The origin(s) of extant amphibians: a review with emphasis on the "lepospondyl hypothesis"

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ABSTRACT

The origins of the extant amphibians (frogs, salamanders, caecilians) remain controversial after over a century of debate. Three groups of hypotheses persist in the current literature: the "temnospondyl hypothesis" (TH) which roots Lissamphibia Haeckel, 1866 (the smallest clade composed of the extant amphibians) within the Paleozoic temnospondyls, the "lepospondyl hypothesis" (LH) which postulates a monophyletic Lissamphibia nested within the Paleozoic lepospondyls, and the "polyphyly hypothesis" (PH), according to which the frogs and the salamanders are temnospondyls while the caecilians are lepospondyls. The discovery of the Middle Jurassic to Pliocene albanerpetontids, which are very similar to the extant amphibians, has complicated rather than resolved this situation. We present a review of recent publications and theses in this field, several of which show more support for the LH than for the TH and considerably more than for the PH. In addition, we show that there is no particular attraction between long-bodied lissamphibians (caecilians) and long-bodied lepospondyls (such as the lysorophians): when they are removed from two published matrices, reanalyses nonetheless find the LH. In one case the LH is found even when all salamanders are removed as well. We furthermore propose that the complex of characters called the salamander mode of autopodium development is (in its less extreme forms) plesiomorphic for limbed vertebrates, so the apparent presence of this mode of development in temnospondyls cannot support the TH or the PH. Still, a consensus will not be reached soon, despite the increasing

range of data and types of analysis that are used (morphological, molecular and combined phylogenetics, development biology, molecular divergence dating, paleontological supertree dating, combined dating, and calculation of confidence intervals on first appearances in the fossil record). We present examples of pertinent character state distributions and explore a large gap in the fossil record of small stegocephalians.

RÉSUMÉ
L(es) origine(s) des amphibiens actuels : une synthèse avec emphase sur l'« hypothèse lépospondyle ».
Les origines des amphibiens actuels (anoures, urodèles et gymnophiones) restent discutées après plus d'un siècle de débats. Trois groupes d'hypothèses persistent dans la littérature actuelle : l'« hypothèse temnospondyle » (TH) qui enracine Lissamphibia Haeckel, 1866 (le plus petit clade composé des amphibiens actuels) parmi les temnospondyles paléozoïques, l'« hypothèse lépospondyle » (LH) qui propose un Lissamphibia monophylétique issu des lépospondyles paléozoïques, et l'« hypothèse de polyphylie » (PH), selon laquelle les anoures et les urodèles sont des temnospondyles alors que les gymnophiones sont des lépospondyles. La découverte des albanerpetontidés, maintenant connus du Jurassique moyen jusqu'au Pliocène, qui sont très similaires aux amphibiens actuels, a plus contribué à compliquer cette situation qu'à la résoudre. Nous présentons une synthèse des publications et thèses récentes sur ce sujet ; plusieurs d'entre elles renferment des données qui soutiennent un peu plus la LH que la TH, et bien plus que la PH. De plus, nous montrons qu'il n'existe pas d'attraction particulière entre les lissamphibiens à corps allongé (gymnophiones) et des lépospondyles à corps allongé (tels que les lysorophiens) ; si on les enlève de deux matrices de données publiées, des réanalyses soutiennent toujours la LH. Dans un cas, la LH est soutenue même si on enlève tous les urodèles aussi. Nous proposons également que le complexe de caractères appelé le mode urodèle de développement de l'autopodium est (dans des formes moins extrêmes) plésiomorphiques pour les tétrapodes au sens large. La présence présumée de ce mode de développement ne soutient donc pas la TH ou la PH. Néanmoins, on n'atteindra pas de consensus de sitôt, malgré la diversité croissante des données et des types d'analyses utilisées (phylogénétique morphologique, moléculaire et combinée, biologie du développement, datation moléculaire, datation paléontologique utilisant des arbres de synthèse et datation mixte, calcul d'intervalles de confiance de la date d'apparition) pour départager les hypothèses. Nous présentons des exemples de distributions d'états des caractères pertinents et explorons une grande lacune dans le registre fossile des stégocéphales de petite taille.

INTRODUCTION

Much has been written since the late 19th century on the origins of the frogs, salamanders, and caecilians, a problem further complicated since the 1970s by the discovery of a fourth clade of unclear relationships, the Middle Jurassic to Pliocene albanerpetontids (salamander-shaped, somewhat elongate, scaly animals). Exciting advances have been made recently, such as the discovery of new fossils (cited below), the

development of new methods (Marjanović & Laurin 2007, 2008a; Germain & Laurin 2009; Pyron 2011), the use of data from development biology (e.g., Hinchliffe & Vorobyeva 1999; Johanson *et al.* 2007), the use of previously inaccessible anatomical data revealed by computed microtomography (Maddin *et al.* 2011, 2012; Maddin & Anderson 2012), and progress in molecular (Zhang *et al.* 2005; Frost *et al.* 2006; Marjanović & Laurin 2007; Hugall *et al.* 2007; Roelants *et al.* 2007; Igawa *et al.* 2008; San Mauro 2010; Pyron 2011) as well as morphological phylogenetics (cited below). Despite this, three groups of hypotheses persist in the literature today (Fig. 1).

The most widespread one is surely the "temnospondyl hypothesis" (TH hereinafter; Fig. 1A-D), recently supported by Ruta & Coates (2007), Sigurdsen & Green (2011), Maddin & Anderson (2012) and Maddin *et al.* (2012). It posits that the frogs (crown-group: Anura, total group: Salientia), the salamanders (crown-group: Urodela, total group: Caudata), and the caecilians (crown-group: Gymnophiona, total group: Gymnophionomorpha – see below) form a clade called Lissamphibia Haeckel, 1866, which also either contains or is the sister-group of Albanerpetontidae Fox & Naylor, 1982, and is nested within the amphibamid and/or branchiosaurid dissorophoid temnospondyls. The amphibamids, an intensively studied group (Schoch & Rubidge 2005; Huttenlocker *et al.* 2007; Sigurdsen 2008, 2009; Anderson *et al.* 2008a, b; Fröbisch & Reisz 2008; Sigurdsen & Bolt 2009, 2010; Clack & Milner 2010; Bourget & Anderson 2011; Werneburg 2012), are known from the Late Carboniferous to the Early Triassic. They differ from other temnospondyls in their small body sizes and various traits that are in many cases shared by some or all lissamphibians (and in many cases lepospondyls); some of these traits are adaptations to a terrestrial lifestyle. The Late Carboniferous to Early Permian branchiosaurids, recently (Fröbisch & Schoch 2009a) shown to be nested within Amphibamidae Moodie, 1916, are mostly known from larvae and neotenic adults that resemble modern neotenic salamanders (Schoch 2009). According to this hypothesis, the diadectomorphs, lepospondyls, seymouriamorphs and usually anthracosaurs (embolomeres) are stem-amniotes.

Another is the "lepospondyl hypothesis" (LH). In its modern form (Fig. 1E; Vallin & Laurin 2004; Pawley 2006: app. 16, figs 88, 89, 91, 92; Germain 2008a: chapter V; Marjanović & Laurin 2008b, 2009; Marjanović 2010: chapter 5; Pyron 2011), it postulates a close relationship between Lissamphibia (again ignoring the exact position of the albanerpetontids) and certain lepospondyls, especially the eel-like Late Carboniferous to Early Permian lysorophians as well as (recently) the coeval "nectrideans" (a possibly paraphyletic assemblage of mostly aquatic animals of small size and diverse shapes) and aïstopods (small, snake-like animals, at least some of which were probably terrestrial). More distant relationships are hypothesized to exist with the "microsaurs", a diverse, probably paraphyletic assemblage of mostly terrestrial to amphibious animals, some of them burrowing (Anderson *et al.* 2009). Temnospondyli is a clade of stem-tetrapods under the LH, and the tetrapod crown-group is smaller than according to the other hypotheses; it includes diadectomorphs (on the amniote stem), and lepospondyls (along the amphibian stem) but not seymouriamorphs or anthracosaurs.

The third is the "polyphyly hypothesis" (PH), most recently supported by Anderson *et al.* (2008b; Fig. 1G; but see Maddin & Anderson [2012] and Maddin *et al.* [2012]). Under this hypothesis, there is no Lissamphibia, because the frogs are considered to be amphibamid temnospondyls and the caecilians to be "microsaurian" lepospondyls (closely related to the elongate, possibly burrowing Early Permian *Rhynchonkos* Schultze & Foreman, 1981). The salamanders were originally advocated to be "microsaurs" (Carroll & Holmes 1980; Fig. 1F), but are now thought to be branchiosaurid temnospondyls (Carroll 2007; Fig. 1H) or found, together with the albanerpetontids, to be the sister-group of the frogs (Anderson *et al.* 2008b). Less plausible variants of the PH (Fig. 1H) were found by McGowan (2002) and Carroll (2007: fig. 77).

Reviews of the current state of research on the phylogeny of limbed vertebrates in general and the origin of the extant amphibians in particular have recently been published by proponents of the PH (Carroll *et al.* 2004; Carroll 2007; Anderson
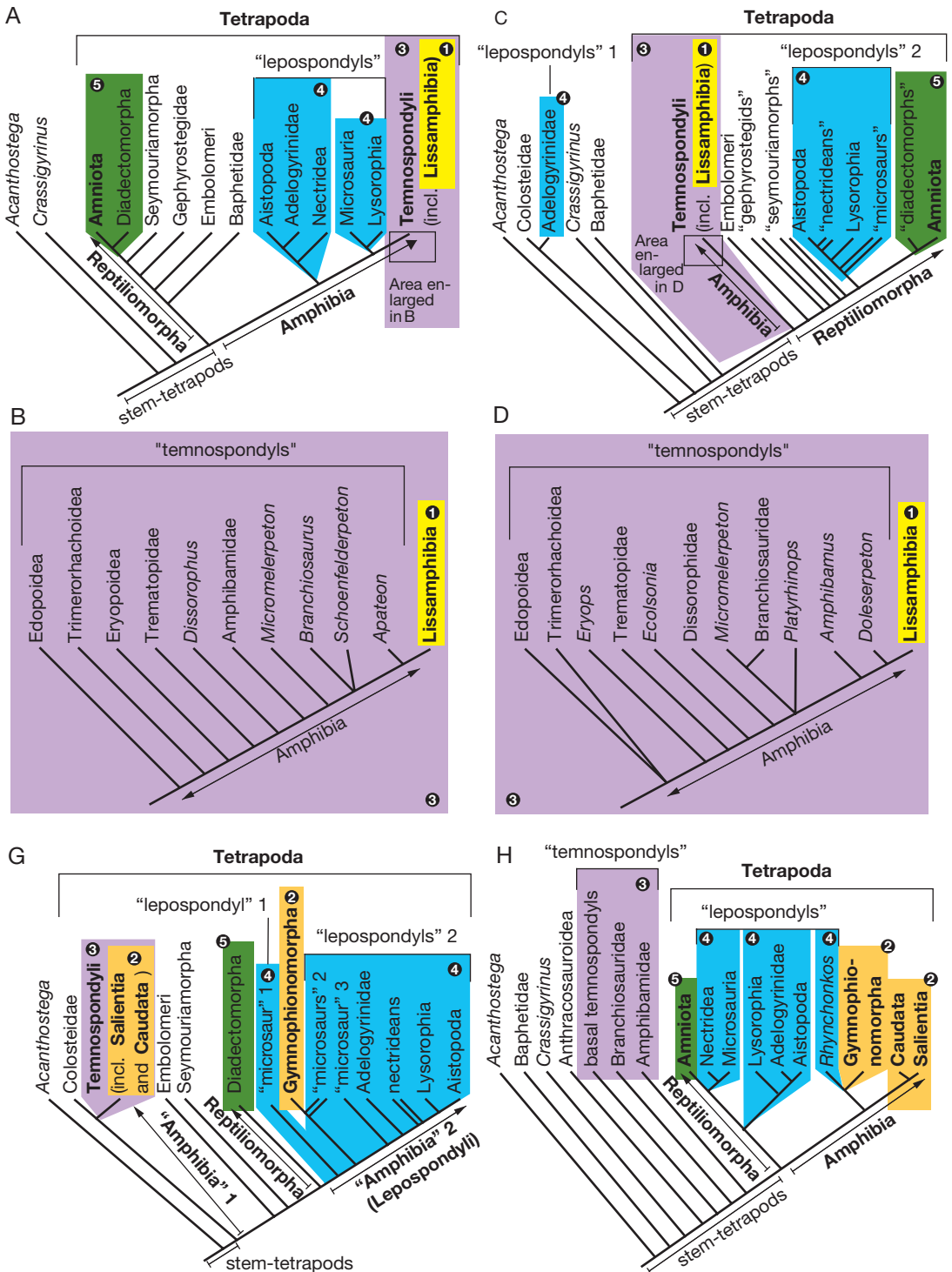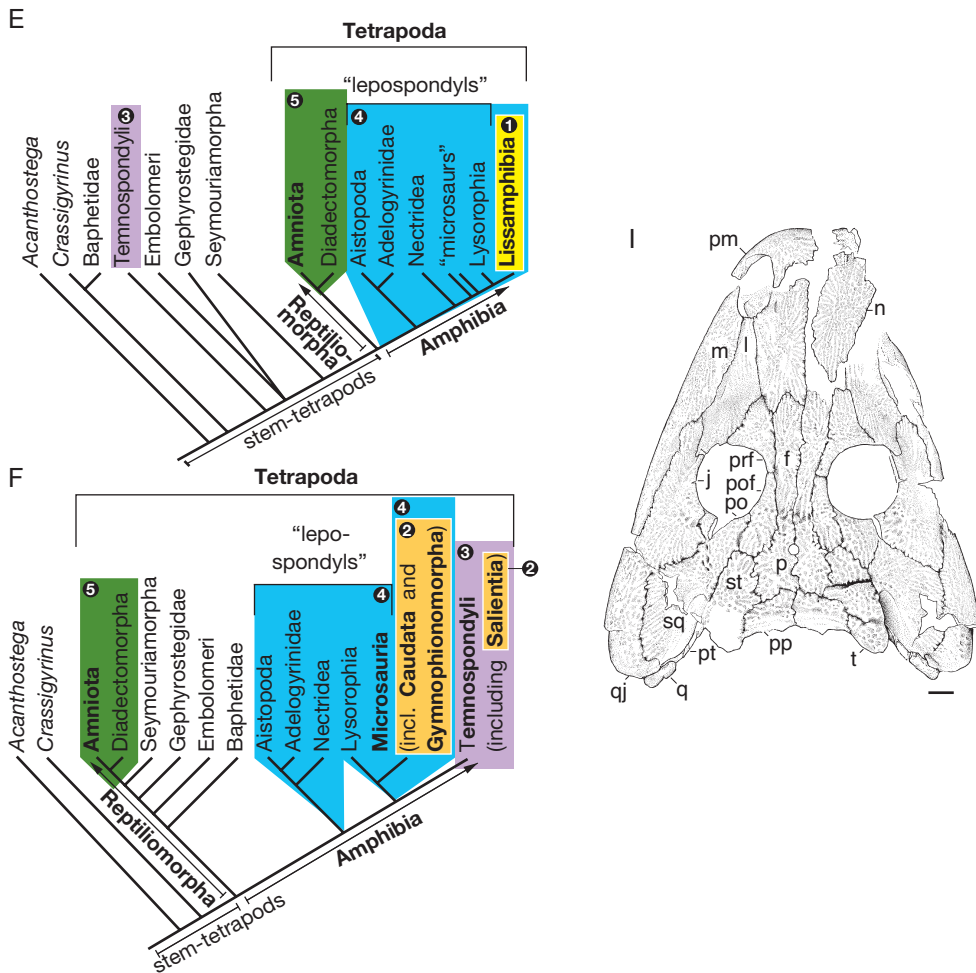
Fig. 1. — Hypotheses on the origin of Lissamphibia in the recent literature (modified from Marjanović & Laurin 2008b: fig. 1). Extant taxa in bold; extant amphibians underlain in yellow (❶) if monophyletic (Lissamphibia) or pastel orange (❷) if polyphyletic, temnospondyls underlain in violet (❸), lepospondyls in cyan (❹), the amniote-diadectomorph clade in green (❺): **A**, **B**, Temnospondyl hypothesis (TH) as of the late 1980s and early 1990s; **B**, simplified from Trueb & Cloutier (1991); **C**, **D**, TH, simplified from Ruta & Coates (2007); **E**, Lepospondyl hypothesis (LH), simplified from Vallin & Laurin (2004); **F**, Polyphyly hypothesis (PH), simplified from Carroll & Holmes (1980) through Carroll *et al.* (2004); **G**, PH simplified from Anderson *et al.* (2008b); the name Amphibia does not apply to any clade under this topology; **H**, a version of the PH, simplified from Carroll (2007: fig. 77), where extant amphibians and "lepospondyls" are nested inside the "temnospondyls"; "Anthracosauroidea" is an OTU that includes Embolomeri, Gephyrostegidae and Seymouriamorpha; "basal temnospondyls" is an OTU composed of *Dendrerpeton* and *Balanerpeton*; the "Microsauria" OTU consists of all "microsaurs" except *Rhynchonkos*; **I**, skull roof of the temnospondyl *Iberospondylus schultzei*, modified from Laurin & Soler-Gijón (2001). Scale bar: 1 cm. The authors of all taxon names are listed in Appendix 11.

2008) and of the TH (Ruta *et al.* 2003; Schoch & Milner 2004; Ruta & Coates 2007; Coates *et al.* 2008), but not the LH. We would like to provide a complementary review and summarize information contained in recent publications.

WHY IS THE ORIGIN OF THE LISSAMPHIBIANS SO CONTROVERSIAL?

Our inability to reach a phylogenetic consensus is often attributed to the notorious incompleteness of the fossil record. Indeed, our knowledge of the

fossil record of lissamphibians and their potential closest relatives contains considerable gaps (Fig. 2A). The caecilians have almost no fossil record; apart from isolated vertebrae from the Late Cretaceous through Miocene and an isolated Miocene skull, all of which belong to the crown-group (Gymnophiona) or close relatives of it (Rage & Pickford 2011), there is disarticulated Early Cretaceous material from a stem-group representative (*Rubricacaecilia* Evans & Sigogneau-Russell, 2001) and a number of articulated partial skeletons of an Early Jurassic stem-caecilian (*Eocaecilia* Jenkins & Walsh, 1993; Jenkins *et al.* 2007; Maddin *et al.* 2012). The fossil record of salamanders reaches down into the Middle Jurassic, where it is fairly diverse (Skutschas & Krasnolutskii 2011) – but then it just stops, unless the badly preserved, superficially described, and tiny *Triassurus* Ivachnenko, 1978 (Ivachnenko 1979), from the Late Triassic of Kyrgyzstan, is a caudate (Ruta & Coates [2007] mention one potential unique synapomorphy) rather than a temnospondyl larva (Schoch & Milner 2004). The albanerpetontids likewise have no known fossil record before the Middle Jurassic. Stem-salientians are known from the Early Jurassic and later, and from the Early Triassic forms *Triadobatrachus* Kuhn, 1962, and *Czatkobatrachus* Borsuk-Białynicka & Evans, 1998 (Evans & Borsuk-Białynicka 2010).

All potential sister-groups of Lissamphibia or of its main constituent clades are much older (Fig. 2). Under all hypotheses, a gap of at least 70 Ma must be inferred at the base of the group(s). Dissorophoid temnospondyls are not known after the Early Permian, with the sole exceptions of the Early Triassic amphibamids *Micropholis* Huxley, 1876, and *Tungussogyrinus* Efremov, 1939 (a branchiosaurid), and perhaps the undescribed "branchiosaurid-like temnospondyl" mentioned by Gao *et al.* (2004); *Micropholis* (Schoch & Rubidge 2005) has never been considered particularly close to any extant amphibians, and while caudate affinities had been suggested for *Tungussogyrinus* (Schoch & Milner 2004), its latest redescription (Werneburg 2009) argues strongly against this. Lepospondyls are rare after the Early Permian; they are represented by an undescribed presumed "microsaur" from the Middle or Late Permian of Russia (Ivakhnenko *et al.*

1997: 14), by a diplocaulid "nectridean" from the Middle to Late Permian of Morocco (Dutuit 1988; Germain 2010), and by unspecified "lepospondyl amphibians" from the Early Triassic of China (Gao *et al.* [2008]; called "a microsaur-like lepospondyl" by Gao *et al.* [2004]). If lissamphibians and lysorophians (or "nectrideans") are sister-groups, or if the lissamphibians are nested within the branchiosaurs (Trueb & Cloutier 1991), a stem-lissamphibian ghost lineage into the Late Carboniferous is required. A shorter but still sizable gap is required under the TH if *Doleserpeton* Bolt, 1969, or *Gerobatrachus* Anderson, Reisz, Scott, Fröbisch & Sumida, 2008 (Anderson *et al.* 2008b; Sigurdsen & Green 2011; Maddin *et al.* 2012), are closely related to some or all extant amphibians. The PH requires two or three ghost lineages extending down to the Early Permian or earlier. Barring future surprises from the purported Middle/Late Permian and Triassic lepospondyls, wide gaps separate the oldest known lissamphibians from all of their potential closest relatives, and similarly wide gaps exist in our knowledge of the early history of Lissamphibia itself. However, the subsequent history of Lissamphibia, from the Early Cretaceous onwards, is documented by a reasonably rich fossil record (Marjanović & Laurin 2007, 2008a).

In analogy to "Romer's Gap" (Coates & Clack 1995), we would like to introduce the term "Carroll's Gap" for the time from the Middle Permian to the Early Jurassic which has so far yielded almost no fossils of lissamphibians or any of their potential close relatives (Laurin 1998a; Carroll *et al.* 2004; Carroll 2007). Both gaps are illustrated in Figure 2.

On their own, such gaps need not be a problem. Phylogenetic analysis can be, and is almost always, done without taking stratigraphic data into account. In this case, however, fossils from the mentioned gaps would show whether all three main lissamphibian clades converge on a single ancestral morphotype, as predicted by the TH and the LH, or not, as suggested by the PH. In the former case, such fossils would also narrow down the diversity of possible character combinations for the ancestral lissamphibians, which would help discriminate between the TH and the LH. Two examples should suffice to illustrate this.
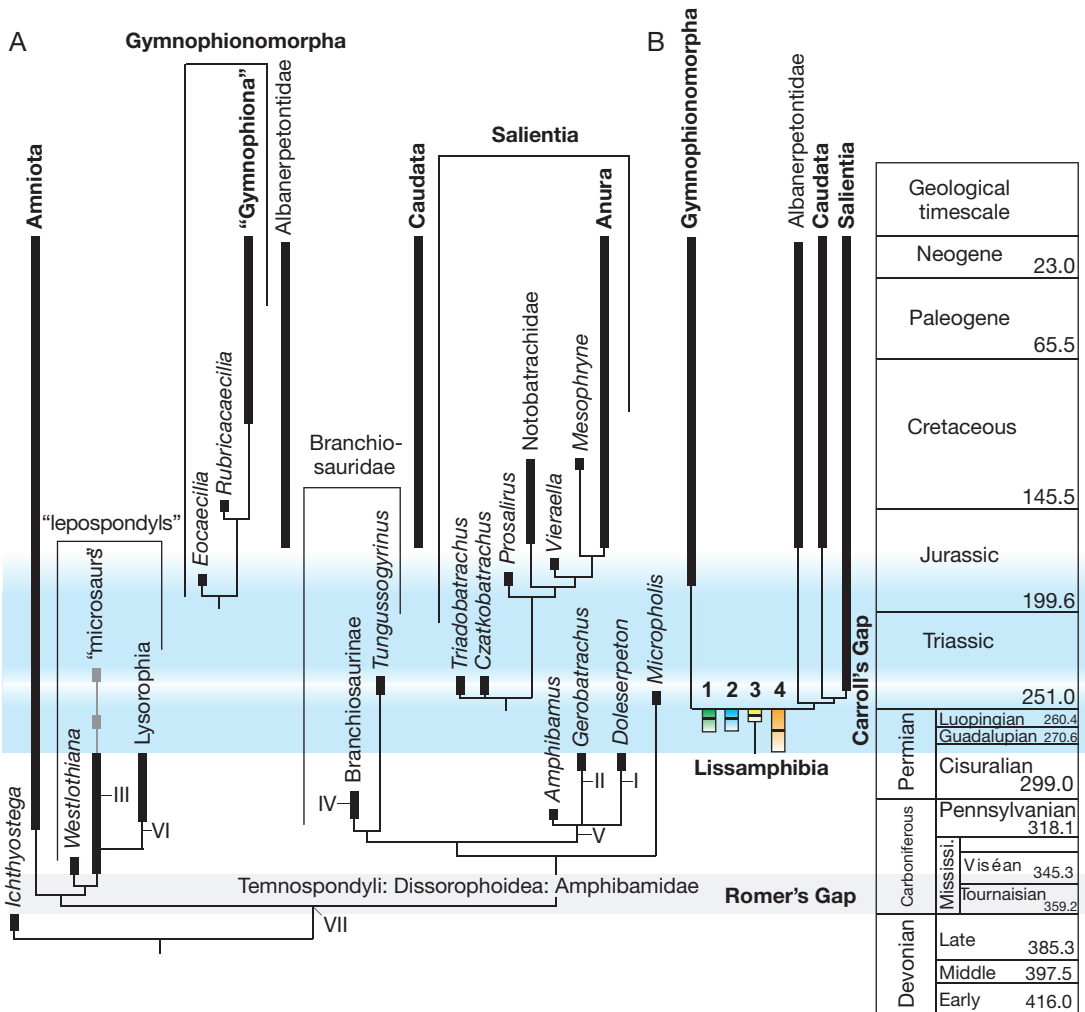
Fɪɢ. 2. — Time-calibrated trees showing Romer's and Carroll's Gaps. Names of extant taxa in bold. Known stratigraphic ranges, including uncertainties, are shown by thick lines. The timescale follows Gradstein *et al.* (2004); the unlabeled stage is the Serpukhovian, which began 326.4 ± 1.6 Ma ago. **Mississi.**, Mississippian. **A**, a phylogeny of early limbed vertebrates and extant amphibians. The "microsaurs" are likely paraphyletic with respect to Lysorophia; their gray extension consists of the undescribed possible representatives from the mid-late Permian of Russia and the Late Early Triassic of China (see text). The undescribed possible branchiosaurid from the late Early Triassic of China (Gao *et al.* 2004) is not shown, because *Tungussogyrinus* has about the same age. The position of *Gerobatrachus* in a trichotomy follows Fröbisch & Reisz (2008) and Marjanović & Laurin (2008b, 2009); that of *Tungussogyrinus* is taken from Werneburg (2009); the oldest known "microsaur" is *Kirktonecta*, named and described by Clack (2011). Note that all lepospondyls, amphibamids, or lissamphibians from Carroll's Gap are restricted to four or possibly five representatives from the Early Triassic, with the single exception of the purported Russian "microsaur"; their age range is shown as a bleached zone in Carroll's Gap. "Gymnophiona" includes Gymnophiona and all fossils that either belong to it or represent its closest known relatives; see Marjanović & Laurin (2007: fig. 3, as "Apoda") and Rage & Pickford (2011). The Roman numerals represent possible origins of Lissamphibia or parts thereof, placed as high in the geological section as possible: **I**, Lissamphibia (**TH**), Batrachia (**PH**), or Salientia (**PH**); **II**, Batrachia (**PH**); **III**, Gymnophionomorpha (**PH**); **IV**, Lissamphibia (**TH**) or Caudata (**PH**); **V**, Lissamphibia (**TH**), Batrachia (**PH**), or Salientia (**PH**); **VI**, Lissamphibia (**LH**); **VII**, basal split between the extant amphibians (**PH**). **B**, Time-calibrated phylogeny of Lissamphibia showing stratigraphic estimates of the age of that clade. The rectangles **1** to **4** represent the confidence intervals on the origin of Lissamphibia calculated under four different assumptions on the presumed severity of the impact of mass extinction events (Permian-Triassic, Triassic-Jurassic, and Cretaceous-Paleogene boundaries) on lissamphibian diversity. The bottom of each rectangle shows the older limit of the 75% confidence interval, the black bar the older limit of the 50% confidence interval. Note that none of the rectangles extends beyond the base of Carroll's Gap, while the PH predicts a date within Romer's Gap (VII in A) for the split between Gymnophionomorpha and Salientia. From Marjanović & Laurin (2007: fig. 9b; 2008a: fig. 4C). The authors of all taxon names are listed in Appendix 11.

TABLE 1. — Sizes of the latest few data matrices for tetrapod phylogenetics in "genealogical" and chronological order (matrices that are based on each other follow each other in chronological order and lie between the same horizontal lines). Matrices that do not contain any lissamphibians are omitted. On the other hand, some publications appear several times in this Table because they analyzed several matrices. Treatment as morphologically immature (= sexually immature or paedomorphic) means that presumably ontogeny-dependent characters are scored as unknown unless the state associated with morphological maturity is present (based on the approach recommended by Wiens et al. [2005]); note that this does not need to concern the entire skeleton (it is possible to be peramorphic in some characters and paedomorphic in others at the same time). Finding out the exact number of parsimony-informative characters in the analyses by Pawley (2006) is not easy, so we present the total number of characters, but Pawley (2006: 205) mentions that all characters were parsimony-informative, apparently in all analyses. Maddin & Anderson (2012) and Maddin et al. (2012) stated the number of parsimony-informative characters in the text. Trond Sigurdsen kindly told DM the number of parsimony-informative characters in the supermatrix by Sigurdsen & Green (2011). For all other references, we either inspected the matrix by eye to find uninformative characters and subtract them from the total or used PAUP* 4.0b10 (Swofford 2003) to determine their number.

Publication	Supported hypothesis	No. of OTUs (outgroups included)	No. of parsimony-informative characters	Comments
Laurin (1994)	LH	38	150	Lissamphibia sister to Lysorophia, nested among "microsaurs"; Batrachia, with frogs nested inside paraphyletic salamanders
Laurin & Reisz (1997)	LH	38	154	Publication of the above with some characters added; caecilians and frogs form a polytomy with the three salamander OTUs
Laurin (1998a)	LH	43	153	The above with *Doleserpeton*, *Apateon*, *Eryops*, *Westlothiana*, and *Karaurus* added, some characters corrected, some added, some deleted; Procera, with caecilians nested inside paraphyletic salamanders
Laurin & Reisz (1999)	LH	45	154	The above with *Solenodonsaurus* and *Tulerpeton* added, one character added, many cells corrected (table 3; this includes corrections by Laurin 1998b)
Vallin & Laurin (2004: fig. 6)	LH	49	159	The above with *Microbrachis*, *Asaphestera*, *Cardiocephalus* and *Utaherpeton* added, some cells corrected (table 3), five characters added, several characters recoded
Sigurdsen & Green (2011: 460, supplementary information)	LH	49	147	Many changes to individual cells of the matrix of Vallin & Laurin (2004); some characters excluded; no bootstrap support, mediocre support from Bayesian analysis of 150 characters
Pyron (2011)	LH	49	inapplicable	Bayesian analysis of the 161 characters of the matrix by Vallin & Laurin (2004); topology very similar to that found by Vallin & Laurin (2004), posterior probability of 1.0 for Lissamphibia, for a lissamphibian + "lepospondyl" + amniote + diadectomorph clade, and for Temnospondyli; adding 2652 characters from the gene RAG1 of the 8 extant taxa had no effect on these results, neither did adding 26 additional extant taxa coded only for RAG1
Anderson (2001)	PH or LH	48 or 49	181	Almost complete sample of lepospondyls, but no salientians or caudates and few other taxa in the matrix; *Eocaecilia* sister-group to brachystelechid "microsaurs"
Vallin & Laurin (2004: fig. 7)	PH or LH	48	181	The above with some changes (Vallin & Laurin 2004: 66-68); almost complete loss of resolution among "microsaurs"
Anderson (2007)	PH	62	196	Matrix from Anderson (2001) with extant amphibians, albanerpetontids, and dissorophoids added; see text
Anderson et al. (2008b)	PH	54	216	Taxa and characters from the above and Anderson et al. (2008a) with omission of the most poorly known lepospondyls
Marjanović & Laurin (2009: electronic supplementary material)	LH	54	211	Taxa and characters from Anderson et al. (2008b), but many changes to individual cells, some states redefined, many multistate characters ordered, four characters deleted; supports the LH

TABLE 1. — Continuation.

Publication	Supported hypothesis	No. of OTUs (outgroups included)	No. of parsimony-informative characters	Comments
Sigurdsen & Green (2011: 460)	LH	54	206	Many changes to individual cells from Anderson *et al.* (2008b), some taken from Marjanović & Laurin (2009); some characters excluded; bootstrap support exists, but Bayesian analysis of 213 characters did not converge on a result at all.
Maddin & Anderson (2012)	TH	55	207	A few changes to individual cells from Anderson *et al*. (2008b); only one change parallels any of those suggested by Marjanović & Laurin (2009), and only four correlated ones parallel any of those suggested by Sigurdsen & Green (2011) – neither paper is cited; one new character and Gymnophiona ("caecilians") added; Lissamphibia sister to *Gerobatrachus*; Procera, with Albanerpetontidae and Gymnophionomorpha as sister-groups.
Maddin *et al*. (2012)	TH	64	274	Merger of the matrices of Maddin & Anderson (2012) and Maddin *et al*. (2011); several changes to the former (not directly to Anderson *et al*. [2008b], as the supplementary information claims – the main text is correct); only one change each parallels any of those suggested by Marjanović & Laurin (2009) or Sigurdsen & Green (2011) – neither paper is cited; five new characters and *Karaurus* added; *Gerobatrachus* found as a stem-batrachian within Lissamphibia, which is nested among the remaining amphibamid temnospondyls.
McGowan (2002)	PH	20	41	Gymnophionomorpha nested among "microsaurs", together forming sister-group of Batrachia + Albanerpetontidae; all together nested inside Dissorophoidea; all-zero ancestor modeled after basal temnospondyls; no other taxa in the matrix
Marjanović & Laurin (2008b: fig. 6a)	TH	21	38	Taxa and characters from the above, but all-zero ancestor replaced by two real taxa, characters split and fused, states redefined, and many changes to individual cells
Marjanović & Laurin (2008b: fig. 6c)	LH	22 or 23	39	As above, but addition of *Brachydectes* and optionally *Gerobatrachus* (not shown in the figure)
Marjanović & Laurin (2008b: fig. 6e)	LH	21 or 22	38	As above, but *Doleserpeton* and, when added, *Gerobatrachus* (not shown in the figure) interpreted as morphologically immature; *Brachydectes* not added
Ruta *et al.* (2003)	TH	90	308	Lissamphibia nested in Temnospondyli
Pawley (2006: app. 16)	LH	90	352	Main source is the above, but many additions of characters (including cranial characters that seem correlated to others), as well as removal of ontogeny-dependent and parsimony-uninformative ones and many changes to individual cells; Lissamphibia sister to *Phlegethontia*, whether characters are reweighted (fig. 89) or not (fig. 88)
Pawley (2006: app. 16)	LH	90	371 or 376	Same as above, but cranial characters unmodified from Ruta *et al*. (2003), only postcranial ones modified; Lissamphibia-Albanerpetontidae clade sister to *Brachydectes* (Lysorophia), nested in "nectridean"-aïstopod-*Acherontiscus*-adelospondyl clade (fig. 91; *Acherontiscus*); reweighting resolves basal polytomy of that clade to nectridean monophyly (fig. 92); the text of app. 16 (p. 389) says 376 characters, while tables 16 and 17 say 371

TABLE 1. — Continuation.

Publication	Supported hypothesis	No. of OTUs (outgroups included)	No. of parsimony-informative characters	Comments
Ruta & Coates (2007)	TH	102	333	Addition of taxa and addition and removal of characters to/from Ruta *et al.* (2003), but only two changes to any cells
Germain (2008a: fig. 5.15)	LH	102	330	Taxon and character list identical to Ruta & Coates (2007), except for merger of five correlated characters; many changes to individual cells; Lissamphibia-Albanerpetontidae clade sister to *Brachydectes* (Lysorophia); TH is one step less parsimonious (fig. 5.16)
Marjanović (2010: ch. 5: "fig." 1)	LH	102	289	Many changes to individual cells from Germain (2008a), mergers of many correlated characters; TH ("fig." 2) is 8 steps less parsimonious than LH; further changes have increased the difference to 12 steps
Marjanović (2010: ch. 5: "fig." 3)	LH	111	289	Same as above with added taxa such as *Gerobatrachus*; TH ("fig." 4) is 10 steps less parsimonious than LH; addition of more taxa has increased the difference to 14 steps
Sigurdsen & Green (2011: 460)	TH	102	320	Many changes to individual cells from Ruta & Coates (2007); strong bootstrap support, but Bayesian analysis of 326 characters did not converge on a result at all
Carroll (2007)	PH	23	113	Similar results to McGowan (2002); see text
Sigurdsen & Green (2011: figs 2B, 3B, 4)	TH	25	335	All characters from modified matrices of Vallin & Laurin (2004), Ruta & Coates (2007) and Anderson *et al.* (2008b) applied to the taxa shared by all three; few correlated characters merged within each of those matrices; mediocre bootstrap support, strong support from Bayesian analysis of 504 characters

All extant amphibians as well as the albanerpetontids lack the paired postparietal and tabular bones at the caudal edge of the skull roof – yet *Eocaecilia*, the oldest and basalmost known caecilian, possesses well developed postparietals as well as a pair of extra bones which are most parsimoniously interpreted as tabulars (Jenkins *et al.* 2007). On the other hand, postparietals are missing in the brachystelechid "microsaurs" (Carroll 1991; Maddin *et al.* 2011) and apparently in lysorophians (Fig. 3; Marjanović & Laurin 2008b). Anderson *et al.* (2008b) scored *Triadobatrachus* as possessing postparietals and tabulars, although our own inspections of the specimen have failed to replicate this observation.

Similarly, the jugal bone is absent in all extant amphibians and in lysorophians, and appears remarkably late and slowly in the ontogeny of the branchiosaurid temnospondyls (Schoch 2002, and references therein), yet *Eocaecilia* (Jenkins *et al.* 2007) and albanerpetontids (McGowan 2002; Venczel & Gardner 2005) possess jugals.

An alternative way to assess the origin of extant amphibians might be to turn to evidence independent of morphology, that is, molecular data. However, so many of the relevant taxa are extinct that sequence-based analyses cannot distinguish between the TH and the LH – both predict lissamphibian monophyly with respect to Amniota. This only discriminates between monophyly (TH or LH) on one hand and the PH on the other.

Lissamphibian monophyly with respect to Amniota has indeed been found in every molecular analysis we are aware of (Laurin 2002; Anderson 2008; San Mauro 2010; Pyron 2011), despite the wide diversity of genes (nuclear and mitochondrial), techniques, and taxon samples that have been used (the only partial exception are the ambiguous results
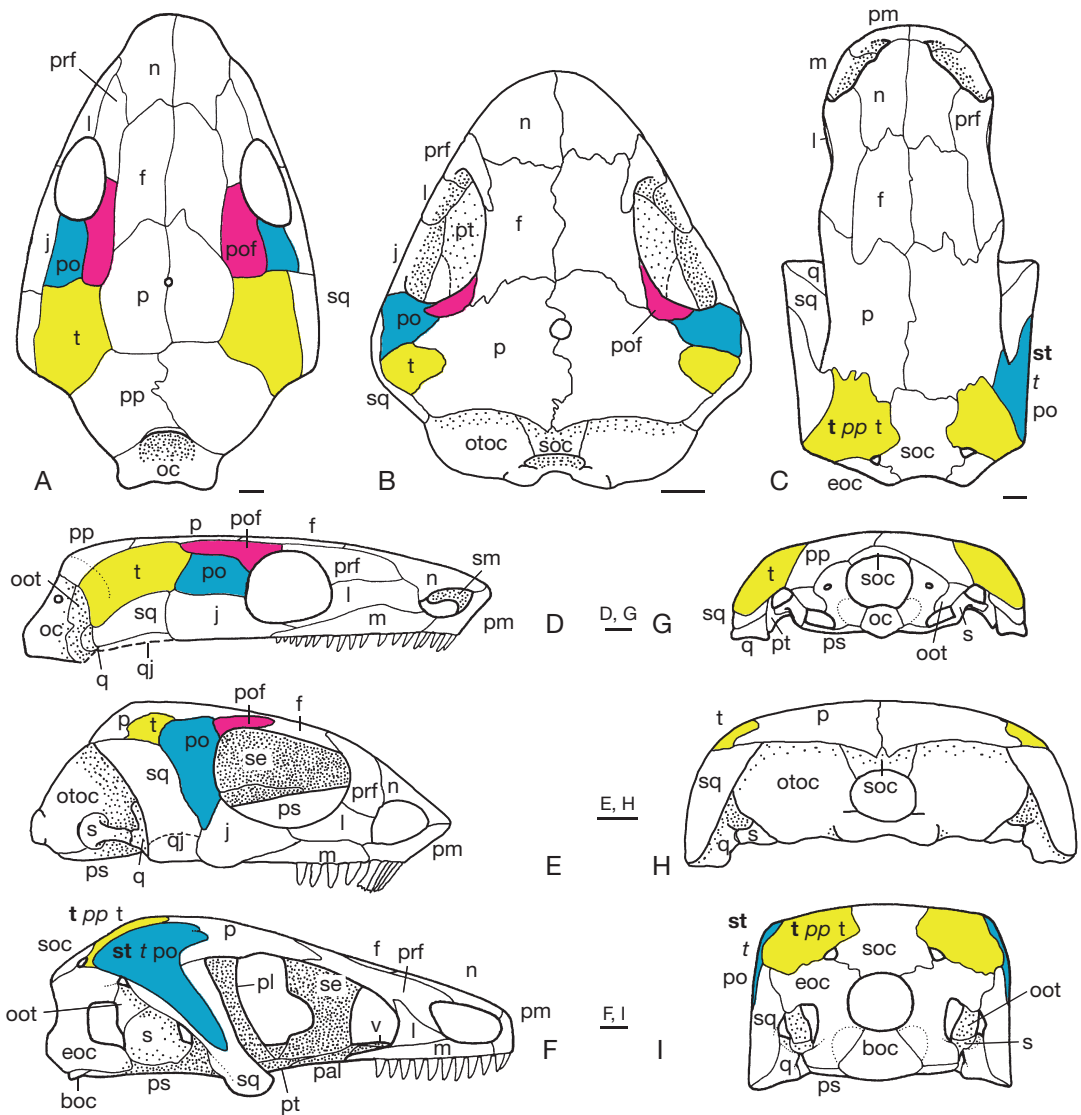
FIG. 3. — Reinterpretation of the skull roof of the lysorophian lepospondyl *Brachydectes* (**C**, **F**, **I**) in comparison to the "microsaurian" lepospondyls *Rhynchonkos* (**A**, **D**, **G**) and *Batropetes* (**B**, **E**, **H**); **A-C**, dorsal view; **D-F**, right lateral view; **G-I**, caudal (occipital) view. Where interpretations of *Brachydectes* differ, those by Sollas (1920), Romer (1966) and Bolt & Wassersug (1975) are in bold, those by Wellstead (1991) are in italics, and ours (Marjanović & Laurin 2008b) are in regular typeface; they are always shown in this order. The colored bones are, in our interpretation, the tabular (yellow/light gray), the postorbital (cyan/middle gray), and the postfrontal (magenta/dark gray). Abbreviations: **boc**, basioccipital; **eoc**, exoccipital; **f**, frontal; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **oc**, fusion of ex- and basioccipital; **oot**, opisthotic; **otoc**, fusion of pro- and opisthotic to ex- and basioccipital; **p**, parietal; **pal**, palatine; **pl**, pleurosphenoid; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pp**, postparietal; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **s**, stapes; **se**, sphenethmoid; **sm**, septomaxilla; **soc**, suproccipital; **sq**, squamosal; **st**, supratemporal; **t**, tabular; **v**, vomer. Scale bar: 1 cm. Modified from Marjanović & Laurin (2008b: fig. 4).

by Fong *et al.* [2012]). Lissamphibian monophyly with respect to Amniota is incompatible with the PH because all large phylogenetic analyses of early limbed vertebrates (Table 1; Fig. 1) show that the lepospondyls are closer to the amniotes than to the temnospondyls. Thus, the PH predicts paraphyly of the extant amphibians in molecular trees.

Morphological phylogenetics so far leads to several mutually contradicting results. This could in part be due to differences in character and taxon sampling in the published data matrices, but also to different approaches to coding characters or to questionable scores. Recently, our lab (Germain 2008a: chapter V; Marjanović & Laurin 2008b, 2009; Marjanović 2010: chapter 5) has started to explore the latter possibility. In the data matrices by McGowan (2002), Ruta & Coates (2007) and Anderson *et al.* (2008b), we have found many scores we disagree with. These range from differences of interpretation over different state delimitations to, apparently, cases where entire clades were scored as having the same state but not every member was checked, momentary confusions of states 0 and 1, cases where the right state was entered in the wrong column, and probable typographic errors. Having at least partially rescored the abovementioned matrices to reflect the descriptive literature, we have found that they all support the LH (Table 1).

Detailed assessment of the reasons for topological incompatibilities was not undertaken until recently because it is a time-consuming task. For instance, our reappraisal of McGowan's (2002) small matrix fills 51 pages of mostly fine print (Marjanović & Laurin 2008b). That matrix is well suited as a test case: it is so small (21 taxa, 41 characters) that it was feasible to scrutinize each cell, to perform seven different analyses (including bootstrapping) based on different assumptions and thus five different matrices, and to use time-consuming methods, most notably stepmatrix gap-weighting (Wiens 2001), on some characters. We found and documented many cases where, e.g., all temnospondyls or all "microsaurs" had been given the same character state even though the character is not known in some of these OTUs or even though (occasionally) another state is known to be present; the matrix by McGowan (2002) contains many scores that differ from published descriptions, and this, it seems, had a large influence on the results.

NOMENCLATURE

A few short comments on nomenclature are necessary because some taxon names mentioned below have multiple meanings and some taxa have more than one name in the recent literature.

The caecilian crown-group (e.g., Schoch & Milner 2004; Marjanović & Laurin 2007; Maddin *et al.* 2012) and sometimes the total group (Cannatella & Hillis 1993; Pyron 2011) have been called Apoda Oppel, 1811. However, *Apoda* Haworth, 1809, is the name of a moth genus. To avoid confusion (especially in search engines), we prefer not to use the name Apoda for a clade of tetrapods. For this reason, we now (Marjanović & Laurin 2008b) follow the other common usage, i.e. calling the caecilian crown-group (rather than the total group) Gymnophiona. In the same paper we also proposed the new name Gymnophionomorpha that is intended to apply to the largest clade that includes the caecilians but excludes the frogs, salamanders, albanerpetontids, and lepospondyls.

Under the International Code of Zoological Nomenclature (ICZN 1999), family names remain valid if they are based on genus names that have been sunk into synonymy. The nomenclature of lepospondyls contains no less than three such cases: Gymnarthridae Case, 1910, is named after a junior synonym of *Cardiocephalus* Broili, 1904, Brachystelechidae Carroll & Gaskill, 1978, after a junior synonym of *Batropetes* Carroll & Gaskill, 1971, and Cocytinidae Cope, 1875, after a junior synonym of *Brachydectes* Cope, 1868. Perhaps by analogy, Ruta *et al.* (2003), Carroll (2007 and earlier), and Anderson (2008) continued to use the name Goniorhynchidae Carroll & Gaskill, 1978, for the monotypic family that contains *Rhynchonkos stovalli* (Olson, 1970). However, *Goniorhynchus* Olson, 1970, is not a junior synonym of *Rhynchonkos*; instead, *Rhynchonkos* Schultze & Foreman, 1981, is a replacement name for *Goniorhynchus* Olson, 1970, which was preoccupied by the beetle *Goniorhynchus* Hampson, 1896. If a taxon is to be named Goniorhynchidae, it must have the valid genus *Goniorhynchus*, not the invalid one, as its type; therefore, Goniorhynchidae Carroll & Gaskill, 1978, has always been invalid and should never have been
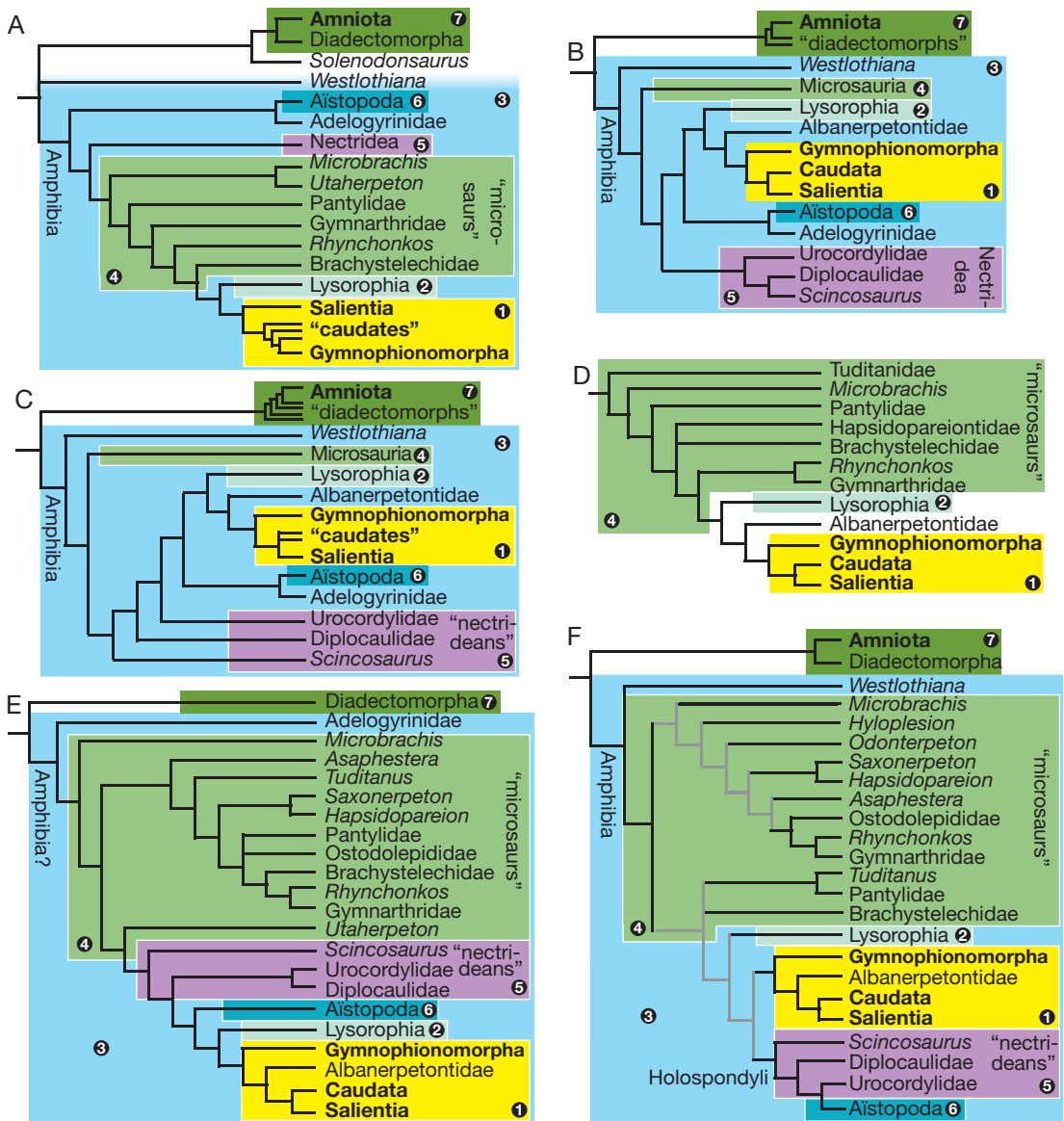
FIG. 4. — Crown-group tetrapod phylogeny according to analyses that support the LH, showing diversity within the LH. All are simpli-fied from their sources (by collapsing suprageneric taxa), and the names are made comparable. Internal topology of Microsauria in B and C not shown. Colored boxes: yellow (❶), Lissamphibia; pastel green (❷), Lysorophia; cyan (❸), Amphibia; olive (❹), "microsaurs"; violet (❺), "nectrideans"; blue (❻), Aïstopoda; dark green (❼), amniotes and diadectomorphs. **A**, Vallin & Laurin (2004: fig. 6); **B**, Pawley (2006: fig. 92), with the taxon sample and cranial characters of Ruta *et al.* (2003) but Pawley's own set of postcranial characters, and reweighting; **C**, Germain (2008a: fig. 5.15); **D**, Marjanović & Laurin (2008b: fig. 6c), Tuditanidae, and Hapsidopareiontidae are OTUs that may not be monophyletic, their composition was not tested, but carried over from McGowan (2002); **E**, Marjanović & Laurin (2009: supplementary figure); **F**, Marjanović (2010: chapter 5), unconstrained analysis without added taxa. The majority-rule consensus is shown; internodes absent from the strict consensus are gray.

erected (ICZN 1999: art. 39). Accordingly, Zanon (1988) coined the replacement name Rhynchonkidae. This is the name that should be used if one is not content to refer to the only known genus and species directly by their own names.

Finally, the smallest or almost smallest clade that includes the "nectridean" lepospondyls *Keraterpeton* Etheridge, 1866, and *Diplocaulus* Cope, 1877, is more often called Keraterpetontidae than Diplocaulidae in recent literature; yet, Diplocaulidae Cope, 1881, has clear priority over Keraterpetontidae Jaekel, 1902.

THE CURRENT STATES
OF THE LEPOSPONDYL AND
THE POLYPHYLY HYPOTHESES

Anderson (2008) and Sigurdsen & Bolt (2009), among others, suggested that the lepospondyl hypothesis on the origin of lissamphibians (LH) is only supported by ML and his collaborators. This is incorrect, even though the LH certainly lacks broad support at present. Working without our knowledge, Pawley (2006: figs 88, 89, 91, 92) reviewed the matrix of Ruta *et al.* (2003), which initially supported the TH, and performed a large number of analyses on it. In all analyses with the same taxon sampling as Ruta *et al.* (2003), presented in app. 16, she found support for the LH, except in the analysis without postcranial characters, which led to a large polytomy encompassing all temnospondyls, seymouriamorphs, lepospondyls, and amniotes (Pawley 2006: fig. 90). Even in that latter analysis, Amphibamidae is monophyletic with respect to Lissamphibia + Albanerpetontidae – a result that is compatible neither with any version of the temnospondyl hypothesis (TH) proposed in the last 15 years, where Lissamphibia is thought to be nested within Amphibamidae, nor with the polyphyly hypothesis (PH). In the analyses with her own preferred taxon sampling, which are presented in chapter 6 of the thesis, Pawley omitted all extant amphibians, but she did mention (Pawley 2006: 239) that the postcranial evidence favors the LH over the TH. Unfortunately, the reasons for many of Pawley's coding decisions are not better documented than those of Ruta *et al.* (2003).

Unsurprisingly, some diversity now exists within the LH concerning which lepospondyls are the closest relatives of Lissamphibia and where Albanerpetontidae fits (Fig. 4). Vallin & Laurin (2004) found the lysorophians to be sister-group of Lissamphibia, followed by the brachystelechid "microsaurs" and then various other "microsaurs" (Fig. 4A). Other studies (Germain 2008a: chapter V; Marjanović & Laurin 2008b, 2009; Fig. 4C-E) generally also have Lysorophia as the sister-group of Lissamphibia (or Lissamphibia + Albanerpetontidae, when the latter lies outside Lissamphibia), but the topology varies among more distant relatives of Lissamphibia. When she replaced the postcranial dataset of Ruta *et al.* (2003) by her own, but kept their taxon sample, Pawley (2006: figs 91, 92; Fig. 4B) found the closest relatives of Lissamphibia to be Albanerpetontidae, followed by lysorophians and a clade composed of aïstopods and adelogyrinids; all these are nested among the "nectrideans" (Pawley 2006: fig. 91) or form their sister-group (Pawley 2006: fig. 92). Most trees in Marjanović (2010: ch. 5; majority-rule consensus in Fig. 4F), a study based on a modified version of the matrix of Germain (2008a), itself derived from Ruta & Coates (2007), show Lissamphibia (including Albanerpetontidae) as the sister-group to a "nectridean"-aïstopod clade (Holospondyli Schwarz, 1908), with the next closest relative being Lysorophia followed by the paraphyletic "microsaurs". A monophyletic Microsauria Dawson, 1863, was found by Pawley (2006: figs 88, 89, 91, 92) and Germain (2008a).

Similarly, there are considerable differences between the versions of the polyphyly hypothesis (PH) by Anderson (2007) and Anderson *et al.* (2008b) on one hand and Carroll (2007 and earlier) on the other: while both agree on frogs and salamanders being temnospondyls (exception: Carroll & Holmes 1980) and caecilians being lepospondyls (Fig. 1H), Anderson (2007) and Anderson *et al.* (2008b) found Salientia and Caudata as more closely related to each other than to any Paleozoic taxon (Fig. 1G), while Carroll derived the frogs from amphibamids and the salamanders from branchiosaurids. Carroll (2007: fig. 78) also considered lepospondyl intrarelationships to be quite different from those found by Anderson (2001, 2007) and Anderson *et al.* (2008b).

PHYLOGENY OF LISSAMPHIBIA

As if the confusion about the origin(s) of the extant amphibians were not enough, there is no broad consensus in the current literature on whether the frogs or the caecilians are the extant sister-group of the salamanders. The first hypothesis recognizes Batrachia Latreille, 1800, a clade formed by anurans and urodeles; the second recognizes Procera Feller & Hedges, 1998, formed by urodeles and gymnophionans. The position of the albanerpetontids is even less clear, with all possible positions except a sister-group relationship to the frogs having been supported by phylogenetic analyses within the last ten years. To some degree, as pointed out in the literature, these hypotheses interact with the abovementioned hypotheses on the origin of Lissamphibia, because several character states present in amphibamids (especially *Doleserpeton* or *Gerobatrachus*) or lepospondyls (especially lysorophians) are present in some but not all lissamphibians.

BATRACHIA OR PROCERA?

Anderson (2008) portrayed the Procera hypothesis as part of the LH. This is indeed the topology that best fits the results of Vallin & Laurin (2004; Fig. 4A) and earlier installments of the LH, as well as (arguably) those of the morphology-only analysis by Pyron (2011), but the Batrachia hypothesis is strongly supported by the Bayesian analyses with combined data by Pyron (2011) and the bootstrap analyses of Marjanović & Laurin (2008b: fig. 6d; 2009: supplementary figure; see also Fig. 4D, E). Likewise, Germain (2008a) found the Batrachia hypothesis (frogs and salamanders as sister-groups to the exclusion of caecilians) to be better supported (Fig. 4C), as did Marjanović (2010; Fig. 4F). Pawley found the same result in some (Pawley 2006: figs 90-92; Fig. 4B) but not others of her analyses (fig. 89 shows Procera; fig. 88 shows a polytomy between Salientia, the gymnophionomorph *Eocaecilia*, Caudata, and Albanerpetontidae). In fact, as pointed out by Bolt (1991), Ruta *et al.* (2003) and Schoch & Milner (2004), the Procera hypothesis is more compatible with the TH because certain character states are shared only by salientians and dissoro-phoid temnospondyls; a possible example is the tympanic middle ear, of which any trace is lacking in Caudata and Gymnophionomorpha (and, as far as can be determined, Albanerpetontidae), but which several authors believe to have been present in many or most temnospondyls, including all terrestrial and amphibious dissorophoids (e.g., Bolt & Lombard 1985). Indeed, Maddin & Anderson (2012) found the Procera hypothesis in combination with the TH (although Maddin *et al.* [2012] did not). Under the Batrachia hypothesis combined with the TH, homology of the salientian and the putative dissorophoid tympanum would require two (or, depending on the position of the albanerpetontids, more likely three) independent losses that resulted each time in convergence with the stapedial morphology and spatial relationships seen in lepospondyls and early amniotes but not any temnospondyls. In any case, the presence of a tympanum in temnospondyls is debatable; Laurin & Soler-Gijón (2006) reviewed evidence that most temnospondyls lacked a tympanum, and Witzmann & Schoch (2006) showed that if the terrestrial dissorophoid temnospondyl *Acanthostomatops* Credner, 1883, possessed a tympanum, it must have been rather different in size, shape and position from that seen in frogs and commonly reconstructed in *Doleserpeton*.

The Batrachia hypothesis appears to be better supported than the Procera hypothesis by both morphological (Ruta & Coates 2007; Germain 2008a; Marjanović & Laurin 2008b, 2009; Marjanović 2010; Sigurdsen & Green 2011; Maddin *et al.* 2012) and, to a lesser extent, molecular data (Marjanović & Laurin 2007; Anderson 2008: table 2; San Mauro 2010). The combined analyses by Pyron (2011) concur – this is important because combined analyses do not necessarily yield results supported by any of their constituent data sets when these are analyzed in isolation; sometimes, three (Lee 2009) or even "forty-five wrongs make a right" (Gatesy & Baker 2005). Except for Maddin & Anderson (2012), which we consider superseded by Maddin *et al.* (2012), no analysis which included albanerpetontids has ever found Procera; but all of these have so far lacked molecular data altogether.

The phylogenetic position of Albanerpetontidae

Unfortunately, the confusion summarized by Marjanović & Laurin (2008b: 169) still reigns. The albanerpetontids were long interpreted as stem-caudates (Trueb & Cloutier 1991) and were again found in such a position by Anderson (2007), Anderson *et al.* (2008b) and Maddin *et al.* (2012). Arguing against this hypothesis, McGowan & Evans (1995) and McGowan (2002), as well as Marjanović & Laurin (2009: ESM 2 [supplementary figure]; Fig. 4E) and Marjanović (2010; Fig. 4F), found Albanerpetontidae and Batrachia as sister-groups. Ruta & Coates (2007) and Maddin & Anderson (2012) recovered Albanerpetontidae and Gymnophionomorpha as sister-groups. Finally, Pawley (2006: app. 16; Fig. 4B) and Marjanović & Laurin (2008b; Fig. 4D) found Albanerpetontidae and Lissamphibia as sister-groups, an arrangement called "only slightly longer" than an albanerpetontid-batrachian clade by McGowan & Evans (1995: 145) and contained in at least one of the 64 most parsimonious trees found by Ruta *et al.* (2003).

Potential reasons for this lack of consensus are easy to find: despite their vast stratigraphic distribution, most albanerpetontids are known only from isolated frontal or jaw bones. Complete skeletons (with fully articulated scales, possible femoral glands, and a body outline; McGowan 2002) have only been found for the Early Cretaceous *Celtedens* McGowan & Evans, 1995, and these are preserved in two dimensions; worse yet, all of these specimens have been split through the bone, which hampers interpretation of certain features (such as most of the skull).

QUANTITY AND QUALITY OF DATA IN MATRICES

Quantity

Schoch & Milner (2004: 355), Anderson (2008: 234) and Maddin & Anderson (2012: 70) pointed out that the matrix of Vallin & Laurin (2004), which supports the LH, is considerably smaller than those which support the TH (Ruta *et al.* 2003; Ruta & Coates 2007) or some that support the PH (Anderson 2007; Anderson *et al.* 2008b) and used this as an argument against the LH.

However (Table 1), the matrices by Pawley (2006: app. 16) that support the LH are much bigger than that of Vallin & Laurin (2004), ranking highest and second highest in numbers of parsimony-informative morphological characters among all analyses of the phylogeny of limbed vertebrates conducted so far. They also rank third in the number of OTUs (together with the source of that taxon list, the matrix by Ruta *et al.* 2003). The second rank in OTU number goes to Ruta & Coates (2007), ranking fourth in character number and supporting the TH, Germain (2008a), ranking fifth in character number and supporting the LH, and the analysis without added OTUs by Marjanović (2010), which supports the LH but ranks eighth in the number of characters. The first rank in OTU number, and again the eighth in character number, goes to the analysis with added OTUs by Marjanović (2010), which likewise supports the LH. The TH is supported by the analysis with the third rank in character number but the fourth lowest number of OTUs, namely 25 (the analysis with merged matrices by Sigurdsen & Green 2011). By quantity alone, thus, there are no consistent differences in size between the largest matrices which support the LH and the TH.

Importantly, character counts can be inflated in ways that mean they should not be taken at face value. One example is the "atomization" of characters by coding correlated features separately. To include correlated characters in a matrix has the same effect as weighting some characters higher than others and should therefore be strictly avoided. Of course, which characters are correlated is usually a difficult or at least time-consuming question to answer, but some cases in the literature appear obvious to us. The probably most extreme example consists of characters 313 through 316 of Ruta *et al.* (2003), which are quoted below and are identical to characters 333 through 336 of Ruta & Coates (2007):

"313. Absence (0) or presence (1) of digits.

314. Absence (0) or presence (1) of no more than four digits in manus.

315. Absence (0) or presence (1) of no more than five digits in manus.

316. Absence (0) or presence (1) of no more than three digits in manus."

If an animal has no more than three fingers per hand, it also has no more than four and no more than five. This was not taken into account in the matrices; all OTUs with state 316(1) were also scored as 314(1), 315(1) and 313(1). Accordingly, Germain (2008a) merged these characters into a single multistate character, which follows (translated):

"333. Primitive absence of fingers (0), more than five fingers (1), five fingers (2), four fingers (3), three fingers (4), secondary absence of fingers (5)."

This can probably still be improved. Most evidently, as Marjanović (2010) did, the wordings "primitive absence" and "secondary absence" should be modified so as to avoid assumptions of secondary homology in the coding of primary homology (perhaps as "fin present" and "extremity absent", respectively), and the character should be given a stepmatrix that orders states 0 to 4 and counts every transition to state 5 as a single step (as also done by Marjanović 2010). Some of these concerns were addressed by Ruta & Bolt (2006: 157), who used a single (but unordered) multistate character. However, as mentioned, Ruta & Coates (2007) did not.

QUALITY
It has been argued that data quality is at least as important as data quantity for testing phylogenetic hypotheses (Jenner 2001; Marjanović & Laurin 2008b: 167; Morrison 2009; Sigurdsen & Green 2011). In this perspective, several recent studies have focused on scrutinizing published data matrices to ensure that they were of comparable scoring quality.

To verify the data supporting the TH, Germain (2008a) checked the accuracy of the scoring of part of the data matrix of Ruta & Coates (2007), found the scoring of many cells to be incompatible with the descriptive literature, and rescored them. Analysis of the resulting matrix suggests that the LH (Germain 2008a: fig. 5.15) is more parsimonious than the temnospondyl hypothesis (TH), but only by one step. More recently, an extension of this work by DM (Marjanović 2010) increased the gap to eight steps (ten steps if *Gerobatrachus* and eight other OTUs are added)); this is being continued, and the gap has currently reached 12 steps (14 steps if *Gerobatrachus* and 35 others are added).

Two matrices supporting the PH have recently been scrutinized in this way. The first (McGowan 2002) initially supported a version of the PH that was replicated only by Carroll (2007). Not only, however, was this matrix tiny (20 ingroup OTUs, 41 characters); it was also riddled with codings that contradict the descriptive literature. We (Marjanović & Laurin 2008b) checked every cell against the literature and specimens of *Micromelerpeton* Bulman & Whittard, 1926, *Apateon* von Meyer, 1844, *Microbrachis* Fritsch, 1875, and *Triadobatrachus*, and changed the scoring of 35% of the cells (which includes redefining the state limits of some characters and splitting or fusing others). Every change to the matrix is documented and justified in appendix 1 of Marjanović & Laurin (2008b). The resulting version of McGowan's matrix supports either the TH or the LH, the latter if either the lysorophian *Brachydectes* is added or the described material of *Doleserpeton* is considered immature or paedomorphic (see below) – adding *Gerobatrachus* has no effect, though we must caution that several of the apomorphies it shares with some or all lissamphibians are not included in the matrix.

The second matrix supporting the PH to be re-examined recently, that of Anderson *et al.* (2008b) which accompanied the description of *Gerobatrachus*, was scrutinized in less detail because of its much larger size, but rescoring following the same methods resulted in a matrix that supports the LH (Marjanović & Laurin 2009: electronic supplementary material).

The third matrix supporting the PH (Caroll 2007) has not been subjected to the same scrutiny. However, we find several problems to be readily apparent. For instance, many characters (Carroll 2007: app. 3) contain "inapplicable" *as a state*, so that the loss of limb bones and the pelvic girdle is coded several times for the same OTU, which amounts to arbitrarily weighting such characters higher than all others. The extreme is nine times each for the humerus (characters 69 through 77, which describe the humerus, all contain a state called "does not apply") and the rest of the forelimb (characters 78 through 86); furthermore, these losses are not independent, because the humerus is never lost when the lower forelimb is still present, so that a single

loss of the forelimb counts as eighteen apomorphies. As is otherwise universal practice, these cells should be scored as "inapplicable", that is, "unknown".

Many characters in Carroll's (2007) matrix have extremely high numbers of states. The extreme is twelve states each for characters 19 and 45; there are only 23 OTUs in the matrix, which means, for these characters, on average less than two OTUs for each state. "All characters are unordered" (Carroll 2007: 119), so these characters are almost parsimony-uninformative – an unordered character of which each state only occurred in one OTU would be uninformative.

The taxon list contains suprageneric OTUs that Carroll himself (2007) explicitly considers paraphyletic with respect to other OTUs, for example "Microsauria" with respect to "*Rhynchonkos*" or "Basal Temnospondyls" with respect to "Branchiosauridae" and "Amphibamidae".

Finally, we think that some (perhaps many) codings seem difficult, if not impossible, to justify. For example, characters 115 (ossification of whole dermal skull at once vs two orders of sequential ossification) and 116 (ossification of neural arches before centra or not) are scored as known for most lepospondyls. In fact, the only lepospondyl of which even a partial skull ossification sequence (three stages) is known is the highly apomorphic aïstopod *Phlegethontia* Cope, 1871 (Anderson 2002, 2007; see also Marjanović & Laurin 2008b: 158), and the only known lepospondyl of which even a small part of the vertebral ossification sequence is known is *Utaherpeton* Carroll, Bybee & Tidwell, 1991 (suggested to be a basal "microsaur": Carroll *et al.* 1991; Carroll & Chorn 1995). The fact that the smallest known specimens of a taxon already possess all skull bones does not mean that these bones all formed at the same time; it simply means that we have not found even younger, smaller, and less well mineralized individuals yet.

This review shows that, contrary to the impression that could be gathered by counting the number of published matrices, papers, or paleontologists which support the PH or, to some extent, the TH, neither hypothesis is nearly as well supported as it might seem at first glance. Conversely, the LH, although so far supported by the smallest number of studies or scientists, appears to have fairly strong support from data matrices.

SIGURDSEN & GREEN (2011): A STEP TOWARDS CONSENSUS?

We applaud the recent far-reaching attempt by Sigurdsen & Green (2011) to fill in missing data and improve codings in the matrices by Vallin & Laurin (2004), Ruta & Coates (2007) and Anderson *et al.* (2008b) using the descriptive literature and specimens, and to unite these three matrices to overcome the large differences in character sampling. We are pleasantly surprised that they used terms like "uncorrected", "corrected", "critiqued", "misinterpretation", and "incorrect or misleading" to describe scoring in matrices, because several referees have objected to use of such wording in our manuscripts. These corrections include "many of the changes suggested by Marjanovic [sic] & Laurin (2009) to correct the data set of Anderson *et al.* (2008b)" (Sigurdsen & Green 2011: 459). Furthermore, the extremely high ratio of parsimony-informative characters to taxa (13.4) bears pointing out – many recent analyses have ratios close to 3 or even 2, which raises concerns about accidental sampling bias. Still, it is clear that their analysis cannot be regarded as having solved the question.

The largest issue we see is taxon sampling. Sigurdsen & Green (2011) used only those OTUs that are shared by all three of the matrices they investigated; this left only 25 OTUs, including the outgroup *Acanthostega* Jarvik, 1952. As Sigurdsen & Green (2011: 459) noted, this meant that *Gerobatrachus* had to be excluded in spite of its potential importance for the PH. It also meant that Albanerpetontidae had to be excluded, even though that taxon has great potential to break up long branches around the base of Lissamphibia, retains plesiomorphies that are rare in the other modern amphibians, and is more strongly attracted to the lepospondyls than *Eocaecilia*, the frogs or the salamanders (DM, pers. obs. on a matrix almost identical to that of Marjanović [2010: ch. 5]).

Moreover, Sigurdsen & Green (2011: 459) did not order any characters, despite good arguments that potentially continuous and meristic characters should be ordered (Wiens 2001). One of their sources, Vallin & Laurin (2004), had ordered several characters.

Finally, we are disappointed that, on the last two pages of their paper – after the discussion of analyses and results –, Sigurdsen & Green (2011) revert to the conceptual framework of "key taxa" (table 4), "informative characters" that are (table 4) chosen independently of the results of their analyses, subjective "evolutionary implausibilities" (467) of unassessed objective probability, and the idea that character states that have clearly evolved often are less convincing synapomorphies than states that may have evolved only twice and/or are "unique among tetrapods" (466). This latter argument in particular strikes us as indefensible. As far as can be known today, the probability that a character state evolves stays the same every time it evolves anew; it does not depend on the number of times it has already appeared. The hypothesis that, e.g., tooth pedicely (found in osteoglossomorph actinopterygians, some amphibamid temnospondyls, and most lissamphibians) evolved twice is more parsimonious than the hypothesis that it evolved three times if this character is considered in isolation, but only congruence of the totality of evidence can tell us which hypothesis is globally more parsimonious.

"Informative character distributions" and "key taxa"

To facilitate comparison of our review to previously published ones, we discuss a few characters that have been argued to support various hypotheses about lissamphibian origins by Anderson (2008) and/or Sigurdsen & Green (2011: table 4), as well as a few other relevant characters that have traditionally been neglected or had mostly unknown distributions until recently. The complete list of apomorphies that support one of the most parsimonious trees by Marjanović (2010: chapter 5) forms Appendices 1-10.

Tooth pedicely

Pedicellate teeth occur in osteoglossomorph actinopterygians, the amphibamids *Doleserpeton* and possibly (but see Sigurdsen & Bolt 2010) *Amphibamus* Cope, 1865, and (plesiomorphically) in caecilians, salamanders, and frogs but not albanerpetontids. Unless the tentative reports of possibly pedicellate teeth in the "microsaurian" lepospondyl *Carrolla*

Langston & Olson, 1986 (Maddin *et al.* 2011), or the aïstopod lepospondyl *Phlegethontia* (Germain 2008b), can be substantiated, this character supports the TH.

We have previously (Marjanović & Laurin 2009) pointed out that Milner (1980: 392) called the teeth of the "nectridean" *Scincosaurus* Fritsch, 1876, "pedicellate […] without a line of abscission". This was a reference to the long, cylindrical bases of its tooth crowns (which could be called "pedicels"); the teeth indeed lack "a line of abscission" and are thus not pedicellate (A. C. Milner, pers. comm. to DM, September 2009; Milner & Ruta 2009). However, we would like to draw attention to the fact that very few lepospondyls – and indeed not that many temnospondyls either – have been investigated in enough detail to determine whether they have pedicellate teeth. As a target for future research, we would once more like to suggest the aïstopod *Oestocephalus* Cope, 1868, of which Carroll (1998: figs 4B, 8A) illustrates a dentary and maxillae where many teeth seem to be broken off at the same level, as if crown tips had fallen off from pedicels (seen in many fossil lissamphibians and *Doleserpeton* but not *Amphibamus* or *Gerobatrachus*) – Carroll (1998: 158) even mentions this resemblance explicitly.

Number of presacral vertebrae

Crown-group frogs (anurans) are notorious for their extremely short presacral columns; the highest number of presacral vertebrae, found in *Ascaphus* Stejneger, 1899, and *Leiopelma* Fitzinger, 1861, is 9. Among stem-frogs (stem-salientians), *Notobatrachus* Reig *in* Stipanicic & Reig, 1955, has 9, *Vieraella* Reig, 1961, has 9 or 10, and *Triadobatrachus* still only reaches 14 (Roček & Rage 2000; Carroll 2007). This overlaps the range of Mesozoic salamanders, which reaches from 13 in the stem-caudate *Karaurus* Ivachnenko, 1978 (pers. obs. on a cast in the Muséum national d'Histoire naturelle, Paris, March 2010) to 17 in the early urodele *Valdotriton* Evans & Milner, 1996 (Evans & Milner 1996). The only albanerpetontid with a completely known presacral column, *Celtedens ibericus* McGowan & Evans, 1995 (McGowan 2002), was less abbreviated (21 or 22 vertebrae, depending on how the archless "axis" is

interpreted). Most temno- and lepospondyls have 25 or (sometimes) a few more presacral vertebrae, but there are exceptions among the amphibamids: branchiosaurids have 19-24 (Boy & Sues 2000), *Doleserpeton* has at least 22, probably 24 (Sigurdsen & Bolt 2010), *Amphibamus* has 21 (Anderson 2008), *Gerobatrachus* has only 17 (Anderson *et al.* 2008b). 24 or fewer presacrals are also found in the pantylid and the brachystelechid "microsaurs". In stark contrast, the caecilians are greatly elongate animals; the lowest presacral count, 49, is estimated for *Eocaecilia* (Jenkins *et al.* 2007) and resembles those of elongate "microsaurs" (Ostodolepididae Romer, 1945, *Rhynchonkos*, Gymnarthridae) and lysorophians. This character appears to require about six steps (depending on "microsaur" phylogeny) under all hypotheses. Probably the signal is primarily ecological: the presacral column is shortened in terrestrial walkers and possible burrowers with unreduced limbs (amphibamids including metamorphosed branchiosaurids; brachystelechids; pantylids; albanerpetontids; batrachians plesiomorphically), further shortened in jumpers (salientians other than *Triadobatrachus*; anurans which later adapted to walking, limb-based burrowing or hindlimb-propelled swimming had no selection pressure to secondarily lengthen their presacral columns), and lengthened in terrestrial (elongate "microsaurs"; caecilians) and aquatic (lysorophians) burrowers with reduced limbs.

Tusks on the palate
Plesiomorphically, tetrapodomorphs possess teeth on the vomer and the palatine that are taller and/or broader at the base than the marginal teeth and the teeth in the vomerine and palatine toothrows (when such toothrows are present). Usually, there is only one such enlarged tooth per bone, paired with an empty alveolus that represents the previous and the next tooth generation. Such "tusks" or "fangs", as they are usually called, are absent in lissamphibians, and much has been made of the fact that *Doleserpeton* lacks them as well (Bolt 1969, 1979, 1991; Schoch & Milner 2004; Sigurdsen & Bolt 2010), as does *Gerobatrachus* (Anderson *et al.* 2008b). However, tusks are also absent in premetamorphic and juvenile postmetamorphic specimens of its close

relative *Amphibamus*, being known to be present only in the largest known specimen (Daly 1994: 27). This may be evidence that the loss of tusks in *Doleserpeton* and *Gerobatrachus* is a consequence of their miniaturization (paedomorphosis in the dermal skeleton; Sigurdsen 2008, Sigurdsen & Bolt 2010), so that *Doleserpeton* should be scored as unknown for this character in phylogenetic analyses (Marjanović & Laurin 2008b: 157, 180, 193 – see below).

Be that as it may, palatal tusks are absent throughout the amniote-diadectomorph-lepospondyl clade (the tetrapod crown-group according to the LH), with only three reversals (all of them among "microsaurs"): *Crinodon* Carroll & Gaskill, 1978, has fairly large teeth scattered in irregular rows or fields on the vomers, palatines, ectopterygoids and pterygoids (Carroll & Gaskill 1978: fig. 11); *Asaphestera* Steen, 1934, has a toothrow on the palatine (and possibly the vomer) that is parallel to the much smaller teeth of the maxilla (Carroll & Gaskill 1978: fig. 7); and *Pantylus* Cope, 1881, though it lacks tusks on the extremely narrow vomers, has a large one on each palatine (Carroll & Gaskill 1978: fig. 25). Evidently, this pair of characters is equally compatible with all three phylogenetic hypotheses.

The radial condyle/capitulum/capitellum/capitate eminence on the humerus
In many limbed vertebrates, the radius articulates with a hemispherical condyle on the humerus; a comparable condyle for the ulna seems to be restricted to amniotes. Along with other features of the humerus, this was described in detail by Sigurdsen & Bolt (2009). In lissamphibians (including *Eocaecilia*) and *Doleserpeton*, the radial condyle is especially large, and the epicondyles are small enough that the condyle lies close to the medial edge of the bone and occupies about half of the width of its distal end. Sigurdsen & Bolt (2009) pointed out that this condition has not so far been found in a "microsaur" and thus supports the TH. We think the situation is more complicated.

In the "microsaurs" *Pantylus* (Carroll & Gaskill 1978: fig. 122B) and *Trihecaton* Vaughn, 1972 (DM pers. obs. of CM 47681 [Carnegie Museum of Natural History, Pittsburgh], November 2012; *contra* Carroll & Gaskill 1978: fig. 123K), the con-

dyle lies very close to the medial edge of the bone (the ectepicondyle is very narrow) and occupies close to half of its distal width if the enormous entepicondyle (as wide as the radial condyle) is not taken into account. The "nectridean" *Scincosaurus* (Milner & Ruta 2009) shows a condition similar to that seen in lissamphibians and *Doleserpeton* but with a wider ectepicondyle and a proximodistally considerably taller entepicondyle reminiscent of the mediolaterally much broader one of *Pantylus* and *Trihecaton*. Size and shape of the condyle and the epicondyles should probably not be treated as a single character as Sigurdsen & Bolt (2009) have done.

The main problem in coding this character is that the condyle ossifies late in ontogeny, if ever, remaining cartilaginous in many aquatic and small amphibious forms including many extant salamanders (Sigurdsen & Bolt 2009). Very few lepo- or temnospondyls thus preserve the condyle at all. Moreover, the sizes of the epicondyles, and thus the distal width of the humerus relative to the radial condyle, appear correlated to power (larger epicondyles) versus speed (smaller ones), so that small epicondyles and therefore a relatively large radial condyle are found in animals with long, gracile limbs and short presacral vertebral columns (see above), such as amphibamids, lissamphibians, and lizard-shaped amniotes like Paleozoic diapsids and varanopids. Thus, this character is of uncertain phylogenetic significance if it is treated separately from other adaptations to terrestrial locomotion.

Participation of the palatines in the margin of the interpterygoid vacuities

Usually, the interpterygoid vacuities are formed by the pterygoids and the parasphenoid alone, with occasional participation of the vomer in forms with wider snouts. In lissamphibians, the palatines form part of the margins of the vacuities (or are entirely missing as in some frogs and in metamorphosed salamanders, so that the vacuity reaches all the way to the maxilla and is open laterally between the maxilla and the pterygoid), and the same is seen in dissorophoid temnospondyls other than trematopids and the possible trematopid *Ecolsonia* Berman, Reisz & Eberth, 1985. Even given the LH, the occurrences in the diplocaulid "nectrideans" *Diplocaulus*

and *Diploceraspis* Romer, 1952, are unlikely to be homologous to that in Lissamphibia, as are those in the aïstopods *Oestocephalus* and *Phlegethontia* (which lacks a distinguishable palatine altogether); thus, this character supports the TH.

Clear convergence is also found in some dvinosaurian temnospondyls and in plagiosaurid stereospondyl temnospondyls.

Contribution of the jugal to the ventral skull margin

Plesiomorphically, the caudal end of the maxilla is sutured to the quadratojugal, excluding the jugal from the ventral margin of the skull. Sigurdsen & Green (2011: table 4) distinguish four states in this character: the caudal end of the maxilla can contact the quadratojugal (0), the jugal (1), the palatine (2) or end freely (3). They assign state 0, the plesiomorphy, to *Doleserpeton*, *Eocaecilia* and Salientia, state 1 to amniotes and "microsaurs", state 2 to Lysorophia and state 3 to Caudata; interpreted this way, this character would support the TH, because the LH and the PH would require a reversal in frogs and/ or *Eocaecilia*. However, this character is not applicable to lysorophians, frogs or salamanders, because they lack the jugal – a jugal that is not there cannot contribute to the ventral skull margin, so state 1 is impossible in these animals. Lysorophians and most salamanders further lack the quadratojugal, precluding state 0; metamorphosed salamanders lack even the palatine, so they cannot have state 2 and are logically restricted to having state 3 by default (a contact between maxilla and pterygoid is sometimes found). Most frogs possess a maxilla-quadratojugal contact, and the missing jugal leaves a fenestra; however, this difference from salamanders and lysorophians is better expressed by making states 2 and 3 a separate character that describes whether the ventral skull margin is complete, as done for instance by Ruta & Coates (2007). After all, the ventral skull margin can be incomplete even when the jugal is present (and attaches dorsally rather than caudally to the caudal end of the maxilla), which occurs in ostodolepidid "microsaurs" and in many sauropsid amniotes. The presence or absence of the palatine in salamanders (and the aïstopods *Oestocephalus* and *Phlegethontia*) is likewise better accommodated elsewhere.

Thus, this character should have only two states, and the only lissamphibians to which it can be applied are *Eocaecilia* and the albanerpetontids. The latter apparently possess state 1 – while it is not known if a quadratojugal was present, a bone identified as the jugal is present and forms about half of the ventral margin of the skull (McGowan 2002; Venczel & Gardner 2005). *Eocaecilia* shows state 0 instead (Jenkins *et al.* 2007). State 0 is retained by most temnospondyls, in particular all dissorophoids; state 1 is an autapomorphy of a clade formed by *Solenodonsaurus* Broili, 1924, Seymouriamorpha, Amniota, Diadectomorpha, and the lepospondyls, with three or four reversals among lepospondyls in the "microsaur" *Euryodus primus* Olson, 1939 (Carroll & Gaskill 1978: 63; unknown in *E. dalyae* Carroll & Gaskill, 1978), the urocordylid "nectrideans" *Urocordylus* Huxley, 1866, and *Sauropleura* Cope, 1868, and the aïstopod *Oestocephalus*, as well as several reversals among Paleozoic amniotes. This makes the TH and the LH equally parsimonious: under the TH, *Eocaecilia* retains state 0, and Albanerpetontidae gains state 1 in parallel to the abovementioned clade of lepospondyls and their relatives; under the LH, Albanerpetontidae retains state 1 from that clade, and *Eocaecilia* has undergone a reversal.

Length and width of the vomers
Table 4 of Sigurdsen & Green (2011) contains a character "Vomers narrow anteriorly", which has the state "No" in *Acanthostega*, *Doleserpeton*, Salientia, Caudata, and *Eocaecilia*, and the state "Yes" in Amniota, "Microsauria" and Lysorophia. This is probably correct, but unfortunately Sigurdsen & Green (2011) did not quantify this character, and their taxon sample oversimplifies the picture.

Ruta & Coates (2007) defined two cutoff ratios of vomer length to width. Unfortunately, they made two characters out of them. Merging them (Marjanović 2010: chapter 5, character 106) yields a character with three states: "Vomer approximately as wide as long or wider (0), intermediate (1), at least 2½ times longer than wide (2) (ordered)." State 1 is the plesiomorphy, homologous from *Eusthenopteron* Whiteaves, 1881, through most temnospondyls and further present in *Eocaecil-*

ia, the seymouriamorph *Utegenia* Kuznetsov & Ivakhnenko, 1981, one or two clades of "microsaurs", and all holospondyls ("nectrideans" and aïstopods) except the long-snouted *Sauropleura*; state 0 occurs in *Ventastega* Ahlberg, Lukševičs & Lebedev, 1994, *Colosteus* Cope, 1869, *Baphetes* Owen, 1859, Amphibamidae (not including Branchiosauridae Fritsch, 1883), the seymouriamorph *Ariekanerpeton* Ivachnenko, 1981, and Batrachia (unknown in Albanerpetontidae); state 2 is found in some (maybe most) anthracosaurs, the remaining seymouriamorphs, Amniota + Diadectomorpha, "microsaurs" plesiomorphically, Lysorophia, and the abovementioned "nectridean" *Sauropleura*. Under the LH, state 1 is homologous between *Eocaecilia* and Holospondyli, at least if Lysorophia stays outside the Lissamphibia-Holospondyli clade, and state 0 is convergent between Batrachia and Amphibamidae; under the TH, state 0 is homologous between Batrachia and the other amphibamids, and state 1 in *Eocaecilia* is a reversal. Both arrangements are equally parsimonious, and the character supports the PH by one step.

The craniovertebral joint: cranial side
In lissamphibians, there are two separate occipital condyles, apparently formed by the exoccipitals and articulating with two separate cotyles on the atlas; the basioccipital appears to be entirely absent at least in adults (Rose 2003). This configuration has long been claimed to connect lissamphibians and temnospondyls. Yet, the only temnospondyls that really possess such an occiput are the stereospondyls (for instance *Gerrothorax* Nilsson, 1934, in which the exoccipitals meet in a ventral suture, showing that there is no basioccipital between them: Jenkins *et al.* 2008) and the amphibamid *Micropholis* (Schoch & Rubidge 2005). Stereospondyls have not been considered close to the origins of any extant amphibians since at least the early 20th century, and *Micropholis* has never been considered particularly close to any extant amphibians either.

In dissorophoids other than *Micropholis* (*Acheloma* Cope, 1882: Olson [1941: 162]; *Phonerpeton* Dilkes, 1990: Dilkes 1990; *Ecolsonia*: Berman *et al.* 1985; *Doleserpeton*: Sigurdsen [2008]), there are two condyles (or flat surfaces), but they touch in the

sagittal plane, and it is currently impossible to tell which ossification(s) make(s) up the unitary bone called "exoccipital-basioccipital complex" on which the condyles lie. To the best of our knowledge, this state does not occur anywhere else.

Two widely spaced exoccipital condyles do, however, occur in many lepospondyls, most notably the diplocaulids and their fellow "nectridean" *Scincosaurus*. Among "microsaurs", *Carrolla* (Maddin *et al.* 2011), *Batropetes* (according to the reconstruction by Carroll [1991: fig. 5], which looks very similar to its fellow brachystelechid *Carrolla*), *Asaphestera* (as far as we can interpret Carroll & Gaskill [1978: fig. 6E]), and *Rhynchonkos* (Carroll & Gaskill [1978: fig. 65E, F]) share this condition. *Llistrofus* Carroll & Gaskill, 1978 (Bolt & Rieppel 2009) shows an intermediate state probably shared by *Hapsidopareion* Daly, 1973 (Carroll & Gaskill [1978: 27, 28]).

Thus, this character supports the LH by one step over the TH and the PH.

The remaining "microsaurs" and lysorophians have a unique but similar state in which the two cotyles (or flat articulating surfaces) on the exoccipitals form a continuous articulating surface with a deeper cotyle on the basioccipital; this cotyle articulates with a process on the atlas (see below). The occiput is apparently unknown in all urocordylids (but see below); the aïstopods have a circular occipital cotyle the composition of which is unknown because there are no sutures in aïstopod braincases.

The craniovertebral joint: vertebral side
In most salamanders and in albanerpetontids, the atlas has a process (of widely varying size) that reaches between the exoccipital condyles, variously called "odontoid process" (not to be confused with the mammalian structure of the same name), "interglenoid tubercle" or "intercotylar tubercle". This process has long been compared to the indistinguishable one of "microsaurs" (see above). It is also present in stereospondyl temnospondyls (like *Gerrothorax*: Jenkins *et al.* 2008). Although unknown in extant caecilians or frogs, it was recently discovered in the stem-caecilians *Eocaecilia* and *Rubricacaecilia* Evans & Sigogneau-Russell, 2001 (Evans & Sigogneau-Russell 2001; Jenkins *et al.* 2007), the stem-frogs *Notobatrachus* (Báez & Basso

1996) and *Prosalirus* Shubin & Jenkins, 1995 (Jenkins & Shubin 1998), and the probable stem-frogs *Gobiates* Špinar & Tatarinov, 1986 (Roček 2008), and *Liaobatrachus* Ji & Ji, 1998 (Roček *et al.* 2012: fig. 2) – it may well be present but overlooked in yet more Mesozoic frogs. Clearly, the intercotylar tubercle is plesiomorphically present in modern amphibians and was lost in gymnophionans, most anurans, and a few paedomorphic caudates.

The tubercle further occurs in the diplocaulid "nectridean" *Diploceraspis* and the urocordylid "nectridean" *Ptyonius* Cope, 1875, but these are isolated occurrences (as far as known). More recently, it has been discovered in *Gerobatrachus* (Anderson *et al.* 2008b), making it the first dissorophoid known to possess the tubercle.

The presence of this feature is correlated to the shape of the occiput. The abovementioned cotyle on the basioccipital of lysorophians and most "microsaurs" that articulates with the intercotylar process obviously requires the presence of the latter; on the other hand, single, undivided occipital cotyles or condyles do not leave any space for it and thus preclude its presence (very deep cotyles excepted). If treated as a character in phylogenetic analyses, it has to be considered inapplicable in all those cases, which together cover the vast majority of taxa; only when there are two occipital condyles can the tubercle be present or absent. For this reason, it requires the same number of steps under all three hypotheses, even when *Gerobatrachus* is not taken into account.

Doleserpeton (Bolt 1991: fig. 5) and the Early Triassic stem-frog *Czatkobatrachus* (Evans & Borsuk-Białynicka 2010: fig. 1) should likewise be scored as inapplicable (unknown), because in them the entire area where an intercotylar tubercle could occur is occupied by an extremely large, unrestricted notochordal canal, which is even dorsally open (confluent with the neural canal) in *Doleserpeton*.

Position of the jaw articulation
Plesiomorphically, panderichthyids and limbed vertebrates were predators of large prey, so their jaw joints lie caudal to the occiput. In seymouriamorphs, diadectomorphs and lepospondyls (with

a few reversals in each), the jaw articulation lies more or less directly lateral to the craniovertebral articulation; this is paralleled in some dvinosaurian temnospondyls. The jaw joint lies rostral to the occiput in some "microsaurs", in lissamphibians (with reversals in some frogs such as *Triadobatrachus*, in which the jaw joints have a caudal position), in *Scincosaurus*, in diplocaulids, and independently in the aïstopod *Phlegethontia*. As this condition is not known in any adult Paleozoic temnospondyl except the presumed adults of the heavily paedomorphic branchiosaurid *Schoenfelderpeton* Boy, 1986, this character supports the LH over the TH, though not the PH, by no less than two steps (if the character is ordered, as it should be, being potentially continuous [Wiens 2001]; otherwise, the difference shrinks to one step).

Loss of the postsplenial

Although this is one of the dreaded "loss characters" (see below), this bone of the lower jaw is retained in all temnospondyls but lost in amniotes + diadectomorphs (with a possible reversal in the diapsid amniote *Petrolacosaurus* Lane, 1945: Reisz 1981), in the "microsaurs" *Euryodus* Olson, 1939, and *Hapsidopareion* (twice independently), and in *Brachydectes*, lissamphibians, and holospondyls. Thus, this character supports the LH by one step.

Loss of the coronoid III in adults

The caudalmost (distalmost) coronoid is retained everywhere outside of lysorophians, lissamphibians, holospondyls (but see below; unknown in *Scincosaurus*), and a few Meso- and Cenozoic amniotes. All temnospondyls, as far as known, retain it. This character supports the LH by one step.

The coronoid III reappears in diplocaulids (of all documented ontogenetic ages). This puzzling reversal might be a paedomorphic feature of these aquatic holospondyls: a coronoid of unclear homology but rather caudal position is present in larval and paedomorphic salamanders and is only lost (with its toothrow) at metamorphosis (Rose 2003). However, lysorophians lack coronoids (Wellstead 1991) in spite of showing paedomorphosis at least postcranially (see below).

Loss of denticles on the vomer

Very small teeth (distinctly smaller than the marginal tooth row) which are arranged at random in narrow fields or even over almost the entire palate are retained on the vomer in most temnospondyls, including *Doleserpeton* and *Amphibamus* (Sigurdsen & Bolt 2010) and arguably *Gerobatrachus* (Marjanović & Laurin 2009; Sigurdsen & Bolt 2010). They are absent in "nectrideans" (unknown or inapplicable in all aïstopods), lissamphibians, lysorophians, and some "microsaurs"; this distribution supports the LH by one step. Importantly, there is no reason to suspect that loss of the vomerine denticles is correlated to paedomorphosis: on the contrary, some temnospondyls lost theirs during ontogeny (Sigurdsen & Bolt 2010).

Fusion of neural arch and (pleuro)centrum in the second vertebra

Arch and centrum of the axis apparently never fuse outside a clade consisting of amniotes, diadectomorphs, lepospondyls and lissamphibians (the tetrapod crown-group according to the LH), and always do so within that clade, except in the "microsaur" *Hapsidopareion* and in lysorophians. In the former, this may be a sign of immaturity of the known material (as it would be in amniotes), rather than a genuine reversal. In the latter, all neural arches are sutured rather than fused to their centra, and even the left and right neural arches of the same vertebra are separated by a suture throughout the vertebral column, so the lysorophians should be scored as inapplicable for this character, which in any case supports the LH by one step.

Gills

Plesiomorphically, gnathostomes (and indeed craniates) possess internal gills. Aquatic larvae of extant amphibians instead possess external gills that are lost at metamorphosis even if the animals remain aquatic and even if metamorphosis is incomplete (as it is in cryptobranchids and *Amphiuma* Garden, 1821, where at least one pair of gill slits stays open); they are retained throughout life only in fully neotenic salamanders that do not metamorphose at all. External gills are outgrowths from the septa between the internal gills (and thus between

the gill slits). In lepidosirenid lungfishes, external gills are present on two gill arches in larvae; they are then lost, and the internal gills attached to the other two gill arches take over their function (together with the lungs). Extant amphibians, on the other hand, never possess internal gills – the gills of tadpoles are homologous to external, not internal, gills, even though they are soon covered by a soft operculum which may be homologous to the common osteichthyan one (Schoch & Witzmann 2010, and references therein).

The external gills of lissamphibians and lepidosirenids are probably not homologous; they seem to develop from different parts of the gill septa and are absent in *Neoceratodus* Castelnau, 1876, as well as in the more distantly related *Latimeria* Smith, 1939 (which is viviparous, but viviparous caecilians often have very large external gills in the fetus stage). The questions thus are when in the ancestry of lissamphibians the external gills evolved and when the internal ones were lost.

As reviewed by Schoch & Witzmann (2010), external gills have been discovered in exceptionally preserved fossils of a wide variety of temnospondyl larvae as well as paedomorphic adult branchiosaurids and larvae of seymouriamorphs. Therefore, external gills are not an autapomorphy of Lissamphibia, must have been present in ancestors of Amniota, and cannot distinguish between the TH, LH and PH.

Acanthostega shows evidence of internal gills (Coates & Clack 1991). It possesses a caudoventral groove on each ceratobranchial bone; this groove carries a branchial artery in extant vertebrates with internal gills. The cleithrum, which forms most of the shoulder girdle, retains the postbranchial lamina (Pawley 2006: fig. 70-1.1), against which a gill lid may have been able to close the gill chamber (even though the opercular bone, which stiffens the gill lid in most osteichthyans with internal gills, was absent). This discovery of evidence for internal gills in a limbed vertebrate, which caused some surprise at that time, set off a search for these features in more crownward limbed vertebrates. While the ceratobranchials often did not ossify or were otherwise lost before fossilization, a postbranchial lamina on the cleithrum has now been found in the late Early Carboniferous colosteid *Greererpeton*

Romer, 1969 (Godfrey 1989: fig. 17b; recognized by Coates 1996), *Ichthyostega* Säve-Söderbergh, 1932 (Jarvik 1996; recognized by Clack 2002), the middle Early Carboniferous whatcheeriid *Whatcheeria* Lombard & Bolt, 1995 (Lombard & Bolt 1995), the Late Carboniferous baphetid *Baphetes* (Milner & Lindsay 1998; Milner *et al.* 2009), and, remarkably, the Early Permian anthracosaur *Archeria* Case, 1915 (Pawley 2006: chapter 6, fig. 70-2.2,4). It may be yet more widespread, but the cleithrum of limbed vertebrates is hardly ever illustrated in cranial or caudal view, and the lamina is invisible in lateral and difficult to recognize (at best) in medial view. On the other hand, we are not aware of research on what sizes and shapes a postbranchial lamina can have if it is to function as described above; *Ventastega*, for instance, has a narrow lamina (Ahlberg *et al.* 2008: figs 2b, 3e), yet the text of the same paper says a postbranchial lamina is absent because the lamina is deemed too small for unstated reasons, as Coates (1996) did with the purported postbranchial lamina of *Whatcheeria*.

Certain aquatic dvinosaurian and stereospondyl temnospondyls of the Permian and Triassic have often been suggested to be paedomorphic like the branchiosaurids and many extant salamanders, and to have retained external gills like them; osteological evidence for open gill slits and functional gills was used to support this notion. However, these temnospondyls had internal, not external, gills as adults (Schoch & Witzmann 2010). Their ceratobranchials possess grooves – the ceratobranchials of extant amphibians, and of temnospondyls with semiaquatic (*Onchiodon* Geinitz, 1861) or terrestrial (*Acanthostomatops*) adults, are never grooved –, and they have a postbranchial lamina on the clavicle (figured in, e.g., Hellrung 2003; Pawley 2007; Jenkins *et al.* 2008).

Schoch & Witzmann (2010) further report possible preservation of a soft-tissue gill lid in two dvinosaurian temnospondyls. In the stereospondyl *Gerrothorax*, no soft tissue is preserved, but the caudal extremities of the jaws may have taken over part of this function (Hellrung 2003).

No evidence of internal gills has so far been reported from lepospondyls, including permanently aquatic ones like the abovementioned "microsaur"

Microbrachis or the diplocaulid "nectrideans". If this is not due to mere lack of research (and indeed, the well-ossified ceratobranchials of the apparently aquatic lysorophians lack grooves: Wellstead 1991; Schoch & Witzmann 2010), the absence of internal gills could be homologous between lepospondyls and lissamphibians (amniotes should be coded as inapplicable because they are plesiomorphically terrestrial). This would bolster the LH. On the other hand, maybe the paedomorphosis of branchiosaurs indicates that dissorophoids, too, had lost the ability to develop internal gills and could only become aquatic by paedomorphosis. Unfortunately, the largest paedomorphic specimen of the branchiosaurid *Apateon caducus* (Ammon, 1889) (Fröbisch & Schoch 2009b) does not preserve soft tissue; its branchial denticles show that it retained open gill slits, but if it had external, internal or no gills cannot be determined – the hyobranchial skeleton is not ossified, and the poorly formed clavicles are only exposed in ventral view.

Forelimb digit identities

As far as known, all salientians, caudates, albanerpetontids (McGowan 2002) and temnospondyls as well as most lepospondyls (including lysorophians and *Rhynchonkos*) have four fingers per hand. Parsimony dictates considering them all homologous until evidence to the contrary is found. Such evidence has recently been reported. In the hindlimbs of frogs and salamanders, as well as in the limbs of amniotes (Fröbisch & Shubin 2011, and references therein; Vargas *et al.* 2011) the first digit does not express HoxD-11, while all others do. The same is apparently true for the first digit of the forelimb of the salamander *Ambystoma mexicanum* (Shaw, 1789) (Torok *et al.* 1998). In the frog *Xenopus laevis* (Daudin, 1802), however, the "first" finger does express HoxD-11, even though the first toe, as usual, does not (Satoh *et al.* 2006). This agrees with the well-known fact that, in development apart from HoxD-11 expression (see below), the fingers of salamanders are very similar to the first four toes, while the fingers of frogs develop in ways more similar to the last four toes of frogs and to the last four digits of all limbs of amniotes. Taken at face value, this means that

salamanders have fingers I through IV, while frogs have fingers II through V – in other words, the fingers of frogs and salamanders are not entirely homologous, so the first batrachian must have retained all five fingers. This surprising conclusion clashes with the abovementioned fact that albanerpetontids, all temnospondyls (unless the five-fingered *Caerorhachis* Holmes & Carroll, 1977, is the basalmost temnospondyl; Pawley 2006), and all lepospondyls except a few "nectrideans" possess only four per hand, the fact that frog, salamander, albanerpetontid, and temnospondyl hands are morphologically quite similar, and the fact that these hands are morphologically more similar to the first four fingers of other limbed vertebrates and the four fingers of lepospondyls. This conundrum has only begun to be investigated (Vargas *et al.* 2011).

Fröbisch *et al.* (2007) and arguably Fröbisch & Shubin (2011), none of whom cited Satoh *et al.* (2006), implied that Torok *et al.* (1998) or some reference therein had found lack of HoxD-11 expression in the "first" finger of frogs. In fact, Torok *et al.* (1998) did not mention frog development at all.

STRANGE ATTRACTIONS TESTED
BY TAXON DELETION ANALYSES

There is evidence from squamate phylogenetics that elongate tetrapods with reduced or absent limbs and, in many cases, a burrowing lifestyle often cluster together in morphological cladistic analyses even when other (e.g., molecular) evidence indicates they are not close relatives at all. For example, the analysis by Conrad (2008), which is based on a matrix with a very large number of taxa but relatively few characters, found a clade consisting of snakes, amphisbaenians, dibamids, and limbless and limb-reduced skinks to be nested among the skinks with unreduced limbs – a result that is most likely wrong, judging from molecular (Townsend *et al.* 2004, Vidal & Hedges 2005) and morphological evidence (Lee 2005, 2009). Gymnophionomorphs are burrowers with reduced limbs (*Eocaecilia*, probably *Rubricacaecilia*) or no limbs and girdles at all (Gymnophiona), and albanerpetontid skulls and necks show adaptations to burrowing (even though their limb proportions and vertebral column

TABLE 2. — Hypotheses supported by the MPTs that result when selected taxa are deleted from the matrix of Marjanović & Laurin (2009). Note that the TH and the PH become topologically indistinguishable when *Eocaecilia* is deleted. Abbreviations: **Ad**, Adelogyrinidae; **Aï**, Aïstopoda; **Al**, Albanerpetontidae; **Br**, *Brachydectes* (Lysorophia); **Eo**, *Eocaecilia* (Gymnophionomorpha); **RMA**, remaining modern amphibians (whichever lissamphibians and albanerpetontids that were not deleted); **Ut**, *Utaherpeton* ("microsaur"). The authors of all taxon names are listed in Appendix 11.

Deleted taxa	Supported hypotheses
none	LH; Lissamphibia sister to Br, followed by Aï; Al sister to Batrachia
Eo	LH; RMA sister to Br, followed by Aï; Al sister to Batrachia
Eo, Br	LH; RMA sister to Aï, both nested among "nectrideans", then Ut; Al sister to Batrachia
Eo, Br, Aï	all equally parsimonious; if LH, Al sister to Batrachia; if TH/PH, Al sister to Caudata
Eo, Aï, Ad, Al	LH; RMA sister to Nectridea/Holospondyli, then Br, then *Hapsidopareion* ("microsaur")
Eo, Br, Aï, Ad	LH; RMA sister to Ut, Nectridea/Holospondyli or Diplocaulidae + Urocordylidae ("nectrideans")
Eo, Br, Aï, Ad, Al	TH/PH; RMA sister to *Gerobatrachus*, then *Doleserpeton* or (*Platyrhinops* + *Amphibamus*)
Eo, Caudata, Aï, Ad, Al	TH/PH; RMA (= Salientia) sister to *Gerobatrachus*, then *Doleserpeton*; Br sister to *Hapsidopareion*
Eo, Al	LH; RMA (= Batrachia) sister to Aï, then polytomy with "nectrideans", then Br
Eo, Al, Caudata	TH/PH; RMA (= Salientia) sister to *Gerobatrachus*, then *Doleserpeton*, within dissorophoid polytomy, but there is no Temnospondyli in the strict consensus; Lepospondyli almost perfectly resolved
Eo, Al, Aï	LH; RMA (= Batrachia) sister to Br, then some or all "nectrideans", or to Nectridea/Holospondyli, then Br

lengths are unremarkable; Wiechmann 2000, and references therein). Similarly elongate and/or burrowing animals are found among the lepospondyls (Gymnarthridae, *Rhynchonkos*, Ostodolepididae: elongate terrestrial burrowers with short limbs; Lysorophia: eel-like aquatic animals that are often found in their aestivation burrows just like coeval and extant lungfishes; Aïstopoda: elongate, limbless, remarkably long-tailed, at least in part probably terrestrial snake-like animals [Anderson 2002; Germain 2008b]; Adelogyrinidae Brough & Brough, 1967: poorly known elongate aquatic animals which may have lacked limbs and may or may not be lepospondyls). In comparison, all temnospondyls are short and squat (some aquatic ones like *Trimerorhachis* possess up to 35 presacral vertebrae, but this is already the extreme). It is therefore possible that, given the strong support for Lissamphibia, the caecilians (and perhaps the albanerpetontids) pull Lissamphibia as a whole from the temno- into the lepospondyls in the phylogenetic analyses that find the LH. We have tested this by removing varying combinations of the mentioned taxa from the matrices by Marjanović & Laurin (2009) and Vallin & Laurin (2004), which support the LH, and reanalyzing them.

In the matrix of Marjanović & Laurin (2009) (Table 2), the PH/TH (in the absence of *Eocaecilia*, the only gymnophionomorph in that matrix, the TH and the PH are not distinguishable) becomes more parsimonious than the LH only if *Eocaecilia*, the albanerpetontids, and either the salamanders or all of *Brachydectes* (the only lysorophian in the matrix), the aïstopods, and the adelogyrinids are removed.

When *Eocaecilia*, *Brachydectes* and Aïstopoda are removed from the same matrix, the LH and the TH/PH become equally parsimonious. Interestingly, in the MPTs that support the LH, Albanerpetontidae and Batrachia are sister-groups, while in the others albanerpetontids and salamanders cluster together as they did in Anderson *et al.* (2008b). Surprisingly, when the adelogyrinids are additionally removed, the LH is restored as the single most parsimonious outcome.

Within the LH, when *Brachydectes* is present, the (remaining) lissamphibians are not always its sister-group; they sometimes appear next to some or all "nectrideans", the aïstopods (which are then nested inside the "nectrideans"), or the somewhat elongate "microsaur" *Utaherpeton*.

Clearly, if there is an attraction of any particular modern amphibians to elongate lepospondyls, those

TABLE 3. — Hypotheses supported by the MPTs that result when selected taxa are deleted from the matrix of Vallin & Laurin (2004), which does not contain albanerpetontids or *Gerobatrachus* and contains a single OTU called "Nectridea". *Siren* and *Proteus* are long-bodied caudates with reduced limbs (*Siren* even lacks hindlimbs). Note that the TH and the PH become topologically indistinguishable when *Eocaecilia* is deleted. Abbreviations: **Gy**, Gymnophionomorpha (OTUs *Eocaecilia*, Rhinatrematidae, Ichthyophiidae); **Ly**, Lysorophia (an OTU). The authors of all taxon names are listed in Appendix 11.

Deleted taxa	Supported hypotheses
none	LH; Lissamphibia sister to Ly, followed by Brachystelechidae
Gy	LH; RMA (= Batrachia) sister to Ly, followed by Brachystelechidae; slightly decreased resolution elsewhere among "microsaurs"
Gy, *Siren*	LH; RMA (= Batrachia) sister to Ly, followed by Brachystelechidae; resolution elsewhere among "microsaurs" as above
Gy, *Siren*, *Proteus*	LH; RMA (= Batrachia) sister to Ly, followed by Brachystelechidae; resolution elsewhere among "microsaurs" as above
Gy, Caudata	LH; RMA (= Salientia) sister to Ly, followed by Brachystelechidae; resolution elsewhere among "microsaurs" slightly improved

modern amphibians are not the caecilians but the caudates, the oldest and basalmost representatives of which had very short bodies, long, well-formed limbs, and no known adaptations to burrowing (summarized in Marjanović & Laurin 2008b, 2009: electronic supplementary material)!

The matrix by Vallin & Laurin (2004) contains two extant long-bodied caudates with reduced limbs, *Siren* Österdam, 1766, and *Proteus* Laurenti, 1768, as OTUs. Deleting them, or even deleting all of Caudata and Gymnophionomorpha (so that the salientians are the only remaining modern amphibians), has no effect on the MPTs (Table 3).

Even in this latter version of the matrix with maximum deletion, the Salientia-Lysorophia clade retains a bootstrap value of 0.67; the highest bootstrap value that keeps Salientia out of Temnospondyli is 0.76. Only 10 nodes in the entire ingroup of 41 OTUs have bootstrap values > 0.76. We did not delete long-bodied lepospondyls from this matrix because, as far as we can imagine, they cannot be attracted to Salientia.

When the non-elongated salamanders (*Karaurus* and Hynobiidae Cope, 1859) are restored, the bootstrap value of the Lysorophia-Batrachia clade is 0.87. This value is not surpassed outside Batrachia, except by a clade of amphibamids that includes the branchiosaurid *Apateon* but not any lissamphibians, by Seymouriamorpha, and by the ingroup as a whole without *Panderichthys* Gross, 1941. Temnospondyli has a bootstrap value of 0.82.

The matrix by Vallin & Laurin (2004) forms the supplementary information to the present article. It has not been published in one piece before; Vallin & Laurin (2004) only published the changes they had made to the matrix by Laurin & Reisz (1999) (see Table 1); Laurin & Reisz (1999) themselves only published the changes they had made to the matrix by Laurin (1998a), which has only been published in text form and not as a NEXUS file. Starting with Laurin & Reisz (1999), all these matrices also incorporated the additions mentioned in Laurin (1998b).

EVO-DEVO

Ontogeny evolves. This means that Haeckel's "Biogenetic Fundamental Law" ("ontogeny recapitulates phylogeny") is wrong, so phylogeny cannot be reconstructed by merely observing ontogeny. On the other hand, it also means we can use shared derived similarities in the ontogeny of different taxa as evidence in phylogenetics – as characters in a data matrix for phylogenetic analysis. Some morphologists (Carroll 2007; Anderson 2008; Olori 2011; Werneburg & Sánchez-Villagra 2009) have argued that this should be done more often than it is.

For instance, Anderson (2008: 242) reviewed the two main well-known patterns of distal limb formation in extant tetrapods (Schmalhausen 1915; Holmgren 1933; Shubin & Alberch 1986; Cohn *et al.* 2002; Johanson *et al.* 2007: 759, 765). The first occurs in

TABLE 4. — Correlation between ossification and chondrification sequence in the manus and pes of four extant tetrapod species. Spearman's r and probabilities appear as reported by Fröbisch (2008: fig. 8), r², and probability rank (sorted in increasing order; ranks averaged in case of ties). The latter is used in the analysis of false-discovery rate (see Table 5). The authors of all taxon names are listed in Appendix 11.

Taxon, body part	Spearman's r	r²	Probability	Probability rank
Ambystoma mexicanum manus	0.92778	0.86077573	0.001	2
Ambystoma mexicanum pes	0.92828	0.86170376	0.001	2
Rana temporaria manus	0.72862	0.5308871	0.044	6
Rana temporaria pes	0.94458	0.89223138	0.001	2
Chelydra serpentina manus	0.67511	0.45577351	0.041	4
Chelydra serpentina pes	0.68644	0.47119987	0.047	7
Mus musculus manus	0.71131	0.50596192	0.041	5
Mus musculus pes	0.64222	0.41244653	0.06	8
Average	0.7805425	0.6238725	0.0295	

frogs and amniotes. Their limbs chondrify in a predominantly proximal-to-distal sequence, with most of the mesopodium forming before the autopodium, which in turn develops in a mostly caudal-to-cranial sequence: digital ray IV forms first (and appears to grow from the ulnare/fibulare), followed by III and V, then II, and then I. The second occurs to varying degrees in salamanders. There, the digital rays appear in a mostly cranial-to-caudal sequence, so that II and then I appear first and without direct contact to more proximal elements, later followed by III, then IV, and then (in the foot) V, and only afterwards is the chondrification of the carpus/tarsus completed (from both sides, proximal and distal). Thus, limb development includes two partly linked characters: the order in which digits appear (cranial to caudal or the reverse), and the proximo-distal development sequence (proceeding in a proximo-distal order or proceeding to an extent from the metapodials proximally).

The abovementioned second pattern may occur, as far as its ossification sequence suggests, in the temnospondyl *Apateon* (Fröbisch *et al.* 2007). This inference is uncertain because the correlation between chondrification and ossification that Fröbisch (2008) demonstrated is extremely variable, ranging from nearly perfect in the pes of *Rana temporaria* Linnaeus, 1758 (r² = 0.89), to rather poor, as in the pes of *Mus musculus* Linnaeus, 1758 (r² = 0.41), with an average explained variance (r²) of 0.62 (Table 4). In these discussions, and in Table 4, we emphasize r² rather

TABLE 5. — Correction of Table 4 for multiple testing following the False-Discovery Rate procedure (applied to a 0.05 probability threshold). The hypothesis tested is that the position in the chondrification sequence is random with respect to the position in the ossification sequence.

Threshold for individual tests	Ranks	Actual probabilities, sorted	Significant?
0.00625	1	0.001	yes
0.0125	2	0.001	yes
0.01875	3	0.001	yes
0.025	4	0.041	no
0.03125	5	0.041	no
0.0375	6	0.044	no
0.04375	7	0.047	no
0.05	8	0.06	no

than r because the former indicates how much of the variance in the dependent character (here, position in the ossification sequence) is explained by the independent character (here, position in the chondrification sequence). Fröbisch (2008) reported the probabilities that the correlation results from chance alone in eight graphs (four taxa, each for the hand and foot). Applying correction for multiple testing (because here, the hypothesis that the sequence of ossification reflects the sequence of chondrification is tested eight times) in the form of False Discovery Rate (Benjamini & Hochberg 1995), as done in recent papers from our lab that use statistics (e.g., Laurin *et al.* 2009), shows that only three of the eight results are statistically significant (Table 5). Moreover,

Fröbisch (2008) did not assess correlation between sequence of ossification and sequence of prechondrogenic condensation at all. Yet, the latter is the focus of most evo-devo work on the limb skeleton. The correlation between these two sequences is probably somewhat lower than that between ossification and chondrification because the distance in ontogenetic time is greater, but this clearly needs to be assessed.

Furthermore, as pointed out by Fröbisch & Shubin (2011), "the salamander pattern" is not monolithic, and this complicates the discussion of these characters. In the salamandrid *Triturus marmoratus* (Latreille, 1800) (Blanco & Alberch 1992), as well as in *Ambystoma mexicanum* (Franssen *et al.* 2005), the basale commune (distal carpals/tarsals 1 + 2, see below) becomes a separate cartilaginous element before all other mesopodials, so that much of the mesopodium forms from distal to proximal, very much unlike in amniotes or frogs. In *Salamandrella* Dybowski, 1870, a hynobiid and thus a generally rather plesiomorphic salamander, as well as in the highly nested plethodontid *Desmognathus aeneus* Brown & Bishop, 1947 – which has direct development rather than a free-swimming larva – the mesopodium forms mostly in a proximal-to-distal sequence (though the centralia form last) (Vorobyeva & Hinchliffe 1996; Hinchliffe & Vorobyeva 1999; Franssen *et al.* 2005).

CRANIOCAUDAL CONDENSATION
SEQUENCE OF DIGITS

It has been suggested that the cranial-to-caudal pattern of salamanders is due to natural selection on pond-dwelling larvae that use their forelimb buds for locomotion while the digits are developing (Schmalhausen 1915; Hinchliffe & Vorobyeva 1999; Cohn *et al.* 2002; Franssen *et al.* 2005; Stopper & Wagner 2005; Fröbisch & Shubin 2011). The digits at the cranioventral corner of the limb – I and II – are thus predicted to form first because they are located most closely to the substrate and hence are the most solicited in larval locomotion. *Salamandrella* larvae have a long "fin" that is supported by the developing fingers I and II, while *Ambystoma mexicanum* and *Triturus marmoratus* larvae touch the substrate directly with the tips of those fingers; this could

explain the differences among salamanders with pond-dwelling larvae. As hinted at by Stopper & Wagner (2005), amniotes and frogs lack selection pressure for precocious development of I and II and are free to emphasize the digit that is longest and strongest in the adult, namely IV, from the beginning of development. In *Desmognathus aeneus*, a salamander that spends the entire "larval" stage in the egg and hatches fully metamorphosed, finger III acquires much of its cartilaginous skeleton before that of finger I starts forming (although II is still the first); in the adult, as in the soft anatomy of the embryo, II and III are equal in length and much longer than I and IV (Franssen *et al.* 2005). *Desmognathus aeneus* further resembles amniotes and frogs in that the digits form as a paddle that later subdivides by apoptosis; in other salamanders such as *Ambystoma mexicanum*, every digit is a separate outgrowth from its limb bud (Franssen *et al.* 2005).

We suggest that the use of the developing forelimbs in locomotion is plesiomorphic for limbed tetrapods (already noted as a possibility slightly less parsimonious than their preferred hypothesis by Fröbisch & Shubin 2011). While difficult to test, this hypothesis is supported by the antiquity of the "salamander pattern" of development (*Apateon* is Pennsylvanian in age; Fröbisch *et al.* 2007) and the fact that free-swimming, pond-dwelling larvae without the specializations of tadpoles are optimized as plesiomorphic for limbed vertebrates. Such larvae with a long median fin (representing the fused dorsal, caudal, and anal fins) and external gills are shared at least by lungfishes (though see above), temnospondyls, and seymouriamorphs. This morphotype, together with any use of developing forelimbs, was lost in frogs due to the evolution of the gill lid which covers the forelimb bud in tadpoles almost all the way to metamorphosis, and independently in amniotes and direct-developing salamanders because the entire larval stage was transferred into the egg (or into the mother).

There is no known outgroup that could be used to polarize this character. Under the TH, the LH, and Anderson's version of the PH, it therefore requires at least three steps (appearance of digits included), regardless of what the ancestral condi-

tion is. Under Carroll's version of the PH, where the caudates are branchiosaurids, the frog-amniote pattern is optimized as ancestral (two steps). Thus, in isolation, this character supports Carroll's version of the PH over all alternatives, as noted by Fröbisch *et al.* (2007, 2010) – unless arguments such as our suggestion above can support the salamander pattern as ancestral.

Circumstantial evidence for the salamander pattern being indeed plesiomorphic comes from Early Carboniferous stem-tetrapods like the colosteid *Greererpeton* (Godfrey 1989) and the anthracosaur *Proterogyrinus* Romer, 1970 (Holmes 1980, 1984). In the foot of *Greererpeton*, all proximal and central tarsals are ossified, while of the distal ones, only the first is present even in articulated specimens. In *Proterogyrinus*, the only carpals to ossify at all (even though all tarsals are ossified) are the first and the second distal ones – strongly reminiscent of the carpus of a not quite adult specimen of the temnospondyl *Sclerocephalus* Goldfuß, 1847 (SMNS 90055: Schoch & Witzmann 2009). In contrast, in the Early Permian diadectomorphs *Tseajaia* Vaughn, 1964, and *Orobates* Berman, Henrici, Kissel, Sumida & Martens, 2004 (close relatives of the amniotes), the only ossified distal tarsal is the fourth (Moss 1972; Berman & Henrici 2003; Berman *et al.* 2004), as expected for the frog/amniote pattern.

Proximodistal condensation sequence of appendages

Johanson *et al.* (2007) provided the novel suggestion that the metapodial-to-mesopodial condensation pattern is the plesiomorphic one. Based on their study of the development genetics of the Australian lungfish (*Neoceratodus forsteri* Castelnau, 1876), they suggested that the "independent radials" are homologous to digital rays. The radials form without connection to the rest of the fin skeleton and only later form joints with it – just as in salamanders, in which the digital rays form independently of the rest of the limb skeleton and only later connect to it by the appearance of the missing carpals/tarsals (Johanson *et al.* 2007: 765). This suggests that it is plesiomorphic for the digital rays to form independently of the rest of the limb as observed

in salamanders (Johanson *et al.* 2007: 765, 766). This hypothesis is equally parsimonious under all current phylogenetic hypotheses.

As Johanson *et al.* (2007: 766) noted, the salamander pattern being primitive could explain why the chondrification and the ossification sequence do not match in frogs and amniotes (Tables 4, 5; Fröbisch 2008). Like those of *Apateon* and salamanders, the anuran and amniote metapodials and digits ossify before the carpals/tarsals, while the chondrification sequence is different. The chondrification sequence, it seems, has undergone more evolution than the ossification sequence. If the independence of the proximal and the distal parts of the limb shown by the salamander pattern is plesiomorphic, that would further explain why the number of centralia in the carpus and tarsus of limbed vertebrates in general is so unstable (ranging from 0 to 4 even in cases where fusion events can be excluded) and why these bones do not line up with the distal carpals/tarsals – the more space there is between the digital rays and the unconnected rest of the limb, the more centralia can form (Johanson *et al.* 2007: 765–766).

The basale commune

The *os basale commune*, which represents distal carpals/tarsals 1 and 2 (they condense, chondrify, and ossify as a unit), is present in all salamanders. It was unknown elsewhere until Anderson *et al.* (2008b) reported the presence of a basale commune in the tarsus of the amphibamid temnospondyl *Gerobatrachus*. Its presence, tentatively accepted by Sigurdsen & Green (2011), is a potential synapomorphy of *Gerobatrachus* and salamanders which could bolster the PH (though not Anderson's particular version of it). As we have explained previously (Marjanović & Laurin 2008b: 168, 169; 2009: electronic supplementary material 1: character 207), we are not convinced that either of the two preserved tarsals in the feet of *Gerobatrachus* is a basale commune. Judging from comparisons of the drawings and photos of Anderson *et al.* (2008b) to the few known sufficiently complete tarsi of other temnospondyls (among which we had overlooked *Eoscopus* Daly, 1994: Daly [1994: fig. 11]; for *Sclerocephalus*, see also Schoch & Witzmann [2009: fig. 8E]), other stem-tetrapods, and salamanders, the most likely

identity of the supposed basale commune is the centrale 2. There are several other slightly less plausible possibilities, of which a basale commune is only one. Comparing the very incompletely preserved tarsus of *Gerobatrachus* only to the tarsi of salamanders and determining the homologies of the tarsals of *Gerobatrachus* on that basis would amount to assuming a close relationship between *Gerobatrachus* and salamanders *a priori*. Before all else, we think, *Gerobatrachus* should be compared to its fellow amphibamids *Eoscopus* and *Micropholis*, followed by their fellow dissorophoid *Ecolsonia*, and then all other temnospondyls. Nonetheless, scoring *Gerobatrachus* as possessing a basale commune in the matrix of Marjanović & Laurin (2009) has no effect on the (LH-supporting) results except for adding a step to the four most parsimonious trees; even the Bremer value of Amphibia (i.e. the "lepospondyl"-lissamphibian clade) does not decrease.

Sigurdsen & Bolt (2009, 2010) report the absence of a basale commune in the carpus of *Doleserpeton*, a close relative (perhaps the sister-group) of *Gerobatrachus*. This indicates that the basale commune, if present in *Gerobatrachus*, is not widespread among amphibamids.

It may seem bold of us to suggest anatomical reinterpretations of a specimen that we have not examined, and indeed, an anonymous referee of an earlier draft criticized this. Still, our interpretation of the ankle of *Gerobatrachus* is based on the anatomical data provided in the description (Anderson *et al.* 2008b), and examination of the only known specimen by Trond Sigurdsen (Sigurdsen & Bolt 2010: 1372, 1376; Sigurdsen & Green 2011) has corroborated another of our reinterpretations (Marjanović & Laurin 2008b: 169, 179; 2009: electronic supplementary material 1: character 99), namely the absence of pedicellate teeth in that specimen.

Paedomorphosis, peramorphosis, miniaturization: cases where "ontogeny discombobulates phylogeny"

Paedomorphosis is the presence of character states in the adult that were, in ancestors of the taxon in question, restricted to earlier ontogenetic stages; peramorphosis is the opposite, namely the exag-geration of adult features that fail to stop their development. Importantly, both can be restricted to parts of the body and therefore occur in the same animal. For instance, compared to the ancestral ape condition, the human head shape is paedomorphic while human hindlimb length relative to the rest of the body is peramorphic. However, paedomorphosis is commonly an organism-wide phenomenon caused by neoteny (slowed-down development of all of the body except the sexual organs) or progenesis (precocial development of the sexual organs truncating the development of the rest of the body). This is expected to result in the correlated appearance of many juvenile character states in the same adult, and convergent evolution of paedomorphosis should thus result in many convergent similarities between the adults of disparate taxa. This may be exemplified by the "absence characters" of Schoch & Milner (2004), "loss features" of Anderson (2008: 240; see Marjanović & Laurin 2009: Electronic Supplementary Material 1), or "shared absences" and "loss"es of Sigurdsen & Green (2011). If these character states are all taken at face value in a phylogenetic analysis, they will be counted as large numbers of correlated and therefore spurious synapomorphies between paedomorphic taxa. Wiens *et al.* (2005: 96) suggested three methods for dealing with paedomorphosis in phylogenetic analysis and found disadvantages to all of them, but recommended to score the adult morphology of paedomorphic OTUs as unknown.

We have tried (Marjanović & Laurin 2008b, 2009; Marjanović 2010) to implement a modified version of this approach when scoring taxa that are known to exhibit paedomorphosis and taxa known only from immature and/or paedomorphic individuals (a common occurrence in the fossil record). The modification is to score only those characters as unknown that are known to be influenced by ontogeny, and even then only if the observed state is limited to immature stages in close relatives. This eliminates the main disadvantage of the method recommended by Wiens *et al.* (2005), which is that we would end up without any data for some OTUs. However, it combines the disadvantages of the other methods, even

though we still think it combines the highest number of advantages.

Naturally, determining which individuals are immature or paedomorphic is not always trivial. Wiens *et al.* (2005) worked on extant taxa with known ontogenies and a clear-cut metamorphosis that makes it relatively easy to determine whether a species is paedomorphic and whether a character is affected by this (even though there are phenomena like the partial metamorphosis of cryptobranchids and *Amphiuma*, or the miniaturization – see below – of some direct-developing plethodontids such as *Thorius* Cope, 1869, and *Oedipina* Keferstein, 1868). Moreover, Urodela is a fairly closely-knit taxon of reasonably obvious monophyly, which means that inferences can easily be drawn from the ontogeny of one species to that of another. Among Paleozoic limbed vertebrates, reasonably complete growth series are known only from a few temnospondyls (including, among the dissorophoids, several branchiosaurids and micromelerpetontids), and a clearly delimited metamorphosis has been described only in the branchiosaurid *Apateon* (Werneburg 1991; Schoch & Fröbisch 2006), while other temnospondyls developed in more gradual ways (Schoch 2001, 2009). Among lepospondyls, the ontogeny of the postcranial skeleton is known in some detail from a few representatives such as the aquatic "microsaurs" *Hyloplesion* Fritsch, 1883 (Carroll & Gaskill 1978), and *Microbrachis* (Olori 2011), but a skull ossification sequence has been discovered only for the aïstopod *Phlegethontia*, and that sequence comprises only three known stages (Anderson 2002, 2007). The ontogeny of other taxa can at present only be inferred by phylogenetic bracketing, and this method quickly reaches its limits, as the following example will illustrate.

When discussing the LH, Schoch (2002: 294) suggested that lysorophian "lepospondyls" in general and *Brachydectes* (the only well-known lysorophian) in particular are "heavily paedomorphic", and that this feature could be responsible for the position the lysorophians occupy in the LH by resulting in correlated derived states shared by lysorophians and some or all lissamphibians.

As previously pointed out (Marjanović & Laurin 2008b: 157, 158), *Brachydectes* indeed shows several features that indicate paedomorphosis in osteichthyans generally, such as the persistent suture between left and right neural arches (Wellstead 1991). Whether other features could be due to paedomorphosis is, however, difficult to ascertain.

One case is the absence of the jugal bones in lysorophian skulls ("leaving" a gap in the lateroventral margin of the skull). The jugal is likewise missing in frogs, salamanders, and extant caecilians (but not *Eocaecilia* or albanerpetontids), and appears late in temnospondyl ontogeny, staying small and apparently never reaching the (paedomorphically short) maxilla in the highly paedomorphic branchiosaurid *Schoenfelderpeton*. It is therefore tempting to attribute the lack of jugals in lysorophians (and perhaps their short maxillae) to their paedomorphosis. But such an inference would be based on an assumption of a close relationship to temnospondyls. To interpret the lysorophian skull from an evo-devo perspective, we need to examine the ontogeny of at least one (other) close relative of lysorophians, ideally another unquestioned lepospondyl, which can at present only be *Phlegethontia* (see above). In *Phlegethontia*, the jugal is present in the second of the three known stages, before even the premaxilla; as previously pointed out, the ontogeny of *Phlegethontia* does not lead through a stage that resembles the adult (and only known) condition of lysorophians (Marjanović & Laurin 2008b: 158).

We suspect that the absence of the jugal is not paedomorphic in lysorophians, but may be related to jaw mechanics instead – the "orbitotemporal fenestra" is drastically enlarged caudally, apparently providing space for jaw-closing muscles caudal to the eye (Wellstead 1991: fig. 2E).

The jugal is of particular interest because its absence in frogs and salamanders (and, before the discovery of *Eocaecilia*, caecilians) has often been thought to be explicable by paedomorphosis from a dissorophoid temnospondyl ancestor which truncated its ontogeny before the jugal and several other dermal bones of the skull and shoulder girdle ossified (Schoch & Milner 2004; Carroll 2007). In

turn, this paedomorphosis has itself been suggested to be part of miniaturization – peramorphosis of the endochondral skeleton leading to truncation of growth and paedomorphosis of the dermal skeleton, as observed in certain especially tiny extant plethodontid salamanders (the aforementioned *Thorius* and *Oedipina*). But because lepospondyl skull ossification sequences are unknown apart from *Phlegethontia*, to accept this scenario would amount to assuming a close relationship between dissorophoids, frogs and salamanders (in other words, the TH or the PH). We have therefore continued to score the jugals in frogs and salamanders as absent (Marjanović & Laurin 2008b, 2009; Marjanović 2010).

Other features might be paedomorphic, but have a more complex distribution: "for example, the arrangement of the vomerine teeth of *Brachydectes* (Wellstead 1991: fig. 2B) is identical to that of larval and paedomorphic salamanders, but never seen in anuran or gymnophionan ontogeny" (Marjanović & Laurin 2008b: 157), let alone temnospondyl ontogeny. Lepospondyl ontogeny is too poorly known for comparisons.

Finally, as their name suggests, many "microsaurs" are so small that miniaturization effects may be expected (e.g., Carroll 2007). Unfortunately, the ontogeny of large as well as small "microsaurs" – and lepospondyls in general – is (as mentioned) so poorly known that only vague suggestions have ever been made as to which characters could be affected by this. In our phylogenetic analyses, we have therefore taken "microsaur" anatomy at face value. We hope that this tacit assumption will become testable by new discoveries.

Skull ossification sequences, or: phylogenetics with two taxa

Carroll and various coauthors have pointed out the close similarities (but see Anderson 2007: 191) between the cranial ossification sequences of the extant hynobiid salamander *Ranodon* Kessler, 1866, and the branchiosaurid dissorophoid temnospondyl *Apateon* and drawn the conclusion that salamanders are branchiosaurids (Carroll *et al.* 1999, 2004; Schoch & Carroll 2003; Carroll 2007; see also Schoch & Fröbisch 2006). However, this argument suffers from problems inherent in both its method and its data.

Firstly, this argument requires the assumption that the skull ossification sequences of salamanders are more similar to those of branchiosaurids than to those of other amphibamids, the lepospondyls *Rhynchonkos* and *Brachydectes*, and other potentially relevant taxa. This assumption cannot be tested at present, because the skull ossification sequences of all these animals are unknown (see above on *Phlegethontia*). This alone invalidates the entire argument (Ruta & Coates 2007).

Furthermore, it appears that many of the character states that *Ranodon* shares with *Apateon* but not with frogs or caecilians are not synapomorphies, but symplesiomorphies: Schoch (2006) found them to be shared by the actinopterygians *Amia* Linnaeus, 1766, *Acipenser* Linnaeus, 1758, and *Polypterus* Lacépède, 1803, as well as the lungfish *Neoceratodus*. Indeed, his phylogenetic analysis of cranial ossification sequences (Schoch 2006: fig. 1) recovered *Apateon* as a stem-tetrapod; as Schoch (2006: 529) noted, this is predicted by the LH but not compatible with the TH or the PH.

Lastly, the mentioned argument requires the assumption that *Ranodon* has conserved the ancestral urodelan skull ossification sequence. While this animal is generally rich in plesiomorphies, it is not the ancestral urodele (crown-group salamander), let alone the ancestral caudate (total-group salamander).

Reconstruction of the ancestral urodelan skull ossification sequence using a novel method based on squared-change parsimony and phylogenetically independent contrasts shows that, for four bones, the 95% confidence interval excludes *Apateon* even though those intervals are for the most part very broad (Germain & Laurin 2009). According to simulations in the same publication, the new method outperforms the most sophisticated previously existing method, event-pair cracking using Parsimov (Jeffery *et al.* 2005), in both type I error rate and power. Nonetheless, Parsimov yields a similar range of most parsimonious ossification times for the ancestral urodele (unlike the new method, it cannot calculate confidence intervals), except that even *Ranodon* is sometimes found to lie outside that range. Thus, the similarities in the skull ossification sequences between *Apateon* and the

ancestral urodele are smaller than implied in most studies. Incidentally, Germain & Laurin (2009: fig. 5) confirm Anderson's (2007: 191) statement that *Apateon* and *Ranodon* are not very similar to each other either – for many bones they lie on opposite sides of the midpoint of the confidence interval for the ancestral urodele.

New discoveries of fossils will most likely be necessary if cranial ossification sequences are to become a significant source of information in the phylogenetics of early limbed vertebrates. The lack of known cranial ossification sequences is not restricted to lepospondyls – even in the famous *Eusthenopteron*, which could otherwise serve as an appropriate outgroup for such studies, the smallest known specimens already have a full complement of fully ossified dermal skull bones, even though changes in proportions and the gradual ossification of the postcranial skeleton have been studied in detail in large collections of larger individuals (Schultze 1984; Cote *et al.* 2002).

HOMOLOGIES IN THE LYSOROPHIAN SKULL ROOF

With the publication of Laurin & Reisz (1997), the lysorophian lepospondyls regained a prominent position in the discussion on the origin of the extant amphibians. One of the characters that supported the finding of lysorophians and lissamphibians as sister-groups (Laurin 1994, 1998a; Laurin & Reisz 1997, 1999; Vallin & Laurin 2004; Pawley 2006: figs 91, 92, app. 14) was their shared lack of postorbital bones in the skull.

Recently (Marjanović & Laurin 2008b: 155-157), however, we offered a new interpretation of the identities of the bones that make up the caudal part of the skull roof in lysorophians; that is, we think the bones identified as the tabular and postparietal by Wellstead (1991) can be more parsimoniously considered the postorbital and tabular, respectively. In sum, this interpretation (Fig. 3) makes the lysorophians slightly less lissamphibian-like than Wellstead's (1991): although the postparietals are absent (like in all known lissamphibians except *Eocaecilia*), the

postorbitals are present, unlike in all known lissamphibians, including *Eocaecilia* (Jenkins *et al.* 2007).

Importantly, this interpretation does not depend on the assumption of a close relationship between lysorophians and brachystelechid "microsaurs"; the latter (*Batropetes* in Figure 3) should merely be considered an example of a lepospondyl with large orbits and a rostrocaudally narrow cheek region, a condition which we expect to lead to dorsoventrally long and rostrocaudally narrow postorbitals and squamosals.

As an interesting byproduct, our interpretation allows more confident identification of the putative posttemporal foramen of *Brachydectes*. In our interpretation, the tabular borders this foramen as in most early limbed vertebrates. In Wellstead's (1991) interpretation, the postparietal contributes to its margin, which is unusual; this led Wellstead (1991: 18) to doubt the identification of the foramen in question as homologous to the posttemporal fenestra. Moreover, our interpretation restores the contact between tabular and exoccipital, another widespread plesiomorphy.

DATING THE APPEARANCE OF LISSAMPHIBIA

Assuming monophyly, the age of Lissamphibia is highly contentious. Some authors (San Mauro *et al.* 2005; Roelants *et al.* 2007) proposed an origin of Lissamphibia in the Late Devonian (360-370 Ma ago). Hugall *et al.* (2007) found mid-Carboniferous (323 ± 19 Ma based on nucleotide data) or Late Carboniferous/Early Permian ages (292 ± 28 Ma based on amino acid data), about both of which they cautioned that, "[g]iven that all the lissamphibian nodes are outside the most basal calibration employed, they may be prone to being over- (rather than under-) estimated" (Hugall *et al.* 2007: 558). Using three methods for molecular dating and his preferred set of calibration points, San Mauro (2010: table 3) found Late Carboniferous point estimates surrounded by 95% confidence intervals that sometimes extend into the Early Carboniferous and/or the Early or

TABLE 6. — Estimated date of appearance of selected taxa in the supertree of Marjanović & Laurin (2007) under various assumptions of branch lengths. The dates, in Ma ago, have a precision of *c.* 2 Ma, resulting from the resolution of the scale displayed in Mesquite. When only one number is given, stratigraphic fit was used (a given species is assumed to have been present throughout at least one geological stage regardless of its duration). When two numbers are given, the first one is the minimal internal branch length (as under stratigraphic fit) and the second is the minimal terminal branch length (the species are not assumed to have existed throughout at least a given geological stage, but to have lasted at least a given number of years before the end of the geological stage in which they have been preserved). For the taxa that have a branch-based definition, the dates reported represent the beginning of the differentiation of the taxon (the oldest known node in it), not the appearance of its branch (or stem). All calculations were performed using Stratigraphic Tools (Josse *et al.* 2006). *, Branch length assumptions used to produce the supertree of Marjanović & Laurin (2007: figs 3-7). Note that the divergence between *Hyla*, and *Bufo*, may be too old, because the oldest fossil in this clade that was included in the supertree was *Baurubatrachus*, which is Maastrichtian (70.6-65.5 Ma) rather than Campanian (83.5-70.6 Ma) in age (Roček 2000; Fernandes & Coimbra 2000; Gradstein *et al.* 2004). Gymnophionomorpha and Gymnophiona were called "Gymnophiona" and "Apoda", respectively, by Marjanović & Laurin (2007); see the "Nomenclature" section of the present paper. From Marjanović & Laurin (2007: app. 4). The authors of all taxon names are listed in Appendix 11.

Taxa	0.1 Ma	1 Ma	2 Ma	3 Ma*	5 Ma	0.1 Ma/ 0.1 Ma	0.1 Ma/ 1 Ma	0.1 Ma/ 5 Ma	1 Ma/ 0.1 Ma	1 Ma/ 1 Ma	1 Ma/ 5 Ma	5 Ma/ 0.1 Ma	5 Ma/ 1 Ma	5 Ma/ 5 Ma
Lissamphibia	252	254	258	260	267	246	248	250	248	249	253	261	262	266
Gymnophionomorpha	190	190	190	190	190	183	183	188	183	184	189	183	184	189
Gymnophiona	100	100	100	100	100	94	94	99	94	95	100	94	95	100
Batrachia	252	253	254	254	257	246	247	250	247	248	251	250	251	256
Urodela	157	159	160	162	166	152	153	156	153	154	158	161	162	166
Cryptobranchoidea	140	141	142	143	146	138	139	144	138	140	147	141	144	150
Salamandridae	60	62	66	70	84	57	58	62	60	61	65	76	77	81
Salientia	252	252	252	252	252	246	247	250	246	247	250	246	247	250
Anura	169	171	174	178	183	166	168	174	168	170	188	180	183	190
Bombinanura	169	170	172	175	178	166	168	174	167	169	187	175	178	185
Pipanura	158	160	162	165	171	152	153	156	153	156	159	166	168	171
Neobatrachia	85	91	99	108	124	72	73	77	78	79	83	111	112	116
Hyloidea	85	91	99	105	119	72	73	77	78	79	83	106	107	111
(*Hyla*, *Bufo*)	85	89	94	99	109	72	73	77	77	78	82	96	97	101
Ranoidea (*Microhyla*, *Rana*)	38	42	50	58	74	34	36	40	37	38	42	69	70	74
Microhylidae	29	31	34	38	44	23	24	28	26	27	31	39	40	44
Ranidae	38	40	47	52	65	35	36	40	35	36	40	59	60	64
Aglaioanura	38	38	43	46	55	35	36	40	33	34	38	49	50	54

even Middle Permian. Our results (Marjanović & Laurin 2007, 2008a) suggest a yet more recent, Permian age (300-255 Ma).

Molecular dating offers a way of answering the question of when a cladogenesis happened without having to rely entirely on the imperfect fossil record. Dates estimated this way for the origin of Lissamphibia have been advanced as support for the TH (Zhang *et al.* 2005) and the PH (Lee & Anderson 2006; Anderson 2008). While these particular arguments relied on a misunderstanding of the literature about the fossil record of temno- and lepospondyls in the first case and on questionable decisions about calibration points in both cases (Marjanović & Laurin 2007), divergence dates can be used to discriminate between phylogenetic hypotheses (as also noted by San Mauro [2010], who used his molecular date estimates for cautiously arguing against the PH).

Despite being imperfect, however, the fossil record itself can also provide estimates of divergence dates if used as the input for methods that take its sampling density into account. We have developed two such approaches (Marjanović & Laurin 2007, 2008a), which are summarised below along with recent work in molecular dating.

Contrary to what San Mauro (2010: 556) claimed, we have never made an "assertion that the lissamphibian fossil record is complete enough to be read literally". It is not; this is why two such complex approaches are necessary.

Fossil-based supertree

Any taxon is at least as old as its oldest known fossil representative. How much older it is depends on how many internodes (branches) separate that fossil from the origin of the taxon, and on how long those internodes are. The first question can be approximately answered by a phylogenetic tree with the fossil in it; the answer to the second can be estimated by testing if different arbitrary but realistic values give similar results.

Therefore, we (Marjanović & Laurin 2007) used a set of 14 assumptions about minimal branch lengths (Table 6) on a hand-made supertree of Lissamphibia. The minimal length of terminal branches ranged from 0.1 to 5 Ma or a whole geological stage (regardless of its duration), and the minimal length of terminal branches varied from 0.1 to 5 Ma (a 50-fold range of values). Because of these wide ranges, the age of clades with a poor fossil record, such as Ranoidea Rafinesque, 1814 (Table 6), depends strongly on the assumptions about minimal branch lengths. This is because in such cases the oldest fossil is usually deeply nested, and the method yields a minimal clade age equal to the age of the oldest fossil plus the sum of all internal branches connecting it to the root of the clade. Thus, the age of Ranoidea varied between 34 and 74 Ma (Table 6). Conversely, clades with a fairly good fossil record typically have fossils close to the base, and in such cases assumptions about minimal branch lengths have little impact. For Lissamphibia, this procedure yielded ages that varied from 246 to 267 Ma ago (Fig. 2C; Table 6). The variation of about 21 million years found for the origin of Lissamphibia yielded by this method is almost identical to the size of the 95% confidence interval of the date of origin of Lissamphibia found by the molecular dating study of Zhang *et al.* (2005), suggesting that it is not artificially narrow.

We also (Marjanović & Laurin 2007) assessed the impact of phylogenetic uncertainty (in the form of polytomies) by randomly resolving each polytomy in our supertree ten times and comparing the average age of several crown-clades under these random resolutions with the age under the preferred tree. The results show that the use of polytomies tends to slightly inflate the age of most clades (Table 7).

These results are significant with respect to the PH: the date of origin of Lissamphibia is incompatible with the PH, a fact that *does not automatically follow* from lissamphibian monophyly and therefore constitutes *additional* evidence against the PH.

Stratigraphy-based, phylogeny-free dating

Marjanović & Laurin (2008a) modified a method first proposed by Marshall (1997) and used it to date the appearance of Lissamphibia. This method calculates a confidence interval on the appearance of a taxon based on the stratigraphic distribution of the horizons or localities that have yielded fossils of this taxon (1207 localities in this case) and the following factors that determine how many fossils we should expect to be known from each geological stage: the relative area of exposed rocks from the relevant stages, exponential-growth models that differ by the assumed starting date of lissamphibian diversification, and the assumed effects of mass extinctions taken from the literature and based on observed extinction rates in various taxa (too little is currently known about the history of lissamphibian diversity to estimate this from their fossil record). In order to sample a broad range of biologically plausible models and assumptions, we performed two sets of calculations of stratigraphic confidence intervals; their respectively Devonian and Early Carboniferous starting dates were taken from Roelants *et al.* (2007) and Zhang *et al.* (2005). Realistic settings for the other variables result in 75% confidence intervals that stay within the Permian and 50% confidence intervals that begin no later than the Middle (Guadalupian) or even Late Permian (Luopingian) (Fig. 2B; Marjanović & Laurin 2008a: fig 4C1-4).

In the future, this method could be improved by taking changes in the ratio of terrestrial to marine sediments over time into account (it was assumed to be constant in Marjanović & Laurin [2008a]), but we do not expect this to result in large changes to the results: our models explained from 85 to 90% of the variance in the temporal distribution of fossiliferous localities that have yielded lissamphibians.

TABLE 7. — Estimated date of appearance of selected taxa under ten random resolutions of the polytomies in the supertree of Marjanović & Laurin (2007) produced by the equiprobable model of MacClade 4.06 (Maddison & Maddison 2003). All dates are in Ma ago and rounded to 1 Ma. The "undoubted pelodytid" is mentioned as such by Rage & Roček (2003); it comes from the Bartonian of France. For the taxa whose names have a branch-based definition, the dates reported represent the oldest known node in the taxon, not the appearance of the taxon as a whole. From Marjanović & Laurin (2007: app. 5). The authors of all taxon names are listed in Appendix 11.

Designation of polytomy	Taxa included in the polytomy	Relevant taxa	Age of relevant taxa on random trees			Age on reference tree
			Average	Minimal	Maximal	
Gymnophiona	Wadi Milk caecilian, Pajcha Pata caecilian, *Apodops*, Rhinatrematidae, Stegokrotaphia	Gymnophiona	70	11	109	100
Salientia	*Triadobatrachus, Czatkobatrachus,* other Salientia	Batrachia	257	257	257	254
		Lissamphibia	263	263	263	260
Discoglossoidea	*Eodiscoglossus, Callobatrachus, Bombina, Opisthocoelellus, Latonia,* Discoglossidae	Discoglossoidea (crown)	146	34	180	171
		Anura	183	177	186	177
Bombina	*Bombina* spp.	*Bombina* (crown)	19	2	26	23
Discoglossus	*Discoglossus* spp.	*Discoglossus* (crown)	21	5	34	28
	Discoglossus, Alytes	Discoglossidae (crown)	33	31	37	31
Pelobatidae	*Pelobates, Eopelobates, Scotiophryne*	(*Pelobates* + *Eopelobates*)	81	55	87	84
	Pelobatidae, Megophryidae, Pelodytidae, Scaphiopodidae	Pelobatoidea	95	93	96	93
Pelodytidae	*Pelodytes, Miopelodytes, Tephrodytes*, Quercy pelodytid, "undoubted pelodytid"	Pelodytidae	46	43	49	40
Pelobates	*Pelobates* spp.	*Pelobates* (crown)	33	17	43	34
Rana (*Pelophylax*)	*Rana* (*Pelophylax*) *ridibunda, R.* (*P.*) *saharica*, Möhren green frog	*Rana* (*Pelophylax*) (crown)	27	2	37	34
		Ranoidea	60	58	61	58
Telmatobiinae	*Telmatobius, Eupsophus, Neoprocoela,* Itaboraí telmatobiine	Telmatobiinae (crown)	67	65	68	62
Hylidae	Hylinae, Itaboraí hylid, (Pelodryadinae + Phyllomedusinae)	Hylidae (crown)	54	37	65	62
		(Hylidae + *Rhinoderma*)	67	65	68	65
Cryptobranchidae (crown)	Cryptobranchidae except *Chunerpeton*	Cryptobranchidae (crown)	55	31	68	59
Siren	*Siren* spp.	*Siren* (crown)	37	2	52	49
		Sirenidae (crown)	54	52	55	52
Ambystoma	*Ambystoma* spp.	*Ambystoma* (crown)	28	2	40	34
Salamandra	*Salamandra* spp.	*Salamandra* (crown)	36	18	43	37
		Salamandrinae (crown)	43	40	46	40
Average			77	59	86	80

MOLECULAR DATING, CHOICE OF CALIBRATION DATES

Some molecular estimates of the time of origin of Lissamphibia suggest Early Carboniferous (Viséan or earlier) or even Devonian dates of origin of Lissamphibia (references in Anderson [2008] and San Mauro [2010]). The choice of characters (that is, genes: mitochondrial or nuclear, coding for a wide variety of proteins, tRNAs and/or rRNAs) does not seem to have a noticeable effect on the

divergence date estimates. Brochu (2004a, b, 2006) and Marjanović & Laurin (2007) showed that the calibration points are most critical, and that it is necessary to use multiple calibrations, both shallow and deep, both within and outside the clade of interest. Indeed, several of the most recent studies (Roelants & Bossuyt 2005; San Mauro *et al.* 2005; Roelants *et al.* 2007; Marjanović & Laurin 2007; Vieites *et al.* 2007; Igawa *et al.* 2008; some of the analyses by San Mauro 2010) have used such a combination of calibration constraints. An important difference between the studies, however, lies in the use of maximum ages which most of the recent studies used only for external constraints. Rodríguez-Trelles *et al.* (2002) suspected this fact of artificially inflating molecular divergence date estimates and predicted that the use of maximum ages would bring these estimates into much closer accord with the fossil record. Marjanović & Laurin (2007) used maximum age constraints for two or three internal calibration points (the origins of Urodela, Bombinanura Cannatella & Hillis, 1993, and in some analyses the tetrapod crown-group) in all analyses that resulted in Permian dates of origin for Lissamphibia. (We also proposed [Marjanović & Laurin 2007: 381, 382] maximum ages for the origins of Batrachia and Pipoidea Gray, 1825, but did not use them in any analysis.) The prediction by Rodríguez-Trelles *et al.* (2002) was further confirmed by San Mauro (2010: Table 3). San Mauro's preferred analyses had only external calibration points and found the abovementioned early Late Carboniferous dates for the origin of Lissamphibia, with confidence intervals of various sizes as mentioned. When he added internal calibration points with maximum ages from Marjanović & Laurin (2007), a narrow 95% confidence interval (320-292 Ma ago; latest Early Carboniferous to earliest Permian) resulted, with a best estimate of only 305 Ma ago (latest Carboniferous); adding internal calibration points without maximum ages instead resulted in older divergence date estimates than those found by the preferred analyses.

Use of the internal calibration constraints was validated by testing the overall quality of the lissamphibian fossil record using the time-calibrat-ed supertree mentioned above. We chose those maximum ages based on the the presence of older sister-taxa of the clade of interest (Fig. 5), as suggested by Raaum *et al.* (2005). We furthermore selected only dates that did not strongly depend on assumptions about minimum branch lengths (Table 6). This method is based on the assumption that the fossilization potential of lineages within and outside the crown-groups should be comparable.

We seem to have failed to make sufficiently clear that we used these selection criteria to select upper bounds of calibration constraints (Marjanović & Laurin 2007: 380). For instance, Anderson (2008: 242) asked: "How can one be certain that *Eocaecilia* is placed in the fossil record close to the real time of divergence with no ghost lineage, when above it in the stratigraphic column there are two known ghost lineages totaling approximately 90 million years?" Similarly, San Mauro (2010: 556) has argued against using *Eocaecilia* to constrain a calibration point. In reality, it is not *possible* to use the Early Jurassic *Eocaecilia* to constrain a calibration point: *Eocaecilia* is practically alone on the long gymnophionomorph stem, making it useless for calibration points within Gymnophionomorpha – and Batrachia (*Triadobatrachus* and *Czatkobatrachus*) is known to be older than *Eocaecilia*, making *Eocaecilia* useless for calibration points within Batrachia or any clade that contains the latter. Therefore we deliberately did not use *Eocaecilia* as a calibration constraint.

San Mauro (2010: 556), however, gives an entirely different reason for why *Eocaecilia* should not be used to constrain a calibration point: its "phylogenetic affinities are still equivocal (Anderson 2008; Jenkins *et al.* 2007)". In fact, in their monographic redescription of *Eocaecilia*, Jenkins *et al.* (2007) have shown that numerous gymnophionomorph autapomorphies are present in *Eocaecilia* and confirmed the consensus that its phylogenetic position is as shown in Figure 2A. Anderson (2008) explicitly agreed that *Eocaecilia* is closely related to Gymnophiona, and the monographic description of the braincase coauthored by him (Maddin *et al.* 2012) has further confirmed this hypothesis. The phylo-
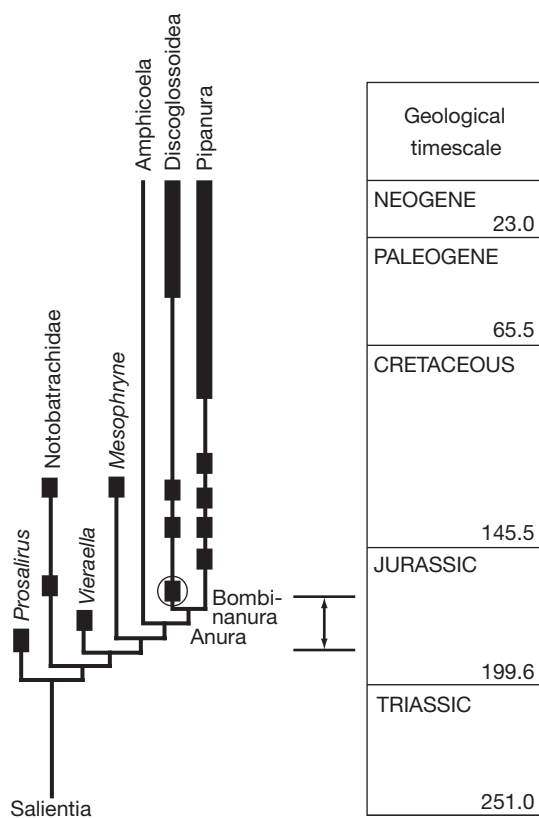
FIG. 5. — Criteria for choosing calibration points and determining their minimum and maximum ages (after Raaum *et al.* 2005: fig. 2) exemplified by the origin of Bombinanura (i.e. the cladogenesis in which Discoglossoidea and Pipanura originated). Known stratigraphic ranges shown by thick lines. The minimum age is the age of the oldest known bombinanuran fossil, the discoglossoid *Eodiscoglossus oxoniensis* (circled). The maximum age is more difficult to constrain, but is probably close to the bottom of the interval marked by the double arrow, from which bombinanurans are not known, even though closely related and presumably ecologically similar salientians (*Prosalirus* and *Vieraella*) were present. That fossils of the *Mesophryne* lineage older than *Eodiscoglossus* have not been discovered, and that Amphicoela (*Ascaphus* and *Leiopelma*) lacks a known pre-Pleistocene fossil record altogether, is unfortunate, but has little relevance for the above argument. The root of this tree extends down to the approximate age of the oldest known salientians, *Triadobatrachus* and *Czatkobatrachus*. The authors of all taxon names are listed in Appendix 11.

genetic position of *Eocaecilia* is unclear only to the extent that the position of Gymnophionomorpha is controversial, which depends only on the adopted hypothesis of extant amphibian inter- (TH, LH, or PH) and intrarelationships (Batrachia hypothesis,

Procera hypothesis, or again PH). There is a fair amount of phenetic distance between *Eocaecilia* and Gymnophiona, but this had to be expected from the former's Early Jurassic age (*c.* 190 Ma).

The global test on the quality of the fossil record that we performed on our dataset consists of comparing the order of appearance of taxa expected from the topology of the reference tree to the observed stratigraphic order of appearance of the taxa. Similar comparisons are done for populations of trees in which the stratigraphic ranges of taxa have been randomly permuted. Significance is established by the proportion of randomized trees that have at least as good a match as the reference tree. This test was performed using Ghost (Wills 1999), and it yielded a highly significant correlation (p = *c.* 0.0001; Marjanović & Laurin 2007: 380).

The significance of this test seems not to have been fully appreciated. Anderson (2008: 242) doubted the relevance of the result, claiming that Huelsenbeck (1994) "demonstrated that a relatively low number of consistent nodes (four in his example) are necessary to find significant consistency of the tree with the fossil record, and this significant consistency remains present in all trees several steps from most parsimonious". However, Huelsenbeck (1994: 476, fig. 2) explained the results of his analyses of one particular dataset; he did not draw any generalizations from it – to the contrary, his table 1 lists two trees that are inconsistent with the stratigraphic record even at the p ≤ 0.1 level despite having 7 and 25 nodes that are consistent with the stratigraphy (out of 10 and 37 possible nodes). Thus, the lissamphibian record – although highly incomplete in absolute terms! – is "probably not too incomplete" (Marjanović & Laurin 2007: 385) to supply maximum ages for a few carefully selected calibration points.

Igawa *et al.* (2008), who used minimum and maximum ages for two (out of five) internal and all external calibration points, nonetheless found Lissamphibia to be 335 (352-317) Ma old. This result is very similar to the one by Zhang *et al.* (2005), who used an earlier version of the same dataset (with fewer taxa) and the same programs, but only two calibration points, both of them external. At first sight, this might be taken to mean

that the number and maximum ages of calibration points do not matter much. In contrast, we would like to point out that some of the calibration dates used by Igawa *et al.* (2008: table 2) are based on misunderstandings of the paleontological literature. An external and two internal calibration constraints shall serve as examples:

The origin of Archosauria Cope, 1869 (the divergence between the crocodile and bird lineages) was put at 252-257 Ma ago by Igawa *et al.* (2008), and Reisz & Müller (2004) were cited as the source. In fact, Reisz & Müller (2004) attributed this age to the crocodile-squamate (archosauromorph-lepidosauromorph) divergence, which preceded the crocodile-bird divergence. Reisz & Müller (2004) did not mention the latter much; Müller & Reisz (2005) suggested maximum and minimum ages of 251 and 243 Ma for the crocodile-bird divergence based on the presence of numerous stem-archosauriforms but the absence of archosaurs in the Early Triassic record, and the presence of one stem-archosauriform but no archosaurs in the Permian sediments investigated so far (thus fulfilling the criteria by Raaum *et al.* 2005). Nesbitt (2011: 249, fig. 58A) found the late Early Triassic (probably older than 247 Ma) *Xilousuchus* Wu, 1981, and possibly the coeval *Vytshegdosuchus* Sennikov, 1988, to be archosaurs; he consequently recommended (Nesbitt 2011: 253) that "a date greater than 245 Ma should be used to calibrate molecular divergence dates". His figure 58A implies a maximum age of 250 or 249 Ma, in the middle Early Triassic, and puts the Permian/Triassic boundary at 252.3 Ma ago. In short, the crocodile-bird split may have happened as recently as 245-250 Ma ago.

Igawa *et al.* (2008) further attributed a minimum age of 168 Ma to the divergence between Discoglossidae Günther, 1859, and Bombinatoridae Gray, 1825, citing Milner (1993) who called *Eodiscoglossus oxoniensis* Evans, Milner & Mussett, 1990, the earliest known discoglossid. This reflects the imprecise taxon delimitation in rank-based nomenclature (Laurin 2008): for much of the 20th century it was usual to use the name Discoglossidae for what is now more often called Discoglossoidea, a clade that includes both Discoglossidae in the current sense and Bombinatoridae (formerly Bombinatorinae). *Eodiscoglossus* Villalta, 1957, is at present a discoglossoid incertae sedis, and there is no reason to assume it is a discoglossid. It is potentially useful to molecular dating as the oldest known crown-group frog (Fig. 5; Marjanović & Laurin 2007), but cannot presently be used to date cladogeneses within Discoglossoidea. In fact, the minimal divergence date between Discoglossidae and Bombinatoridae is poorly constrained by the fossil record because the affinities of most relevant fossils are uncertain (Marjanović & Laurin 2007: fig. 5) – it could be as recent as Lutetian (middle Eocene, less than 49 Ma ago).

Finally, both the minimum and the maximum dates given for the divergence between Rhacophoridae Hoffman, 1932, and Mantellidae Laurent, 1946, by Igawa *et al.* (2008: table 2) are not directly based on the fossil or the geological record. Instead, they are *results* of the molecular dating analysis by Bossuyt & Milinkovitch (2001). To use such a date as a calibration point for molecular divergence dating is suboptimal (e.g., Graur & Martin 2004).

Incidentally, Anderson (2008: table 2) cited Igawa *et al.* (2008) as having found Lissamphibia to be 355 (370-340) and Batrachia to be 335 (352-317) Ma old, which would be more compatible with the PH than with the LH or the TH. In fact, the latter is the age of Lissamphibia found by Igawa *et al.* (2008); the former is the age of the tetrapod crown-group, in other words, the divergence between the ancestors of Lissamphibia and those of Amniota (Igawa *et al.* 2008: 123).

Altogether, keeping in mind the caveats discussed above, it appears that molecular dating refutes, rather than supports, the PH, as noted by San Mauro (2010).

DATING OF A COMBINED ANALYSIS WITH TERMINAL TAXA AS CALIBRATION CONSTRAINTS

Pyron (2011) merged the morphological data matrix of Vallin & Laurin (2004) with a molecular dataset, conducted a phylogenetic analysis of this combined matrix, and obtained a tree that supports the LH (and in general a topology almost entirely compatible with that found by Vallin & Laurin 2004). He then dated the nodes of that tree by giving all OTUs their known geological

ages – instead of using any nodes as calibration constraints – and applying a recently developed program for molecular dating that can deal with noncontemporaneous terminal branches. In effect, thus, every OTU acted as a minimum age for the node from which it stems; branch length estimates, including those of extinct taxa (for which length was computed as steps in the morphological characters), were used in the dating procedure. The only "maximum age" in the tree was the root, set as a 95% confidence interval from the earliest fossils of the closest finned outgroups (Late Devonian) to the earliest evidence of limbed vertebrates (Niedźwiedzki *et al.* 2010; early Middle Devonian). The resulting 95% confidence interval for the age of Lissamphibia reaches from 278 Ma ago (Early Permian) to 332 Ma ago (middle Early Carboniferous), with a best estimate at 305.5 Ma ago (late Late Carboniferous). As Pyron (2011: 474) noted, these dates – as well as those of many nodes inside Lissamphibia – are consistent with the results by Marjanović & Laurin (2007, 2008a) and San Mauro (2010; see above) and much younger than those found by most other studies.

It remains to be tested to what degree this encouraging result depends on the data matrix by Vallin & Laurin (2004). That dataset was designed for parsimony analysis, so that – unlike in the molecular part of the combined dataset – almost all characters are parsimony-informative; the deliberate exclusion of parsimony-uninformative characters may have led to underestimated branch lengths.

POSSIBLE FUTURE SURPRISES

In a conference abstract, Pardo (2011) reported a few results of his reinvestigation of specimens of the diplocaulid "nectridean" *Diploceraspis*. Several of these contradict the latest published description (Beerbower 1963), including the line drawings therein. "Relationships of *Diploceraspis* were investigated with cladistic analysis of several existing matrices, including matrices heavily sampling both lepospondyls and temnospondyls. Strong support is found for a temnospondyl

origin of *Diploceraspis*, and by extension other nectrideans, within the Dvinosauria […]. No strong support exists for a monophyletic Lepospondyli, suggesting important and previously understated instability in the phylogeny of early tetrapods." If this decidedly heterodox claim can be substantiated, in particular if not too many of the similarities between diplocaulids and dvinosaurian temnospondyls turn out to be due to convergence among obligatorily aquatic ambush predators, the terms TH, LH and PH may lose much of their meaning if lissamphibians are closely related to nectrideans. But in any case, even according to published descriptions, quite a few character states are shared between some or all holospondyls (notably the amphibious or terrestrial *Scincosaurus*, which is not a diplocaulid, although it may be their sister-group), some or all temnospondyls, and some or all lissamphibians (see the section 'Informative character distributions' and 'key taxa' above, and Appendices 1-10).

CONCLUSIONS

At present, the lepospondyl hypothesis on the origin of the extant amphibians (LH) appears to be somewhat better supported than the temnospondyl hypothesis (TH) and considerably more so than the polyphyly hypothesis (PH), based on several independent lines of evidence including phylogenetics (despite the often complex, if not confusing, distribution of character states) and three, arguably four, methods of dating the divergence of the extant amphibians from each other. The complex of characters called the salamander mode of autopodium development is, in its less extreme forms, likely plesiomorphic for limbed vertebrates and was independently and to varying degrees lost in direct-developing salamanders, frogs, and amniotes; if accurate, this means that reports of this mode of development in temnospondyls cannot be used to argue for the TH or the PH. Taxon deletion analyses suggest that the LH is not due to convergence between long-bodied limbless lissamphibians (caecilians, *Siren*, *Proteus*) and long-bodied lepospondyls with reduced limbs

(lysorophians, aïstopods, various "microsaurs"). If correct, this implies that, while thousands of (mostly endangered) species of "lepospondyl" descendants are still with us, the temnospondyls are entirely extinct and lie outside the tetrapod crown-group.

NOTE ADDED IN PROOF

While Figure 5 correctly explains what we did in our 2007 paper, it is outdated : there are amphicoelan fossils from the Miocene and the Late Cretaceous, and, most importantly, *Eodiscoglossus* is not a bombinanuran and may not even be an anuran (Báez 2013). The oldest bombinanurans are thus the pipanuran *Rhadinosteus* Henrici, 1998 (shown as a black rectangle in Figure 5), and the coeval discoglossoid *Enneabatrachus* Evans & Milner, 1993 (not shown). The minimum age of Bombinanura, is thus younger, and its maximum age better constrained, than shown in Figure 5. This and similar issues that concern Tables 6 and 7 as well as pages 243 and 247 will be discussed in an upcoming paper.

REFERENCES

AHLBERG P. E., CLACK J. A., LUKŠEVIČS E., BLOM H. & ZUPIŅŠ I. 2008. — *Ventastega curonica* and the origin of tetrapod morphology. *Nature* 453: 1199-1204.

ANDERSON J. S. 2001. — The phylogenetic trunk: maximal inclusion of taxa with missing data in an analysis of the Lepospondyli (Vertebrata, Tetrapoda). *Systematic Biology* 50: 170-139.

ANDERSON J. S. 2002. — Revision of the aïstopod genus *Phlegethontia* (Tetrapoda: Lepospondyli). *Journal of Paleontology* 76: 1029-1046.

ANDERSON J. S. 2007. — Incorporating ontogeny into the matrix: a phylogenetic evaluation of developmental evidence for the origin of modern amphibians, *in* ANDERSON J. S. & SUES H.-D. (eds), *Major transitions in Vertebrate Evolution*. Indiana University Press, Bloomington, 182-227.

ANDERSON J. S. 2008. — The origin(s) of modern amphibians. *Evolutionary Biology* 35: 231-247.

ANDERSON J. S., HENRICI A. C., SUMIDA S. S., MARTENS T. & BERMAN D. S 2008a. — *Georgenthalia clavinasica*, a new genus and species of dissorophoid temnospondyl from the Early Permian of Germany, and the relationships of the family Amphibamidae. *Journal of Vertebrate Paleontology* 28: 61-75.

ANDERSON J. S., REISZ R. R., SCOTT D., FRÖBISCH N. B. & SUMIDA S. S. 2008b. — A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. *Nature* 453: 515-518.

ANDERSON J. S., SCOTT D. & REISZ R. R. 2009. — *Nannaroter mckinziei*, a new ostodolepid "microsaur"(Tetrapoda, Lepospondyli, Recumbirostra) from the Early Permian of Richards Spur (Ft. Sill), Oklahoma. *Journal of Vertebrate Paleontology* 29: 379-388.

BÁEZ A. M. 2013. — Anurans from the Early Cretaceous Lagerstätte of Las Hoyas, Spain : New evidence on the Mesozoic diversification of crown-clade Anura. *Cretaceous Research* 41: 90-106.

BÁEZ A. M. & BASSO N. G. 1996. — The earliest known frogs of the Jurassic of South America: review and cladistic appraisal of their relationships. *Münchner geowissenschaftliche Abhandlungen Reihe A (Geologie und Paläontologie)* 30: 131-158.

Beerbower J. R. 1963. — Morphology, paleoecology, and phylogeny of the Permo-Pennsylvanian amphibian *Diploceraspis*. *Bulletin of the Museum of Comparative Zoology at Harvard College* 130: 33-108.

Benjamini Y. & Hochberg Y. 1995. — Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)* 57: 289-300.

Berman D. S & Henrici A. C. 2003. — Homology of the astragalus and structure and function of the tarsus of Diadectidae. *Journal of Paleontology* 77: 172-188.

Berman D. S, Reisz R. R. & Eberth D. A. 1985. — *Ecolsonia cutlerensis*, an Early Permian dissorophid amphibian from the Cutler Formation of north-central New Mexico. *Circular* 191 *of the New Mexico Bureau of Mines and Mineral Resources*: 1-31.

Berman D. S, Henrici A. C., Kissel R. A., Sumida S. S. & Martens T. 2004. — A new diadectid (Diadectomorpha), *Orobates pabsti*, from the Early Permian of central Germany. *Bulletin of Carnegie Museum of Natural History* 35: 1-36.

Blanco M. J. & Alberch P. 1992. — Caenogenesis, developmental variability, and evolution in the carpus and tarsus of the marbled newt, *Triturus marmoratus*. *Evolution* 46: 677-687.

Bolt J. R. 1969. — Lissamphibian origins: possible protolissamphibian from the Lower Permian of Oklahoma. *Science* 166: 888-891.

Bolt J. R. 1979. — *Amphibamus grandiceps* as a juvenile dissorophid: evidence and implications, *in* Nitecki M. H. (ed.), *Mazon Creek fossils*. Academic Press, London, 529-563.

Bolt J. R. 1991. — Lissamphibian origins, *in* Schultze H.-P. & Trueb L. (eds), *Origins of the higher groups of tetrapods—controversy and consensus*. Cornell University Press, Ithaca, 194-222.

Bolt J. R. & Lombard R. E. 1985. — Evolution of the amphibian tympanic ear and the origin of frogs. *Zoological Journal of the Linnean Society* 24: 83-99.

Bolt J. R. & Rieppel O. 2009. — The holotype skull of *Llistrofus pricei* Carroll and Gaskill, 1978 (Microsauria: Hapsidopareiontidae). *Journal of Paleontology* 83: 471-483.

Bolt J. R. & Wassersug R. J. 1975. — Functional morphology of the skull in *Lysorophus*: a snake-like Paleozoic amphibian (Lepospondyli). *Paleobiology* 1: 320-332.

Bossuyt F. & Milinkovitch M. C. 2001. — Amphibians as indicators of early Tertiary "Out-of-India" dispersal of vertebrates. *Science* 292: 93-95.

Bourget H. & Anderson J. S. 2011. — A new amphibamid (Temnospondyli: Dissorophoidea) from the Early Permian of Texas. *Journal of Vertebrate Paleontology* 31: 32-49.

Boy J. A. & Sues H.-D. 2000. — Branchiosaurs: larvae, metamorphosis and heterochrony in temnospondyls and seymouriamorphs, *in* Heatwole H. & Carroll R. L. (eds), *Amphibian Biology*. Volume 4: *Palaeontology*. Surrey Beatty & Sons, Chipping Norton, 1150-1197.

Brochu C. A. 2004a. — Calibration age and quartet divergence date estimation. *Evolution* 58: 1375-1382.

Brochu C. A. 2004b. — Patterns of calibration age sensitivity with quartet dating methods. *Journal of Paleontology* 78: 7-30.

Brochu C. A. 2006. — Empirical exploration of calibration sensitivity in molecular dating methods – maximising the role of palaeontology in molecular evolution, *in* Yang Q., Wang Y. & Weldon E. A. (eds), *Ancient life and modern approaches* [abstract volume of the 2nd International Palaeontological Congress]. University of Science and Technology of China Press, Beijing, 138 p.

Cannatella D. C. & Hillis D. M. 1993. — Amphibian relationships: phylogenetic analysis of morphology and molecules. *Herpetological Monographs* 7: 1-7.

Carroll R. L. 1991. — *Batropetes* from the Lower Permian of Europe – a microsaur, not a reptile. *Journal of Vertebrate Paleontology* 11: 229-242.

Carroll R. L. 1998. — Cranial anatomy of ophiderpetontid aïstopods: Palaeozoic limbless amphibians. *Zoological Journal of the Linnean Society* 122: 143-166.

Carroll R. L. 2007. — The Palaeozoic ancestry of salamanders, frogs and caecilians. *Zoological Journal of the Linnean Society* 150 (Suppl. 1): 1-140.

Carroll R. L. & Gaskill P. 1978. — *The order Microsauria*. American Philosophical Society, Philadelphia, 311 p.

Carroll R. L. & Holmes R. 1980. — The skull and jaw musculature as guides to the ancestry of salamanders. *Zoological Journal of the Linnean Society* 68: 1-40.

Carroll R. L. & Chorn J. 1995. — Vertebral development in the oldest microsaur and the problem of "lepospondyl" relationships. *Journal of Vertebrate Paleontology* 15: 37-56.

Carroll R. L., Bybee P. & Tidwell W. D. 1991. — The oldest microsaur (Amphibia). *Journal of Paleontology* 65: 314-322.

Carroll R. L., Kuntz A. & Albright K. 1999. — Vertebral development and amphibian evolution. *Evolution & Development* 1: 36-48.

Carroll R. L., Boisvert C., Bolt J., Green D. M., Philip N., Rolian C., Schoch R. R. & Tarenko A. 2004. — Changing patterns of ontogeny from osteolepiform fish through Permian tetrapods as a guide to the early evolution of land vertebrates, *in* Arratia G., Wilson M. V. H. & Cloutier R. (eds), *Recent advances in the origin and early radiations of vertebrates*. Dr. Friedrich Pfeil, München, 321-343.

Clack J. A. 2002. — *Gaining Ground. The Origin and Evolution of Tetrapods*. Indiana University Press, Bloomington, 369 p.

Clack J. A. 2011. — A new microsaur from the Early Carboniferous (Viséan) of East Kirkton, Scotland,

showing soft-tissue evidence. *Special Papers in Palae-ontology* 86: 45-55.

Clack J. A. & Milner A. R. 2010. — Morphology and systematics of the Pennsylvanian amphibian Platyrhinops lyelli (Amphibia: Temnospondyli). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 100: 275-295.

Coates M. I. 1996. — The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 87: 363-421.

Coates M. I. & Clack J. A. 1991. — Fish-like gills and breathing in the earliest known tetrapod. *Nature* 352: 234-236.

Coates M. I. & Clack J. A. 1995. — Romer's gap: tetrapod origins and terrestriality. *Bulletin du Muséum national d'Histoire naturelle de Paris, 4ème série* 17: 373-388.

Coates M. I., Ruta M. & Friedman M. 2008. — Ever since Owen: changing perspectives on the early evolution of tetrapods. *Annual Review of Ecology, Evolution, and Systematics* 39: 571-592.

Cohn M. J., Lovejoy C. O., Wolpert L. & Coates M. I. 2002. — Branching, segmentation and the metapterygial axis: pattern versus process in the vertebrate limb. *BioEssays* 24: 460-465.

Conrad J. L. 2008. — Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History* 310: 1-182.

Cote S., Carroll R., Cloutier R. & Bar-Sagi L. 2002. — Vertebral development in the Devonian sarcopterygian fish *Eusthenopteron foordi* and the polarity of vertebral evolution in non-amniote tetrapods. *Journal of Vertebrate Paleontology* 22: 487-502.

Daly E. 1994. — The Amphibamidae (Amphibia: Temnospondyli), with a description of a new genus from the upper Pennsylvanian of Kansas. *The University of Kansas Museum of Natural History Miscellaneous Publication No.* 85: i-iv + 1-59.

Dilkes D. W. 1990. — A new trematopsid amphibian (Temnospondyli: Dissorophoidea) from the Lower Permian of Texas. *Journal of Vertebrate Paleontology* 10: 222-243.

Dutuit J.-M. 1988. — *Diplocaulus minimus* n. sp. (Amphibia: Nectridea), lépospondyle de la formation d'Argana, dans l'Atlas occidental marocain. *Comptes Rendus de l'Académie des Sciences de Paris* 307: 851-854.

Evans S. E. & Borsuk-Białynicka M. 2010. — The Early Triassic stem-frog *Czatkobatrachus* from Poland. *Palaeontologica Polonica* 65: 79-105.

Evans S. E. & Milner A. R. 1996. — A metamorphosed salamander from the Early Cretaceous of Las Hoyas, Spain. *Philosophical Transactions of the Royal Society of London, Series B* 351: 627-646.

Evans S. E. & Sigogneau-Russell D. 2001. — A stem-group caecilian (Lissamphibia: Gymnophiona) from the Lower Cretaceous of north Africa. *Palaeontology* 44: 259-273.

Fernandes L. A. & Coimbra A. M. 2000. — Revisão estratigráfica da parte oriental da Bacia Bauru (Neocretáceo). *Revista Brasileira de Geociências* 30: 717-728.

Fong J. J., Brown J. M., Fujita M. K. & Boussau B. 2012. — A phylogenomic approach to vertebrate phylogeny supports a turtle-archosaur affinity and a possible paraphyletic Lissamphibia. *PLoS ONE* 7: e48990

Franssen N. A., Marks S., Wake D. & Shubin N. 2005. — Limb chondrogenesis of the seepage salamander, *Desmognathus aeneus* (Amphibia: Plethodontidae). *Journal of Morphology* 265: 87-101.

Fröbisch N. B. 2008. — Ossification patterns in the tetrapod limb – conservation and divergence from morphogenetic events. *Biological Reviews of the Cambridge Philosophical Society* 83: 571-600.

Fröbisch N. B. & Reisz R. R. 2008. — A new Lower Permian amphibamid (Dissorophoidea, Temnospondyli) from the fissure fill deposits near Richards Spur, Oklahoma. *Journal of Vertebrate Paleontology* 28: 1015-1030.

Fröbisch N. B. & Schoch R. R. 2009a. — Testing the impact of miniaturization on phylogeny: Paleozoic dissorophoid amphibians. *Systematic Biology* 58: 312-327.

Fröbisch N. B. & Schoch R. R. 2009b. — The largest specimen of *Apateon* and the life history pathway of neoteny in the Paleozoic temnospondyl family Branchiosauridae. *Fossil Record* 12: 83-90.

Fröbisch N. B. & Shubin N. H. 2011. — Salamander limb development: integrating genes, morphology, and fossils. *Developmental Dynamics* 240: 1087-1099.

Fröbisch N. B., Carroll R. L & Schoch R. R. 2007. — Limb ossification in the Paleozoic branchiosaurid *Apateon* (Temnospondyli) and the early evolution of preaxial dominance in tetrapod limb development. *Evolution & Development* 9: 69-75.

Fröbisch N. B., Olori J. C., Schoch R. R. & Witzmann F. 2010. — Amphibian development in the fossil record. *Seminars in Cell & Developmental Biology* 21: 424-431.

Frost D. R., Grant T., Faivovich J., Bain R. H., Haas A., Haddad C. F. B., Sá R. O. de, Channing A., Wilkinson M., Donnellan S. C., Raxworthy C. J., Campbell J. A., Blotto B., Moler P., Drewes R. C., Nussbaum R. A., Lynch J. D., Green D. M. & Wheeler W. C. 2006. — The amphibian tree of life. *Bulletin of the American Museum of Natural History* 297: 1-370.

Gao K., Fox R., Li D. & Zhang J. 2004. — A new vertebrate fauna from the Early Triassic of northern Gansu Province, China. *Journal of Vertebrate Paleontology* 24 (Suppl. to issue 3): 62A.

Gao K., Fox R., Zhou C. & Li D. 2008. — A new non-mammalian eucynodont (Synapsida: Therapsida) from the Lower Triassic of China, and its biostrati-

graphic implications. *Journal of Vertebrate Paleontology* 28 (Suppl. to issue 3): 82A.

GATESY J. & BAKER R. 2005. — Hidden likelihood support in genomic data: can forty-five wrongs make a right? *Systematic Biology* 45: 483-492.

GERMAIN D. 2008a. — *Anatomie des Lépospondyles et origine des Lissamphibiens* [doctoral thesis]. Muséum national d'Histoire naturelle, Paris, 398 p.

GERMAIN D. 2008b. — A new phlegethontiid specimen (Lepospondyli, Aistopoda) from the Late Carboniferous of Montceau-les-Mines (Saône-et-Loire, France). *Geodiversitas* 30 (4): 669-680.

GERMAIN D. 2010. — The Moroccan diplocaulid: the last lepospondyl, the single [sic] one on Gondwana. *Historical Biology* 22: 4-39.

GERMAIN D. & LAURIN M. 2009. — Evolution of ossification sequences in salamanders and urodele origins assessed through event-pairing and new methods. *Evolution & Development* 11: 170-190.

GODFREY S. J. 1989. — The postcranial skeletal anatomy of the Carboniferous tetrapod *Greererpeton burkemorani* Romer, 1969. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 323: 75-133.

GRADSTEIN F. M., OGG J. G. & SMITH A. G. 2004. — *A Geologic Time Scale 2004.* Cambridge University Press, Cambridge.

GRAUR D. & MARTIN W. 2004. — Reading the entrails of chickens: molecular timescales of evolution and the illusion of precision. *Trends in Genetics* 20: 80-86.

HELLRUNG H. 2003. — *Gerrothorax pustuloglomeratus*, ein Temnospondyle (Amphibia) mit knöcherner Branchialkammer aus dem Unteren Keuper von Kupferzell (Süddeutschland). *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* 330: 1-130.

HINCHLIFFE J. R. & VOROBYEVA E. I. 1999. — Developmental basis of limb homology in urodeles: heterochronic evidence from the primitive hynobiid family, *in* HALL B. K. (ed.), *Homology*. John Wiley & Sons, Chichester, 95-109.

HOLMES R. 1980. — *Proterogyrinus scheelei* and the early evolution of the labyrinthodont pectoral limb, *in* PANCHEN A. L. (ed.), *The Terrestrial Environment and the Origin of Land Vertebrates.* Academic Press, London, 351-376.

HOLMES R. 1984. — The Carboniferous amphibian *Proterogyrinus scheelei* Romer, and the early evolution of tetrapods. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 306: 431-527.

HOLMGREN N. 1933. — On the origin of the tetrapod limb. *Acta Zoologica* 14: 185–295.

HUELSENBECK J. P. 1994. — Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology* 20: 470-483.

HUGALL A. F., FOSTER R. & LEE M. S. Y. 2007. — Calibration choice, rate smoothing, and the pattern of tetrapod diversification according to the long nuclear gene RAG-1. *Systematic Biology* 56: 543-563.

HUTTENLOCKER A. K., SMALL B. J. & PARDO J. D. 2007. — *Plemmyradytes shintoni*, gen. et sp. nov., an Early Permian amphibamid (Temnospondyli: Dissorophoidea) from the Eskridge Formation, Nebraska. *Journal of Vertebrate Paleontology* 27: 316-328.

IGAWA T., KURABAYASHI A., USUKI C., FUJII T. & SUMIDA M. 2008. — Complete mitochondrial genomes of three neobatrachian anurans: A case study of divergence time estimation using different data and calibration settings. *Gene* 407: 116-129.

IVACHNENKO M. F. 1979. — Urodelans from the Triassic and Jurassic of Soviet central Asia. *Paleontological Journal* 1978: 362-368.

IVAKHNENKO M. F., GOLUBEV V. K., GUBIN M. YU., KALANDADZE N. N., NOVIKOV I. V., SENNIKOV A. G. & RAUTIAN A. S. 1997 — [*Permian and Triassic tetrapods of eastern Europe*]. Moscow: GEOS (in Russian with English abstract and Table of contents).

JARVIK E. 1996. — The Devonian tetrapod *Ichthyostega*. *Fossils & Strata* 40: 1-206.

JEFFERY J. E., BININDA-EMONDS O. R. P., COATES M. I. & RICHARDSON M. K. 2005. — A new technique for identifying sequence heterochrony. *Systematic Biology* 54: 230-240.

JENKINS F. A. JR & SHUBIN N. H. 1998. — *Prosalirus bitis* and the anuran caudopelvic mechanism. *Journal of Vertebrate Paleontology* 18: 495-510.

JENKINS F. A. JR, WALSH D. M & CARROLL R. L. 2007. — Anatomy of *Eocaecilia micropodia*, a limbed caecilian of the Early Jurassic. *Bulletin of the Museum of Comparative Zoology, 158*, 258-365.

JENKINS F. A. JR, SHUBIN N. H., GATESY S. M. & WARREN A. 2008. — *Gerrothorax pulcherrimus* from the Upper Triassic Fleming Fjord Formation of east Greenland and a reassessment of head lifting in temnospondyl feeding. *Journal of Vertebrate Paleontology* 28: 935-950.

JENNER R. A. 2001. — Bilaterian phylogeny and uncritical recycling of morphological data sets. *Systematic Biology* 50: 730-741.

JOHANSON Z., JOSS J., BOISVERT C. A., ERICSSON R., SUTIJA M. & AHLBERG P. E. 2007. — Fish fingers: digit homologues in sarcopterygian fish fins. *Journal of Experimental Zoology B (Molecular Development and Evolution)* 308: 757-768.

JOSSE S., MOREAU T. & LAURIN M. 2006. — *Stratigraphic tools for Mesquite. Ver. 1.0* [software]. Available via http://mesquiteproject.org/packages/stratigraphicTools

LAURIN M. 1994. — *The Osteology of Seymouriamorphs and its Implications for the Origin of Amniotes* [doctoral thesis]. University of Toronto, Toronto, xviii + 366 p.

LAURIN M. 1998a. — The importance of global parsimony and historical bias in understanding tetrapod evolution. Part I. Systematics, middle ear evolution, and jaw suspension. *Annales des Sciences Naturelles, Zoologie, Paris, 13e Série* 19: 1-42.

Laurin M. 1998b. — A reevaluation of the origin of pentadactyly. *Evolution* 52: 1476-1482.

Laurin M. 2002. — Tetrapod phylogeny, amphibian origins, and the definition of the name Tetrapoda. *Systematic Biology* 51: 364–369.

Laurin M. 2008. — The splendid isolation of biological nomenclature. *Zoologica Scripta* 37: 223-233.

Laurin M. & Reisz R. R. 1997. — A new perspective on tetrapod phylogeny, *in* Sumida S. & Martin K. (eds), *Amniote Origins – Completing the Transition to Land*. Academic Press, San Diego, 9-59.

Laurin M. & Reisz R. R. 1999. — A new study of *Solenodonsaurus janenschi*, and a reconsideration of amniote origins and stegocephalian evolution. *Canadian Journal of Earth Sciences. Revue canadienne des sciences de la Terre* 36: 1239-1255.

Laurin M. & Soler-Gijón R. 2001. — The oldest stegocephalian from the Iberian Peninsula: evidence that temnospondyls were euryhaline. *Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la vie/ Life sciences* 324: 495-501.

Laurin M. & Soler-Gijón R. 2006. — The oldest known stegocephalian (Sarcopterygii: Temnospondyli) from Spain. *Journal of Vertebrate Paleontology* 26: 284-299.

Laurin M., Canoville A. & Quilhac A. 2009. — Use of paleontological and molecular data in supertrees for comparative studies: the example of lissamphibian femoral microanatomy. *Journal of Anatomy* 215: 110-123.

Lee M. S. Y. 2005. — Squamate phylogeny, taxon sampling and data congruence. *Organisms Diversity & Evolution* 5: 25-45.

Lee M. S. Y. 2009. — Hidden support from unpromising data sets strongly unites snakes with anguimorph 'lizards'. *Journal of Evolutionary Biology* 22: 1308-1316.

Lee M. S. Y & Anderson J. S. 2006. — Molecular clocks and the origin(s) of modern amphibians. *Molecular Phylogenetics and Evolution* 40: 635-639.

Lombard R. E. & Bolt J. R. 1995. — A new primitive tetrapod, *Whatcheeria deltae*, from the Lower Carboniferous of Iowa. *Palaeontology* 38: 471-494.

Maddin H. C. & Anderson J. S. 2012. — Evolution of the amphibian ear with implications for lissamphibian phylogeny: insight gained from the caecilian inner ear. *Fieldiana Life and Earth Sciences* 5: 59-76.

Maddin H. C., Olori J. C. & Anderson J. S. 2011. — A redescription of *Carrolla craddocki* (Lepospondyli: Brachystelechidae) based on high-resolution CT, and the impacts of miniaturization and fossoriality on morphology. *Journal of Morphology* 272: 722-743.

Maddin H. C., Jenkins F. A. Jr. & Anderson J. S. 2012. — The braincase of *Eocaecilia micropodia* (Lissamphibia, Gymnophiona) and the origin of caecilians. *PLoS ONE* 7: e50743.

Maddison D. R. & Maddison W. P. 2003. — *MacClade: Analysis of Phylogeny and Character Evolution.*

Ver. 4.06 [software]. Sunderland: Sinauer Associates.

Marjanović D. 2010. — *Phylogeny of the Limbed Vertebrates with Special Consideration of the Origin of the Modern Amphibians* [doctoral thesis]. Université Pierre et Marie Curie, Paris, and Universität Wien, Vienna (Austria), 324 p. Available via http://othes.univie.ac.at/12920/

Marjanović D. & Laurin M. 2007. — Fossils, molecules, divergence times, and the origin of lissamphibians. *Systematic Biology* 56: 369-388.

Marjanović D. & Laurin M. 2008a. — Assessing confidence intervals for stratigraphic ranges of higher taxa: the case of Lissamphibia. *Acta Palaeontologica Polonica* 53: 413-432.

Marjanović D. & Laurin M. 2008b. — A reevaluation of the evidence supporting an unorthodox hypothesis on the origin of extant amphibians. *Contributions to Zoology* 77: 149-199.

Marjanović D. & Laurin M. 2009. — The origin(s) of modern amphibians: a commentary. *Evolutionary Biology* 36: 336-338.

Marshall C. R. 1997. — Confidence intervals on stratigraphic ranges with nonrandom distributions of fossil horizons. *Paleobiology* 23: 165-173.

McGowan G. J. 2002. — Albanerpetontid amphibians from the Lower Cretaceous of Spain and Italy: a description and reconsideration of their systematics. *Zoological Journal of the Linnean Society* 135: 1-32.

McGowan G. J. & Evans S. E. 1995. — Albanerpetontid amphibians from the Cretaceous of Spain. *Nature* 373: 143-145.

Milner A. C. 1980. — A review of the Nectridea (Amphibia), *in* Panchen A. L. (ed.), *The Terrestrial Environment and the Origin of Land Vertebrates*. Academic Press, London, 377-405.

Milner A. R. 1993. — Amphibian-grade Tetrapoda, *in* Benton M. J. (ed.), *The Fossil Record 2*. Chapman & Hall, London, 665-679.

Milner A. C. & Lindsay W. 1998. — Postcranial remains of *Baphetes* and their bearing on the relationshps of the Baphetidae (= Loxommatidae). *Zoological Journal of the Linnean Society* 122: 211-235.

Milner A. C. & Ruta M. 2009. — A revision of *Scincosaurus* (Tetrapoda, Nectridea) from the Moscovian of Nýřany, Czech Republic, and the phylogeny and interrelationships of nectrideans. *Special Papers in Palaeontology* 81: 71-89.

Milner A. C., Milner A. R. & Walsh S. A. 2009. — A new specimen of *Baphetes* from Nýřany, Czech Republic, and the intrinsic relationships of the Baphetidae. *Acta Zoologica (Stockholm)* 90 (special issue): 318-334.

Morrison D. A. 2009. — Why would phylogeneticists ignore computerized sequence alignment? *Systematic Biology* 58: 150-158.

Moss J. L. 1972. — The morphology and phylogenetic relationships of the Lower Permian tetrapod *Tseajaia*

campi Vaughn (Amphibia: Seymouriamorpha). *University of California Publications in Geological Sciences* 98: 1-71.

MÜLLER J. & REISZ R. R. 2005. — Four well-constrained calibration points from the vertebrate fossil record for molecular clock estimates. *BioEssays* 27: 1069-1075.

NESBITT S. J. 2011. — The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History* 352: 1-292.

NIEDŹWIEDZKI G., SZREK P., NARKIEWICZ K., NARKIEWICZ M. & AHLBERG P. E. 2010. — Tetrapod trackways from the early Middle Devonian period of Poland. *Nature* 463: 43-48.

OLORI J. C. 2011. — *The Evolution of Skeletal Development in Early Tetrapods: Anatomy and Ontogeny of Microsaurs (Lepospondyli).* Doctoral thesis. The University of Texas at Austin, Austin (Texas), xxiii + 518 p. Available via http://repositories.lib.utexas.edu/handle/2152/ETD-UT-2011-05-3535

OLSON E. C. 1941. — The family Trematopsidae. *Journal of Geology* 49: 149-176.

PARDO J. 2011. — The morphology and relationships of the Carboniferous-Permian nectridean *Diploceraspis burkei*. *Journal of Vertebrate Paleontology* (online suppl.): 170, 171.

PAWLEY K. 2006. — *The Postcranial Skeleton of Temnospondyls (Tetrapoda: Temnospondyli)* [doctoral thesis]. La Trobe University, Melbourne, 442 p. Available via http://hdl.handle.net/1959.9/57256

PAWLEY K. 2007. — The postcranial skeleton of *Trimerorhachis insignis* Cope, 1878 (Temnospondyli: Trimerorhachidae): a plesiomorphic temnospondyl from the Lower Permian of North America. *Journal of Paleontology* 81: 873-894.

PYRON R. A. 2011. — Divergence time estimation using fossils as terminal taxa and the origins of Lissamphibia. *Systematic Biology* 60: 466-481.

RAAUM R. L., STERNER K. N., NOVIELLO C. M., STEWART C.-B. & DISOTELL T. R. 2005. — Catarrhine primate divergence dates estimated from complete mitochondrial genomes: concordance with fossil and nuclear DNA evidence. *Journal of Human Evolution* 48: 237-257.

RAGE J.-C. & PICKFORD M. 2011. — Discovery of a Gymnophionan [sic] skull (?Caeciliidae, Amphibia) in the Early [sic] Miocene of Uganda. *Geo-Pal Uganda* 4: 1-9.

RAGE J.-C. & ROČEK Z. 2003. — Evolution of anuran assemblages in the Tertiary and Quarternary of Europe, in the context of palaeoclimate and palaeogeography. *Amphibia-Reptilia* 24: 133-167.

REISZ R. R. 1981. — A diapsid reptile from the Pennsylvanian of Kansas. *Publications of the Museum of Natural History of the University of Kansas* 7: 1-74.

REISZ R. R. & MÜLLER J. 2004. — Molecular timescales and the fossil record: a paleontological perspective. *Trends in Genetics* 20: 237-241.

ROČEK Z. 2000. — Mesozoic anurans, *in* HEATWOLE H. & CARROLL R. L. (eds), *Amphibian Biology*. Volume 4. *Palaeontology*. Surrey Beatty & Sons, Chipping Norton: 1295-1331.

ROČEK Z. 2008. — The Late Cretaceous frog *Gobiates* from Central Asia: its evolutionary status and possible phylogenetic relationships. *Cretaceous Research* 29: 577-591.

ROČEK Z. & RAGE J.-C. 2000. — Proanuran stages (*Triadobatrachus*, *Czatkobatrachus*), *in* HEATWOLE H. & CARROLL R. L. (eds), *Amphibian Biology*. Volume 4. *Palaeontology*. Surrey Beatty & Sons, Chipping Norton: 1283-1294.

ROČEK Z., WANG Y. & DONG L. 2012. — Post-metamorphic development of Early Cretaceous frogs as a tool for taxonomic comparisons. *Journal of Vertebrate Paleontology* 32: 1285-1292.

RODRÍGUEZ-TRELLES F., TARRÍO R. & AYALA F. J. 2002. — A methodological bias toward overestimation of molecular evolutionary time scales. *Proceedings of the National Academy of Sciences of the United States of America* 99: 8112-8115.

ROELANTS K. & BOSSUYT F. 2005. — Archaeobatrachian paraphyly and Pangaean diversification of crown-group frogs. *Systematic Biology* 54: 111-126.

ROELANTS K., GOWER D. J., WILKINSON M., LOADER S. P., BIJU S. D., GUILLAUME K., MORIAU L. & BOSSUYT F. 2007. — Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences of the United States of America* 104: 887-892.

ROMER A. S. 1966. — *Vertebrate Paleontology*. 3rd edition. University of Chicago Press, Chicago.

ROSE C. S. 2003. — The developmental morphology of salamander skulls, *in* HEATWOLE H. & DAVIES M. (eds), *Amphibian Biology*. *Volume 5. Osteology*. Surrey Beatty & Sons, Chipping Norton: 1684-1781.

RUTA M. & BOLT J. R. 2006. — A reassessment of the temnospondyl amphibian *Perryella olsoni* from the Lower Permian of Oklahoma. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 97: 113-165.

RUTA M. & COATES M. I. 2007. — Dates, nodes and character conflict: addressing the lissamphibian origin problem. *Journal of Systematic Palaeontology* 5: 69-122.

RUTA M., COATES M. I. & QUICKE D. L. J. 2003. — Early tetrapod relationships revisited. *Biological Reviews* 78: 251-345.

SAN MAURO D. 2010. — A multilocus timescale for the origin of extant amphibians. *Molecular Phylogenetics and Evolution* 56: 554-561.

SAN MAURO D., VENCES M., ALCOBENDAS M., ZARDOYA R. & MEYER A. 2005. — Initial diversification of living amphibians predated the breakup of Pangaea. *The American Naturalist* 165: 590-599.

SATOH A., ENDO T., ABE M., YAKUSHIJI N., OHGO S., TAMURA K. & IDE H. 2006. — Characterization of

Xenopus digits and regenerated limbs of the froglet. *Developmental Dynamics* 235: 3316-3326.

SCHMALHAUSEN I. I. 1915. — [The development of the extremities in amphibians and their significance to the question of the origin of extremities in terrestrial vertebrates]. *Contributions of the Imperial University of Moscow: Section of Natural History* 37: 1-263 (in Russian).

SCHOCH R. R. 2001. — Can metamorphosis be recognised in Palaeozoic amphibians? *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 220: 335-367.

SCHOCH R. R. 2002. — The early formation of the skull in extant and Paleozoic amphibians. *Paleobiology* 28: 278-296.

SCHOCH R. R. 2006. — Skull ontogeny: developmental patterns of fishes conserved across major tetrapod clades. *Evolution & Development* 8: 524-536.

SCHOCH R. R. 2009. — Evolution of life cycles in early amphibians. *Annual Review of Earth and Planetary Sciences* 37: 135-162.

SCHOCH R. R. & CARROLL R. L. 2003. — Ontogenetic evidence for the Paleozoic ancestry of salamanders. *Evolution & Development* 5: 314-324.

SCHOCH R. R. & FRÖBISCH N. B. 2006. — Metamorphosis and neoteny: alternative pathways in an extinct amphibian clade. *Evolution* 60: 1467-1475.

SCHOCH R. R. & MILNER A. R. 2004. — Structure and implications of theories on the origin of lissamphibians, *in* ARRATIA G., WILSON M. V. H. & CLOUTIER R. (eds), *Recent Advances in the Origin and Early Radiations of Vertebrates*. Dr. Friedrich Pfeil, Munich, 345-377.

SCHOCH R. R. & RUBIDGE B. S. 2005. — The amphibamid *Micropholis* from the Lystrosaurus Assemblage Zone of South Africa. *Journal of Vertebrate Paleontology* 25: 502-522.

SCHOCH R. R. & WITZMANN F. 2009. — Osteology and relationships of the temnospondyl genus *Sclerocephalus*. *Zoological Journal of the Linnean Society* 157: 135-168.

SCHOCH R. R. & WITZMANN F. 2010. — Bystrow's Paradox – gills, fossils, and the fish-to-tetrapod transition. *Acta Zoologica (Stockholm)* 92: 251-265.

SCHULTZE H.-P. 1984. — Juvenile specimens of *Eusthenopteron foordi* Whiteaves, 1881 (osteolepiform rhipidistian, Pisces) from the Late Devonian of Miguasha, Quebec, Canada. *Journal of Vertebrate Paleontology* 4: 1-16.

SHUBIN N. & ALBERCH P. 1986. — A morphogenetic approach to the origin and basic organization of the tetrapod limb. *Evolutionary Biology* 20: 319-387.

SIGURDSEN T. 2008. — The otic region of *Doleserpeton* (Temnospondyli) and its implications for the evolutionary origin of frogs. *Zoological Journal of the Linnean Society* 154: 738-751.

SIGURDSEN T. & BOLT J. R. 2009. — The lissamphibian humerus and elbow joint, and the origins of modern amphibians. *Journal of Morphology* 270: 1443-1453.

SIGURDSEN T. & BOLT J. R. 2010. — The Lower Permian amphibamid *Doleserpeton* (Temnospondyli: Dissorophoidea), the interrelationships of amphibamids, and the origin of modern amphibians. *Journal of Vertebrate Paleontology* 30: 1360-1377.

SIGURDSEN T. & GREEN D. M. 2011. — The origin of modern amphibians: a re-evaluation. *Zoological Journal of the Linnean Society* 162: 457-469.

SKUTSCHAS P. P. & KRASNOLUTSKII S. A. 2011. — A new genus and species of basal salamanders from the Middle Jurassic of western Siberia, Russia. *Proceedings of the Zoological Institute of the Russian Academy of Sciences* 315: 167-175.

SOLLAS W. J. 1920. — On the structure of *Lysorophus*, as exposed by serial sections. *Philosophical Transactions of the Royal Society of London, Series B* 209: 481-527.

STOPPER G. F. & WAGNER G. P. 2005. — Of chicken wings and frog legs: A smorgasbord of evolutionary variation in mechanisms of tetrapod limb development. *Developmental Biology* 288: 21-39.

SWOFFORD D. L. 2003. — *PAUP*: Phylogenetic analysis using parsimony (* and other methods). Ver. 4.0b10* [software]. Sinauer Associates, Sunderland.

TOROK M. A., GARDINER D. M., SHUBIN N. H. & BRYANT S. V. 1998. — Expression of *HoxD* genes in developing and regenerating Axolotl limbs. *Developmental Biology* 200: 225-233.

TOWNSEND T. M., LARSON A., LOUIS E. & MACEY R. J. 2004. — Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Systematic Biology* 53: 735-757.

TRUEB L. & CLOUTIER R. 1991. — A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli), *in* SCHULTZE H.-P. & TRUEB L. (eds), *Origins of the Higher Groups of Tetrapods – Controversy and Consensus*. Cornell University Press, Ithaca, 223-313.

VALLIN G. & LAURIN M. 2004. — Cranial morphology and affinities of *Microbrachis*, and a reappraisal of the phylogeny and lifestyle of the first amphibians. *Journal of Vertebrate Paleontology* 24: 56-72.

VARGAS A., SOTO-ACUÑA S., WEISS C. & OSSA-FUENTES L. 2011. — The status of morphological and developmental evidence on digit identity in the hand of Anura. *Journal of Vertebrate Paleontology* (online suppl.): 208.

VENCZEL M. & GARDNER J. D. 2005. — The geologically youngest albanerpetontid amphibian, from the lower Pliocene of Hungary. *Palaeontology* 48: 1273-1300.

VIDAL N. & HEDGES S. B. 2005. —The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. *Comptes Rendus de l'Académie des sciences – Biologies* 328: 1000-1008.

VIEITES D. R., MIN M.-S. & WAKE D. B. 2007. — Rapid diversification and dispersal during periods of global warming by plethodontid salamanders. *Proceedings of the National Academy of Sciences of the United States of America* 104: 19903-19907.

VOROBYEVA E. I. & HINCHLIFFE J. R. 1996. — Developmental pattern and morphology of *Salamandrella keyserlingii* limbs (Amphibia, Hynobiidae) including some evolutionary aspects. *Russian Journal of Herpetology* 3: 68-81.

WELLSTEAD C. F. 1991. — Taxonomic revision of the Lysorophia, Permo-Carboniferous lepospondyl amphibians. *Bulletin of the American Museum of Natural History* 201: 1-90.

WERNEBURG R. 1991. — Die Branchiosaurier aus dem Unterrotliegend des Döhlener Beckens bei Dresden. *Veröffentlichungen des Naturhistorischen Museums Schleusingen* 6: 75-99.

WERNEBURG R. 2009. — The Permotriassic branchiosaurid *Tungussogyrinus* Efremov, 1939 (Temnospondyli, Dissorophoidea) from Siberia restudied. *Fossil Record* 12: 105-120.

WERNEBURG R. 2012. — Dissorophoide Amphibien aus dem Westphalian [sic] D (Ober-Karbon) von Nýřany in Böhmen (Tschechische Republik) – der Schlüssel zum Verständnis der frühen ‚Branchiosaurier'. *Semana – Naturwissenschaftliche Veröffentlichungen des Naturhistorischen Museums Schloss Bertholdsburg Schleusingen* 27: 3-50.

WERNEBURG I. & SÁNCHEZ-VILLAGRA M. R. 2009. — Timing of organogenesis support [sic] basal position of turtles in the amniote tree of life. *BioMed Central Evolutionary Biology* 9, 9 p.

WIECHMANN M. F. 2000. — The albanerpetontids from the Guimarota mine, *in* MARTIN T. & KREBS B. (eds), *Guimarota – A Jurassic ecosystem*. Dr. Friedrich Pfeil, München, 51-54.

WIENS J. J. 2001. — Character analysis in morphological phylogenetics: problems and solutions. *Systematic Biology* 50: 689-699.

WIENS J. J., BONETT R. M. & CHIPPINDALE P. T. 2005. — Ontogeny discombobulates phylogeny: paedomorphosis and higher-level salamander relationships. *Systematic Biology* 54: 91-110.

WILLS M. A. 1999. — Congruence between phylogeny and stratigraphy: randomization tests and the gap excess ratio. *Systematic Biology* 48: 559-580.

WITZMANN F. & SCHOCH R. R. 2006. — Skeletal development of the temnospondyl *Acanthostomatops vorax* from the Lower Permian Döhlen Basin of Saxony. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 96: 365-385.

ZANON R. T. 1988. — A replacement name for the family Goniorhynchidae Carroll and Gaskill, 1978 (Amphibia: Microsauria). *Journal of Paleontology* 62: 317.

ZHANG P., ZHOU H., CHEN Y., LIU Y. & QU L. 2005. — Mitogenomic perspectives on the origin and phylogeny of living amphibians. *Systematic Biology* 54: 391-400.

APPENDICES

Appendices 1-10 list the apomorphies in a matrix almost identical to that of Marjanović (2010: chapter 5, without added taxa) that support a tree compatible with Figure 4F (the abstract by Pardo [2011] has thus not been taken into account). *Batropetes*, the only brachystelechid in the matrix, is the sister-group of the *Tuditanus*-Pantylidae clade. As in all most parsimonious trees from this matrix, the branching pattern within Lissamphibia is (*Eocaecilia*, (Albanerpetontidae, ((*Karaurus*, *Valdotriton*), (*Triadobatrachus*, (*Notobatrachus*, *Vieraella*)))))). The TH is nine steps less parsimonious than the LH according to this matrix (1,857 as opposed to 1,848 steps). Unless stated otherwise, the character optimization for ambiguous apomorphies is DELTRAN (delayed transformation), which favors convergence over reversals.

APPENDIX 1. — Autapomorphies of Lissamphibia, contradicting the polyphyly hypothesis. Note that none of these autapomorphies of Lissamphibia is unique within this tree. Homoplasy is frequent and omnipresent. *, Character states that are not autapomorphies of Lissamphibia under the TH. The authors of all taxon names are listed in Appendix 11.

Character state change	Convergence in:
Loss of postorbital (unambiguous)	*Oestocephalus* + *Phlegethontia* (Amphibia: Holospondyli: Aïstopoda), *Adelospondylus* (Adelogyrinidae). In keeping with its huge orbitotemporal fenestrae, *Brachydectes* is traditionally (Wellstead 1991) interpreted as lacking postorbitals, but we disagree with this interpretation (Marjanović & Laurin 2008b; this paper).
Quadratojugal rostrocaudally elongate and bar-like (unambiguous)	A clade of "microsaurs" composed of *Odonterpeton*, Hapsidopareiontidae, *Asaphestera* (reversal), Ostodolepididae, *Rhynchonkos* (unknown) and Gymnarthridae (unknown in *Cardiocephalus*). The state of this character is unknown or inapplicable in all lissamphibians other than *Eocaecilia* and *Karaurus*; the character would thus fit the PH (the state of *Batropetes* is unknown).
Loss of separate angular (unambiguous)	A separate angular cannot be distinguished in *Phlegethontia*, but reappears in the stem-caudate *Karaurus.*
Loss of separate surangular (unambiguous)	*Phlegethontia.*
Loss of pineal foramen (ambiguous)	The absence of the pineal foramen in lissamphibians is optimized as possibly homologous with that in *Brachydectes* (although this would, in this topology, require a reversal in Holospondyli) and even that in the "microsaur" *Pantylus* (which would require additional reversals in *Batropetes* and *Stegotretus*). Clearly convergent losses of the pineal foramen characterize the ostodolepidid "microsaurs" and the cochleosaurid edopoid temnospondyls. Finally, *Triadobatrachus* is difficult to interpret; as there are two dubious candidate features that could be the pineal foramen or part of the dermal sculpture of the skull roof (pers. obs.), we have scored it as unknown.
Vomer-maxilla contact rostral to choana (ambiguous)	ACCTRAN only. Under ACCTRAN, *Notobatrachus* shows a reversal; under DELTRAN, the condition has evolved separately in *Eocaecilia* and *Valdotriton*. In any case it also occurs in *Ventastega*, *Ichthyostega*, *Ossinodus*, *Crassigyrinus*, *Trimerorhachis*, *Neldasaurus*, *Cochleosaurus*, and *Eoscopus.*
Loss of separate opisthotics and/or exoccipitals (ambiguous)	This condition is shared with *Eusthenopteron* (so it may be a reversal; unknown in *Panderichthys*) and *Phlegethontia*. It is an ambiguous autapomorphy of Lissamphibia because it might instead be synapomorphic of Lissamphibia and *Phlegethontia*: the condition is unknown in all other holospondyls except *Diploceraspis*.
Scapula and coracoid separate (ambiguous)	Possibly homologous in *Brachydectes*. Not homologous in *Whatcheeria* + *Pederpes*, *Caerorhachis*, *Trimerorhachis* (Temnospondyli), *Seymouria* + Discosauriscidae, *Captorhinus* (Amniota), *Tseajaia* + Diadectidae, *Micraroter* (gymnarthrid "microsaur"), *Microbrachis* ("microsaur"). Reversed in Caudata, though this is an artefact of taxon sampling. — Ontogenetic fusion makes this character difficult to interpret, it may be much more widespread, although ossification sequences in which the entire scapulocoracoid ossifies gradually from a single center are known for some temnospondyls, see Marjanović & Laurin (2008b: 185) and references therein.

APPENDIX 1. — Continuation.

Character state change	Convergence in:
Maxilla participates in orbit margin (unambiguous)*	*Adelogyrinus* (Adelospondyli); Amphibamidae (Temnospondyli: Dissorophoidea) except *Doleserpeton*; amphibians: *Cardiocephalus* ("Microsauria": Gymnarthridae) and the holospondyl taxa *Batrachiderpeton* (Diplocaulidae), *Diceratosaurus* (ditto), *Sauropleura* (Urocordylidae) and Aïstopoda. Not applicable to *Brachydectes* or the frogs *Notobatrachus* and *Vieraella*, because some of the circumorbital bones are absent in these taxa; Albanerpetontidae is polymorphic.
Palatine participates in margin of interpterygoid vacuity or is absent (unambiguous)*	State 3 or higher of this ordered character with 6 states is found in Lissamphibia (where known), *Diplocaulus* + *Diploceraspis* (Amphibia: Holospondyli: Diplocaulidae), *Oestocephalus* + *Phlegethontia*, *Broiliellus* + (Amphibamidae + (*Micromelerpeton* + Branchiosauridae)) (Temnospondyli: Dissorophoidea), and *Isodectes* (Temnospondyli: Dvinosauria).
Pterygoid entirely caudal to palatine (ambiguous)*	ACCTRAN only. This is state 4 of the above character; state 4 or higher occurs in all lissamphibians except Albanerpetontidae, as well as in *Isodectes* and *Doleserpeton* + (*Amphibamus* + *Platyrhinops*) among temnospondyls and *Diploceraspis* and *Oestocephalus* + *Phlegethontia* among holospondyls.
Interpterygoid vacuities concave along their entire rostral, lateral and caudal margins (unambiguous)*	*Caerorhachis*; Temnospondyli (reversed in *Edops*); amphibians: *Hyloplesion*, *Diplocaulus* + *Diploceraspis* (Holospondyli: Diplocaulidae), *Urocordylus* and *Ptyonius* (Urocordylidae). – This is a multistate character; interpterygoid vacuities with concave margins come in different widths – *Eocaecilia* has the narrowest state, like *Caerorhachis*, *Hyloplesion* and *Urocordylus* and unlike any temnospondyl; frogs and salamanders (unknown in albanerpetontids) share the broadest state with *Diplocaulus* + *Diploceraspis* and the temnospondyl taxa *Balanerpeton*, *Capetus*, *Cochleosaurus*, and Dissorophoidea other than Trematopidae; the intermediate state is found in the remaining temnospondyls and *Ptyonius.*
Pedicellate teeth (ambiguous)*	ACCTRAN only (with reversal in Albanerpetontidae); under DELTRAN, the occurrences in *Eocaecilia* and Batrachia are convergent. Not homologous in *Doleserpeton* and *Amphibamus*, although under ACCTRAN it is homologous between these two (and *Platyrhinops* has reversed).
Teeth with two or more labiolingually arranged cusps (ambiguous)*	ACCTRAN only (with reversal in Albanerpetontidae); under DELTRAN, the occurrences in *Eocaecilia* and *Notobatrachus* are convergent. Not homologous in *Doleserpeton* + (*Amphibamus* + *Platyrhinops*) and in Diadectidae.
Ectepicondyle ridge absent (ambiguous)*	Possibly homologous in *Brachydectes* and maybe the "microsaurs" *Hyloplesion* and *Saxonerpeton* (Hapsidopareiontidae), therefore ambiguous. (In this case, the ridges of the "nectridean" *Diplocaulus* and maybe the "microsaurs" *Pelodosotis* [Ostodolepididae], *Euryodus* [Gymnarthridae], *Asaphestera* and *Pantylus* represent two reversals.) Not homologous: *Balanerpeton* (Temnospondyli), *Broiliellus* + Amphibamidae (except *Platyrhinops*) + "Branchiosauria" (Temnospondyli), and the "microsaur" *Rhynchonkos.*
Humerus length more than 3 times maximum distal width (unambiguous)*	Small-bodied taxa with terrestrial adults that are not limbless – Amphibamidae, *Apateon* and *Leptorophus* (but not *Schoenfelderpeton*), *Paleothyris* + *Petrolacosaurus*. Remarkably, *Eocaecilia* possesses the derived state in spite of its very small limbs.
Humerus longer than 2 ½ midtrunk vertebrae (unambiguous)*	Reversal to the plesiomorphy which is retained by all temnospondyls. Separate reversals occur in Hapsidopareiontidae + (*Asaphestera* + (Ostodolepididae + (*Rhynchonkos* + Gymnarthridae))) and in *Batropetes* + (*Tuditanus* + Pantylidae).
Straight ribs (unambiguous)*	Ribs that are not curved ventrally are found in *Eusthenopteron*, *Panderichthys*, *Acanthostega* but not *Ichthyostega*, *Ossinodus* (?Whatcheeriidae), *Pederpes* (Whatcheeriidae) but not *Whatcheeria*, *Greererpeton* but not the adelospondyls, *Eucritta*, temnospondyls except *Trimerorhachis*, the seymouriamorphs *Seymouria* and *Discosauriscus*, but not *Kotlassia* (or *Karpinskiosaurus*), *Ariekanerpeton* or *Utegenia*, *Diplocaulus*, and Aïstopoda.

APPENDIX 1. — Continuation.

Character state change	Convergence in:
Longest ribs shorter than 3 successive vertebrae in adults (unambiguous)*	Temnospondyli: *Balanerpeton*, *Dendrerpeton*, *Acheloma* (Trematopidae), Amphibamidae, *Apateon*. Lepospondyli: *Rhynchonkos* + Gymnarthridae, *Oestocephalus* + *Phlegethontia*. This character is compatible with those versions of the PH where *Rhynchonkos* is the sister-group of some extant amphibians. Interestingly, it is neither correlated to body size (*Acheloma* is much larger than the other mentioned taxa) nor to body elongation (*Brachydectes* has very long ribs).

APPENDIX 2. — Synapomorphies of Lissamphibia and Holospondyli ("Nectridea" including Aïstopoda). *, Character states that require the same number of steps under the LH and the TH. The authors of all taxon names are listed in Appendix 11.

Character state change	Convergence in:
Basioccipital not participating in craniovertebral joint (or entirely absent), exoccipital condyles not touching each other (unambiguous)	This state has a complex distribution among "microsaurs", apparently occurring in *Batropetes*, *Rhynchonkos*, *Asaphestera*, *Hapsidopareion*, possibly *Saxonerpeton*, and probably *Odonterpeton*; this is optimized as two (ACCTRAN) or three (DELTRAN) counts of convergence. – The aïstopods, where known, possess a very different state of this character. – We consider the condition found in dissorophoid temnospondyls (other than *Micropholis*), including *Doleserpeton*, a different state of this multistate character; see discussion in main text.
Vomers less than two ½ times as long as wide (unambiguous)*	Reversal; reversed again in *Sauropleura* (Holospondyli: Urocordylidae). Plesiomorphically present in temnospondyls. Also reversed in the discosauriscid seymouriamorph clade *Utegenia* + *Ariekanerpeton* and in two "microsaur" clades (Amphibia). – This is an ordered multistate character; the vomers are at least as wide as long in *Ventastega*, *Colosteus* (Colosteidae), *Baphetes* (Baphetidae), Amphibamidae (Temnospondyli), *Ariekanerpeton* (Seymouriamorpha), and frogs + salamanders. Unknown in Albanerpetontidae.
Loss of (caudal exposure of) suproccipital (unambiguous)*	Gymnarthridae. This character can only be coded for two holospondyls (*Diploceraspis* and *Oestocephalus*); the temnospondyls in this matrix lack (where known) the suproccipital plesiomorphically, so this character does not distinguish between the TH and the LH – although it does distinguish between different versions of the LH (*Brachydectes* and most non-gymnarthrid microsaurs, including *Batropetes* and *Rhynchonkos* which are important for the PH, are known to possess a suproccipital).
Tallest ossified part of neural arch of caudal trunk vertebrae lies dorsal to cranial half or middle of centrum (unambiguous)*	This, too, is a reversal that is itself reversed in the frog *Notobatrachus*. Further reversals to this state occur in *Diadectes* and Discosauriscidae. The state is plesiomorphically present in all temnospondyls (except – of all things – *Doleserpeton*!), so this character does not distinguish between the TH and the LH – although it does distinguish between different versions of the LH (*Brachydectes* and most non-gymnarthrid microsaurs, including *Batropetes* and *Rhynchonkos* which are important for the PH, possess the other state). – Outside of seymouriamorphs and crown-tetrapods, the other state (tallest part located dorsal to the caudal half of the centrum or caudal to the entire centrum) is found in *Caerorhachis*, *Ossinodus*, *Ichthyostega* and *Acanthostega*.

APPENDIX 3. — Synapomorphies of Lissamphibia, Holospondyli, and *Brachydectes*. *****, Character states that require the same number of steps under the LH and the TH; ******, the character state that requires fewer steps to be explained by the TH – at the cost of additional steps in other characters – than by the LH. The authors of all taxon names are listed in Appendix 11.

Character state change	Convergence in:
Prefrontal entering nostril margin (ambiguous)	Possibly homologous in *Batropetes*, in which case *Tuditanus* + Pantylidae show a reversal. Not homologous in *Crassigyrinus*, Colosteidae + *Acherontiscus* + Adelogyrinidae, the temnospondyl taxa *Isodectes*, Trematopidae and *Ecolsonia*; reversed in the diplocaulids *Batrachiderpeton* and *Diplocaulus* and in the aïstopod *Lethiscus*. Unfortunately, only two lissamphibians in this matrix can be scored for this character: the stem-caudate *Karaurus* and the deeply nested albanerpetontid *Albanerpeton pannonicum*.
Jaw articulation rostral to occiput (ambiguous)	Possibly homologous in the "microsaurs" *Batropetes* and *Stegotretus*; in this case, *Pantylus* and *Tuditanus* show reversals. Unambiguously reversed in *Triadobatrachus* and Urocordylidae + Aïstopoda; reversed again in the aïstopod *Phlegethontia*. Paralleled in the "microsaur" taxa *Odonterpeton*, *Hapsidopareion*, and Ostodolepididae + (*Rhynchonkos* + Gymnarthridae) – these three cases may be homologous with each other, in which case *Asaphestera* and the hapsidopareiontid *Saxonerpeton* show reversals.
Loss of postsplenial (unambiguous)	Amniota + Diadectomorpha as well as the "microsaurs" *Euryodus* (Gymnarthridae) and *Hapsidopareion*. Peculiar reversal in the diapsid amniote *Petrolacosaurus*.
Loss of caudal coronoid in adults (unambiguous)	Reversed in Diplocaulidae. In salamanders, the coronoid III is present in larvae and disappears at metamorphosis; in taxa without metamorphosis, it persists, but paedomorphic salamanders are not present in this matrix (and should be counted as not morphologically adult anyway; see discussion in main text).
Radius not shorter than ulna (unambiguous)	This is a reversal shared with many temnospondyls but not amphibamids (or *Eryops* or the dvinosaur *Neldasaurus*). Further such reversals are found in the anthracosaur *Proterogyrinus*, possibly *Eucritta* (could be plesiomorphic; ambiguous optimization), discosauriscid seymouriamorphs, and the "microsaurs" *Microbrachis* and *Odonterpeton* (twice separately). The "nectridean" *Scincosaurus* has reversed again and has radii shorter than its ulnae.
Loss of sigmoid profile of rostralmost part of medial margin of postorbital in dorsal or lateral view (unambiguous)*	This character cannot be scored for any lissamphibians and therefore cannot distinguish between the LH, the TH and the PH. The sigmoid shape occurs in *Westlothiana*, all "microsaurs" (where known) except Ostodolepididae, and convergently in the ?whatcheeriid *Ossinodus*.
Postorbital region of skull table less than 1/3 wider than long (ambiguous)*	ACCTRAN only. Under ACCTRAN, the condition is lost in Batrachia, *Scincosaurus*, and *Diplocaulus* + *Diploceraspis*; under DELTRAN, it arose separately in *Brachydectes*, *Eocaecilia* and Diplocaulidae + (Urocordylidae + Aïstopoda) before reversing in *Diplocaulus* + *Diploceraspis*. – This state is itself a reversal; separate reversals occur in Edopoidea, and *Captorhinus*, while the occurrences in Dvinosauria and *Dendrerpeton* could be plesiomorphic. – As batrachians and dissorophoids share the other state of this character to the exclusion of *Eocaecilia* (see above), this character supports the PH.
Loss of contact between pterygoids (unambiguous)**	This is a reversal to the condition found in *Eusthenopteron* and *Panderichthys*. Parallel reversals have happened in Temnospondyli (reversed in *Edops*), *Bruktererpeton* (?Gephyrostegidae), *Limnoscelis*, and *Orobates* (Diadectomorpha), and the "microsaurs" *Hyloplesion* and *Pelodosotis*. Reversals in Urocordylidae and the diplocaulid *Batrachiderpeton* (both Holospondyli). – This is a multistate character; the next state in the retreat of the pterygoid, participation of the palatine in the margin of the interpterygoid vacuity, is reached in Lissamphibia among others (Appendix 1).
Parasphenoid without elongate, broad posterolateral processes (unambiguous)*	This is a reversal to a condition retained by the temnospondyls. Such processes are found in seymouriamorphs, amniotes, diadectomorphs except *Limnoscelis*, *Westlothiana*, "microsaurs", and the urocordylid holospondyl *Ptyonius*.

Appendix 3. — Continuation.

Character state change	Convergence in:
Ventral plate of parasphenoid (caudal to basal articulations) more or less rectangular (unambiguous)*	*Panderichthys*; most anthracosaurs; most non-dvinosaurian temnospondyls including *Doleserpeton* and *Amphibamus*; *Gephyrostegus*; and the "microsaurs" *Hyloplesion*, *Odonterpeton* and *Micraroter*. Reversed or otherwise modified in salamanders, diplocaulids (where known), the urocordylid *Ptyonius*, and the aïstopods (inapplicable to *Phlegethontia*).
Loss of parasternal process of interclavicle (unambiguous)*	Reversal to the state found in *Eusthenopteron* and *Panderichthys*. Other reversals are seen in Colosteidae + (*Acherontiscus* + Adelogyrinidae), some specimens of *Eucritta*, and Temnospondyli except *Isodectes*. The interclavicle is lost in Lissamphibia.
Loss of entepicondyle foramen (unambiguous)*	Reversed in the "nectrideans" *Scincosaurus* and *Urocordylus*. Parallelled twice in Temnospondyli (Dvinosauria, *Eryops* + *Edops* + Dissorophoidea), in the seymouriamorph *Kotlassia* (or *Karpinskiosaurus*?), and twice among "microsaurs" (*Rhynchonkos* + Gymnarthridae and the pantylid *Stegotretus*).
Dorsal iliac process absent (unambiguous)*	Reversal to the condition seen in *Eusthenopteron*. Also found in *Greererpeton* (Colosteidae), Temnospondyli except the branchiosaurid *Schoenfelderpeton*, Sauropsida/Amniota, and Ostodolepididae, *Rhynchonkos*, *Saxonerpeton*, *Hyloplesion*, and *Pantylus* among "microsaurs".

APPENDIX 4. — Synapomorphies of Lissamphibia, Holospondyli, *Brachydectes*, and a clade formed by the "microsaurs" *Batropetes* (the only brachystelechid in the matrix), *Pantylus*, *Stegotretus* (Pantylidae), and *Tuditanus*. *, Character states that require the same number of steps under the LH and the TH. The authors of all taxon names are listed in Appendix 11.

Character state change	Convergence in:
Loss of postparietals (ambiguous)	ACCTRAN only. Reversed in *Tuditanus* + Pantylidae, *Eocaecilia*, and Diplocaulidae + Urocordylidae + Aïstopoda with a secondary loss in *Phlegethontia*; under DELTRAN, the postparietals were lost separately in *Batropetes*, *Brachydectes*, Albanerpetontidae + Batrachia, *Scincosaurus* and *Phlegethontia*. – Anderson *et al.* (2008b) scored *Triadobatrachus* as possessing postparietals, but we cannot substantiate this (pers. obs.; Marjanović & Laurin 2009: Electronic Supplementary Material 1).
Loss of denticles on vomer (ambiguous)	Reversal. Possibly homologous in Amniota + Diadectomorpha, in which case most "microsaurs" have reversed the reversal. Parallelled by *Crassigyrinus*, *Greererpeton*, Embolomeri, Dvinosauria, the "branchiosaurs" (but not Amphibamidae), *Rhynchonkos*, *Cardiocephalus*, and *Hapsidopareion* (though see Bolt & Rieppel 2009). Denticles reappear in the diapsid amniote *Petrolacosaurus* (and many amniotes not represented in the matrix).
Loss of middle coronoid (unambiguous)	*Balanerpeton* (Temnospondyli), Amniota, *Diadectes*. – This character is rather sparsely documented, and when fewer than three coronoids are present, it can be difficult to homologize them.
Halves of atlas neural arch fused (unambiguous)	*Rhynchonkos*, one of the two species of *Euryodus*, some specimens of *Eryops*. Reversed in Urocordylidae + Aïstopoda. Inapplicable to *Brachydectes* (scored as unknown) – the halves are unfused, but so are those of all neural arches (including the proatlas), which is probably due to paedomorphosis; it is not known if a hypothetical skeletally adult *Brachydectes* would have fused halves of the neural arch of the atlas.
Loss of ectopterygoid (unambiguous)*	Paralleled in *Captorhinus*. Reversed in *Ptyonius*; possibly also reversed in several extant caecilians that are lacking from this matrix. *Doleserpeton* has traditionally been reconstructed without an ectopterygoid; if this is correct, this character cannot differentiate between the TH, the LH and the PH. However, Sigurdsen & Bolt [2010] report that the presence of a small ectopterygoid, perhaps like that of *Gerobatrachus*, cannot be ruled out.
Loss of denticles on palatine (unambiguous)*	This is a reversal. Separate reversals are seen in Anthracosauria, *Trimerorhachis*, "branchiosaurs" and *Doleserpeton* (but not *Amphibamus*), *Kotlassia*, *Ariekanerpeton* + *Utegenia*, *Captorhinus*, *Tseajaia* + Diadectidae, *Rhynchonkos*, *Cardiocephalus*, and *Hapsidopareion* (though see Bolt & Rieppel 2009). Denticles reappear in the holospondyl *Scincosaurus*.
Loss of trunk intercentra (ambiguous)*	Possibly homologous in *Microbrachis*; if so, the Ostodolepididae + (*Rhynchonkos* + Gymnarthridae) clade has undergone a reversal. Not homologous in Adelogyrinidae and the diadectid *Orobates*. Reversed in *Eocaecilia*. – In many lepospondyls and lissamphibians, this had to be scored as inapplicable, because there is no evidence of more than one kind of centrum in them (as opposed to evidence from close relatives, which would be circular in a phylogenetic analysis); in theory, the single centrum in those forms could be the pleuro- or the intercentrum.

Appendix 5. — Synapomorphies of the clade mentioned in Appendix 4 with a clade formed by all remaining "microsaurs"; in other words, autapomorphies of a clade formed by all amphibians except *Westlothiana*. *, Character states that require the same number of steps under the LH and the TH. The authors of all taxon names are listed in Appendix 11.

Character state change	Convergence in:
Frontals shorter than parietals (unambiguous)	Reversal to the condition found in *Eusthenopteron* and *Panderichthys*. Also seen in some temnospondyls (*Neldasaurus* + *Isodectes*, *Eryops*, *Edops*, *Broiliellus* – not any amphibamid) and the seymouriamorphs *Kotlassia* and *Microphon*. Reversed again in most "microsaurs" (but not *Microbrachis*, *Hyloplesion*, *Pelodosotis*, Gymnarthridae, or *Batropetes*), Albanerpeton-tidae, *Diceratosaurus* + (*Diplocaulus* + *Diploceraspis*), Urocordylidae, and *Lethiscus* (Aïstopoda).
Loss of supratemporal (unambiguous)	*Acherontiscus* + Adelogyrinidae. Reversed in Urocordylidae + Aïstopoda.
Articulating surfaces of exoccipi-tals dorsolateral to basioccipital, basioccipital cotyle articulating with interglenoid tubercle of atlas (ambiguous)	This state is only documented in Ostodolepididae, Gymnarthridae, *Micro-brachis*, Pantylidae, *Tuditanus*, and *Brachydectes*. However, it may well be a possible starting point for the evolution of the next state, a cranioverte-bral joint that consists only of exoccipital condyles that articulate with the atlas without help from the basioccipital. That state unites Lissamphibia and Holospondyli (Appendix 2).
Postorbital irregularly polygonal (unambiguous)*	Reversal shared with *Anthracosaurus*, *Trimerorhachis*, *Chenoprosopus*, *Phonerpeton*, *Kotlassia*, *Seymouria*, *Captorhinus*, and *Tseajaia*. Reversed again in *Brachydectes*. This character is not applicable to lissamphibians, because they lack postorbitals (Appendix 1).
Parasphenoid without single median depression (ambiguous)*	Reversal; possibly homologous in Temnospondyli, *Seymouria* + Discosau-riscidae, *Limnoscelis* and *Tseajaia*. In other words, the fossa occurs only in *Whatcheeria*, *Crassigyrinus*, *Eucritta*, Anthracosauria, *Caerorhachis*, *Kot-lassia*, Amniota, Diadectidae, and *Westlothiana.*
Posterior coronoid not exposed in lateral view (ambiguous)*	Reversal shared with *Trimerorhachis* and *Ariekanerpeton* + *Utegenia*. (The bone is exposed in lateral view in the remaining temnospondyls, the re-maining seymouriamorphs, *Gephyrostegus*, Amniota and *Diadectes*.) This generally poorly known character is not applicable to (metamorphosed) lissamphibians, because they lack coronoids.
Supraglenoid foramen enlarged (ambiguous)*	*Acanthostega*, *Ventastega* (which may or may not be its sister-group), *Eosco-pus* (Temnospondyli: Amphibamidae). Reversed in *Pantylus* and *Eocaecilia*
Loss of supinator process on humerus (unambiguous)*	Reversal shared with *Broiliellus* + (Amphibamidae + "branchiosaurs"), Dis-cosauriscidae, and *Captorhinus*; reversed again in *Scincosaurus* and the urocordylid *Sauropleura*.
Internal trochanter not separated from general femur surface by fossa (ambiguous)*	Possibly homologous in Diadectomorpha, *Paleothyris* + *Petrolacosaurus*, and *Discosauriscus*; if so, reversed in *Kotlassia*, *Captorhinus*, and *Westlo-thiana*. Not homologous in *Ichthyostega*, *Pederpes*, *Proterogyrinus*, *Arche-ria*, *Neldasaurus*, and *Eryops* + Dissorophoidea (reversed in *Eoscopus* and *Doleserpeton*). Reversed in *Euryodus*, *Batropetes*, and *Stegotretus*.
Loss of L-shaped proximal tarsal bone (ambiguous)*	ACCTRAN only. Under DELTRAN, this is simply a plesiomorphy. A proximal tarsal (the intermedium or astragalus) is L-shaped in *Tulerpeton*, Embo-lomeri, *Caerorhachis*, Gephyrostegidae, Amniota, Diadectidae, *Westlo-thiana*, and *Tuditanus*; except for the latter, this condition is homologous in all under ACCTRAN.

APPENDIX 5. — Continuation.

"Odontoid process" (tuberculum interglenoideum/processus interglenoideus) on atlas (ambiguous)*	With most states of the character that describes the occipital condyle(s)/cotyle, this character can only have one state. We therefore had to score it as inapplicable to most taxa in the matrix and cannot even reconstruct the condition at the root – only one taxon outside the clade described in this table, the anthracosaur *Eoherpeton*, can be scored for it (and that likely only because its occiput is unknown). Either way, loss in Holospondyli, regain in the holospondyls *Diploceraspis* (Diplocaulidae) and *Ptyonius* (Urocordylidae). – An interglenoid tubercle is present in several temnospondyls that are not part of this matrix, most notably *Gerobatrachus* (Anderson *et al.* 2008b). – It is absent in extant caecilians and extant frogs, but present in the stem-gymnophionomorph *Eocaecilia* and the stem-salientian *Notobatrachus* which are included in the present matrix, as well as in the stem-gymnophionomorph *Rubricacaecilia* (Sigogneau-Russell 2001), the stem-salientian *Prosalirus* (Jenkins *et al.* 1998), and *Gobiates* (Roček 2008: fig. 2E) and *Liaobatrachus* (Roček *et al*. 2012: fig. 2), which are close relatives or members of the crown-group Anura. Possession of the tubercle is thus clearly plesiomorphic for each of the four large clades of modern amphibians.
Loss of swollen neural arches (unambiguous)*	Neural arches with distinctly convex dorsolateral surfaces occur only in seymouriamorphs, *Captorhinus*, diadectomorphs, and *Westlothiana*.
Capitular facets lie on caudal rim of mid-trunk centra (unambiguous)*	Adelogyrinidae. Reversed in Ostodolepididae + (*Rhynchonkos* + Gymnarthridae), Albanerpetontidae + Batrachia, and Diplocaulidae + (Urocordylidae + Aïstopoda). Present in *Eocaecilia* (Jenkins *et al.* 2007).
Loss of fifth finger (ambiguous)*	*Colosteus*, Temnospondyli. The fifth finger is regained in *Diceratosaurus* (DM, pers. obs. July 2009; Marjanović & Laurin 2009) and *Urocordylus*. See discussion in main text.

APPENDIX 6. — Autapomorphies of Amphibia. *, Character states that require the same number of steps under the LH and the TH. The authors of all taxon names are listed in Appendix 11.

Character state change	Convergence in:
Parietal/nasal length ratio > 1.45 (unambiguous)*	*Panderichthys*, *Ichthyostega*, Colosteidae, *Balanerpeton* + Dvinosauria (reversed in *Neldasaurus*), *Amphibamus*, Branchiosauridae, and *Discosauriscus*. Reversed in Ostodolepididae, *Rhynchonkos*, *Hapsidopareion*, *Tuditanus*, *Eocaecilia*, *Ptyonius*, and at least one species of *Sauropleura*.
Supratemporal at least three times as long as wide (unambiguous)*	*Orobates* (Diadectomorpha). Within Amphibia, only applicable to *Westlothiana*, *Ptyonius*, *Sauropleura*, *Lethiscus* and *Oestocephalus* (unknown in *Urocordylus*).
Sigmoid profile of rostralmost part of medial margin of postorbital in dorsal or lateral view (unambiguous)*	*Ossinodus*. Reversed in Ostodolepididae and in *Brachydectes* + (Lissamphibia + Holospondyli), not applicable to Lissamphibia because they lack postorbitals; see above.
Loss of flange on pterygoid (unambiguous)*	Reversal; separate reversals are found in *Trimerorhachis*, *Isodectes*, *Amphibamus* and the "branchiosaurs". A caudolateral flange like that seen in the remaining temnospondyls reappears in *Microbrachis*, Hapsidopareiontidae, *Euryodus*, *Eocaecilia*, and *Notobatrachus* + *Vieraella*. This character supports the PH.
Humerus shorter than 2½ midtrunk vertebrae (unambiguous)*	*Eusthenopteron*, *Panderichthys*, *Crassigyrinus*, Colosteidae. Reversed in Hapsidopareiontidae + (*Asaphestera* + (Ostodolepididae + (*Rhynchonkos* + Gymnarthridae))), in *Batropetes* + (*Tuditanus* + Pantylidae), and in Lissamphibia (see above).
Loss of transverse pelvic ridge (ambiguous)*	Possibly homologous in *Paleothyris* + *Petrolacosaurus*; if so, Diadectomorpha shows a reversal. Not homologous in *Balanerpeton* + Dvinosauria and in Dissorophoidea.
Lack of distinct rugose area on fourth trochanter of femur (unambiguous)*	*Eusthenopteron*, Whatcheeriidae, Dissorophoidea, Gephyrostegidae, *Discosauriscus*, *Paleothyris* + *Petrolacosaurus*, *Orobates*. Reversed in *Urocordylus*. – This character is poorly documented and can be scored for few taxa
Height of neural arch in midtrunk vertebrae smaller than distance between pre- and postzygapophyses (unambiguous)*	*Kotlassia*, *Captorhinus*. Reversed in Diplocaulidae + (Urocordylidae + Aïstopoda) and in Albanerpetontidae + Batrachia; reversed again in *Notobatrachus* + *Vieraella*.

APPENDIX 7. — Autapomorphies of the tetrapod crown-group – in other words, synapomorphies of Amphibia and Amniota + Diadectomorpha. *, Character states that require the same number of steps under the LH and the TH. The authors of all taxon names are listed in Appendix 11.

Character state change	Convergence in:
Caudolateral edge of skull straight or convex (unambiguous)	Colosteidae and *Acherontiscus*, and *Isodectes*. A dorsoventrally tall embayment evolves from this state in Adelogyrinidae, *Tseajaia* + Diadectidae, and Salientia; this is a reversal to the condition seen in most temnospondyls, *Gephyrostegus*, *Solenodonsaurus*, and most seymouriamorphs, and which appeared independently in *Silvanerpeton*. The plesiomorphy, a dorsoventrally narrow notch, appears in *Capetus* + (*Eryops* + Edopoidea) (with a reversal to the broad embayment of other temnospondyls in *Cochleosaurus*), in *Phonerpeton*, in *Seymouria*, and in *Microphon*.
Loss of rostral coronoid (unambiguous)	Reversed in *Microbrachis*; unknown in *Doleserpeton* (Sigurdsen & Bolt 2010). — Homologizing coronoids is usually difficult when fewer than three are present.
Axis arch fused to axis (pleuro)-centrum (unambiguous)	Reversed in *Hapsidopareion*. – We have scored *Brachydectes* as inapplicable because none of its arches are fused to their centra (or even to each other at the symphysis), probably due to paedomorphosis, see above.
Loss of intertemporal (ambiguous)*	Possibly homologous in *Solenodonsaurus*; not homologous in *Acanthostega*, *Ichthyostega*, Colosteidae + (*Acherontiscus* + Adelogyrinidae), *Megalocephalus* (Baphetidae), *Eryops*, and Dissorophoidea. – There are, however, two possible results of the loss of the intertemporal. This clade fills the theoretical hole by a contact between the parietal and the postorbital; so do *Solenodonsaurus* (possibly homologous), *Acanthostega*, *Ichthyostega*, and Colosteidae, while *Megalocephalus*, *Eryops* and Dissorophoidea use a postfrontal-supratemporal contact instead. These are two different states of this multistate character – and both are not applicable to lissamphibians, which lack the supratemporal (see above).
Supratemporal-squamosal suture smooth (unambiguous)*	Reversal to the condition of *Eusthenopteron*, *Panderichthys* and *Ventastega*. Also seen in *Ossinodus*, *Crassigyrinus*, Anthracosauria except *Anthracosaurus*, *Isodectes*, *Capetus*, *Broiliellus*, *Amphibamus*, *Doleserpeton*, Gephyrostegidae, and Discosauriscidae. Not applicable to Lissamphibia.
Combined width of parietals greater than distance between caudal margin of skull roof (measured in the sagittal plane) and caudal margin of orbit (ambiguous)*	Possibly homologous in *Seymouria* + Discosauriscidae; if so, reversed in *Kotlassia*. Not homologous in *Pederpes*, Amphibamidae, and *Apateon* (Branchiosauridae); reversed in *Captorhinus*, *Odonterpeton*, *Rhynchonkos* + Gymnarthridae, Pantylidae, *Eocaecilia*, *Keraterpeton*, *Diceratosaurus*, and Urocordylidae + Aïstopoda (possibly homologous between the last three).
Loss of tusks on vomer (unambiguous)*	*Ossinodus*, *Pholiderpeton* spp. + *Anthracosaurus*, *Broiliellus*, *Doleserpeton*, *Leptorophus* + *Schoenfelderpeton*, and *Microphon*; reversed in *Euryodus*.
Loss of tusks on palatine (ambiguous)*	Possibly homologous in *Kotlassia*; if so, *Seymouria* + Discosauriscidae have regained the tusks. Not homologous in *Doleserpeton* and *Leptorophus* + *Schoenfelderpeton*; reversed in Pantylidae.
Suproccipital present (unambiguous)*	Reversed in Gymnarthridae and Lissamphibia + Holospondyli, see above.
Entepicondyle width less than half humerus length (unambiguous)*	*Baphetes*, *Silvanerpeton*, *Pholiderpeton scutigerum*, Amphibamidae + "branchiosaurs". Reversed in *Limnoscelis*, *Pelodosotis*, *Pantylus*, Diplocaulidae, and *Urocordylus*.

APPENDIX 8. — Synapomorphies of the tetrapod crown-group and Seymouriamorpha. *, Character states that require the same number of steps under the LH and the TH. The authors of all taxon names are listed in Appendix 11.

Character state change	Convergence in:
Jaw articulation not caudal to occiput (unambiguous)	*Eusthenopteron*, *Acherontiscus* + Adelogyrinidae. Reversed in *Utegenia*, *Orobates*, *Westlothiana*, *Tuditanus*, *Triadobatrachus*, *Sauropleura*, *Lethiscus* and *Oestocephalus.*
Interorbital width not smaller than half of skull width (unambiguous)*	*Eusthenopteron*, *Pederpes*, *Ossinodus*, *Colosteus*, *Silvanerpeton*, *Eoherpeton*, *Dendrerpeton*, *Capetus*, *Chenoprosopus*. Reversed in *Discosauriscus*, Amniota, *Tseajaia*, Albanerpetontidae + Batrachia (with reappearance in *Notobatrachus* + *Vieraella*), *Diplocaulus* + *Diploceraspis*, and Urocordylidae + Aïstopoda (reversed again in *Oestocephalus*). This character would support the "inverse PH".
Loss of tusks on ectopterygoid (ambiguous)*	Unknown in *Solenodonsaurus*. Parelleled in *Acanthostega*, *Ichthyostega*, *Ossinodus*, *Adelospondylus*, *Trimerorhachis*, and the "branchiosaurs". Not applicable to taxa that certainly or possibly lack the ectopterygoid, such as Lissamphibia and *Doleserpeton.*
Angular reaches caudal end of lower jaw (unambiguous)*	*Acherontiscus* + Adelogyrinidae, *Isodectes*, Dissorophoidea. Inapplicable to Lissamphibia, which lack the angular.
Less than 30 teeth in the maxilla (unambiguous)*	*Ichthyostega*, *Whatcheeria* + *Pederpes*, *Eucritta*, *Eoherpeton*, *Anthracosaurus*, *Edops*, *Ecolsonia*. Reversed in *Paleothyris* + *Petrolacosaurus*, *Westlothiana*, *Eocaecilia*, *Notobatrachus*, and *Lethiscus.*
Supinator process on humerus present (ambiguous)*	*Eryops*, *Edops*, Trematopidae, *Ecolsonia* (homologous between these). Reversed in *Broiliellus* + (Amphibamidae + "branchiosaurs"), Discosauriscidae, *Captorhinus*, and the clade formed by all amphibians except *Westlothiana*; the process reappears in the holospondyls *Scincosaurus* and *Sauropleura.*
Swollen neural arches (unambiguous)*	Reversed in *Paleothyris* and Amphibia except *Westlothiana*, see above.
Tallest ossified part of neural arch of caudal trunk vertebrae lies dorsal to caudal half of centrum or caudal to the centrum (unambiguous)*	*Acanthostega*, *Ichthyostega*, *Ossinodus*, *Caerorhachis*, *Doleserpeton*; reversed in Discosauriscidae, *Diadectes*, and Lissamphibia + Holospondyli; reversed again in the stem-frog *Notobatrachus.*

APPENDIX 9. — Synapomorphies of Amphibia, Amniota + Diadectomorpha, Seymouriamorpha, and *Solenodonsaurus*. *****, Character states that require the same number of steps under the LH and the TH; ******, the character state that requires fewer steps to be explained by the TH – at the cost of additional steps in other characters – than by the LH. The authors of all taxon names are listed in Appendix 11.

Character state change	Convergence in:
Rostrocaudal diameter of orbit shorter than distance between caudal margin of orbit and rostralmost point of caudolateral edge of skull (ambiguous)	Reversal to the condition of *Eusthenopteron*, *Panderichthys* and *Ichthyostega*. Possibly homologous in Dvinosauria, *Dendrerpeton*, and *Capetus* + (*Eryops* + Edopoidea); if so, *Gephyrostegus* has reversed again. Not homologous in Colosteidae + (*Acherontiscus* + Adelogyrinidae), *Eoherpeton*, and both species of *Pholiderpeton*. Reversed again in Discosauriscidae, *Paleothyris* + *Petrolacosaurus*, *Tseajaia* + Diadectidae, *Asaphestera*, and *Batropetes*.
Trunk pleurocentra fused middorsally (unambiguous)	*Whatcheeria*, *Acherontiscus* + Adelogyrinidae, *Archeria* + *Pholiderpeton* spp. + *Anthracosaurus*.
Caudal end of maxilla rostral to caudal margin of orbit (ambiguous)**	Possibly homologous in *Gephyrostegus*. Not homologous in *Eoherpeton*, *Archeria* + *Pholiderpeton scutigerum*, *Eryops*, and *Cochleosaurus*. Reversed in *Odonterpeton*, *Euryodus*, *Stegotretus*, *Eocaecilia* and *Notobatrachus* (not known in other lissamphibians in this matrix), Urocordylidae and *Oestocephalus*.
Parietal-tabular contact (unambiguous)*	Inapplicable to lissamphibians, because they lack supratemporals, tabulars (except *Eocaecilia*) and postparietals (except *Eocaecilia*). Paralleled in Anthracosauria and within the temnospondyl *Micromelerpeton* (sometimes the two sides of one individual exhibit the two states of this character); reversed (supratemporal-postparietal contact) in *Tseajaia*.
Jugal contributes to ventral skull margin (unambiguous)*	The contact between maxilla and quadratojugal is also lost in *Adelospondylus*, *Baphetes*, the anthracosaurs *Silvanerpeton*, *Proterogyrinus*, *Archeria* and *Pholiderpeton attheyi* (possibly homologous between them), *Neldasaurus* + *Isodectes*, and Cochleosauridae. Reversed in *Euryodus primus* (unknown in *E. dalyae*), *Eocaecilia*, (*Sauropleura* + *Urocordylus*), and *Oestocephalus*. Several reversals within Amniota are not represented in this matrix. Not applicable to Batrachia, where the jugal is absent.
Interorbital distance greater than maximum orbit diameter (unambiguous)*	Reversal to the condition seen in *Eusthenopteron*, *Panderichthys* and *Ichthyostega*. Also in Colosteidae, *Eoherpeton*, *Neldasaurus* + *Isodectes*, *Dendrerpeton*, *Capetus* + (*Eryops* + Edopoidea), and *Platyrhinops*. Reversed again in *Utegenia*, *Discosauriscus*, Amniota, *Tseajaia*, *Batropetes*, *Triadobatrachus*, *Diplocaulus* + *Diploceraspis* and Urocordylidae + Aïstopoda. The only lissamphibian other than *Triadobatrachus* that can be scored for this character is *Eocaecilia*; the character supports the PH.
Less than 40 teeth in the maxilla (unambiguous)*	*Ichthyostega*, Whatcheeriidae, *Crassigyrinus*, *Adelogyrinus*, Baphetidae, *Eucritta*, *Silvanerpeton*, and *Eoherpeton* (homologous between all of these); *Anthracosaurus*, Edopoidea, *Ecolsonia*. Reversed in *Eocaecilia* and *Notobatrachus*.
Interclavicle wider than long (excluding parasternal process, if present) (unambiguous)*	*Ichthyostega*, Whatcheeriidae, *Ecolsonia*, *Apateon*. Reversed in *Tuditanus*, *Pantylus*, and Diplocaulidae + (Urocordylidae + Aïstopoda). Not applicable to Lissamphibia (or Aïstopoda) due to loss of the interclavicle.
Neural arches of trunk vertebrae fused to their centra (unambiguous)*	*Platyrhinops*, *Doleserpeton*. Reversed in Discosauriscidae; in all "microsaurs" except *Asaphestera*, *Rhynchonkos*, *Euryodus*, the most mature specimen of *Batropetes*, and *Tuditanus* (unknown in *Hyloplesion*); and in *Brachydectes* (which should arguably be scored as unknown, see above).

APPENDIX 10. — Synapomorphies of Amphibia, Amniota + Diadectomorpha, Seymouriamorpha and *Solenodonsaurus* with *Gephyrostegus* and *Bruktererpeton*. The sister-group of this clade is Temnospondyli. *, Character states that require the same number of steps under the LH and the TH. The authors of all taxon names are listed in Appendix 11.

Character state change	Convergence in:
Caudodorsal process of premaxilla occupies the entire available medio-lateral width at its base (as opposed to no distinct process, an alary process, or a very long, narrow process) (unambiguous)	*Tulerpeton*, *Crassigyrinus*, *Silvanerpeton*, both species of *Pholiderpeton* and *Anthracosaurus*. Reversed (to the absence of a distinct process) in Discosauriscidae, one species of *Euryodus*, *Keraterpeton*, *Batrachiderpeton*, and Urocordylidae. An alary process appears in *Ichthyostega*, arguably Colosteidae and *Dolichopareias*, Temnospondyli (with two reversals and see below), and the stem-caudate *Karaurus*. A very long, narrow process is known from the temnospondyl *Phonerpeton*, Diadectidae, the other species of *Euryodus*, and the urodele *Valdotriton*. – It is difficult to partition this character into states (see Marjanović & Laurin [2008b, 2009] for some discussion); it will require more attention in the future.
Premaxillae less than two-thirds as wide as skull (ambiguous)	Possibly homologous in Anthracosauria (if so, all temnospondyls show a reversal); not homologous in *Ventastega*; reversed in *Brachydectes*, Batrachia, and Diplocaulidae + (Urocordylidae + Aïstopoda), with reappearances in *Diplocaulus* + *Diploceraspis* and *Oestocephalus*.
Postorbital region of skull table at least 1/3 wider than long (ambiguous)*	Possibly homologous in *Balanerpeton*, *Capetus*, *Eryops*, and Dissorophoidea. Reversed in *Brachydectes*, *Eocaecilia* and Diplocaulidae + (Urocordylidae + Aïstopoda) before reversing again in *Diplocaulus* + *Diploceraspis*; see above under the synapomorphies of *Brachydectes*, Lissamphibia and Holospondyli. – As batrachians and dissorophoids share the other state of this character to the exclusion of *Eocaecilia* (see above), this character supports the PH.
Loss of mesial tusks on dentary (unambiguous)*	Adelogyrinidae, *Silvanerpeton*, *Archeria*, *Pholiderpeton attheyi*, *Anthracosaurus*, *Acheloma*, *Doleserpeton*. Reversed in *Captorhinus*, *Limnoscelis*, *Microbrachis* and Pantylidae.
Parasternal process of interclavicle parallel-sided for most of its length (ambiguous)*	*Ichthyostega*, Whatcheeriidae, *Archeria*. Ambiguous because the process is present, though (except in *Archeria*) not parallel-sided, in Anthracosauria, unknown in *Caerorhachis*, and absent in Temnospondyli except *Isodectes*. Reversed in the "microsaur" *Asaphestera*, process lost in *Brachydectes* + (Lissamphibia + Holospondyli), interclavicle lost in Lissamphibia, see above.
Radial condyle ventral on humerus (unambiguous)*	*Ichthyostega*, *Proterogyrinus*, Dissorophoidea + (*Eryops* + *Edops*). Reversed in Discosauriscidae.

APPENDIX 11. — List of taxon names mentioned in this article and their authors.

Acanthostega Jarvik, 1952
Acanthostomatops Credner, 1883
Acheloma Cope, 1882
Acherontiscus Carroll, 1969
Acipenser Linnaeus, 1758
Adelogyrinidae Brough & Brough, 1967
Adelogyrinus Watson, 1928
Adelospondylus Carroll, 1967
Aïstopoda Miall, 1875
Albanerpetontidae Fox & Naylor, 1982
Alytes Wagler, 1830
Ambystoma Tschudi, 1838
Ambystoma mexicanum (Shaw, 1789)
Amia Linnaeus, 1766
Amphibamidae Moodie, 1916
Amphibamus Cope, 1865
Amphicoela Noble, 1931
Amphiuma Garden, 1821
Anthracosaurus Huxley, 1863
Anura Duméril, 1806 (as Anoures)
Apateon von Meyer, 1844
Apoda Haworth, 1809
Apoda Oppel, 1811
Apodops Estes & Wake, 1972
Archosauria Cope, 1869
Ariekanerpeton Ivachnenko, 1981
Asaphestera Steen, 1934
Ascaphus Stejneger, 1899
Balanerpeton Milner & Sequeira, 1994
Baphetes Owen, 1859
Baphetidae Owen, 1865
Batrachia Latreille, 1800
Batrachiderpeton Hancock & Atthey, 1871
Batropetes Carroll & Gaskill, 1971
Baurubatrachus Báez & Perí, 1989
Branchiosauridae Fritsch, 1883
Bombina Oken, 1816
Bombinanura Cannatella & Hillis, 1993
Bombinatoridae Gray, 1825
Brachydectes Cope, 1868
Brachystelechidae Carroll & Gaskill, 1978
Broiliellus Williston, 1914
Bruktererpeton Boy *in* Boy & Bandel, 1973
Bufo Laurenti, 1768
Caerorhachis Holmes & Carroll, 1977
Callobatrachus Wang & Gao, 1999
Capetus Steen, 1938
Captorhinus Cope, 1895
Cardiocephalus Broili, 1904
Carrolla Langston & Olson, 1986
Caudata Scopoli, 1777
Celtedens McGowan & Evans, 1995
Celtedens ibericus McGowan & Evans, 1995
Chelydra serpentina (Linnaeus, 1758)

Chenoprosopus Mehl, 1913
Chunerpeton Gao & Shubin, 2003
Cochleosaurus Fritsch, 1885
Cocytinidae Cope, 1875
Colosteidae Cope, 1875
Colosteus Cope, 1869
Crassigyrinus Watson, 1926
Crinodon Carroll & Gaskill, 1978
Cryptobranchidae Fitzinger, 1826
Czatkobatrachus Borsuk-Białynicka & Evans, 1998
Dendrerpeton Owen, 1853
Desmognathus aeneus Brown & Bishop, 1947
Diadectidae Cope, 1880
Diceratosaurus Jaekel, 1902
Diplocaulidae Cope, 1881
Diplocaulus Cope, 1877
Diploceraspis Romer, 1952
Discoglossidae Günther, 1859
Discoglossus Otth, 1837
Discosauriscus Kuhn, 1933
Discosauriscidae Romer, 1947
Dissorophoidea Boulenger, 1902
Doleserpeton Bolt, 1969
Dolichopareias Watson, 1928
Ecolsonia Berman, Reisz & Eberth, 1985
Edopoidea Romer, 1945
Edops Romer, 1936
Embolomeri Cope, 1885
Enneabatrachus Evans & Milner, 1993
Eocaecilia Jenkins & Walsh, 1993
Eodiscoglossus Villalta, 1957
Eodiscoglossus oxoniensis Evans, Milner & Mussett, 1990
Eoherpeton Panchen, 1975
Eopelobates Parker, 1929
Eoscopus Daly, 1994
Eryops Cope, 1877
Eucritta Clack, 1998
Eupsophus Fitzinger, 1843
Euryodus Olson, 1939
Euryodus dalyae Carroll & Gaskill, 1978
Euryodus primus Olson, 1939
Eusthenopteron Whiteaves, 1881
Gephyrostegidae Jaekel, 1909
Gephyrostegus Jaekel, 1902
Gerobatrachus Anderson, Reisz, Scott, Fröbisch & Sumida, 2008
Gerrothorax Nilsson, 1934
Goniorhynchidae Carroll & Gaskill, 1978 (invalid)
Goniorhynchus Hampson, 1896
Goniorhynchus Olson, 1970 (junior homonym of *Goniorhynchus* Hampson, 1896; replaced by *Rhynchonkos* Schultze & Foreman, 1981)
Gymnarthridae Case, 1910
Gymnophiona Müller, 1832

APPENDIX 11. — Continuation.

Gymnophionomorpha Marjanović & Laurin, 2008
Hapsidopareion Daly, 1973
Hapsidopareiontidae Daly, 1973
Holospondyli Schwarz, 1908
Hyla Laurenti, 1768
Hylidae Rafinesque, 1815
Hyloplesion Fritsch, 1883
Hynobiidae Cope, 1859
Iberospondylus schultzei Laurin & Soler-Gijón, 2001
Ichthyophiidae Taylor, 1968
Isodectes Cope, 1895
Karaurus Ivachnenko, 1978
Karpinskiosaurus Sushkin, 1925
Keraterpeton Etheridge, 1866
Keraterpetontidae Jaekel, 1902
Kotlassia Amalitzky, 1921
Latonia von Meyer, 1843
Leiopelma Fitzinger, 1861
Leptorophus Bulman & Whittard, 1926
Lethiscus Wellstead, 1982
Limnoscelis Williston, 1911
Lissamphibia Haeckel, 1866
Llistrofus Carroll & Gaskill, 1978
Lysorophia Romer, 1930
Mantellidae Laurent, 1946
Megalocephalus Barkas, 1873
Megophryidae Bonaparte, 1850
Mesophryne Gao & Wang, 2001
Micraroter Daly, 1973
Microbrachis Fritsch, 1875
Microhyla Tschudi, 1838
Microhylidae Günther, 1858
Micromelerpeton Bulman & Whittard, 1926
Micropholis Huxley, 1876
Microphon Ivachnenko, 1983
Microsauria Dawson, 1863
Miopelodytes Taylor, 1941
Mus musculus Linnaeus, 1758
Nectridea Miall, 1875
Neldasaurus Chase, 1965
Neoceratodus forsteri Castelnau, 1876
Neoprocoela Schaeffer, 1949
Notobatrachus Reig *in* Stipanicic & Reig, 1955
Odonterpeton Moodie, 1909
Oedipina Keferstein, 1868
Oestocephalus Cope, 1868
Opisthocoelellus Špinar, 1976
Ossinodus Warren & Turner, 2004
Ostodolepididae Romer, 1945
Paleothyris Carroll, 1969
Panderichthys Gross, 1941
Pantylidae *Case, 1911*
Pantylus Cope, 1881
Pederpes Clack, 2002
Pelobates Wagler, 1830

Pelobatidae Bonaparte, 1850
Pelodosotis Carroll & Gaskill, 1978
Pelodytes Bonaparte, 1838
Pelodytidae Bonaparte, 1850
Pelodryadinae Günther, 1858
Phlegethontia Cope, 1871
Pholiderpeton Huxley, 1896
Pholiderpeton attheyi (Watson, 1926)
Pholiderpeton scutigerum Huxley, 1896
Phonerpeton Dilkes, 1990
Phyllomedusinae Günther, 1858
Pipanura Cannatella & Hillis, 1993
Pipoidea Gray, 1825
Platyrhinops Steen, 1931
Polypterus Lacépède, 1803
Procera Feller & Hedges, 1998
Proterogyrinus Romer, 1970
Proteus Laurenti, 1768
Rana Linnaeus, 1758
Rana (*Pelophylax*) (Fitzinger, 1843)
Rana (*Pelophylax*) *ridibunda* Pallas, 1771
Rana (*Pelophylax*) *saharica* Boulenger in Hartert, 1913
Rana temporaria Linnaeus, 1758
Ranodon Kessler, 1866
Ranoidea Rafinesque, 1814
Rhacophoridae Hoffman, 1932
Rhadinosteus Henrici, 1998
Rhinatrematidae Nussbaum, 1977
Rhinoderma Duméril & Bibron, 1841
Rhynchonkos Schultze & Foreman, 1981
Rhynchonkidae Zanon, 1988 (replacement name for
    Goniorhynchidae Carroll & Gaskill, 1978)
Rhynchonkos stovalli (Olson, 1970).
Rubricacaecilia Evans & Sigogneau-Russell, 2001
Salamandra Laurenti, 1768
Salamandrella Dybowski, 1870
Salamandridae Goldfuß, 1820
Salientia Laurenti, 1768
Sauropleura Cope, 1868
Saxonerpeton Carroll & Gaskill, 1978
Scaphiopodidae Cope, 1865
Schoenfelderpeton Boy, 1986
Scincosaurus Fritsch, 1876
Sclerocephalus Goldfuß, 1847
Scotiophryne Estes, 1969
Seymouria White, 1939
Seymouriamorpha Watson, 1917
Silvanerpeton Clack, 1994
Siren Österdam, 1766
Sirenidae Gray, 1825
Solenodonsaurus Broili, 1924
Stegokrotaphia Cannatella & Hillis, 1993
Stegotretus Berman, Eberth & Brinkman, 1988
Telmatobiinae Fitzinger, 1843
Telmatobius Wiegmann, 1834

APPENDIX 11. — Continuation.

Tephrodytes Henrici, 1994
Thorius Cope, 1869
Trematopidae Williston, 1910
Triadobatrachus Kuhn, 1962
Triassurus Ivachnenko, 1978
Trihecaton Vaughn, 1972
Trimerorhachis Cope, 1878
Triturus marmoratus (Latreille, 1800)
Tseajaia Vaughn, 1964
Tuditanidae Cope, 1875
Tuditanus Cope, 1874
Tulerpeton Lebedev, 1986
Tungussogyrinus Efremov, 1939

Urocordylidae Lydekker, 1889
Urocordylus Huxley, 1866
Urodela Duméril, 1806 (as Urodèles)
Utaherpeton Carroll, Bybee & Tidwell, 1991
Utegenia Kuznetsov & Ivakhnenko, 1981
Valdotriton Evans & Milner, 1996
Ventastega Ahlberg, Lukševičs & Lebedev, 1994
Vieraella Reig, 1961
Vytshegdosuchus Sennikov, 1988
Westlothiana Smithson & Rolfe, 1990
Whatcheeriidae Clack, 2002
Xenopus laevis (Daudin, 1802)
Xilousuchus Wu, 1981