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An updated paleontological timetree of lissamphibians, with comments on the anatomy of Jurassic crown-group salamanders (Urodela)

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We present an update of our time-calibrated supertree of extant and extinct lissamphibians (Marjanović D, Laurin M. 2007. Fossils, molecules, divergence times, and the origin of lissamphibians. *Syst Biol* 56(3):369–388) and of the divergence dates that can be inferred from it. The present version contains 319 extinct species or possible species of lissamphibians, compared to 223 previously. Discoveries of new fossiliferous sites, advances in phylogeny and recently obtained radiometric dates have offered opportunities to test our results, including the conclusion that the fossil record of Lissamphibia is dense enough to provide reliable calibration constraints for molecular divergence dating. By and large, the results are upheld. Some of the divergence dates we infer from the tree are up to 15 Ma younger than we previously published, some are up to 15 Ma older, some have had their range of uncertainty drastically reduced and the maximum age for the origin of Urodela (the salamander crown group) is no longer well constrained. The dermal bone plates in the gill region of the Jurassic urodeles *Beiyuanerpeton*, *Seminobatrachus* and *Chunerpeton* and the grooves for the lateral line organ on the skull of the first require either unexpected reversals or several independent losses in other lissamphibians and indeed other urodeles.

Keywords: Lissamphibia; Caudata; Urodela; supertree; timetree; calibration

Introduction

In 2007, we published a hand-made time-calibrated supertree of Lissamphibia, containing 223 extinct species or possible species. The main use of this tree was to derive minimal divergence date estimates from it; indeed, the paper has been cited most often by molecular dating (e.g. Matsui et al. 2008; Zhang and Wake 2009) or comparative studies (e.g. Gomes et al. 2009; van Buskirk 2009) that needed such time calibration. However, we also proposed maximal divergence date estimates for four of the clades for which close older relatives were known (Marjanović and Laurin 2007 – ‘ML07’ hereinafter). Here we test the impact of recent discoveries – in particular new fossils (e.g. Báez, Gómez, Ribeiro, et al. 2012; Gao and Shubin 2012a; complete list in Table 1) as well as advances in phylogeny (e.g. Pyron and Wiens 2011; Gao and Shubin 2012a; Báez 2013; complete list in Table 1) – on this supertree and the divergence dates it supports. The supertree now contains 319 extinct species or possible species. We emphasise that our timetree directly yields minimal divergence date estimates; maximal or actual divergence dates are much more difficult to derive, and rigorous methods to assess these are cumbersome and have rarely been used (Marjanović and Laurin 2008a; Wilkinson and Tavaré 2009; Wilkinson et al. 2011; Pyron 2011;

Ronquist et al. 2012), although there are exciting developments in this field (reviewed in Laurin 2012).

Thus, the figures below should be considered to supersede those of ML07. To facilitate comparisons, we have organised the illustrations in a similar way; Figures 1–5 correspond to figures 3–7 of ML07, as far as possible. There are minor differences because the affinities of some early lissamphibians have been revised, as mentioned earlier; for instance, *Iridotriton*, which was placed on the salamandroid stem in ML07 (figure 3), is now placed on the hynobiid stem (Figure 1) to reflect the findings of Gao and Shubin (2012a).

In addition to adding taxa and modifying the supertree in keeping with advances in lissamphibian phylogeny, we have updated the timescale used to calibrate the supertree. The present version is based on the current International Chronostratigraphic Chart (International Commission on Stratigraphy 2013).

At this opportunity, we attempt to clarify the significance of our findings about the chronology of lissamphibian diversification. This is evidently needed because some statements in recent papers (e.g. Anderson 2008, 2012; Gao and Shubin 2012a) reflect misunderstandings about our results, perhaps caused in part by their presentation in a very dense paper (ML07). Some of these misunderstandings were subsequently corrected (Gao and

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Table 1. References used to update the tree of ML07.

<i>Newly described and previously overlooked taxa (red and orange in Figures 1–5)</i>	
Gymnophionomorpha:	Rage and Pickford (2011).
Albanerpet(ont)idae:	Buscalioni et al. (2008), Martín et al. (2012), Sweetman and Gardner (forthcoming). Stratigraphic ranges follow Gardner and Böhme (2008).
Caudata:	Čkhikvadze (1982), Sanchiz (1998a), Evans and McGowan (2002), Venczel (2008), Rage and Dutheil (2008), Zhang et al. (2009), Skutschas and Krasnolutskii (2011), Skutschas and Gubin (2012), Gao and Shubin (2012a), Martín et al. (2012), Gardner (2012), Vasilyan et al. (2013), Schoch and Rasser (2013) and Gao et al. (2013).
Salientia:	Hossini (2000), Roček and Rage (2000), Rage (2003), Venczel and Csiki (2003), Prasad and Rage (2004), Báez and Harrison (2005), Henrici and Haynes (2006), Evans et al. (2008), Rage and Dutheil (2008), Báez et al. (2009), Szentesi and Venczel (2010, 2012), Gómez et al. (2011), Roček et al. (2011), Martín et al. (2012), Báez, Gómez, Ribeiro, et al. (2012), Báez (2013), Venczel et al. (2013) and Folie et al. (forthcoming).
<i>Phylogeny (including placement of previously excluded taxa, brown in Figures 1–5)</i>	
Position of Albanerpet(ont)idae:	Ruta and Coates (2007) and Marjanović and Laurin (2008b, 2009, 2013).
Intrarelationships of Albanerpet(ont)idae:	Sweetman and Gardner (forthcoming).
Caudata:	Evans and McGowan (2002), Venczel (2008), Zhang et al. (2008), Skutschas (2009), Pyron and Wiens (2011), Gao and Shubin (2012a), Böhme et al. (2012), Gardner (2012), Vasilyan and Böhme (2012), Schoch and Rasser (2013) and Vasilyan et al. (2013).
Salientia:	Venczel and Csiki (2003), Báez and Harrison (2005), Bever (2005), Henrici and Haynes (2006), Báez and Sanchiz (2007), Buscalioni et al. (2008), Roček (2008), Báez et al. (2009), Szentesi and Venczel (2010, 2012), Gómez et al. (2011), Pyron and Wiens (2011), Ruane et al. (2011), Martín and Sanchiz (c2010–2011), Báez, Gómez, Ribeiro, et al. (2012), Roček et al. (2012), Wuttke et al. (2012) and Báez et al. (2013).

Notes: Both categories include references from which we derived range extensions or age changes.

Shubin 2012b), but a more general clarification about our methods and results seems warranted. Most significantly, we argue below that recently found lissamphibian fossils indicate that the fossil record for this taxon is reasonably good because these new finds do not significantly change the implied divergence dates between the extant taxa, contrary to what has recently been suggested (Anderson 2012). To illustrate this, we have selected the example of *Beiyanerpeton jianpingense*, which was rather extensively discussed by Anderson (2012).

Last but not least, we have incorporated the results of recent radiometric dating studies of various fossiliferous localities that have yielded lissamphibian remains (Henrici and Haynes 2006; Liu et al. 2006; Yang and Li 2008; Peng et al. 2012).

Methods

We have generally followed our previous methods (ML07, appendix 1).

Taxon sampling

We have been able to add a large number of extinct amphibian taxa from the sources cited in Table 1 to the supertree of ML07. This includes taxa that were described after 2007 (in red in Figures 1–5), taxa that were described earlier which we had overlooked (in orange) and taxa that we had not been able to place in the phylogeny, but that can

now be positioned with some confidence (in brown). It goes without saying that there remain taxa that we had, and still have, not included for lack of confidence, e.g. *Monsechobatrachus*, a frog known from a complete but very poorly preserved skeleton from the Barremian of Catalonia, or *Tregobatrachus*, an isolated left frog ilium of unique shape from the Miocene of Kansas. We have now additionally removed three taxa included in our 2007 tree: the Oligocene ‘*Eupsophus* sp.’ is an indeterminate frog that needs further research (Nicoli 2012); the poorly known *Scotiophryne* is likewise an indeterminate frog according to Roček (2000); *Opisthocoelellus hessi* most likely belongs to *Latonia*, possibly *Latonia ragei* (Sanchiz, pers. comm., 27 Mar 2013; Martín and Sanchiz c2010–2011 and references therein).

Sanchiz (1998b) and Rage and Roček (2003) found that a systematic revision of Palaeobatrachidae (Pipoidea) and *Latonia* (Discoglossidae) was required. Such a revision has only partially been done for Palaeobatrachidae (Wuttke 2012; Wuttke et al. 2012; Venczel et al. 2013) and not at all, to the best of our knowledge, for *Latonia*. We have therefore continued our previous practice (ML07, appendix 1) of keeping the representatives of *Latonia* restricted to the oldest known, the youngest known and some of the best-known material (Figure 3); ‘*Opisthocoelellus hessi*’ does not increase the temporal range of *Latonia*. Of the Cenozoic palaeobatrachids, we include *Palaeobatrachus grandipes*, one of the best-understood nominal species, *Palaeobatrachus langhae* (formerly its own genus *Pliobatrachus*), the youngest known representative, and additionally those with a relatively well-understood phylogenetic position (Figure 3).

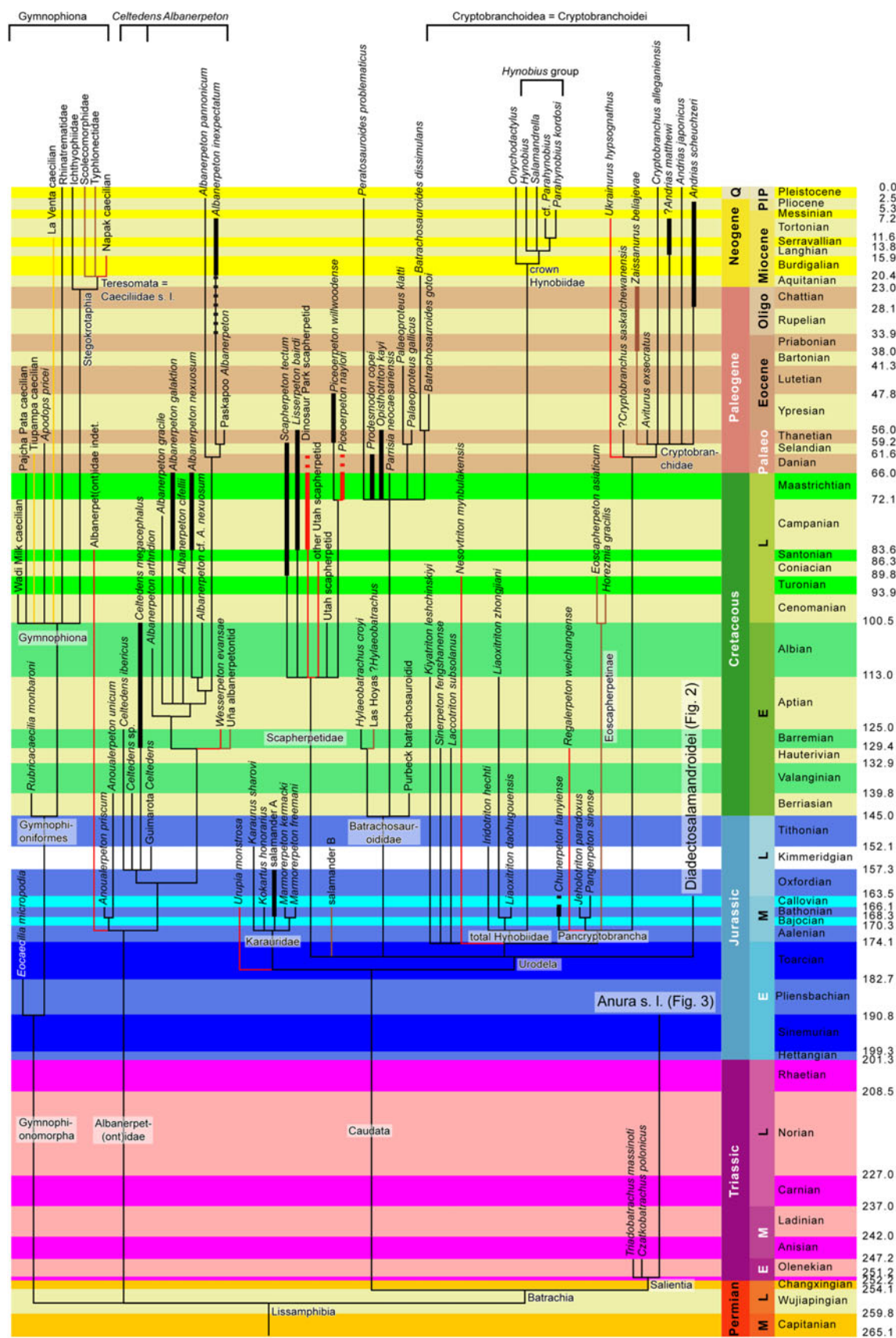


Figure 1.

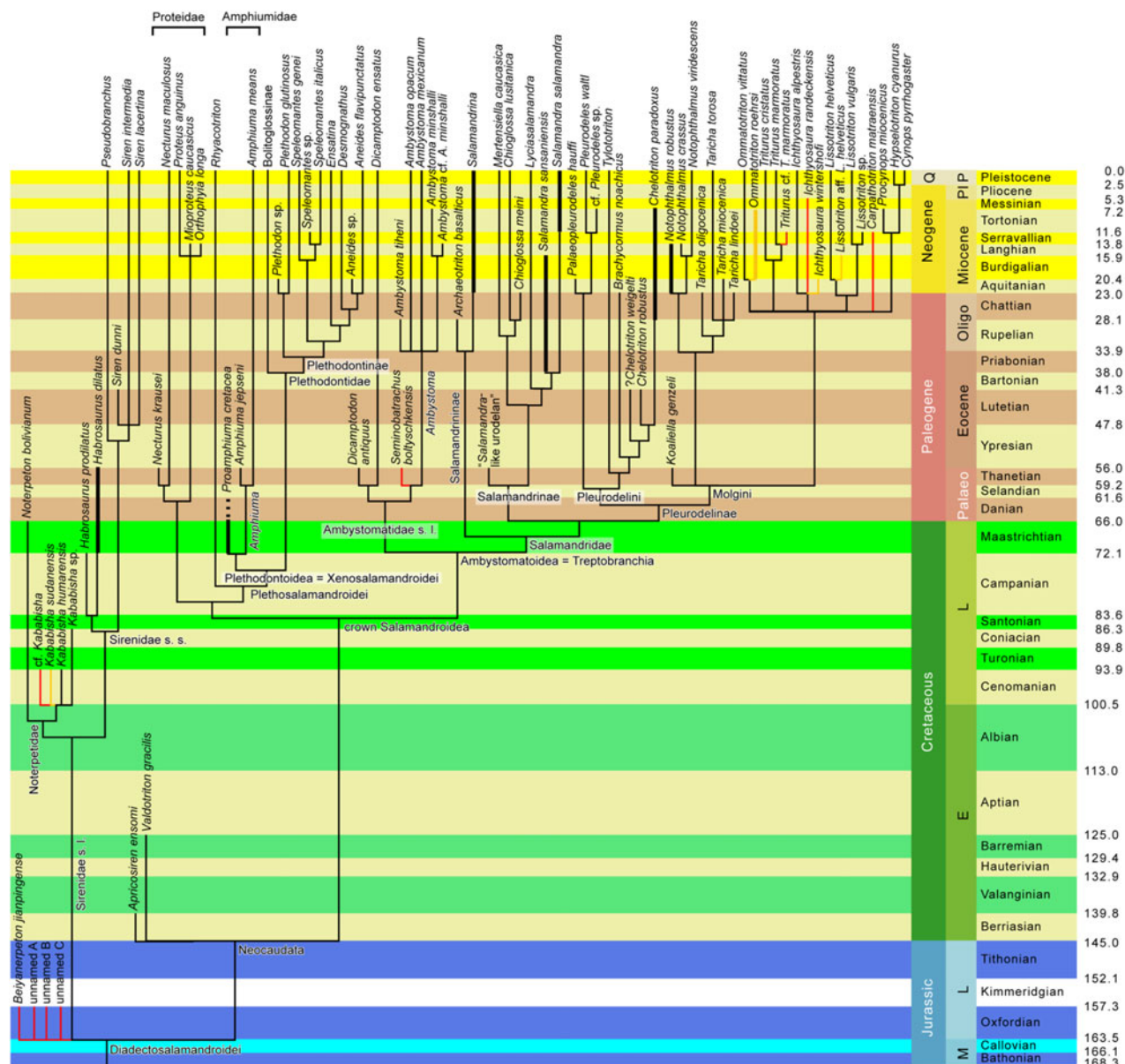


Figure 2. Diadectosalamandroidei. Colours, branch thicknesses and abbreviations as in Figure 1.

Figure 1. Lissamphibia other than Anura sensu lato and Diadectosalamandroidei (which are shown in Figures 2–5). All terminal branches occupy at least an entire geological stage, all internodes are at least 3 Ma long (this is just a graphic convention to make several nested taxa with the same oldest members visible). As stated in ML07, clades without a fossil record are collapsed or reduced to a single representative species to save space, and all polytomies represent uncertainty (they are soft polytomies). Red branches indicate fossils published after ML07; orange shows taxa we had previously overlooked; brown highlights taxa we had previously omitted because their phylogenetic positions were unclear, but are now clearer. Thin branches represent terminal taxa that are only known from the last stage through which their branches extend. Thick branches represent the ranges of terminal taxa that are known from two or more stages; the karaurid caudate genus *Marmorerpeton* extends into the Oxfordian, but this is not marked, because our source (Evans and McGowan 2002) does not mention which species is known from the Oxfordian, assuming the material can even be assigned to a species. Possible extensions are represented by thick stippled branches. Notes: Definite fossil stegokrotaphians were unknown in 2007, so we represented this taxon as a single branch; we now show Ichthyophiidae, Scolecomorphidae and Typhlonectidae (the latter two marked in brown) explicitly, so we can provide context for the Napak caecilian as a member of Teresomata = Caeciliidae sensu lato (Rage and Pickford 2011). The ‘Guimarota *Celtdens*’ is the same as ‘cf. *Celtdens* sp.’ of ML07 (figure 3). Abbreviations: s. l., sensu lato; s. m., sensu medio; s. s., sensu stricto; E, Early; M, Middle; L, Late; Palaeo, Palaeocene; Oligo, Oligocene; Pl, Pliocene; P, Pleistocene; Q, Quaternary. The unlabelled stage at the beginning of the Triassic is the Induan.

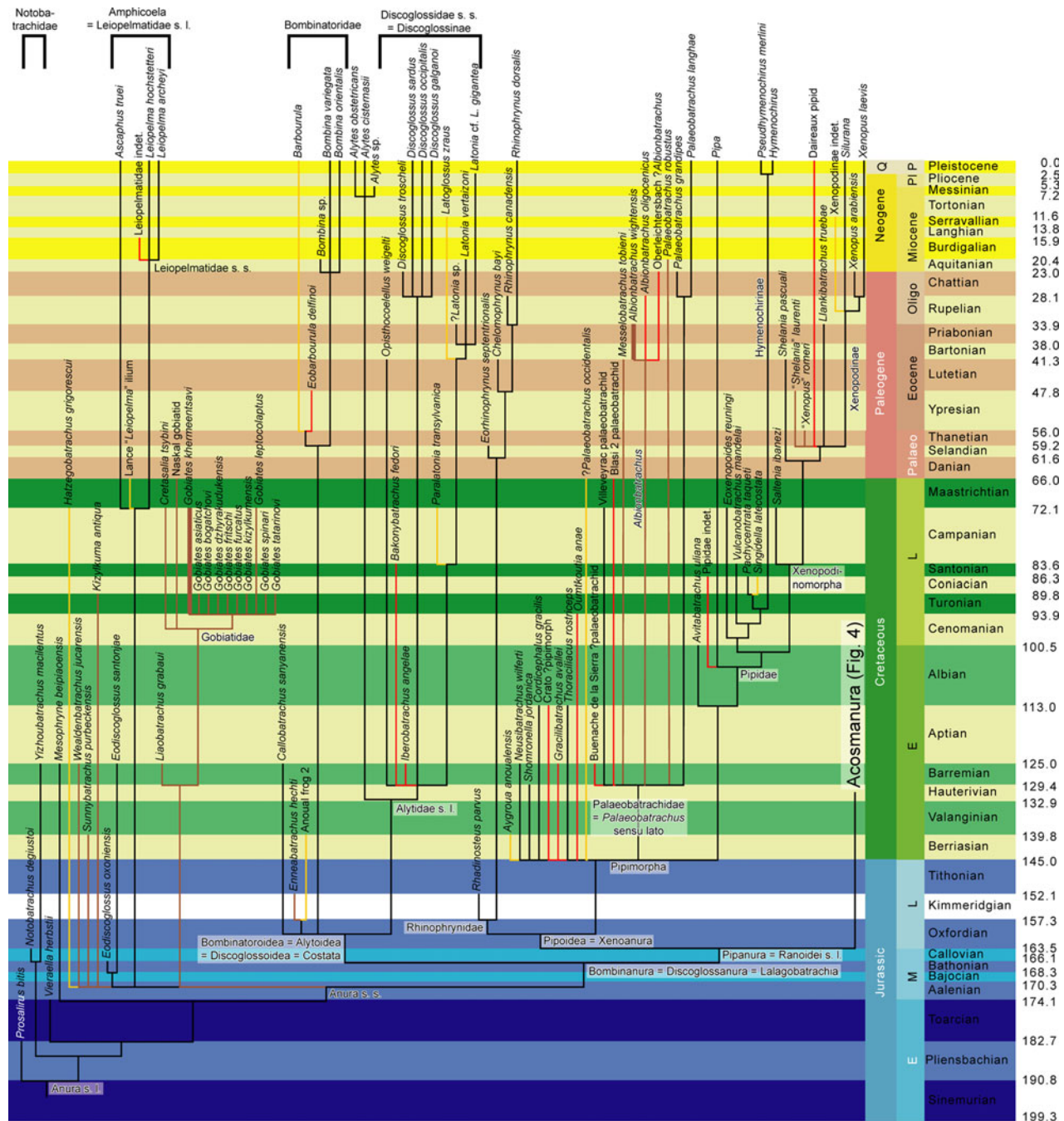


Figure 3. Anura sensu lato except Acosmanura (which is shown in Figures 4 and 5). The enormous polytomy at the base of Pipimorpha is mostly due to conflicting phylogenetic analyses in our sources. Colours, branch thicknesses and abbreviations as in Figure 1. Note: *Palaeobatrachus langhae* died out some 500,000 years ago (Wuttke et al. 2012, figure 8), the Daireaux pipid (Báez, Gómez, and Taglioretti 2012; marked in red) is only known from the late Pleistocene. We have, however, also added the extant *Barbourula*, marked in orange, to show more clearly that the early Miocene '*Bombina* sp.' is a crown bombinatorid and to show the position of the newly discovered *Eobarbourula* (Folie et al. forthcoming).

Most of the missing species probably form a clade with *Palaeobatrachus grandipes* and *Palaeobatrachus langhae* (Wuttke et al. 2012), but their synonymies have, for the most part, yet to be worked out – let alone their phylogeny.

The holotype of *Bufo tihen* is 'a fragmentary sacral vertebra'; '[f]ive ilia from the same locality were tentatively

referred to this species although they are rather variable among themselves' (Roček and Rage 2000, p. 1374). We see little to no basis for these referrals, and note that Bever (2005, table 5) has found the ilia to be indistinguishable from those of several extant species of *Bufo* sensu lato that are referred to *Anaxyrus* or *Incilius* by those who adopt the splitting of

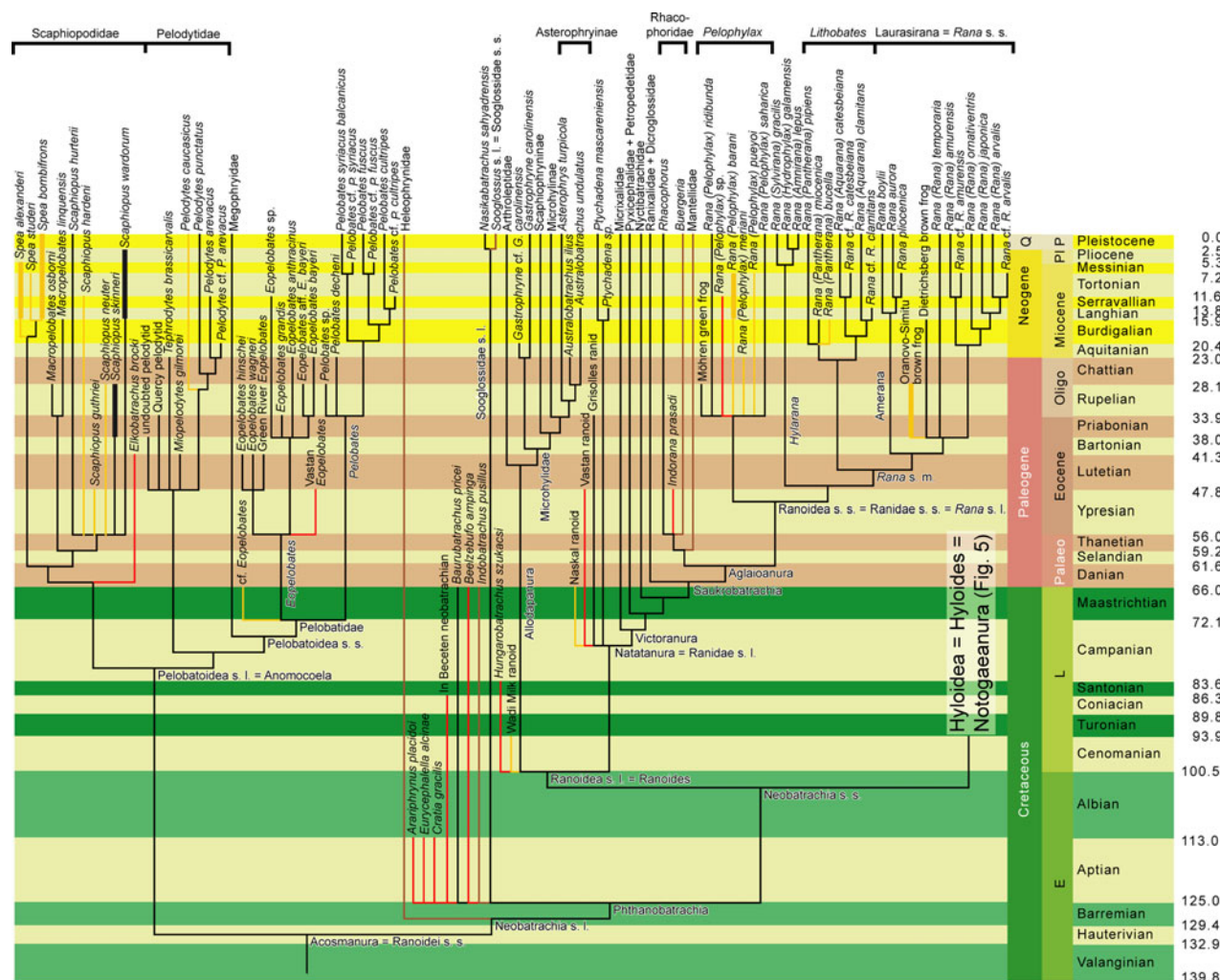


Figure 4. Acosmanura except Hyloidea sensu lato/Hyloides (which is shown in Figure 5). Colours and abbreviations as in Figure 1. Notes: Pre-Pleistocene members of the Rhacophoridae–Mantellidae clade were unknown in 2007, so we represented this clade as a single branch; we now show *Rhacophorus*, *Buergeria* and Mantellidae (the latter two marked in brown) explicitly, so we can provide context for *Indorana* as a (stem- or crown-group) rhacophorid (Folie et al. forthcoming). We have similarly added the extant *Pelodytes caucasicus*, marked in orange, to show that the Miocene *Pelodytes arevacus* is a crown-pelodytid (Sanchiz 1998a), and the extant heleophrynids, likewise marked in brown, in order to better constrain the phthanobatrachian polytomy. Note also the Eocene rather than Miocene age of *Miopolodytes* (Henrici and Haynes 2006).

Bufo by Frost et al. (2006), meaning there is no evidence that they represent a single species. Accordingly, we have removed *Bufo tihenii* from our tree. Several species of *Bufo* sensu lato that remain in our tree, as well as presumed Miocene records of extant species, may have to be treated the same; for the time being, we have kept them in the supertree to illustrate the fact that bufonid fossils are known from several stages of the Miocene.

In contrast, we previously (ML07, appendix 1) explicitly excluded the gobioid frogs because their phylogenetic position was too poorly known. They have meanwhile been revised (Roček 2008). Although no phylogenetic analysis was performed, it is now fairly clear that they most likely lie just inside or outside the crown group of frogs (Roček 2008, Roček et al. 2012); we now

show them in the crown-anuran polytomy in Figure 3, next to their sister-group *Liaobatrachus* (Roček et al. 2012), which we had previously also excluded, for similar reasons. To the gobioid frogs mentioned by Roček (2008), we have added the gobioid material from Naskal described by Prasad and Rage (2004), which was not discussed or cited by Roček (2008).

Nicoli (2012, p. 237) cited us (ML07) as having used the above-mentioned '*Eupsophus* sp.' as a 'calibration point'. This is incorrect; this taxon was incorporated in our tree (ML07, figure 7), but it was not one of the calibration constraints that we used in our molecular dating analyses. Neither did this Oligocene (probably Rupelian) fossil constrain the ages of clades in our palaeontological timetree analyses, because it was attached to a branch stemming

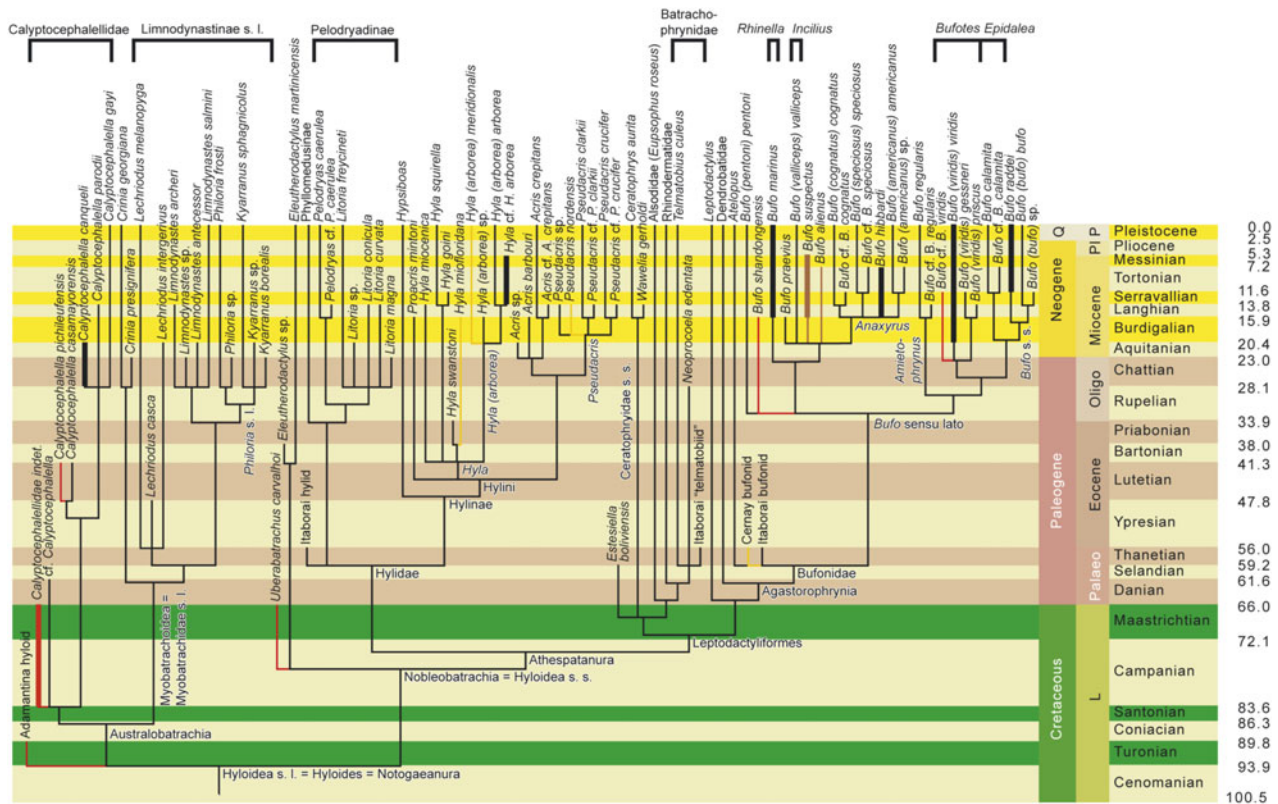


Figure 5. Hylidae sensu lato = Hylidae. Colours, branch thicknesses and abbreviations as in Figure 1. Notes: We have added the extant *Hyla (arborea) meridionalis*, marked in orange, to provide more context for the early Miocene *Hyla (arborea)* remains (Sanchiz 1998a).

from a polytomy at the base of Telmatobiinae (now Batrachophryinae) that also comprised the geologically much older (latest Palaeocene or earliest Eocene: Oliveira and Goin 2011) Itaboraí ‘telmatobiine’. Thus, the removal of ‘*Eupsophus* sp.’ (Figure 5) improves the factual accuracy of our tree, but does not change the implied timing of any cladogenesis visible on that tree.

In Figure 4, we have replaced the extant *Spea multiplicata* by the likewise extant *Spea bombifrons* which has a fossil record that we had overlooked (Roček and Rage 2000).

For name changes, see the Nomenclature section below.

The phylogenetic position and age of Gerobatrachus

Maddin et al. (2012) found the Permian amphibamid temnospondyl *Gerobatrachus* to be a lissamphibian, in particular a stem-batrachian. Being of probably Kungurian (late Early Permian) age (Wardlaw 2004; Anderson et al. 2008), it is some 25–30 Ma older (International Commission on Stratigraphy 2013) than the oldest uncontroversial lissamphibians, the Early Triassic *Triadobatrachus* and *Czatkobatrachus*. It is also some 10–15 Ma older than the range of ages for Lissamphibia derived from our supertree

(ML07, figure 9, table 2), and lies around the beginnings of the 75–95% confidence intervals on the origin of Lissamphibia calculated by Marjanović and Laurin (2008a, table 4) under the most realistic sets of assumptions. Most of the many molecular dates for the origin of Lissamphibia calculated by ML07 (table 2) do encompass it.

However, we question whether *Gerobatrachus* is indeed a lissamphibian. The data matrix used by Maddin et al. (2012) in their phylogenetic analysis is based on that by Anderson et al. (2008), yet Maddin et al. (2012) did not address the modifications proposed by Marjanović and Laurin (2009: Electronic Supplementary Material 1) or those suggested by Sigurdson and Green (2011: appendix S3). Implementing our modifications places *Gerobatrachus* (like all other temnospondyls) as a stem-tetrapod (Marjanović and Laurin 2009, Electronic Supplementary Material 2); implementing those by Sigurdson and Green places it (again like all other temnospondyls) as a stem-amphibian. Addition of *Gerobatrachus* (Marjanović 2010, chapter 5; Marjanović, Germain and Laurin, ongoing work) to a data matrix based on that by Ruta and Coates (2007) has not so far placed *Gerobatrachus* as a member – or even the sister-group – of Lissamphibia, not even when the lissamphibians are

Table 2. Summary of recommendations about the calibration dates proposed by ML07 (mostly table 1).

Clade	Main content	ML07		This paper		Comments
		Min	Max	Min	Max	
Batrachia	Salientia, Caudata	250	275	250	275	Unchanged
Anura (crown)	Amphicoela, Bombinanura	170	185–215	155–166	185	<i>Eodiscoglossus</i> may not be a (crown-)anuran
Bombinanura	Bombinatoroidea/Alytoidea/Discoglossoidae/Costata, Pipanura	170	185–215	152	170–185	<i>Eodiscoglossus</i> is not a bombinanuran
Pipoidea	Rhinophrynidae, Pipimorpha	155	175	155	175	Unchanged
Urodela	Cryptobranchioidea, (Sirenidae sensu lato + Neocaudata)	155	170–200	165	275	Redating of ‘Daohugou Beds’ has changed min, made max much older

Notes: Minimum and maximum ages (min, max) in Ma. See main text for more information.

constrained to be temnospondyls. We await the ongoing full description of *Gerobatrachus* with great interest and encourage further study of published data matrices.

Phylogeny

We have followed the phylogeny by Pyron and Wiens (2011) for all taxa it contains, except for the molgine salamandrids; we represent that clade as a polytomy, because the relatively poorly supported tree by Pyron and Wiens (2011), based on three mitochondrial and nine nuclear genes, the more strongly supported tree by Zhang et al. (2008), based on complete mitochondrial genomes, the tree by Venczel (2008), based on morphological data, and the tree by Schoch and Rasser (2013), based on a partially overlapping set of morphological data, all disagree. The positions we show for extinct taxa (which are of course not considered in molecular phylogenies) follow the most recent literature as closely as possible; we have continued our convention (ML07) of assigning taxa of moderately uncertain position to a polytomy formed from the basal dichotomy of the largest clade they can be assigned to – almost all polytomies in our trees represent such situations. The used literature is cited in Table 1.

Uncertainties about geological ages

Many sites cannot be dated with enough precision to confidently assign them to a single geological stage. In such cases, we have followed our convention (ML07, p. 374) of placing the taxa in question at the end of the oldest geological stage they could date from. For instance, the salamander *Chunerpeton* (discussed below) could be Bathonian, Callovian or Oxfordian in age, so we have placed it at the end of the Bathonian, the earliest of these three stages (Figure 1).

This practice should introduce a bias towards older divergence dates; we expect this bias to partly counteract

the bias towards younger divergence dates that is caused by the incompleteness of the fossil record (discussed below).

Some sites can be dated with greater precision than a geological stage. In the cases of albanerpetontids (Gardner and Böhme 2008), this is shown (approximately) in Figure 1, but it was not taken into account in our analyses.

Branch lengths

The fossil record being incomplete, we cannot assume that any fossil is the earliest member of its lineage, directly representing the age of a cladogenesis. Rather, we must assume some leeway. Similarly, we cannot assume that internodes had a length of zero so that successive cladogeneses would occur at the same time. Unfortunately, there is no objective way of directly deriving branch lengths from supertrees; however, we have applied a range of realistic values to the tree and recorded the resulting ages of various nodes. This is easy to do in Mesquite (Maddison and Maddison 2011) with Stratigraphic Tools (Josse et al. 2006); hereinafter we call this procedure a ‘branch length sensitivity analysis’.

These analyses were conducted in the same way as in our 2007 paper, namely by varying minimal internal and terminal branch lengths between 0.1 and 5 Ma or by setting minimal terminal branch lengths to occupy at least one whole geological stage (‘stratigraphic fit’). All modified paleontological dates for clades larger than a single species reported below are assessed in this way, unless mentioned otherwise. The figures show stratigraphic fit and a minimal internal branch length of 3 Ma.

Nomenclature

This paper is not issued for purposes of zoological nomenclature; any nomenclatural act herein is invalid according to Article 8.2 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). In particular, if this paper

appears in print before Folie et al. (forthcoming) or Sweetman and Gardner (forthcoming), it must not be considered as publishing the new genus and species names coined in those articles. We do comment on correct spellings below, but all of these cases follow automatically from the Code (Article 29) and do not require nomenclatural acts – we merely wish to bring those spellings to the attention of the community.

Mynbulakia surgayi is a junior synonym of *Eoscapherpeton asiaticum*, with much of the referred material now being called *Nesovtriton mynbulakensis* (Skutschas 2009). The name *Pachybatrachus* was preoccupied and has been replaced by *Pachycentrata* Báez and Rage, 2004; *Macropelobates* ‘cratus’, so called in our 2007 paper, is correctly *Macropelobates linquensis* (Roček et al. 2011).

Pyron and Wiens (2011) cite us (ML07) for the claim that the splitting of *Bufo* and *Rana* by Frost et al. (2006) is controversial. Although this claim is clearly true, we do not wish to be seen as taking sides in it. (Being vertebrate palaeontologists, we do prefer genera that are monophyletic and small enough to handle, but neobatrachians are far outside our field.) We therefore continue to apply our previous convention in Figures 4 and 5: the traditional names are given for species, but the new genus names are shown at their nodes. We note that acceptance of the splitting by Frost et al. (2006) seems to be spreading – Martín et al. (2012) presupposed it, amphibiaweb.org adopted most of it in 2012, and Wikipedia is inconsistent as of early May 2013.

Within this splitting of *Bufo*, three of the names used by ML07 (figure 7) are incorrect: *Chaunus* is now referred to *Rhinella* (Chaparro et al. 2007), *Cranopsis* was both preoccupied and a junior synonym of *Incilius* (Frost et al. 2009), and *Pseudepidalea* is a junior synonym of *Bufotes* (Dubois and Bour 2010).

Because the tree by Pyron and Wiens (2011) is largely congruent with that by Frost et al. (2006), we have applied much of the latter’s nomenclature for higher taxa in Figures 1–5. Some clades are therefore designated by several synonyms.

As previously explained (Marjanović and Laurin 2008b, 2013), we prefer not to use the name *Apoda* Oppel, 1810, for a clade of caecilians, because it is a homonym of *Apoda* Haworth, 1809, which designates a genus of moths; instead, we adopt the other common convention in Figure 1, which is to use *Gymnophiona* for the caecilian crown group. *Gymnophioniformes* Marjanović and Laurin, 2008b, applies to the smallest clade that contains *Gymnophiona* and the Early Cretaceous *Rubricacaecilia*; *Gymnophionomorpha* Marjanović and Laurin, 2008b, applies to the largest clade that contains *Gymnophioniformes* but not *Salientia*, *Caudata*, *Albanerpetontidae* or the currently known Paleozoic tetrapods.

We accept the corrections by Martín et al. (2012) of incorrect original spellings; to these, we have to add the

corrections of *Regalerpeton weichangensis* to *Regalerpeton weichangense* Zhang et al., 2009, and of *Beiyanerpeton jianpingensis* to *Beiyanerpeton jianpingense* Gao and Shubin, 2012a, because (as mentioned by Martín et al. 2012) the Ancient Greek *herpetón* is neuter (originally the neuter form of an adjective to ‘creep’). Furthermore, Martín et al. (2012) pointed out that the original spelling *Scapherpetidae* is grammatically correct and must be retained instead of the more widespread subsequent spelling ‘*Scapherpetontidae*’. Article 29 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999) mandates that the grammatically incorrect original spellings ‘*Eoscapherpetontinae*’ and ‘*Noterpetontidae*’ must similarly be corrected to *Eoscapherpetinae* Nesov, 1981, and *Noterpetidae* Rage, Marshall and Gayet 1993. However, according to the same article, the likewise grammatically incorrect original spelling *Amphiumidae* Gray, 1825, is to be retained because it ‘is in prevailing usage’. It is not clear to us if this argument applies to the grammatically incorrect original spelling *Albanerpetontidae* Fox and Naylor, 1982: although no other spelling has ever been used, there is not much literature on the taxon it designates, so it could be argued that there has not been enough usage to count as ‘prevailing’. Consequently, we use the spelling ‘*Albanerpet(ont)idae*’ hereinafter and in the figures.

Results and discussion

Divergence dating

In this section, we revise the divergence dates presented in figure 9(b) of ML07, and the calibration constraints proposed in its table 1, where recent discoveries have made this necessary. Our new recommendations about these calibration constraints are summarised in Table 2.

Anura sensu stricto,

Bombinanura/Discoglossanura/Lalagobatrachia

It used to be thought (e.g. Roček 2000) that *Eodiscoglossus oxoniensis* from the Bathonian (late Middle Jurassic) of England was an alytoid/discoglossoid/costatan and therefore the oldest known bombinanuran/discoglossanuran, indeed the oldest anuran in the strict sense. We positioned it as such in our supertree and consequently found *Bombinanura* to be 166–185 Ma old in our branch length sensitivity analyses (ML07, figure 5, table 2, appendix 4; figure 9(b) has slightly erroneous values). In the same paper (table 1), we went on to propose the origins of *Anura* and *Bombinanura* as a calibration constraint with a minimum age of ~170 Ma, based on the age of *Eodiscoglossus oxoniensis*, and a maximum age of ~185 Ma, based on the presence of several clades of stem frogs but the absence of crown frogs in the Early and early Middle Jurassic

(Figure 3). However, as we pointed out (ML07, p. 381), the much later appearance of the sister group of Anura, *Mesophryne* (Figure 3), creates a ghost lineage of at least 55 Ma on that branch. This, along with the complete lack of known amphicoelans before the Maastrichtian (~70 Ma ago; Figure 3) and the absence of salientians between the middle Early Jurassic and the Early Triassic, raised the possibility that Bombinanura and Anura are older than our supertree suggests. Accordingly, we had repeated those runs of r8s (the program we had used for molecular dating), where the origin of Bombinanura was used as a calibration constraint, assuming that the distance between the minimal and the maximal age was twice or three times as large as proposed there (i.e. a maximal age of 200 or 215 My).

However, the hypothesis that *Eodiscoglossus oxoniensis* belongs to this clade had never been tested by a phylogenetic analysis till Báez (2013) included *Eodiscoglossus santoniae*, the much better known type species of *Eodiscoglossus*, in her analysis and found it to lie outside of Bombinanura. Assuming that *Eodiscoglossus santoniae* and *Eodiscoglossus oxoniensis* should still be regarded as sister-groups, we have moved *Eodiscoglossus* to the crown-anuran polytomy. Thus, as now depicted in Figure 3, the oldest known bombinanurans (and undoubted crown anurans) are the indeterminate costatan *Enneabatrachus* and the stem-rhinophrynid pipoid *Rhadinosteus*, both from the Morrison Formation (western USA) and thus Late Jurassic, probably Kimmeridgian to Tithonian, in age. Bombinanura consequently appears to be 152–172 Ma old, according to a branch length sensitivity analysis.

Consequently, we propose to move the minimum age of this calibration constraint to ~152 Ma, and have increased confidence in its maximum age of ~185 Ma because there are no longer any known Middle Jurassic bombinanurans; even a maximum age of ~175 Ma may be reasonable. Given the uncertainty over the placement of *Eodiscoglossus*, we cannot at present recommend the use of a minimum age for the origin of crown-group Anura (other than the minimal age of Bombinanura) as a calibration constraint – however, the only extant non-bombinanuran anurans (*Ascaphus* and *Leiopelma*) are seldom, if ever, included in molecular divergence date analyses, so this is not a great loss; the maximum age, however, is still realistic.

Neobatrachia, Ranoidea sensu lato/Ranoides

As presented in the previous version (ML07, figures 6 and 7), Neobatrachia had no Mesozoic fossil record except for the supposedly Campanian (late Late Cretaceous) presumed hyloid *Baurubatrachus* (on which see below in the Athespatanura section), and the earliest known ranoid dated only from the end of the Eocene. Given this absence of constraints, different branch length settings resulted in

very wide age ranges for these clades – 72–124 Ma for Neobatrachia in the strict sense and 34–74 Ma for the basal node of Ranoidea in the wide sense/Ranoides. This situation has radically changed (Báez, Gómez, Ribeiro, et al. 2012, and references therein).

The oldest known definite neobatrachian sensu stricto is the ranoid from Wadi Milk (Sudan), dating from the Cenomanian (earliest Late Cretaceous), which is now thought to have lasted from 100.5 to 93.3 Ma ago. This falsifies the younger half of the range for Neobatrachia and, because of our convention about the use of polytomies, the entire range for the basal node of Ranoidea (Figure 4) proposed by ML07. The next younger neobatrachian may be the hyloid from the Adamantina Formation (Brazil), which may be as old as Turonian (Figure 5). A Santonian (middle Late Cretaceous) site in Hungary has yielded the probable ranoid *Hungarobatrachus* (Figure 4); *Baurubatrachus* has left the picture (see below), but Campanian hyloid material may be known in the form of isolated bones tentatively assigned to Calyptocephalellidae (Gómez et al. 2011); such material is also known from the Maastrichtian, as is the likely nobleobatrachian *Uberabatrachus* (see below) and the ranoid from Naskal (Prasad and Rage 2004). As depicted in Figures 4 and 5, the Palaeocene and Eocene record of Neobatrachia has also improved, and the late Eocene holds not only an indeterminate ranid in the widest sense but also a member of *Rana* in the strictest sense (a ‘brown frog’). The updated fossil record of Neobatrachia (sensu stricto) suggests a minimal age in the range of 94–104 Ma (94–99 Ma for the basal node of Ranoidea sensu lato and 90–99 Ma for the basal node of Hyloidea sensu lato) according to branch length sensitivity analyses.

Several Cretaceous phthanobatrachians of uncertain placement (Figure 4) may be neobatrachians in the strict sense (in other words, ranoids or hyloids). Noteworthy among these, because of their late Early Cretaceous age, are *Arariphrynus*, *Eurycephalella* and *Cratia* from the late Aptian or possibly early Albian of Brazil – the oldest known acosmanurans.

Athespatanura

In our 2007 paper, we found that our fossil-based supertree consistently gave younger ages than the molecular divergence dating analysis by Zhang et al. (2005), except for the divergence between *Bufo* (and relatives) and *Hyla* (and relatives), which we found to have happened 72–101 Ma ago (Campanian to Albian; Late to latest Early Cretaceous) depending on the branch length settings (ML07, figure 9(b)). This exception was the result of two errors.

First, we had assigned a Campanian age to the presumed ceratophryid *Baurubatrachus*. This was taken from our source, Roček (2000). As this source correctly

mentions, however, *Baurubatrachus* was found in the Marília Formation of southern Brazil, famous for its dinosaurs and terrestrial crocodyliforms; it has long been considered to belong to the Maastrichtian, the following stage (Fernandes and Coimbra 2000; briefly mentioned by Marjanović and Laurin 2013, table 6). As *Baurubatrachus* was the only Mesozoic member of Athespatanura (the smallest clade that contains *Hyla* and *Bufo*), this means the age range our tree gave was too old; the Maastrichtian, the last stage of the Cretaceous, ended only 66 Ma ago.

Second, Ruane et al. (2011) have cast great doubt on the identification of *Baurubatrachus* and the similar *Beelzebufo* from the Maastrichtian of Madagascar (Evans et al. 2008) as ceratophryids. When *Baurubatrachus* and *Beelzebufo* are removed from Athespatanura (we have included them in the Phthanoatrachia polytomy in Figure 4), there are no Mesozoic athespatanurans left, and the oldest known athespatanuran is the Danian (early Paleocene) *Estesiella*. Varying the minimal branch lengths between 0.1 and 5 Ma as done in ML07 yields a range of minimal ages for Athespatanura between 62 and 90 Ma, about 10 Ma less than our previous estimates.

Uberabatrachus, likewise from the Marília Formation, is apparently a nobleobatrachian, thus a hyloid closer to *Hyla* and/or *Bufo* than to *Calyptocephalella* and Myobatrachidae, but ‘it remains unclear whether it lies within this clade or is part of its stem’ (Báez, Gómez, Ribeiro, et al. 2012, p. 1148). If it lies within Athespatanura, a Maastrichtian minimum age is restored.

The unnamed hyloid from the post-Cenomanian Late Cretaceous Adamantina Formation, known from ‘four articulated specimens’ (Báez, Gómez, Ribeiro, et al. 2012, p. 1148), has not been described to the extent that it could be placed more precisely. Should this taxon belong to Athespatanura, the minimum age of Athespatanura may move close to the beginning of the Late Cretaceous – or not, given the uncertainty about the age of the Adamantina Formation.

Urodela, Cryptobranchoidea

We have proposed the use of the origin of Urodela (the salamander crown group) as a calibration constraint for molecular divergence dating, suggesting a minimum age of ~155 Ma based on what we considered the earliest known urodele (the probably Kimmeridgian or Tithonian – middle or late Late Jurassic – *Iridotriton*: Evans et al. 2005) and a maximum age of ~170 Ma based on the presence of several karaurids (nonurodelan caudates) and the supposed absence of urodeles in the Middle Jurassic (ML07, p. 382, table 1). We stated on the same page that the complete absence of known older caudates was not encouraging, given the size of the gap implied by the oldest known salientians (Figure 1). Accordingly, as with

Bombinanura, we had repeated those molecular divergence date analyses in which we used the origin of Urodela as a calibration constraint, under the assumption that the distance between the minimal and the maximal age was twice or three times as large as we initially proposed (i.e. a maximal age of 185 or 200 My).

From fossils alone, we had dated the origin of Urodela to 152–166 Ma ago under different branch length settings for our supertree (ML07, figure 9(b), table 2); in those molecular analyses where we did not use it for calibration, we found it to have occurred more than 170 Ma ago (ML07, table 2), because the analysis of the molecular data by r8s pushed that age to its upper constraint except when that constraint was very high (e.g. 200 Ma).

Anderson (2012) stated instead that we had dated the origin of Urodela to 143 Ma ago. Perhaps Anderson had read the column titled ‘Cry’ instead of the column titled ‘Uro’ just to its left in table 2; it is the origin of crown-group Cryptobranchoidea (the divergence between Hynobiidae and Cryptobranchidae) that we had estimated to 138–150 Ma ago from our supertree (ML07, table 2, appendix 4; figure 9(b) in that paper had slightly erroneous values). The age of 143 Ma was obtained through a stratigraphic fit (every terminal branch occupies at least an entire geological stage) and a minimum internode length of 3 Ma, which was the setting used to provide our ‘best guess’ dates in figure 9(b).

Our finding that the crown group of Cryptobranchoidea was around 143 Ma old relied on the idea that the ‘Daohugou Beds’ of easternmost Inner Mongolia (northeastern China), which have yielded the pancryptobranchian *Chunerpeton*, were of Valanginian age and therefore at most 140 Ma old (ML07, p. 382) – incidentally, this is the age that Gao and Shubin (2012a, but see 2012b) mistakenly cited as the age we had found for Urodela.

The age of the ‘Daohugou Beds’, now considered part of the Tiaojishan/Lanqi Formation (Liu et al. 2006; Yang and Li 2008; Peng et al. 2012) or the underlying Jiulongshan/Haifanggou Formation (Gao and Shubin 2003, 2012a; Gao et al. 2013), was a point of controversy and confusion for a long time, as reported by ML07 (pp. 382, 388). A radiometric date of 164 ± 4 Ma ago has now been obtained from the middle of the ‘Daohugou Beds’, right under the salamander-bearing layer (Liu et al. 2006; Yang and Li 2008; Gao and Shubin 2012a); this corresponds to a Bathonian to Oxfordian age (middle Middle to early Late Jurassic), with a midpoint in the Callovian (late Middle Jurassic). The Valanginian maximum age we assigned (ML07, figure 3) to the crown-group cryptobranchoids (Gao and Shubin 2012a) *Jeholotriton*, *Liaoxitriton daohugouensis* and *Chunerpeton* is thus clearly wrong; we have placed them in the Bathonian (their maximal possible age) in Figure 1. *Pangerpeton*, from Reshuitang, is only slightly younger (Callovian: Gao et al. 2013).

However, the impact of this finding on our estimates of the age of Urodela is limited (*contra* Anderson 2012 and Gao and Shubin 2012a; acknowledged by Gao and Shubin 2012b). The age of the above-mentioned four oldest known urodeles still broadly overlaps with the age range determined from our 2007 supertree (152–166 Ma ago; ML07, figure 9, table 2); the age range derived from the update we present here ranges from 167 to 186 Ma ago, 12 to 16 Ma more than our initial estimate. This slightly greater age results from redating previously known fossils rather than the discovery of older fossils, which suggests that the lissamphibian fossil record is reasonably good (*contra* Anderson 2008, 2012).

Believing that our molecular divergence dating analyses had found Urodela to be younger than its oldest known members, Anderson (2012) speculated that it might have helped if we had used soft instead of hard maximum ages for those calibration constraints to which we assigned maximum ages. We fully agree that soft maxima are in the vast majority of cases more realistic than hard maxima – unfortunately, soft maxima were not implemented in the software available to us at the time. All we were able to do, as quoted above, was to vary the maximum ages of two calibration constraints (to up to 200 Ma for Urodela, which is still well above the minimum age estimated here) and run separate analyses.

Beiyannerpeton, newly introduced into our tree (described by Gao and Shubin 2012a), is a non-cryptobranchoid urodele from the Oxfordian or possibly Kimmeridgian (early Late Jurassic) of Liaoning (also northeastern China). It is most likely older than *Iridotriton*, but in any case younger than the crown-cryptobranchoids from Daohugou (Gao and Shubin 2012a), regardless of whether the ‘Daohugou Beds’ are considered to belong to a lower part of the same formation (the Tiaojishan/Lanqi Formation) or not. Thus, the discovery of *Beiyannerpeton* does not change the implied minimal origin date of crown urodeles.

‘Salamander B’ from the Bathonian of England may lie inside or close to Urodela; this uncertainty is shown in Figure 1. If it is a urodele, it is one of the oldest known urodeles, but not (or hardly) older than the Daohugou cryptobranchoids.

In sum, we propose to move the minimum age of this calibration constraint to ~167 Ma; given the fact that there are no longer any known caudates that are definitely older than the oldest known cryptobranchoids, the maximum age should be considered to be 275 Ma (late Artinskian), which makes this information useless as a dating constraint. This may change as the dating of the Daohugou cryptobranchoids becomes more precise.

Comments on the anatomy of *Beiyannerpeton*

Gao and Shubin (2012a) and Anderson (2012) mentioned that *Beiyannerpeton* has grooves for the lateral-line organ on its skull, but did not comment on the importance of this finding. The lateral-line organ, which senses vibrations in water, is plesiomorphic for vertebrates and is retained in aquatic lissamphibians today – in aquatic adults as well as in aquatic larvae that metamorphose into terrestrial adults and lose the organ during metamorphosis (Duellman and Trueb 1986; Schoch 2001). However, in contrast to the plesiomorphic condition that was retained by many Palaeozoic and Mesozoic aquatic limbed vertebrates (temnospondyls, ‘lepospondyls’, etc.), the lateral-line organ has never been documented to leave traces (grooves or closed canals) on the skulls of lissamphibians other than *Beiyannerpeton*; it lies entirely in the skin.

Although gills (Gao and Shubin 2012a; *contra* Anderson 2012) or other soft tissue are not preserved in *Beiyannerpeton*, it is one of only three lissamphibians known to retain ossified plates on the ceratobranchials (the latter often remain cartilaginous themselves and are not preserved in these cases). The other two are the pancryptobranchian *Chunerpeton* (Gao and Shubin 2003) and the ambystomatid *Seminobatrachus* (Skutschas and Gubin 2012). These dermal bones are plesiomorphically retained in several temnospondyls (reviewed by Schoch and Witzmann 2011) and the ‘lepospondyl’ *Microbrachis* (Olori 2011), where they plesiomorphically bear small teeth. *Contra* Gao and Shubin (2012a, p. 5768), they are not homologous (Schoch 2001, pp. 353–354; Schoch and Witzmann 2011, and references therein) to the ‘gill rakers’, projections of the ceratobranchials that apparently never ossify and are plesiomorphically retained in extant aquatic salamanders.

There is no further evidence (Gao and Shubin 2012a) that *Beiyannerpeton* or *Chunerpeton* might be stem amphibians or stem salamanders; we conclude that lateral-line grooves and (as *Chunerpeton* and *Seminobatrachus* already suggested) dermal bone plates on the ceratobranchials must have been lost several times independently within Lissamphibia and even within Urodela. Indeed, rudiments of the mentioned dermal bone plates may transiently appear during the development of the extant *Rhyacotriton* (Worthington and Wake 1971).

Discussion and conclusions

In a qualitative sense, the shortcomings of the fossil record of continental tetrapods are well known, and this record has been argued to be especially poor for lissamphibians (summarised by Fara 2004). It is incomplete, biased (e.g. towards lakes and floodplains and away from rainforests, mountains and soils) and it exhibits a strong diversity dependence, meaning that – all else being equal – taxa of low taxonomic diversity are more difficult to find than

more speciose ones, and young fossil-bearing localities are much more common than old fossil-bearing localities (documented for lissamphibians by Marjanović and Laurin 2008a). In our 2007 paper, we tried to answer the question if these problems make it impossible to derive divergence dates (with reasonably small ranges of uncertainty) from the fossil record of lissamphibians. The number of extinct species or possible species – 223 – we managed to place in our supertree may seem insignificant compared to the 7129 known extant species of lissamphibians (amphibia-web.org as of 10 May 2013), and the biases are manifest: the aquatic pipimorph frogs, encompassing 33 extant species (amphibia-web.org as of 10 May 2013), are represented by a minimum of 26 extinct species over 145 Ma (Figure 3; increased from 2007), whereas the burrowing caecilians, counting 192 species today (amphibia-web.org as of 10 May 2013), are known from a total of eight extinct species over 190 Ma (Figure 1; three more than in our 2007 paper). In spite of all this, our supertree had a highly significant stratigraphic fit (ML07), showing that the biases for or against certain clades have their limits, and confidence intervals on the origin of Lissamphibia are calculable (Marjanović and Laurin 2008a), showing that the incompleteness and biases in the fossil record do not make the situation hopeless either.

Encouraged by these findings, surprising though they are (Anderson 2008, 2012), we went on to propose calibration constraints for molecular divergence dating (ML07, table 1), derived from our supertree. These proposals and the changes required by recent discoveries are summarised in Table 2. Of the five constraints we proposed that lie within Lissamphibia, two (the origins of Batrachia and Pipoidea) are unchanged (the effects of revisions to the geological timescale are minimal), one (Bombinanura) has its minimum age decreased by 15 Ma while its maximum age is more firmly established than before, another (Anura, with previously identical dates to Bombinanura) has a reduced minimum but unchanged maximum age and the fifth (origin of Urodela) has its minimum age increased by 10 Ma and its maximum age greatly extended.

Among the other divergences we explicitly dated, the origins of crown Neobatrachia and Ranoidea sensu lato/Ranoidea – both previously poorly constrained by fossils – now have a much smaller range of uncertainty than before, and the origin of Athespatanura (the *Bufo*–*Hyla* divergence) seems to have occurred about 10 Ma later than we had previously estimated.

Maddin et al. (2012) found the amphibamid temnospondyl *Gerobatrachus*, which is late Early Permian in age (Wardlaw 2004; Anderson et al. 2008; International Commission on Stratigraphy 2013), to be a lissamphibian. Being considerably older than the oldest uncontroversial lissamphibians (Early Triassic), it would lie outside the range of ages our supertree suggests for the origin of

Lissamphibia. However, we question the results of the phylogenetic analysis by Maddin et al. (2012): they are inconsistent with ours (Marjanović and Laurin 2009) based on the same matrix (Anderson et al. 2008), but lack the modifications proposed by us as well as those by Sigurdson and Green (2011). We await the ongoing full description of *Gerobatrachus*.

All taken together, we reaffirm our previous conclusion that the fossil record of Lissamphibia is good enough to derive calibration constraints for molecular divergence dating from it. The changes explained above are small; the large number of added species (the total number of extinct species or possible species is now 319), improvements in the dating of certain fossiliferous sites and advances in our understanding of lissamphibian phylogeny have not significantly rearranged the tree or led to other sizable surprises – they have mostly filled known gaps and resolved or created polytomies.

The Jurassic crown-group salamanders *Beiyangerpeton* and *Chunerpeton* retained the plates of dermal bone on their ceratobranchials (Gao and Shubin 2003, 2012a), as did the much younger *Seminobatrachus* (Skutschas and Gubin 2012); rudiments of such plates may transiently appear in the extant *Rhyacotriton* (Worthington and Wake 1971), but are otherwise, to the best of our knowledge, entirely unknown in any lissamphibian. *Beiyangerpeton* in addition retains the plesiomorphic tetrapod condition of grooves for the lateral-line organ on its skull; the organ is ubiquitous in aquatic lissamphibians today, but never leaves traces on the skull. These features may have been lost several times independently within Lissamphibia and indeed within Urodela, or reappeared in *Seminobatrachus*, *Beiyangerpeton* and *Chunerpeton*.

Erratum

Marjanović and Laurin (2013, pp. 270 and 271) attributed the names *Bufo* and *Salamandra* to Laurenti, 1768. Dubois and Bour (2010) showed that they were in fact first validly coined by Garsault, 1764.

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