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Estimating minimum global species diversity for groups with a poor fossil record: a case study of Late Jurassic–Eocene lissamphibians

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Abstract

Estimates of past diversity using palaeontological evidence can be achieved within two main analytical frameworks. The traditional ‘taxic approach’ makes a straightforward use of stratigraphic ranges at a given taxonomic level, whereas the ‘phylogenetic approach’ derives palaeodiversity estimates from both phylogenetic topologies and stratigraphic occurrences. At lower taxonomic levels, the taxic and phylogenetic approaches have limitations for several groups because of the incompleteness of the fossil record and the frequent absence of stable, comprehensive phylogenetic hypotheses. In particular, fossil specimens unidentifiable at lower taxonomic levels are frequently discarded from both kinds of diversity analysis. However, these specifically or generically indeterminate occurrences may prove crucial for recovering minimal lineage-level diversity patterns, especially for groups with poor fossil records. Diversity counts can be achieved by a simple, intuitive protocol that incorporates all fossil occurrences and minimal principles of evolutionary continuity. This method, intermediate between the taxic and the phylogenetic approaches, has received little attention among palaeobiologists so far although it holds great promises for diversity studies. Here this alternative method is extended, generalised, and tested. When empirical occurrence data are artificially degraded, the technique captures an equal or a better part of the original diversity signal than the taxic approach.

This method is applied here to an original locality-level compilation of fossil lissamphibians occurring in the Late Jurassic–Eocene interval. This empirical study provides the first global lineage-level palaeodiversity estimate ever made for this group, and it shows that specifically indeterminate occurrences and evolutionary continuity can increase species diversity estimates by 400%. The major implications of this work are that (1) palaeontological reports and datasets should record *all* fossil occurrences, regardless of the taxonomic level at which they are diagnostic; (2) it seems preferable to abandon the old commitment of using only taxa assigned to the same rank in diversity analyses; (3) the clade Lissamphibia has experienced a virtually extinction-free gradual rise during the Late Jurassic–Eocene interval; (4) long-term climatic disruptions for the K/T bio-event and hypothetical megabiases in the Late Cretaceous fossil record of small terrestrial vertebrates are unlikely.

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1. Introduction

The history of biodiversity is a central theme in palaeobiology and the fossil record is essential to our understanding of the processes that have shaped modern biodiversity through geological time. However, the nature of the stratigraphic record and limited access to the parameters defining fossil organisms (mainly morphology) put specific constraints on the study of past taxonomic diversity. The assessment of palaeodiversity is rendered difficult by at least three interrelated factors. The first one is the ‘absolute heterogeneity’ of the fossil record, that is, preservation is biased over space and time by varying sedimentological and taphonomical parameters (e.g., Raup, 1972; Lasker, 1976; Signor, 1990; Holland and Patzkowsky, 1999; Smith, 1994, 2001a, 2003; Smith et al., 2001; Peters and Foote, 2001, 2002). The second factor is the ‘gnostic heterogeneity’, which represents our uneven knowledge of the record (Fara, 2001a,b). It stems from variable sampling regimes and unequal study across geographic areas, stratigraphic units, and taxonomic groups (Durham, 1967; Koch, 1978, 1998; Paul, 1998; Jackson and Johnson, 2001; Smith, 2001a). The third factor is the little-known analytical framework required for the whole enterprise. Which taxonomic entities should be counted? What treatments and metrics should be employed in the analysis? Such questions form the basis of a research programme that has received increasing attention in the last decade (Sepkoski and Kendrick, 1993; Smith, 1994; Foote, 1994, 1996, 2000; Robeck et al., 2000; Alroy, 1996, 1998, 2000a; Alroy et al., 2001). Recent methodological advances include better database systems recording information at the locality level (e.g., Alroy, 1996, 2003; Markwick, 1998; Alroy et al., 2001; Fara, 2001b; Markwick and Lupia, 2002), rarefaction techniques and more advanced subsampling algorithms (Miller and Foote, 1996; Alroy, 1996, 1998, 1999, 2000a; Alroy et al., 2001), as well as the application of capture/recapture models to palaeontological data (Nichols and Pollock, 1983; Nichols et al., 1986; Connolly and Miller, 2001).

So far, the exploration of diversity in the geological record has mostly relied on the observed stratigraphic ranges of taxa. This is why Levinton (1988) named this practice the ‘taxic approach’. The attractiveness of the latter stands in its apparent simplicity. A taxo-

nomic compilation of first and last occurrences in a series of time intervals (or time ‘bins’) is sufficient for determining diversity, as well as extinction and origination rates. However, this approach is not assumption-free (e.g., see Smith, 2001a). In the face of many methodological problems (database accuracy, definition of temporal units, choice of the metrics, heterogeneity of the fossil record), most workers assumed that potential noises cancel out and that large datasets still contain the original signals without any directional distortion (e.g., Sepkoski, 1981; Benton, 1989, 1995; Adrain and Westrop, 2000).

In addition, new insights have been brought to the study of palaeodiversity with the widespread acceptance of cladistic principles. This is what Smith (1994) termed the ‘phylogenetic approach’, in contrast to the taxic approach. Partisans of the phylogenetic approach claim that it can compensate for the deficiencies of the fossil record. This is achieved by correcting the known stratigraphic ranges of taxa to conform to the predictions of phylogenetic hypotheses (Norell, 1992, 1993; Smith, 1988, 1994). The tree-based extensions of taxic ranges (‘ghost lineages’ sensu Norell, 1993) inflate diversity estimates, despite the absence of these inferred lineages in the fossil record. The correction of diversity by phylogenetic considerations is intuitive because (1) the fossil record is known to be incomplete, and (2) evolutionary processes are continuous.

Nevertheless, and despite a century of effort in quantitative palaeontology, a disappointing observation must be made. At present, the lower-level taxonomic diversity of some major clades of organisms remains virtually unknown. Why is it so?

The first reason is the rarity of accurate compilations upon which large-scale specific diversity estimates could be established. The second, related, reason stands in the serendipitous nature of the species fossil record. For many groups, species occurrences are too patchy to secure reliable studies of broad-scale evolutionary patterns (e.g., Sepkoski, 1978, 1984; Raup and Boyajian, 1988; Valentine, 1990; Koch, 1991; Benton, 1995; Robeck et al., 2000; Smith, 1994, 2001b). As Robeck et al. (2000) put it: “unfortunately, classification biases cannot be avoided by simply counting species to estimate diversity patterns. When sampling is poor, counting species results in one of the worst correlation with underlying lineage diversity”. For vertebrates, such an argument has been

put forward to explain the current lack of diversity estimates for clades such as frogs, salamanders, or snakes (Estes, 1981; Rage, 1984a; Evans, 1995; Kardong, 1997; Sanchíz, 1998). Since their species fossil record is deemed too poor to make robust inference on diversity patterns, the latter must be deduced from the study of higher taxa. But simply grouping species into genera or families is as inefficient because the number of units upon which diversity is assessed becomes too small. In addition, problems inherent to higher classifications (e.g., equivalence of ranks, paraphyly) come into play. As a result, we stand in a methodological cul-de-sac. So far, global taxic studies thus represent a compromise between sample size and the preservation/sampling probability of their taxonomic units.

The ‘correction’ of diversity estimates by the phylogenetic approach is also problematic. First, the asymmetrical, bottom-oriented, inflation of the taxonomic counts may result in fatal distortions of the underlying diversity patterns (e.g., Wagner, 2000; and unpublished simulations by the late Jack Sepkoski). Second, a robust cladistic analysis can only afford a limited number of Operational Terminal Units (OTUs), both because of computational problems and missing data. As a result, the OTUs represent only a *restricted sample* of the known taxonomic diversity for practical reasons.

At a time when we need to know the historical trajectory of biodiversity, the above-mentioned problems must find practical solutions. Many limitations of the taxic and the phylogenetic approaches for estimating lower-level taxonomic diversity can be overcome by a third, logically distinct method that was first introduced by Alroy (1996) in a regional study of North American mammals. Here I discuss this method, I extend it, and I provide a generalised framework for its application on a global scale. These methodological aspects are illustrated with a group for which no global palaeodiversity estimate is currently available: lissamphibians. This clade comprises all living amphibians, that is, frogs (Anura), salamanders (Caudata), caecilians (Gymnophiona), as well as the extinct, enigmatic albanerpetontids (Allocaudata). All the authors agree on the scarcity of the lissamphibian fossil record (e.g., Carroll, 1977; Estes, 1981; Milner, 1994, 2000; Sanchíz, 1998; Evans and Sigogneau-Russell, 2001), and their phylogenetic relationships

remain problematic at various levels of the hierarchy (e.g., Feller and Hedges, 1998; Sanchíz, 1998; but see Zardoya and Meyer, 2001). However, fossil occurrences demonstrate that the salientan lineage (Proanura + Anura) was already differentiated by the Early Triassic (Rage and Rocek, 1989; Sanchíz, 1998; Evans and Borsuk-Bialynicka, 1998), salamanders and albanerpetontids are unambiguously present in the Middle Jurassic (Evans et al., 1988; Evans and Milner, 1994), and the Early Jurassic *Eocaecilia* witnesses the existence of the clade Gymnophiona by this time (Jenkins and Walsh, 1993). The present study concerns the diversity patterns of lissamphibians from the Late Jurassic to the end of the Eocene. This time span is interesting because it presents the rise of lissamphibians and it permits an overview of their Cretaceous–early Tertiary fossil record. The latter is widely debated since some molecular data have suggested major gaps in the continental record of vertebrates prior to the Cretaceous/Tertiary (K/T) mass extinction (e.g., Cooper and Fortey, 1998; Kumar and Hedges, 1998; Easteal, 1999), an assertion that is strongly challenged by palaeontological evidence (e.g., Alroy, 1999; Foote et al., 1999; Fara and Benton, 2000; Fara, 2002). Although much of the debate revolves around the fossil record of birds and mammals, the suggested global biasing factors (poor preservation, poor sampling, high sea level) should alter even more the fossil record of other continental vertebrates with delicate skeletons (Benton, 1999; Fara and Benton, 2000). In such a context, the early fossil record of lissamphibians offers an interesting taphonomic control.

2. The importance of specifically indeterminate occurrences

In palaeontology, reported faunal lists usually contain a heterogeneous array of taxonomic statements: some specimens show characters that are diagnostic at the species level, others display synapomorphies diagnosing a genus, and many others will be indeterminate at the generic level. These common records, such as ‘Family A indet.’, or ‘Clade B indet.’, are often reported to witness the alpha diversity (sensu Sepkoski, 1988) of the assemblages under study. Paradoxically, these specifically indeterminate occur-

rences (referred hereafter as ‘SIOs’) are often neglected when it comes to diversity and/or turnover estimates on a larger scale. Moreover, there is certainly a bias against the reporting of such occurrences in the palaeontological literature, and specimens diagnostic at lower taxonomic levels generally receive more attention than others. When not included in detailed faunal lists, the SIOs are usually mentioned on their own only when they bear important palaeobiogeographical or temporal information. For example, some SIOs are important for assigning the oldest occurrences of supraspecific groups when the latter are used as terminals in phylogenetic trees.

Yet, should the phylogenetic analysis use other terminal taxa or the taxic approach consider a lower taxonomic rank, then these SIOs will be wrongly discarded. Consider Fig. 1. Three species (A, B, and C) are presented with their phylogenetic relationships and their observed stratigraphic ranges. Traditional taxonomic ranks are used here to clarify the explanations, but note that these ranks are simply used to

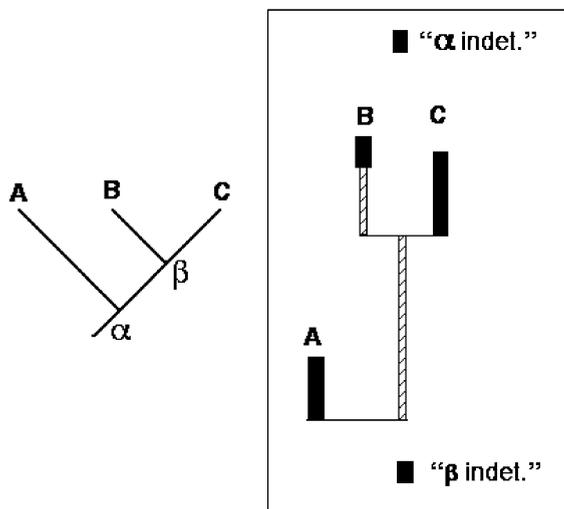


Fig. 1. The problem of indeterminate occurrences. The left figure shows the phylogeny of clade α ; the right figure shows the stratigraphic occurrences reported for the members of clade α . If the terminal taxa A, B, and C are assigned to the same rank (e.g., species), the taxic approach would only consider the observed stratigraphic ranges (black bars) to estimate the diversity at this rank. The phylogenetic approach would first correct the ranges of these terminal taxa by adding adequate ghost lineages (stippled bars). Both methods do not integrate the occurrences ‘ α indet.’ and ‘ β indet.’ despite the fact that the latter represent at least one lineage belonging to clade α .

represent successive hierarchical levels of inclusiveness. Species B and C belong to genus β and species A is placed in its own genus. Both genera are included into the monophyletic family α . Along with the stratigraphic records of the three species, the SIOs ‘ β indet.’ and ‘ α indet.’ are also displayed in Fig. 1. A traditional taxic study made at the species level would consider only the observed ranges of A, B, and C for estimating the diversity, extinction, and origination patterns. A typical phylogenetic approach, despite adding the implied ghost lineages, would probably also dismiss the two SIOs because they do not correspond to the definition of terminal taxa. Both approaches would be incorrect here because they do not use all the available fossil evidence when inferring the species diversity of clade α . The two SIOs are discarded because they lack diagnostic characters defining the taxonomic entities employed in the studies. This is a methodological error that might strongly underestimate the diversity of groups with poor fossil records. Whether named or not, all fossil specimens should be considered, simply because a monophyletic group is an evolutionary continuum.

The same principle applies when the known species of a monophyletic group have their stratigraphic ranges disjunct: at least one *lineage* (or species) of this group can be inferred in the corresponding gaps, unless the study is made at the regional or local scale. For example, besides some generically indeterminate records in the Late Cretaceous and Early Palaeocene, the extant amphibian group Gymnophiona is known from only three named fossil genera that occur in the Early Jurassic, the Early Cretaceous, and the Late Palaeocene (Estes, 1981; Jenkins and Walsh, 1993; Evans and Sigogneau-Russell, 2001). Consequently, at least one lineage of gymnophionan can be counted in all intervals from the Early Jurassic to the Recent at the global scale.

Therefore, both evolutionary continuity and SIOs must be used to infer the minimal lineage diversity of a group. One of the very few diversity studies following such an objective counting is the work on North American mammals by Alroy (1996, 1998, 2000b). Because the species data taken at face value were not as robust as the generic data, this author elaborated a ‘lineage-level’ diversity curve by employing simple rules. First, ‘at any point within the age range of a genus, the number of extant lineages is either equal to

the number of extant species, or, if no named species in a genus is extant, to one' (Alroy, 1996). Second, when the extinction or origination of named species is followed (or preceded) by the occurrence of unnamed species within the same genus, the extinction (or origination) is deemed a pseudo-extinction (or pseudo-origination). In this methodological framework, the lineage-level diversity data of Alroy (1996, 1998, 2000b) captured all the information of the species-level data without the biases inherent to this level of study, and the resulting diversity curve was similar to that at the genus level.

However, Alroy (1996, 1998, 2000b) could not pursue the same line of reasoning for the occurrences identified at higher taxonomic levels because his studies were limited to the North American continent. Indeed, the intercontinental migration rate of mammals is too high for assuming continuous age ranges at high taxonomic levels. Clearly though, the rules implemented in Alroy's studies must be extended and placed in a broader taxonomic context. This will be crucial for recovering more accurate lineage-level diversity patterns (*sensu* Alroy, 1996), especially for groups with so-called 'poor' fossil records.

3. Method

3.1. Assumptions

The method described therein is intermediate between the taxic and the phylogenetic approaches. Contrary to the latter, it does not assume that sister groups arise at the same time. By minimally connecting the stratigraphic ranges of sister taxa, the procedure is equivalent to regarding all taxa as hypothetical ancestors (Eldredge, 1979; Smith, 1994). As such, the diversity estimate is the *minimal* number of lineages present in a time interval given the observed occurrences. Provided there is a comprehensive and fully resolved phylogeny, and if all clades can be characterised by their own set of autapomorphies, then a companion method could level the first occurrences of sister groups by using appropriate ghost lineages. However, these criteria may be difficult to fulfil in practice, especially for large datasets (Smith, 1994). The protocol described thereafter is thus a practical solution for making a maximal use of fossil occur-

rences based on minimal assumptions of evolutionary continuity.

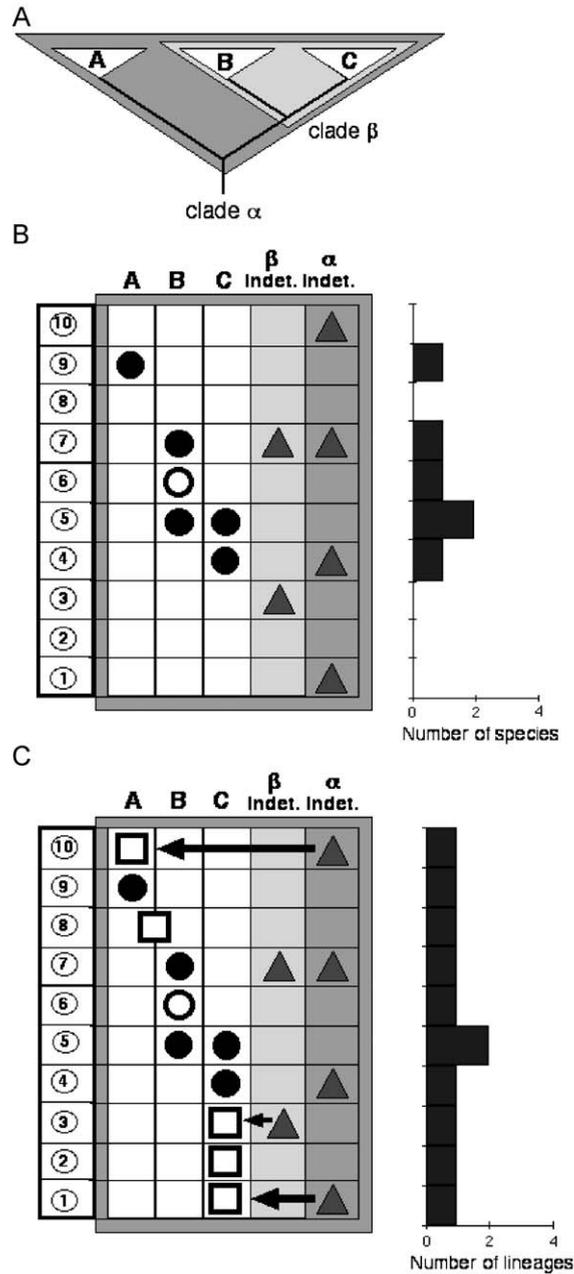
3.2. Protocol

The protocol requires a phylogenetic classification of all the species belonging to a given clade. A phylogeny fully resolved at the species level is not necessary. However, some hierarchical levels of inclusiveness must be established and named in accordance to the fossil occurrences reported at these levels. The distribution of all fossil occurrences is also needed, whatever their level of diagnosticity.

For simplicity, the protocol is described for a small clade α that contains only three species (A, B, and C). The phylogeny of clade α is recalled in Fig. 2A, along with all the stratigraphic occurrences of the members of this clade in a series of 10 time intervals (1 to 10, Fig. 2B). The 'raw' species diversity estimate corrected for the 'Lazarus effect' (Jablonski, 1986) is indicated on the right side of Fig. 2B. Note that it does not take indeterminate occurrences (' β indet.' and ' α indet.')

into account. The method proceeds by drawing inferences from the least inclusive to the most inclusive clades. After intra-range corrections for the Lazarus effect are made for each species, the next level of inclusiveness is considered. Clade β includes species B and C. The stratigraphic ranges of these two species overlap, and so no minimal inference of evolutionary continuity is necessary to link them. Then, occurrences of the type ' β indet.' come into play. One of these records is present in time interval 7 (Fig. 2B), and it could represent species B, or species C, or another, unknown, species of clade β . The latter option is disregarded for the minimal estimate of species-lineage diversity, and this record is therefore viewed as redundant with the known presence of species B in time interval 7. In contrast, the oldest occurrence of clade β is found in interval 3, where neither species B nor C is known. Therefore, the presence of one species belonging to clade β is inferred in that interval. The inferences being completed for clade β and taxon A, the next higher level of inclusiveness (clade α) is tackled. First, we must make sure that a minimal evolutionary continuum is maintained between the previously recognised components of clade α . Since the latest known occurrence of clade β is in

interval 7 and that species A occurs only in interval 9, a species of clade α can be safely inferred in interval 8. Finally, the occurrences ‘ α indet.’ are considered. In intervals 4 and 7, they are redundant with the distribution of less inclusive clades. By contrast, the records of clade α in intervals 1 and 10 are used to infer the presence of one species in both intervals and



in interval 2 (Fig. 2C). Because the method infers minimal species-lineage diversity, the occurrence ‘ α indet.’ in interval 10 is used to extend the latest occurrence of clade α previously recognised (taxon A from interval 9, in our example). In the same way, the occurrence ‘ α indet.’ in interval 1 is juxtaposed to the earliest occurrence previously recorded (occurrence ‘ β indet.’ in interval 3 here). In this particular case, the occurrence ‘ α indet.’ would have been enough to infer the minimal *number* of lineages in intervals 1 to 3, but the record ‘ β indet.’ in interval 3 provides more precise information about the *nature* of this diversity in that interval (see below). Finally, by considering all taxonomic occurrences, the minimal inferences extend at both ends the range distribution obtained with the traditional taxic approach (compare the two diversity profiles in Fig. 2B and C). The minimal lineage diversity is the highest inferable baseline above which lies the true specific diversity.

Specifically indeterminate occurrences (SIOs) could be used also to minimally correct diversity estimates derived from a traditional phylogenetic approach. Some SIOs minimally extend the appropriate species ranges toward the Recent, while others are used to calibrate the minimal age of splitting events. Fig. 3 illustrates this procedure. A ghost lineage (sensu Norell, 1993) is inferred in interval 4 in order to make the species B and C arise at the same time. The phylogenetic approach would also minimally extend the range of species A to this level and it would stop the inference there. By considering the record ‘ β indet.’ in interval 3, however, the minimal age of clade β is pushed backward into that interval. As a result, the ghost lineage of species A is also extended back to reach interval 3. Finally, the minimal age of the whole clade α is determined by the

Fig. 2. Inference of minimal lineage diversity. (A) Phylogeny of clade α . (B) Stratigraphic records of named species (full circles) and specifically indeterminate occurrences (triangles) of the members of clade α in a succession of 10 time intervals (1 to 10). Species ranges are corrected for the ‘Lazarus effect’ (open circles), but specifically indeterminate occurrences are not considered into raw species diversity counts (right histogram). (C) Principles of evolutionary continuity and occurrences of the type ‘ β indet.’ and ‘ α indet.’ are successively used to conservatively infer missing lineages (squares). Arrows show the inferences based on specifically indeterminate occurrences. The corrected lineage diversity of clade α is shown on the right histogram. See text for details.

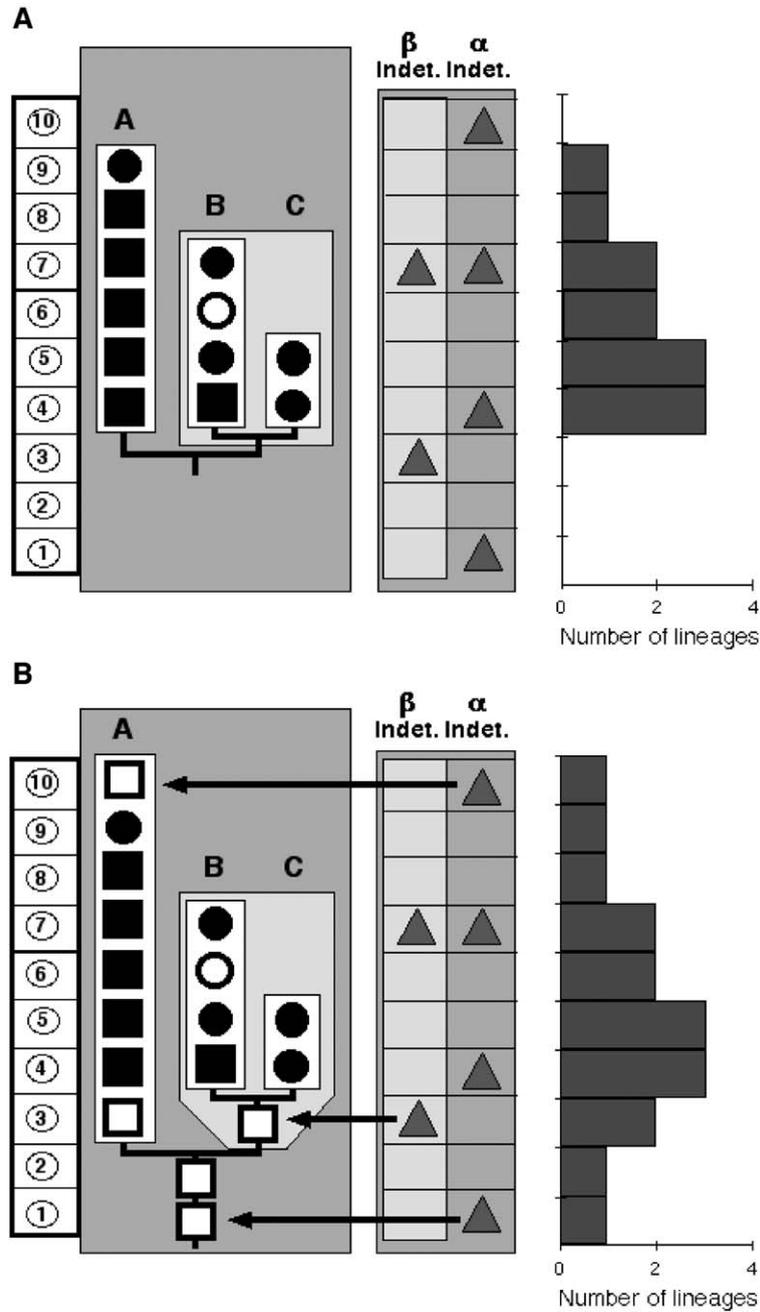


Fig. 3. Phylogenetic approach and specifically indeterminate records. The phylogenetic tree refers to clade α (see Fig. 2A). (A) Traditional phylogenetic approach and its corresponding diversity profile. (B) Phylogenetic approach minimally corrected with specifically indeterminate records and the resulting diversity estimate. Filled squares represent the ghost lineages (sensu Norell, 1993) that would be deduced from a traditional phylogenetic approach, and open squares are the inferred lineages based on indeterminate records. Other symbols as in Fig. 2.

occurrence ‘ α indet.’ in interval 1. This procedure yields a minimal lineage diversity estimate that makes direct use of the phylogenetic hypothesis. Similar to the phylogenetic approach, its main drawback is the need for a fully resolved phylogenetic hypothesis of all species within a clade. This is a major limitation in practice.

3.3. Paraphyletic groups

Because minimal lineage diversity is estimated by consideration of more and more inclusive groups, the premise about the monophyly of these nested entities needs to be addressed. To what extent can this assumption be relaxed? This is an important issue

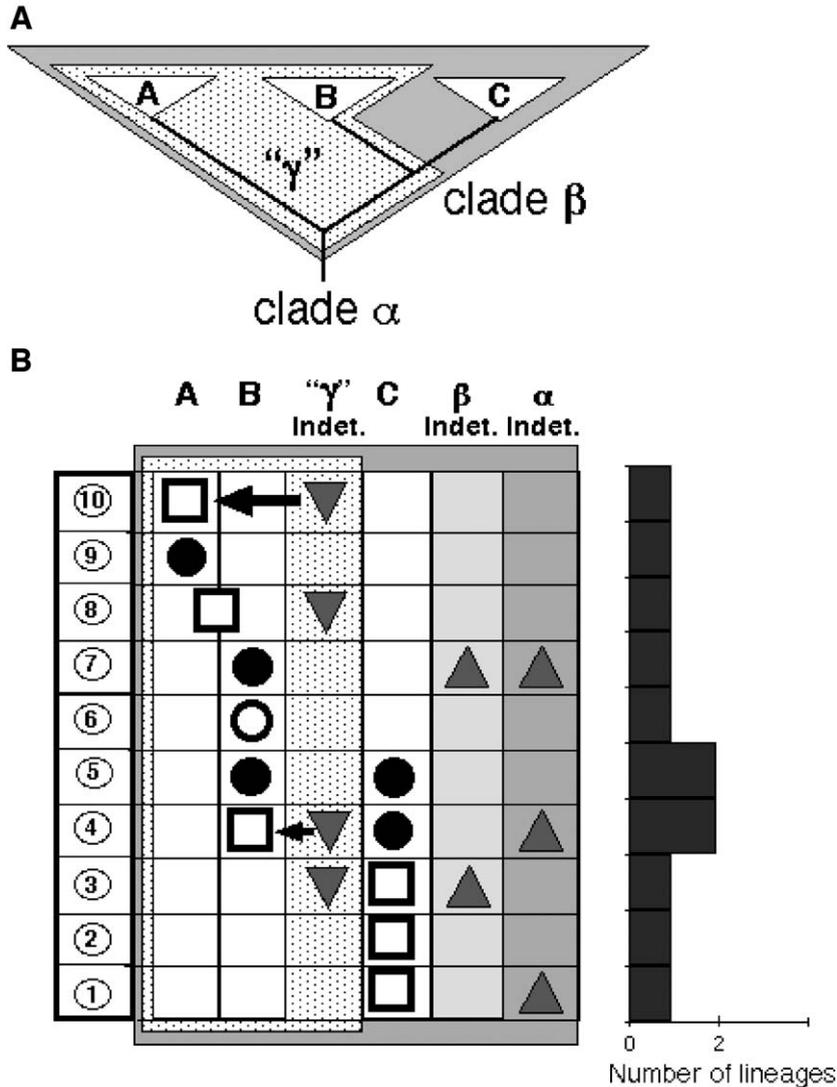


Fig. 4. Potential use of paraphyletic groups for inferring minimal lineage diversity. (A) An old (or competing) classification gathers taxa A and B into a group “ γ ” that is viewed as paraphyletic according to a modern classification (see Fig. 2A). (B) Reported occurrences of the members of clade α in both the old and modern systematic contexts. The occurrence ‘ γ indet.’ in interval 10 is informative because it conservatively witnesses the presence of clade α in that interval. Also, the occurrence ‘ γ indet.’ in interval 4 is informative relative to the occurrence of taxon C. On the contrary, the occurrence ‘ γ indet.’ in interval 3 is not informative because group “ γ ” and clade β overlap. Conventions are as in Fig. 2.

since many current taxonomic frameworks are ‘a chaotic mixture of monophyletic, paraphyletic, polyphyletic, and monotypic taxa’ (Smith, 1994).

Let us consider Fig. 4A. Several fossil occurrences were reported with reference to an old (or competing) classification that gathers taxa A and B into group “ γ ”. Together with taxon C, the latter formed clade α . Alternatively, a modern phylogenetical hypothesis regards B and C as sister taxa, making γ a paraphyletic group. The question is: can a fossil occurrence previously reported as ‘ γ indet.’ be informative for inferring the minimal lineage diversity of clade α in a modern context? At least three main situations can be distinguished.

Situation 1: the occurrence is the single report of clade α in a time interval. This is the case for interval 10 in Fig. 4B. In this situation, the occurrence of the paraphyletic group γ can conservatively be regarded as representative of clade α , and it is therefore informative.

Situation 2: the record ‘ γ indet.’ co-occurs with taxon C (e.g., interval 4 in Fig. 4B). Since γ can be defined as clade α minus taxon C (non-overlapping definitions), and that these two records are found in the same time interval, the record ‘ γ indet.’ is informative. For instance, the monophyletic Squamata contains several groups of ‘lizards’ sensu lato and the monophyletic snakes (e.g., Lee, 1997). The term “lizard” (or “Lacertilia”) is a convenient denomination for ‘non-snake squamates’ (a paraphyletic assemblage), and it abounds in the palaeoherpetological literature. If a same fossil horizon (i.e., ideally a single time slice) yields an indeterminate unequivocal ‘lizard’ and a snake, at least two specific entities must be considered in a minimal diversity count. This inference is possible because the well-defined, monophyletic, clade of snakes does not overlap with the paraphyletic group ‘lizards’.

Situation 3: In the same time interval, a record ‘ γ indet.’ juxtaposes another record of the type ‘ β indet.’ Because the definitions of the groups γ and β overlap (they share taxon B), a conservative approach must be adopted and only one lineage of clade α is counted in that time interval (see, for example, interval 3 in Fig. 4B).

Therefore, paraphyletic groups might be informative when minimal taxonomic diversity is inferred. In cases where their definition is ambiguous with regard

to contemporaneous monophyletic clades (situation 3 and eventually situation 2), a conservative count should be made. This is achieved by safely placing the problematic records into a non-controversial, more inclusive clade.

4. Testing the method

The method outlined here is fairly intuitive, but it involves several assumptions which could affect its utility. When the fossil record is poor, what part of the original diversity signal is captured by lineage-level estimates? One way to explore this issue is to compare diversity patterns established before and after an artificial degradation of the record. A simple three-step approach was adopted here: (1) computation of the taxic and lineage-level diversity estimates for well-sampled biological groups; (2) artificial degradation of the fossil records of those groups in terms of number of occurrences and diagnosticity; (3) re-computation of the diversity estimates.

This test was performed using data on Ruminantia and Eusuchia. Note, however, that the corresponding diversity patterns obtained before degradation are only standard references for our methodological investigation, an actual diversity study for these two groups being well beyond the scope of this paper.

The data on Ruminantia were downloaded from the *Paleobiology Database* on 8 October 2003 ([Paleobiology Database Project](#)) using the group name ‘Ruminantia’ and the following parameters: Authorizer = John Alroy; Time interval = Eocene–Pleistocene; Continent = North America; and lists with poor temporal data were excluded. For the purpose of the test, this dataset was treated as if it were global in scale. This yielded 1187 revised occurrences, out of which only 18,5% are indeterminate at the genus level. The phylogenetic hierarchy follows [McKenna and Bell \(1997\)](#). The occurrence data for eusuchian crocodiles are from [Markwick \(1998\)](#) and the corresponding phylogenetic structure follows [Brochu \(1999\)](#). Data for the Recent were removed, and this left 897 eusuchian occurrences in the Cretaceous–Pleistocene interval.

When necessary, the temporal distribution of these records was refined at the subepoch level for both

datasets, either by consulting published literature, or by evenly distributing the records into each subepoch.

Each dataset was artificially degraded by three different procedures:

- *Degradation 1*: 90% of the occurrences are randomly discarded from the dataset, and diversity is recomputed with the remaining 10%.
- *Degradation 2*: The diagnosticity (taxonomic assignment) of 50% of the original occurrences is randomly pushed back of one level in the

taxonomic hierarchy (for example, the occurrence of a named species becomes the occurrence of the specifically indeterminate genus, etc.), and diversity is then recomputed from the entire dataset.

- *Degradation 3*: 80% of the occurrences are randomly discarded, and the diagnosticity of 50% of the remaining ones is lowered of one hierarchical level.

For the two taxonomic groups, each of these degradation procedure was repeated 10 times and

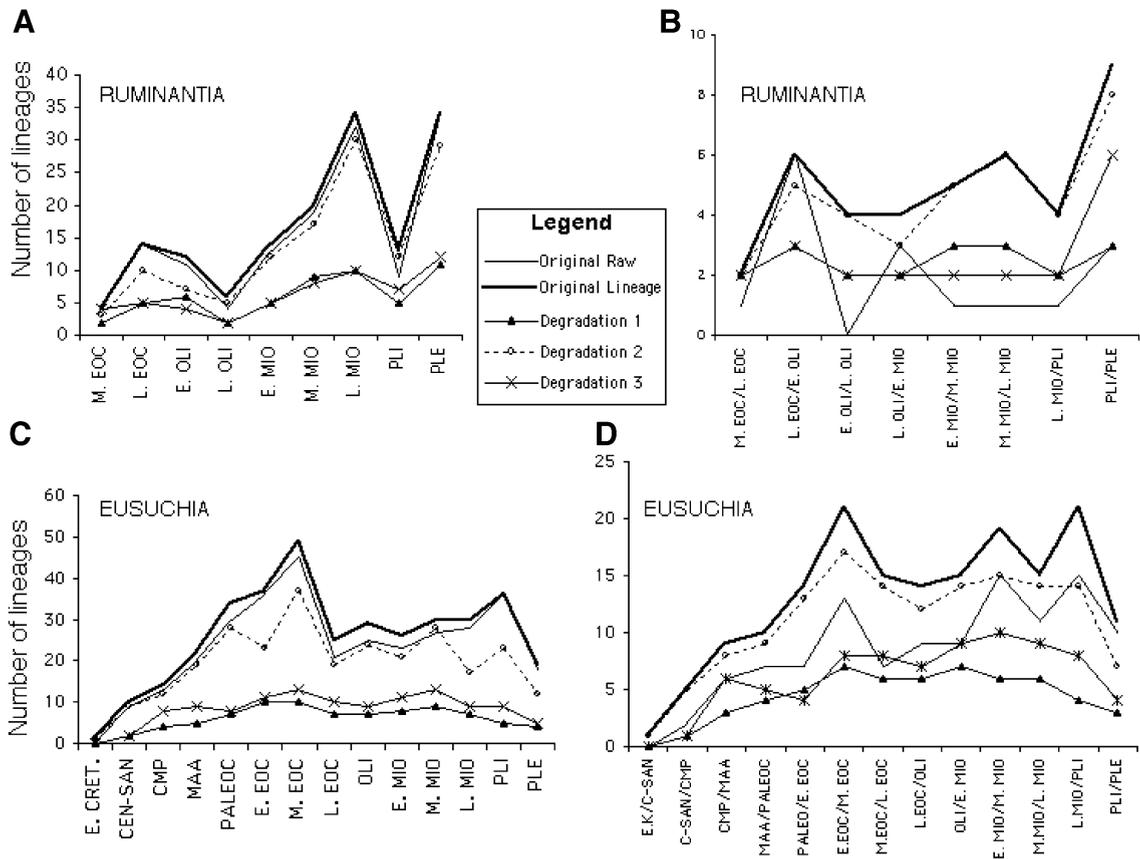


Fig. 5. Original diversity of Ruminantia and Eusuchia compared with the lineage diversity estimated after artificial degradations of their fossil records. Degradation 1 randomly discards 90% of the original occurrences, Degradation 2 randomly pushes back diagnosticity of one level in the taxonomic hierarchy for 50% of the original occurrences, Degradation 3 randomly discards 80% of the original occurrences and it pushes back of one hierarchical level the diagnosticity of 50% of the remaining occurrences. Each degradation procedure was applied 10 times on random samples and the median value of the resulting diversity estimates was used to construct the curves. For comparison, the original raw species diversity ("Original raw") is shown on each graph. (A) Diversity of Ruminantia for sampled-in-bin taxa. (B) Diversity of Ruminantia for boundary crossers. (C) Diversity of Eusuchia for sampled-in-bin taxa. (D) Diversity of Eusuchia for boundary crossers. Note that the method of counting minimum lineage diversity still captures a fair part of the original signal after artificial degradation of the record. C/SAN: Cenomanian–Santonian; CMP: Campanian; CRET: Cretaceous; E.: early; EOC: Eocene; L.: late; M.: middle; MAA: Maastrichtian; MIO: Miocene; OLI: Oligocene; PALEO: Palaeocene; PLE: Pleistocene; PLI: Pliocene.

the median value of the corresponding diversity estimates was computed for each temporal bin.

The diversity estimated by the traditional range-through taxic approach is referred to as the ‘raw’ diversity, whereas the ‘lineage diversity’ applies to the inferred minimal count of lineages as described above. Diversity curves are established either by counting the number of taxa in each temporal bin, or by inferring the number of taxa crossing boundaries between bins (‘boundary crossers’; Carr and Kitchell, 1980). Both these approaches have advantages and drawbacks, and an exploration of their properties is beyond the scope of this work (see Foote, 2000 and Alroy et al., 2001 for a discussion). In general, boundary-crosser curves show less variation than sampled-in-bin curves, and Alroy et al. (2001) observed this pattern in their recent study of Phanerozoic marine invertebrates. This is because the boundary-crosser technique eliminates ‘singletons’ (sensu Alroy, 1996, i.e., taxa restricted to single time units) from diversity counts, but it is never clear to what extent these taxa represent sampling/analytical artefacts or genuine short-lived taxa (Foote, 2000; Alroy et al., 2001).

Fig. 5 shows that the original lineage and raw species diversities of eusuchians and ruminants are virtually identical for sampled-in-bin curves, implying that the consideration of evolutionary continuity and SIOs is not essential at this point. For boundary crossers, those two curves have a similar shape for

crocodilians (Spearman rank–order correlation coefficient $r_s = 0.922$, $p < 0.001$; Fig. 5D), although the raw curve stands at a lower diversity level. The raw species curves of ruminants fails to cross the Early/Late Oligocene boundary, but the raw generic and lineage data are similar for this taxonomic group ($r_s = 0.949$, $p < 0.005$; Fig. 5B).

In all situations, the degradation 2 procedure has little effect on the lineage curve, both in terms of shape and of overall diversity level. In contrast, this global diversity level is strongly diminished by the more stringent degradation 1 and degradation 3. The corresponding lineage curves still tend to follow the original diversity variations (Spearman rank–order correlation tests, Table 1), but they do not succeed in capturing the correct magnitude. Interestingly, these degraded lineage curves come close to the diversity level recorded by the original raw boundary-crossing species curve (Fig. 5B and D). Further analysis shows that, compared to lineage diversity, raw sampled-in-bin species diversity captures a smaller part of the original signal after degradation (r_s [lineage diversity] $> r_s$ [raw species diversity] in all cases). This is more evident for boundary crossers since raw species diversity remains close to zero after artificial degradation. In contrast, lineage and raw generic data both track the original diversity variations in a similar manner after degradation (Table 1). However, as soon as there is not a 1:1 species to genus ratio, lineage data

Table 1

Correlation between original lineage-level diversity and diversity estimated after artificial degradation of the fossil record of Ruminantia and Eusuchia

	Diversity data	Lineage		Genus	
		r_s	Signif.	r_s	Signif.
Sampled-in-bin data	Degrad. 1 Eusuchia	0.823	$p < 0.001$	0.920	$p < 0.001$
	Degrad. 2 Eusuchia	0.860	$p < 0.001$	0.9536	$p < 0.001$
	Degrad. 3 Eusuchia	0.707	$p < 0.01$	0.664	$p < 0.02$
	Degrad. 1 Ruminantia	0.875	$p < 0.005$	0.939	$p < 0.001$
	Degrad. 2 Ruminantia	0.958	$p < 0.001$	0.890	$p < 0.005$
	Degrad. 3 Ruminantia	0.915	$p < 0.005$	0.945	$p < 0.001$
Boundary-crosser data	Degrad. 1 Eusuchia	0.780	$p < 0.005$	0.919	$p < 0.001$
	Degrad. 2 Eusuchia	0.950	$p < 0.001$	0.904	$p < 0.001$
	Degrad. 3 Eusuchia	0.825	$p < 0.002$	0.726	$p < 0.01$
	Degrad. 1 Ruminantia	0.901	$p < 0.01$	0.673	N.S.
	Degrad. 2 Ruminantia	0.963	$p < 0.002$	0.898	$p < 0.01$
	Degrad. 3 Ruminantia	0.731	N.S.	0.711	N.S.

See text for details. Degrad. = Degradation; r_s = Spearman rank–order correlation coefficient; signif. = significance level; N.S. = non-significant ($p > 0.05$).

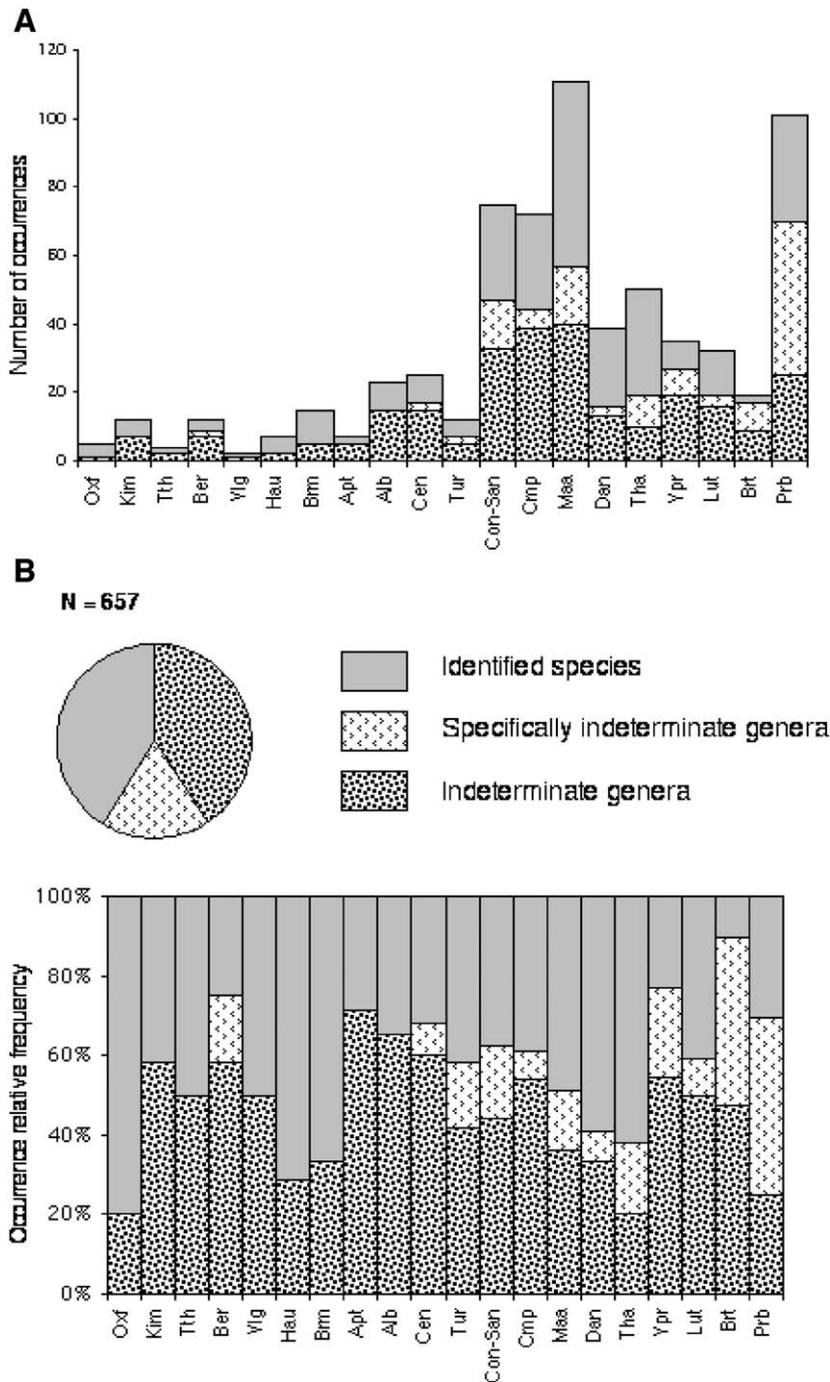


Fig. 6. Diagnosticity of liassamphibian occurrences in the Oxfordian–Priabonian interval. (A) Absolute frequencies. (B) Relative frequencies. Occurrences are divided into records diagnostic at the species level, at the genus level, and above the genus level. The pie chart summarises these proportions for the entire Oxfordian–Priabonian interval. N is the total number of occurrences. Stage abbreviations (x-axis) after Harland et al. (1990).

will always be closer to the original species diversity level than generic data.

Overall, this test on empirical occurrence data suggests that the method of counting minimal lineage diversity is an appropriate alternative in the face of a poor fossil record.

5. Diversity of Late Jurassic–Eocene lissamphibians

5.1. Data

A comprehensive compilation of the literature about lissamphibians known to have existed in the Late Jurassic–late Eocene interval was made using an original, relational database called ‘Vertebase’ (Fara, 2001b). This dataset records the distribution of 240 taxonomic entities within 250 localities, forming a total of 657 fossil occurrences in that

time span. Further informative occurrences were compiled outside the studied interval in order to ensure evolutionary continuity across its boundaries. Anuran taxonomy is based on the recent reviews of the group by Sanchíz (1998), Rocek (2000), Rocek and Rage (2000), and Báez (2000). The main phylogenetic scheme follows the work of Ford and Cannatella (1993) as modified by Sanchíz (1998). Caudate, albanerpetontid, and gymnophionan taxonomy and phylogenetic hierarchy rely mainly on Estes (1981), Larson and Dimmick (1993), Evans and Milner (1996), Milner (2000), Gardner (2000, 2002), and Evans and Sigogneau-Russell (2001). These major taxonomic frameworks were completed with more detailed taxonomic studies published up to August 2003. Note that for the many controversial areas of lissamphibian phylogeny, a conservative approach was adopted. The resulting synoptic phylogenetic taxonomy of lissamphibians and the corresponding occurrences in the Late Jurassic–Eocene interval

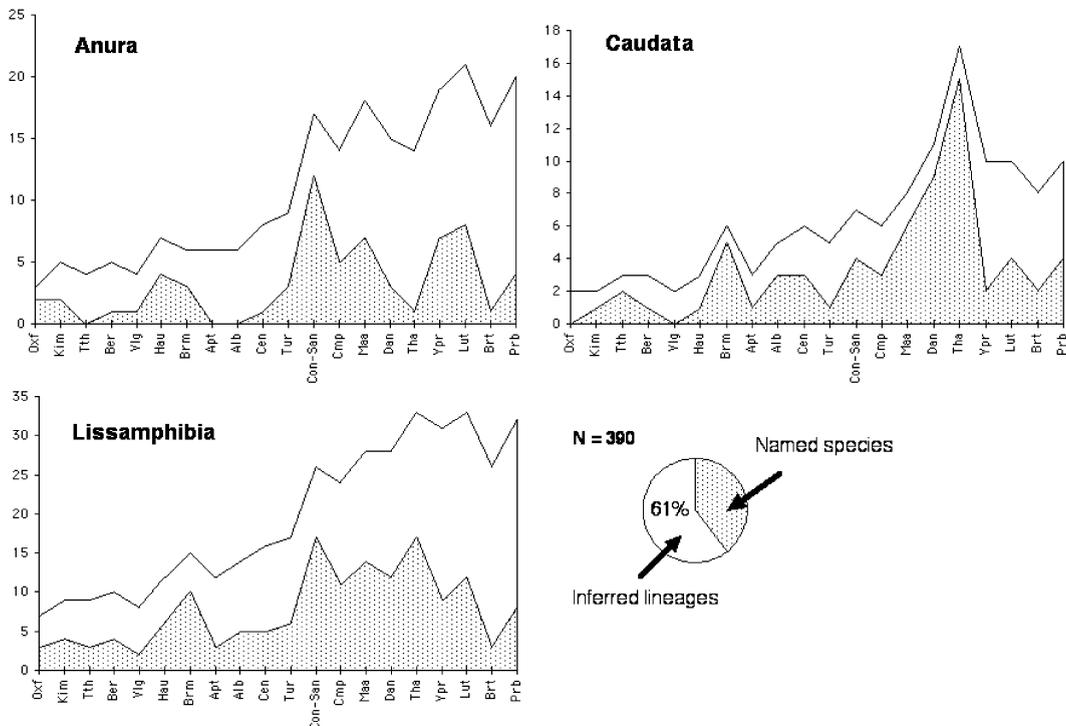


Fig. 7. Raw species diversity (in grey) and minimal lineage diversity (upper line) of anurans (upper left graph), caudates (upper right graph), and all lissamphibians (lower left graph) in the Oxfordian–Priabonian interval. The pie chart shows the proportion of named species and inferred lineages for all lissamphibians. N is the total number of lineages in the studied interval. Ordinate axes not to scale. Stage abbreviations after Harland et al. (1990).

are given at web site <http://paleodb.org/public/data/lissamphibia>.

The timescale used in the analyses includes the 20 standard marine stages ranging from the Oxfordian to the Priabonian, at the exception of the Coniacian and Santonian that were lumped into a single unit in order to reduce the variance in durations (6.28 ± 2.6 myr). Poorly dated occurrences were homogeneously fitted within these stages, but alternative temporal distributions yield similar diversity patterns (Fara, 2001b). The Jurassic–Cretaceous part of the timescale is taken from Gradstein et al. (1994, 1995, 1999), the Palaeocene–Eocene part relies on Berggren et al. (1995). The correlation of the North American Land Mammal Ages (NALMA) in the Upper Cretaceous follows the scheme used in Foote et al. (1999). The biochronological correlations of NALMA in the Palaeogene are taken from Woodburne and Swisher (1995), McKenna and Bell (1997), and Prothero (1998). The South American Land Mammal Ages (SALMA) follow the work of Flynn and Swisher (1995), and the correlation of the European Land Mammal Ages is based on Legendre and L ev eque (1997) and McKenna and Bell (1997).

In terms of analytical choices, the qualifiers of open nomenclature ‘cf.’ and ‘?’, and the words ‘tentatively’ or ‘probably’ were not considered to affect the taxonomic assignments, so that statements such as ‘Taxon A’ and ‘cf. Taxon A’ were deemed equivalent. In contrast, the qualifier ‘aff.’ was regarded as defining particular taxonomic entities (i.e., ‘Taxon A’ and ‘aff. Taxon A’ were considered two different taxa). Note that these analytical choices have virtually no impact on the results presented below. Similarly, the role of probable paraphyletic groups (e.g., Discoglossoidei, Mesobatrachia, see Sanch ız, 1998) proved to be negligible when computing the lineage diversity of lissamphibians.

5.2. Results

The first point of interest is the temporal distribution of fossil occurrences and the taxonomic level at which they are diagnostic. This was investigated by computing, for each time unit, the absolute and relative frequency of lissamphibian records diagnostic at the species level, records of genera indeterminate at the species level, and records indeterminate at the generic level. Fig. 6A shows the heterogeneous dis-

tribution of lissamphibian occurrences through time. There are few records prior to the Turonian, but that changes dramatically in the Coniacian/Santonian–Maastrichtian interval. In the Palaeogene, the pre-Priabonian stages show a number of occurrences in between these two Mesozoic extremes (about 30–40 records per stage). The high number of Priabonian occurrences is mainly due to detailed reports of the prolific sites from the Quercy region, France (Fara, 2001b). Despite this absolute heterogeneity in the number of occurrences, there are, on average, as many occurrences of species as occurrences indeterminate at the generic level throughout most of the Oxfordian–Priabonian interval (Fig. 6B). Records of genera indeterminate at the species level are virtually absent before the Cenomanian, and they represent on average only 18% of all lissamphibian occurrences. By contrast, two thirds of the records in the Aptian–Cenomanian interval are indeterminate at the genus level. As a whole, specifically indeterminate occurrences (SIOs) account for about 60% of the total number of reported lissamphibian records.

Fig. 7 shows raw and lineage diversity of anurans, caudates, and all lissamphibians in the Oxfordian–Priabonian interval. The raw species diversity pattern illustrates the major shortcoming of the taxic approach. Indeed, there are several gaps in the temporal distribution of the large clades Anura and Caudata, since there

Table 2

Autocorrelation coefficients r (measured for a lag of 1) and their significance level for lineage and raw species diversity curves

Diversity data	r	Significance level
<i>Sampled-in-bin data</i>		
Raw Anura	0.271	N.S.
Lineage Anura	0.865	$p < 0.001$
Raw Caudata	0.367	N.S.
Lineage Caudata	0.767	$p < 0.001$
Raw Lissamphibia	0.452	$p < 0.05$
Lineage Lissamphibia	0.924	$p < 0.001$
<i>Boundary-crosser data</i>		
Raw Anura	0.401	N.S.
Lineage Anura	0.942	$p < 0.001$
Raw Caudata	0.549	$p < 0.02$
Lineage Caudata	0.933	$p < 0.001$
Raw Lissamphibia	0.45	N.S.
Lineage Lissamphibia	0.964	$p < 0.001$

N.S. = non-significant.

are no *named* species of frogs unambiguously reported from the Tithonian, Aptian, and Albian stages; and the same is true for caudates in the Valanginian stage. The nonsense of nil species diversity *within* the range of these clades clearly underscores the problem of discarding evolutionary continuity at a given taxonomic level. Raw species diversity curves also show local peaks in the Coniacian–Santonian and Thanetian stages for anurans and caudates, respectively. The former diversity peak is clearly linked to [Rocek and Nessov's \(1993\)](#) prolific description of new fossil frogs from Uzbekistan, and this single reference accounts for 75% of species diversity in that time interval. The latter diversity peak corresponds to the fortuitous reports of 15 caudate species from 22 localities in North America, Europe, and Asia.

[Fig. 7](#) illustrates the major impact that specifically indeterminate occurrences (SIOs) and principles of minimal evolutionary continuity have upon lineage diversity estimates. Inferred lineages ensure the temporal continuity of large clades throughout their range,

and they represent 61% of the corrected lissamphibian diversity (pie chart in [Fig. 7](#)). Among these inferred lineages ('corrections'), 40% are based only on SIOs (mainly specifically indeterminate genera), while the remaining 60% can be inferred from minimal evolutionary continuity alone (even when intervening SIOs could be used).

Lineage diversity curves show broadly similar patterns to raw diversity curves, although they differ more substantially in later stages. In order to quantify this overall shape similarity, the non-parametric Spearman rank–order correlation coefficients were computed for each pair of curves ($r_s = 0.686$ [Anura]; $r_s = 0.824$ [Caudata]; and $r_s = 0.772$ [Lissamphibia]). However, the significance of these values is difficult to assess since most of the time series studied here show autocorrelation ([Table 2](#), see also [McKinney, 1990](#); [Alroy, 2000b](#); [Alroy et al., 2000](#) for discussions).

Whether due to Lagerstätten or monographic/taxonomic effects, biases affecting the diversity within particular time units should partly vanish when

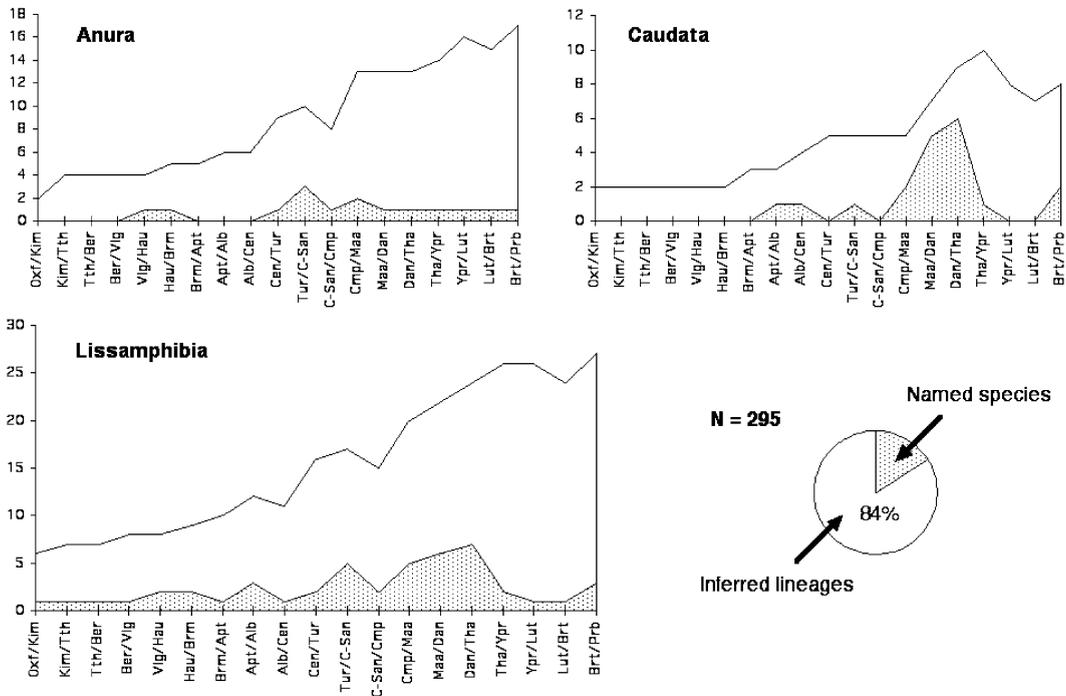


Fig. 8. Raw species diversity (in grey) and minimal lineage diversity (upper line) computed for boundary crossers among anurans (upper left graph), caudates (upper right graph), and all lissamphibians (lower left graph) in the Oxfordian–Priabonian interval. The pie chart shows the proportion of named species and inferred lineages for all lissamphibians. *N* is the total number of boundary-crossing lineages in the studied interval. Ordinate axes not to scale. Stage abbreviations after [Harland et al. \(1990\)](#).

boundary crossers are employed. However, this approach is also expected to reduce raw taxonomic samples because of short stratigraphic ranges, especially at species level. Fig. 8 shows the effect of counting boundary crossers instead of sampled-in-bin taxa. By discarding singletons, the approach decreases the amplitude of most diversity peaks observed with temporal bins (see Fig. 7 for a comparison). For anurans, the monographic effect

previously observed in Coniacian–Santonian stages partly remains at the Turonian/Coniacian boundary because the Bissekty Formation studied by [Rocek and Nessov \(1993\)](#) encompasses this limit. Although boundary crossers yield most diversity patterns observed for taxa in temporal bins, the resulting reduction in taxonomic sample size becomes intolerable here for raw estimates (–69% for named lissamphibian species throughout the Oxfordian–Priabo-



Fig. 9. Comparison of raw species diversity (dotted line), raw genus diversity (thick line), and minimal lineage diversity (plain line) of lissamphibians in the Oxfordian–Priabonian interval. (A) Computations made for taxa present in time bins. (B) Computations made for taxa crossing inter-stage boundaries. Note that generic counts are higher than raw species estimates in both cases.

nian interval). Fig. 8 shows how the use of boundary crossers aggravates the above-mentioned problem of intra-range discontinuity for lissamphibian groups. For example, raw species diversities of anurans and caudates are virtually nil throughout most of the Late Jurassic and Early Cretaceous, although species of both clades were evidently present in that time span. It is therefore not surprising to see SIOs and evolutionary continuity considerably inflating lineage diversity patterns. Fig. 8 confirms this dramatic influence for lissamphibians, since the corrections affect all groups and they bring 84% of the corrected *minimum* lineage diversity. Also, shape similarity for each pair of raw and lineage diversity curves is less pronounced than for sampled-in-bin curves (Spearman rank–order correlation coefficients: $r_s = 0.654$ [Anura]; $r_s = 0.591$ [Caudata]; and $r_s = 0.493$ [Lissamphibia]).

As expected, boundary-crosser curves show less variation than sampled-in-bin curves (see discussion in Section 4), and they both have globally similar amplitudes for lineage diversity estimates.

Finally, how does the minimal lineage-level diversity compare with the raw generic diversity? Fig. 9 presents the raw species and generic diversities of lissamphibians together with the conservative count of lineages. The observation that there are larger raw samples of genera than of species in most time bins (Fig. 9A) and for all temporal boundaries (Fig. 9B) can seem awkward, since a genus contains at least one species (see also Alroy, 1996). This pattern stems from both a low species/genera ratio and from the occurrences of specifically indeterminate genera (18% of all lissamphibian occurrences in the studied interval, see Fig. 6). This counter-intuitive result does not arise from the ‘poor’ fossil record of species per se, it rather stems from the commitment to work at a given taxonomic level without integrating phylogenetic information and fossil evidence diagnostic at higher taxonomic levels (SIOs). Fig. 6 shows that records diagnosable at the species level represent only 40% of all known lissamphibian occurrences. By using such restricted samples and by discarding evolutionary continuity, the taxic approach is the source of the problem. Whether for temporal bins or boundary crossers, the lineage diversity curve captures the same signal as the raw generic curve, and with a logically larger sample (Fig. 9). Interestingly, this result repli-

cates the observations made by Alroy (1996, 1998) with his dataset on North American mammals.

6. Discussion

6.1. Analytical aspects

In the face of the lissamphibian fossil record, the minimal lineage-level method seems to be the only practical solution for assessing diversity. This does not make the fossil record any better, but at least it extracts the most information from available palaeontological and phylogenetical evidence. This is true for clades with abundant occurrences (see for example Alroy’s (1996, 1998, 2000b) studies on Cenozoic North American mammals), but it becomes of primary importance for clades with scanty occurrences. The method discussed here assesses diversity at the lowest taxonomic level, thus maximizing the sample of taxonomic units (whether named or inferred). It defines a conservative baseline above which lies the true species diversity and it integrates (1) all informative occurrences, whatever their level of diagnosticity, and (2) the phylogenetic background that maintains a minimal evolutionary continuity among these units. For lissamphibians, these two factors minimally increase raw species diversity by 300–400%. In fact, we can expect these proportions to become even larger as our knowledge of phylogenetic relationships improves, since higher phylogenetic resolution means turning more hypothetical lineages into sister taxa.

Although the lineage-level diversity estimates are based on a much larger taxonomic sample than raw estimates, they both capture the same overall patterns for sampled-in-bin lissamphibian taxa (Figs. 7 and 9A). A similar observation was made by Alroy (1996) in his study of Tertiary North American mammals, with the difference that Alroy’s lineage diversity estimate was sampling-standardised and was corrected only with occurrences of specifically indeterminate genera. The test presented in Section 4 further suggests that the lineage method is appropriate for capturing the temporal variations of diversity when the amount of data is randomly reduced and the diagnosticity of occurrences is randomly degraded.

Estimating minimal lineage diversity does not, however, solve all the problems. First, Fig. 5 shows

a major limitation of the approach: the correct magnitude of diversity variations is poorly recovered. The discrepancy between the original and the reconstructed diversity patterns might therefore vary in time, merely because sampling is itself heterogeneous in time (e.g., Raup, 1972; Smith, 2003). In turn, this might prevent the recovery of the accurate temporal pattern of diversity. On that issue, further theoretical investigations will be necessary for comparing the performance of the lineage method with the taxic and the phylogenetic approaches. Also, the effect of parameters such as phylogenetic structure, time-bin duration, species to genus ratio, and diagnosticity remains to be examined.

Second, sampling-standardisation techniques for locality-level compilations (Miller and Foote, 1996; Alroy, 1996, 2000a,b; Alroy et al., 2001) could not be applied here because the sample of lissamphibian occurrences is too small. The same is true for extinction and origination rates. They are not described here because the samples are by far too small, even at the stage level, and this problem is exacerbated because the method decreases the number of turnovers by discarding some of them as possible pseudo-turnovers (see also Alroy, 1996).

Third, a lineage-level study focusing on a limited time interval requires a compilation of occurrences within that time span, and also of some informative occurrences outside it. When extant representatives are used to infer past lineages, one might fear a 'pull of the Recent' effect (Cutbill and Funnell, 1967; Raup, 1972). One alternative consists of taking known fossil occurrences instead of extant taxa (e.g., Jablonski et al., 2003). Here, a huge majority of the range extensions towards the Recent are based on actual post-Priabonian fossil occurrences of lissamphibians. Indeed, virtually all lissamphibian groups have fossil representatives in the Oligocene–Pleistocene interval (e.g., Estes, 1981; Sanchíz, 1998; Fara, unpublished data). Finally, note that the method used in this work is always sound for *global* diversity estimates. Regional or local diversity surveys cannot systematically assume lineage continuity because of migrations, range contractions, and local extinctions. Therefore, this problem becomes particularly crucial at higher taxonomic levels (compared to a species, a family is more likely to become locally extinct and to reinvade the area).

Robeck et al. (2000) suggested that taxa assigned to different taxonomic levels should be used in diversity analyses in order to compensate for the vagaries of the fossil record and for variable sampling regimes. Here, I advocate inferring diversity at the lowest taxonomic level by considering fossil occurrences and phylogenetic information at all levels of the hierarchy. Nevertheless, both studies reach a similar conclusion: it seems preferable to abandon the old commitment of working at a single taxonomic level in diversity analyses.

6.2. *Lissamphibian palaeodiversity*

Lissamphibian lineage diversity seems to have increased exponentially from the end of the Jurassic to the Eocene. Indeed, linear regressions through the log transformed diversity values show good fits, with a Pearson's product–moment correlation coefficient r of 0.96 for sampled-in-bin diversity taken at both stage mid-points and end-points, and with an r of 0.98 for boundary-crosser diversity (Fig. 10). In turn, this suggests a constant rate of diversification for the clade, i.e. speciation and extinction rates seem to have remained roughly constant through the studied interval. However, more data are required to see whether this evolutionary dynamics has remained the same throughout the entire history of the clade. Concurrent diversity estimates based on boundary crossers and sampled-in-bin taxa suggest that a majority of local variations are due mostly to Lagerstätten or monographic effects (e.g., local diversity maxima in the Barremian and Coniacian/Santonian stages; Fig. 7).

The absence of any diversity drop at the Jurassic/Cretaceous and Cenomanian/Turonian boundaries is hardly surprising since no significant global extinctions have been recognised for continental vertebrates at these times (Benton, 1985; Hallam and Wignall, 1997; Fara, 2000). The survival of virtually all lissamphibian lineages at the Cretaceous/Tertiary (K/T) boundary is more compelling. The present work demonstrates the strength of this evolutionary signal, despite the fact that the study incorporates phylogenetic information and is conducted at the lowest taxonomic level. This survival pattern is impressively consistent across analyses made at various temporal, geographic, and taxonomic scales. Indeed, peculiar survival of amphibians, and more generally of fresh-

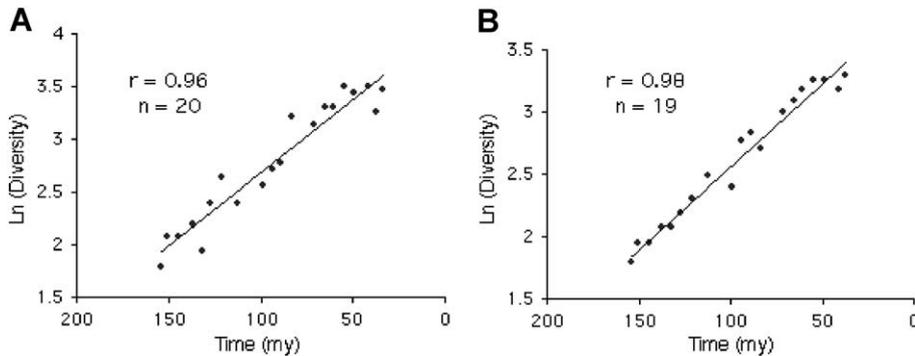


Fig. 10. Log lissamphibian diversity plotted against geological time in the Oxfordian–Priabonian interval. (A) Sampled-in-bin diversity plotted at geological stage end-points. The pattern and the statistics are similar when the geological stage mid-points are taken for the x -axis. (B) Boundary-crosser diversity. In both cases, linear regressions show good fits, suggesting an exponential diversification pattern for the clade Lissamphibia. r : Pearson's product–moment correlation coefficient; n : sample size.

water taxa, has been observed in both local and global studies (Bakker, 1977; Van Valen and Sloan, 1977; Hutchinson, 1982; Clemens, 1986; Sheehan and Hansen, 1986; Sheehan and Fastovsky, 1992; Buffetaut, 1984, 1990; Archibald and Bryant, 1990; Prasad and Khajuria, 1995; Markwick, 1998; Fara, 2000; Bossuyt and Milinkovitch, 2001). The most plausible explanation is that freshwater habitats mainly rely on allochthonous resources, and the latter were less affected by temporary drops in primary productivity at the K/T boundary (see Sheehan and Hansen, 1986; Sheehan and Fastovsky, 1992; Hallam and Wignall, 1997; Fara, 2000 and Milner et al., 2000 for discussions). However, these models are not sufficient for explaining the survival of other parts of the fauna, such as terrestrial squamates (e.g., Archibald and Bryant, 1990; Kardong, 1997; Milner et al., 2000; Fara, 2001b).

So far, the main arguments against long-term, climate-related hypotheses for K/T extinctions have come mainly from the crocodylian fossil record (Buffetaut, 1980, 1984, 1990; Markwick, 1994, 1996, 1998; but see also Milner et al., 2000). Because lissamphibians have been rather conservative in their morphology, ecology, and certainly physiology since they first appeared (Sanchíz, 1998; Rocek, 2000), their fossil record may also be reconsidered in view of modern ecological data. In particular, the recent interest in environmental distress syndromes related to modern global warming has stimulated a large number of ecological studies on frogs and salamanders, (e.g.,

Beebee, 1995; Pounds, 2001; Pounds et al., 1999; Andrews, 2000; Kiesecker et al., 2001). For these groups, population decline, shifts in breeding/nesting strategy, and sensitivity to pathogen outbreaks are commonly climate-induced, although the mechanisms involved are extremely complex and may have different scaling (Beebee, 1995; Pounds, 2001; Pounds et al., 1999; Kiesecker et al., 2001). Together with the results presented here, these observations suggest that long-term climatic disruption is not a viable hypothesis for the K/T extinctions. Finally, note that the amphibian extinction event mentioned for the Eocene/Oligocene boundary (Rage, 1984b; Rocek and Rage, 2000) has a very low amplitude and it is limited to Europe.

Although the diversity of lissamphibians increased gradually through the Late Jurassic–Eocene interval, this pattern does not correspond to a gradual improvement of the quality of their fossil record. In particular, early Tertiary occurrences do not outnumber Late Cretaceous ones, and their preservation quality—in terms of diagnostic completeness—is not superior (Fig. 6). A similar observation can be made with the fossil record of other tetrapod groups, such as crocodylians (Markwick, 1996, 1998) and squamates (Fara, 2001b). This is in contradiction with hypothetical megabiases affecting the distribution and preservation of Cretaceous continental tetrapods, as suggested by some authors (e.g., Cooper and Fortey, 1998; Kumar and Hedges, 1998; Eastal, 1999; Smith, 2001a; Smith and Peterson, 2002). In the

debates on the apparent Cenozoic radiation of modern birds and mammals, it seems that a *general* biasing factor for the Cretaceous fossil record is not a viable hypothesis. Otherwise, why should these modern groups be dramatically absent from Cretaceous rocks when other terrestrial tetrapods, found in similar assemblages, are homogeneously represented on both sides of the K/T boundary?

7. Conclusions

Current paradigms on the trajectory of biodiversity through time are either based on studies made at high taxonomic level and/or they are restricted to groups with an abundant fossil record (e.g., Sepkoski, 1984, 1996; Benton, 1995). But things are changing. Global locality-level compilations are emerging in the prospect of a more comprehensive and accurate picture of palaeodiversity (see, for example, Alroy et al., 2001 and Alroy, 2003), and this endeavour is paralleled with the development of more sophisticated analytical methods (e.g., Foote, 2000; Alroy, 2000a). However, the fossil records of many groups are still deemed too poor for diversity analysis, especially at the species level. It is argued here that practical solutions must be found for integrating as many data as possible in diversity estimates. This seems to require the abandonment of old commitments such as working at high taxonomic levels, disregarding poorly diagnostic occurrences, and neglecting current phylogenetic knowledge. Clearly, this will not revolutionize palaeodiversity estimates of clades such as foraminiferans, bivalves, or North American Cenozoic mammals, but it might prove essential for groups with taxonomically and diagnostically poorer fossil records. The present study advocates that (1) fossil occurrences should be equally reported whatever their level of diagnosticity; (2) maximum taxonomic details should be provided in faunal and floral studies. This includes the number of ‘forms’ thought to be present at a locality, as well as the eventual taxonomic exclusions within inclusive clades (e.g., ‘non-discoglossid anuran’); (3) database systems should allow SIOs to be compiled and treated in the same way as other taxonomic records; and (4) a minimal phylogenetic continuum must be maintained among the taxonomic units used in the analysis.

The present work provides the first quantitative assessment of lissamphibian diversity and it shows the virtually extinction-free gradual rise of this clade during the Late Jurassic–Eocene interval. It argues not only against a long-term climatic disruption at the K/T boundary, but also against hypothetical megabiases in the Late Cretaceous fossil record of small terrestrial vertebrates.

At a time when the impact of human activities upon modern biodiversity is a major concern, much work remains to be done for adequately placing this crisis into historical perspective. We can just agree with Foote (2000) when he writes: ‘the fact that methods for uncovering these [diversity] signals are still being developed attests to the vibrancy of paleontology today’. It will be interesting to see to what extent this methodological Renaissance will affect the main results that traditional approaches have offered so far.

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