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EXTINCTION EVENTS AMONG MESOZOIC MARINE REPTILES

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Marine reptiles are an adaptive assemblage including a mosaic of forms with fully marine groups (ichthyosaurs, "nothosaurs", plesiosaurs, placodonts, thalattosaurs and hupehsuchians), as well as groups containing continental representatives (turtles, crocodiles, lizards and snakes). Forty-six families of marine reptiles are recorded during the Mesozoic. The fossil record of marine reptiles is punctuated by two major extinctions at the Middle-Late Triassic transition (loss of 64% of families) and at the Cretaceous-Tertiary boundary (36% of families died out). The Ladinian-Carnian boundary event coincides with an important regressive phase and affects essentially coastal forms. The K/T boundary is characterized by selective extinctions among marine reptiles, probably linked with a break in the food chain.

KEY WORDS: Marine reptiles, Mesozoic, diversity, extinctions.

INTRODUCTION

Most studies on diversity and mass extinctions have essentially been focused on marine invertebrates on the basis of their good fossil record. Among vertebrates, similar studies have recently been attempted on groups with poorer fossil records, such as terrestrial tetrapods (Benton, 1985, 1987). As for marine reptiles, they have been included in papers on global diversity (Benton, 1988), especially concerning the Cretaceous/Tertiary (K/T) crisis (Russell, 1977; Sullivan, 1987) or modes of predation and swimming (Massare, 1987, 1988). Nevertheless, information on their global diversity fluctuations during the Mesozoic has not hitherto been synthesized.

Marine reptiles do not represent a monophyletic group but an adaptive assemblage, which developed a similar response to the same environment: the sea. The different groups of marine reptiles are here considered as a natural entity, only in terms of a good reflection of changes in their environment and thus on which diversity analysis may be attempted with a quantitative approach (*sensu* van Valen, 1978, 1985; Sepkoski, 1984, 1987).

The purpose of this paper is to provide some information on the quality of the fossil record of Mesozoic marine reptiles, including a revised list of familial stratigraphic ranges. Extinction events are discussed, with comments on disappearing and surviving taxa.

DATA AND METHOD

Data on both systematics and stratigraphic range of marine reptile groups are scattered in several hundred papers. On the other hand, synthetic data, essentially from Romer

(1966), Harland *et al.* (1967), Sepkoski (1982a) and Carroll (1987), remain often imprecise both systematically (because of the rapid increase in our knowledge) and stratigraphically (because the temporal interval is generally longer than the stage). Recent improvements in the fossil record of selachians (Cappetta, 1987) and non-marine tetrapods (Benton, 1987, 1988) reveal significant differences in data bases compared with the above mentioned previous works.

This works has been directed in the following way: bibliographical study, review of collections and study of newly discovered material have been complemented by contact with specialists on the groups involved. The present paper is part of a global research project on Mesozoic marine reptiles, that includes refining and improvement of the fossil record as well as study of patterns of evolution and extinction (Bardet, 1992a).

The marine reptile diversity graphs (families, genera and species levels) through time have been based on the new data set. The stage has been used as a standard stratigraphic interval. Extinction and origination rates (Re and Rs respectively) have been calculated globally at familial level. These rates were calculated as the number of families that disappeared (E) or appeared (S) during a stratigraphic stage, divided by the estimated duration of that stage (Dt). The timescale of Harland *et al.* (1989) has been used for stage durations in My.

THE FOSSIL RECORD OF MARINE REPTILES

Perspective (Figure 1)

Aquatic adaptation is a common trend in amniote history, as exemplified by reptiles during the Mesozoic and by mammals (cetaceans, pinniped carnivores and sirenians) during the Cenozoic.

Reptiles are a primarily terrestrial group and the pioneers which first developed aquatic adaptations are known from Permian deposits. These are the Mesosauridae, a family with unclear affinities, found in South Africa and Brazil (Carroll, 1987) and the Claudiosauridae from Madagascar, postulated ancestors of the Sauropterygia (Carroll, 1981). These families have not been included in this study.

Forty-six families of marine reptiles are recorded during the Mesozoic (Figure 1), some being fully aquatic and others including also continental members. Marine reptiles have played an important role as active predators in Mesozoic marine ecosystems. The thalattosaurs, "nothosaurs", placodonts, hupehsuchians and *Helveticosaurus* are restricted to the Triassic while the ichthyosaurs, plesiosaurs and pliosaurs are known during a large part of the Mesozoic Era. Turtles have adapted to marine life with near-shore forms during the Late Jurassic and mainly pelagic ones during the Late Cretaceous. As for marine mesosuchian crocodiles, they are mainly represented by the thalattosuchians, ranging from the Early Jurassic to the Early Cretaceous, but other groups have occasionally invaded the marine realm, such as the dyrosaurs in the Late Cretaceous as well as the pholidosaurs in Albian-Cenomanian times. Finally, some families of both snakes and lizards (mainly the huge and greatly diversified mosasaurs) have colonized the marine environments during the Late Cretaceous.

The earliest record of marine reptiles during the Mesozoic is from the Smithian, with the oldest mention of ichthyosaurs (Cox & Smith, 1973; Callaway & Brinkman, 1989). Since the Spathian, the fossil record of marine reptiles is richer and represented by ichthyosaurs, "nothosaurs", placodonts and thalattosaurs. This high diversity during Spathian time implies an unknown older terrestrial origin as well as problems of palaeobiogeographical dispersal for these groups (Mazin, 1988).

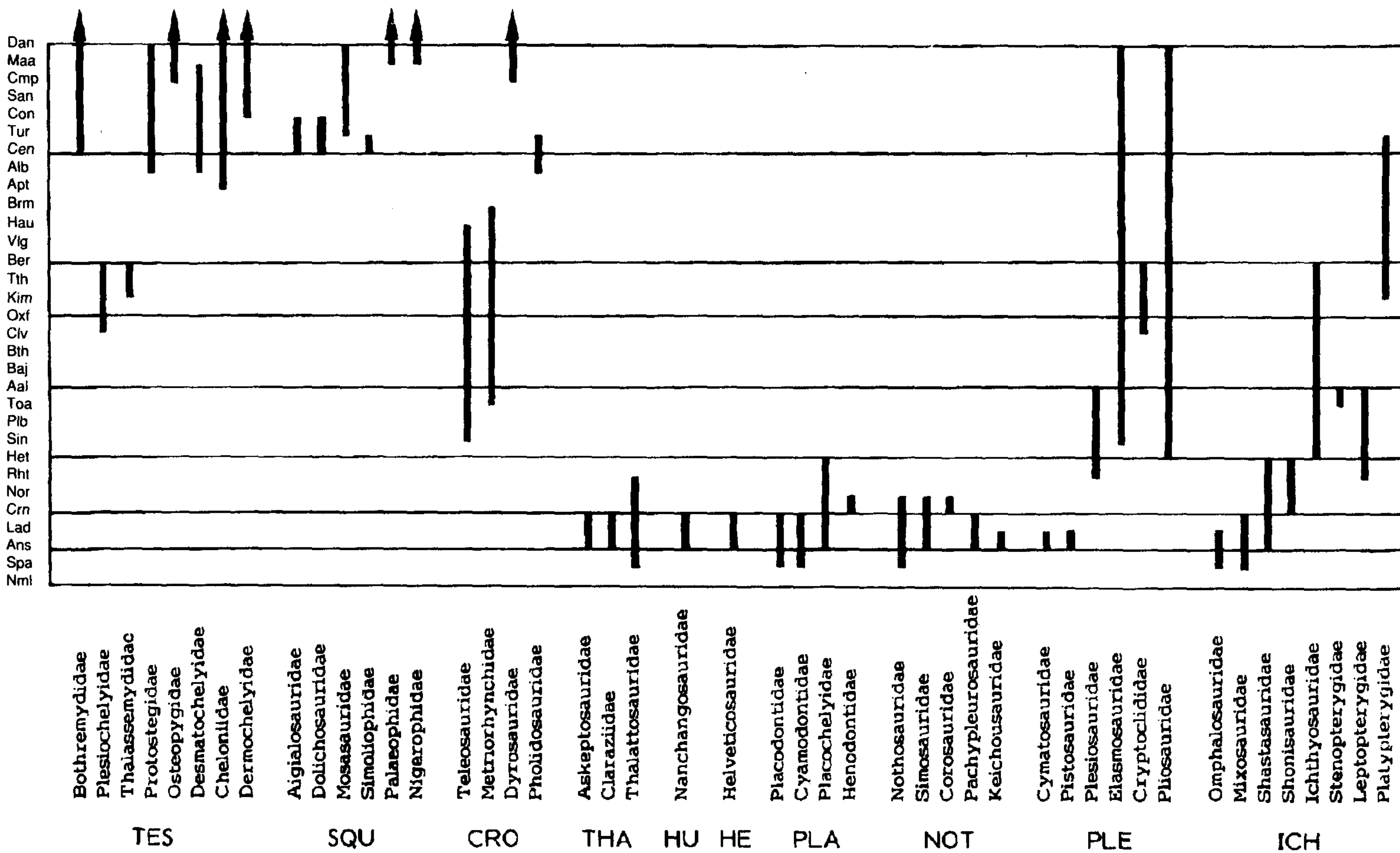

Figure 1 Stratigraphical ranges of Mesozoic marine reptile families. The data are part of Bardet (1992a) compilation. Timescale of Harland *et al.* (1989) has been used for stage abbreviations.

The Quality of the Fossil Record (Table 1)

The fossil record of marine reptile groups is not equal in quality from stage to stage. Some stratigraphical intervals, i.e. the Aalenian-Bathonian (Middle Jurassic) and Berriasian-Aptian (Lower Cretaceous), have yielded scanty remains. These intervals represent 28% of the Mesozoic Era duration but have yielded only 8% of the number of genera. The percentage of families is higher (24%) because this taxonomic level includes fewer 'Lazarus taxa' than lower taxonomic levels. On the other hand, stages such as the Anisian-Ladinian (Monte San Giorgio), Toarcian (Holzmaden), Callovian (Oxford Clay), Tithonian (Solnhofen) and Campanian-Maastrichtian (North American outcrops) show an apparent high diversity because of 'Lagerstatten' and 'monographic' effects.

To estimate quantitatively the completeness of the marine reptile record, the SCM (Paul, 1982) has been calculated by examining the number of families which ought to be present (Table 1). The more 'Lazarus taxa' (Jablonski, 1986) that are present in a stage, the more incomplete is the fossil record. The SCM ranges from 0% (Bajocian, Barremian) to 100% (Spathian, Carnian-Sinemurian, Callovian, Aptian). Most of the values are located between 50% and 100%, but some fall below 50% in the Pliensbachian, Aalenian, Bathonian, Oxfordian, Berriasian and Coniacian.

Table 1 Completeness of the fossil record (SCM) of marine reptiles measured by stratigraphic stage. The families known by fossils (FF) divided by the total number of families (TF) provided the SCM, expressed in percentage.

Stages	FF	TF	SCM
Spa	6	6	100
Ans	16	17	94
Lad	12	13	92
Crn	8	8	100
Nor	4	4	100
Rht	5	5	100
Het	4	4	100
Sin	6	6	100
Plb	1	6	16
Toa	7	8	87
Aal	1	5	20
Baj	0	5	0
Bth	2	5	40
Clv	7	7	100
Oxf	3	7	42
Kim	7	9	77
Tth	7	9	77
Ber	2	5	40
Vlg	3	5	60
Hau	2	4	50
Brm	0	3	0
Apt	4	4	100
Alb	5	7	71
Cen	9	11	81
Tur	8	9	88
Con	2	8	25
San	7	8	87
Cmp	9	10	90
Maa	10	11	90
Dan	3	7	43

The recognition of intervals characterized by gaps and 'Lazarus taxa' is of interest because it could focus the attention of palaeontologist on where stratigraphical efforts should be made.

DIVERSITY ANALYSIS

Diversity Changes (Figure 2)

High diversity among marine reptiles occurred mainly during the Mid Triassic and the Late Cretaceous. The Anisian-Ladinian and Campanian-Maastrichtian intervals, which represent less than 14% of the Mesozoic duration, have yielded approximately 63% of the total number of families, and 50% of genera and species known. These periods are characterised by a good fossil record, probably in relation with global transgressive phases and interest of palaeontologists. Minor diversification events have been recognised during the Kimmeridgian-Tithonian and Santonian stages.

As previously mentioned, marine reptiles are very poorly represented during the Aalenian to Bathonian and Berriasian to Aptian intervals, probably related to a change in the quality of the fossil record.

There seem to be at least two significant declines in marine reptile diversity, tentatively attributable to mass-extinction events: Ladinian-Carnian and Maastrichtian-Danian. During the Mid-Late Triassic transition, 64% of families and 83% of general died out. The Cretaceous-Tertiary boundary is marked by the disappearance of 36% of families and 88% of genera. Minor extinction events occurred during the Tithonian-Berriasian and Cenomanian-Turonian transitions.

Extinction and Origination Rates (Figure 3)

Familial extinction rates are particularly high in the Ladinian, Tithonian, Cenomanian-

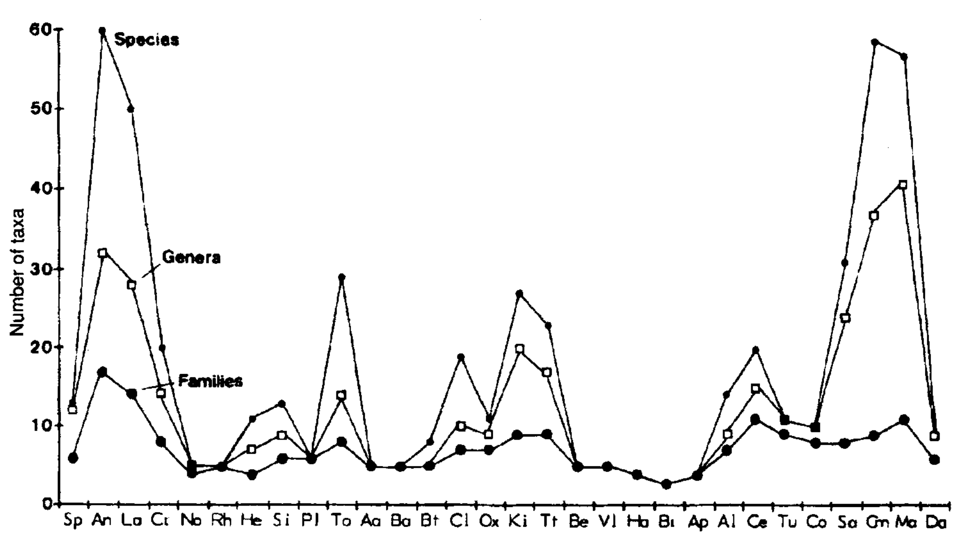

Figure 2 Global diversity with time spans (Spathian-Danian) for families, genera and species of marine reptiles. Timescale of Harland *et al.* (1989) has been used for stage abbreviations.

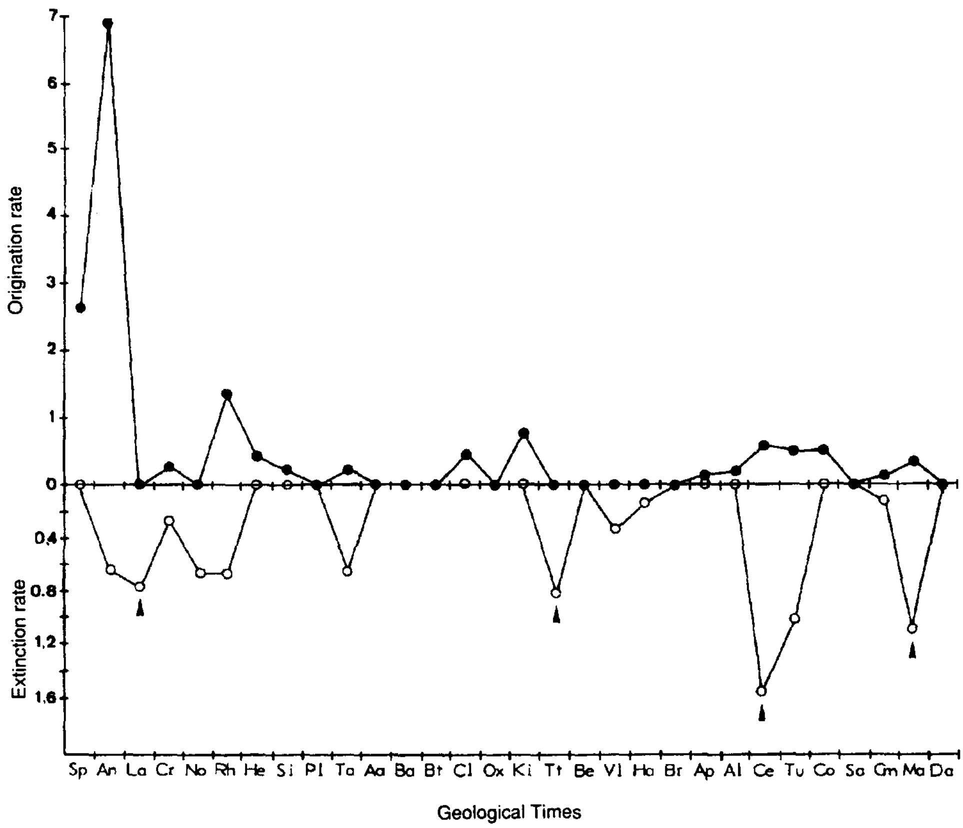

Figure 3 Total extinction and origination rates for marine reptile families calculated stage by stage (Spathian-Danian). Timescale of Harland *et al.* (1989) has been used for stage abbreviations and durations.

Turonian and Maastrichtian stages and they correspond to phases of global diversity drops previously mentioned.

Familial originations rates are important in the Spathian, Anisian, 'Rhaetian' and Kimmeridgian.

Reliability of the Fossil Record (Figure 2, 4)

Comparisons of global diversity fluctuations show that the familial curves correlate globally with the generic and specific ones (Figure 2). The reliability of the fossil record at the family level is thus warranted in some degree, because these families are able to reflect lower taxonomic levels (Sepkoski, 1987).

On the other hand, a comparison of the curve based on all families with that based only on families considered as well defined and monophyletic, shows minor differences (Figure 4). The intervals where the two curves overlap correspond globally to periods with poor fossil record. On the contrary, curves do not overlap during the intervals with a good fossil record. Minor differences are noted for the Triassic, Toarcian and Kimmeridgian-Tithonian intervals, whereas differences are important during the Late Cretaceous. So, this could focus the attention of palaeontologists on where systematic efforts should be made.

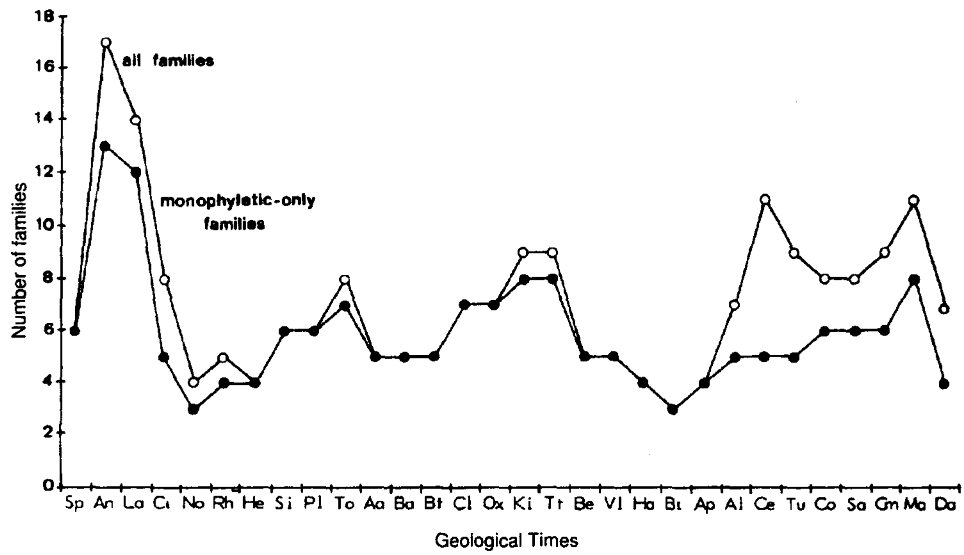

Figure 4 Global diversity with time spans (Spathian- Danian) for total number of families compared with well defined and monophyletic-only families of marine reptiles. Timescale of Harland *et al.* (1989) has been used for stage abbreviations.

EXTINCTION EVENTS

A mass extinction should satisfy criteria of timing (brief event relative to the average duration of the taxa involved), breadth (event affecting a variety of higher taxa on taxonomic, and thus presumably on ecological and biogeographic points of view) and magnitude (elevated extinction rates) (Jablonski, 1986). The combination of major drops in overall diversity with times of unusually high extinction rates permits to detect mass extinction events.

The fossil record of Mesozoic marine reptiles is punctuated by major extinction events, tentatively attributable to mass-extinctions, as well as minor extinction events, as follows:

Middle-Late Triassic (Ladinian-Carnian)

Nine families of marine reptiles died out during this event:

- "Nothosauria": Pachypleurosauridae, Keichousauridae;
- Ichthyopterygia: Mixosauridae;
- Placodontia: Placodontidae, Cyamodontidae;
- Thalattosauria: Askeptosauridae, Claraziidae;
- Hupehsuchia: Nanchangosauridae;
- Helveticosauroidea: Helveticosauridae.

The "nothosaurs" are the most affected: only three genera among the 13 currently known during the Ladinian persist into the Carnian (Bardet, 1992a). Placodonts and thalattosaurs show faunal replacement with loss of diversity. As for hupehsuchians, cymatosaurs and pistosaurs, they are not currently known in the fossil record after the Mid Triassic. Ichthyosaurs seem less affected during this transition and they diversify in the Carnian, with the appearance of pelagic forms and the decrease of littoral ones (Mazin, 1988).

The Ladinian-Carnian boundary corresponds to the beginning of a great regressive phase (Haq *et al.*, 1987). It leads to an important restriction of the epicontinental realm, where most of these marine reptiles lived. This regression could have mainly affected coastal forms such as nothosaurs, placodonts, thalattosaurs and some ichthyosaurs. Only pelagic forms (ichthyosaurs such as shastasaurids) seem not to have been directly affected.

Raup & Sepkoski (1986) have argued that the Late Triassic extinction consisted of a single event located in the Late Norian ('Rhaetian'). This event, leading to the extinction of 20% of families and 48% of genera of marine invertebrates, affected essentially cephalopods, bivalves, gastropods, brachiopods and conodonts (Sepkoski, 1982b, 1986). On the contrary, Benton (1986a, 1986b) has identified at least two phases of extinction in the fossil record of tetrapods, ammonoids and other groups, respectively at the Carnian-Norian transition and at the Triassic-Jurassic boundary. An extinction event has also been detected for ammonoids, bivalves, conodonts, echinoids and crinoids at the end of the Early Carnian (Benton, 1991). Regarding marine reptiles, the time of extinction seems to occur anywhere between the end of the Ladinian and the beginning of the Carnian, but stratigraphical details are not accurately known. It is not excluded that extinction among marine reptiles may be correlated with the Early Carnian event. However, the Late Triassic to Triassic-Jurassic boundary do not correspond to a period of extinction for marine reptiles but rather to an important faunal turnover interval (Bardet, in prep).

Latest Jurassic (Tithonian-Berriasian)

Four families died out during this event:

- Plesiosauria: Cryptoclididae.
- Ichthyopterygia: Ichthyosauridae.
- Chelonia: Plesiochelyidae, Thalassemydidae.

The coastal turtles are the group most affected, as the two families dissappear from the fossil record. Plesiosaurs and ichthyosaurs are less affected, with the lost of one family each. The thalattosuchians (both teleosaurids and metriorhynchids) persist into the Neocomian with a very low diversity. For all these groups, most of the genera known from the Tithonian are not found in the fossil record after that time (Bardet, 1992a).

A high extinction rate among marine invertebrates, especially ammonoids, bivalves and corals (37% of genera affected), has been detected at the end of the Tithonian (Sepkoski, 1986). This event, especially marked on the dominant group of benthic invertebrates, the bivalves, correlates broadly with evidence of a major regression of shallow epicontinental seas restricted to Europe (Hallam, 1986). At the same time, a widespread transgression occurred in South America. As a result, the bivalve extinction cannot be recognised here (Hallam, 1986). Thus, the marine invertebrate extinction event at the end of the Tithonian occurred on a regional scale and could be related to severe reductions in habitat area caused by regression of epicontinental sea (Hallam, 1986). As for marine reptiles, the main portion of Upper Jurassic taxa has been discovered in Europe. The scenario could thus be the same for marine reptiles as for marine invertebrates in terms of a reduction in habitat area. The effects of the regression could have been particularly marked on coastal forms such as thalassemydid and plesiochelyid turtles, whereas pelagic groups could have been able to survive. The recent discovery of a rich Upper Jurassic fauna of marine reptiles in South America (Fernandez & Fuente, 1989; Gasparini, 1985) could permit a better understanding of this extinction event.

Early Late Cretaceous (Cenomanian-Turonian)

During this event, three families of marine reptiles died out:

- Ichthyopterygia: Platypterygidae.
- Crocodylia: Pholidosauridae.
- Serpentes: Simoliophidae.

The Cenomanian-Turonian transition is marked by the probable extinction of ichthyosaurs, considered by some authors to reach the end of the Cretaceous (Russell, 1977; Sullivan, 1987). In fact, they seem to become rare during the Cenomanian and probably died out during this crisis. A review of post-Cenomanian ichthyosaur remains has revealed that all are doubtful both on systematic and stratigraphic grounds (Bardet, 1992b). As suggested by Baird (1984), the survival of ichthyosaurs into the post-Cenomanian stages of the Late Cretaceous remains to be established.

The Cenomanian-Turonian (C/T) boundary event has been considered as a second-order extinction within Phanerozoic marine families (Raup & Sepkoski, 1986). This crisis corresponds to a global environmental perturbation period, effecting both the marine and continental realms (see Kauffman, 1986). 28% of marine invertebrate genera disappeared during this interval, including cephalopods, bivalves, echinoids, foraminifera and ostracods (Sepkoski, 1986). As for vertebrates, only teleostean fishes show a significant drop in diversity (Benton, 1989).

The perturbations (anoxic events, cooling, upwelling, etc.) which characterized the C/T boundary may have affected marine organisms such as invertebrates, fish and reptiles. A break in the food chain of ichthyosaurs, attested by the great extinction suffered by Tethyan belemnites (Stevens, 1973; Doyle, 1992) is proposed as an extinction scenario (Bardet, 1992b). The fact that plesiosaurs may have been more opportunistic predators than ichthyosaurs (Massare, 1988) could explain why they have not been directly affected. A major reorganisation at some time between the Kimmeridgian and the Late Cretaceous, leading to a replacement of the pliosaur/crocodile dominated fauna by mosasaurs has been proposed by Massare (1987). Concerning pliosaurs, they become rare after the C/T crisis, probably related to the expansion and competition of mosasaurs. Finally, the pholidosaurids and simoliophids as well as dolichosaurs and aigialosaurs remain respectively too sporadic in occurrence or too badly stratigraphically defined to link their disappearance with the C/T event.

Latest Cretaceous (Maastrichtian-Danian)

Four families died out:

- Sauropterygia: Pliosauridae, Elasmosauridae.
- Squamata: Mosasauridae.
- Chelonia: Protostegidae.

The Cretaceous-Tertiary (K/T) crisis among marine reptiles seems to have been selective (Bardet, 1992a; in prep.). Most of the large pelagic forms, such as mosasaurs, elasmosaurs, pliosaurs and protostegid turtles, become extinct. Contrary to Sullivan's (1987) assertion of a gradual extinction for marine reptile groups, the extinction of mosasaurs and elasmosaurs fits rather into a catastrophist than a gradualist model as they are still known and largely widespread in Late Maastrichtian formations (Bardet, 1992a). On the contrary, pliosaurs and protostegid turtles remain very scarce during the Maastrichtian, suggesting that they were already declining.

Direct survivors of the crisis are mainly coastal forms, such as dyrosaurid crocodiles, osteopygid and bothremydid turtles, paleophid and nigerophid snakes. At least some of these forms probably moved on land, as suggested by bothremydids and dyrosaurids found in continental deposits. As for cheloniid and dermochelyid turtles, the data are not good enough during the Late Cretaceous-Palaeogene period, so that their behaviour at the K/T boundary is difficult to surround.

The K/T boundary is characterised by a significant mass extinction affecting both continental and marine organisms, which led to the disappearance of 15% of families and 50% of genera (Sepkoski, 1982b, 1986). Two major controversies have arisen in research on the end-Cretaceous mass extinctions, concerning whether they were sudden or gradual and terrestrially or extraterrestrially induced (see Hallam, 1988 for a summary). In the marine realm, the strong extinction suffered by the phytoplankton, especially that of open ocean surface waters (Thierstein, 1982) may have induced a global break in the food chain. This break is suggested here as an extinction scenario to explain the disapperance of huge pelagic reptiles which are directly based on the phytoplankton chain. It could also explain the survival of littoral groups, not directly affected by this break because probably able to seek refuge in freshwater environments. A similar scenario (break of plant food chain) has been proposed for the continental realm (Buffetaut, 1984).

CONCLUSION

The fossil record of marine reptile groups has been punctuated by two major extinctions, tentatively attributable to mass-extinctions, located at the Ladinian-Carnian and Maastrichtian-Danian transitions. The Mid-Late Triassic crisis affected mainly coastal groups. The Cretaceous-Tertiary extinction was selective, affecting pelagic groups, some implying a catastrophist model of extinction. Two minor events have been recognised at the end of the Tithonian and the Cenomanian but more data are necessary for a better understanding. Even if the vertebrate fossil record is not good enough to test the Raup & Sepkoski (1984, 1986) theory of 26 My extinction periodicity, most of the marine reptiles events, i.e. Tithonian, Cenomanian and Maastrichtian, match those identified by previous authors. However, the Middle-Late Triassic extinction does not fit at all the 26 My cycle. On the other hand, some of the 26 My extinctions postulated by Raup & Sepkoski (1984, 1986), i.e. Pliensbachian and Aptian, have not been recognised for marine reptiles.

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