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Assessing confidence intervals for stratigraphic ranges of higher taxa: The case of Lissamphibia

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To evaluate stratigraphic evidence for the time of origin of the clade of extant amphibians (Lissamphibia), we attempt to establish a confidence interval on the lower bound of the stratigraphic range of this clade. This is based on the stratigraphic distribution of 1207 fossiliferous localities that have yielded lissamphibians, the relative area of sedimentary rocks from various periods (upper Paleozoic to present) exposed on the continents, and ten exponential-growth models of lissamphibian diversity that differ by the assumed effects of three major biological crises and the assumed starting times of lissamphibian diversification. The results suggest a more recent origin of Lissamphibia than advocated in most recent molecular studies. They are also more compatible with monophyly than with polyphyly of the extant amphibians, but heavily depend on poorly constrained assumptions about lissamphibian extinction rates during biological crises. Counts of lissamphibian diversity through time that consider ghost lineages and stage durations show moderate declines across the Cretaceous–Paleogene and Oligocene–Miocene boundaries.

Key words: Lissamphibia, origination time, evolution of biodiversity, stratigraphic range, fossil record, mass extinction.

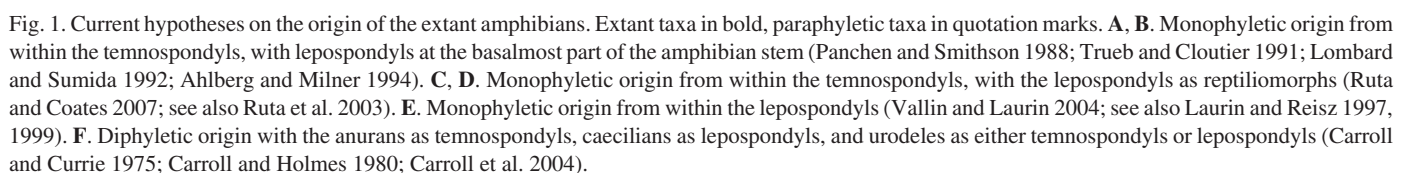
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Introduction

The possible origins of the extant amphibians (Lissamphibia) from temnospondyls (e.g., Ruta et al. 2003; Schoch and Milner 2004; Ruta and Coates 2007), lepospondyls (e.g., Laurin 1998; Vallin and Laurin 2004), or polyphyletically from both (e.g., Carroll et al. 2004; Anderson 2007) have been debated for a long time, but no consensus has emerged (Fig. 1). Recently, Zhang et al. (2005) compared their molecular divergence date estimates with appearance dates of presumed relatives of Lissamphibia in the fossil record in order to determine which hypothesis about lissamphibian origins best fits the molecular estimates. They found that their molecular estimate for the origin of Lissamphibia had the most overlap with what they thought to be the age of the first dissorophoid temnospondyls, and therefore considered the hypothesis that lissamphibians are temnospondyls to be the one best supported by this line of evidence. However, several errors in the paleontological data used by Zhang et al. (2005), and in their interpretation of these data, invalidate this result (Marjanović and Laurin 2007).

The study by Zhang et al. (2005) is but one of several recent attempts made by molecular biologists to date the appearance of lissamphibians (San Mauro et al. 2005; Roelants et al. 2007). All these studies suggest that lissamphibians appeared in the Late Devonian or Early Carboniferous (between about 370 and 335 Ma ago). As pointed out by Lee and Anderson (2006), such an early origin of Lissamphibia would favor a polyphyletic origin for this group, which is in-

compatible with nearly all recently published phylogenies supported by data matrices (Laurin 2002). Conversely, an age of origin of Lissamphibia which clearly postdates the latest possible divergence date for temnospondyls and “lepospondyls” would refute all hypotheses of a polyphyletic origin of Lissamphibia from both of these groups (Marjanović and Laurin 2007). The oldest known lissamphibian dates from the Early Triassic (less than 251 Ma ago), and our time-calibrated supertree of lissamphibians (which includes 223 extinct species), as well as our own molecular dating of the basal divergence of this taxon, suggest a Permian origin (Marjanović and Laurin 2007), less than 300 Ma ago, which in turns implies lissamphibian monophyly. This is not the first time that a major discrepancy is found between the times of origin advocated by molecular phylogeneticists and paleontologists; similar controversies revolve around the timing of the diversification of crown-group birds (Padian and Chiappe 1998; Bleiweiss 1999; Marshall 1999; Chiappe and Dyke 2002; Dyke and van Tuinen 2004; Clarke et al. 2005), placental mammals (Hedges et al. 1996; Kumar and Hedges 1998; Waddell et al. 1999, 2001; van Tuinen and Hadley 2004; Wible et al. 2007), vertebrates (Janvier 1996; Delgado et al. 2001), and other taxa. However, this debate should not be construed as a straightforward disagreement between molecular phylogeneticists and paleontologists because specialists of both fields have sometimes worked together and found that the molecular data were compatible with the relatively recent diversification times indicated by fossil evidence (e.g., Ericson et al. 2006; see also Waddell et al. 2001). Nev-



ertheless, most recent diversification dates of lissamphibians based on molecular data (San Mauro et al. 2005; Zhang et al. 2005; Roelants et al. 2007) are much older than what a literal interpretation of the fossil record suggests, and this suggests that a critical appraisal of the fossil record of lissamphibians would be useful.

Here we calculate confidence intervals on the date of origin of Lissamphibia based on data from the fossil record, using methods proposed by Marshall (1990, 1994, 1997). We propose modifications of these methods required or warranted when the taxon of interest is known from a large number (hundreds) of fossil-bearing horizons and when its diversification presumably impacted significantly on its fossil-recovery potential. Recently Marjanović and Laurin (2007) dated the appearance of this taxon using two methods: a time-calibrated paleontological supertree and molecular dating. The present study takes a third approach which, contrary to the two other methods used by Marjanović and Laurin (2007), does not use phylogenetic information (other than the assignment of a fossil to Lissamphibia) to date the appearance of Lissamphibia. This study was undertaken to determine if all these techniques give consistent results, and to determine which of them is the most precise.

Material and methods

Stratigraphic distribution of fossiliferous localities and analytical methods.—Confidence intervals on the stratigraphic range of taxa can be computed using information about the temporal distribution of the fossil occurrences of a taxon (Marshall 1990, 1994, 1997). Thus, we have compiled a database on the age of 1207 fossiliferous localities that range from the Early Triassic to the Recent. Most of these localities are listed by Sanchíz (1998), but a few more were taken from Estes (1981) and the primary literature (Appendix 1). We then sorted these localities by age. Most of the Mesozoic localities cannot be dated more precisely than the stage level (average duration about 5 Ma); many of the Cenozoic localities (those located in Europe) are dated more precisely using Land Mammal Ages (average duration of about 1.4 Ma). These localities were then assumed to be uniformly distributed throughout the stages or mammal ages to calculate the mean gap size within each stage or biozone. This procedure yields uniform gap sizes within each stage or biozone (Appendix 2, http://app.pan.pl/SOM/app53-Marjanowic_Laurin_SOM.pdf), but considering the large number of time divisions (51) used in our analysis, this should not alter the results substantially. We have assumed that no two localities are exactly of the same age. This assumption may have been occasionally violated, but this effect (probably rare considering the vastness of geological time) is probably more than compensated by our simplifying assumption that each locality has yielded lissamphibian fossils at a single horizon. Thus, the number of localities that we have used is much more likely to underestimate than to overestimate the number of horizons that have yielded

lissamphibian fossils. Consequently, the confidence intervals based on these numbers are likely to be too large, rather than too narrow, and this should minimize the difference between our estimate of the maximum age of Lissamphibia and the deep ages reported by recent molecular studies (San Mauro et al. 2005; Zhang et al. 2005; Roelants et al. 2007). We cannot provide a count of horizons that yielded fossil lissamphibians at each locality because this information is usually not reported (a notable exception is Venczel and Gardner [2005] reporting *Albanerpeton pannonicum* from 25 successive horizons of a single locality). At best, the thickness of sediments that have yielded such fossils is occasionally provided. For instance, fossils of the basal pipimorph frog *Shomronella jordanica* have been found throughout a thickness of 1.5 m (Estes et al. 1978), and the basal pipinomorph frog *Eoxenopoides reuningi* was found over 33 m of sediment (Estes 1977). The amount of time that these layers represent was not reported (and is usually difficult or impossible to determine), but it clearly cannot be very short, at least in the second case.

Unlike many studies that perform molecular divergence date estimates, we used the compilation by Milner (1993) only to check that we had not overlooked relevant data, because Milner (1993) focuses only on first and last occurrences of families, while our study requires data of all relevant fossiliferous localities (not only the oldest and youngest for each taxon). Furthermore, the two other approaches used in our previous study (Marjanović and Laurin 2007) focused on species rather than families or taxa of another particular supraspecific rank because the supraspecific Linnaean categories are entirely artificial and subjective. Comparative studies should focus on evolutionary lineages rather than arbitrary and, in our opinion, meaningless taxonomic levels (Laurin 2005, 2008; Bertrand et al. 2006).

Marshall (1990, 1994, 1997) described a series of methods to infer the confidence interval of the true stratigraphic range of a taxon. These methods are difficult to use in this case because not all their assumptions are met. The first method assumes that “fossil horizons are distributed randomly and that collecting intensity has been uniform over the stratigraphic range” (Marshall 1990:1). The second method offers a partial relaxation of this assumption, but still as-

Table 1. Correlation (as shown by R^2) between gap size and geological age in various subsamples of 1207 localities with lissamphibian fossils.

Cumulative number of localities	End of the interval (in Ma)*	R^2	Probability
1207	0 (Holocene)	0.201	< 0.0001
425	5.33 (Miocene)	0.203	< 0.0001
215	23.03 (Oligocene)	0.203	< 0.0001
78	65.5 (Maastrichtian)	0.212	< 0.0001
43	99.6 (Albian)	0.276	0.0003
20	145.5 (Tithonian)	0.426	0.0018

* End of the time interval represented by the sampling; the interval always starts at the oldest locality (Early Triassic, 251 Ma ago); only the age (stage name and absolute minimum age in Ma) of the youngest locality of each subsample is given.

sumes “no correlation between stratigraphic position and the sizes of gaps between adjacent fossil horizons” (Marshall 1994: 460). When such a correlation is present, this method should only be used as a first-order approximation. Thus, we have tested for such a correlation by performing simple linear regressions between gap size and geological age (Table 1), and by performing a Kolmogorov-Smirnov goodness-of-fit test in Statview® (Caldarola et al. 1998). Because both tests indicated the presence of a correlation between gap size and geological age (see below), neither of these two methods (Marshall 1990, 1994) can provide a reliable confidence interval of the stratigraphic range of Lissamphibia.

The fossil-recovery potential function.—The remaining method (Marshall 1997) requires a recovery potential function; it was suggested that it be based on the exposure surface of fossiliferous rocks or on water depth (for marine organisms whose depth preference is known). The second criterion is obviously inapplicable because many lissamphibians are terrestrial whereas others are aquatic (hence their recovery potential does not vary uniformly with water depth), and there is no convenient way to determine water depth or any comparable parameter in 1207 continental localities. However, Marshall (1997: 169) further indicated that the recovery function should not be based on the empirical distribution of finds (because this would lead to a recovery potential of 0 beyond the known stratigraphic range and thus preclude calculation of a confidence interval). Thus, the data on the evolution of lissamphibian diversity (Fig. 2) cannot be used to determine the recovery potential function.

To determine the exposure surface of fossiliferous rocks, we have digitized the geological world map by Bouysse et al. (2000) which is a flat projection of the globe onto three surfaces: the two poles (in polar views) and the rest of the world (in Mercator projection). Both of these projections cause distortion: in Mercator projection the equatorial areas appear smaller than they should, whereas the high-latitude areas appear too large. The distortion is caused by the 10°-wide longitudinal zones appearing equally wide from 0 to 80° rather than narrower as they should with increasing latitude, and by the height of the 10°-high longitudinal zones being proportional to their latitude rather than constant. To compensate for these distortions, we scaled each band of 5° height to its real area assuming that the Earth is spherical. The polar projections, which covered only 20° (from 70 to 90° in latitude) in the Arctic and 30° in the Antarctic, were considered flat in our calculations; the resulting error must be negligible because the exposure area around the poles is very small. Submarine outcrops were ignored, as they are never prospected for lissamphibian fossils. We used Photoshop® 7 to count the pixels representing the various periods in order to estimate the relative surface covered by sediments of these periods (Table 2).

The geological map by Bouysse et al. (2000) uses a coarse geological scale (i.e., “upper Paleozoic” or “Jurassic and Cretaceous”). To maximize the power of our statistical tests for verifying that the assumptions of Marshall’s (1997)

method were met, we considered it preferable to estimate the area covered by sediments from shorter periods. Thus, we assumed that the amount of sediment deposited during any period was proportional to the duration of the period. This does not require that sedimentation be steady: the assumption is only that sedimentation over long periods of time (at least a few Ma) did not change significantly on a worldwide scale. However, even if this assumption is not met, this is not a serious problem because it only decreases the power of the extra tests that we performed to verify that the assumptions were met; heterogeneities in sedimentation rates would not alter the results of our confidence interval on the stratigraphic range of lissamphibians. For instance, the Paleocene lasted 9.7 Ma and the “Tertiary” lasted 63.7 Ma, so we inferred that the area of Paleocene sediments equaled 0.152 times the area covered by the “Tertiary” ($9.7 \text{ Ma}/63.7 \text{ Ma} = 0.152$). The only exception is for the “Quaternary”: instead of giving the Holocene a minute proportion of the “Quaternary” ($0.0115 \text{ Ma}/1.806 \text{ Ma} = 0.0064$), we arbitrarily assigned it 0.1 of the “Quaternary” record to compensate for the much greater sampling effort that results from the archaeozoological research on historic, protohistoric and late prehistoric sites. This procedure cannot have reduced the power of the test because the Kolmogorov-Smirnov goodness-of-fit test uses the observed maximum difference between predicted and observed values (the observed values being the cumulated number of fossiliferous localities at various periods, starting in the Triassic), and our method does not affect this difference for any of the times for which it can be unambiguously established using the geological map (at the end of the Triassic, at the end of the Cretaceous, and at the end of the Pliocene). The only partial exception is for the end of the Pliocene because part of the Cenozoic sediments is only identified as undifferentiated Cenozoic, so we had to assume that a part of this was from the Pleistocene and Holocene. Thus, our interpolation of the area covered by sediments for shorter periods can only increase the power of the Kolmogorov-Smirnov test; it cannot have adverse effects on any other calculations. This procedure also enables us to better assess the quality of the fit of our recovery potential function using linear regressions.

Preliminary analyses using the Kolmogorov-Smirnov test indicated that the area of exposure of rocks of various ages was a poor predictor of the number of fossiliferous sites yielding lissamphibians ($D_{\max} = 0.38$; $P \leq 0.001$). Results using this function are reported below (CI 6 in Fig. 3 and Tables 3, 4) for comparison purposes, to demonstrate that another

Table 2. Relative area of sedimentary rocks in continental areas.

Period	Relative area
“Quaternary”	0.264
“Tertiary” (including indeterminate Cenozoic)	0.297
Jurassic and Cretaceous	0.264
Triassic	0.034
Upper Paleozoic (Carboniferous and Permian)	0.141

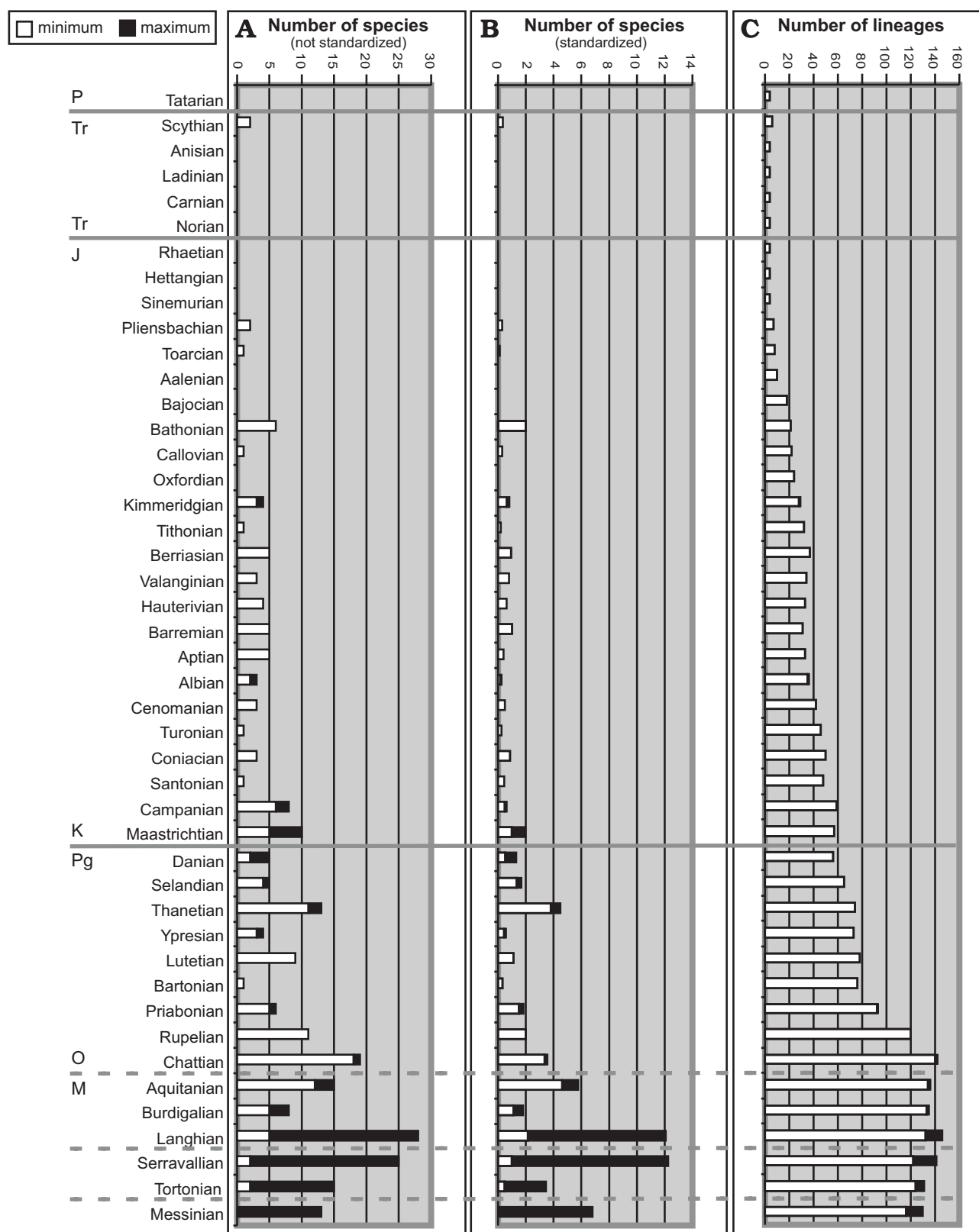


Fig. 2. Lissamphibian biodiversity through time. **A.** Number of species found in each geologic stage. **B.** Standardized species numbers, calculated to account for uneven stage durations. **C.** Number of lineages, obtained by adding the number of recorded species and the number of ghost lineages for each geologic stage. Major biological crises identified in other taxa are shown as continuous gray lines. Minor crises that may have affected lissamphibians are shown as dashed gray lines. Since most post-Miocene species are excluded, this figure ends with the terminal Miocene. Minimum (white) and maximum (black) values have been calculated under various assumptions about the age of several middle Miocene species and the status of specimens with questionable affinities. The geologic timescale follows Gradstein et al. (2004) in all figures. Abbreviations: J, Jurassic; K, Cretaceous; M, Miocene; O, Oligocene; P, Permian; Pg, Paleogene; Tr, Triassic.

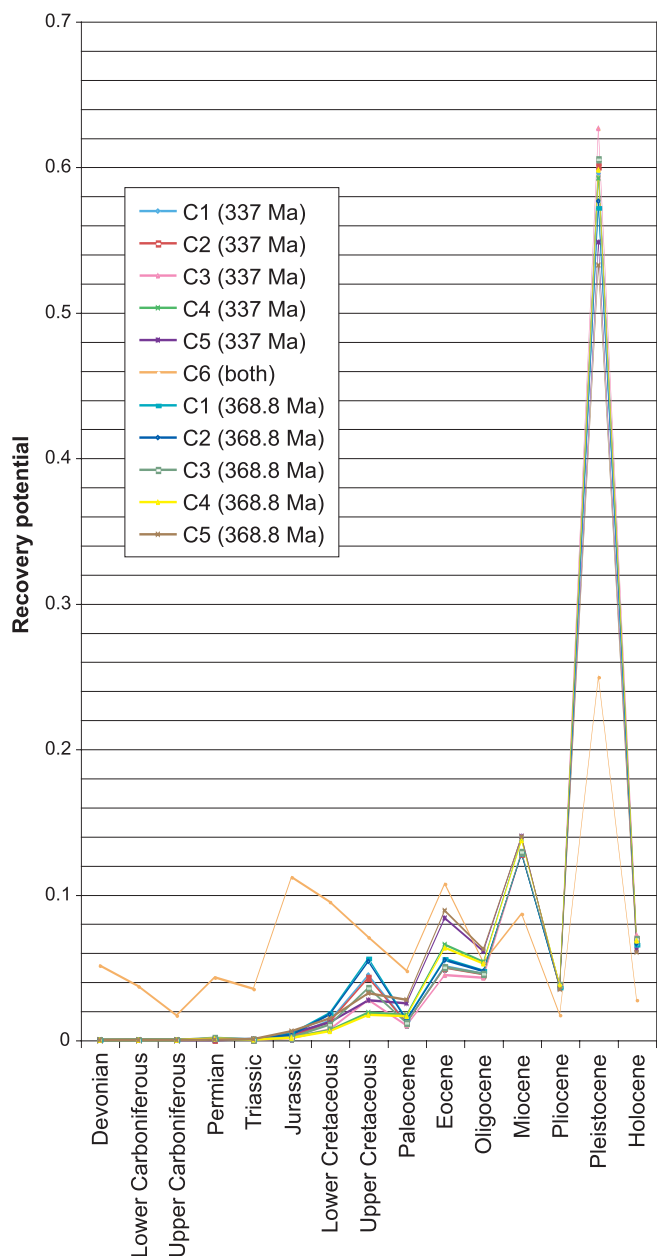


Fig. 3. A histogram of the curves (C) representing the recovery potential functions showing each period's or epoch's fraction of the total recovery potential calculated under eleven different assumptions (Table 4: CI 1–CI 6, which assume six different rates across extinction events and two different ages of origin for each except CI 6 which is independent of the age of origin). A bar chart of these data would be more appropriate than a dot-and-line graph, but much more difficult to read. The total recovery potential under each assumption (i.e., the area under each “curve”) is 1. Note the wide divergence between CI 6, which is based only on the exposure area of sedimentary rocks (Table 1), and all others, which include an exponential model of diversification. The much lower recovery potential of CI 1–CI 5 in the Paleozoic generates correspondingly wider CIs.

approach was required. Thus, we developed a second approach which we combined with the first. This second approach models the increasing lissamphibian diversity through time. During lissamphibian diversification, the number of species present in this clade increased from one to sev-

eral thousand, and this diversification must have been accompanied by a great expansion of the geographic range and the diversity of habitats used by lissamphibians. All these changes must have had major effects on the fossil recovery potential of this group. Several plausible models could be used, including a simple exponential function to model the evolution of biodiversity of lissamphibians through time:

$$B = 2^{t/d} \quad (1)$$

where B is the biodiversity (number of species) at a given time, t is the time (Ma), and d is the time necessary for doubling the number of lineages.

To simplify, we will call the ratio t/d “ g ” (for generations). Thus, the equation becomes:

$$B = 2^g \quad (2)$$

This approach is consistent with Benton's (2001: 227) recent argument that an exponential pattern describes the evolution of terrestrial vertebrate biodiversity since their origin well, but it may greatly overestimate the rate of lissamphibian diversification (see below). Therefore it is significant that equation (2) cannot be adjusted using the lissamphibian fossil record because the quality of the latter is precisely what we are trying to assess. However, the exponential function can be adjusted by inserting today's biodiversity (6157 species; Anonymous 2007) and that of the time at which the diversification started. That time is not known (and it is precisely what we want to infer), but the null hypothesis that we wish to test is the hypothesis suggested by recent molecular studies (San Mauro et al. 2005; Zhang et al. 2005; Roelants et al. 2007) that Lissamphibia started diversifying in the Late Devonian to Early Carboniferous, between 368.8 and 337 Ma ago. The oldest (Table 4, rows 5–8) and most recent (Table 4, rows 1–4) times proposed in these studies were used as the beginning of lissamphibian diversification. The fossil recovery potential (R) between the clade origin (368.8 or 337 Ma ago) and any given time can be obtained by integrating function (2), which gives:

$$R = 2^g / (\ln 2) + C \quad (3)$$

where \ln designates the natural logarithm, and C is a constant common to all indefinite integrals. To obtain the recovery potential between two arbitrary points in time (e.g., the beginning and end of a geological stage), the definite integral of the intervening period must be calculated by simple subtraction. Note that what we call “clade origin” here (368.8 or 337 Ma ago) is the time at which the first cladogenesis occurred within Lissamphibia (this is what molecular studies can date). Thus, our method can yield confidence intervals up to a full generation (g) older. The value of g varies depending on the assumed extinction rates in biological crises, but it is on the order of 20–25 Ma. Thus, our method cannot yield upper bounds older than about 390 or 370 Ma, depending on which of the two ages of clade origin (368.8 or 337 Ma) is used.

The recovery potential values obtained from the exponential growth model can also be divided by the duration of a given geological period as a proxy of average standing

Table 3. Correlation (as shown by R^2) and discrepancy (D) between the predicted number of fossiliferous lissamphibian localities according to various models and the recorded number of localities. CI 1–CI 6 are confidence intervals as distinguished (in the row below) by the extinction percentages at the K/Pg (Cretaceous/Paleogene), P/Tr (Permian/Triassic), and Tr/J (Triassic/Jurassic) boundaries; in parentheses follows the time (in Ma) necessary for doubling the number of species. All numbers were calculated using 337 Ma as the beginning of lissamphibian diversification; using 368.8 Ma instead yields very similar results (not shown).

Period/ epoch	Predicted number of localities						Recorded number of localities
	CI 1	CI 2	CI 3	CI 4	CI 5	CI 6	
	P/Tr 0.9; Tr/J 0.5; K/Pg 0.8 (18.53)	P/Tr 0.9; Tr/J 0.6; K/Pg 0.8 (18.21)	P/Tr 0.95; Tr/J 0.8; K/Pg 0.76 (16.65)	P/Tr 0.8; Tr/J 0.5; K/Pg 0.2 (25.20)	Exponential growth (no extinctions) (29.08)	Surface of exposures only	
Holocene	82.70	83.36	87.29	81.73	75.11	37.07	220
Pleistocene	719.62	724.96	756.78	715.19	661.66	333.67	466
Pliocene	45.16	45.42	46.96	45.62	43.05	23.12	96
Miocene	154.96	154.84	154.72	166.24	168.98	116.07	210
Oligocene	55.08	54.49	51.62	64.75	73.50	71.29	66
Eocene	61.30	60.04	53.87	79.23	101.07	143.63	56
Paleocene	14.68	14.22	12.00	21.06	30.44	63.62	15
Late Cretaceous	54.04	51.53	33.46	22.63	33.81	94.44	35
Early Cretaceous	16.15	15.07	8.70	8.20	14.58	127.12	23
Jurassic	3.05	2.76	1.34	2.08	5.32	149.83	18
Triassic	0.26	0.29	0.23	0.25	0.47	47.15	2
R^2 (log-transformed)	0.892	0.894	0.898	0.882	0.865	0.058	
P (log-transformed)	0.0001	0.0001	0.0001	0.0001	0.0001	0.4746	
D	0.1138	0.1133	0.1304	0.1146	0.1201	0.3994	
$P(D)^*$	5.17 E-14	7.00 E-14	3.06 E-18	3.36 E-14	1.48 E-15	1.18 E-167	

* Computed using equation (5) (see text).

Table 4. Lower (oldest) bounds (Ma ago) of the confidence intervals (CI) for the fossil record-based assessments of the stratigraphic range of Lissamphibia according to various models. CI 1–CI 6 are confidence intervals as distinguished (in the row below) by the extinction percentages at the K/Pg (Cretaceous/Paleogene), P/Tr (Permian/Triassic), and Tr/J (Triassic/Jurassic) boundaries (see also text).

Molecular divergence date estimate (Ma ago)	Confidence level	CI 1	CI 2	CI 3	CI 4	CI 5	CI 6*
		P/Tr 0.9; Tr/J 0.5; K/Pg 0.8	P/Tr 0.9; Tr/J 0.6; K/Pg 0.8	P/Tr 0.95; Tr/J 0.8; K/Pg 0.76	P/Tr 0.8; Tr/J 0.5; K/Pg 0.2	No extinction event	No model of diversity
337 (Zhang et al. 2005)	50%	260 (Capitanian– Wujiapingian boundary)	260 (Capitanian– Wujiapingian boundary)	257 (Wujiapingian)	270 (Roadian)	319 (Serpukhovian)	251 (uppermost Changxingian)
	75%	277 (Artinskian)	274 (Kungurian)	264 (Capitanian)	324 (Serpukhovian)	–	251 (uppermost Changxingian)
	80%	285 (Sakmarian)	281 (Artinskian)	267 (Wordian)	–	–	251 (uppermost Changxingian)
	95%	–	–	304 (Kasimovian– Gzhelian boundary)	–	–	251 (uppermost Changxingian)
368.8 (Roelants et al. 2007)	50%	255 (Wujiapingian)	255 (Wujiapingian)	253 (Changxingian)	260 (Wujiapingian)	280 (Artinskian)	251 (uppermost Changxingian)
	75%	261 (Capitanian)	260 (Capitanian– Wujiapingian boundary)	256 (Wujiapingian)	272 (Kungurian)	378 (Frasnian)	251 (uppermost Changxingian)
	80%	263 (Capitanian)	261 (Capitanian)	257 (Wujiapingian)	277 (Artinskian)	–	251 (uppermost Changxingian)
	95%	279 (Artinskian)	275 (Artinskian–Kungurian boundary)	263 (Capitanian)	381 (Frasnian)	–	251 (uppermost Changxingian)

* CI 6 is based only on the surface of exposed rocks, hence its size is independent of the assumed age of the basal node of Lissamphibia.

lissamphibian biodiversity. This approach seems more appropriate than directly using the fossil recovery potential calculated for a period based on the exponential diversification model because the latter would result in a high potential if a period were very long. In fact, the length of the period is irrelevant; what matters is the abundance of lissamphibians in the former biological communities, and the area of exposed fossiliferous rocks. Whether these rocks represent e.g., 1 Ma or 10 Ma should have no impact on the recovery potential.

The estimated average biodiversity in each period can be multiplied by the area of exposures of rocks of various periods on the continents to yield the recovery potential curve; this is the method that was adopted here (Table 3). With this model, we should be able to determine if the fossil record of lissamphibians is consistent with our starting assumption of lissamphibian origins, i.e., the timings suggested by Zhang et al. (2005) and Roelants et al. (2007), and diversification. We have found that our recovery potential function is adequate using a Kolmogorov-Smirnov test of goodness of fit for continuous distributions. The exact probability for the values of D at our high sample size ($n = 1207$) is not reported in Zar (1984), but it can be computed by isolating α (the probability threshold) in the formula used when n is large:

$$D_{\alpha n} = ([-\ln(\alpha/2)]/2n)^{1/2} \quad (4)$$

From this equation α can be extracted:

$$\alpha = 2e^{-2nD^2} \quad (5)$$

In this case, what is computed is a probability ($\alpha = p$).

We have also tested the correlation between the observed number of localities and the predicted number of localities using our recovery potential functions using a simple linear regression in Statview® (Caldarola et al. 1998) and using a regression with 9999 permutations in Permuto! (Casgrain 2005). We tested normality using Progciciel R (Casgrain et al. 2004). Since the distribution of the localities in the various periods was lognormal rather than normal, the values were log-transformed (Table 3).

Lissamphibians in mass extinction events.—The simple exponential diversification model is probably unrealistic because most taxa that originated in the Paleozoic have suffered mass extinction at least a few times in their history (Nitecki 1984; Hallam and Wignall 1997). The simple exponential function predicts that the number of lissamphibian species will double in the next 15 to 25 Ma, but this seems unlikely because many of these species are currently becoming extinct through habitat loss and introduced diseases in combination with climate change and other causes (Pounds et al. 2006). The models that seem most appropriate include three major crises: the Permian–Triassic boundary (P/Tr), the Triassic–Jurassic boundary (Tr/J), and the Cretaceous–Paleogene boundary (K/Pg) mass extinction events. We have used plausible ratios of species extinction (Tables 3–4: CI 1–CI 3), although they are poorly constrained because nearly nothing is known about how these extinctions affected lissamphibians, with the partial exception of the K/Pg crisis

(Cretaceous/Paleogene, often called K/T for Cretaceous/Tertiary in older literature) which may not have affected lissamphibians as strongly as many other terrestrial vertebrate taxa (Archibald and Bryant 1990; Sheehan and Fastovsky 1992). The end-Permian event is generally considered the most severe (Erwin 1993; Benton 2003), and in one of our analyses we consider that it probably eliminated 90% of the lissamphibian species of that time. A similar percentage of extinction has been calculated for marine metazoans by Hallam and Wignall (1997: table 1.1). Lower extinction levels have been assumed for the end-Triassic and end-Cretaceous events, as suggested by various studies, most of which focused on marine metazoans (Nitecki 1984; Erwin 1993: table 1; Hallam and Wignall 1997: table 1.1). It might be objected that the extinction levels of lissamphibians may not have been comparable to those of marine metazoans; therefore we also assess the implications of lower extinction levels in lissamphibians (Tables 3, 4: CI 4–CI 5).

The K/Pg and Eocene/Oligocene mass extinction events apparently eliminated species of medium to large body size in foraminifera (Norris 1991), and the P/Tr crisis had a similar effect on gastropods (Payne 2005). Thus, given the small size of lissamphibians relative to other tetrapods, it might be suggested that they must have suffered comparatively low extinction levels (for tetrapods) during biological crises. This is congruent with the results presented by Fara (2000), who found that all lissamphibian families survived the K/Pg event. However, vertebrates may be an exception to this rule: an analysis of body size evolution using 93 species of stegocephalians that date from the latest Middle Permian to the Early Triassic has failed to find a statistically significant size decrease across the P/Tr boundary (Laville 2007). (Throughout this paper, Stegocephali refers to the clade composed of the first animal with digits homologous to those of *Homo sapiens* and all descendants of that ancestor; see Laurin, 1998.)

Since the extinction levels are poorly constrained and influence the inferred limits of the confidence intervals on the time of origin of Lissamphibia, four combinations of values were used. We consider the first two the most plausible, while the third one uses values reported by Hallam and Wignall (1997: table 1.1). The fourth set of values assumes that lissamphibians were much less affected by the great biological crises than most other taxa. To calculate the value of the recovery potential, this potential has to be calculated separately in each time interval bounded by two successive mass extinctions. A fifth set of values assumes that lissamphibians were unaffected by biological crises. These five extinction level settings were used to compute confidence intervals under the assumption that the basal split in Lissamphibia occurred 337 or 368.8 Ma ago. The combination of all these settings yields ten models (Tables 3, 4: CI 1–5; Fig. 3). An eleventh model (Tables 3, 4: CI 6; Fig. 3), based only on the surface of exposures, is provided only to illustrate the need for a model of lissamphibian diversification.

Little is known about the evolution of lissamphibian biodiversity through time, but, as mentioned above, our recov-

ery potential function requires information about lissamphibian biodiversity evolution. Therefore, our study would benefit from any improvement in our understanding of lissamphibian biodiversity through time. Thus, we have used the new StratAdd module (Faure et al. 2006) for Mesquite (Maddison and Maddison 2005) to compile three indices of lissamphibian biodiversity through time in order to assess the fate of Lissamphibia around the K/Pg boundary (Fig. 2) using the supertree by Marjanović and Laurin (2007). These indices are: (i) a simple count of observed species in each stage; (ii) a standardized count of observed species in each stage (obtained by dividing the first index by the stage duration in Ma); (iii) a count of all observed species plus all inferred ghost lineages in each stage. The last index incorporates phylogenetic information and is based on our supertree, incorporating the corresponding minimum branch length assumptions (each species occupies at least a whole geological stage, and the minimum internal branch length is 3 Ma). Thus, ghost ranges are longer here than in other studies because they have usually been computed under the assumption that internal branches can have zero length (Wills 1999). Ghost ranges are potentially important in species-level studies on biological crises (as opposed to studies using more inclusive taxa) because species have a relatively short duration (at least among vertebrates), on the order of a single geological stage. Therefore, studies neglecting ghost ranges would be very sensitive to taphonomic artefacts such as the fluctuating quality of the fossil record; in a worst-case scenario, a group with a good fossil record in one stage and no fossil record in the next would appear to have undergone complete extinction. However, if many of the species present in the first (oldest) stage had descendants in later stages and if the phylogeny were reasonably well known, methods that take ghost lineages into consideration would infer much lower extinction rates. Simulations are required to more precisely assess the merits of various approaches to study mass extinctions, but they are beyond the scope of this paper. Most previous studies on extinction patterns in early vertebrates did not incorporate ghost range estimates (Erwin 1993; Hallam and Wignall 1997). Our first two indices do not use any phylogenetic information, but still differ from most previous studies in this field by being done at the species (rather than genus, family or order) level (see Ward et al. 2006 for a partial exception).

Early studies on the evolution of biodiversity did not standardize for stage duration “because of considerable uncertainty in the durations of stages” (Raup and Sepkoski 1984: 801). Over the last twenty years, this uncertainty has greatly diminished for the Cenozoic, so we have calculated these durations from the ages given by Gradstein et al. (2004). In the Mesozoic there are still stages whose beginning and end is associated with uncertainty on the scale of the duration of the stage itself (e.g., the Kimmeridgian, whose duration we consider to be 4.9 Ma, while both its beginning and its end have confidence intervals of ± 4.0 Ma; Gradstein et al. 2004), but we do not try to test for mass extinctions within the Mesozoic. Recent studies have generally standardized for time in

various ways (e.g., Alroy 1999, 2000; Ward et al. 2006); our second biodiversity index is also time-standardized.

We did not calculate either background or total extinction rates because the lifetime of most species is highly uncertain; in most cases, species are known from a single stage, but the actual duration of their lineages (including ghost ranges) may be far greater. Thus, it is very difficult to measure extinction rates; but the minimum biodiversity at any given time can be measured more objectively. Our analysis might indicate whether or not it is appropriate to include extinction events in the model of lissamphibian biodiversity, although, given the paucity of Triassic and Jurassic lissamphibian fossils, only the K/Pg boundary event and less important crises that occurred in the Cenozoic can be studied in this taxon.

Uncertainties about the assignment of fossils to geological stages of the Miocene complicated the analysis because many lissamphibian fossils are only dated to middle Miocene in the literature, whereas our scale divides this interval into Langhian and Serravallian. Therefore, we computed all biodiversity indices using two versions of our supertree, one in which all species of uncertain age were put in the Langhian and another in which these species were placed in the Serravallian. There are also several records of fossils whose taxonomic assignment is questionable and that could represent distinct species or (often) the oldest records of their respective species. Again, we calculated the three biodiversity indices while either considering these specimens of questionable affinities to be distinct species, or excluding them. The latter approach would be justified if these specimens were ancestral to at least some of the other species in our tree, if they belonged to known species not included in our tree, or if they were—as argued by Bever (2005) for many fossils attributed to *Bufo* sensu lato (i.e., not sensu Frost et al. 2006)—based on non-diagnostic material. We then computed the maximum and minimum biodiversity according to the three indices and two versions of the supertree (differing in stage assignment of middle Miocene lissamphibians), and these are the values reported in the Results section.

Results

Evolution of biodiversity in Lissamphibia.—The raw (unstandardized) observed number of species per epoch varies widely and, to a large extent, randomly (Fig. 2A). This index obviously reflects mostly taphonomic artefact and is nearly useless to assess the fate of lissamphibians across the K/Pg boundary. However, this graph shows the stratigraphic distribution of the lissamphibian species that are included in the supertree (which includes most known extinct lissamphibian species, except for those dating from the Pliocene or Pleistocene), and, as such, nicely summarizes this aspect of our data.

The standardized observed number of species (Fig. 2B) also varies widely, but perhaps a little less than the raw number of species (Fig. 2A). The differences between both indices are enlightening. For instance, the raw number of species sug-

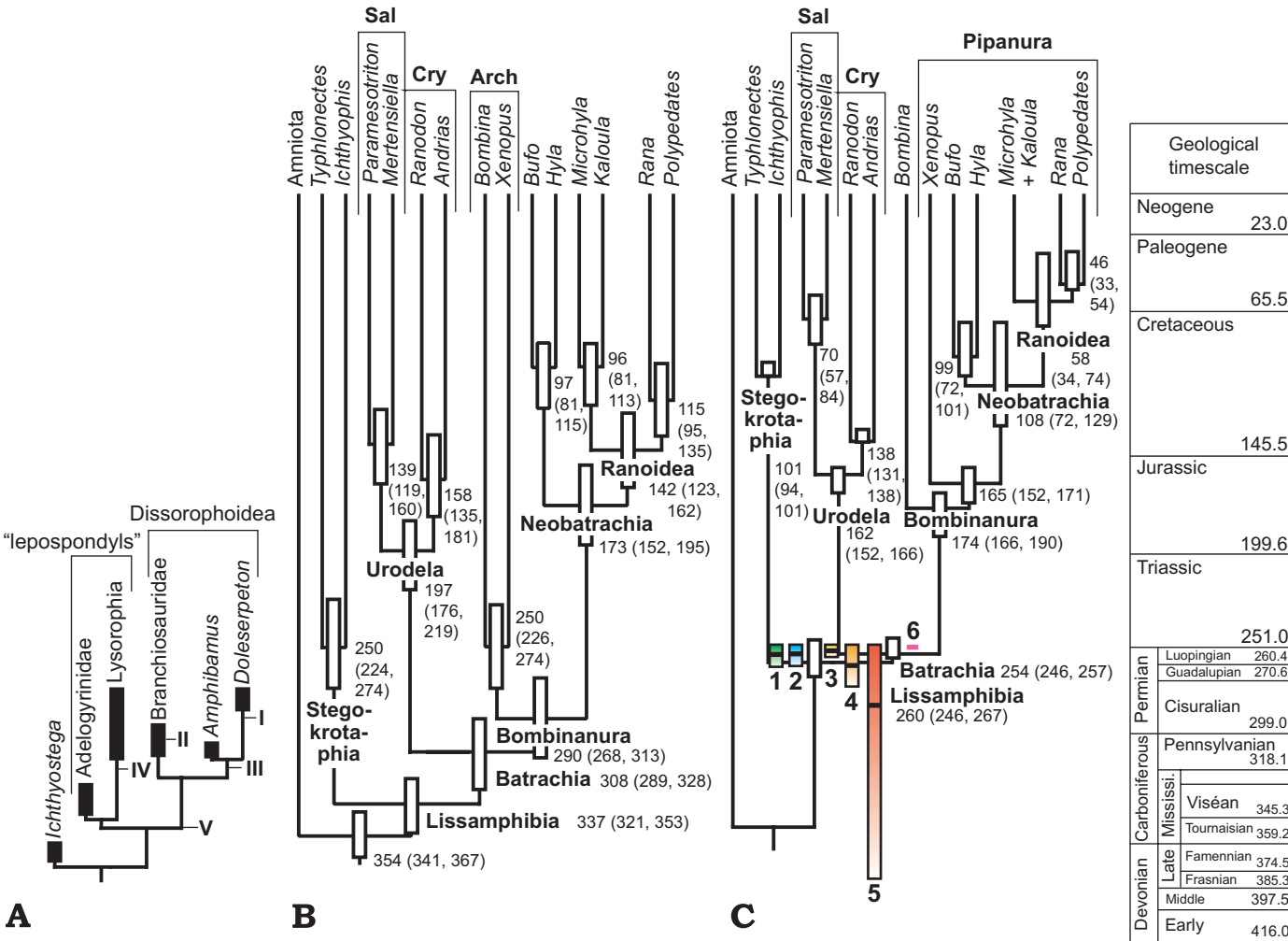


Fig. 4. A comparison of the origination (A–C) and diversification (B, C) times of Lissamphibia according to time-calibrated phylogenetic trees of (A) Stegocephali, (B) Lissamphibia based on the molecular analysis by Zhang et al. (2005), and (C) Lissamphibia based on the fossil record (Marjanović and Laurin 2007). In A, the stem of Lissamphibia is placed as high in the geological section as plausible under the various phylogenetic hypotheses: (I) as the sister-group of *Doleseperpeton*; (II) within Branchiosauridae; (III) as the sister-group of the *Doleseperpeton* + *Amphibamus* clade; (IV) as the sister-group of Lysorophiidae; (V) polyphyletic from within “lepospondyls” (caecilians, or caecilians and caudates) and “temnospondyls”. Known stratigraphic ranges are shown as thick lines, ghost ranges as thin lines. In B, the 95% credibility intervals of molecular dates are represented by blank boxes; the best estimates and lower and upper boundaries of the credibility intervals are also indicated in parentheses. In C, the numbers given next to the nodes represent the age estimates (Ma) based on the assumptions used for the supertree by Marjanović and Laurin (2007: fig. 9b). In parentheses follow the ranges of minimum (rather than actual) divergence dates as obtained using various minimum branch length assumptions (Marjanović and Laurin 2007: appendix 4); these ranges, also represented as blank boxes, are not true confidence intervals. The colored boxes represent the confidence intervals on the lower bound of the stratigraphic range of Lissamphibia calculated in the present paper (1–6 correspond to the lower half of Table 4: CI 1–CI 6), where the bottom of the rectangle shows the lower limit of the 75% confidence interval and the black bar in each colored box corresponds to the lower limit of the 50% confidence interval. Abbreviations: Arch, Archaeobatrachia; Cry, Cryptobranchoidea; Mississi., Mississippian; Sal, Salamandridae.

gests a 50% diversity drop at the K/Pg boundary, but the standardized values suggest a more moderate reduction. Similarly, the raw values suggest moderate drops in lissamphibian diversity in three Cenozoic time intervals (Chattian/Aquitainian, Langhian/Serravallian, and Tortonian/Messinian), but the standardized values show moderate increases in diversity, which suggests that these variations in raw values mostly represent taphonomic artefacts. However, even the standardized observed numbers of species are probably affected by taphonomic factors, as shown by comparisons with the observed number of lineages (see below).

The count of lineages appears to be much less affected by taphonomic artefacts, judging by the smooth shape of the diversity curve (Fig. 2C). However, the signal in this index is probably overwhelmed to a large extent by the numerous ghost ranges that lead to extant species. This is illustrated by the number of observed species (5 to 10) and high number of lineages (57) in the Maastrichtian; there are about 50 ghost lineages in that stage, and most of them lead to extant species. Thus, this index should have a low power to detect extinction events. Nevertheless, four drops in diversity are visible. The first occurs between the Campanian (59 lineages) and the

Danian (56 lineages). The second drop (from about 140 to about 135 lineages) is across the Chattian/Aquitania (Oligocene/Miocene) boundary that is not considered a time of major biological crisis (Hallam and Wignall 1997), although many species of corals became extinct at that time (Edinger and Risk 1995). Another slight reduction in number of lineages (from about 140 to about 130) is across the Langhian/Serravallian boundary, in the middle Miocene. An extinction event at that time was recognized by Raup and Sepkoski (1984). The fourth slight drop (from about 127 to about 123 lineages), between the Tortonian and the Messinian (late Miocene), may result partly from our deliberate omission of the Pliocene and Quaternary (sub)fossils, but it may also reflect a genuine reduction in lissamphibian biodiversity because an extinction event in North American mammals has long been recognized at that time (Webb and Barnoski 1989). The three possible Tertiary crises identified on the basis of the number of lineages, and the K/Pg event, also appear as times of elevated extinction level according to the first index, i.e., the raw number of observed species (Fig. 2A).

Comparison of the three indices suggests that there was a slight reduction in lissamphibian diversity across the K/Pg boundary, but the other reductions we detected in the Cenozoic could be artefacts.

Confidence interval of the stratigraphic range of Lissamphibia.—The confidence interval of the stratigraphic range of Lissamphibia had to be computed using a method that can cope with nonrandom distribution of fossil horizons (Marshall 1997) because the correlation between gap size and geological age in our data is highly significant, as shown by simple linear regressions (Table 1). A Kolmogorov-Smirnov goodness-of-fit test on the 78 Mesozoic localities also indicates a strong deviation from an even temporal distribution of localities ($p < 0.001$). A method that assumes there is no such correlation (Marshall 1994) suggests that there is a 99% probability that the 80% confidence interval of the stratigraphic range of Lissamphibia extends no more than 425,000 years beyond the first appearance of fossils, i.e., beyond the beginning of the Triassic (into the very latest Permian). In this method, the limits of confidence intervals have confidence probabilities.

More plausible results were obtained by the fossil recovery potential curve using the method advocated by Marshall (1997). The fossil recovery potential functions based on an exponential diversification model and on the area of exposed rock (Table 3) show moderate discrepancies between predicted and observed number of localities ($D_{\max} = 0.11$ or 0.12). These deviations are highly significant ($P < 0.001$), but this largely reflects the high number of localities (1207) used to compute this statistic. Marshall's (1997) method seems to have been designed for cases where far fewer localities are known, and accordingly, his test maximizes the power to find deviations between the predicted and the observed number of localities; with several hundred localities, obtaining a recovery potential function without significant deviations from the

observed number of localities and obtained independently from the distribution of localities seems extremely unlikely. Our linear regression using *Permute!* (Casgrain 2005) shows that most of our recovery potential functions explain at least 85% of the observed variance in the observed number of localities; the associated probability for this being a random pattern is less than 0.0001 (Table 3). Thus, we conclude that the recovery potential functions are adequate, and we report the results of these calculations, with the caveat that one of the recommendations by Marshall (1997) cannot be followed exactly as he suggested.

The functions that assume that lissamphibians were affected by biological crises to about the same extent as most metazoans (Table 4: CI 1–CI 3; Fig. 4) yield a 50% confidence limit of lissamphibian origins extending down to the Late Permian (Wujiapingian or Changxingian; 253 to 260 Ma ago, depending on model and molecular estimate adopted). The 75% confidence limit still also implies much younger dates of lissamphibian origin than suggested by most recent molecular studies (San Mauro et al. 2005; Zhang et al. 2005; Roelants et al. 2007), with an earliest possible time of appearance between 256 and 277 Ma ago (Wujiapingian to Artinskian). Three other functions, including one that does not predict the number of localities well (Table 3: CI 6), have highly variable lower bounds to their confidence intervals and give highly variable results (Table 4: CI 4–CI 6; Fig. 4). Assuming that the great biological crises had minor or no effects on lissamphibians (CI 4–CI 5) gives a 50% confidence limit ranging from the Wujiapingian (260 Ma ago) to the Serpukhovian (319 Ma ago; late Mississippian). The 75% confidence limit under the same assumptions (CI 4–CI 5) ranges from 272 Ma ago (Kungurian) to 378 Ma ago (Frasnian, Upper Devonian). Since digits may not have appeared before the Famennian (Laurin et al. 2000) and the earliest known crown-tetrapods date from the Viséan (Laurin 2004), and because the fossil record of the Upper Devonian is quite good (Janvier 1996), an origin of lissamphibians in the Frasnian is highly unlikely. The model incorporating only the exposure area of sediments has a poor fit (Table 3: CI 6) and gives a ridiculously recent confidence interval (terminal Changxingian). This result is provided only to illustrate the need to have an adequate recovery potential function.

Discussion

Evolution of biodiversity and the fate of Lissamphibia across mass extinction events.—We have found large differences in the reconstructed pattern of lissamphibian biodiversity shown by raw and standardized observed number of species. Earlier studies of biodiversity through time (e.g., Smith 1994 and references therein) did not standardize for stage duration; the need for standardization was recognized by Alroy (1998, 1999, 2000) and Alroy et al. (2001), who used absolute ages instead of stage assignments and also standardized for sampling intensity (Alroy 1999, 2000; Alroy et al. 2001). Unfortunately, we know too little about the sam-

pling of the lissamphibian fossil record in collections and in the literature to standardize for this.

Incorporation of extinction events into the models is supported to an extent by the literature and by our new analyses. Among taxa that have been interpreted as stem-amphibians (= stem-lissamphibians), the temnospondyls suffered a great reduction in biodiversity towards the end of the Permian, although their record is not good enough to determine if this was a slow decline or a result of the end-Permian crisis (Milner 1990, 1991). The “lepospondyls” also declined steadily in diversity in the Permian, but in their case, complete extinction (except for the lineage which probably led to the lissamphibians) seems to have occurred well before the end of the Permian (contra Zhang et al. 2005: figs. 2, 3) because only a few species persist into the Middle to Late Permian (Carroll 2000). Less is known about how lissamphibians fared in times of biological crises. Aquatic vertebrates, especially those living in freshwater, may have been little affected by the K/Pg boundary event (Clemens 1982; Fara 2000); however, this conclusion is based mostly on turtles and crocodilians, which have a much better fossil record.

Our data suggest that lissamphibian biodiversity dropped (but only moderately) at least twice (biological crises before the K/Pg boundary cannot be studied because critical data are lacking): between the Maastrichtian (or possibly the Campanian) and the Danian, and across the Oligocene/Miocene boundary (Fig. 2). Thus, lissamphibians may have been moderately affected by the K/Pg event, and a literal reading of lineages (Fig. 2C) suggests a gradual decline rather than a catastrophic extinction event, although the two other indices suggest a more rapid reduction in diversity consistent with a catastrophic K/Pg event (Fig. 2A, B). The apparently gradual decline in lissamphibian diversity suggested by the lineage count in that interval (Fig. 2C) may also be due to the Signor-Lipps effect (Signor and Lipps 1982), reflecting the relatively scanty fossil record of lissamphibians in the Mesozoic. This interpretation is consistent with the stratigraphic range extension of *Albanerpeton galaktion* from the Campanian to the Maastrichtian (Gardner 2000).

These results give moderate support to our incorporation of major biological crises into the recovery potential function because our data suggest that lissamphibian diversity did not undergo unchecked exponential diversification through time; some periods seem to show at least moderate decline. Our study did not focus on biological crises and we do not want to emphasize our results on how extinction events affected lissamphibians because our database was not primarily compiled for this purpose. We have found limited evidence that, contrary to previous suggestions (Clemens 1982; Archibald and Bryant 1990; Fara 2000), lissamphibians were affected by biological crises, at least by the K/Pg boundary event; however, the effect of this crisis appears to have been modest in this clade, at least by comparison with dinosaurs.

The difference between our results and those of Fara (2000) reflect the taxonomic level at which the studies were performed. Fara (2000) found that all lissamphibian families

survived the K/Pg boundary, and we too have found the extinction of only one clade that is sometimes considered a family (Noterpetontidae, not documented in Fara's source: Milner 1993). However, at the species level, the extinction event was more noticeable, with five or six species becoming extinct at or near that boundary. Archibald and Bryant (1990) found few extinctions in lissamphibian species from north-eastern Montana at the K/Pg boundary, but a new species from the Maastrichtian of Bolivia (*Noterpeton bolivianum*) was subsequently described (Rage et al. 1993), and the stratigraphic range of *Albanerpeton galaktion* extended (Gardner 2000).

Comparisons with molecular dating of the origin of Lissamphibia.

—Those recovery potential functions that best predict the observed number of localities and assume plausible extinction levels of lissamphibians in biological crises (Table 4, CI 1–CI 4) yield moderately different lower (older) limits on the stratigraphic range of Lissamphibia (Fig. 4), most of which are significantly younger than the results of Zhang et al. (2005). None of the 80% confidence intervals are compatible with the Late Devonian age of Lissamphibia which was the point estimate by San Mauro et al. (2005) and Roelants et al. (2007), or even with the Mississippian age calculated by Zhang et al. (2005). However, the credibility intervals on these molecular dates span the interval from 417 to 328 Ma ago, thus including the entire Devonian and most of the Mississippian (San Mauro et al. 2005). They are even wider if the penalized-likelihood dating by Roelants et al. (2007: online supplementary dataset) is considered; in that analysis, the age of Lissamphibia is estimated at 352 Ma, with a credibility interval which ranges from 370 to 304 Ma ago (a timespan that includes most of the Carboniferous as well as the end of the Devonian). Still, of all confidence intervals, only the 95% confidence interval of CI 4 overlaps these molecular dates (entirely so in the case of Zhang et al. 2005).

All these ancient molecular dates of lissamphibian diversification, which are difficult to reconcile with the fossil record, can be explained by the choice of calibration dates. Zhang et al. (2005) used only two external, ancient calibration points, namely the divergence between dipnomorphs and tetrapodomorphs and the origin of Amniota, which they placed at 400 Ma ago and 300–320 Ma ago, respectively (see Marjanović and Laurin [2007] for a discussion of these dates). Roelants et al. (2007) used 24 calibration dates, including 22 within Lissamphibia, but only two, the origins of crown Tetrapoda (sensu Laurin and Anderson 2004) and Amniota, had estimated upper bounds. All other calibration points, i.e., all those within Lissamphibia, had only minimum (lower) bounds. Such a choice of calibration dates has been found to yield unrealistically ancient dates (Brochu 2004a, b, 2006; Marjanović and Laurin 2007). Furthermore, the upper bound used for Tetrapoda (385 Ma ago) is probably too old; this is the beginning of the Late Devonian (385–359 Ma ago), from which several stem-tetrapods, but no tetrapods, are known (Laurin et al. 2000). A few more stem-tetrapods,

some of them closer to the crown-group than all known Devonian ones, have also been found in Tournaisian strata (359–345 Ma old), where tetrapods are so far still unknown, and this suggests that 360 Ma is a more appropriate upper bound for Tetrapoda (Marjanović and Laurin 2007). San Mauro et al. (2005) used Amniota (set at 338–288 Ma ago), Batrachia (at least 230 Ma ago), Cryptobranchioidea (at least 161 Ma ago, but see Wang et al. [2005]), Anura (at least 140 Ma ago), and several more; however, only a single external (Amniota) and a single internal calibration date (the divergence between *Mantidactylus wittei* and *Mantidactylus* sp. from the Comoro islands, not more than 15 Ma ago) had an upper bound. All these factors probably explain the very ancient dates obtained by Zhang et al. (2005) and Roelants et al. (2007), and to a lesser extent those of San Mauro et al. (2005) (since those authors used one internal calibration date with an upper bound). In contrast, the most recent molecular divergence date estimates (Hugall et al. 2007: fig. 5, table 3) approach or include the Permian–Carboniferous boundary (nucleotides: 322 ± 19 Ma ago; amino acids: 292 ± 28 Ma ago) even though its calibration points are all external to Lissamphibia. This may, as Hugall et al. (2007: 552) point out, be due to the fact that nuclear genes were used because “mtDNA divergences typically saturate at these timescales” so that the basal branches of mitochondrial-DNA trees are too short and the other branches too long. However, Hugall et al. (2007) chose no less than five calibration points and used all of them as fixed ages (i.e., they had an upper bound); this probably contributed to yielding reasonable ages.

There is no irreconcilable difference between paleontological and molecular dates. Our own molecular dating which incorporates internal and external calibration dates with lower and (in a few cases) upper bounds yields results compatible with evidence from the fossil record (Marjanović and Laurin 2007). These dates result from a reanalysis of the data of Zhang et al. (2005) using penalized likelihood (Sanderson 2003) and several combinations of calibration dates, of topologies (with mono- or paraphyletic “Archaeobatrachia”), of evolutionary models, and of smoothing factors (the smoothing factor in penalized likelihood determines how much the rates of evolution are allowed to differ between sister-groups). Our results were presented briefly, but because of the complexity and number of the analyses involved (Marjanović and Laurin 2007: table 2 and appendix 10), a summary highlighting our most relevant findings may be useful. The set of calibration dates which yielded the most plausible results included both external (Dipnomorpha–Tetrapodomorpha divergence, fixed at 410 Ma ago, and Amniota, at least 310 Ma ago) and internal calibration dates. The latter included only minimum (lower) bounds in most cases, such as Cryptobranchioidea (at least 140 Ma ago), and, depending on topology, Pipanura (at least 155 Ma ago) or “Archaeobatrachia” (at least 170 Ma ago) and Batrachia or Lissamphibia (both set to at least 250 Ma ago). When the upper bound was reasonably well constrained, we used both upper and lower bounds, but varied the upper bound to test its impact on the molecular dates. Thus, the age

of Urodela was constrained between 155 Ma ago (lower bound) and 170, 185 or 200 Ma ago (upper bound), and the age of Bombinanura was set between 170 Ma ago (lower bound) and 185, 200, or 215 Ma ago (upper bound). These 22 analyses yielded ages of Lissamphibia ranging from 250 to 291 Ma ago, with an average of 272 Ma ago, which suggest a Permian origin for Lissamphibia (Gradstein et al. 2004).

Confidence interval on the origination time of Lissamphibia using the fossil record.

—We have tried to compute confidence intervals on the stratigraphic range of Lissamphibia to determine its probable earliest time of appearance based on its fossil record. Because of the numerous assumptions made in these calculations, we do not wish to put too much confidence into these results, although these assumptions are perhaps not more unreasonable than those used for molecular divergence dating (Lee 1999; Shaul and Graur 2002; Brochu 2004a, b; Graur and Martin 2004; Britton 2005). The requirements about the distribution of fossiliferous localities that enable application of the methods proposed by Marshall (1990, 1994, 1997) are severely limiting; none of the proposed methods was entirely suitable for our purpose, although the latest one (Marshall 1997) is adequate when modified as suggested above. The recommendation to use a Kolmogorov–Smirnov goodness-of-fit test for continuous distributions in order to detect deviations between observed and predicted number of localities (Marshall 1997) was proposed for situations in which relatively few localities were known. In Marshall’s (1997) example, the species are represented in 10 horizons. Thus, a Kolmogorov–Smirnov test may be too stringent when many localities exist, because significant deviations will almost always be found. For example, the deviations between our various functions and the observed number of localities were always highly significant ($D = 0.11$ to 0.13 ; $p < 0.0001$) because Lissamphibia is represented by 1207 localities. However, the same value of the D statistic yields non-significant results ($p > 0.05$) with a lower sample of 120 localities, which is still much higher than the cases envisioned by Marshall (1997). When a taxon is present in a large number of horizons, we suggest using regressions (with permutations, if the distribution of observed number of localities is not normal) to verify that the recovery potential function predicts the actual number of localities well. In this case, we suggest that the coefficient of determination (R^2) be examined; even if the relationship is significant ($p < 0.05$), we do not recommend using this method if the R^2 is less than about 0.8 (admittedly an arbitrary threshold). In our case, this method suggests that our recovery potential functions incorporating geological age, an exponential model, and the surface of exposure of sedimentary rocks, are adequate. The other model that uses only the exposure surface is clearly inadequate, as shown by its much lower coefficient of determination in the linear regression. Establishing confidence intervals of stratigraphic ranges of taxa remains an open problem, but this is hardly surprising because much relevant information is usually missing, such as the

sampling effort in the field, the exact age of the fossiliferous localities, and the abundance of the relevant taxa in their former biological communities.

The confidence intervals CI 5 and to a lesser extent CI 4 extend deep into the past because our exponential function yields a very low lissamphibian biodiversity in the Paleozoic, ranging from two species in the Viséan (337 Ma ago) or Famennian (368.8 Ma ago) to a maximum of 72 species at the end of the Permian. Thus, despite the fairly extensive Permian exposures, the lissamphibian recovery potential for that period is much smaller than for the Cenozoic, in which lissamphibian diversity has grown (according to our preferred model) from 400 to 6157 species. Other biodiversity models, such as logistic or steady-state models, would have yielded greater biodiversity in the Paleozoic and, hence, much smaller confidence intervals. A steady-state model that can be exemplified by taking only the exposure area of sedimentary rocks into consideration gives ridiculously short confidence intervals (Table 4: CI 6; Fig. 4) and is inconsistent with the evolution of estimated lissamphibian biodiversity using any of the three indices used here (Fig. 2) or with the observed number of localities (Table 3). The model that assumes that lissamphibians were unaffected by all biological crises and diversified exponentially gives an excessively long 75% confidence interval that extends into the Late Devonian in one case and is not calculable in the other (Table 4: CI 5; Fig. 3), yet it fits the observed number of localities almost as well as the other exponential models that incorporate the effect of biological crises, which yield drastically smaller confidence intervals (Table 4: CI 1–CI 4; Fig. 3). Thus, this method is less conclusive (in this case) than obtaining minimum paleontological ages from a time-calibrated supertree (Marjanović and Laurin 2007), but the results obtained by both of these methods, and by our molecular dating (Marjanović and Laurin 2007), are all compatible. Furthermore, we should point out that recent divergence date estimates from molecular data (Zhang et al. 2005; Roelants et al. 2007; Marjanović and Laurin 2007) encompass a similarly large range of dates, ranging from 368.8 to 255 Ma ago.

Other methods could have been used to compute confidence intervals on the origin of Lissamphibia. For instance, Foote et al. (1999) assessed various scenarios on the timing of placental mammal diversification by using a model of diversification which assumes a constant probability of cladogenesis and extinction, and uses only biodiversity at present and at the first time of appearance in the fossil record as input. It might be interesting to test this method using our data, but we preferred using Marshall's (1997) method because it uses all the data on the stratigraphic distribution of the relevant fossils. By contrast, since only two Triassic localities have yielded lissamphibian fossils, the method of Foote et al. (1999) would use only about 0.17% of the available data (2/1207) presented in Appendix 2 (SOM). We expect that discarding over 99.8% of our data would result in wider confidence intervals, although this would have to be verified by applying the method. Furthermore, the assumption of constant diversification and extinction rates required by the

method of Foote et al. (1999) may not be realistic over the studied geological timespan, because several mass extinction events may have affected lissamphibians.

The method we use here does not distinguish node-, apomorphy- and branch-based taxa, and hence, the confidence intervals calculated here do not necessarily apply to Lissamphibia (the amphibian crown-group). Marshall (1999) stated that the time of origin that he obtained (for some bird taxa) were "actually the origination time of the first diagnosable synapomorphy". In the case of Lissamphibia, the situation is a little different because the name of this taxon has had a clear phylogenetic meaning for at least a few decades (the amphibian crown-group). However, contrary to molecular divergence dating that clearly dates a cladogenesis, the confidence interval based on stratigraphy could also be conceived of as dating the branch-based taxon that includes Lissamphibia and all unknown extinct taxa that are more closely related to Lissamphibia than to its closest known relatives (lysoophians and/or dissorophoids). In that case, the basal dichotomy in Lissamphibia may be younger than our calculations suggest. Globally, our calculations of the confidence interval on the stratigraphic range of Lissamphibia suggest that this taxon is younger than advocated by San Mauro et al. (2005) and Roelants et al. (2007). However, our calculations give less precise results than a time-calibrated supertree (Marjanović and Laurin 2007) and, under some assumptions on the impact of mass extinction events (Table 4: CI 4–CI 5), cannot exclude the divergence times inferred by Zhang et al. (2005). Globally, the molecular and the paleontological evidence are most compatible with an origin of Lissamphibia sometime in the Permian, between about 290 and 255 Ma ago.

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Appendix 1

List of localities that have yielded lissamphibian fossils

Localities represented by a number instead of a name bear the same number in Sanchíz (1998: 146–180), and this citation is not repeated for them. Correlation of terrestrial deposits across continents is usually difficult. We have kept the original stratigraphic designation of each site (that is, mostly those used by Sanchíz 1998). For the correlation of these, apart from the primary literature, we have relied on Sanchíz

(1998: 3) and simplified it. For example, in Sanchíz (1998) the Casamayoran, a South American Land Mammal Age, begins and ends a bit earlier than the Ypresian, an official (Gradstein et al. 2004) stage, does; because we lack evidence to the contrary, we have considered all Casamayoran sites to be Ypresian in age and therefore show them in the same cell. Abbreviations: Fm, Formation.

Geological stage	Number of localities	Duration of stage(s) (Ma)	Name of localities and reference, or locality number in Sanchíz (1998)
Lower Triassic	2	6	108, Czatkowice (Evans and Borsuk-Białynicka 1998)
Pliensbachian or Toarcian	1	14	561
Pliensbachian	1	6.6	367
Toarcian	1	7.4	?896
Bajocian	1	3.9	Upper Bajocian: 348
Bathonian	at least 5	3	Qýzýlsu (Nessov 1988); Upper Bathonian: 543, 1027, 1154

Geological stage	Number of localities	Duration of stage(s) (Ma)	Name of localities and reference, or locality number in Sanchíz (1998)
Upper Bathonian to Callovian, or possibly lower Oxfordian	1	~6.5	70
Callovian to Oxfordian	3	9	585, 653, 1079
Kimmeridgian	3	4.9	Karabastau suite (Milner 2000), Guimarota and Porto Dinheiro (Estes 1981)
Kimmeridgian or Tithonian	1	10.2	846
Tithonian	1	5.3	Lower Purbeck (Ensom et al. 1991)
Lower Cretaceous indet.	4	45.9	157, 380, 465, 788
Berriasian	1	5.3	Anoual (Gardner et al. 2003)
Upper Berriasian or lower Valanginian	1	< 9.1	939
Hauterivian or Barremian	1	11.4	960
Hauterivian	2	6.4	1095, Bernissart (Estes 1981) Not counted: Fengshan (Dabeigou Fm, Hauterivian rather than Barremian according to He et al. 2006)
Barremian	> 6	5	461, 627, Calizas de la Huérguina Fm (McGowan 2002) Lower B.: 347; Barremian-Aptian boundary: all localities of the Yixian Fm
Aptian	>3	13	?327, ?710, all localities of the Jiufotang Fm
Aptian or Albian	3	25.4	34, 536, ?779
Albian	3	12.4	183, Pietraroia (McGowan 2002); Upper Albian: 537
Late Cretaceous indet.	1	34.1	646
Cenomanian	4	6.1	1145, 886 (assuming this is <i>Avitabatrachus</i> – Báez et al. 2000); Lower Cenomanian: 538, 953
Turonian	1	< 4.2	Upper Turonian: 289
“Late Turonian to Santonian”	1	<10	547
Coniacian	4	3.5	285, 287, 288; Upper Coniacian: 286
Coniacian to Santonian	1	5.8	472
Santonian	1	< 2.3	Lower Santonian: 516
Santonian to Campanian	1	15.2	534
Campanian or Maastrichtian	3	18	15, 23, 797
Campanian	6	12.9	18, 346, 501, 1135; Upper Campanian: 337, 338
Upper Campanian or lower Maastrichtian	1	< 18	664
Maastrichtian	11	5.1	46, 203, 335, 359, 433, 591, 718, 816, 940, Pajcha Pata (Gayet et al. 2001); Upper Maastrichtian: 588
Maastrichtian and Danian hopelessly mixed	1	8.9	147
“undetermined Tertiary”	1	63.694	447
Paleocene indet.	1	9.7	586
Danian/“Lower Paleocene”	5	3.8	?410, 845, 1055; Puercan: 1087; Torrejonian: 1063
Selandian/“Middle Paleocene”	3	3	323; Riochican: 485; Tiffanian: 328
Thanetian/“Upper Paleocene”	5	2.9	584, 708, Naran-Bulak Suite (Gubin 1991), Ravenscrag Fm (Estes 1981); MP6: 185
Eocene or Oligocene	2	32.77	184, 798
Eocene indet.	4	21.9	11, ?349, 630, 686
Ypresian/“Lower Eocene”	9	7.2	?130, 952, 1176, 1182; Casamayoran: 170, 808; MP7: 273, 971; MP10: 1222
Lutetian	13	8.2	Mustersan: 780; Bridgerian: 1028; “Middle Eocene”: 80, 372; MP11: 667; MP11–13: 351; MP13: 53; Uintan: 320, 353, 424, 833, 863, 996
Upper Eocene or Oligocene	1	14.87	73
Upper Eocene or lower Oligocene	1	12	763
Upper Eocene indet.	4	6.5	98, 223, 1099, 1181
Bartonian	6	3.2	Duchesnean: ?242; “Duchesnean or Chadronian”: 1056; MP16: 137, 383, 595, 893
Priabonian	22	3.3/4	MP17: 51, 128, 427, ?428, ?429, 430, 451, 598, 635, 803, 834, 905, ?1073, Hordle Cliff (Holman and Harrison 2003); MP18: 373, 915; MP19: 213, 311, 431, 904, 975; MP20: 1168

Geological stage	Number of localities	Duration of stage(s) (Ma)	Name of localities and reference, or locality number in Sanchíz (1998)
Oligocene or Miocene	3	28.568	633, 755, 768
Oligocene indet.	5	10.87	60, 324, 821, 826, 1059
Chadronian	1	6	?473
Rupelian	24	5.5	78, 165, 306, 463, 490, 575, 691, ?965, ?1105, 1109, 1121; MP21: 444, 449, 862, 902, 999; MP22: 647, 681; MP23: 191, 486, 791; Orellan: 319; Whitneyan: 344
“Middle Oligocene”	3	10.87	151, 416, 579
Chattian	19	5.37	95, 397, 399, 774, 1040, 1199; MP27: 129; MP28: 303, 343, 790; MP29: 682; Deseadan: 881, 921; MP30: 214, 764, 906, 1010; “uppermost Oligocene”: 642; Arikarean: 811
“Neogene indet.” = Miocene or Pliocene	13	21.224	507, 616, 632, 758, 819, 857, 868, 869, 887, 934, 1083, 1093, 1108
“late Oligocene or early Miocene”	4	< 12.43	400, 435, 890, 1163
“Oligocene-Miocene boundary”	11	very little	153, ?511, 557, 573, 619, 674; MN0: 442, 748, 1022, 1118, 1207
Miocene indet.	8	17.698	8, 123, 180, ?364, 527, 572, 706, 1074
“Lower or middle Miocene”	1	11.422	1191
Lower Miocene indet.	15	7.06	14, 145, 300, 321, 497, 590; Arikarean: 161, 162, 644, 655, 1184; Agenian or Orléanian: 411, 483, 509, 767
Agenian	14	maybe 3	24, ?88, 375; MN1: 786, 1157, 1158; MN1–2: 759, 877, 1062; MN2: 422, 594, 1094; MN2a: 916; MN2b: 721
Burdigalian	30	4.46 or more	?626; MN3: 462, 663, 719, 987, 1014, 1066; MN4: 20, 271, 861, 900, 908, 1104; MN4a: 44, 149; MN4b: 227, 1020; MN4–5: 1125; MN5: 97, 333, ?393, 818, 856, 1002; Shanwangian: 951; Hemingfordian: 1052; Colhuehuapian: 187, 216; Santacrucian: 883, 884
Burdigalian or middle Miocene (“late Orléanian or early Astaracian”)	2	< 8.822	MN5–6: 702; MN5–7: 22
Middle Miocene	53	4.362	168; Barstovian: 29, 116, 215, 295, 361, 363, 458, 550, 736, 740, 852, 898, 1078; Friasian: 392, 476, 583, 1113; Tungurian: ?1188; Astaracian: MN6: 265, 282, 334, 637, 933, 936, 1071; MN6–8: 7, 50, ?107, 109, Hasznos, Szentendre, Sámsonháza 3.; Mátraszőlős 1, M. 2, Felsőtárkány 1, F. 3/2 (Venczel 2004); MN7: 100, 386; MN7–8: 186, 312, 624, 750, 761, 840, 937, 1007, ?1129; MN8: 217, 385, 549; “Upper Astaracian”: 994
Middle or upper Miocene	22	?4	891; Friasian or Chasicoan: 77; Barstovian or Clarendonian: 301; Clarendonian: 113, 374, 615, 679, 1137, 1149; Vallesian: ?605; MN9: 28, 55, 169, 384, 1070, 1107; MN9–10: 159, 576; MN10: 27, 600, 652, 1018
Upper Miocene	60	6.276	503, 1186; “Vallesian-Turolian”: 787; “Upper Vallesian or middle Turolian”: MN 10–12: 1069; Turolian: MN11: 10, 47, 243, 267, 567, 744, 800, 909, 1103, 1140; MN11–13: 206, 247, 326, 684; MN12: 21, 221, 222, 240, 249, 639, 650, 742, 810, 938, 1034, 1080; MN12–13: 194, 976; MN13: 30, ?40, 140, 241, 299, 339, 640, 651, 683, 825, 922, 1102, 1114; Hemphillian: 264, 278, 294, ?318, 408, 603, 613, 625, 832, 859, 874, 899, 941, 1178, 1193
Upper Miocene and/or Pliocene	5	9.802	195, 398, 753; “Upper Miocene or lower Pliocene”: 230, 310
Pliocene indet.	14	3.562	112, ?518, 544, 1160; Ruscinian or Villanyian: MN14–16: 1172; Blancan: 89, 102, 114, 331, 404, 452, 873, 930, 1167
“Lower Pliocene”	31	2.744	Montehermosan: 229, 481, 688, 848; Ruscinian: MN14: 17, 629, 769, 799, 820, 841; MN14–15: 174, 520, 570, 1126; MN15: 41, 167, 228, 245, 315, 369, 489, ?510, 562, 596, 749, 842, 942, 948, 949, 1000, 1165
“Middle or upper Pliocene”	1	1.794	648
“Upper Pliocene”	37	0.782	556, 589, 814, 1225, 1227, 1229, 1230; Youhean: 150; Chapadmalalan: 844; Villanyian: 545, ?1092; MN16: 39, 67, 68, 103, 105, 201, 313, 345, ?370, 395, 412, 657, 738, 864, 879, 1075, 1077, 1166, 1198; MN16–17: 1110; MN17: 504, 610, 694, 712, 1130, 1132
“Upper Pliocene or Pleistocene”	2	2.5765	989, 1015
“Pliocene-Pleistocene boundary”/“Upper Pliocene or Lower Pleistocene”	7	1.807	71, 136, 322, 519, 568, 796, 1133
Pleistocene and/or Holocene	9	1.806	261, 263, 620, 666, 737, 782, 885, 978; “Lower Pleistocene to Holocene”: 355

Geological stage	Number of localities	Duration of stage(s) (Ma)	Name of localities and reference, or locality number in Sanchíz (1998)
Pleistocene indet.	62	1.7945	19, 38, 117, 199, 220, 248, 259, 293, 389, 443, 502, 505, 513, 517, 521, 529, 530, 531, 532, 533, 553, 554, ?559, 566, 569, 582, 629, 634, 654, 660, 662, 678, 680, 689, 701, 709, 730, 751, 802, 809, 815, 827, 912, 927, 944, 957, 959, 964, 966, 973, 977, 1004, 1049, 1050, 1058, 1106, 1123, 1156, 1164, 1185, 1205, 1211, 1213
Lower and/or middle Pleistocene	4	1.68	467, 614, 1086, 1203
Lower Pleistocene	62	1.025	57, 84, 91, 104, 106, 118, 181, 188, 202, 234, 246, ?283, 358, 366, 418, 445, 446, 478, 482, 496, 512, 539, 541, 558, 560, 563, 581, 602, 612, 649, 713, 714, 746, 754, 764, 871, 925, 946, 979, 984, 993, 1013, 1017, 1041, 1084, 1085, 1098, 1115, 1131, 1134, 1142, 1155, 1171, 1189, 1194, 1197, 1200, 1206, 1214, 1215, 1226, 1228
Middle and/or upper Pleistocene	9	0.7695	42, 276, 407, 450, 687, 995, 1036, 1047, 1170
Middle Pleistocene to Holocene	1	0.781	597
Middle Pleistocene	81	0.655	1, 9, 16, 25, 37, 43, 63, ?66, 76, 90, 127, 132, 152, 158, 198, 219, 250, 251, 253, 268, 271, 280, 281, 291, 302, 307, 329, 341, 365, 376, 379, 396, 413, 419, 421, 440, 455, 460, 479, 515, 526, 593, 606, 618, 685, 690, 693, 700, 717, 725, 747, 757, 762, 801, 828, 829, 851, 865, 876, 931, 982, 988, 997, 1001, 1005, 1006, 1019, 1021, 1024, 1044, 1064, 1076, 1096, 1117, 1128, 1141, 1161, 1162, 1175, 1192, 1221
Upper Pleistocene	206	0.1145	2, 12, 35, 56, 59, 61, 64, 65, 72, 75, 81, 82, 87, 96, 115, 120, 121, 122, 125, 126, 135, 139, 146, 154, 156, 164, 172, 176, 178, 182, 193, 204, 205, 207, 208, 210, 211, 218, 231, 232, 235, 238, 239, 252, 254, 257, 258, 270, 277, 279, 290, 292, 297, 305, 308, 317, 330, 332, 336, 342, 352, 354, 360, 368, 382, 387, 390, 394, 401, 402, 409, 415, 426, 434, 437, 439, 464, 469, 470, 477, 480, 484, 487, 488, 491, 492, 494, 495, 498, 499, 522, 523, 525, 542, 551, 555, 578, 580, 587, 601, 604, 607, 617, 621, 631, 641, 659, 661, 665, 671, 672, 673, 675, 677, 696, 697, 704, 716, 720, 724, 728, 729, 731, 732, 734, 735, 739, 743, 745, 756, 776, 777, 781, 789, 793, 794, 795, 805, 824, 830, 831, 835, 836, 838, 839, 855, 866, 867, 882, 894, 897, 901, 910, 911, 923, 926, 928, 929, 932, 947, 955, 956, 961, 962, 972, 974, 980, 981, 983, 985, 990, 998, 1003, 1008, 1009, 1011, 1012, 1025, 1026, 1029, 1035, 1038, 1046, 1048, 1053, 1057, 1068, 1088, 1091, 1097, 1100, 1112, 1124, 1127, 1139, 1153, 1173, 1177, 1183, 1195, 1196, 1202, 1204, 1208, 1210, 1217
Upper Pleistocene and/or Holocene	61	0.126	36, 45, 58, 69, 99, 141, 148, 155, 177, 196, 200, 224, 226, 275, 340, 350, 423, 438, 448, 459, 528, 540, 622, 623, 636, 656, 668, 676, 705, 722, 766, 773, 804, 806, 813, 817, 853, 854, 858, 870, 880, 945, 969, 991, 1039, 1042, 1045, 1090, 1116, 1120, 1122, 1147, 1179, 1180, 1187, 1190, 1201, 1212, 1216, 1224; "Pleistocene-Holocene boundary": 1089
Holocene	189	0.0115	3, 4, 5, 6, 26, 31, 32, 33, 52, 54, 57, 62, 74, 79, 83, 85, 86, 92, 94, 101, 110, 111, 124, 131, 134, 138, 143, 144, 160, 163, 166, 171, 173, 175, 179, 189, 190, 192, 209, 225, 236, 237, 244, 255, 256, 260, 262, 266, 269, 274, 284, 298, 304, 309, 314, 316, 325, 356, 357, 362, 377, 378, 381, 388, 391, 403, 405, 406, 414, 417, 420, 425, 432, 436, 441, 453, 454, 456, 457, 466, 468, 471, 474, 475, 493, 500, 506, 524, 535, 546, 548, 552, 565, 571, 574, 592, 599, 611, 638, 643, 645, 658, 669, 670, 692, 695, 698, 699, 707, 711, 715, 723, 726, 727, 733, 741, 752, 760, 770, 771, 772, 775, 778, 783, 784, 785, 807, 812, 822, 823, 837, 843, 847, 849, 850, 860, 872, 875, 878, 888, 892, 895, 903, 907, 913, 914, 917, 919, 920, 954, 958, 967, 968, 970, 986, 992, 1016, 1023, 1030, 1031, 1032, 1033, 1037, 1051, 1054, 1061, 1065, 1067, 1072, 1081, 1101, 1111, 1119, 1136, 1138, 1143, 1144, 1146, 1148, 1150, 1151, 1152, 1159, 1169, 1174, 1218, 1219, 1220, 1223