1 0 0 0 1 0 2    1 1 0 0 0 0 0 0 1 0    0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 1 0 1    ? 0 0 0 0 0 0 0 0 1    0 0 0 0 1 0 0 0 0 0    1 1 1 0 0 ? 0 0 0 0    1 0 0 0 0 1 1 0 0 2    2 0 3 0 0 0 0 0 0 c
4 1 ? ? 0 ? ? ? 0 ?    ? ? 0 0 1 0 0 0 0 0    0 1 ? 0 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    0 0 0 ? ? ? 0 0 0 0    0 1 0 0 1 0 0 1 0 1
0 2 0 0 0 0 0 ? ? ?    ? 1 0 0 0 0 0 1 1 ?    0 ? 1 0 1 0 0 0 1 0    ? 0 ? 0 ? 0 1 0 1 0    1 0 1 0 ? ? 1 0 0 1    0 1 0 0 0 0 1 1 1 1
0 0 0 0 0 0 1 1 1 0    0 1 0 1 0 1 2 0 1 0    1 1 0 0 1 1 1 1 1 0    1 1 0 1 1 0 1 1 0 1    0 1 1 2 0 0 0 1 1 0    2 1 1 1 0 0 1 0 0 0
0 0 0 0 0 0 0 0 0 1    1 0 0 0 0 0 0 0 0 0    0 1 1 1 1 1 1 0 0 0    0 0 1 0 1 0 1 1 1
```

Ptyonius marshii
```
0 ? ? 0 0 0 0 1 ? 1    0 0 0 0 0 0 0 0 1 0    0 0 0 1 0 1 0 0 0 0    0 0 1 1 0 0 1 1 1 2    1 0 0 1 1 0 0 0 1 0    0 0 0 0 0 0 0 1 ?
? ? 0 0 1 0 0 0 ? 1    ? 0 0 0 0 0 1 0 0    0 1 1 0 1 0 0 0 0 0    1 0 1 0 0 0 0 0 0 ?    1 0 0 0 0 1 1 0 0 0    2 0 ? 0 0 0 0 0 0 4
4 0 1 0 0 ? 1 1 0 0    0 0 1 0 0 0 0 0 0 0    1 0 0 0 0 0 0 0 0 1    0 0 0 0 0 0 0 0 0 0    1 0 0 0 0 2 ? 0 0 ?    0 1 0 0 ? 1 0 0 1 0
0 2 0 0 0 0 1 ? ? ?    ? ? 1 0 0 0 0 ? ? ?    ? ? ? 0 ? ? 1 0 1 0    ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 0    0 0 0 0 2 0 1 1 1 0
0 1 0 0 ? ? 1 1 ? 0    ? ? 1 1 ? ? ? 0 1 0    1 1 1 1 1 0 0 1 1 0    1 0 0 ? 0 0 1 1 2 ?    ? ? ? 2 ? 0 0 1 ? ?    ? ? ? ? 0 ? 1 0 0 0
0 ? 1 1 1 1 1 1 1 ?    ? ? 0 1 0 ? ? 0 0 0    0 1 1 1 1 1 1 0 0 1    0 0 1 1 0 0 1 1 1
```

Rhynchonkos stovalli

```
0??0110101   0000000000   0000001?00   0012000102   1100000001   010000111?
??1???0000   0001000000   1001100000   101000???0   1000000000   go?1000004
4?10001100   0010000000   1010000000   0000001000   0000021001   0100000010
02000021??   ?1100000?1   0110101010   01???01100   1?????1000   00002?????
???????0   1?111??110   1111110120   10010011?1   0012000100   2?11011000
011100???1   11010000??   11111??01?   001???111
```

Sauropleura pectinata / S. scalaris

```
0??00001?1   fof0100010   0001010100   0001001112   100110000?   000000001?
??001000?0   0000000100   0110100000   0010000000   1000011000   2010000004
4110?01100   001000000?   ??????000?   0000000000   000002?000   0100?00000
02000001??   ?11000001??   1??0?01010   0???????1   ??????1000   0000201110
0100??11?1   ??11???010   1111100110   100?00112?   ????2?001??   ?0?10?1000
0010111111?   ??010??000   0111111001   001100111
```

Saxonerpeton geinitzi

```
0??01001?1   0000000000   0000001?00   0012?00102   110000000?   000000101?
??1???0000   0010000000   100?000000   101000011?   1000000000   20?100000?
a111?01100   0011?0000?   ??????001?   0000000000   000002????   ?????00010
02000001???   ?1100000???   ???0??1???   ?????????   ???????001   0000201112
10001??1?0   1?011??110   1111110120   10010011?1   001g000100   2011001000
0??100????   ??0?0??0??   111????11?   0011001?1
```

Schoenfelderpeton prescheri

```
1?100001?1   0110010000   100000?110   1010100002   110110010?   000000001?
??000?0??1   ?000?00001   0000101000   101000000?   1101111001   20?1000004
4010101110   10100?1100   101?100000   0011100000   111002????   ?????10000
0200112???   ?1?00000??   0110101010   ???????0   ???1111?00   00000????0
100??????0   ??111??1?0   ????1?0110   0?0??01???   ?????????   ?????????
????00????   ??????0??   ?11?????0?   001100??1
```

Scincosaurus crassus

```
0??00001?1   0010000010   0000011000   0110000102   1101?1????   ?????0101?
??1???00?0   00?0000000   1100100010   1010010000   1000020000   20?1000004
401???1110   0011100001   ??????0000   0000000000   000002?100   0100?00000
02000001???   ?????????   ?????????   ?????????   ???????000   ?000201100
0000?111?1   1?0???110   1111100120   100?001121   0012000 1??   ????0?1000
0?10111101   110101?000   0111111001   001???111
```

Seymouria baylorensis / S. sanjuanensis

```
0??0100111   0000000000   0000001000   0011000102   1100000f01   0000000001
1000010001   ?010000001   0000100000   1010010001   1000020000   2011000004
4101001100   0001100000   1110?1011   0000000000   0000020000   010000?120
02000011??   ?110000111   0110101010   0010101010   1011111001   0000201102
?001101111   1101012110   1100110120   1111101110   ?102000110   2011000000
0000000001   1111000000   1111111000   001010111
```

Silvanerpeton miripedes

```
0??010?;??1   0000000000   0000000000   0011000102   110000000?   0000000000
0000000101   0000000001   0010100000   1?1000000?   1000?21001   10?0000004
?101??1100   0?01100 00?   ??????0001   0000000000   000??2????   ?100?00101
02000000???   ?110000 1??   0110??0010   ?????0???0   10100?1000   000010?111
0000?????0   ??0101?000   1111100120   010??011??   ???2???1??   2011001000
0???000001   1000000000   ?11??????0   001010111
```

Solenodonsaurus janenschi

```
????1??1?1   0000??0000   0000001000   0?11001112   1101100???   000000001?
??00010???   ?000?00001   0000100070   1?1000000?   10?0010000   20?1000004
?????????   ?????????   ?????0????   ?????????   ?????????   ?????????
??????0???   ??????0???   ???0???010   ?????????   ???????000   ?0001011?2
10?0??????   1?010121?0   110?110120   0????????   ?????????   ????001000
0???000001   110100?000   011????000   001???1?1
```

Stegotretus agyrus

```
0??0110101   0000000000   0000000001   0012000102   1100000001   010000101?
??1???0000   ?001000000   1001?00000   1011000000   1000000000   10?1000004
?110001100   0001100001   ??????0001   ?000000000   0000021001   0100000020
02000002???   ??00000???   ???0??1010   ?????????   ??????1001   00012????c
10000?11??   ??1????1?0   ?????10120   110??01111   1011000???   ?????????
???1000001   110001?000   111????110   001???1?1
```

Triadobatrachus massinoti

```
? ? ? ? ? ? ? ? 1     ? ? ? ? ? ? ? ? ?     ? ? ? ? ? ? ? 1 1 0   1 ? ? ? 1 1 ? ? ? ?   0 ? 1 ? ? 1 ? ? ? ?   ? ? ? ? ? 1 ? ? 1 ?
? ? 1 ? ? ? 1 ? ? ?   ? ? 1 ? ? ? 1 ? ? ?   ? ? ? ? ? 0 1 0 0 1   ? ? ? ? ? ? ? ? ? ?   1 ? ? ? ? 1 1 ? 0 1   ? 0 ? 1 0 0 0 0 0 ?
? ? ? ? ? ? ? 1 ?     ? ? 1 0 1 ? ? 1 0 1   ? ? ? ? ? ? 0 0 0 0   1 0 1 1 0 0 0 0 0 0   1 1 1 ? ? ? 0 1 0   1 1 0 0 ? 0 0 0 0 0
0 2 1 0 1 1 0 ? ? ?   ? ? ? ? ? 1 0 ? ? ?   1 ? ? 1 ? ? ? 1 ? ?   ? 1 ? ? ? 1 ? ? ? 1   ? ? ? ? ? ? ? ? ?   ? ? ? ? ? 0 1 1 ? ?
? ? ? 1 ? ? ? 1 ? 0   1 ? 1 1 1 ? ? 1 ? 1   1 1 1 1 1 0 0 1 1 0   1 0 0 ? 0 1 1 1 ? 0   ? 0 ? 2 0 0 0 1 0 0   c 0 ? ? 0 0 0 0 0 0
1 1 ? 0 0 0 0 0 0 ?   ? ? 0 1 0 1 ? 0 0 0   1 1 1 1 1 1 1 ? 1 0   0 0 1 ? ? ? 1 1 1
```

Trimerorhachis insignis

```
1 0 0 0 0 0 0 1 ? 1   0 0 0 0 0 0 0 0 0 0   0 0 0 0 0 0 0 0 0 0   0 0 1 0 0 0 0 0 0 2   1 0 0 0 0 0 0 0 0 1   0 0 0 0 0 0 0 0 0 0
0 1 0 0 0 1 0 0 0 f   0 0 0 0 0 0 0 0 0 0   0 1 0 0 0 1 0 0 0     0 0 1 0 0 0 0 0 0 0   1 0 0 0 0 1 1 0 0 0   0 0 1 0 0 0 0 0 0 d
? ? 0 0 1 1 1 1 0 0   0 0 0 0 0 0 0 0 0 0   1 0 0 0 0 0 1 0 0 0   0 0 0 0 0 0 0 0 0 0   1 1 0 0 0 1 0 0 0 0   0 1 0 0 0 1 0 0 0 0
0 2 0 0 0 0 1 1 ? ?   ? 1 0 0 0 0 0 0 1 1   0 1 1 0 1 0 0 0 1 0   1 0 1 ? ? 0 1 0 f 0   1 0 f 1 0 0 1 0 0 0   0 0 0 0 a ? ? ? 1 0
0 1 0 1 ? 0 ? 1 ? 0   1 1 1 1 0 1 2 1 0 0   1 1 0 1 1 1 0 1 1 0   1 0 0 1 0 0 1 1 ? 1   1 ? ? 1 ? 0 0 1 0 0   ? ? ? ? 0 0 1 0 0 0
0 ? ? ? 0 0 0 0 0 1   0 ? 0 0 0 0 0 0 0 0   0 1 0 ? ? ? ? 0 0 0   0 0 1 1 0 0 1 1 1
```

Tseajaia campi

```
0 ? ? 0 1 0 ? 1 ? 1   0 0 0 0 0 0 0 0 0 0   0 0 0 0 0 0 1 0 0 0   0 0 1 1 0 0 0 0 1 2   1 1 1 1 0 0 0 1 0 0   0 0 0 0 0 0 0 0 1 ?
? ? 0 0 0 0 0 0 0 1   ? 0 1 0 0 0 0 0 0 0   0 0 0 0 1 0 ? 0 0 0   1 ? 1 0 0 0 0 0 0 ?   1 0 0 0 0 0 0 0 0 1   0 0 ? 1 0 0 0 0 0 4
? 1 ? ? ? ? 1 ? 0 0   0 0 1 ? ? 0 0 0 0 ?   ? ? ? ? ? ? c 0 1 ?   0 0 0 0 0 ? 0 0 0 0   0 0 0 0 0 2 ? 0 0 0   0 1 0 0 ? 0 0 0 2 0
0 2 0 ? 0 0 0 ? ? ?   ? 1 1 0 0 0 0 1 ? ?   1 ? ? 0 1 0 1 0 1 0   0 ? ? ? ? 0 1 0 1 0   1 0 1 1 ? 1 1 0 0 1   0 0 0 0 2 0 1 1 0 1
1 ? 0 1 1 0 1 ? ? 1   ? ? 0 1 0 1 2 1 1 0   1 1 ? 0 1 0 0 1 2 0   1 1 1 1 1 0 1 1 1 0   0 1 1 2 0 0 ? 1 ? ?   2 0 1 ? 0 ? f 0 0 0
0 0 1 0 0 ? ? ? ? 1   1 1 1 1 0 0 0 0 ? 0   1 1 1 ? ? ? ? 0 f 0   0 0 1 0 1 0 1 1 1
```

Tuditanus punctulatus

```
? ? ? ? ? ? ? 1 ? 1   0 0 0 0 0 0 0 0 ? 0   0 0 0 1 0 0 1 ? 0 0   0 ? 1 1 0 0 0 1 0 2   1 1 0 0 0 0 ? ? ? ?   0 ? ? ? 0 0 1 ? 1 ?
? ? 1 ? ? ? 0 ? ? 0   0 0 1 ? ? 0 0 0 0 0   1 0 0 1 0 0 0 0 0 0   1 ? 1 0 0 0 0 0 0 ?   1 0 0 ? 0 2 0 0 0 0   ? 0 ? 1 0 0 0 0 0 ?
? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? 0 ? ? ? ?   ? ? ? ? ? ? 0 0 0 ?   ? ? 0 0 0 ? 0 0 0 0   0 0 0 ? ? ? ? 0 0 1   0 1 0 0 ? 0 0 0 1 0
0 2 0 0 0 0 0 ? ? ?   ? ? ? 0 0 0 0 ? ? ?   ? ? ? 0 ? ? 1 0 1 0   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? 0 0 1   0 0 0 0 2 0 1 1 1 2
1 0 0 ? ? ? ? ? ? 0   ? ? 0 1 ? ? ? 1 0 0   1 1 1 1 1 1 0 1 c 0   ? 1 0 1 0 0 1 1 1 1   0 0 1 ? 0 0 0 1 0 0   c a 1 ? 0 1 1 0 0 0
0 ? ? 1 0 0 ? ? ? ?   ? ? 0 1 0 ? ? 0 ? ?   1 1 1 1 ? ? ? ? 1 ?   0 0 1 1 0 0 1 1 1
```

Tulerpeton curtum

```
? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?
3 ? 0 1 ? ? 0 1 ? 0   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? 0 ? ? ? ?   ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?   ? 1 0 0 0 0 ? ? ? ?   ? ? ? 0 0 ? 0 ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? 0 0 ?   ? 0 0 0 ? 0 ? 1 0 c
0 0 0 0 1 0 1 0 1 0   0 0 0 1 0 1 1 0 0 0   1 1 0 0 0 ? ? 1 1 0   1 ? ? ? ? ? ? ? ? 1   1 1 0 2 0 0 1 1 0 1   2 1 1 1 ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? 1   0 0 ? ? 0 0 0 0 ? ?   ? ? ? ? ? ? ? ? ? ?   ? 0 1 0 0 0 ? ? ?
```

Urocordylus wandesfordii

```
0 ? ? 0 0 0 ? 1 ? ?   ? ? ? ? ? ? ? ? ? ?   ? 0 0 1 0 1 0 0 0 0   0 ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? 0 0 ? 0   0 0 ? ? 0 0 0 1 0 0   ? 1 1 0 ? 0 0 0 0 0   0 0 1 0 ? 0 0 0 0 ?   1 ? ? ? ? ? ? 0 ? 0   ? ? ? 0 0 0 0 ? 0 ?
? ? ? ? ? ? ? ? ? ?   ? ? 1 ? 0 ? 0 0 0 ?   ? ? ? ? ? ? ? 0 ? ?   ? 0 ? 0 0 ? ? 0 0 0   0 0 0 ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?   ? 1 1 0 0 0 0 ? ? ?   ? ? ? 0 ? ? 1 0 1 0   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? 0 0 0   ? 0 0 0 2 0 1 1 1 0
0 1 0 0 ? ? ? 1 ? 0   ? ? 0 1 ? ? ? 0 1 0   1 1 0 0 1 0 0 1 1 0   1 0 0 ? 0 ? 1 1 2 1   0 1 1 2 0 0 0 1 ? ?   ? ? ? ? 0 ? 1 0 0 0
0 ? 1 0 1 1 1 1 1 ?   ? ? 0 1 0 1 ? 0 0 0   0 1 1 1 1 1 1 0 0 1   0 0 1 1 0 0 1 1 1
```

Utegenia shpinari

```
0 ? ? 0 1 0 0 1 0 1   0 0 0 0 0 0 0 0 0 0   0 0 0 0 0 0 1 0 0 0   0 0 1 1 0 0 f 1 0 2   1 1 0 0 0 0 0 1 0 ?   0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 1 0 1   ? 0 1 0 1 0 0 0 0 1   0 0 0 0 1 0 0 0 0 0   1 0 1 0 0 0 0 0 0 ?   1 0 0 0 0 2 1 0 0 1   2 0 1 1 0 0 0 0 0 3
d 1 0 1 0 0 1 1 0 0   0 0 0 1 0 0 0 0 0 0   1 1 1 0 0 0 1 0 1 ?   0 0 0 0 0 0 0 0 0 ?   0 0 0 0 0 2 ? 0 0 0   0 ? 0 0 ? 0 1 1 2 0
0 2 0 0 0 0 0 1 ? ?   ? 1 1 0 0 0 0 ? ? ?   0 1 1 0 1 0 1 0 1 0   ? 0 1 0 1 0 1 0 1 0   1 0 1 1 0 0 1 0 0 0   0 0 0 0 2 0 1 1 ? 2
1 0 0 1 ? ? ? ? ? ?   ? ? 0 1 ? ? ? ? ? 0   1 1 ? ? 1 1 0 1 1 0   0 ? 1 ? 1 0 1 1 ? ?   ? ? ? 2 ? 0 ? 1 ? ?   ? ? ? ? 0 0 1 0 0 0
0 ? ? ? 0 0 0 0 0 0   1 f 0 0 0 0 0 0 0 0   0 1 1 1 1 ? ? 0 0 0   0 0 1 0 1 0 1 1 1
```

Valdotriton gracilis

```
1 1 1 0 0 0 0 1 ? 1   0 0 1 0 0 1 0 0 1 1   1 1 ? ? ? ? ? 1 1 0   1 0 1 0 1 0 0 ? ? 0   1 1 ? 0 ? 1 ? ? ? ?   ? ? ? ? ? 1 ? ? 1 ?
? ? 1 ? ? ? 1 ? ? ?   ? ? ? ? ? ? 1 ? ? ?   ? ? ? ? 0 0 0 0 0 1   ? ? ? ? ? ? 1 ? ? ?   1 0 0 1 0 1 1 0 0 1   3 0 ? 1 0 0 0 0 0 4
? 0 1 0 1 1 1 1 1 1   0 1 ? ? ? ? ? ? 1 1   ? ? ? ? ? ? 0 1 0 0   1 ? 0 1 0 0 0 1 1 0   1 1 1 ? ? 2 0 0 1 0   1 1 0 0 ? 0 0 0 0 0
0 2 0 0 1 1 2 1 ? ?   ? 1 1 0 0 0 0 ? ? ?   1 ? ? 1 ? ? ? 1 ? ?   ? 1 ? ? ? 1 ? ? ? 1   ? ? ? ? ? ? ? 1 ? 0   0 0 0 0 ? ? ? 1 ? ?
? ? ? 0 1 1 1 1 ? 0   1 ? 1 1 1 ? ? 1 ? 1   1 1 1 1 1 1 0 1 1 0   0 0 0 ? ? 0 1 1 ? 1   0 ? 1 2 1 0 0 1 0 0   ? ? ? ? 0 0 0 0 0 0
1 ? 1 1 0 0 0 1 0 ?   ? ? 0 1 1 ? ? 0 0 0   0 1 1 1 1 1 1 0 0 0   1 0 1 1 0 0 1 1 1
```

Ventastega curonica

```
0 ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? 0 1 0 0 0 0 0 0 0   0 ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? 0 ? ?   ? ? ? ? 0 ? ? ? ? 0
? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? 0 0 1     1 1 0 1 0 0 0 0 1 0   0 0 0 0 0 0 0 0 0 0   0 0 0 1 0 0 0 1 0 0   1 1 0 0 ? 0 0 0 1   0 0 0 0 0 ? ? ? 0 ?
? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ? ?   ? ? ? ? ? ? ? ? ?
```

Viaerella herbsti

```
1 0 1 0 0 0 0 1 ? 1    ? ? ? 1 ? ? ? ? ? ?    ? 1 ? ? ? ? 1 1 ? 0    0 0 ? ? 1 1 ? ? ? ?    0 ? 0 ? ? 1 ? ? ? ?    ? ? ? ? ? 1 ? ? 1 ?
? ? 1 ? ? ? 1 ? ? ?    ? ? 1 ? ? ? 1 ? ? ?    ? ? ? ? ? 0 ? 0 0 1    ? ? ? ? ? ? ? ? ? ?    1 0 0 1 ? 0 1 ? 0 1    3 0 ? ? 1 0 0 0 0 ?
? 0 1 ? 1 ? 1 1 ? ?    ? 1 ? ? ? ? ? 1 1    ? ? ? ? ? ? 0 0 ? 0    1 ? 1 1 ? 0 0 0 0 0    1 1 1 ? ? ? ? ? ? ?    ? ? ? ? ? ? ? ? ? ?
? ? ? ? 1 1 2 ? ? ?    ? 1 1 0 0 1 0 ? ? ?    1 ? ? 1 ? ? ? 1 ? ?    ? 1 ? ? ? 1 ? ? 1    ? ? ? ? ? ? ? 1 ? ?    ? 0 0 0 2 0 1 1 ? ?
? ? ? 1 ? ? ? 1 ? 0    ? ? 1 1 1 0 ? 1 ? 1    1 1 1 1 1 0 0 ? ? 1    1 ? ? ? ? 1 ? ? ? ?    ? ? ? 2 ? ? ? ? ? ?    ? ? ? ? 0 ? 0 0 1 0
1 1 ? ? 0 ? ? ? ? ?    ? ? 0 1 0 1 ? 0 ? 0    0 1 1 ? ? ? ? 0 1 0    0 0 1 1 0 0 1 1 1
```

Westlothiana lizziae

```
0 ? ? 0 1 0 0 1 0 1    1 0 0 0 ? 0 0 0 ? 0    0 0 ? ? 0 ? 1 ? ? 0    0 ? 1 1 0 0 0 1 1 2    1 1 0 0 0 0 0 0 0 ?    0 0 0 0 0 0 0 ? 1 ?
? ? 0 0 0 0 0 ? ? 1    ? 0 1 0 ? 0 0 0 0 1    0 0 0 1 ? 0 0 0 0 0    ? ? 1 0 0 0 0 0 0 0    1 0 0 0 0 2 ? 0 0 b    2 0 ? 1 0 0 0 0 0 ?
? ? ? ? ? ? ? ? 0 ?    ? ? ? 1 1 ? 0 0 0 0    1 1 ? 1 0 0 0 0 0 ?    ? 0 0 0 0 0 0 0 0 0    0 0 0 ? ? ? 1 ? ? ?    ? ? ? ? ? 0 0 0 ? 1
0 2 0 0 0 0 1 ? ? ?    ? ? 1 0 0 0 0 ? ? ?    ? ? ? 0 ? ? 1 0 1 0    ? ? ? ? ? ? ? ? ? ?    ? ? ? ? ? ? ? 0 0 0    0 0 0 0 1 ? ? 1 ? ?
? ? ? 0 ? ? ? ? 1 1    1 1 0 1 0 1 2 1 ? 0    1 1 1 1 1 0 0 1 2 0    1 1 0 1 0 0 1 1 1 1    1 0 1 2 0 0 1 1 0 0    2 1 1 1 0 ? 1 0 0 0
0 ? ? ? 0 0 0 0 0 1    1 1 1 1 0 0 0 0 0 0    1 1 1 1 1 1 1 0 1 0    0 0 1 ? ? ? 1 1 1
```

Whatcheeria deltae

```
0 ? ? 0 0 0 ? 1 ? 1    0 0 0 0 0 0 0 0 0 0    0 0 ? 0 0 0 0 0 0 0    0 ? 1 1 0 0 1 0 0 1    1 1 0 0 0 0 0 0 1 0    0 0 0 0 0 0 0 0 0 1
1 0 0 0 0 1 0 1 0 1    ? 0 0 0 0 0 0 0 0 0    0 0 0 0 1 0 0 0 ? 0    ? ? 1 0 1 ? 0 0 0 ?    1 0 0 0 0 1 1 1 1 1    0 0 1 0 0 0 0 0 0 2
2 ? 0 1 0 ? ? ? ? ?    ? ? 0 1 0 0 ? ? 0 0    0 1 ? 0 0 0 0 0 ? 0    ? ? ? ? ? ? ? 0 0 ?    ? ? ? ? ? 2 ? ? ? ?    ? ? ? ? ? 0 ? ? 0 1
0 2 ? ? ? ? 0 0 0 1    1 1 0 0 0 0 0 ? ? ?    0 0 1 0 ? ? 0 ? ? ?    ? 0 1 0 0 0 1 1 0 0    ? 1 0 0 1 ? 0 0 0 1    0 0 0 0 2 0 0 1 0 2
1 0 0 1 ? 0 1 1 0 0    1 1 0 1 0 1 1 0 0 0    1 1 0 0 1 ? 1 ? ? 0    1 1 0 1 0 0 1 1 0 0    ? ? 0 ? 0 1 0 1 0 1    ? ? ? ? 0 1 1 1 0 0
0 ? ? 0 0 0 0 0 1    0 1 0 0 0 0 0 0 0 0    0 1 1 ? ? ? ? 0 0 0    0 0 1 ? ? ? 1 ? 1
```

Appendix 4: List of character-state changes for selected nodes

For each labelled node in Fig. 5, we have included the number of the character (as it appears in the character list), consistency index and character-state transformation (all apomorphy lists have been generated using the accelerated transformation in PAUP). The double arrow denotes that the related change is unambiguous on that tree. The single-line arrow implies an ambiguous change on the tree.

Node A (Fig. 5) subtending *Amphibamus*, *Doleserpeton* and Lissamphibia (decay index = 2; no bootstrap support in a 50 % majority-rule consensus):

3 (0.25; 1 → 0); 68 (0.091; 1 ⇒ 0); 70 (0.111; 1 → 0); 105 (0.111; 1 → 0); 123 (0.143; 0 → 1); 133 (0.167; 0 ⇒ 1); 183 (0.25; 0 ⇒ 1); 193 (0.091; 0 → 1); 228 (0.5; 0 ⇒ 1); 229 (0.333; 0 ⇒ 1).

Node B (Fig. 5) subtending *Doleserpeton* plus Lissamphibia (decay index = 1; no bootsrap support compatible with a 50 % majority-rule consensus):

130 (0.5; 0 → 1); 140 (0.25; 0 ⇒ 1); 151 (0.333; 0 → 1); 152 (0.333; 0 → 1); 311 (0.333; 0 ⇒ 1); 312 (0.2; 0 → 1); 314 (0.167; 0 ⇒ 1).

Node C (Fig. 5) subtending Lissamphibia (decay index = 8; bootsrap = 67 %):

3 (0.25; 0 → 1); 19 (0.083; 0 ⇒ 1); 34 (0.074; 1 ⇒ 0); 43 (0.143; 0 → 1); 48 (0.125; 1 → 0); 56 (0.333; 0 → 1); 63 (0.2; 0 ⇒ 1); 77 (0.25; 0 ⇒ 1); 87 (0.143; 1 → 0); 91 (0.071; 0 → 1); 100 (0.125; 1 → 0); 111 (0.125; 2 ⇒ 3); 124 (0.091; 1 ⇒ 0); 126 (0.143; 0 → 1); 131 (0.2; 1 → 0); 154 (0.5; 0 ⇒ 1); 176 (0.2; 1 ⇒ 0); 187 (0.083; 0 ⇒ 2); 201 (0.167; 0 ⇒ 1); 204 (0.25; 0 → 1); 208 (0.5; 0 → 1); 212 (0.333; 0 ⇒ 1); 216 (0.333; 0 → 1); 220 (0.333; 0 → 1); 281 (0.071; 0 → 1); 285 (0.5; 0 → 1); 302 (0.25; 0 ⇒ 1); 304 (0.167; 0 → 1); 316 (0.2; 0 → 1).

Node D (Fig. 5) subtending total group Salientia (decay index = 6; bootstrap = 97 %):

2 (0.25; 1 → 0); 14 (1; 0 → 1); 36 (1; 0 → 1); 41 (0.2; 1 ⇒ 0); 87 (0.143; 0 → 1); 126 (0.143; 1 → 0); 196 (1; 0 → 1); 244 (0.1; 0 ⇒ 1): presence of a separate scapular ossification; 245 (0.111; 1 → 0); 266 (0.091; 1 ⇒ 0); 276 (1; 0 → 1); 280 (0.143; 1 ⇒ 0); 285 (0.5; 1 → 0); 304 (0.167; 1 → 0); 321 (0.143; 0 → 1); 329 (0.2; 0 ⇒ 1).

Node subtending total group Caudata (in some trees only) (decay index = 0; bootstrap = 61 %):

148 (1; 0 ⇒ 1); 158 (1; 0 ⇒ 1); 159 (1; 0 ⇒ 1); 315 (0.5; 0 ⇒ 1); 331 (0.333; 0 → 1).

Node E (Fig. 5) subtending Albanerpetontidae plus Gymnophiona (decay index = 2; no bootsrap support in a 50 % majority-rule consensus):

1 (0.5; 1 ⇒ 0); 12 (0.167; 1 ⇒ 0); 16 (0.5; 1 ⇒ 0); 73 (0.077; 1 → 0); 104 (0.2; 1 → 0); 107 (0.105; 1 → 0); 110 (0.105; 1 → 0); 130 (0.5; 1 → 0); 138 (0.5; 1 → 0); 151 (0.333; 1 → 0); 153 (0.167; 1 → 0); 163 (0.2; 1 → 0); 165 (0.333; 1 → 0); 183 (0.25; 1 → 0); 69 (0.133; 1 → 2).

Node subtending Batrachia (Fig. 5) (decay index = 3; bootstrap = 80 %):

20 (0.25; 0 → 1); 22 (0.333; 0 → 1); 29 (0.5; 0 ⇒ 1); 46 (0.25; 0 ⇒ 1); 67 (0.2; 0 ⇒ 1); 85 (0.111; 1 → 0); 90 (0.5; 0 ⇒ 1); 97 (0.333; 0 → 1); 98 (0.333; 0 → 1); 99 (0.333; 0 → 1); 135 (0.111; 0 → 1); 139 (0.333; 0 → 1); 149 (0.071; 1 → 0); 152 (0.333; 1 → 0); 155 (0.5; 1 ⇒ 0); 271 (0.071; 0 → 1); 303 (0.333; 0 ⇒ 1).

Node subtending the clade Procera in the shortest suboptimal trees compatible with such clade

43 (0.167; 0 ⇒ 1); 316 (0.2; 1 → 0); 331 (0.5; 0 ⇒ 1).

Node subtending Procera plus Albanerpetontidae in the shortest suboptimal trees that are compatible with Procera

1 (0.333; 1 → 0); 12 (0.167; 1 ⇒ 0); 87 (0.167; 1 ⇒ 0); 126 (0.167; 0 → 1); 138 (0.5; 1 → 0); 151 (0.333; 1 → 0); 153 (0.2; 1 → 0); 183 (0.25; 1 → 0); 285 (1; 0 → 1); 304 (0.2; 0 ⇒ 1); 321 (0.143; 1 → 0).