Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the Cretaceous–Tertiary boundary

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Abstract

Fishes are often thought to have passed through mass extinctions, including the Cretaceous–Tertiary (KT) event, relatively unscathed. We show that neoselachian sharks suffered a major extinction at the K/T boundary. Out of 41 families, 7 became extinct ($17\pm12\%$). The proportional measure increases at lower taxic levels: $56\pm10\%$ loss of genera (loss of 60 out of 107) and $84\pm5\%$ loss of species (loss of 182 out of 216). However, the Maastrichtian and Danian are characterized by a high number of singleton taxa. Excluding singletons we have calculated a $34\pm11\%$ loss of genera and a $45\pm9\%$ loss of species. The simple completeness metric (SCM) for genera displays a decrease from the Maastrichtian (94%) to the Danian (85%) indicating a rather complete fossil record of neoselachian genera. The extinctions were heavy among both sharks and batoids (skates and rays), but most severe among batoids, which lost almost all identifiable species. There were equal losses among open marine apex predators (loss of Anacoracidae, Cretoxyrhinidae, and Scapanorhynchidae) and durophagous demersal forms from the continental shelf and shallow seas (Hypsobatidae, Parapaleobatidae, Sclerorhynchidae, Rhombodontidae). Benthopelagic and deep-sea forms were apparently little affected. New families with similar ecological roles (Carcharhinidae, Isuridae, Torpedinidae) replaced these families in the Danian, and full diversity of the different shark and batoid groups had been recovered by the end of the Paleocene or early Eocene. Sharks and rays suffered levels of extinction entirely in line with other groups of organisms at the K/T extinction event.
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1. Introduction

The K/T extinction represents probably the most famous of all mass extinction events in the fossil record. According to recent data, the K/T boundary mass extinction ranks well among the Phanerozoic Big Five with a loss of $76\pm5\%$ species, $47\pm4\%$ genera, and $16\pm2\%$ families (Jablonski, 1991; Sep-

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koski, 1991). Major extinction of tetrapods and aquatic invertebrates at the K/T boundary is well documented (e.g., Benton, 1987, 1995, 1999; Keller et al., 1995; Håkansson and Thomsen, 1999; Dupuis et al., 2001; Kiessling and Claeys, 2001; Alegret et al., 2002; Fara, 2002). The currently favored hypothesis involves a meteorite that collided with the Earth (impact theory) roughly 65 Ma ago creating the Chicxulub crater in Yucatán, Mexico (e.g., Alvarez et al., 1980). This impact changed the climate dramatically as dust and ashes clouded the sky blocking the sun out and reducing photosynthesis, generating toxins, and destroying the ozone layer resulting in short-term extinction events within <1 year of the impact (Hildebrand et al., 1998; Hildebrand, 2003).

Despite broad acceptance of a major extinction event its consequence for organisms is still controversial in terms of timing (sudden versus gradual), severity of the extinction of taxa, and the relative completeness of K/T boundary sections (e.g., Keller and Barrera, 1990; Keller et al., 1998; Stinnesbeck, 1996; Stinnesbeck et al., 1999, 2001; Keller et al., 2001). Alternative hypotheses explaining diversity fluctuations and extinction patterns at the end of the Cretaceous include multi-event scenarios such as extended periods of volcanism, changes in sea level, and climatic changes as well as certain local factors (e.g., Prasad and Khajuria, 1995; Keller et al., 2002, 2003; Stinnesbeck, personal communication). A central question in recent debates is whether the quality of the fossil record is good enough to accept observed diversity and extinction quantity and whether rock volume is actually the controlling factor of patterns of abundance and diversity of fossils (e.g., Peters and Foote, 2001, 2002).

Ideally, the diversity pattern of aquatic vertebrates such as actinopterygians and selachians across the K/T boundary follows that of other organisms resulting in high extinction rates. For instance, the effect of the K/T boundary event on actinopterygians is rather similar to that of neoselachians with 19% of families becoming extinct (Cavin, 2001). However, mainly specialized forms were affected (Cavin and Martin, 1995; Cavin, 2001). Previous works on neoselachians suggest, conversely, mass extinction of taxa at the end of the Cretaceous although the rates differ significantly between studies and the level of resolution between these analyses ranges from global (e.g., Cappetta, 1987a) to local scale (Archibald and Bryant, 1990; Noubhani and Cappetta, 1997) or considers only certain groups (Zhelezko, 1999; Zhelezko and Kozlov, 1999).

Here, with an emphasis on global diversity patterns, we re-evaluate the extinction and origination rates of neoselachians at all taxonomic levels across the K/T boundary based on updated data. The underlying causes for the diversity fluctuations are considered to assess whether the observed patterns are real or an artefact. Hybodontoid sharks are not considered. According to the present knowledge, a single hybodont species is known from the late Maastrichtian. Most hybodonts seem to vanish before the Maastrichtian. Only a single species is known from the Maastrichtian.

2. Methods and data

Neoselachians are a well-defined monophyletic clade that represents one of the most successful groups of selachians (e.g., Compagno, 1977) with a fossil record that encompasses almost 250 Ma and extends back at least to the Early Triassic (Thies, 1982) although rare isolated teeth from Paleozoic strata may represent plesiomorphic members of this group (e.g., Duffin and Ward, 1983; Turner and Young, 1987). Earlier systematic concepts of fossil neoselachians (e.g., Cappetta, 1987b) were critically scrutinized and updated on the basis of works by Siverson (1999), Cappetta et al. (1993), Shirai (1996), Carvalho (1996), McEachran et al. (1996), Noubhani and Cappetta (1997), Adnet and Cappetta (2001), and Kriwet (in press). The database used here (electronic appendix see Background Data Set) was compiled from a vast literature on fossil and extant neoselachians (e.g., Cappetta, 1987b; Ward, 1988; Siverson, 1992; Zhelezko and Kozlov, 1999), and considerable generic and species revision based on recent publications was carried out. This resulted in re-arrangements of taxa or changes in supra-generic taxonomic composition. For instance, a single genus, *Cretoxyrhina*, is assigned to Cretoxyrhinidae according to Siverson (1999). A total of 12 orders, 45 families, 164 genera, and 448

species, 64 of which are in open nomenclature were assessed.

The severity of extinction and recovery relates unquestionably to whether or not specimens found in a time slice are genuine or reworked and to the completeness of the fossil record. *Deania*, cf. *Oxynotus*, *Eostegostoma*, *Gymnura*, *Pachygaleus*, and *Pseudodontaspis*, for instance, are Lazarus taxa known from Cretaceous and/or Paleogene strata that have not been recovered in the Maastrichtian so far. The Mesozoic occurrences of *Mesiteia* (considered here a typical Cenozoic taxon) and the Paleogene records of *Orectoloboides*, *Scapanorhynchus*, and sclerorhynchid sawfishes (characteristic Cretaceous taxa) are arguable and were subsequently omitted from the analyses. The presence of *Cretalamna appendiculata* in post-Coniacian, of *Cretoxyrhina mantelli* in post-Campanian, and of *Squalicorax kaupi* in late Maastrichtian strata may be arguable (C. Underwood personal communication).

Chlamydoselachus, *Thrinax*, *Echinorhinus*, *Deania*, *Centroscymnus*, *Somniosus*, cf. *Oxynotus*, *Brachaelurus*, *Odontaspis*, *Pseudodontaspis*, *Pachygaleus*, and *Gymnura* are considered here Lazarus taxa for the Danian.

Species in open nomenclature were only considered in the final analyses when they are the only records of the corresponding supraspecific taxon. At the species level these entries were completely ignored. These refinements of the original database resulted in a slightly reduced data set of 12 orders (9 sharks, 3 batoids), 45 families (30 sharks, 15 batoids), 161 genera, and 415 species.

Two different approaches to scrutinize the effect of the K/T boundary event on neoselachians are available. Quantitative methods investigate rates of extinction and recovery whereas qualitative methods

consider paleoecological data. Quantitative indices used in this study are those of Sepkoski (1978) and Lasker (1978):

rate of origination $r_0 = (1/D) \times (S/t)$

rate of extinction $r_e = (1/D) \times (E/t)$

where D indicates the number of taxa present in a specific interval, S is the number of taxa originations, E is the number of taxa extinctions, and t is the time interval (in Ma). The rates of diversification ($r_d = r_o - r_e$) and recovery ($r_t = r_o + r_e$), respectively, are calculated to establish the diversity of neoselachians in the latest Cretaceous and the Early Paleogene.

Unfortunately, sufficient data on the exact temporal and spatial distribution of last (LAP) and first appearances (FAP) of taxa as well as additional age occurrences are not available. Only a few publications indicate the exact stratigraphic position of Maastrichtian neoselachians (e.g., Siverson, 1993; Noubhani and Cappetta, 1997). Consequently, it is not possible to employ resampling methods and all LAPs are considered here to be Maastrichtian. LAPs, FAPs, and SURs (taxa living unaffected through the K/T boundary) for all taxonomic levels in percentages were determined (Table 1). Singleton taxa (those occurring only in the Maastrichtian and Danian, respectively) introduce unacceptable biases and were subsequently omitted to reduce the noise and to obtain more realistic biological signals. We find 27 genera and 86 species to occur only in the Maastrichtian and 21 species and 6 genera only in the Danian.

The simple completeness metric (SCM) of Benton (1987) is used to assess the diversity dynamics and completeness of the fossil record for genera.

The 68% and 95% confidence intervals for neoselachians in total, sharks, and batoids at family,

Table 1
Absolute neoselachian and shark and batoid last appearance (LAP), survival (SUR), and first appearance (FAP) percentages at family, generic, and species levels

	LAP (Maastrichtian)			SUR			FAP (Danian)		
	Total (%)	Sharks (%)	Batoids (%)	Total (%)	Sharks (%)	Batoids (%)	Total (%)	Sharks (%)	Batoids (%)
Family	17.1	7.3	9.7	82.9	61	21.9	7.3	4.1	3.2
Genus	56.1	19.6	36.6	43.9	37.4	6.5	29.0	15.9	13.1
Species	84.3	45.8	38.5	15.7	14.4	1.3	44.4	31.0	13.4

Ratios of shark and batoid patterns are calculated as percentages of the total proportion whereas the percentages in the text refer to the actual numbers of taxa and therefore differ.

genus, and species levels were calculated according to Raup (1991) with the help of a computer program developed by W. Kiessling (personal communication) (Table 2). The errors of 95% binominal confidence interval are given in the text. For corresponding errors of 68% binominal confidence interval refer to Table 2.

The establishment of qualitative data (diet, environmental preferences) is more difficult. The concept of durophagous versus piscivorous and marine versus brackish/freshwater seems insufficient to describe the trophic specializations. Consequently, the mode of life and bathymetric occurrence were distinguished. The attribution of these ecological parameters (e.g., demersal, pelagic including oceanic and neritic forms, benthopelagic, and bathydemersal) to exclusively fossil taxa known only by their dentitions is, nevertheless, problematical and often incoherent. To minimize possible errors we classified families and genera more broadly (e.g., Carcharhinidae predominantly pelagic, which can include littoral occurrences also).

The inferred durations of the time intervals are based on the Geological Time Scale compiled by Palmer and Geissman (1999) and differ slightly from those used by others (e.g., Noubhani and Cappetta, 1997). Duration of 6.3 Ma is given for the Maastrichtian, 4.0 Ma for the Danian, and 3.1 Ma for the Selandian and Thanetian. However, we did not normalize the occurrences for the duration of a stage.

3. Results

3.1. Late Cretaceous to Paleogene neoselachian diversity patterns

The standing diversity of post-Albian to Thanetian neoselachians is shown in Fig. 1 based on published and unpublished information. The lowest diversity is found in the Turonian and Coniacian after rather high diversity in the Cenomanian. A constant increase in taxonomic diversity is recognizable from the end of the Coniacian to the end of the Maastrichtian. The decrease of neoselachians at the end of the Cenomanian might reflect an extinction event that appears to be correlated with an expansion of dysoxic conditions across wide areas of the continental shelves (e.g., Elder, 1989). However, Gale et al. (2000) and Smith et al. (2001) presented convincing evidence that the end-Cenomanian extinction event may in fact be an artefact of a major marine transgression at that time. The intensity of the Coniacian to Santonian recovery phase of neoselachian faunas might, consequently, also be artificial and the smaller disturbances in the diversity curve for most of the Late Cretaceous might not be real. Another reason for the post-Cenomanian decline in neoselachian diversity might be that the Cenomanian has been studied more intensely by bulk sampling than the Turonian and Coniacian. There seems to be no decline when taxa with larger teeth that are more easily collected are considered (C. Underwood, personal communication).

The Maastrichtian heralds the greatest diversity of Late Cretaceous sharks and batoids according to the available data followed by a deep incision at the K/T boundary resulting in a rather low diversity of neoselachians in the Danian. The low diversity in the Selandian probably represents the proposed delayed extinction of taxa. However, the comparison of available data from all Paleogene ages indicates that the Selandian low diversity may be an artefact while the Thanetian displays rapid recovery patterns and an increase of neoselachian diversity (e.g., Cappetta, 1987a; Noubhani and Cappetta, 1997; this study). The standing diversity curve for species essentially follows that of genera (Fig. 1C).

However, the Late Cretaceous diversity pattern of neoselachians presented here must be cautioned. A revision of Cretaceous taxa in terms of stratigraphic

Table 2
Errors of 68% and 95% binominal confidence intervals for neoselachian extinctions in the Maastrichtian (A) and survivals (B) at family, genus, and species levels for total selachian occurrences and for sharks and batoids respectively

	Total		Sharks		Batoids	
	68%	95%	68%	95%	68%	95%
A						
Family	5.9%	11.5%	4.9%	9.6%	8.4%	16.1%
Genus	4.8%	9.4%	5.1%	10.0%	7.1%	13.9%
Species	4.9%	4.9%	4.4%	8.6%	5.2%	10.3%
B						
Family	6.5%	12.7%	9.8%	19.1%	14.3%	27.0%
Genus	7.3%	14.2%	7.7%	15.0%	10.8%	18.3%
Species	6.3%	12.2%	6.3%	12.4%	/	12.8%

The large errors of 95% binominal confidence intervals prevent a conclusive statement and indicate the need for further research.
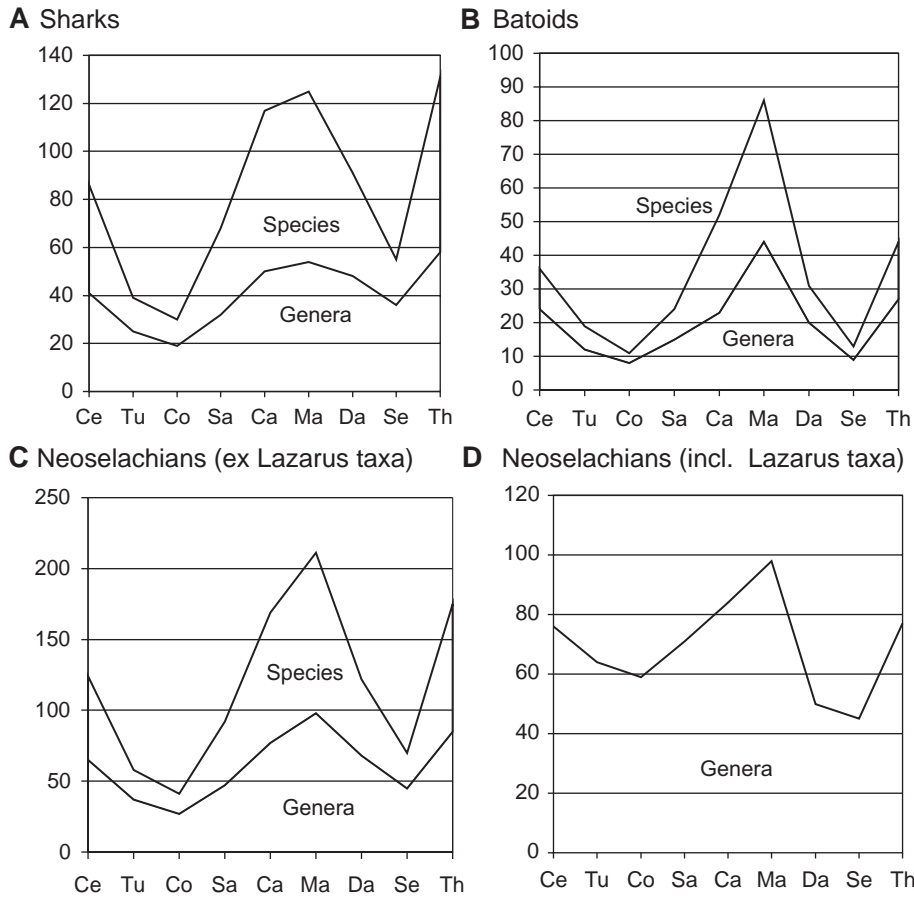
Fig. 1. Patterns of diversification of sharks (A), batoids (B), and neoselachians in general excluding (C) and including (D) Lazarus taxa on generic level in the Late Cretaceous and Paleogene in terms of taxa present per stratigraphic range. Ce, Cenomanian; Tu, Turonian; Co, Coniacian; Sa, Santonian; Ca, Campanian; Ma, Maastrichtian; Da, Danian; Se, Selandian; Th, Thanetian. The low diversity in the Selandian is related to the high number of Lazarus taxa. Singletons are excluded.

occurrences and taxonomy in addition with consideration of age durations and Lazarus taxa results in a slightly different pattern for pre-Maastrichtian selachians (Underwood and Kriwet, manuscript in preparation). The diversity of neoselachians on generic basis including Lazarus taxa (Fig. 1D) follows, however, mostly that excluding Lazarus taxa (Fig. 1C).

3.2. Total Maastrichtian to Danian neoselachian diversity

We measured the extinction, survival, and origination rates of neoselachians at ordinal, family, and species level across the K/T boundary based on global occurrences. At ordinal level, no extinction or turn-

over is recognized. Ordinal diversity increases across the K/T boundary from 11 orders in the Maastrichtian to 12 in the Danian as a result of the first appearance of electric rays (Torpediniformes).

At all other taxonomic levels, extinctions and originations are apparent. Forty-five families are known in the Maastrichtian and Paleogene of which 41 families occur in the Maastrichtian (Table 3). Seven families (17±12%) became extinct in the Maastrichtian (Table 4). Four Paleogene families, Carcharhinidae, Isuridae, Pristidae, and Torpedinidae are absent in the Cretaceous. The family Gymnuridae is interpreted here as a survivor because gymnurids occur in the Cenomanian (Werner, 1989) and Danian (Noubhani and Cappetta, 1997). A total of 37 families

Table 3

Absolute numbers of neoselachian families, genera, and species occurring in the Maastrichtian (M) and Danian (D), and Maastrichtian extinctions (E), Danian originations (O), taxa surviving the K/T boundary event (S), absolute Maastrichtian shark and batoid occurrences (M_S and M_B), absolute shark and batoid extinction numbers (E_S and E_B), absolute Danian shark and batoid occurrences (D_S and D_B), absolute Danian shark and batoid origination numbers (O_S and O_B), absolute numbers of surviving selachians and batoids (S_S and S_B)

	Family	Genus	Species
M	41	107	216
M_S	28	61	130
M_B	13	46	86
E	7	60	182
E_S	3	21	99
E_B	4	39	83
D	37	78	130
D_S	27	57	98
D_B	10	31	32
O	3	31	96
O_S	2	17	67
O_B	1	14	29
S	34	47	34
S_S	25	40	31
S_B	9	7	3

Lazarus taxa are not considered. This results in the apparent differences between ages. See text for discussion on Lazarus taxa.

are documented from the Paleogene (Tables 2 and 4) with two families representing Lazarus taxa (Chlamydoselachidae, Echinorhinidae). Only three (8.1%)

Table 5

Absolute numbers of neoselachian families, genera, and species for the Selandian (Se) and Thanetian (T) expressed as Selandian (SeO) and Thanetian originations (TO), number of Selandian sharks and batoids (Se_S and Se_B), sharks and batoid originations in the Selandian (SeO_S and SeO_B), number of Thanetian sharks and batoids (T_S and T_B), number of Thanetian sharks and batoid originations (TO_S and TO_B)

	Family	Genus	Species
Se	24	45	70
Se_S	18	36	57
Se_B	6	9	13
SeO	4	4	17
SeO_S	2	2	10
SeO_B	2	2	7
T	32	85	175
T_S	21	58	131
T_B	11	27	44
TO	1	13	81
TO_S	0	8	55
TO_B	1	5	26

of these groups are new (Carcharhinidae, Isuridae, Torpedinidae; Table 4). The first modern sawfishes (Pristidae) are known from the Thanetian (3% of the total number of known families in the Thanetian).

The Selandian is characterized by only 24 families (20%), whereas 32 families are present in the Thanetian (25%) (Table 5). This model is similar to that of Cappetta (1987a) but the overall pattern is probably related to collecting bias and the possible

Table 4

Listing of families disappearing at the end of the Cretaceous (LAP), living through the K/T boundary event (SUR), and originating in the Danian (FAP)

LAP	SUR		FAP
Anacoracidae	Scyliorhinidae	Heptranchidae	Carcharhinidae
Cretoxyrhinidae	Triakidae	Hexanchidae	Isuridae
Scapanorhynchidae	Heterodontidae	Pristiophoridae	Torpedinidae
Hypsobatidae	Cretodontidae	Echinorhinidae	
Parapaleobatidae	Alopiidae	Squalidae	
Sclerorhynchidae	Jaekelotodontidae	Orthacodidae	
Rhombodontidae	Mitsukurinidae	Palaeospinacidae	
	Odontaspididae	Squatinidae	
	Otodontidae	Platyrhinidae	
	Serratolamnidae	Rajidae	
	Brachaeluridae	Rhinobatidae	
	Ginglymostomidae	Rhynchobatidae	
	Hemiscyliidae	Dasyatidae	
	Orectolobidae	Mobulidae	
	Parascyliidae	Myliobatidae	
	Rhincodontidae	Gymnuridae	
	Chlamydoselachidae	Rhinopteridae	

presence of Lazarus taxa. Thirty-four families (87 ± 11%) in sum live through the K/T boundary event including all major ecological groups (Tables 1 and 2).

A considerable decrease in genera and species diversity is evident across the K/T boundary (Tables 1 and 2). Sixty neoselachian genera became extinct in the Maastrichtian (61 ± 10%) while only 31 genera are encountered in the Danian for the first time (32%). Forty-seven genera (48 ± 14%) live through the K/T boundary event. The SCM for genera displays a decrease from the Maastrichtian (94%) to the Danian (85%) indicating a rather complete fossil record of neoselachian genera for these stages.

The extinction and origination rates are slightly lower but not significantly different when all genera including dubious records are analyzed. In this case, the extinction rate for the Maastrichtian is 59% and the origination percentage for the Danian is 44%.

A total of 182 species (84 ± 5%) disappear at the end of the Cretaceous compared to 96 species (44 ± 5%) that first emerge in the Danian (Table 1). Only 34 species (13 ± 13%) pass through the K/T boundary.

3.3. Sharks versus batoids

The different responds of sharks and batoids to the K/T boundary event are noteworthy because batoids are mainly bottom dwellers with few benthopelagic or pelagic forms. The differences are modest at ordinal level and indicate a slight increase in diversity from nine shark and two batoid orders in the Maastrichtian to and nine shark and three batoid orders in the Danian to Thanetian.

The loss and origination of sharks and batoids at family level are more pronounced (Tables 1 and 2). Only 25 shark and nine batoid families of formerly 28 shark and 13 batoid families in the Maastrichtian survive the K/T boundary event. 43% of the extinct families are sharks whereas 57% belong to batoids. Two shark families (Carcharhinidae, Isuridae) and a single batoid family (Torpedinidae) first appear in the Danian resulting in a total origination percentage of only 8%.

Batoids were also more strongly affected at generic level. Thirty-nine batoid genera vanish at the end of the Cretaceous resulting in an extinction rate of 65%

whereas only 14 batoid genera (45%) are encountered in the Danian for the first time. Forty-seven of all genera (48 ± 14%) cross the K/T boundary, 85% being sharks (Table 1). Batoids display with 15% a comparably low survival rate.

The results at species level are slightly contradictory. Of 182 (85 ± 5%) extinct species, 99 are sharks (54%) and 83 are batoids (46%) compared to 96 FAPs (77%) in the Danian of which 67 are sharks (70%) and 29 are batoids (30%) (Table 3). Although seven batoid genera cross the boundary six are represented by unspecified finds, only a single named species (*Myledaphus bipartitus*) is reported in both the Maastrichtian and Danian.

3.4. Ecological selectivity

A number of pelagic apex predators such as *Archaeolamna*, *Paranomotodon*, *Squalicorax*, *Cretoxyrhina*, and *Scapanorhynchus* disappeared at the end of the Cretaceous (Table 4). These are medium- to large-sized and mostly fast-swimming predators of the epipelagic and shelf zones with generally rather broad-spectrum diets. However, there are indications that at least several species of *Squalicorax* and *Cretoxyrhina* possibly were considerably specialized (e.g., Schwimmer et al., 1997; Shimada, 1997, 2000). These top predators becoming extinct at the end of the Cretaceous were replaced by other pelagic groups with similar adaptations in the Danian (Carcharhinidae, Isuridae) although extinction and origination rates are not balanced (Table 4).

Other heavily affected groups include demersal shallow-marine forms, the orectolobiforms (e.g., *Paraginglymostoma*, *Cantioscyllium*, *Ganntouria*, *Plicatoscyllium*, *Pseudoginglymostoma*) and batomorphs (Table 4). A selective aspect at generic level is evident. Batoids with grinding-type dentition as adaptation to hard-shelled prey (e.g., *Hypsobatis*, *Pseudohypolophus*, *Pucabatis*, *Rhombodus*, *Youssoubatis*) were heavily affected and became mostly extinct at the end of the Cretaceous but were replaced by other taxa with the same adaptations (e.g., *Hypolophodon*, *Hypolophites*) (Cappetta, 1992, this study).

Less affected are deep-water sharks. However, the interpretation of fossil deep-water sharks is difficult and they are not easily identified in the Cretaceous.

Squalids (e.g., *Centrophorus*, *Dalatias*, *Isistius*, *Squa-lus* spp.) are generally regarded as deep-water forms although several other taxa are known to have occurred in large numbers in shallow water environments in the Cretaceous (Siverson and Cappetta, 2001; J.K., unpublished data). Other extant deep-water selachians are, for instance, *Chlamydoselachus*, *Echinorhinus*, and at least several species of scyliorhinids, rajoids, and dasyatoids. Most of these forms seem not to have been affected by the events at the K/T boundary. However, the taxonomy and fossil record of rajiforms is still poorly understood. Only three squalid genera (*Cretas-cymnus*, *Microetmopterus*, *Proetmopterus*) were wiped out. *Chlamydoselachus*, *Echinorhinus*, and *Eoetmopterus* represent Lazarus taxa in the Danian. The absence of these taxa is certainly related to the lack of corresponding deep-water deposits. The

identity of *Eoetmopterus* in the Cenozoic might, however, be dubious.

Fig. 2 summarizes the impact of the K/T boundary event on neoselachians according to their distribution (ecomorphotypes).

4. Discussion

Considerable progress has been made in resolving the effects of the K/T boundary event on marine and terrestrial organisms. The occurrence of the Chicxulub impact at the K/T boundary is generally accepted although its role and extent is still discussed. For instance, Glasby and Kunzendorf (1996), Keller et al. (2003), and Stinnesbeck (personal communication) reject the Chicxulub impact as being a major factor in
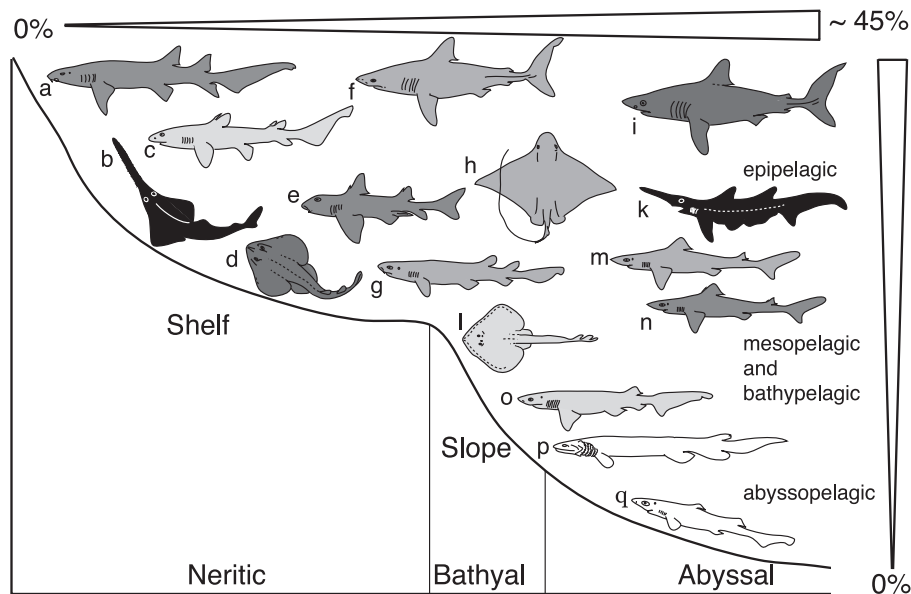

Fig. 2. Diagram displaying the effects of the K/T boundary event on some major neoselachian groups according to their main distribution. For instance, Pristiophoridae and Pristidae that are not affected and Squatinidae, only modestly affected, are not displayed. Some of these groups show rather wide distributions across several habitats (e.g., Squaliformes, Hexanchiformes, Rajidae, Myliobatiformes). Consequently, the diagram provides only a general impression. Four major habitats and corresponding neoselachian faunas are recognized in the Late Cretaceous: continental and insular shelves and open ocean (epipelagic zone), continental and insular slopes (meso- and bathypelagic zone), and deep-sea (abyssopelagic). Six categories in different shadings (white=not affected to black=extinct) are distinguished to indicate the impact of the K/T boundary event on selachians: none (<2%, no), slight (sl, 3–25%), modest (mo, 26–50%), strong (st, 51–75%), severe (se, 76–99%), extinct (ex, 100%). a, Orectolobiformes (st); b, Sclerorhynchidae (ex); c, Synechodontiformes (sl); d, demersal batoids (st–se); e, Heterodontiformes (st); f, lamniforms of the shelf areas (mo-st), g, Scyliorhinidae (mo), h, pelagic batoids (mo-st), i, pelagic lamniforms (se); k, Scapanorhynchidae (ex); l, slope to deep-sea batoids (sl); m, Triakidae (mo); n, Squalidae (st); o, Hexanchiformes (sl); p, Chlamydoselachidae and Echinorhinidae (no); q, deep-sea sharks (no). The effect of the K/T boundary event increases from freshwater (0%) to open oceanic habitats (~45%) and decreases from the epipelagic (~45%) to the abyssopelagic zone (0%).

the extinction event while others (e.g., Sheehan et al., 2000) favor the impact as the only possibility to explain the disappearance of taxa. Toon et al. (1997) and Hildebrand et al. (1998) reviewed and discussed possible effects of such impacts on organisms and concluded that multiple agents triggered the loss of taxa. Major extinction events for calcareous nanno-plankton, planktonic and benthic foraminifera, ammonites, belemnites, bivalves, bryozoans, brachio-pods, echinoids, corals, and probably ostracodes and gastropods are indicated by Kiessling and Claeys (2001). Based on Sepkoski's K/Tbase (Sepkoski, 2002), the extinction and origination rates for bivalve genera is 54.6% and 40.8%, for gastropods 38.6% and 27.4%, and for corals 42.1% and 37.2% (W. Kiessling, personal communication).

It has been shown that the K/T boundary event affected different trophic levels in food webs based on phyto- and zooplankton, which collapsed. This correlates well with the obliteration of pelagic and shallow-marine ecosystems producing severe stress. Consequent extinctions of ecologically important taxa resulted in prominent biomass reductions (Kiessling and Claeys, 2001). This assumption is transferable to marine vertebrates that represent mostly the top end of food pyramids. The disappearance of marine reptiles is well documented (e.g., Benton, 1999). Extinction of actinopterygians is moderate and victims are mainly epipelagic forms with assumed dietary specializations whereas deep-sea, shallow-marine, and freshwater bony fishes were more or less spared (Cavin and Martin, 1995; Cavin, 2001).

The evidence that selachians, on the other hand, were strongly affected by the K/T boundary event is compelling. Hybodontiformes, the predominant sela-chian group of the Paleozoic disappeared finally at the end of the Cretaceous after a long period of declining diversity (J.K., unpublished data). The final disap-pearance seems to have been rather sudden.

In this study, we found that 7 families, 60 genera (56±10%), and 182 species (84±5%) of neosela-chians became extinct (Tables 1–3). Victims were mainly pelagic piscivorous apex predators with rather broad feeding preferences, such as Anacoracidae, Cretoxyrhinidae, and Scapanorhynchidae as well as three groups of benthic dwellers with predominantly durophagous adaptations (Hypsobatidae, Parapaleo-batidae, Rhombodontidae) and the sclerorhynchids

that were more opportunistic in their diet (Kriwet and Kussius, 2001). Groups with similar or identical trophic specializations replace them in the Danian (Carcharhinidae, Isuridae, Torpedinidae). Benthopela-gic species and deep-water forms, on the contrary, are the least influenced. Severe loss of lamniforms is also supported by Zhelezko and Kozlov (1999) in a study of Peri-Tethyan neoselachians. However, the authors did not present detailed data on other neoselachian groups.

Remarkable is the high number of singleton taxa in the Maastrichtian and Danian. Eighty-six species and 27 genera are known only in the Maastrichtian while 21 species and 6 genera occur only in Danian strata. These numbers also include dubious identifications but exclude all taxa in open nomenclature. The reason for the high number of singletons might represent a collecting bias rather than a biological phenomenon.

Excluding all these singletons results in an extinction rate of 45±9% for species and 34±11% for genera. Conversely, 57±10% species and 37± 19% genera originate in the Danian making the turnover more pronounced.

Previous studies illustrate a rather heterogeneous image of neoselachian diversity across the K/T boundary. Only 16% of all chondrichthyan genera died out at the K/T boundary according to Sepkoski's K/T database (W. Kiessling, personal communica-tion), whereas Cappetta (1987a) found that 45% of all genera and three families (Anacoracidae, Sclerorhyn-chidae, Rhombodontidae) became extinct. The results are probably not directly comparable because Sep-koski's data also include chimaeriforms. However, the differences are not only caused by this broader approach here but by usage of different data sets and systematic concepts.

The most dramatic extinction rates for neosela-chians come from the continental Hell Creek For-mation of North America. Here, extinction was complete (Bryant, 1989; Archibald and Bryant, 1990; Archibald, 1996). However, the small sample size (five taxa) and the unique environment that does not represent the typical habitat of most neoselachians do not provide any crucial evidence of selachian extinction in continental environments. This interpre-tation is also strengthened by the occurrence of the batoid *Myledaphus bipartitus*, one of the groups becoming extinct in the Hell Creek Formation, in

other Paleogene sites, being the only named batoid species crossing the K/T boundary.

The most comprehensive study so far reflected the extinction and origination of neoselachians in open marine to near coastal settings in Morocco (Noubhani and Cappetta, 1997). These authors employed similar methods to the present study and provided therefore the only directly comparable result. Accordingly, they indicate extinction of 72.5% of genera (of which 32.5% are sharks and 40% are batoids) and 97% of species (of which 50% are sharks, and 47% are batoids). Conversely, 70% of genera (43% sharks, 27%) and 96% of species (61% sharks, 35% batoids) appeared in the Danian. These extinction and origination rates differ significantly from those in this study especially when singletons are excluded (Table 6). Moroccan genera and species are 75% and 55% more strongly affected. The origination rates are 74% higher at generic and 45% higher at species level in Morocco. In Table 6, the calculated diversity rates at global (this study) and local (Morocco) diversity are shown. Values at genus and species level including and excluding all singletons are displayed to facilitate comparisons. Surprisingly, the ratios including all singletons in this study differ significantly from those of Noubhani and Cappetta (1997) while those excluding all singletons are more similar although Noubhani and Cappetta (1997) incorporated all taxa in their analysis. Exclusion of singletons indeed corrects and lowers values for Morocco, which are, nevertheless, still higher than the rates found at global scale here.

Unfortunately, it is only possible to compare the rates derived for neoselachians with those for

actinopterygians at family level. The corresponding rates have been calculated from the data provided by Cavin (2001). At family level, 19% of actinopterygians became extinct. This rate is rather similar to that of neoselachians, and actinopterygians probably experienced similar losses at other taxonomic levels. The extinction (r_e=0.104), origination (r_o=0.074), diversification (r_d=−0.031), and turnover (r_t=0.178) rates for actinopterygians are, however, significantly dissimilar.

The observed divergences in neoselachian diversity are probably linked with factors that are more significant on a local or regional than on a global scale. It has been frequently argued that regressions and transgressions control deposition of sediments and thus the abundance and diversity of fossils (e.g., Smith, 2001). Local marine faunas are unquestionable affected by those regressions and transgressions that alter the surface area and displace habitats. This may result in apparent local extinctions that mask true extinction events (e.g., Smith et al., 2001). But migration is also an important cause of taxic disappearance. Migration can be assumed for at least some of the Maastrichtian neoselachian taxa of the Hell Creek Formation (e.g., *Myledaphus*) and of Morocco (e.g., *Scyliorhinus elongatus*, *Anomotodon plicata*, *Cretalamna biauriculata*, *Serratolamna serrata*) since they are known from younger strata for other localities. How far other taxa are also affected by this pseudoextinction pattern is difficult to establish. Finding any taxon in question in younger sediments depends strongly on the presence of similar facies somewhere else and the potential of the specimens to be fossilized.

The quality of the fossil record has been debated recently and it was questioned whether the sedimentary record is in fact good enough to accept observed oscillations as reflecting the real pattern. The volume of rocks deposited during a certain time is assumed to be the controlling factor of past diversity by some authors (e.g., Peters and Foote, 2001, 2002). These authors argue that the rapid diversification of life in the sea, and especially on land, in the past 250 Ma is not real and that virtually all mass extinction events, except perhaps the end-Permian and the K/T, could well be taphonomic artefacts. Their hypothesis would imply that diversity and extinction could only rarely be detected by palaeontological studies.

Table 6
Total rates of extinction (re), origination (ro), diversification (rd), and turnover (rt) at family, generic, and species levels and corresponding rates for genus and species levels excluding singletons (*)

	Family	Genus	Genus*	Species	Species*
r_e	0.027	0.089	0.110	0.133	0.222
N and C	–	0.081	–	0.108	–
r_o	0.020	0.099	0.115	0.185	0.220
N and C	–	0.096	–	0.214	–
r_d	-0.007	0.01	0.027	0.052	0.002
N and C	–	0.126	–	0.083	–
r_t	0.047	0.188	0.225	0.318	0.442
N and C	–	0.186	–	0.345	–

N and C: values from Noubhani and Cappetta (1997).

These assumptions are important because they contradict the long-held understanding that the fossil record can document the history of life (e.g., Sepkoski et al., 1981; Benton, 1995, 1999) and the finding that, at coarse taxonomic scale, the fossil record is equally good throughout the Phanerozoic (Benton et al., 2000). However, a generally rising trend of marine diversity since the beginning of the Triassic that opposes the overall falling sea-level curve can be noticed, so that the global increase in diversity since then is probably real (Smith, 2001). In addition, it has been shown in detailed studies of the Cretaceous rock and fossil records that there is actually no linkage between the nature of the rock record and the diversity curve, at least for continental organisms (Fara, 2002). Smith (2001) may be right that many of the smaller perturbations in organismal diversity are not extinction events. Nevertheless, there is no evidence for a major deterioration in the quality of the sedimentary rock record around the K/T boundary, and we are content to accept the patterns we report here are essentially correct reflections of selachian diversity changes.

5. Conclusions

The quantity of data of Maastrichtian and Paleogene selachians has increased since the last analyses of neoselachian diversity across the K/T boundary. A mass extinction event for selachians was assumed by some authors before and is confirmed here although the amplitudes of extinction and recovery differ.

The diversity measures at all analyzed taxonomic levels (family, genus, species) are rather uneven. Extinctions are most significant on species level (Table 2). This reflects the problems when dealing with higher systematic groups when addressing biodiversity and extinction patterns.

Minor specialization aspects of pelagic (epipelagic to littoral) and demersal shelf neoselachians are recognized that may have made these groups more vulnerable to ecological changes and triggered their extinction. However, this remains at the moment rather speculative.

The high extinction and origination rates of Noubhani and Cappetta (1997) and in this study are obviously related to many singletons at generic and species level in the Maastrichtian and Danian. Removal of these taxa leads to a more realistic scenario and is in better accordance with patterns observed in other marine groups.

Causes for the disappearance of taxa are threefold: (1) global extinction, (2) local extinction, e.g., related to transgression/regression events, and (3) migration. Pseudoextinctions may mask true extinction events when analyzing diversity patterns on local to regional scale. Consequently, we favor here analyzing global patterns contrary to Vermeij and Leighton (2003) who suggested evaluating extinction and diversification rates on local to regional scales because global trends mask variations amongst habitats, regions, and among clades.

Surprisingly, the origination rate of neoselachians in the Danian is higher than the extinction rate at the K/T boundary and contradicts the findings in other marine groups.

The observed global extinction event of neoselachians cannot be explained as a consequence of long-term environmental changes (climatic modifications, sea level fluctuations) and we consequently interpret the patterns we found in this study as basically correct reflections of selachian diversity in connection to a major mass extinction event at the K/T boundary with subsequent recovery. However, the ultimate nature of this event (single or multiple impact, volcanism) remains debatable at the moment.

The causes of the disappearance of taxa across the K/T boundary are still controversial and are related to the problem in assessing gradual disappearance and sudden extinction is related to the Signor–Lipps effect (Signor and Lipps, 1982) and the possibility of applying resampling methods. Timing the disappearance of neoselachians requires precise temporal and spatial resolutions of neoselachian occurrences that are not available at the moment. The time span of neoselachian extinction is certainly also influenced by the fact that many studies have been based around hial or condensed deposits (C. Underwood, personal communication). However, the combination of observed extinction patterns by Cappetta (1987a), Noubhani and Cappetta (1997), Zhelezko and Kozlov (1999), and in this study concurs better with the expected consequences of a short-termed disastrous event.

Further analyses of additional faunas at high latitudes (JK and in prep.) and concerning local extinction patterns will provide additional data and will allow depicting a more detailed model of the effects of the K/T boundary event on neoselachian faunas and distinguishing between local and global causes.

Acknowledgments

Appendix A. Supplementary Data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2004.02.049.

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