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# Tertiary mammal turnover phenomena: what happened to the herpetofauna?

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Since the Paleogene and Neogene Mammal Units are based on mammal turnovers that are the expression of more general changes in biodiversity, we question whether other vertebrates might contribute to define the biodiversity dynamics and consequently the limits of the stratigraphic units. Theoretically, due to their high sensitivity to environmental factors, amphibians and reptiles could act as precise signals of changes in biodiversity. How much did the European herpetofauna evolve during the Cenozoic? Did it experience any turnover phenomenon? Is it possible to find any synchrony in mammalian and herpetofaunal turnover? Focusing on some major mammal turnovers (i.e. those limiting different epochs) it appears evident that also the herpetofauna experienced some more or less abrupt changes that are sometimes perceivable at suprabasinal scale but are often detected in relatively restricted areas.

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## INTRODUCTION

Vertebrate paleontologists have a long and rich tradition of placing vertebrate evolution into stratigraphic and biochronologic contexts. However, the term biochronology was rarely used prior to the 1970s, when the application of radiometric dating became widespread in geology, and the distinction was made between radiochronology and biochronology as different aspects of geochronology (*cf.* Berggren & Van Couvering 1974). Based on the original definition of a 'biochron' being 'a time unit whose measure is the endurance of organic character' (Williams 1901), Berggren & Van Couvering (1974)

suggested the application of term 'biochron' for units of geologic time that are based on paleontologic data without reference to lithostratigraphy or rock units. On this conceptual basis, specific mammal biochronologic scales have been constructed for North and South America and Europe extensively, but also for Asia, Africa and Australia (*cf.* Lindsay 2001).

For the Paleogene and Neogene of Europe, mammal paleontologists have developed two unit systems, MP and MN respectively, discussed among others, by Schmidt-Kittler *et al.* (1987), Vianey-Liaud (1997), Mein (1975, 1989) and De Bruijn *et al.* (1992). Although it has been stressed that units lack boundaries

by definition (De Bruijn *et al.* 1992, Sigé & Legendre 1997), an implicit idea of boundaries cannot be denied (Van der Made 1997) so that Agustí (1999) recently proposed "to re-open the discussion on the MN unit system and to re-define and correlate them in terms of faunal dispersals and extinctions (FAD and LAD)". The 'borders' of these units (in other words, the reference localities of each unit) can therefore be defined with the aid of marked changes in the composition of the Tertiary mammal assemblages, changes that are relatively well known (for West Europe: Agustí *et al.* 2001) and frequently described and analysed in terms of dispersal events, turnover, provinciality, similarity and diversity (cf. Bernor *et al.* 1996, Van der Made 1997). Fortelius *et al.* (1996a,b) recently synthesised the theoretical and practical aspects of the study of these changes creating solid bases for well-grounded future analyses.

If one considers that a mammal turnover is simply a signal of complex biodiversity dynamics (e.g. addition of origination and extinction of populations, taxa and communities; McKinney 1998) that results from changes in terrestrial paleoenvironments, it is worth noting that the rest of the terrestrial vertebrate fauna has been taken into little account in the definition of these dynamics, perhaps also because it is usually not studied for stratigraphic purposes. It has been long said that amphibians and reptiles have little or no stratigraphic significance. More in particular, as far as amphibians and reptiles are concerned, the terms 'turnover' and 'biostratigraphy' are seldomly found in the European paleoherpetological literature (interesting exceptions are represented by Vigne *et al.* 1997, and Gleed-Owen 1999). This is perhaps related to the widely accepted opinion that amphibians and reptiles evolved gradually and that in the late Quaternary, contrary to the mammals, they show little or no change (Holman 1995, 1998). In any case, this assumption does not necessarily indicate stability or gradual evolution throughout the Cenozoic. Assuming that synchronous changes between herpeto-

faunas and mammal faunas can be documented, then herpetofaunas should provide considerable new information from both taxonomic and a palaeoecologic points of view. This would improve the resolution of the 'boundaries' between various units based on mammals.

Theoretically, a broad analysis of the changes in the composition of European herpetofaunas is biased by some main aspects:

- the physiographic heterogeneity of different European regions through geologic ages;
- the presence of herpetological biogeographic units in pre-Pleistocene Europe (Barbadillo *et al.* 1997);
- the geographical and chronological non-uniformity of the fossil record (e.g. Paleogene amphibians and squamates are scantily represented in Italy and Central Europe);
- the different status of the paleoherpetological studies in different countries, an aspect directly related to the local research traditions (among others, French, German, Polish and Spanish paleoherpetofaunas are particularly well known).

Taking into consideration the disparities listed above, and limiting the analysis to family and genus level, in order to avoid the doubtful nature of several specific allocations, some general issues can be outlined. For the purposes of the present study crocodylians have not been considered.

## THE MAIN TURNOVERS IN EUROPE

In the past decades, the researches dealing with the fossil faunas of amphibian and reptile from the European Cenozoic have produced a huge amount of data. For example, Italy alone, whose Cenozoic fossil record has not been as extensively studied as those of other countries, offers at present more than 800 taxon/locality data combinations (Delfino 2002). Although the European record has never been object of a detailed wide scale analysis in terms of stratigraphical and geographical distribution, some major changes in the composition of the European Tertiary herpetofauna are easily detectable in correspondence with the limits

between different epochs.

### **Palaeocene/Eocene boundary**

Pleurosternid turtles, which were present in Europe during the late Palaeocene, did not survive into the Eocene. Moreover, dicampodontid salamanders temporarily disappeared from the continent. On the other hand, the earliest Eocene (MP7) is marked by immigrations, newcomers significantly increased the European herpetofauna: pelobatid frogs; podocnemid and geoemydine turtles; iguanid, agamid, gekkonid, varanid, helodermatid and ascertained lacertid lizards; scolecophidian, tropidophiid, and ruseolophiid snakes (Rage & Auge 1993, Rage 1997, Duffaud 2000). As a result, the Palaeocene/Eocene limit represents an important turnover in European herpetofaunas.

### **Eocene/Oligocene boundary**

The limit between the Eocene and Oligocene marks a prominent turnover, at least in Western Europe. Some changes can be detected at the family level, although squamates show considerable modification at the species level. By the end of the Eocene, ruseolophiid snakes became definitively extinct and leptodactylid frogs, podocnemid turtles, and iguanid lizards disappeared from the continent (Lapparent de Broin 2001, Rage & Auge 1993). Pelodytid frogs temporarily withdrew from Europe. At the species level, amphibians and non-squamate reptiles were apparently not prominently affected (Duffaud 2000) but at least three-fourths of the squamate species became extinct at the end of the Eocene (Rage 1984). At the beginning of the Oligocene (MP21), a few survivors and very rare immigrants formed a depauperated herpetofauna. During the Early Oligocene (after MP21), a combination of Asian immigrants and autochthonously evolved species increased herpetofaunal diversity. Prior to the Eocene/Oligocene limit, the European herpetofauna had an Euro-American aspect; after this event, it had an Eurasian aspect. This event is well documented in Western Europe but it is still poorly known in central and

eastern parts of the continent.

### **Oligocene/Miocene boundary**

The transition between the Oligocene and Miocene corresponds to a 'modernisation' of the European herpetofauna but the change was not an abrupt turnover. At family level, only cordylid lizards and tropidophiid snakes disappeared from Europe at the end of the Oligocene (MP30). On the other hand, only one family (viperid snakes) appeared in the earliest Miocene (MN1). However, in Western Europe, a lineage of lacertid lizards with 'molariform' teeth markedly developed during the Oligocene. At the same time the number of erylinc boids (fossorial snakes) strongly increased. Consequently, the squamate fauna at the end of the Oligocene was highly peculiar, with very high percentages of unusual lizards and fossorial snakes. This squamate fauna suddenly disappeared at the Oligocene/Miocene boundary (Rage 1987). Given that "there is not a clear criterion for separating the uppermost Oligocene terrestrial levels from those of the lowermost Miocene, the use of particular lineages excepted" (Agusti 1999; see Agusti *et al.* 2001 for a detailed discussion), the presence/absence of the above mentioned herpetofauna should be investigated in detail since they might be useful markers.

### **Other turnovers**

Apart from the three above-mentioned main turnovers, other changes have been identified, but have not been studied in a comprehensive way yet: MP22 during the Oligocene, early/middle Miocene transition (for snakes see Ivanov 2001), and perhaps MP15/MP16 in the late Eocene. Other minor changes might also be significant from a stratigraphic point of view, mainly in the Eocene and Oligocene.

### **The problem of the late Neogene**

No significant turnover can be detected among the European herpetofauna at the Miocene/Pliocene boundary although global

vegetation and faunal changes have been reported (Cerling *et al.* 1997, and reference therein quoted). Modifications in the herpetological communities are apparently scattered along the transition. As already noticed by Barbadillo *et al.* (1997) and Rage (1997), the late Neogene is apparently less affected by marked faunal changes in the sense that, at least at family level, there are only few entries and, on the whole, it seems to be dominated by a progressive decrease in diversity. The late Neogene herpetofauna consisted of a mixture of taxa that were mainly relics of the thermophilous Miocene fauna, or new immigrants from Asia or North Africa (Bailon 1991): curiously, amphibians show no direct exchange with Africa (Sanchiz 1997) but only with Asia, whereas squamates immigrate from both (Rage & Auge 1993).

All the families (as well as the most of the genera and several species) of the modern European herpetofauna possess a fossil record that goes back at least to the Pliocene when Europe was still inhabited by some families and genera that are now definitely extinct or that we can consider exotic. With the beginning of the climatic deterioration, we can perceive a whole string of extinctions and range re-arrangements. The timing of these changes is hard to define in detail since the late Pliocene (MN17) is represented by a limited number of sites. Assuming that the late Pliocene record is sufficiently informative, a sharp drop in species diversity can be perhaps identified at the middle-late Pliocene transition: after MN 16, cryptobranchid salamanders, varanid lizards, aniliid and elaphid snakes and perhaps chelydrid turtles are not found in Europe (Broin 1977, Rage 1997). This change could have been triggered by the earliest glacial-interglacial cycles and the severe coolings that Europe faced since 2,6 million years (Bertini 1995, Suc *et al.* 1995), coolings that certainly disrupted the faunal assemblages (for Italian mammals see: Gliozzi *et al.* 1997) and particularly affected the herpetofaunal communities, most ecto-

thermic members of which are highly sensitive to temperature and humidity. A general discussion of faunal changes in Europe is discussed in Azzaroli *et al.* (1988) and evidences have been reported from Spain, France, Italy (Alberdi *et al.* 1997, Gliozzi *et al.* 1997) and Eastern European countries (summarised by Vislobokova *et al.* 1993).

Although attractive, this hypothesis is perhaps biased by the fact that the presence in the middle Pliocene (MN16) of one of the more informative Pliocene herpetofaunas (Balaruc II; Bailon 1989, 1991) is not balanced in the late Pliocene (MN17) by any equally representative fauna. Moreover, the recent split of the Pliocene into three parts (Rio *et al.* 1994) is potentially misleading since some of those sites previously considered to be late Pliocene, could be middle Pliocene in age: a critical review of the chronological allocation of several sites is therefore required.

It is worth mentioning that at the same time, several reptile taxa that are now restricted to the Balkans and few Aegean Islands were still present in West Europe (Bailon 1991): Agamidae, Scolecophidia, Boidae, large Viperidae (the 'Oriental vipers'). Starting from the late Pliocene their ranges markedly shrunk leading to a further decrease in diversity mainly in West and Central Europe. This N-S and W-E contraction of the amphibian and reptilian ranges continued during the Quaternary when Europe lost the Hynobiidae (Venczel 1999) and when, at the same time, the family Palaeobatrachidae (Sanchiz 1998) and the genus *Latonia* definitely disappeared (Delfino 2002).

It should be noted that amphibians and reptiles, although traditionally placed together in the herpetofauna since they are the only ectothermic terrestrial vertebrates, display some differences in terms of extinction and survival patterns. The reptilian extinction pattern follows not only a N-S trend but also a marked W-E one. The amphibian extinction pattern appears to be not so directional (e.g. palaeobatrachids survived only in Central

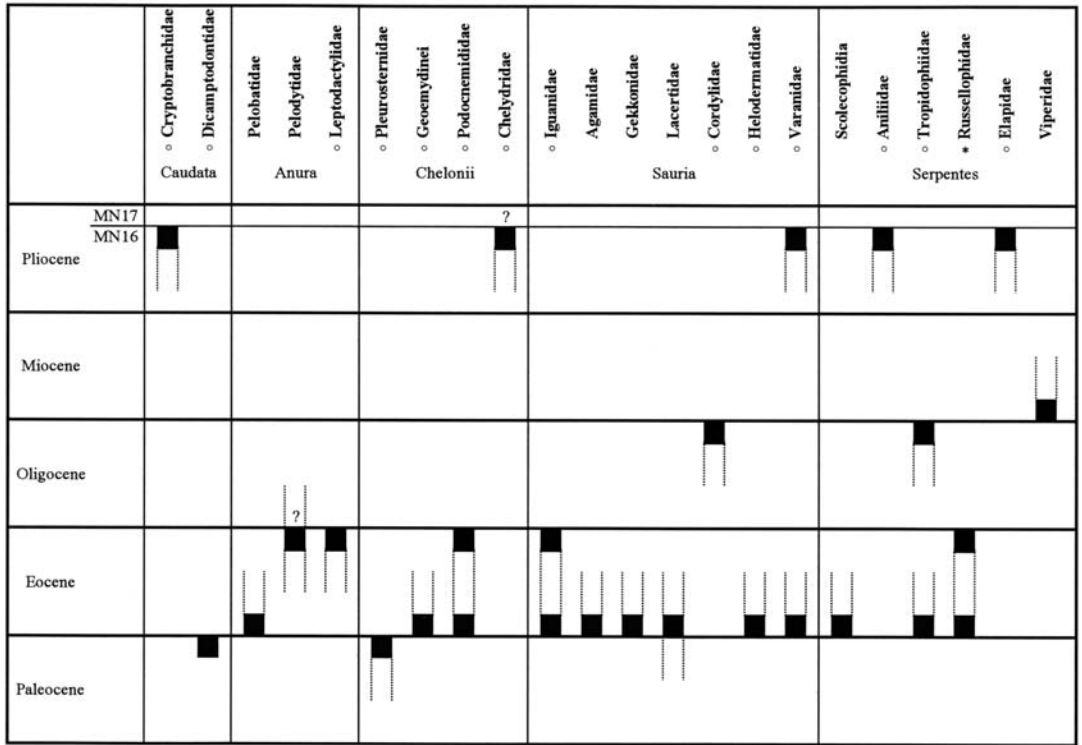


Figure 1 Simplified distribution of selected herpetofaunal taxa of stratigraphic interest (crocodilians are not considered) showing the 'time-slices' in which significant turnover occurred (see text for details). Appearances and extinctions are plotted on the figure only when they correspond to a turnover. When needed, dotted lines have been added to the black squares in order to avoid the false impression of 'flash permanence' of taxa; therefore, they do not represent the real distribution of the taxa. ◦ = taxa extinct in Europe; \* = taxa extinct globally.

Europe before extinction) as they are highly sensitive to the environmental moisture that generally shows a more complex distribution than temperature. As further evidence, we can consider that among those taxa (reptiles only) that deeply restricted their range during the considered time span and that are still present in Europe, many are widespread in the Balkans or in the Aegean Islands only. This apparently contrasts with the fact that Iberia is warmer than the Balkans at present. Concerning this topic, Cheylan (1995) noticed that the centre of dispersion for most of the European taxa was Asia and the speed of the Plio/Pleistocene range shrinkage has been higher in those regions (i.e. Iberia and France) that are the farthest from the centre of dispersion. As a consequence, the analysis

of the fossil record suggests a withdrawal of the ranges from W to E, withdrawal that has not been completed for the taxa that still persist in South Eastern Europe. Therefore, the above-mentioned -often gradual- changes of geographic ranges hamper the use of amphibians and reptiles in the analysis of the late Neogene stratigraphy.

**CONCLUSIONS**

The comparison of the paleoherpetological record of the European Tertiary with that of the mammals is biased by several factors, the main one being the absence of data from various areas and periods from which fossil amphibians and reptiles have not yet been studied, although it may be presumed that their remains have already been collected

along with those of mammals. However, a general analysis of the available record from a chronological point of view allows us to observe that the herpetofauna evolved, at least prior to the late Neogene, through a series of turnovers influenced by the same external forces that, being responsible for more general biodiversity dynamics, shaped the terrestrial palaeoenvironments.

Several turnover episodes, corresponding to some of the limits between different epochs, can be evidenced (Fig. 1): Paleocene/Eocene, Eocene/Oligocene and Oligocene/Miocene boundaries (but also MP 22 during the Oligocene, the early/middle Miocene transition, perhaps MP15/MP16 in the late Eocene, and others). The pattern of evolution of the Tertiary European herpetofauna follows some of the guidelines already identified for mammals. The turnover of herpetological faunas is mainly connected to East-West dispersal events as underlined for mammals by Werdelin & Fortelius (1997).

Due to the fact that the geographic and chronological distribution of the paleoherpetofaunistic data are far from being uniform at the moment, a perusal of aspects such as provinciality and diachrony cannot be easily accomplished. Nonetheless, faunal changes that are markedly perceivable inside one single region (French Late Oligocene; Rage 1987) are, at least partly, the product of broad renewals that left evidences even at supraba-sinial level. For example, the extinction of lizards with 'molariform' teeth at the end of the Oligocene is perhaps a phenomenon restricted to one region (southern France) but, just after the extinction of these lizards, the genus *Vipera* certainly appeared across most of Europe.

Although it is unlikely that the biochronological use of the European Cenozoic herpetofauna will ever attain the resolution of mammals, it may be possible to foresee a role of these vertebrates in augmenting mammals for biochronologic and, even more so, paleoecological characterisations. Because of the high number of taxa involved and the wide range

in terms of time and space, a detailed analysis would benefit from the development of a broad taxon/locality data-set and an accuracy of investigation similar to those that are currently performed by programs such as NOW (Neogene of the Old World; <http://www.helsinki.fi/science/nw/>) and EEDEN (Environments and Ecosystem Dynamics of the Eurasian Neogene; <http://www.esf.org/life/lp/EEDEN/eedena.htm>).

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