



DIVERSITY OF CALLOVIAN-YPRESIAN (MIDDLE JURASSIC-EOCENE) TETRAPOD FAMILIES AND SELECTIVITY OF EXTINCTIONS AT THE K/T BOUNDARY

EMMANUEL FARA

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ABSTRACT - The diversity of tetrapod families increased through the Cretaceous, punctuated by three major extinction events at the Jurassic/Cretaceous, Cenomanian/Turonian, and Cretaceous/Tertiary boundaries. Extinction and survivorship at these times are analysed with regard to taxonomy and ecological categories of diet, habitat and size. Whereas no constant selectivity pattern is found for diet and size through the period, freshwater tetrapods seem to have been less extinction-prone than terrestrial and marine ones. The Cretaceous/Tertiary extinction had less effect on small, omnivorous, and freshwater families than other ecological categories. This strong selectivity signal is consistent with other work made at higher taxonomic and stratigraphic levels of resolution, thus legitimising the use of fossil families in global studies of diversity and palaeoecology.

KEYWORDS: TETRAPODS, CRETACEOUS, EXTINCTION, PALAEOECOLOGY.

RÉSUMÉ - La diversité des familles de tétrapodes a augmenté au cours du Crétacé mais trois épisodes d'extinctions la ponctuent aux limites Jurassique/Crétacé, Cénomaniens/Turonien et Crétacé/Tertiaire. Extinction et survie lors de ces événements sont étudiées pour différentes catégories de régime alimentaire, d'habitat et de taille. Régime alimentaire et taille ne font preuve d'aucun motif constant de sélectivité au cours de la période mais les tétrapodes vivant en eaux douces affichent une survie préférentielle par rapport aux tétrapodes terrestres et marins. La crise Crétacé-Tertiaire a peu affecté les familles de petite taille, omnivores et vivant en eaux douces. Le fort signal de sélectivité écologique corrobore les travaux réalisés à des niveaux de résolution taxinomique et stratigraphique plus élevés, légitimant ainsi l'emploi du niveau familial dans les études globales de diversité et de paléocéologie.

MOTS-CLÉS: TÉTRAPODES, CRÉTACÉ, EXTINCTION, PALÉOÉCOLOGIE.

INTRODUCTION

Major patterns of evolution are documented by palaeontological data, or so it is hoped. Since the time of Simpson (1944, 1953), broad diversity patterns have been investigated by the taxic approach (Levinton 1988; Smith 1994) in the 'nomothetic palaeontology' framework (Raup et al. 1973). Rates of extinction and origination can be deduced from the observed ranges of groups at a chosen taxonomic level. These patterns can be investigated at different geographic and temporal scales, ranging from studies of local sections representing a few million years (my) to global databases covering the entire Phanerozoic (e.g. Raup & Sepkoski 1982, 1984, 1986; Benton 1985, 1989, 1995; Sepkoski 1996). Even if those large-scale non-cladistic approaches suffer from some drawbacks (Patterson & Smith 1987; Smith 1994), their outcomes should not be dismissed (see Sepkoski & Raup 1986; Sepkoski & Kendrick 1993; Sepkoski & Koch 1996; Foote 1996 for discussion). Indeed, congruence in the results is an informative way of testing the robustness of assessed evolutionary patterns. Here, I present an overview of tetrapod familial diversity through the Cretaceous in a so-

called 'taxon counting' perspective and investigate the Cretaceous/Tertiary (K/T) extinction event.

A purely taxonomic approach has its limitations and consideration of survivorship and extinction within ecological categories is advisable for a better understanding of extinction processes (Bakker 1977; Jablonski 1986a,b, 1991; Flessa & Jablonski 1984). Small-scale studies have previously documented the ecological selectivity of extinctions at the K/T boundary for different groups of vertebrates. For instance, differential survival might have favoured freshwater taxa, omnivorous and insectivorous groups as well as small-sized animals (e.g. Buffet 1984; Archibald & Bryant 1990; Sheehan & Fastovsky 1992). However, even if some general conclusions emerge, they remain syntheses of diverse isolated works often restricted to one region or to one group. It thus seems fundamental to test the significance of these selectivity patterns at wider temporal, geographical and taxonomic scales with a single global database, especially at a time when such compilations are becoming readily available. The clade Tetrapoda has been well studied in terms of ecology and it is relevant to tackle this question (Benton 1989). The

ecological selectivity of the K/T event by size, diet and habitat is tested here. The results are compared with other Cretaceous extinction events, those at the Jurassic/Cretaceous and Cenomanian/Turonian transitions.

METHOD

The stratigraphic ranges of Cretaceous tetrapod families (most of them being monophyletic) are taken from The Fossil Record 2 (Benton 1993). The few corrections made to this original dataset are listed in appendix. The timescale is from Harland et al. (1990), which is the standard used in the Fossil Record 2 compilation. Other timescales (Odin 1994; Gradstein et al. 1994, 1999; Berggren et al. 1995) yield similar patterns when extinction and origination rates are calculated. Ecological attributes come from a database compiled by Benton (1996a,b), which is available on the Internet (<http://palaeo.gly.bris.ac.uk/tetrapods/tetrapods.html>). This data set assigns each family to a broad ecological category of diet, habitat and size, based on consideration of all species in the family and taking into account, as far as possible, changing body sizes and diets during growth. Categories used for this study are:

- Diet: tetrapod-eater; fish-eater; invertebrate-eater; omnivorous; herbivorous.
- Habitat: terrestrial; freshwater; marine.
- Size: small (snout-vent length $L < 15$ cm); medium ($15 \text{ cm} < L < 150$ cm); large ($L > 150$ cm).

Clearly, many families can belong to more than one category for each ecological attribute (e.g. small/medium or freshwater/terrestrial, etc.). The stratigraphic ranges have been maximised ('long-range technique'). Families known from a single speci-

men from a single locality (and called here 'singletons') have been removed from the analysis. I thus consider here 345 non-singleton families (20 of amphibians, 138 of reptiles, 42 of birds and 145 of mammals) occurring in the Callovian-Ypresian interval. This large time span allows the study of diversity to be made around 15 million years beyond the period boundaries. Variations in diversity are usually estimated by four metrics. The simple numbers of extinctions (E) and originations (O), and the ratio of these numbers divided by the stage duration (T) (the 'total rates') are the basic measures, but they do not account for the total diversity (D), that is to say the number of taxa 'at risk' in each time-unit. The proportional rates (E/D and O/D) and the per-taxon rates (E/DT and O/DT) correct for this bias but are consequently subject to larger statistical uncertainties (Sepkoski & Koch 1996). Inasmuch as these two latter measures yield very similar patterns to the simple numbers and total rates respectively, they have been preferred here.

In addition, ecological selectivity of extinctions is studied by comparing survival and extinction in each ecological category for the Tithonian/Berriasian (= Jurassic/Cretaceous), Cenomanian/Turonian, and K/T boundaries. In order to test the differential survival of taxa at the end of the Cretaceous, I also applied statistical tests to the proportions of survival for each ecological category. Statistical investigations are not possible for the other events because the sample sizes at the family level are too small. The statistics used here for the K/T boundary are a binomial test comparing the proportion of extinction per category with the random variation of the overall mean proportion (McKinney 1987), and the 95% binomial confidence intervals as proposed by Raup (1991a).

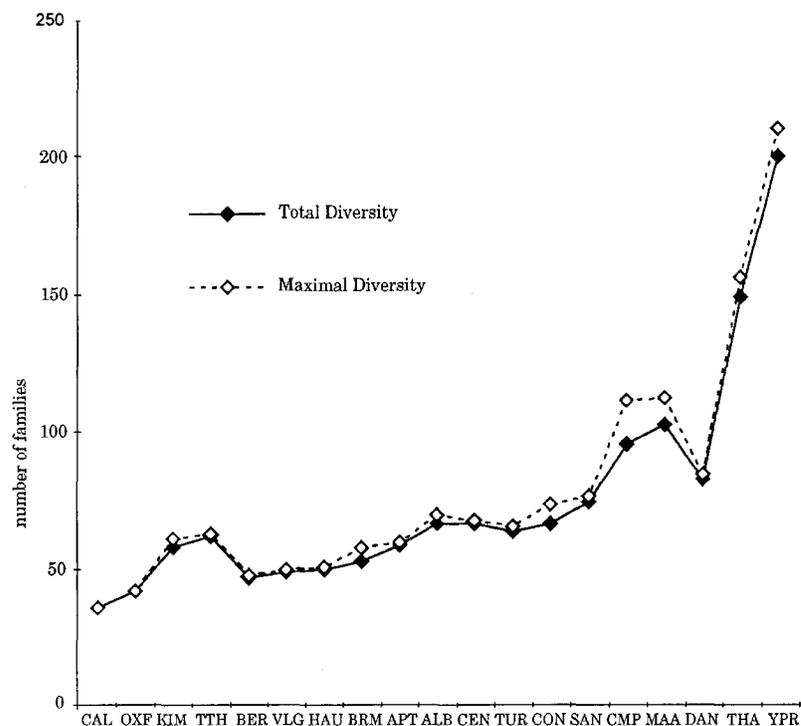


FIGURE 1 - Total and maximal diversity of tetrapod families from the Callovian (Middle-Jurassic) to the Ypresian (Eocene). The maximal diversity corresponds to the total diversity to which the singleton families (known from a single specimen from a single locality) are added. *Diversité totale et maximale des familles de tétrapodes du Callovien (Jurassique Moyen) à l'Yprésien (Éocène). La diversité maximale correspond à la diversité totale à laquelle sont ajoutées les familles 'singleton' (connues par un seul spécimen provenant d'une seule localité).*

RESULTS

OVERALL DIVERSITY

Figure 1 represents the total diversity and the maximal diversity (which corresponds to the total diversity when the 'singleton' families are added) for tetrapod families throughout the Callovian-Ypresian interval. The general increase in diversity is clear and statistically significant (Spearman Rank Correlation, $p < 0.005$), going from 36 families in the Callovian to 201 in the Ypresian, though this diversity growth is not linear, neither exponential (χ^2 test, $p < 0.001$). Three main extinction events are noticeable in the interval, with diversity drops at the Jurassic/Cretaceous boundary (from 62 to 47 families), between the Cenomanian and the Turonian (from 67 to 64 families) and at the Cretaceous/Tertiary transition (from 103 Maastrichtian to 83 Danian families). Note that the total diversity does not differ significantly from the maximal diversity, showing that the singleton families do not create artificial diversity patterns.

EXTINCTION AND ORIGINATION RATES

Figure 2 shows the proportional extinction and origination rates for tetrapods. Although division by the total diversity increases the statistical uncertainty of the ratio, it allows the calculation of the 95% confidence intervals estimated by a binomial procedure as proposed by Raup (1991a) and used in many works (Erwin 1996; Jablonski 1998; Jablonski & Raup 1995; Sepkoski 1996; Sepkoski & Koch 1996). This technique shows that the rates do not differ significantly from one stage to the next, except in the Tithonian (end-Jurassic) and Maastrichtian (end-Cretaceous) where the extinction rates are significantly higher than for adjacent stages. The results are consistent with the traditional use of major bio-events to delimit the main time-units in geology. The local peak in both extinction and origination rates in the Albian can be linked to the long duration of this stage, the longest in the whole Mesozoic (from 12 to 15 my, after Harland et al. 1990; Odin 1994; Gradstein et al. 1994, 1999). Benton (1995) observed a similar result in the Albian for continental organisms but this dubious pattern vanishes when a time-normalisation is

FIGURE 2 - Proportional origination and extinction rates for tetrapod families in the Callovian-Ypresian interval. Error bars represent the binomial 95% confidence intervals calculated following Raup (1991a). *Taux proportionnels d'extinction et d'apparition des familles de tétrapodes dans l'intervalle Callovien-Yprésien. Les barres d'erreur représentent les intervalles de confiance à 95% calculés suivant la méthode binomiale de Raup (1991a).*

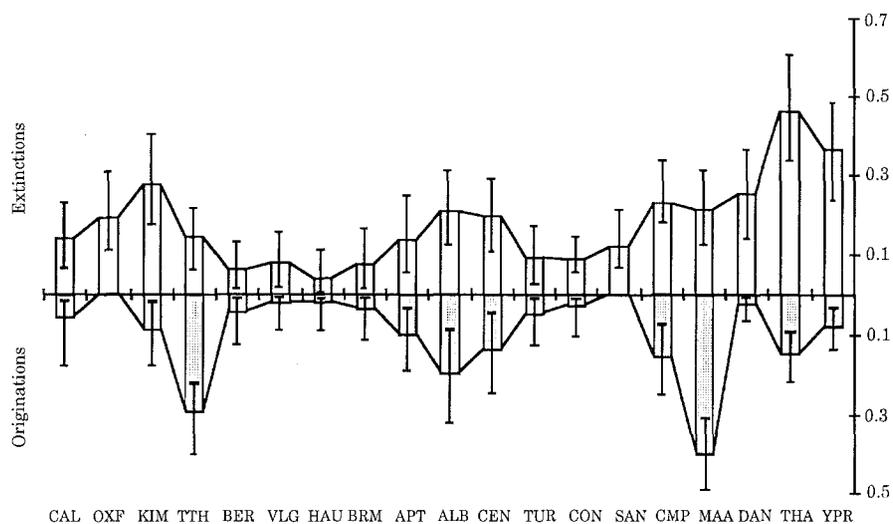
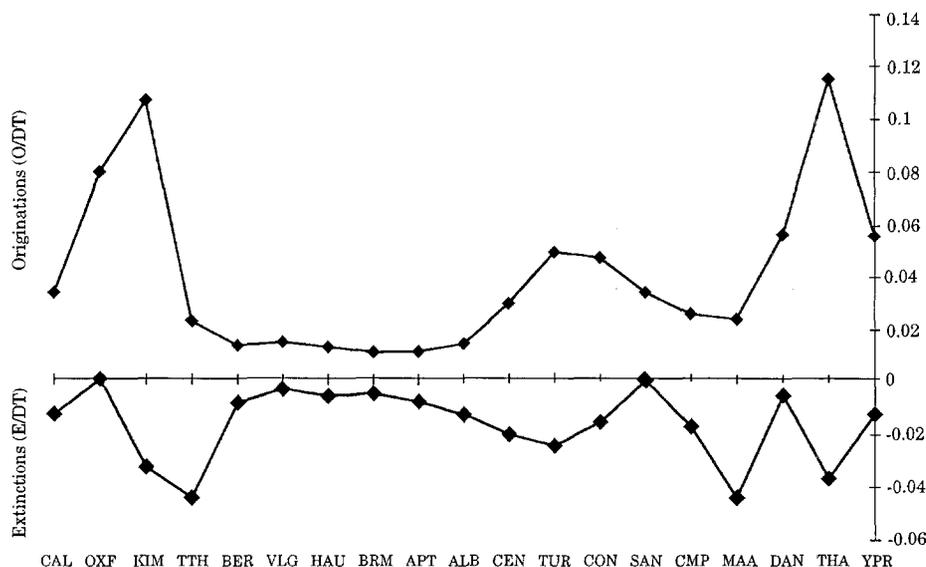


FIGURE 3 - Per-taxon origination and extinction rates for tetrapod families in the Callovian-Ypresian interval. The timescale used is from Harland et al. (1990). *Taux par taxon d'extinction et d'apparition des familles de tétrapodes dans l'intervalle Callovien-Yprésien. L'échelle de temps est celle de Harland et al. (1990).*



applied. Local maxima in origination rate also occur in the Kimmeridgian and in the Thanetian. The former might be due to a 'Lagerstätten effect' and the latter illustrates the end-Palaeocene mammalian turnover, although the ten families restricted to this stage may exaggerate its magnitude.

Further information can be gained from the per-taxon extinction rates (Fig. 3). The end-Jurassic and end-Cretaceous events have similar magnitude with this metric. Compared with the proportional rates, major shifts occur in the Aptian-Coniacian interval where the longest stages adjoin the shortest ones. Artefactual peaks due to time-normalisation have been faced by many authors in this interval (see for instance Sepkoski & Raup 1986; Hubbard & Gilinsky 1992) and stem from the choice among the available timescales. The latter can create artificial local maxima for the Turonian (Harland et al. 1990) or the Coniacian (Odin 1994), but the Cenomanian extinction event carries a strong and stable signal associated with a drop in diversity also recognised in local studies. Time normalisation adds uncertainties linked to the time-scale (Raup 1986; Sepkoski & Raup 1986; Raup & Boyajian 1988; Gilinsky 1991) and per-taxon rates

have been shown to be negatively correlated to the time-units duration under most of realistic extinction models (Foote 1994). It also assumes that extinctions and originations are evenly spread throughout each stage. However, there is no correlation between extinction rate and stage duration here but there is for origination rate (Spearman Rank Correlation, $p < 0.05$) in the Callovian-Ypresian interval, though this correlation is insignificant in the Cretaceous sensu stricto.

EXTINCTION EVENTS AND ECOLOGICAL SELECTIVITY

The following results present survivorship of tetrapod families among ecological categories of diet, habitat and size at the end of the Cretaceous (Maastrichtian/Danian transition), in comparison with the Tithonian/Berriasian and Cenomanian/Turonian events. The figures allow estimates of the absolute as well as the relative importance of extinction in all categories. Statistical significance of extinction and survival is also given for the K/T event.

FIGURE 4 - Extinctions and survivals of tetrapod families at the Jurassic/Cretaceous, Cenomanian/Turonian and K/T boundaries by class. Abbreviations are as follow: Amph= Amphibians; Rept=Reptiles; Bird=Birds; Mamm=Mammals. Statistical significance of selectivity at the K/T boundary according to the binomial test on the overall mean is noted by an asterisk, categories significantly different from all the others according to the binomial 95% confidence interval calculated following Raup (1991a) are noted by §. *Extinction et survie des familles de tétrapodes aux limites Jurassique/Crétacé, Cénomanien/Turonien et Crétacé/Tertiaire par classe. Les abréviations sont les suivantes: Amph=Amphibiens; Rept=Reptiles; Bird=Oiseaux; Mamm=Mammifères. Les catégories écologiques montrant une sélectivité significative lors de la crise K/T sont notées par un astérisque (test binomial sur la moyenne) et/ou par le symbole § [intervalle de confiance binomial à 95% calculés d'après Raup (1991a)].*

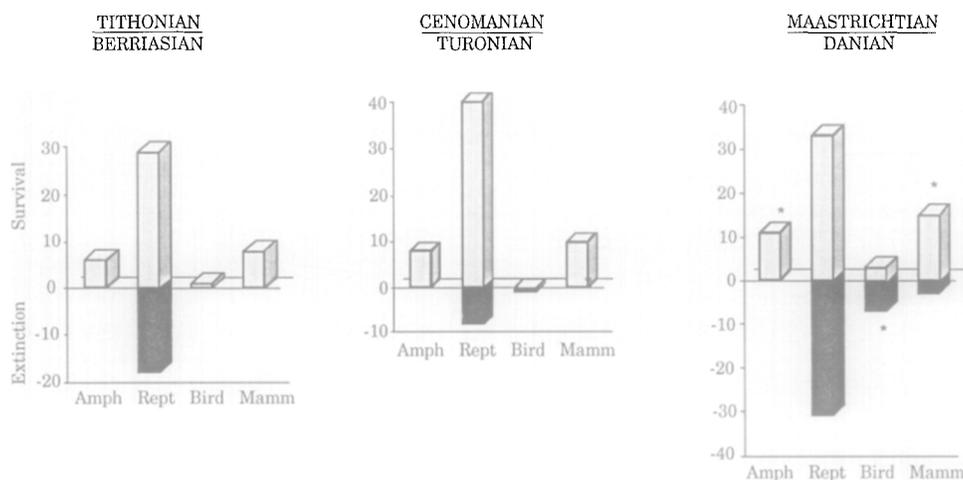
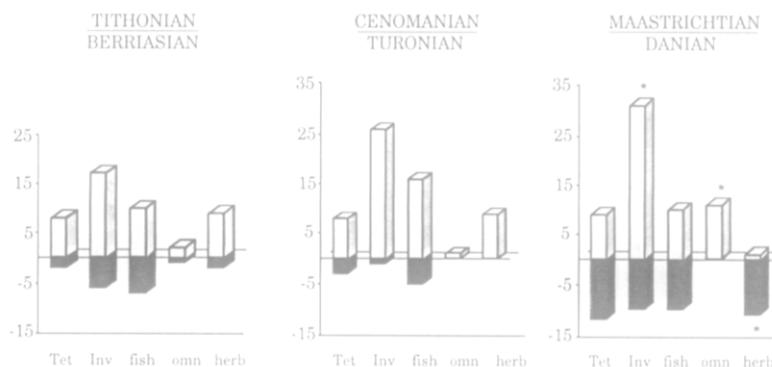


FIGURE 5 - Extinctions and survivals of tetrapod families at the Jurassic/Cretaceous, Cenomanian/Turonian and K/T boundaries by diet. Abbreviations are as follow: Herb=Herbivorous, Omn=Omnivorous, Tet=Tetrapod-eater, Inv=Invertebrate-eater, Fish=Fish-eater. Statistical significance for the K/T event noted as on fig.4. *Extinction et survie des familles de tétrapodes aux limites Jurassique/Crétacé, Cénomanien/Turonien et Crétacé/Tertiaire par régime alimentaire. Les abréviations sont les suivantes: Herb=Herbivore, Omn=Omnivore, Tet=mangeur de tétrapodes, Inv=mangeur d'invertébrés, Fish=piscivore. Catégories statistiquement significatives notées comme sur la fig. 4.*



Taxonomy

Lumping tetrapod families into larger groups (traditional 'classes') reveals some interesting patterns of extinction and survival (Fig. 4). All the extinctions concern the most diverse group during the Cretaceous: Reptilia. However, birds suffered high losses, with 70 % of families becoming extinct at the K/T boundary. However, as Chiappe (1995) pointed out, the fossil record of birds taken at face value could lead to spurious results and figures of extinction must be considered with caution. Although Alroy (1999) found high level of extinction (around 60%) among North American mammal species at the K/T boundary, the data suggest here a significant survival of this class at the family level. Similar observations are made for amphibians, which amazingly cross all the three events studied here without any extinction. Through the whole Cretaceous, only the Chigutisauridae are known to disappear in the Albian. Clemens (1986) also found a high familial survival (7/8) among amphibians in the Western Interior at the K/T boundary. This seems to be a general pattern among amphibians as most of the Mesozoic families are still extant today. Even if their poor fossil record must be treated cautiously, the peculiar resistance of amphibians to extinctions may well be linked to their habitat and diet as I will discuss later.

Diets

The transition from the Maastrichtian to the Danian is marked by important extinctions in all diet categories, except the significant survival of omnivorous families (Fig. 5). Relatively to their diversity, invertebrate-eaters are also little affected at the K/T boundary as well during other Cretaceous extinction events, the sharpest extinction for them being the Tithonian/Berriasian transition. The K/T event is also the most dramatic for herbivorous and carnivorous families, with 92% (n=12) and 57% (n=21) of extinctions respectively. The Tithonian/Berriasian event shows the highest number of extinctions among fish- and invertebrate-eating families whereas fish- and tetrapod-eating families are most affected at the Cenomanian/Turonian boundary.

The nature of the diet and the position of an animal within food webs appear to be determining factors for the survival of many taxa during major crises. For instance, omnivorous sea urchin genera showed significant survival through the K/T event (Smith & Jeffery 1998). Benthic deposit-feeders and detritus-feeding taxa also reached the Tertiary with few taxa being wiped out (Sheehan & Hansen 1986). Nevertheless, bivalves show no differential survival concerning this parameter (Jablonski & Raup 1995). The present results show that omnivorous tetrapods and invertebrate-eaters (including insectivorous taxa) are markedly favoured at the K/T boundary. The diet-selective pattern of extinction is also apparent for the other events. But even if diets are regarded as autonomous characteristics in studies on selectivity, they are directly tied to the habitat.

Habitat

Survival depends on habitat (Fig. 6). Marine tetrapod families show relatively high extinction rates, especially at the K/T boundary (61% of extinction, n=18) where this result is statistically significant. Terrestrial families are severely reduced in diversity at the K/T boundary (43% of extinction, n=68), compared to freshwater-dwelling families that are significant outliers in terms of survival. The few taxa becoming extinct are also terrestrial. Freshwater families exhibit only a slight increase in diversity (16 to 17 families from the Maastrichtian to the Danian). This habitat appears to be protected for all the three events studied here and also for the purely continental Thanetian/Ypresian faunal turnover. Taxa dependent upon humus and freshwater habitat (mainly invertebrate-eaters, detritus-feeders and omnivorous taxa) were little affected during the K/T environmental crisis, even the freshwater fauna and flora found in the infra- and intertrappean beds in India (Prasad & Khajuria 1995). Bakker (1977) also found a huge survival (90%) for tetrapod families (turtles, crocodiles and champsosaurs) at the K/T boundary in freshwater environments, as did Van Valen & Sloan (1977) and Sheehan & Fastovsky (1992). Buffetaut (1990) noted general agreement about the peculiar resistance of freshwater taxa at the end of the Cretaceous.

FIGURE 6 - Extinctions and survivals of tetrapod families at the Jurassic/Cretaceous, Cenomanian/Turonian and K/T boundaries by habitat. Abbreviations are as follow: Mar=Marine, Ter=Terrestrial, Fw=Freshwater. Statistical significance for the K/T boundary noted as on fig. 4. *Extinction et survie des familles de tétrapodes aux limites Jurassique/Crétacé, Cénomanién/Turonien et Crétacé/Tertiaire par habitat. Les abréviations sont les suivantes: Mar=Marin, Ter=Terrestre, Fw=Eaux douces. Catégories statistiquement significatives notées comme sur la fig. 4.*

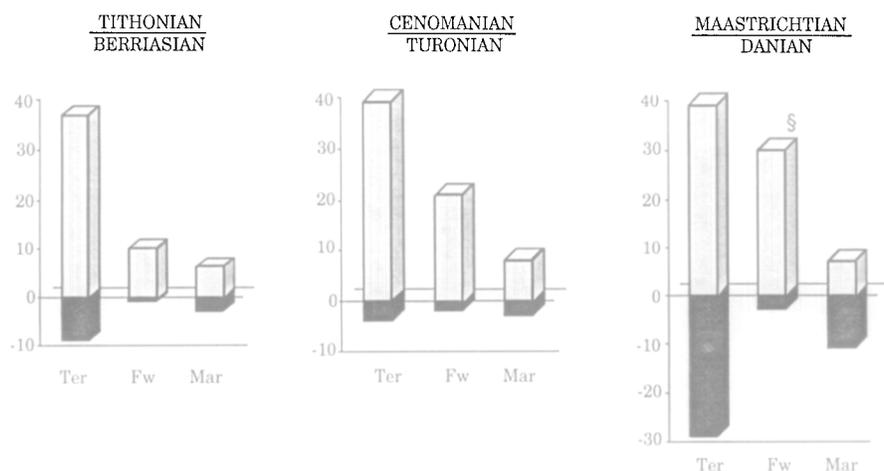
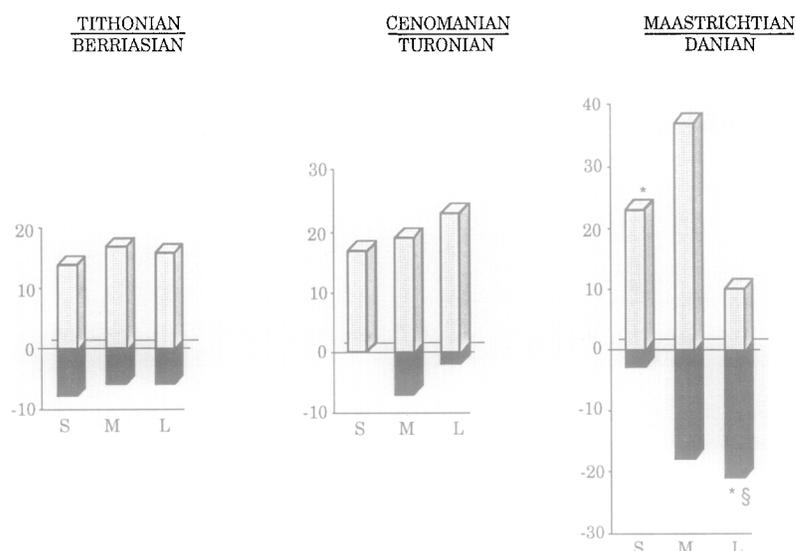


FIGURE 7 - Extinctions and survivals of tetrapod families at the Jurassic/Cretaceous, Cenomanian-Turonian and K/T boundaries by size. Abbreviations are as follow: S=Small, M=Medium; L=Large. Statistical significance for the K/T boundary noted as on figure 4. *Extinction et survie des familles de tétrapodes aux limite Jurassique/Crétacé, Cénomano-Turonienne et Crétacé/Tertiaire par taille. Les abréviations sont les suivantes: S=Petit, M=Moyen, L=Grand. Catégories statistiquement significatives notées comme sur la fig. 4.*



Size

Survivorship also depends on body size (Fig. 7). Whereas the Cenomanian/Turonian extinction affected taxa from the medium-large range of sizes, no selectivity is observed at the Tithonian/Berriasian boundary. Families of large-sized tetrapods were significantly more likely to become extinct at the K/T boundary than the two other categories. Conversely, small-sized tetrapods exhibit a high survival when reaching the Tertiary. Size is a factor traditionally considered in studies about extinction selectivity. It is commonplace to consider large animals as more vulnerable than small ones for proximate causes of extinction, such as during brutal environmental shifts (Bakker 1977; Gingerich 1984; Lawton 1995). Size is indeed directly correlated with metabolism, size of populations and gene pool (Bakker 1977; La Barbera 1986; Raup 1991b; Jablonski 1996). For the K/T boundary, Bakker (1977) noted that the 'size-specificity of this extinction is remarkable', as out of twenty-two 'small' (under 10 kg) families, only two (pediomyid and stagodontid mammals) became extinct. The results presented here further support size selectivity at the K/T boundary for tetrapods.

DISCUSSION

TITHONIAN/BERRIASIAN BOUNDARY

The Jurassic/Cretaceous transition has been considered as a second-order mass extinction and of significant intensity in the study of periodicity (Raup & Sepkoski 1986). Nearly 30 % of marine invertebrate genera, especially cephalopods and bivalves, became extinct (Sepkoski 1996), corresponding to the loss of 19 mollusc families (Sepkoski 1992) and a fall in marine family diversity of 6.5% (Sepkoski & Raup 1986). Benton (1985, 1995) also observed important reductions in diversity at this time for non-marine tetrapod families and similar drops in diversity ranging from 5.1% to 17.6% for

marine and continental organisms. Marine reptiles also suffered important losses (Bakker 1977, 1993; Bardet 1995). The high percentages of extinction among marine fish- and tetrapod-eating taxa found in this work are consistent with these observations, but terrestrial families are also concerned. The global extinction of reptiles between the Tithonian and the Berriasian, with a loss of 24% of families, may be over-estimated because of changes in the quality of the fossil record (Benton 1985, 1989, 1995). 'Lazarus' families indeed appear to be much more numerous in the Berriasian than in the Tithonian (Benton 1987; Bardet 1995; Fara & Benton, in 2000) but proportions are equivalent for all size categories. Lack of differential survival by size also suggests that this parameter is not responsible for any bias in the fossil record at the end of the Jurassic. A rapid marine regression occurred in Europe (Hallam 1978), but no other major faunal turnover is known from elsewhere (Hallam 1986, 1996). Thirteen tetrapod families out of eighteen becoming extinct at the Jurassic/Cretaceous transition have geographic ranges including Europe. Geographic restriction of this pattern should be considered with caution, as most of the studies are themselves confined to Europe. Although Hallam & Wignall (1997) concluded that this event is generally only notable at the species level, significant extinction maxima have been found in global databases of higher taxa. The next challenge will be to estimate the effect of potential biases on the quality of the fossil record and its spatial distribution to explain this signal, especially for terrestrial organisms.

CENOMANIAN/TURONIAN BOUNDARY

Sepkoski (1996) noted a 25% and a 4.5% extinction level for marine genera and families respectively, whereas Benton (1995) obtained a 4.8-5% drop in diversity for all families, but slightly higher for marine families (4.9-5.6%). Similarly, Harries (1993) observed the demise of 7% of marine families. Tetrapod families exhibit similar figures (4.6% in this work). Marine reptiles, especially the

well-known ichthyosaurs, suffered dramatically at the Cenomanian/Turonian transition perhaps because of the decline of their main trophic sources, notably belemnites (Bardet 1995). The results further support a mainly aquatic catastrophe affecting medium-to-large-sized predators of fish and other tetrapods. Severe extinctions have been noted for planktonic and benthic foraminifera (de Gracianski et al. 1984; Hart & Ball 1986; Banerjee & Boyajian 1996), as for coral reefs and molluscs (Kauffmann 1994; Kauffman & Hart 1996). These modifications of micro-, meio- and macrofauna resulted from perturbations in food chains (Hart 1996) that can be linked to the well-documented and correlated environmental shifts known to occur in the Late Cenomanian: high stands in sea level, major anoxic event, abrupt fall in CO₂ and climate cooling (Jenkyns 1980; Haq et al. 1987; Orth 1989; Kauffman 1994; Hüber et al. 1995; Kauffman & Hart 1996; Barnes et al. 1996; Kuypers et al. 1999). The Cenomanian/Turonian boundary corresponds to a key point in the evolution of the global climatic system. Despite poor temporal resolution of the continental fossil record, extinctions among vertebrates were probably caused by the trophic perturbations that affected top predators in the marine realm, but more studies are needed to explain diversity variations on land (Hallam & Wignall, 1997).

CRETACEOUS/TERTIARY TRANSITION

My purpose here is not to discuss the hypotheses (volcanic and/or impact-related) proposed as triggers for the K/T extinction (see for example Sharpton & Ward 1990; Sutherland 1994; MacLeod & Keller 1996; Hallam & Wignall 1997 for reviews) but rather to consider the known ecological aftermath. Both impact and volcanic scenarios for the K/T boundary imply a short-term collapse in primary productivity. A dramatic drop in primary productivity in the oceans has been recognised by many workers (e.g. Hsü & McKenzie 1985; Hsü 1986; Arthur et al. 1987; Zachos et al. 1989; Hansen et al. 1993; Smit 1994) and on land, palynomorphs and fossil leaves witness a similar crisis in continental productivity at the K/T boundary (Orth et al. 1981; Nichols et al. 1990; Tschudy et al. 1984; Wolfe & Upchurch 1986; Saito et al. 1986; Johnson et al. 1989; Johnson & Hickey 1990). This disruption at the base of the ecological pyramid is held to be responsible for the demise of downstream diet categories. This disruption of trophic chains remains a central key argument to explain the selective extinctions of many heterotrophic organisms (Smith & Jeffery 1998, for sea urchins; Cappetta 1987 and Noubhani & Cappetta 1997, for selachians; Bardet 1995, for marine reptiles; Buffetaut 1990; Sheehan & Fastovsky 1992, for terrestrial vertebrates). In the marine realm, Rhodes & Thayer (1991), using bivalves and articulate brachiopods, also supported the hypothesis of reduced primary productivity as the main cause for a selective extinction mechanism. Sheehan & Hansen (1986) proposed a palaeoecological model to explain the differential survival of organisms at the end of

the Cretaceous. Detritus feeding may buffer taxa from extinction at time of drastic but temporary drop in primary productivity. Extinction-buffered taxa either belong to the forest-soil fauna (insectivorous small mammals, lizards and amphibians) or to freshwater stream communities (turtles, crocodiles) relying mainly on detritus from land. This kind of habitat should be buffered during dramatic - but temporary - drops of primary productivity. Freshwater environments are indeed essentially based on allochthonous resources (Sheehan & Hansen 1986; Sheehan & Fastovsky 1992; Sheehan et al. 1996). Archibald & Bryant (1990) and Sheehan & Fastovsky (1992) further tested this hypothesis by comparing the survival of riparian-riverine assemblages with land-dwelling ones, and observed strong differential survival in favour of the freshwater environment among Maastrichtian vertebrate species from Montana. The 90% level of survival obtained here for freshwater tetrapod families is clearly consistent with this hypothesis. This percentage equals (for the same number of taxa) the values independently found by Sheehan & Fastovsky (1992) and Bakker (1977). Importantly, this survivorship appears to be independent of size, supporting Buffetaut (1990), Bakker (1977) Clemens (1986) and Archibald & Bryant's (1990) views that size can not be the single attribute responsible for the differential extinction. Moreover, size is a multivariate factor that implies arbitrary choices to limit convenient categories that are not absolute. According to how the choice is made, one could find a selectivity pattern, or not. One can then readily understand why no general rules can be put forward without having some reserve about this question (Raup 1991b, 1995; Jablonski & Raup 1995; Jablonski 1996). Covariation of ecological attributes also suggests that several of these may explain extinction resistance (Jablonski 1986a; Norris 1992; Harries et al. 1996).

DISCUSSION AND CONCLUSION

Extinction of organisms remains a genuine biological phenomenon. Contemporaneity of environmental shifts does not imply direct cause-effect relations. Major hypotheses indeed come up against the central issue of the selectivity of extinctions (Buffetaut 1984). For instance, selective survival of climate-sensitive animals like eusuchian crocodiles at the K/T boundary casts doubt on long-term climatic hypotheses for this major extinction event (Markwick 1998). Selective survival has been observed in both marine and continental realms. Many factors are usually held to be potentially responsible for the differential survival of taxa at time of extinctions (see Harries et al. 1996 for a review). Surviving taxa seem to be generally associated with wide geographic range (Jablonski 1986a,b), eurytopy (Kauffman & Harries 1996) and high primary productivity of the habitat. Moreover, taxonomic richness, number and size of populations (Lawton 1995), mobility, feeding strategy (Sheehan et al. 1996; Smith &

Jeffery 1998), degree of specialisation (Bakker 1977; Cappetta 1987), reproductive strategy (Gallagher 1991), starvation-resistance (Rhodes & Thayer 1991) and forms of dispersal are important information, when available, that may indicate a selectivity pattern, but the latter is far from constant across groups and through time.

For size, Cretaceous tetrapods show differential survival at the K/T boundary only, but this parameter does not create this pattern independently. The most striking feature observed in this work is the high survivorship in freshwater habitats throughout the period, whatever the extinction intensity. Freshwater communities should be studied in much more detail to further elucidate the extinction selectivity issue. No constant selectivity pattern is found among diet categories during the Cretaceous bio-events. This makes sense as all these extinction events are linked to collapses in food chains related to different environmental shifts. The results presented here are consistent with a dramatic but temporary drop in primary productivity at the end of the Cretaceous, and they support the palaeoecological model of Sheehan & Hansen (1986). The high survival of freshwater tetrapods throughout the period is best explained by the peculiarity of this biotope at times of temporary cessation of primary productivity. It is shown that selective survival also occurs during minor extinction events.

The ecological categories used here are very broad, many families belonging to several of them (homogenisation of the sample) and the taxonomic resolution is low. These data were not originally compiled for such a study, but for a large-scale assessment of the potential amount of competition among tetrapod families (Benton 1996a,b). Rhodes & Thayer (1991) criticised the use of the familial level since families include ecologically diverse sub-groups. Nevertheless, the results are consistent with those obtained at both higher stratigraphic and taxonomic resolutions. The ecological signal of selectivity at the K/T boundary is strong enough to overwhelm the filter of coarse taxonomic and ecological lumping. This legitimises the use of the family level and of ecological categories inferred from fossils as they can accurately feature the past diversity at a global-scale level. Of course, global-scale works complement, but do not replace, other studies made at higher levels of resolution. As soon as the number of taxa is high enough and the study of general scale, the assessed ecological attributes of taxa are helpful to improve our knowledge about the fascinating issue of extinction selectivity.

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E. FARA

Institut des Sciences de l'Évolution
Université de Montpellier II

Present address
Department of Earth Sciences
University of Bristol
U.K., BS8 1RJ Bristol
email: E.Fara@bris.ac.uk
fax: (0044) 117 925 3385

APPENDIX

Corrections made on the original database The Fossil Record 2 (Benton 1993)

L.O.=Lowest Occurrence

H.O.=Highest Occurrence

REPTILIA

Protostegidae: L.O. in the Albian (Bardet 1995; Hirayama 1998).

Plesiochelyidae: L.O. in the Callovian (Fernandez & Fuente 1993)

Augualosauridae: L.O. in the Cenomanian (Bardet 1995)

Mososauridae: L.O. in the Turonian (Bardet 1995)

Nigerophiidae: L.O. in the Maastrichtian (Bardet 1995)

Cryptoleididae: H.O. in the Tithonian (Bardet 1995)

Pliosauridae: H.O. in the Maastrichtian (Bardet 1995)

AVES

Procellaridae: not included into the analysis because the Lowest occurrence (Thanetian) is doubtful.