

SPECIAL

Sea-level variations and the quality of the continental fossil record

E. FARA^{1,2}

¹Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK

²Present address: Institut des Sciences de l'Évolution, Université Montpellier II, Place Eugène Bataillon, 34095 Montpellier cedex 5, France
(e-mail: efara@isem.univ-montp2.fr)

Theoretical and empirical studies suggest that sea-level change was a fundamental parameter determining the distribution of fossil marine organisms. Although a similar relationship is generally assumed for the continental fossil record, this intuition remains speculative. Quantitative evidence reveals no correlation between sea-level variations and the distribution of continental tetrapods in the Late Jurassic–Eocene interval. The quality of the continental fossil record depends on many more factors than just eustatic changes.

Keywords: Sea level, fossil record, Cretaceous, tetrapods.

Since Chamberlin (1909), and most notably after Newell (1967), the frequent correlation between sea-level changes and major extinction events has attracted much attention. The relationship is often explained either by marine regressions and the species-area effect, or by transgressive phases associated with dysoxic/anoxic conditions (e.g. Hallam & Wignall 1999; Smith *et al.* 2001). However, this putative causal relationship has first to pass the test of the stratigraphic record. In this context, the Cretaceous period offers an ideal field of investigation since it witnessed one of the highest sea levels ever reached on a global scale (Haq *et al.* 1988). For example, Smith *et al.* (2001) showed that diversity patterns of mid-Cretaceous macrobenthic invertebrates in Western Europe mainly reflect a taphonomic megabias controlled by sea-level changes rather than genuine evolutionary phenomena. Smith (2001) iterated this cautionary statement in his extended analysis of the relationship linking eustatic level, surface outcrop area, and observed taxonomic ranges in the post-Palaeozoic marine sediments of the same area. These critical studies demonstrate the fundamental role played by sea-level variations in shaping diversity patterns as observed in the *marine* fossil record. But can we extrapolate a similar relationship with the quality of the *continental* fossil record?

Many authors have speculated that the mid-Cretaceous eustatic highstand reduced the number of depositional environments (mainly low-land areas) that are usually favourable to the preservation of terrestrial faunas (e.g. Hedges *et al.* 1996; Sereno 1997; Cooper & Fortey 1998; Smith 2001). Not only did sea-level act directly on the number of these environments, but it also made them more susceptible to erosion by perching them

higher on the landmasses, or so it is claimed (e.g. Estes 1965; Sereno 1997). Although intuitive, the assertion that the quality of the continental fossil record is 'seriously biased by sequence architecture' (Smith 2001) remains speculative and has yet to be quantified. Here, I address this issue from a quantitative viewpoint by comparing global sea-level variations in the Late Jurassic–Eocene interval with (i) the distribution of gaps within the stratigraphic ranges of non-marine tetrapod families and (ii) the distribution of localities yielding lissamphibians and continental lepidosaurs.

Materials and methods. Estimates of Late Jurassic to Eocene long- and short-term sea-levels are taken from Haq *et al.* (1988), along with the alternative estimate of non-marine surface area derived by Smith *et al.* (1994). The time scale follows the work of the former authors. Gap analysis for continental tetrapod families is taken from Fara & Benton (2000), to which the reader is referred for technical details. This approach gives the proportion of 'Lazarus' taxa (Jablonski 1986) relative to the overall diversity in each time interval (see also Fara 2001a). If preservation and sampling quality vary over time with the sea level, then we expect a clustering of Lazarus taxa in time units characterized by eustatic highs.

The problem is also addressed at the locality level and with the power of modern relational databases. A comprehensive compilation was built to record 1957 fossil occurrences of the clades Lissamphibia (frogs, salamanders, caecilians) and Lepidosauria (squamates and rhynchocephalians) in 557 localities within the Late Jurassic–Eocene interval (Fara 2001b). This dataset contains a sample of 227 maximally distinguishable continental lissamphibian- and/or lepidosaur-bearing sites. In order to homogenize the stratigraphic and geographic extent of these localities, some of them were grouped when they belonged to the same stratigraphic unit and were located within a geographic radius of about 50 km. The resulting homogeneous sample of 196 localities is used here, but note that the results presented below are similar for both locality samples. If sea level has any effect on the distribution of continental localities, then we would expect a negative correlation between these two parameters.

Results. Figure 1 compares the estimate of sea-level variations, the land surface area, and the proportion of Lazarus tetrapod families in the Oxfordian (Late Jurassic)–Ypresian (early Eocene) interval. The first two parameters are negatively correlated (see Smith *et al.* 1994), especially before the Campanian–Maastrichtian. At this stage, the non-marine surface area apparently reaches a minimum, before increasing rapidly in the early Tertiary. The sea-level curve of Haq *et al.* (1988) shows less variation in amplitude in that time span. However, as argued by Hallam (1990), the end-Cretaceous regressive phase may have been more pronounced than the results of Haq *et al.* (1988) suggest. As a whole, the independent estimates of sea level and land area are, reassuringly, in good agreement. Because Smith *et al.* (1994) provided numerical values for the latter variable, these data are used in the statistical tests presented below.

The absence of correlation between relative Lazarus frequency and sea-level/non-marine surface area is clear from Figure 1 (Spearman rank-order correlation coefficient $r_s = -0.32$, $n = 18$, one-tailed test, non-significant). Although the Cenomanian–Santonian interval hosts many Lazarus tetrapod families, these are not significantly more frequent than in the early part of the Cretaceous where short- and long-term sea levels reached a local minimum in the Valanginian (Haq *et al.* 1988). Reciprocally, Tithonian and Campanian–Maastrichtian sea-level highs are accompanied by proportions of Lazarus families lower than 25%. Note also that Lazarus frequencies are comparable in the Campanian–Maastrichtian and Danian–Ypresian intervals.

Figure 2 compares sea-level/non-marine surface area with the number of continental lissamphibian- and lepidosaur-bearing

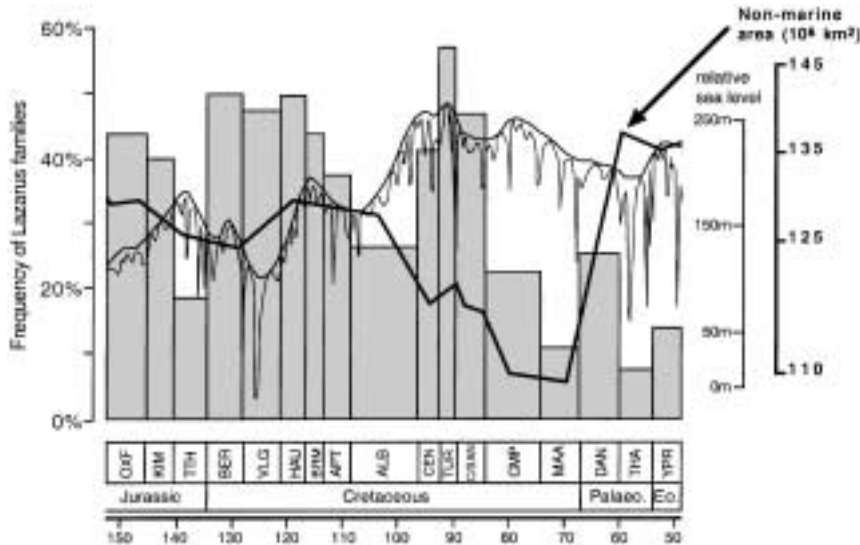


Fig. 1. Relative frequency of Lazarus families among continental tetrapods (histogram) compared with relative short- and long-term sea levels (thin and medium lines, respectively) and non-marine surface area (thick line) in the Callovian–Ypresian interval. Stage abbreviations after Harland *et al.* (1990), Palaeo., Palaeocene; Eo., Eocene. See section ‘Materials and methods’ for references.

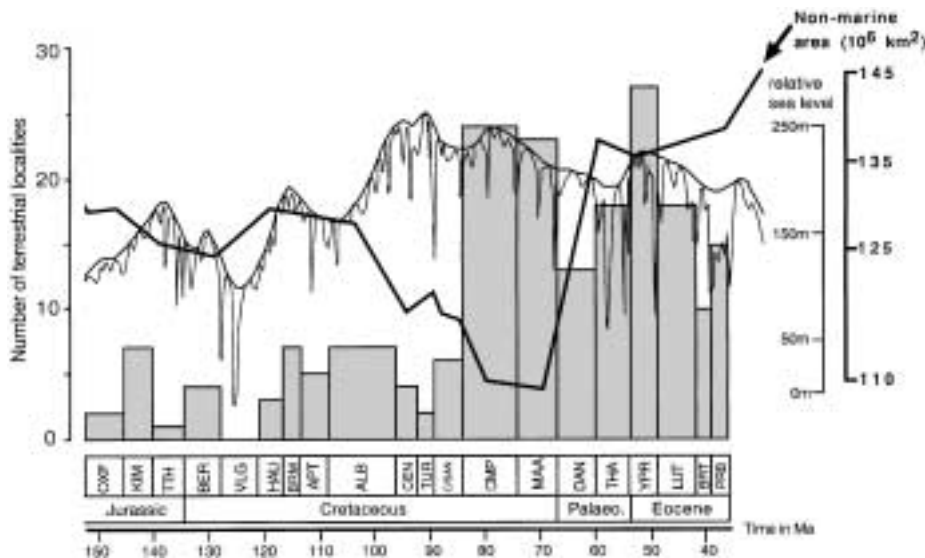


Fig. 2. Number of localities yielding lissamphibians and continental lepidosaurs (histogram) compared with relative short- and long-term sea-levels (thin and medium lines, respectively), and non-marine surface area (thick line) in the Oxfordian–Priabonian interval. Note the absence of any correlation between the former variable and the two latter. Abbreviations and conventions as in Figure 1.

localities in the Oxfordian (Late Jurassic)–Priabonian (late Eocene) interval. Although the two distributions are expected to show some correlation, Figure 2 presents a rather different picture. This graphic impression was tested statistically for the entire interval (20 time units), and for the interval Barremian–Priabonian (14 time units). The latter avoids the small samples observed in preceding time bins and that may affect the investigations (since the number of localities cannot be negative). A Spearman rank-order correlation test supports the lack of correlation between non-marine surface area and the number of fossil localities in both cases ($r_s = 0.231$, $p < 0.25$ (entire interval); and $r_s = 0.169$, $p > 0.25$ (Barremian–Priabonian)).

Discussion and conclusions.

Is sea-level a major factor determining the quality of the continental record? A positive answer to this question is appealing because eustatic highs reduce the emerged surface area. In turn, many palaeontologists have taken this paradigm for granted when they happened to face gaps in the continental Cretaceous fossil record (Estes 1965; Sereno 1997; Wolfe & Kirkland 1998; Smith 2001). This view also prevails among proponents of the

‘molecular clock’ hypothesis, whose results suggest a large hiatus in the distribution of Cretaceous continental tetrapods (Hedges *et al.* 1996; Cooper & Penny 1997; Kumar & Hedges 1998).

The intuitive appeal of a negative correlation between sea-level and the quality of the continental record is also stimulated by studies of fossil marine organisms. For instance, the works of Smith *et al.* (2001) and Smith (2001) demonstrate the close link between eustatic variations and observed distributions of marine invertebrates. Smith (2001) extrapolated these observations to explain the ‘death of Late Cretaceous terrestrial vertebrate faunas worldwide’. However, several lines of evidence render this extrapolation dubious. First, there is a problem of scale. Such very welcome empirical and theoretical studies of stratigraphic ranges and sequence architecture are usually limited in their temporal, geographic, sedimentological, and taxonomic extent (Holland 1995; Goldman *et al.* 1999; Holland & Patzkowsky 1999; Smith *et al.* 2001). Are regional distributions of marine invertebrates really good proxies for drawing inferences about the quality of the continental fossil record on a global scale?

Second, there are many cases suggesting that the continental Cretaceous fossil record is relatively independent from sea-level changes. Eustatic highs in the Campanian and Maastrichtian did not prevent most tetrapod groups from occurring abundantly in these time units (e.g. Weishampel 1990; Markwick 1998; and Figs 1 and 2). Reciprocally, the most distressing hiatus within the distribution of Cretaceous tetrapods occurs in the Berriasian–Hauterivian interval (Fara & Benton 2000), a time when long- and short-term sea levels reached local minima (Haq *et al.* 1988). It remains true, however, that the highest stand in Cenomanian–Turonian times is accompanied by a globally depauperate continental fossil record (Benton 1989; Fara & Benton 2000).

Third, the present study failed to find any correlation between sea-level changes and two alternative estimates of the quality of the continental record. The number of localities has proved a good proxy since it is directly correlated with the number of occurrences and the corresponding taxonomic diversities of lissamphibians and lepidosaurs (Fara 2001b).

And fourth, the independence of the continental record relative to sea levels is not surprising, since many factors can help this decoupling. These include original biotic distributions, taphonomic parameters, erosion processes, sedimentological input, basinal topologies, and sampling. For the continental fossil record, such parameters and their evolution through time cannot be seen as a simple linear series of factors subsidiary to sea-level changes.

Although ‘megabiases in the fossil record continue to mislead palaeontologists’ (Smith *et al.* 2001), it seems also imprudent to extend spatially, temporally, taxonomically, and ecologically regional observations made in the marine fossil record. The extrapolation to the continental realm is intuitive, but it is currently not supported by quantitative evidence. Therefore, sea-level change seems at present a weak argument for the supposed 60 million year-long gap in the Cretaceous fossil record of terrestrial vertebrates as suggested by some molecular results (Hedges *et al.*, 1996; Cooper & Penny 1997; Kumar & Hedges 1998).

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