

Extinctions and faunal renewals among post-Jurassic selachians[†]

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INTRODUCTION.

To this day numerous works on systematics have been devoted to selachians. The studies done over the past two decades have clarified the systematics of this group and brought to light a significant number of new genera, providing evidence of numerous cases of parallel evolution in particular.

However, it is necessary to recognize that despite all this progress, information relative to faunal fluctuations (extinctions and renewals in particular) and accompanied by properly quantified data has been almost nonexistent. According to G.G. Simpson (1969), fish populations, including selachians, have been stable and show neither a definite peak nor a crisis at the K/T transition. C. Arambourg is truly the only author to turn his attention to the question of extinctions among selachians at the K/T boundary—his monograph on the vertebrates from the phosphates of the Maghreb (1952). Even in this case, he confined the extent of his work to the familial level and did not furnish any quantitative data.

It seemed interesting, therefore, on the basis of now available data to analyze in a more thorough manner the phenomena of extinctions and faunal renewals among the selachians while trying to quantify them as well.

Recently, Voigt (1981), Fischer & Arthur (1977) published selachian diversity curves according to data from the “Fossil Record” (Harland et al., 1967). The established curves are at the familial level in the first case and at the generic level, though limited to sharks alone, in the second. Nonetheless, the data used (see below) limits the significance and scope of the results.

I will deal only with post-Jurassic selachians in this study. The Jurassic faunas are still relatively unknown and limited to a small number of deposits, mainly in Europe. It would be illusory on the basis of equally fragmentary documentation to want to evaluate faunal fluctuations of Jurassic forms. At the beginning of the Cretaceous,

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however, and especially from the Aptian, the deposits are much more numerous with rich and diverse faunas, making them much more representative of the selachians existing at that time.

The presentation of evidence of a layer rich in iridium at the K/T boundary (Alvarez et al., 1980) is the origin of a renewed interest in the phenomenon of mass extinctions, particularly the one at the end of the Cretaceous. It is not my intention to review the numerous, submitted hypotheses, whether catastrophist or gradualist in nature. If the iridium is of cosmic origin as supported by Alvarez et al., the enrichment phenomenon was not as sudden as has been claimed. In fact, at the classic site of Stevns Klint in Denmark, the presence of iridium is detectable in a section about one meter thick. This section spans the uppermost Maastrichtian and the base of the Paleocene; the event would not have been instantaneous, therefore, but would have extended over a period of at least 2.5×10^5 years (Rocchia et al., 1984; Renard & Rocchia, 1984). The observations of Zoller et al. (1983) on the significant iridium levels during the course of the Kilauea eruption are somewhat in favor of a terrestrial, non-cosmic source of the iridium. Furthermore, there was the discovery of iridium in the Pliocene of the Antarctic Ocean without apparent relation to the impact of an extraterrestrial object and without associated extinctions (Kyte, Zhou, & Wasson, 1981).

DATABASE.

The database of the post-Jurassic selachian orders, families, genera, and especially their space-time distribution are scattered throughout several hundred articles not easily accessible to non-specialists.

Some isolated works have synthesized this information with the two most used being “Vertebrate Paleontology” (Romer 1966) and the “Fossil Record” (Harland et al., 1967); the data contained in these works are nonetheless old and now completely outdated—as easily applicable to the systematics as to the distribution of taxa—due to the increase in knowledge of the group since their publication.

Recently, Sepkoski (1982) published a “Compendium of marine fossil families,” listing the known fossil marine invertebrate and vertebrate families. The data concerning vertebrates were taken from Romer’s Treatise and from “Fossil Record.” The remarks expressed above naturally apply to the “Compendium”: for the selachians, only 22 of the 49 recognized families since the Early Cretaceous are listed and of those 22, 15 have incorrect stratigraphic distributions; therefore, 68% of the data relative to selachians is not reliable. This comment is noteworthy when one realizes that several authors have used this work recently to establish extinction curves. One can legitimately question the validity of results relying on an incomplete or erroneous database. One should hope that the invertebrates are better treated than the selachians.

The data used in this work (table 1) have been taken from “Handbook of Paleoiichthyology,” Vol. 3B (Cappetta, in press). All valid genera known since the base of the Cretaceous have been accounted for. The stratigraphic distribution of each genus,

and consequently that of each family, have been carefully verified according to the original bibliographic data and numerous unpublished observations regarding the faunas of North and West Africa and North America.

Regarding the stratigraphic distribution of taxa, a genus is considered present between two temporal extremes where it has been well-documented in both. Even if it is not represented in the time intervening, where incomplete fossil documentation does not allow its recognition, the same principle has been applied to families and orders.

The established curves and graphs at the global level basically represent the faunas of the Mesozoic world: the Mesozoic world being from America to Southeast Asia and the paleo-Atlantic with its territories in the Scandinavian province. Nearly all the studied genera came from these regions with the exception of *Pucabatis* and *Pucapristis*, both localized in the Maastrichtian of Bolivia; *Pseudoechinorhinus* and *Ikamauius* known only from New Zealand (in the Early Paleocene and from the Late Eocene to the Pleistocene respectively) and *Pliotrema*, present only in the Neogene of South Africa.

FAUNAL DIVERSITY AT THE GLOBAL LEVEL.

First of all, we are going to examine the faunal diversity of the selachians on a global scale, beginning at the ordinal level, then at the familial, and finally at the generic level.

Ordinal diversity.

Figure 1 shows that the ordinal diversity has varied very little from the Early Cretaceous (10 orders) to the present (11 orders) with a maximum of 12 orders from the Santonian to the Thanetian.

The Squatiniformes, Heterodontiformes, Hexanchiformes, Squaliformes, Orectolobiformes, Lamniformes, Carcharhiniformes, and Rajiformes (being 61.5% of the total) were present throughout this interval. It must be noted that these eight orders were already present in the Jurassic. The hybodonts (7.7%) became extinct at the end of the Cretaceous; the “Palaeospinaciformes” died out at the end of the Paleocene; the Pristiophoriformes are known since the Santonian; the Myliobatiformes have been present since the Cenomanian and the Torpediniformes appeared at the base of the Paleocene. The modern fauna was already in place at the ordinal level during the Early Eocene and there has been no important variation in the number of orders since that time.

Figure 2 shows the importance of each order and its variation percentage over the course of time. One sees the decrease in importance of the Lamniformes across the Late Cretaceous with a correlative increase—weak at first, then much more accentuated—among the Carcharhiniformes, which certainly contributed as well to the disappearance of the “Palaeospinaciformes” at the end of the Paleocene. Throughout the Neogene right up to modern times, the supremacy of the Carcharhiniformes over the

Lamniformes becomes much more pronounced and one notices that the percentages are practically reversed for both orders when comparing the Cenomanian with the Recent.

These same fluctuations are seen between the Rajiformes and the Myliobatiformes: the former declined at the end of the Cretaceous, essentially as a result of the extinction of the Sclerorhynchidae and of the Rhinobatoidei with grinding-type dentitions, whereas the latter became much more prominent thanks especially to the diversification of the Dasyatidae and the Myliobatidae. The other orders remained relatively stable, except for the Hexanchiformes, which experienced a decrease in generic diversity throughout the Cenozoic, and the Squaliformes, which by contrast, diversified during the same period. The fluctuations affecting the other orders are minor and of little significance.

Familial diversity.

The familial diversity curve (fig.1) appears distinctly less regular than the one for the orders. One sees a noticeable increase in the number of families right up to the Campanian with a leveling-off from the Cenomanian to the Campanian, a slight decrease between the Campanian and Maastrichtian (the disappearance of the important Cretaceous family, Ptychodontidae), and a major drop between the Maastrichtian and Dano-Montian, linked to the disappearance of the Hybodontidae, Polyacrodontidae, Anacoracidae, Sclerorhynchidae, and the Rhombodontidae. Then, the diversity clearly increases right up to the Ypresian. It increases again, very slightly, in the Early Oligocene (the appearance the Cetorhinidae) and yet again in the Middle Miocene (the appearance of the Sphyrnidae).

Table 2 shows the stratigraphic distribution of the selachian families. This type of representation gives only limited information, absence or presence of families; it does not give us any indication of the importance and generic diversity of the family at any given time. Yet, when one tries to delineate extinctions and faunal renewals, this type of information would seem fundamental. In fact, the sudden or apparently sudden downfall of a very diverse family at the generic and specific level does not have the same significance as a family represented by one or two monospecific genera. In the case of the very diverse family, one could imagine that there has been an event of sufficient magnitude to threaten a group whose members occupy a variety of ecological niches.

Figure 3 A-D shows the stratigraphic distribution of families, but at the same time providing for each stage their diversity expressed in number of genera.

This figure calls for some remarks and criticisms. The familial content can vary significantly according to various authors (for example, within Lamniformes, Rajiformes, and Myliobatiformes). Among the batoids I assigned some Eocene genera (*Arechia*, *Merabatis*, *Coupatezia*, *Heterotorpedo*) to the Dasyatidae, though perhaps they belong to new families, having the effect of artificially inflating this family between the Dano-Montian and the Late Eocene. On the other hand in the Maastrichtian, the Rajiformes appears to have been a lot less diverse than it was in reality. In fact, I reported that some species within the genus, *Rhinobatos*, bore noticeably different dental morphologies and

should be assigned to new genera which remain to be described. Certain members of Rajiformes with uncertain familial affinities (*Myledaphus*, *Parapalaeobates*, *Protoplatyrhina*, *Squatirhina*) were not integrated into this graph—same for the Eocene genus *Odontorhynchus*, whose ordinal position is uncertain. The earliest indisputable *Alopias* (Alopiidae) appears at the base of the Ypresian. The genus *Paranomotodon*, known from the Cenomanian to the Campanian has been assigned to this family on the basis of morphological similarities which could be due merely to convergence.

The genus *Peyeria* (Cenomanian of Egypt), although assigned to Pristidae could in fact belong to a different family. The earliest uncontested pristids appeared at the base of the Ypresian.

However, despite these reservations, this type of figuration furnishes some direct information on familial diversity. One immediately notices the disappearance of a certain number of families at the end of the Maastrichtian. The Hybodontidae and Polyacrodontidae become extinct, shortly preceded by that of the Acrodontidae and Ptychodontidae. These families were never diverse in the generic sense. The latter, however, in terms of species number and global distribution was an important element in Cretaceous faunas. The disappearance of this family in the Campanian is perhaps related to the decline of the ammonites.

Three other important families also disappeared at the end of the Maastrichtian: the Anacoracidae among the sharks; the Sclerorhynchidae and the Rhombodontidae among the rays. These three families suddenly vanished while they were nearly at their peak of diversity, and it does not appear that these extinctions could be linked to a matter of competition with other groups.

The Orthacodontidae just barely managed to cross the Cretaceous-Tertiary boundary; their disappearance is certainly related to the diversification of the Odontaspidae in the Danian-Montian. The Palaeospinacidae, known since the Rhaetian, became extinct at the end of the Paleocene; this group, which truly flourished during the Cretaceous, is a characteristic element of northern faunas. In fact, it has never been found in any southern faunas of the Mesozoic. It certainly did not live to see the radiation of the Carcharhinidae, which was well under way at the base of the Ypresian, but undoubtedly began in the Paleocene.

Of the 25 families which crossed the K/T boundary without apparent difficulty, six tend to frequent the bathyal zone (Chlamydoselachidae, Hexanchidae, Echinorhinidae, Squalidae, Pristiophoridae, Mitsukurinidae), while five have genera which inhabit the neritic zone and others in the bathyal zone (Odontaspidae, Alopiidae, Scyliorhinidae, Triakidae, Rajidae) with the other families found mainly on the continental shelf.

Some families (Squatinae, Heterodontidae, Hexanchidae, Brachaeluridae) are found all along the time in question without being affected by the events which forced the others to extinction. It must be emphasized that these families are either monotypic (Squatinae, Heterodontidae) or less diverse generically. There is also the fact that they are benthic or bottom-dwelling forms.

One troubling fact which stands out in Figure 3 A-D is the large-scale disappearance of numerous members of Rhinobatidae *s.l.* with crushing-type dentitions

and several genera within *Rhinobatoidei incert. famil.* with grinding-type dentitions. These are benthic forms feeding mainly on shelled or unshelled invertebrates depending on the given group. Their disappearance left open niches which were later occupied by the *Dasyatidae* (crushing-type dentitions) and *Myliobatidae* (grinding-type dentitions).

Generic diversity.

The fluctuations in generic diversity (Fig. 1) are noticeably more pronounced. One sees four peaks of unequal amplitude (Cenomanian, Campanian, Ypresian, Middle Miocene) connected to drops in diversity (Coniacian, Dano-Montian, Early Oligocene, Late Miocene). The drop in faunal diversity seen in the Turonian and Coniacian is quite certainly an artifact of the lack of both deposits and documentation concerning these two stages. It is the same for the Late Miocene and Pliocene, time intervals for which selachian-bearing deposits are rare. The most spectacular decrease is observed at the K/T transition, but basically, the fauna grew steadily.

One can pursue the analysis further by distinguishing between genera that appear, genera that disappear, and those that persist on a stage-by-stage basis. One notices, as in the Turonian, the number of genera that appear is higher than the number that disappear. In the Coniacian one notes a time of great stability: all genera were already present in the Turonian; no genera appear and only the genus *Leptostyrax* disappears. The diversity increases right up to the Campanian, but from this stage onward the number of appearances is less than the number of disappearances. This trend is more pronounced in the Maastrichtian, leading to a thinning-out of the fauna at the base of the Paleocene.

From the Dano-Montian to the Ypresian the number of genera that appear becomes significantly larger than the number that disappear, leading to a discernible enrichment of the fauna. In the Lutetian this trend fades and reverses itself in the Late Eocene, which explains the drop in diversity in the Early Oligocene. During the Oligocene few new genera appear, but at the same time there was no extinction either, so faunal growth progresses.

The Early Miocene is marked by the appearance of a large number of genera while only one disappears. In the Middle Miocene, however, there are as many genera that appear as disappear—same for the Pliocene. In the Late Miocene one observes a time of remarkable stability and if neither an appearance nor an extinction can be evidenced, it is because of a lack of deposits as I have already emphasized.

To conclude this section devoted to variations in the faunal diversity among selachians, it can be maintained that the accuracy of the results depends above all else on the taxonomic level in which one is working. This is clearly shown in Figure 1:

- One observes no significant variation at the ordinal level.
- At the familial level the drop in diversity appears only at the K/T boundary.
- At the generic level the fluctuations are much more distinct and the thinning-out of the fauna at the Eocene-Oligocene boundary is clearly defined, though at the same time, this phenomenon is quite detectable at the familial level.

Down at the species level, the extinction percentages increase sharply at the K/T boundary as we will see later in the phosphates of Morocco.

PERCENTAGES AND RATES OF APPEARANCE AND EXTINCTION.

From the set of data concerning genera (longevity and diversity by stage), it was possible to draw curves which translate the faunal fluctuations. These fluctuations are expressed in percentages (percentages of genera that appear or those that disappear in relation to the total number of genera during a given stage) and in appearance and extinction rates (number of genera that appear or disappear per Ma).

In Figure 5 one notes three peaks of decreasing importance regarding appearances: in the Cenomanian (41%), in the Ypresian (35%), and in the Early Miocene (13%). It is necessary to note an additional peak in the Maastrichtian with 22%, a peak artificially accentuated by the fact that in the Coniacian, there is no appearance percentage. These peaks are the result of a normal diversification in one or two previous stages, similar to the one in the Early Miocene, which follows a drop in the appearance percentages throughout the Oligocene. On the other hand, on the whole no disappearances are observed during this epoch. The balance remained positive, and globally, the number of genera grows across the Oligocene.

For extinctions one notes four stages where the percentage is higher than the appearance percentage: Coniacian, Campanian, Maastrichtian, Late Eocene. The percentage for the Maastrichtian is very important at 43%. This corresponds to the mass disappearance of the Sclerorhynchidae (*Ctenopristis*, *Dalpaiazia*, *Ganopristis*, *Ischyrhiza*, *Pucapristis*, *Schizorhiza*), Anacoracidae (*Pseudocorax*, *Paracorax*, *Squalicorax*), Rhombodontidae (*Rhombodus*, *Pucabatis*), *Scapanorhynchus*, *Cretodus*, Rhinobatoidei (*Parapalaeobates*, *Squatirhina*), Hybodontidae (*Lissodus*, *Hybodus*), and Myliobatidae (*Igdabatis*, *Brachyrhizodus*). It should be noted also that these extinctions are true extinctions, except for *Scapanorhynchus* and Myliobatidae.

The drop in generic diversity in the Coniacian is probably artificial and corresponds to a lack of deposits, especially outside of Europe. In the Late Eocene extinctions primarily affected the Lamniformes (Odontaspidae and Mitsukurinidae), Dasyatidae (*Heterotorpedo*), and Carcharhinidae (*Abdounia*). Carcharhinidae benefited from the losses among the Lamnidae and Odontaspidae.

The data can be equally expressed as appearance and extinction rates, represented in Figure 6. The rates can vary quite noticeably according to the given chronological calibration. In fact, for the same number of appearing or disappearing genera, the rate will be all the more important because the duration of the stage will be shorter. The durations of the stages are entered on Table 1. It can be noted that the appearance rates regularly increase until the Cenomanian, dropping to zero in the Coniacian, but as indicated above, that is certainly an artifact of the lack of documentation for this stage. The rates vary later between values of 1.5 and 2.5 and for the Maastrichtian, one notes an appearance rate that can qualify as being high since it reached 2.4. The most striking feature is the

observed peak in the Ypresian, where it attains an appearance rate near 5.4. It is incontestably the time when the fauna diversified and the recovery reached its peak, particularly with the mass arrival of the Carcharhinidae and the great blossoming of the Dasyatidae and Myliobatidae. The appearance rates fall sharply, slipping to a very weak value (0.3) in the Late Eocene.

With the extinction rates one obtains a curve comparable enough to the one obtained for the extinction percentages. Moreover, the fluctuations are more marked than they are at the level of the appearances. The clear fact that remains is the strong extinction rate of the Maastrichtian with a value of 4.9. This high extinction rate, the most important in the history of post-Jurassic selachians, explains the generic losses observed in the Dano-Montian.

The extinction rate of the Ypresian on the order of 3.1 is the most important one outside of that of the Maastrichtian, but its effects are counterbalanced by a strong appearance rate. For that reason no spectacular losses are detected at the base of the Oligocene.

The rates of faunal renewal (which correspond to the mean $TA+TE/2$) show a peak in the Cenomanian, Santonian, Maastrichtian, and Ypresian with irregular but rather weak fluctuations in the Late Paleogene and Neogene. The renewal rate is on the other hand very weak in the Coniacian, weak and diminishing during the Oligocene, on the increase right up to the Middle Miocene, and at zero in the Late Miocene.

In the end drops in faunal diversity always result from negative balances between extinctions and appearances.

DURATION OF GENERIC LONGEVITY.

It is quite variable as a whole. One can see in the reading of Figure 7 that 61.6% of the genera have a longevity less than or equal to five stages, and that 22.7% are found only in one stage as far as we know.

Four genera have particularly long chronological ranges: *Squatina*, *Heterodontus*, *Hexanchus*, and *Brachaelurus*. The first three, present since the Jurassic, have survived to this day without apparent morphological modifications so they can be considered true living fossils; note that these are cases of genera with benthic (bottom-dwelling) habits. The genus *Brachaelurus*, which appeared at the base of the Cretaceous, is also a benthic form.

Genera with long chronological ranges are seen mainly among the Hexanchidae, Triakidae, Rhinobatidae, and Dasyatidae.

Two stages offer a particularly high percentage of genera which were exclusive to them: the Cenomanian with 20.4% of genera living only during that stage and the Maastrichtian with 17%.

As a matter of fact, the interpretation of the data relative to generic longevity is very delicate at a point, where in numerous cases, it cannot be established with certainty if the observed extinctions are true extinctions or pseudoextinctions. Furthermore, within

the chronological scale being used, that is to say, stages of an average duration of 4 to 6 million years, there is not sufficient data for every stage. In regard to the Moroccan phosphates it has been noticed that certain species are confined to a part of a stage, so one can imagine that the same could be true of certain genera.

A REGIONAL EXAMPLE: SELACHIAN FAUNAS OF THE MOROCCAN PHOSPHATES.

After having examined the extinctions and faunal renewals on a global scale, we are now going to see what happened at the regional level, particularly in the phosphate basins of Morocco.

These basins constitute a prime location to evaluate fluctuations that affected the selachians. This is true for several reasons:

— There exists a stratigraphic series ranging from the Early Maastrichtian to the Late Ypresian (an interval of 20 million years), offered over a vast area of natural and artificial exposures (the latter due to phosphate mining). As a matter of fact, the Lower Lutetian is represented in the Ganntour and Meskala Basins near Chichaoua; the fauna of this stage, however, is too poor and too fragmentary compared to the other stages and could not be factored into the evaluations of extinctions that took place between the Ypresian and the Lutetian.

— Vertebrate remains, selachians in particular, are abundant and diverse as a whole in this series: 80 genera and approximately 140 species have been recognized.

— The presence of a phosphate series over a period as long as this one implies a consistency of conditions favorable to phosphatogenesis. Therefore, the observed faunal variations do not seem to be attributed to local or even regional modifications of the environment.

The phosphate deposits of Morocco (fig. 8) are divided into two principal basins currently being mined: the Ouled Abdoun Basin, situated about 100 km to the southeast of Casablanca, extends about 80 km from west to east and over 60 km from north to south; the Ganntour Basin about 100 km to the east of Safi spreads over about 110 km from west to east and over about 10 km from north to south. It is bordered to the north by Paleozoic formations of the Rehamma and by those of the Jebilet to the south. As a matter of fact, these basins are only the broken-up vestiges from the erosion of an immense phosphatic gulf which spread out over at least 350 km from west to east, as the phosphate layers continue as far as the Mid Atlas (Timhadite region) at the base of the Maastrichtian Black Shales.

The northern Atlas basins, scattered between Chichaoua and Imin Tanoute and the small southern Atlas basins of the Oued Erguita and the region of Ouarzazate, are much more fragmented with the surface area often reduced and affected by tectonic activity. They present, however, places of great paleontological interest because of their richness in fossil vertebrates.

The northern gulf series (Ganntour + Ouled Abdoun) are characterized by an important reduction in thickness from west to east: 160 m at Youssoufia, 134 m at

Benguerir (with, however, in the intermediate area of El Ouata a distinct thinning of the series coming down to 76 m indicating the presence of a shoal), 84 m in the Tessaout region, only about 20 meters in the Oued-Zem region (Arambourg, 1952; Boujo, 1976). Towards the east subsequent to the compression of the series, the thickness of the phosphate layers thins out noticeably and the Maastrichtian deposits in particular are limited to the upper part of the stage (fig. 9).

As far as the samples of the compressed series are concerned, the reduced thickness can lead to errors in the precise stratigraphic origin of the genera and species. This remark is important when one tries to evaluate the extinctions and faunal renewals from one stage to another and all the more so at the level of the K/T boundary. In this regard the Ganntour and Ouled Abdoun Basins provide us with an excellent example.

In the Sidi Daoui area near Oued-Zem in the eastern part of the Ouled Abdoun the base of the Dano-Montian (= Montian *sensu* Arambourg, 1952) is represented by a soft, light-colored phosphate bed extremely rich in selachian teeth. The fauna, based on Arambourg's collections and our recent collections, includes a certain number of Cretaceous species (*Cretolamna* cf. *carai-bea*, *Ginglymostoma* sp., *Pteroscylidium* sp., "*Raja*" *mucronata*, *Rhombodus binckhorsti*, *R. microdon*, *Ctenopristis nougareti*, and *Coupatzia fallax*) associated with some species from the base of the Paleocene (*Striatolamia whitei*, *Odontaspis speyeri*, *Synodontaspis tingitana*, *S. substriata*, cf. *Anomotodon*, *Ginglymostoma subafricanum*, *Paleogaleus brivesi*, Hemigaleidae nov. gen., *Dasyatis tetraedra*, and *D. hexagonalis*). This mixed fauna composed of Maastrichtian and Dano-Montian species had led Arambourg to assert that the transition from the Cretaceous to the Tertiary was very gradual and that the base of the Paleocene still contained a certain number of Cretaceous survivors. When one moves into the Yousoufia region to the west of the Ganntour Basin, the Dano-Montian phosphatic layer with a typical Paleocene fauna is separated from the terminal Cretaceous or "Sillon X" (about 40 cm thick) by a boundary layer (1.25 m thick) made up of hard marls and flint beds. The "Sillon X," formed from a loose, light-colored phosphate, is very fossiliferous and contains a typical Maastrichtian fauna which has species found in the "Dano-Montian" of Sidi-Daoui. The mixed fauna of Daoui, therefore, does not correspond to a transitional fauna as Arambourg thought. It is in actuality a mixture of Cretaceous and Tertiary species linked to the compression of thin layers. Since the Cretaceous fossils are in the same state of preservation as the Paleocene ones, the hypothesis of a redeposition after erosion of a Cretaceous bed can be rejected. This can lead one to think that the mixture of faunas is the result of significant bioturbation in very loose, thin sediments. The result of this in particular is that "*Raja*" *mucronata*, which was considered by Arambourg to be a Paleocene species, is in fact a species of the terminal Maastrichtian and that *Synodontaspis tingitana* is a strictly Paleocene species.

Throughout the basin no trace of marine regression is seen in the series even at the K/T boundary. A terminal Maastrichtian regression, even a weak one, would have led to significant erosion on the margins of the basin. Some layers as loose and thin as the "Sillon X" would have disappeared. Furthermore, no discontinuity is seen between the Late Maastrichtian and the Early Paleocene; there is never a transgressive facies with very

abraded elements at the base of the Paleocene Arambourg, 1952; Boujo, 1976 and 1985 *in litteris*; pers. obs.). These remarks, however, do not exclude the possibility of gaps in sedimentation which are very difficult to detect in the absence of an angular Unconformity.

Analysis of the faunas.

The Maastrichtian fauna (fig. 10) includes 54 species, of which only two, *Hexanchus microdon* and *Cretolamna appendiculata*, survive into the Dano-Montian. The first of these two is known in Europe since the Cenomanian, the second since the Albian—this one is also the sole representative of the Cretoxyrhinidae to survive the Maastrichtian and the origin of an important radiation of the group in the Eocene. Among the 52 species which became extinct (96.3% of the fauna), only four are quite probably direct ancestors of Dano-Montian species: *Palaeogaleus* sp., *Scyliorhinus* sp., *Squalus* sp., and *Dasyatoidea* nov. gen. nov. sp. In the graphs one can take into consideration that the appearances in the Maastrichtian are regional in nature as there is no Campanian age fauna in the phosphate series.

At the generic level (fig. 11 A,B) one counts 32 taxa, of which 22 (68.7%) become extinct at the K/T boundary and only 10 are present in the Dano-Montian. All the orders are affected by the generic extinctions and three important families (Anacoracidae, Sclerorhynchidae, and Rhombodontidae) disappear without any known descendants. Among the sharks the small forms with “semi-benthic” habits such as *Palaeogaleus*, *Scyliorhinus*, and *Ginglymostoma* seem less affected than the large nectic predators such as *Scapanorhynchus*. All except one species of *Cretolamna*, all *Squalicorax*, and all *Pseudocorax* die out. Among the batoids, however, all the groups are severely affected, the Rajiformes in particular: outside of the total disappearance of the Sclerorhynchidae, the Rhinobatidae sees its diversity diminish dramatically. No adaptive group was spared and the extinctions are equally severe among the groups with grinding-type dentitions.

In the Dano-Montian 14 genera appear (58.3% of recoveries). One sees that there are, however, five generic extinctions (*Palaeohypotodus*, cf. *Anomotodon*, *Palaeogaleus*, Hemigaleidae nov., and “*Dasyatis*” *globidens*—20.8%) in this stage. At the species level of the 31 listed species, 29 (93.5% of the fauna) make their first appearance; 21 of these species (67.7%) did not reach the Thanetian.

In the Thanetian the generic recovery is about 42.8% with 15 of the 35 recognized genera being new. The most notable fact is the appearance of large predators such as *Otodus* and *Palaeocarcharodon*; the former would become the ancestor of *Carcharocles*, known from the Middle Eocene to Pliocene, and counting among its species the largest known predator among the sharks, *Carcharocles megalodon*. The Squalidae diversify as do the batoids with the appearance of the genera *Gymnura*, *Burnhamia*, and *Archaeomanta*. At the species level of the 47 recognized species, 18 disappear (38.3% and an extinction rate of 2.8). These extinctions mostly affected the Orectolobiformes, the Scyliorhinidae, and Batoidea. Of note is the disappearance of a large predator,

Palaeocarcharodon, due to competition with *Otodus*, a predator with a comparable tooth type but of larger size.

Of the 44 genera present in the Ypresian, 20 are new (45.4% with an appearance rate of 4.4). The most remarkable fact is the invasion of the Carcharhinidae (*Abdounia*, *Rhizoprionodon*, *Physogaleus*, and *Galeocerdo*) which later increase their generic and specific significance to the detriment of the Lamniformes. It is equally necessary to note the appearance of the modern Pristidae and especially an important adaptive radiation of the Myliobatidae which was on its way to developing very specialized dental morphologies (*Lophobatis* and *Leidybatis*).

At the level of specific diversity (fig. 11 C,D) of the 59 listed species 30 are new in relation to the Thanetian (50.8% with an appearance rate of 6.7). The groups within which the specific recovery is very weak or even nonexistent are the Hexanchidae, the Odontaspidae, the Cretoxyrhinidae, the Otodontidae, and the Lamnidae, which correspond at the ordinal level to the Hexanchiformes and the Lamniformes; the greatest stability is seen, therefore, in the large nectic predators. Regarding the Ypresian extinctions it is impossible to furnish reliable data since the Lutetian fauna, limited to a Gantour Basin deposit, is very sparse and therefore not very representative of the sharks and batoids which were living during that epoch.

In relation to the global variation curves of generic diversity expressed in appearance and extinction percentages, one notes that at the regional level the extinctions are clearly more significant in the Maastrichtian, the Dano-Montian, and the Thanetian. At the regional level as well the appearance percentages are clearly higher in the Dano-Montian, Thanetian, and Ypresian.

For the faunal variations expressed in rates on a regional scale the extinction values are distinctly on the same order as at the global level for the Maastrichtian. They are in contrast slightly higher for the Thanetian and slightly lower for the Ypresian. The appearance rates are higher at the regional level for the Dano-Montian, on the same order for the Thanetian, and weaker for the Ypresian. However, despite these few differences in amplitude, the curves are on the whole comparable and translate as well to the regional level as to the global level, illustrating a significant decrease in the diversity of selachians at the K/T boundary.

DISCUSSION.

In the marine food chains the selachians constitute one of the most important predator groups due to their diversity and their prey's taxonomic variety; nearly all the groups are found in their diet: annelids, peanut worms, sea squirts, crustaceans, mollusks (cephalopods, gastropods, and bivalves), teleosts, selachians, marine birds, and marine mammals other than whales. Regarding diet, therefore, they are a lot less selective than odontocete whales which prey mainly on fish and cephalopods, not counting killer whales which feed primarily on pinnipeds.

The selachian group, because of its wide range of prey and from the fact that it is an apex predator at the top of the food chain, subjecting itself to only very weak predator pressure (exception made certainly for the selachians of the Maastrichtian which must have been regularly preyed upon by large mosasaurian reptiles), is therefore very sensitive to any change in the food chain. The massive extinction of phytoplankton and zooplankton at the K/T boundary, put into evidence in nearly all the studied sections, is certainly the origin of a profound change in the marine ecosystems with dramatic consequences for the predators at the top of the food chain. This disruption of the food chain would explain the disappearance of the large mosasaurian reptiles and the large predaceous teleosts such as the Enchodontidae.

Various explanations, often quite hypothetical, have been submitted to try to explain the mass extinction which affected numerous invertebrate and vertebrate groups at the K/T boundary. The catastrophist explanation with its impact of an extraterrestrial body seems to have enough supporters (Alvarez et al., 1980; Ganapathy, 1980; Hsu, 1980). It has often been cited that there was a generalized marine regression coupled with a decrease in temperature at the end of the Maastrichtian, which would have led to the disappearance of epicontinental seas with the assumed consequences on the neritic faunas and terrestrial ecosystems. This hypothesis, appealing at first glance, has been put forth by Ginsburg (1967, 1984) and by Kauffman (1984), relying mainly on the studies of the Cretaceous basins of North America. It does not seem, however, that Kauffman's observations can be generalized. In fact, on the African continent a transgression starts in the Maastrichtian and ends in the Paleocene (Reyment & Morner, 1977). The geologic studies done in Morocco (Arambourg, 1952; Boujo, 1976; pers. obs.) seem to confirm the absence of regression during the K/T transition, at least in the Ganntour and Ouled Abdoun Basins.

Some authors have proposed a certain periodicity of extinctions with an interval of 26 million years (Raup & Sepkoski, 1984) or of 30 ± 1 million years (Rampino & Stothers, 1984). These results, however, have been contested (Thaddeus & Chanan, 1985) and a periodicity of impacts has not been proven (Weissman, 1985). Furthermore, an impact-extinction relationship is far from being established (Kerr, 1985). Other authors have imagined a relationship between mass extinctions and inversions in the earth's magnetic field (Raup, 1985). Finally, others envision a period of intense volcanic activity at the K/T boundary (Officer & Drake, 1985), attested by the enormous lava flows of the Deccan Traps in India. This hypothesis would explain in part the iridium anomaly from the recent discoveries of Zoller et al. (1983) on the Kilauea volcano, and a darkening of the atmosphere from the expulsion of volcanic ash.

Whatever the considered scenarios may be, the oceanic environments were gravely affected at the K/T boundary as is testified by the mass extinction of the phytoplankton and zooplankton at that time (Smit & Hertogen, 1980). Among the hypotheses submitted those that call for a darkening of the atmosphere, leading to a noticeable decrease in sunlight penetration, could explain the disappearance of the phytoplankton via stoppage of photosynthesis. This darkening would be linked to the impact and disintegration of an extraterrestrial object in the opinion of the catastrophists, while

according to others (Renard & Rocchia, 1984), this dust of interstellar origin would be the result of the passage of the earth into an arm of the galaxy.

These extinctions at the phytoplankton and zooplankton level would have gravely altered the whole marine food chain. Those particularly affected would have been the predators at the top of the food chain, such as the selachians or the large marine reptiles. For the marine invertebrates, excluding plankton, there is available data on the ammonites, cheilostome bryozoans, and bivalves. All these groups decline drastically or even vanish, as was the case with the ammonites (Alvarez, Kauffman, et al., 1984). Among the selachians one notes that genera are lost in all families. An entire group at the ordinal level at least, the Hybodontes, disappears. Three families (Anacoracidae, Sclerorhynchidae, and Rhombodontidae) die out without leaving any descendants. The Palaeospinacidae and Orthacodontidae persist respectively into the Late Paleocene and Early Paleocene, but become very rare and localized in the northern realm.

The extinctions affect, therefore, all the trophic adaptations, all the ecological niches: the nectic as well as the benthic groups; the ichthyophages along with the conchyliophages; the littoral and the pelagic forms.

The causes of the extinctions at the Eocene-Oligocene boundary lend themselves less to controversy. In this case they seem to be the result of gradual climatic degradation with the appearance of the first ocean glaciers (Corliss et al., 1984; Vergnaud-Grazzini, 1984; Pomerol, 1985). The discovery of microtectites in the Caribbean, the Pacific, and the northeast Indian Ocean of that age does not seem to be able to be correlated with the extinctions (Sanfilippo, Riedel et al., 1985). The selachians were in fact little affected during the Eocene-Oligocene transition with the drop in faunal diversity being more important between the Lutetian and Late Eocene than between the Late Eocene and the Early Oligocene.

CONCLUSION.

At the K/T boundary one notes the final disappearance of several families - certain thinned-out groups with already long fossil histories, and others quite the opposite, diversified and individualized for a much shorter length of time. Nearly all the adaptive groups are tapped by this phenomenon of extinction, affecting the littoral forms as much as the pelagic ones. It is necessary to note that it was the families with very specialized dentitions (Anacoracidae, Rhombodontidae, Rhinobatidae with grinding-type dentitions), or exhibiting a particular adaptation (Sclerorhynchidae), which especially suffered at the K/T transition. The fallen adaptive types of that time were replaced by comparable types but incarnated among families without a direct phyletic link to the extinct forms. For example, the Eocene Pristidae replaced the Sclerorhynchidae, and the Eocene Carcharhinidae succeeded the Anacoracidae. It must be noted further that the niches left open were not immediately reoccupied. It always takes the passing of several million years before the rebirth of an adaptive type.

The K/T boundary is characterized by a strong percentage of generic extinctions at the global level and a percentage of specific extinctions still more significant at the regional level.

Unfortunately, the duration of the phenomenon cannot be calculated precisely because of the utilized chronological scale.

In the end the selachians, as far as the group is concerned, endure the K/T transition quite well. This assertion may seem to be in contradiction to what has been stated above, but it must be remembered all the same, that more than 50% of the genera crossed the K/T boundary and that from that important stock of survivors, the selachians were able to rediversify.

References

N.B. The bibliography which follows is intentionally brief. The reader will find numerous references on the extinctions and the various proposed scenarios in the cited symposia and in the article by A. Hoffmann (1984).