

## Diversity of radiolarian families through time

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*Key Words.* – Radiolaria, Family, Diversity, Palaeozoic, Mesozoic, Cenozoic, Extinction, Radiation, Protocists.

*Abstract.* – The examination of radiolarian biodiversity at the family level through Phanerozoic time reveals some general trends known in other groups of organisms, especially among plankton, while some other trends seem to be quite peculiar. The Permian/Triassic crisis that is one of the most important in the evolution of marine organisms, is marked in radiolarian assemblages by the extinction of two orders (Albaillellaria and Latentifistularia) towards the end of the Permian, and mostly by the tremendous diversification of Spumellaria and Nassellaria in the early-mid Triassic. Radiolarian diversity increased from Cambrian to Jurassic, remained quite stable during the Cretaceous and has decreased slightly since then.

## Diversité des familles de radiolaires au cours du temps

*Mots clés.* – Radiolaires, Famille, Diversité, Paléozoïque, Mésozoïque, Cénozoïque, Extinction, Radiation, Protoctistes.

*Résumé.* – L'examen de la biodiversité des radiolaires, au niveau de la famille au cours du Phanézoïque révèle quelques tendances générales connues chez d'autres groupes d'organismes, surtout dans le plancton, alors que d'autres tendances leur sont particulières. La crise permo-triasique, l'une des plus importantes dans l'évolution des organismes marins, est marquée chez les radiolaires par l'extinction de deux familles (Albaillellaria et Latentifistularia) vers la fin du Permien, mais surtout par une énorme diversification des spumellaires et nassellaires au Trias inférieur et moyen. La diversité des radiolaires s'accroît du Cambrien au Jurassique, reste relativement stable au Crétacé et décroît légèrement depuis.

## INTRODUCTION

Much of our ability to discriminate among various hypotheses explaining the evolutionary changes within geologic times depends on careful and detailed comparisons of evolutionary patterns, recognised in trophically, ecologically, reproductively, and developmentally different groups of organisms.

Since they have existed since the Cambrian, radiolarians provide a unique and important record that may produce answers to some fundamental evolutionary problems : origination/extinction rates, speciation patterns, and environmental and palaeoceanographic influences. During their long history, radiolarians have exhibited a wide variety of evolutionary patterns related to different processes operating at different periods within different time-scales.

Radiolaria biodiversity has remained unclear for many years because of insufficient data and because the taxonomy of higher ranking taxa has not been unified. Some evaluation of biodiversity was attempted several years ago for all fossil groups [Benton, 1993] and this included radiolarians [Hart and Williams, 1993]. This tentative analysis is, however, disappointingly poor and does not present a correct

image of the radiolarian world : only 35 families are referred to for the whole geologic period whereas almost twice this number is known for the Cretaceous period alone. A recent work has homogenised the taxonomic criteria used for the Palaeozoic, Mesozoic and Cenozoic, and updated stratigraphic ranges for all families have been proposed. We can now recognise 131 families for the whole Phanerozoic [De Wever *et al.*, 2001]. Hence, we have a good opportunity to survey family biodiversity through time.

Present knowledge of the fossil record confirms that mineralised skeletons of many different kinds and composition appeared very rapidly in a number of clades at the beginning of the Phanerozoic [Gingerich, 1985]. The apparent absence of biominerals in the ediacaran fauna and the nearly simultaneous "skeletalization" of cyanobacteria, algae, protists (foraminifers and radiolarians), and metazoans, implies that the radiation of biomineralising taxa was a major aspect of early Phanerozoic radiation.

As mentioned earlier [De Wever, 1982] under environmental stresses, some radiolarian species seem to be able to adopt a regressive/primitive character. Often this process happens along with a reduction of skeleton (fig 1). If this re-

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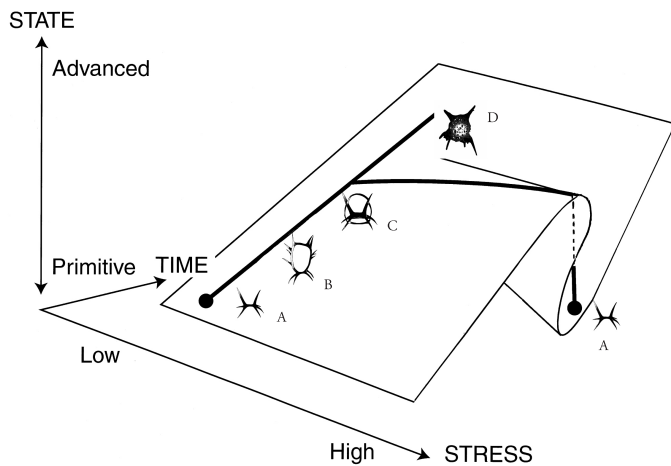


FIG. 1. – Evolutionary model with regressive phase connected to an increasing stress [adapted from Guex, 1981]. In a normal stage, form A evolves to B then C and D. But if at stage C a strong stress is intervening, then a regression to form A is possible.

FIG. 1. – *Modèle d'évolution avec des phases de régression morphologique liées à des augmentations de stress [adapté de Guex, 1981]. Dans un état normal la forme A évolue vers B puis vers C et D. Si au stade C intervient un stress important, alors une régression vers A est possible.*

duction corresponds to no-test at all, it becomes difficult to notice this intervening effect! Conversely, evolutionary processes during radiation phases give rise to homeomorphy as is the case between Triassic fauna (Squinabolella, as illustrated by Carter [1993]) and some Cenomanian fauna (Sciadiocapsa, as illustrated by O'Dogherty [1994]), or as between some Liassic (e.g. some Foremanellidae) and Maastrichtian fauna (e.g. Lithomelissa).

Because of its non-crystalline, isotropic nature and intracellular method of formation, opal ( $\text{Si}_2\text{O}_3(\text{OH}_2)$ ) has had limited potential as a skeletal material except in very small organisms [Runnegar and Bengtson, 1990]. It is in fact most widespread among protists. The only metazoans known to form it are the hexactinellid sponges and demosponges, which use it for spicule formation. They are probably the most abundant organism remains in the Cambrian. Most biogenic opal formed today is either dissolved in the water column before it is incorporated in the sediment or dissolved during early diagenesis, but under certain circumstances opaline skeletons may be preserved, usually as microcrystalline quartz or replacement by other minerals.

The distribution of opal among the earliest skeletal fossils differs significantly from that of calcium carbonate and phosphate. Only four groups of silica-producing organisms are known from the early Phanerozoic time period: hexactinellids, demosponges, chrysomonadines, and radiolarians. All appeared during the Cambrian or earlier and are extant. The significance of this apparent "immortality" of opal-producing lineages is unknown but a small number of clades is involved. The pattern differs considerably from that of calcareous and phosphatic groups. In the latter two groups, the Cambrian radiation appears to have produced a large number of taxa of which only a few survived.

## MATERIAL AND METHODS

The guiding principle of the classification of radiolarians presented in the book authored by De Wever *et al.* [2001] is that the structure of the initial skeletal elements is the most conservative during evolution and should be the foundation of the family level systematics. In this work the authors have tried to make family definitions uniform in accordance with currently published data and their own, mostly unpublished, results. For each family a stratigraphic range has been revised according to the new definition and included genera from worldwide data are listed.

The fundamental data forming the basis for biostratigraphic ranges are records of occurrence of individual fossil taxa at specific localities. The quality of the range thus depends on the consistency with which taxa can be recognised, and the confidence that can be placed in a record of occurrence or non-occurrence. Since, in this study, only records of presence or absence have been used, stratigraphic ranges, thus represented, are maximum extensions.

For several years, numerous researchers have been greatly interested in the study of biodiversity and its evolution through time. These studies pointed out several crisis periods. Nevertheless, it must be mentioned that the results depend on the methodology used. Some researchers simply counted the number of taxa presented in a publication without any taxonomic analysis. That is to say that the number of taxa in a particular work often depends on the taxonomic point of view of the author(s) of the used publications. Hence simple counting might be a source of mistakes. It is, therefore, important that counting of taxa be done by one or several specialists with practice in the respective group and after a thorough taxonomic review. The current study is based on an integrated taxonomic review of radiolarians at the family level [De Wever *et al.*, 2001].

## BIODIVERSITY CHANGES

### Origin of complex skeleton forms in Radiolaria

The oldest microfossils that can be considered as genuine radiolarians were recently described by Won and Below [1999] from the Middle Cambrian of Queensland, Australia. These radiolarians, which are very well preserved and diverse, consist of one or more point-centred spicules quite similar in structure and morphology to siliceous sponge spicules. Similar forms had previously been described by Bengtson [1986] from the Upper Cambrian of Queensland, Australia, and by Kozur *et al.* [1996a] from the lowermost Ordovician (Tremadocian) of Nevada. Due to the types of spicules, Bengtson interpreted these microfossils as skeletons of hexactinellid propagate sponges (phylum Porifera), but Kozur *et al.* [op. cit.] considered them to be primitive radiolarians. All these ancient morphologies characterised by one or more point-centred spicules are presently assigned to the radiolarian order of Archaeospicularia by Dumitrica *et al.* [2000]. The Archaeospicularia appear to be the ancestral representatives of the radiolarians, occurring in the Cambrian and becoming extinct at the end of the Silurian or possibly in the early Devonian, or later. Unlike representatives of other orders of radiolarians, which have either a single internal spicule or a microsphere, the skeleton of Archaeospicularia is built of one or several inter-

locked or fused point-centred spicules. A spicular composition of the skeleton is characteristic of the siliceous sponges which also have a skeleton made of free, interlocked or fused spicules. The similarity of the spicules in sponges and radiolarians suggests a phylogenetic relationship. Although sponges are multicellular organisms, they are generally not regarded as true metazoans. They are of a grade of organisation between protozoans and metazoans. They are sometimes referred to as parazoans [Clarkson, 1998], and it is widely believed that they were derived from a protozoan ancestor. Is this ancestor a radiolarian or do both groups have a common ancestor? This is a question that we cannot answer at present. The two groups, which are presently living, are also distinguished by their mode of living: whereas radiolarians are planktic, sponges are benthic, but some authors believe that the first radiolarians were also benthic [Petrushevskaya, 1977].

The observation of living colonies of radiolarians provides some examples of the relatively high degree of organization these unicellular organisms can reach. For example *Lampoxanthium pandora*, and *Sphaerozooom punctatum* differentiate within their colonies some areas where faecal remains are stored [Swanberg, 1979; Anderson, 1983]. Often colonies share the ectoplasmic part of their cell that includes numerous spicules. In such an organisation it is impossible to know which individual generated a certain skeleton. These structures are usually called colonies but correspond to a syncytium (as in sponges), resulting from the fusion of several cells and, therefore, the cell limits are fuzzy.

One would easily imagine that when such spicules happen to be gathered (agglomerated) in a certain way they would form a spherical shape similar to that of Archaeospicularia [Dumitrica *et al.*, 2000]. This way of life could explain an evolution leading from isolated spicules to shells made by interlocked or even fused spicules, either of one form or several forms as is known in the oldest order Archaeospicularia.

Some living species are reported to have several types of spicules. *Rhapidozooom acuferum* illustrated by Amaral-Zettler *et al.* [1999] is characterised by having both simple and radiate spines. One can easily imagine that when one species is involved – with one type of spicule – the result will be an aggregate of one type of spicule while if several species are involved, several types of spicules can be present. Although we do not know the antiquity of colonial radiolarians because the colonies disintegrate, we can hypothesise that the skeletons were derived from an ancestor with spines which merged to form a skeletal structure. Historically, the colonial spumellarians have been grouped together taxonomically solely on the basis of their ability to form colonies. Classically, the phylogenetic relationships of the colonial Radiolaria, as with other skeleton-bearing groups, have been based on analyses of shell morphology. Morphological analyses, however, have not always been effective in resolving phylogenetic relationships among these species. Recent molecular studies [Amaral-Zettler *et al.*, 1997, 1999] indicate that the ability to form colonies may have evolved more than once in the evolution of radiolarians [contrary to what was supposed until now [Anderson and Swanberg, 1981]].

### Palaeozoic biodiversity

The biodiversity of radiolarians increased constantly throughout the Palaeozoic. The appearance of representatives of all orders, and 28 groups or families characterised by different internal structures can be successively recognised over approximately 270 m.y., from the Mid Cambrian to the late Permian (fig. 2). In the Cambrian, it seems that most radiolarians belonged to, at least, two families: the Echidniniidae, placed into the Archaeospicularia [Dumitrica *et al.*, 2000] and the Archaeoentactiniidae, some forms of which have one or two initial spicules inside a shell (itself made of several spicules) (e.g. *Fungomacula barbatula* Won, 1999, pl. 9, fig. 10 in Won and Below [1999]). This group diversified during the Ordovician and probably gave rise to the Secuicollactidae and Pseudorotasphaeridae.

A noticeable change in radiolarian assemblages took place at the beginning of the Ordovician with the appearance of the first representatives of Entactinaria (Entactiniidae and Inaniguttidae). During Ordovician times the number of species increased and well defined representatives of Entactinaria co-occurred with different representatives of archaeospicularians (Secuicollactidae and Pseudorotasphaeridae) from which they are probably derived. The Entactinaria may have evolved from the Archaeospicularia by the reduction of the number of spicules to a single one which is usually bar-centred (or by fusion of two spicules of triaxon type) and by the building of a shell starting from the branches or verticils of this spicule whose centre is located, in most cases, within the cavity of the shell. This group had a continuous and regular diversification during the rest of the Palaeozoic, and crossed the Permian/Triassic boundary to be rather common and diversified in the Mesozoic.

During the early Silurian or late Ordovician [Danelian, 1999], the first Albaillellaria [Ceratoikiscidae] appeared. It seems quite likely that they descended from some Archaeospicularia by reduction of the multi-spicular skeleton [Dumitrica *et al.*, 2000] to a structure composed of three bar-shaped spicules that intersected and fused at the point of intersection, in the same way that the Secuicollactidae have a pseudo-cortical shell. As in Secuicollactidae, the original albaillellid spicules were probably not similar. Rather, one of them bore one or more pairs of spines that subsequently became the caveal ribs. Evolution within the Albaillellaria seems to have been continuous and regular during the Palaeozoic. Major changes occurred in the Devonian with the development of a shell partly covering the triangular spicule and its ribs (*Holoeciscus* in the Mid Devonian and Albaillellidae at the end of the Devonian). During the Carboniferous and the Permian, the Albaillellidae underwent a great and biostratigraphically important diversification, including in the Lower Carboniferous the development of a more complex structure, as for *Albaillella* (e.g. *A. cartalla*), and in the Upper Carboniferous, simplification of the internal spicule (loss of a bar, or presence of a single intersector: first appearance of *Pseudoalbaillella*) to give rise to the last Albaillellaria (Follicucullidae and Palacantholitidae). During the Upper Permian the evolution of some albaillellarians took two different directions: one was to build a complex shell (*Neoalbaillella*), the other was to simplify this shell (*Follicucullus*).

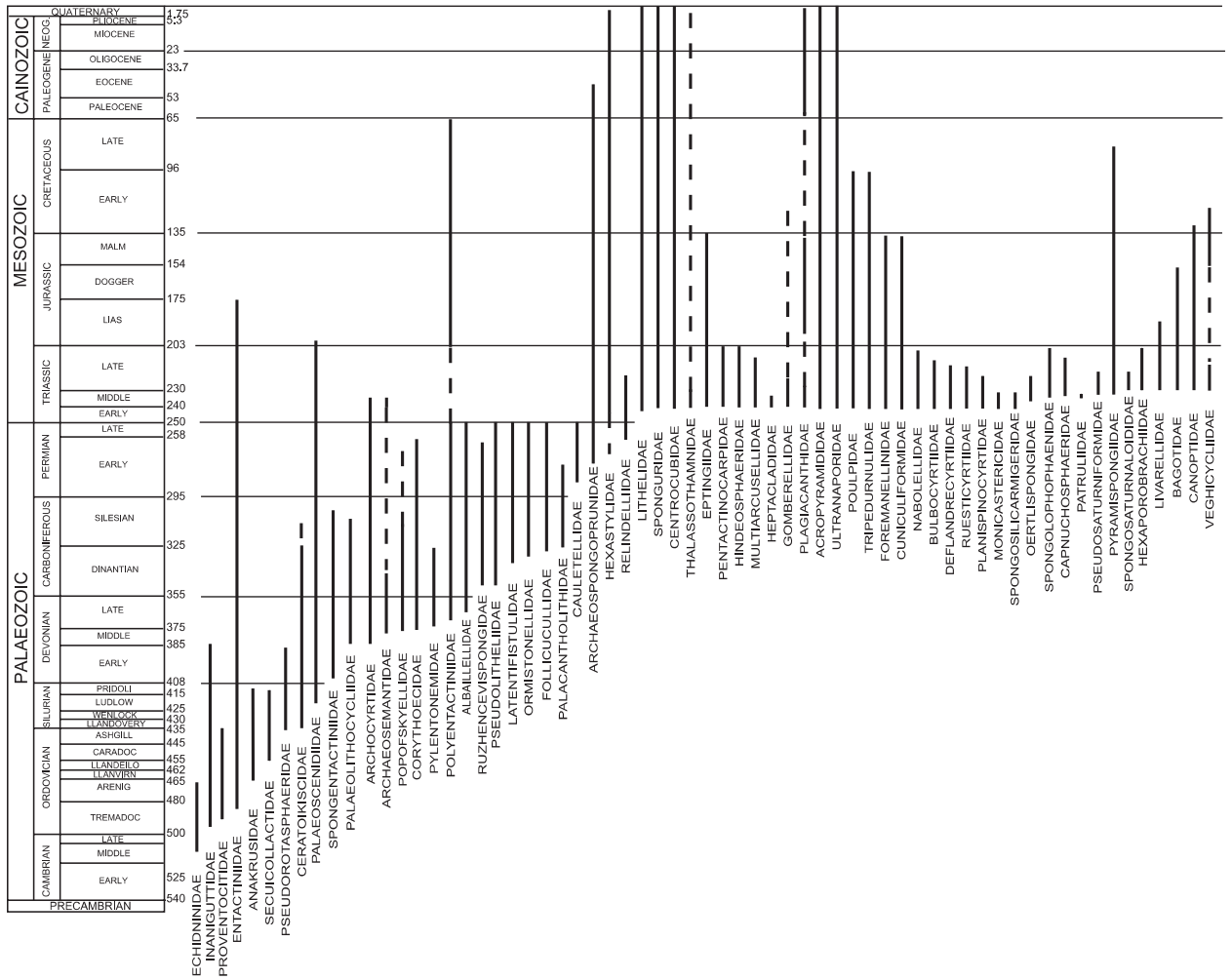


Fig. 2. – Stratigraphic ranges of radiolarian families through time [adapted from De Wever *et al.* 2001]

The Devonian is marked by the appearance of the first representatives of primitive nassellarians. All of them (Archocyrtidae, Archaeosemantidae, and Popofskyellidae) have nassellarian-type internal spicules, but their skeletons still have some entactinarian characteristics [De Wever *et al.*, 2001]. The evolution of these nassellarians was very slow during the Upper Palaeozoic, and they practically disappeared during the Permian so that one can say that the main nassellarian groups appeared during the Triassic.

The last major change in the composition of Palaeozoic radiolarian assemblages occurred during the Lower Carboniferous with the appearance of the order Latentifistularia. Their origin is not known with certainty, but we see a probable origin of this order in some Entactiniidae [Dumitrica *et al.*, 2000]. Early in the Carboniferous, forms with three or four spines are present, but their representatives also have a spongy surrounding shell (Latentifistulidae, Pseudolitheliidae). From this group there arose the Ruzhencevispongidae in the Upper Carboniferous and the Cauletelidae (a group with three tubular, lamellar and partitioned arms) in the Upper Permian. From the same ancestors, during the Permian, there arose a branch with a lamellar shell and four to five (rarely more) arms.

The Permian is not marked by the appearance of new orders of radiolarians, although some representatives of

probable Relindellidae and Archaeospongoprundidae (radiolarians with spongy shells and large external spines whose Permian representatives are tentatively grouped into the Spumellaria) occur together with the last Latentifistularia (Cauletelidae). However, except for the latest Permian, the occurrence of undoubted Spumellaria in the Permian, and in fact in nearly the whole Palaeozoic, is questionable. Many of the Palaeozoic spherical radiolarians previously considered to be Spumellaria contain the remains of an inner spicule, indicative of Entactinaria [De Wever *et al.*, 2001]. Therefore, it is possible that Spumellaria only appeared during the latest Permian and diversified during the Mesozoic.

Palaeozoic radiolarians are abundant in sedimentary rocks that can be compared to shelf sediments [Dong *et al.*, 1997 ; Won and Below, 1999]. Their skeletons are the principal component of the siliceous rocks from many Palaeozoic formations. Among Palaeozoic plankton, remains of radiolarians (together with those of acritarchs) are particularly abundant, although representatives of other planktonic groups such as tintinnids and chrysophytes are found sporadically. Radiolarians became morphologically complex through time (like the foraminifera) with the number of species increasing significantly in the Ordovician and Devonian.



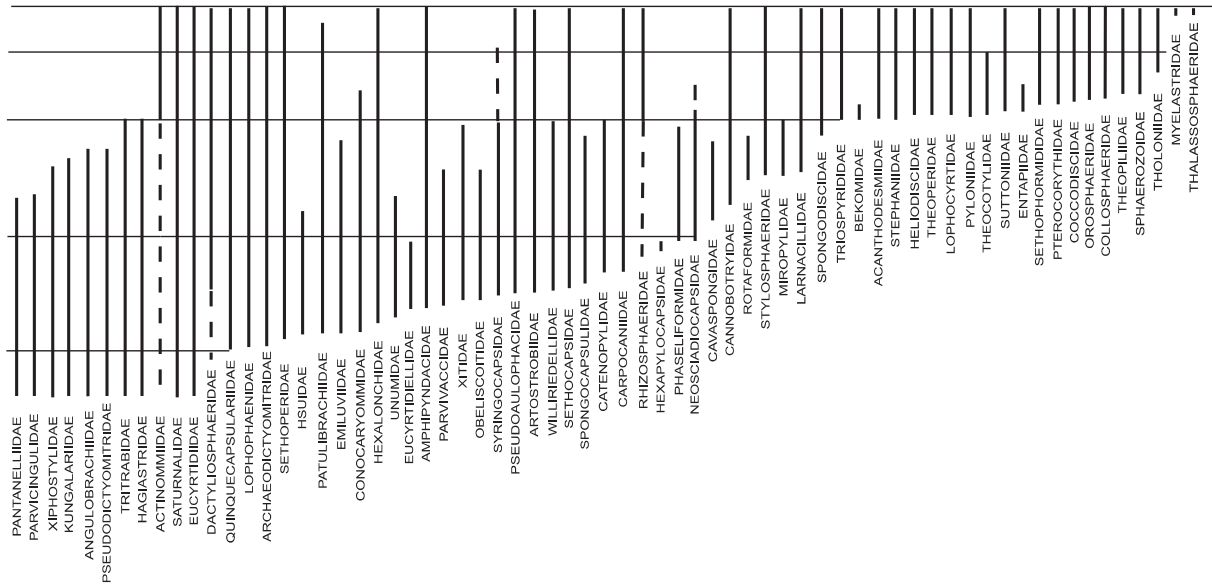


FIG. 2. – Extension stratigraphique des radiolaires [d'après De Wever *et al.*, 2001]

### Mesozoic biodiversity

During the Mesozoic, planktonic protists underwent remarkable evolutionary innovations and radiations. Radiolarians, dinoflagellates, calcareous nannoplankton, diatoms, silicoflagellates, and planktonic foraminifers either appeared and radiated for the first time, or diversified from pre-existing forms into a greater variety of new types.

If we assume that the Upper Permian Relindellidae and Archaeospongoprunidae are spumellarians, no new order of radiolarians appeared during the Mesozoic, but existing lineages of radiolarians produced an impressive number of new morphotypes grouped into new families. Of the 18 families known from the Permian, 8 continued to exist in the Mesozoic and among the 56 families known in the Triassic, 48 appeared during the early and mid Triassic. In the Jurassic 60 families are recognised (27 originations), and in the Cretaceous among the 60 families recorded 9 originated in that time period (fig. 2). The Mesozoic was undoubtedly the main epoch for radiolarian radiation (figs. 3,4).

What could have caused these tremendous radiations and evolutionary innovations? For the most part the causes remain uncertain, but one of them could be the break-up of continents and the partitioning of the world's oceans that produced strengthened circulation, as suggested by hydrologic modelling, and inducing upwelling of nutrients [Cottreau, 1992; De Wever *et al.*, 1994]. It is known that during the Mesozoic, modern oceanic basins began to form, with the creation of the Atlantic Ocean basin and with the beginning of the geographic separation of the Indian plate from the Gondwana. Numerous microplates began their separation in the Tethys Ocean, creating new seaways in the western Tethys and modifying oceanic circulation. The huge Mega Lhasa block (6000 km long including Iran, Mega Lhasa *s.s.*, Qian-Tang, Burma and westernmost Thai-

land; Marcoux *et al.*, 1993], for example, that barred the Tethyan Ocean, was migrating from the centre of the Tethyan Ocean towards South East Asia [Vrielynck and Bouysse, 2001].

Following the mass extinction at the end of the Permian, when the last representatives of the orders Albaillellaria and Latentifistularia completely disappeared, the Lower Triassic faunas were characterised by low diversity and poor preservation [Sashida 1983, 1991; Sashida and Igo, 1992; Sugiyama, 1992, 1997; Kozur *et al.*, 1996b]. These faunas mostly contain robust entactinarians and some sparse monocyrtid nassellarians. However, because of poor preservation, the information that is now available about Lower Triassic faunas should be considered quite incomplete. Forms with thin skeletons have not been preserved, or they appeared and evolved elsewhere, in, for example, less anoxic environments, during this time of environmental crisis. How else can one explain the sudden appearance of so many new groups (families, genera and species) since the beginning of the Mid Triassic when the preservation of radiolarian skeletons improved dramatically? This diversification event generally corresponds to the rise in carbon isotope values which attained positive values in the lowermost Anisian when major changes took place in ocean circulation patterns and when biological recovery after the mass extinction of the terminal Permian was significantly accelerated [Atudorei and Baud, 1997].

Usually radiolarian diversity minima occur simultaneously with the  $\delta^{13}\text{C}$  positive excursion [O'Dogherty and Guex, 2002]. During the Changxingian a minor positive peak is concomitant with the end Permian extinction [cf. Holser *et al.*, 1991], but just after the Permo-Triassic boundary a conspicuous negative carbon isotopes excursion (5-6‰) is recorded. On the other hand, for many authors

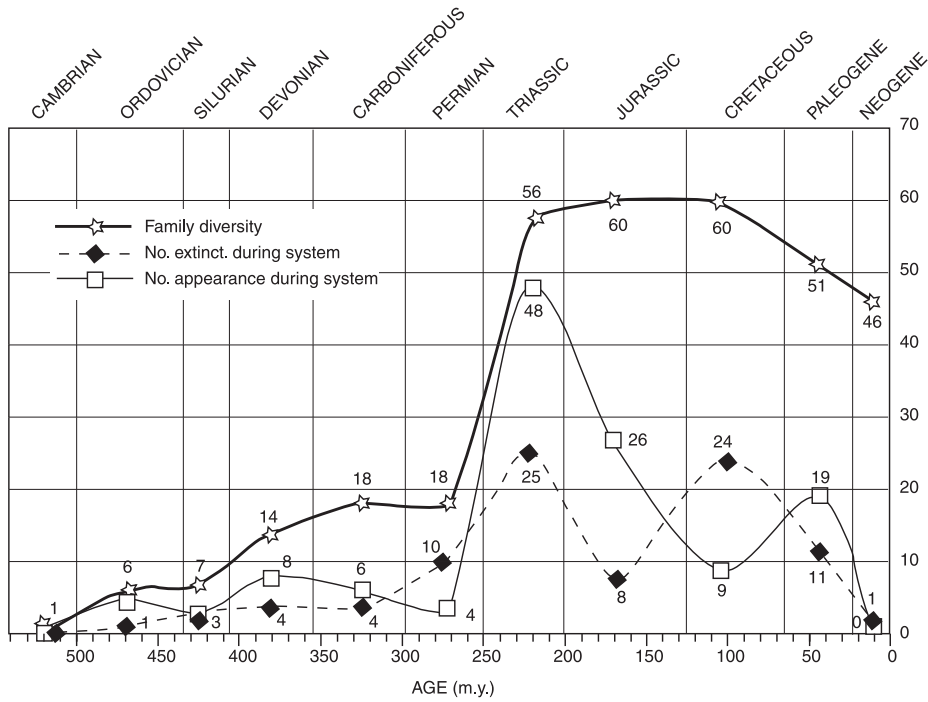


FIG. 3. – Radiolarian families through time comprising the total number of families and the number of families originating and extinct in each period. The major event is the spectacular diversification during the Triassic.

FIG. 3. – Nombre de familles de radiolaires au cours du temps, comprenant le nombre total, le nombre d'apparitions et d'extinctions pour chaque période. L'événement majeur est incontestablement la diversification spectaculaire du Trias.

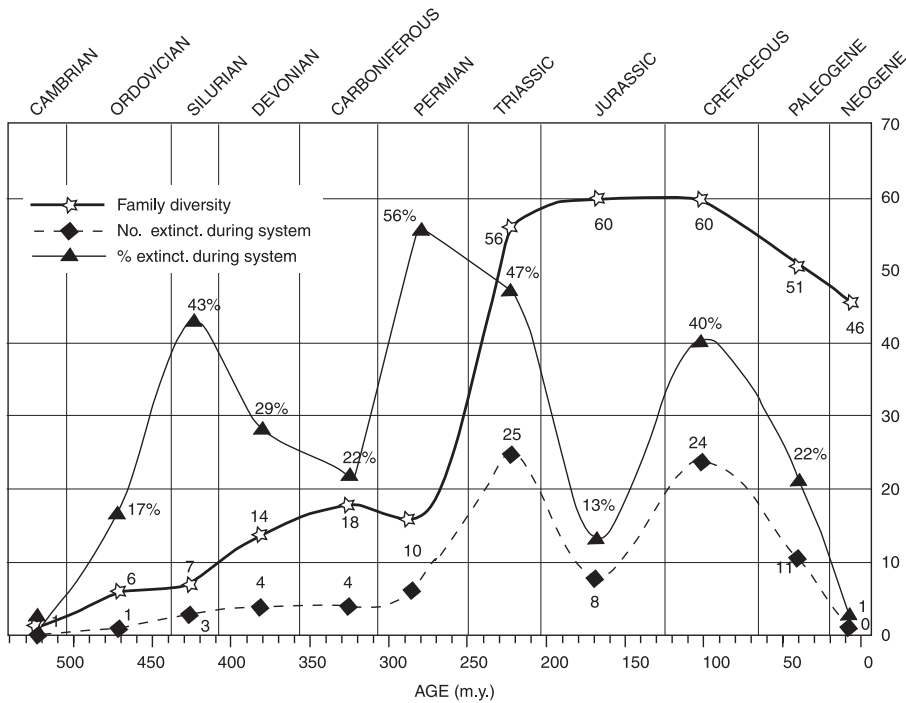


FIG. 4. – Radiolarian family extinctions through time : numbers and percentages of extinct families are plotted against total family diversity. The curve of percentage of extinct families clearly shows four major periods of extinction in decreasing order : the Permian (56 %), the Triassic (47 %), the Silurian (43 %) and Cretaceous (40 %). Note that extinctions figures here do not represent modifications at certain boundaries but took place within successive time periods.

FIG. 4. – Nombre d'extinctions familiales au cours du temps : le nombre et les pourcentages de familles éteintes La courbe des pourcentages d'extinctions montre clairement quatre périodes d'extinctions, qui sont, dans un ordre décroissant : le Permien (56 %), le Trias (47 %), le Silurien (43 %) et le Crétacé (40 %). Il est à noter que les extinctions représentées ici ne sont pas celles qui interviennent à certaines limites, mais celles qui ont eu lieu au cours des périodes successives.

[Hallam and Wignall, 1997 ; Wang *et al.*, 1994] the extinction event seems to be correlated with the negative shift which in turn is related to a dramatic fall in primary productivity. We can observe only at the family level a direct correlation between a diversity minimum (during the end-Permian, cf. fig. 7) and positive values of  $\delta^{13}\text{C}$ . It is still difficult to explain this correlation, as well as that at the Permian-Triassic (P/T) boundary, because they are contrary to what we generally know concerning the relationship between the carbon curve and radiolarian diversity. During the whole Jurassic and the Cretaceous the lowest rate of radiolarian diversity coincides with positive values of  $\delta^{13}\text{C}$  [O'Dogherty and Guex, 2002 ; Bartolini A. *et al.*, 1999]. Probably, in order to explain this we need more precise data concerning diversity curves at the genus and species levels. Irrespective of this correlation, the mid Triassic is a period of unprecedented blooming and accelerated evolution of Entactinaria, Nassellaria and Spumellaria.

Entactinaria represent the most numerous radiolarian group that crosses the P/T boundary and the Lower Triassic crisis. Recent work on the latest Permian of South China [Shang *et al.*, 2001] reveals that some nassellarian-like skeletons and true spumellarians [e.g. Pantanelliidae) seem to be already present before the P/T boundary.

The oldest Triassic species are rather simple, of the *Entactinia* type [Kozur *et al.*, 1996b], and are recorded in the Lower-Middle Scythian, but because of its poor preservation this fauna must be considered as unrepresentative of the fauna living at that time. Spathian entactinarians so far described [Sashida, 1983, 1991 ; Bragin, 1991 ; Sugiyama, 1992, 1997 ; Nagai and Mizutani, 1993] represent a more diverse assemblage with entactiniids, archaeosemantids, and eptingiids. Since the Anisian and Ladinian the entactinarians diversified simultaneously with other radiolarians resulting in new families (Pentactinocarpidae, Multiarcusellidae, Hindeosphaeridae, Centrocubidae, etc.) that became extinct later, during the Triassic, Jurassic or much later. Work in progress by Dumitrica and Zügel shows that some new families also appeared later in the Jurassic. However, by comparison with Nassellaria and Spumellaria, entactinarians decreased in number after the Triassic.

Nassellarians represent the group of radiolarians with the most rapid evolution and diversification during the Triassic and later. Some authors [Holdsworth, 1977] consider that they are absent in the Palaeozoic, but in agreement with others [Cheng, 1986], we consider that the first nassellarians appeared in the Devonian (Archocyrtiidae and Popofskyellidae), diversified during the Carboniferous, and are practically absent, but not extinct, in the Permian. The archocyrtiids seem to be the only nassellarians to have crossed the P/T boundary. The earliest nassellarians of this type are Upper Spathian [Sugiyama, 1992, 1997]. In the lower Anisian the first multisegmented nassellarians appeared (Ruesticyrtiidae), and since then (middle Anisian to Ladinian) the number of species, genera and families of Nassellaria has multiplied at a rate far greater than in any other group of Radiolaria. Most nassellarian families have their origin in the Middle and Upper Triassic, although a high number also appeared during the Lower and Middle Jurassic.

With regard to Spumellaria, their presence in the Palaeozoic is still uncertain. Since their identification de-

pends on the study of the innermost skeleton, and in most cases this skeleton is absent or not well preserved, they could be confused with some entactinarians (in which the initial spicule is dissolved), with which they share their morphology. One could consider, for example, that they are represented by some many-layered spongy skeletons occurring in the Permian. If so, they also crossed the P/T boundary. In the Triassic undoubted spumellarians are much more frequent, with one of the most typical groups being that of the Pantanelliidae. Pyloniacean spumellarians also occur since the Anisian, and Ladinian, and especially in the Upper Triassic where they are represented by Hagiastriidae, Angulobracchiidae and Pseudoaulophacidae, although because of their sudden appearance their origin remains obscure. In any case, pyloniaceans diversified enormously during the Jurassic and Cretaceous and practically disappeared at the end of the Cretaceous, although some of them did give rise to other families of Pyloniacea (Larnacillidae, Pyloniidae, etc.) common in the Cenozoic.

### Cenozoic biodiversity

Radiolarians were abundant and widespread in the oceans throughout the Cenozoic, but their diversity was comparatively reduced since their representatives can be grouped into 53 families (51 in the Palaeogene, 46 in the Neogene) from which 2 are known from the Permian and 10 from the Triassic (fig. 2). This lower diversity at the family level, by comparison with that during the Mesozoic, could also be a result of the fact that the greatest part of the systematics at the family level in the Cenozoic is that founded by Haeckel [1887] and it was also only partly taken into account [De Wever *et al.*, 2001] because of the difficulty in using the morphological characters considered by Haeckel.

Major features of the Cenozoic protistan record can be related to the significant climatic and plate tectonic changes that characterise this era, especially as these changes affected patterns of productivity and circulation of water masses in the oceans. Particularly important to protistan evolution were changes in the structure and properties of oceanic water masses at the end of the Eocene, and the general cooling of the Earth's polar regions from the Oligocene onwards.

The most dramatic evolution in the Palaeocene occurred among the planktic protists and larger foraminifers inhabiting shallow water, with all groups of plankton regaining the high diversities that existed during the Cretaceous. During the late Eocene, the Antarctic began to cool markedly, altering oceanographic and atmospheric circulation patterns. Protists and other groups changed in response to these changes. Diatoms, in particular, radiated significantly in the cold, nutrient-rich surface waters of high latitudes [Barron, 1996]. Major biotic patterns in the Neogene principally involved shifting biogeographic distributions. Warm-water biota were increasingly restricted to equatorial latitudes, while new, cool-water biota evolved in the far south and later in the north. Cool water itself may not have been the most significant factor in the evolution of this biota. The extreme seasonal character of primary productivity in high latitudes combined with oceanographic isolation probably allowed for the evolution of completely new assemblages adapted in many ways to these singular environments. Deep-sea biota also changed during this period of time as

the world's sea floors became bathed in cold water that originated in high latitudes, chiefly near Antarctica. Indeed, the Oligocene and younger biota of the Antarctic regions are unique, apparently having evolved in place as a result of the new conditions there.

Although particularly strong changes in the structure and properties of oceanic water masses occurred at the end of the Eocene with the general cooling induced by the first glaciation of Antarctica, no large variations in the diversity of radiolarian families occurred (no families became extinct at that time) but new species evolved from tropical stocks [Barron, 1996]. Later, despite environmental changes that culminated in the great Pleistocene ice sheets, there were no major pulses of extinction or appearance although background turnover was essentially continuous throughout the interval. Only two families represented by very fragile skeletons (Myelastridae and Thalassosphaeridae) are recorded exclusively in Recent sediments.

Although radiolarian communities from the Palaeocene are not well known because well-preserved assemblages are relatively rare, the early Cenozoic radiolarian fauna differs from the late Cretaceous fauna by the absence of 9 families, and is more allied to the Neogene fauna by the first appearance of 19 new families out of a total of 21 families restricted to the Cenozoic. Representatives of these new families are well represented in deposits from the Eocene to the Recent (Acanthodesmiidae, Helioidiscidae, Pyloniidae, Pterocorythidae, Collosphaeridae, Coccodiscidae, etc.) Some representatives of these families, however, have their first occurrence in the latest Cretaceous [Hollis, 1997]. Species from two families (Bekomidae and Entapiidae) are mostly characteristic of the Palaeocene.

Eocene and Oligocene radiolarian faunas are more or less similar to Neogene associations. Four new families (Tholoniidae, Theopilidae, and probably Sphaerzoidae and Orosphaeridae) make their first appearance in this time interval. Colonial radiolarians become fairly common for the first time. No family is, however, restricted to this period.

The limit with the Neogene is only marked by the disappearance of the Theocotylidae. The Neogene radiolarian assemblages are different from the Oligocene ones primarily at the generic and species levels.

Cenozoic radiolarian assemblages yield some of the best known lineages, because of their widespread distribution, their abundance in deep-sea drilling and piston core material, and their commercial use in biostratigraphy. They display a wide variety of evolutionary tempos and modes, but gradual changes seem relatively common [De Wever *et al.*, 2001]. Because Pleistocene populations appear to have had environmental tolerances little different from their living descendants, plankton distribution can be useful in the reconstruction of climatic and oceanic circulation during the ice ages. Much of our present knowledge of Pleistocene climate is derived directly or indirectly from such micropaleontologic data. Microfossils and isotopic analyses of their skeletons indicate that the Pleistocene climate has fluctuated between intervals that were warmer or cooler than today's climate. Importantly, this record provides a basis for prediction of the Earth's climate in the next few hundred to thousands of years.

## EVOLUTIONARY CRISES AND MAJOR BOUNDARIES

Biodiversity changes in the palaeontological record show that mass extinctions and appearances occurred during some relatively short time intervals. These events (fig. 8) are named and analysed as "evolutionary crises" [i.e. Lethiers, 1998]. Three major mass extinction events are recognised in the Phanerozoic : one is recorded at the Permian/Triassic boundary, one at the Triassic/Jurassic boundary, and another one at the Cretaceous/Tertiary (K/T) boundary [Lethiers, 1998]. As seen above (figs 2-4), rapid changes in the biodiversity of radiolarian assemblages appear to be fairly rare throughout the geological record except during the Lower to Middle Triassic. During this time interval of nearly 20 m.y. abundant representatives of 47 family groups (more than a third of the total number of radiolarian families recognised from the Cambrian to Present) occurred for the first time.

### Palaeozoic extinctions

The three mass extinctions known during the Palaeozoic are usually recorded in marine invertebrate assemblages at the end of the Ordovician, during the late Devonian, and at the Permian/Triassic boundary. The first two of these extinctions are not reflected by changes in protist assemblages in general, and radiolarian populations were only slightly affected although it is difficult to know with confidence since there are insufficient data available at present.

Some discrepancies do exist : while major extinctions affected both the phytoplankton and benthic calcareous algae near the end of the Devonian, radiolarians (and most foraminifers) appear to have been little affected at the family level. A relatively high percentage of representatives of the families present during the Ordovician were extinct by the end of the period, but the number of extinct families is relatively small (figs 2-4). During most of the Palaeozoic, the biodiversity of radiolarian families increased regularly. According to data from where the Frasnian-Famennian extinction event is detectable [Nazarov and Ormiston, 1985, 1986 ; Racki, 1999 ; and Vishnevskaya and Kostyuchenko, 2000], the picture is not exactly the same as far as species are concerned. It is difficult to compare our results with those of other authors such as Kiessling and Tragelehn [1994], or Umeda [1998] among others, and particularly Vishnevskaya and Kostyuchenko [2000] since their taxonomic base is not the same (see figs 5 and 6).

### The Permian-Triassic (P/T) crisis

The end of the Permian is marked by the greatest extinction known in the fossil record. As many as 95 % of all marine species disappeared at that time, including many marine protists. Interpretation of the carbon isotope record suggests a catastrophic collapse of primary productivity in the late Changxingian (latest Permian) [Wang *et al.*, 1994 ; Hallam and Wignall, 1997]. At that time radiolarian cherts that were common in the deep marine sections of South China, Japan, and western Canada, disappeared abruptly. They reappeared only in the Middle Triassic after a "chert gap" of 7 to 8 m.y. An important change in radiolarian composition can be related to this "chert gap" [Isozaki, 1994]. The



mechanisms responsible for this gap in siliceous sedimentation are not entirely understood.

According to the Permian palaeogeography [e.g. in Scotese and Langford, 1995 ; Fluteau *et al.*, 2001], only one continent (Pangea) was present at that time and surrounded by only one super-ocean (Panthalassa). This concomitant drastic decrease of shelf surface added to the Permian glaciation and, with its resultant fall in sea level, an important dynamic change in the dynamics of the ocean circulation occurred [Fluteau *et al.*, 2001]. Progressively, during the Lower Triassic, in concert with changes in plate tectonics and climatic conditions, the ocean environment found a new stability and a tremendous diversification flourished from rare survivors.

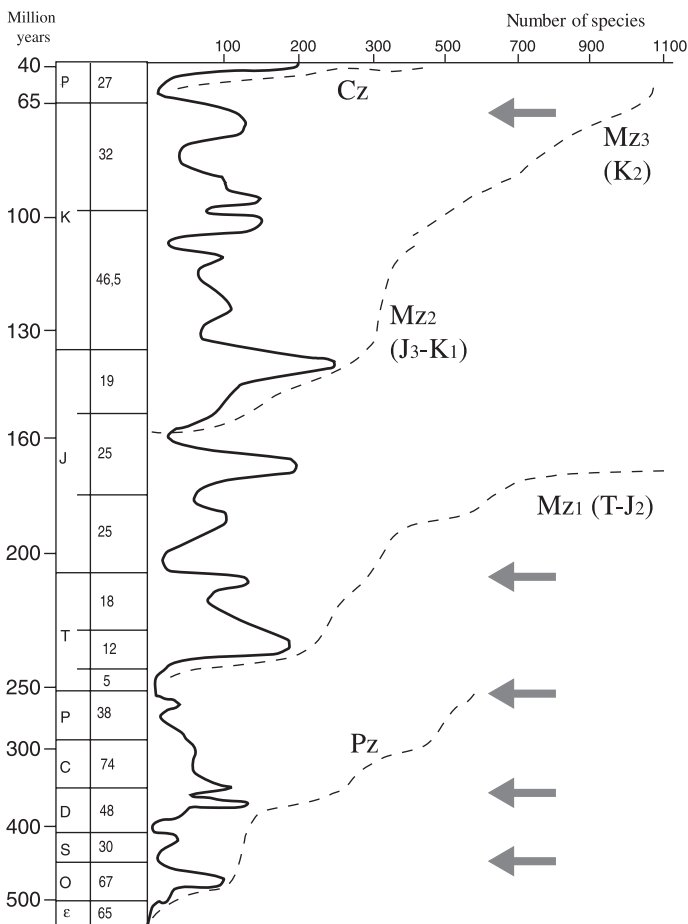


FIG. 5. – Radiolarians species diversity through time according to Vishnevskaya and Kostyuchenko [2000]. The continuous line shows the number of species in the epoch, the dashed line indicates the added up number of species (cumulative curves for three periods). The age scale is logarithmic. First column indicates by abbreviation the successive systems, second column shows the duration of subdivisions as chosen by these authors. Arrows corresponding to the five main marine extinctions at family level are added.

FIG. 5. – Diversité des radiolaires au niveau spécifique au cours du temps selon Vishnevskaya et Kostyuchenko [2000]. La ligne continue montre le nombre d'espèces pour chaque époque, la ligne en tirets indique le nombre cumulé d'espèces (courbes cumulatives pour trois périodes). L'échelle des âges est logarithmique. La première colonne indique les abréviations des étages successifs, la deuxième colonne montre la durée des subdivisions choisies par ces auteurs. Nous avons ajouté les flèches qui soulignent les 5 principales extinctions marines.

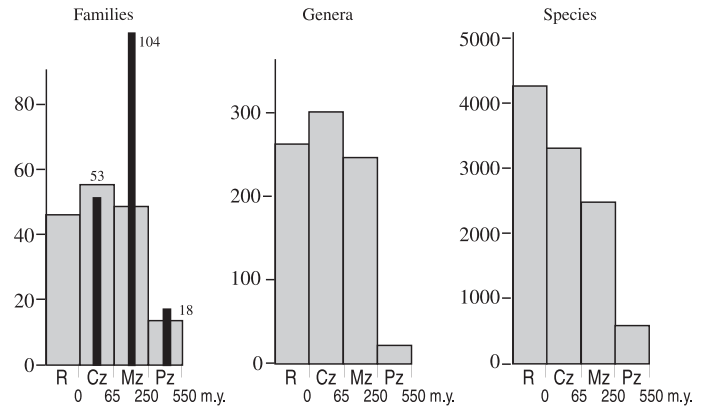


FIG. 6. – Distribution of the number of families, genera, and species of Palaeozoic, Mesozoic, Cenozoic and Recent radiolarians (according to Vishnevskaya and Kostyuchenko [2000]). Our data (black bars), concerning families, are plotted against Vishnevskaya and Kostyuchenko's data (grey boxes) suggesting a strong discrepancy.

FIG. 6. – Distribution du nombre de familles, de genres et d'espèces au Paléozoïque, Mésozoïque, Cénozoïque et dans le Récent [d'après Vishnevskaya et Kostyuchenko, 2000]. Nos données (barres noires) concernant les familles, reportées en face de celles de Vishnevskaya et Kostyuchenko (en gris) révèlent une grande disparité.

Palaeozoic radiolarian families underwent extinctions towards the end of the Permian, and the lowest diversity was attained in the earliest Triassic (fig. 2).

Following the “chert gap”, the rapid diversification of Triassic radiolarian assemblages during the early to late Triassic is the most prolific that has ever been recorded in the Phanerozoic. The extinctions of radiolarians in Japan [Yao and Kuwahara, 1997] between the Permian and Triassic seems to have been a slow and progressive phenomenon (52 % of families, 25 % of genera and 66 % of species disappear at this period, fig. 7). The cause of this big crisis, that probably lasted several million years, would be different from the explanations for other extinctions such as that at the K/T boundary (Cretaceous-Tertiary) since it may be two successive crises separated by 5 million years : late Guadalupian and late Tatarian [Stanley and Yang, 1994].

Events that affected radiolarians will have to be documented in far greater stratigraphic and biogeographic detail before the similarities and differences between different fossil records are useful in constraining theories of evolutionary change in Palaeozoic oceans. Recent data by Shang *et al.* [2001] seem to indicate that species crossing the P/T boundary do not constitute a drastic change but rather a progressive one, from Changxingian to Spathian (fig. 8).

The most distinctive feature for this event is not the diminishing number of taxa (6 families extinct near the P/T boundary), but rather an important diversification that followed it during the Triassic : 18 families are recorded during the Permian, and 56 families by the end of the Triassic, of which 48 appeared in the early and mid Triassic. Examples of detailed lineages or divergence are not known since data are still rare. Some morphological characteristics of the radiolarian tests recognised in different species from this time interval offer however, interesting hypotheses. Among many new morphological characters one can mention the strongly twisted spines occurring in many different species and genera although slightly twisted spines do exist in Palaeozoic and Cretaceous species. This feature is so

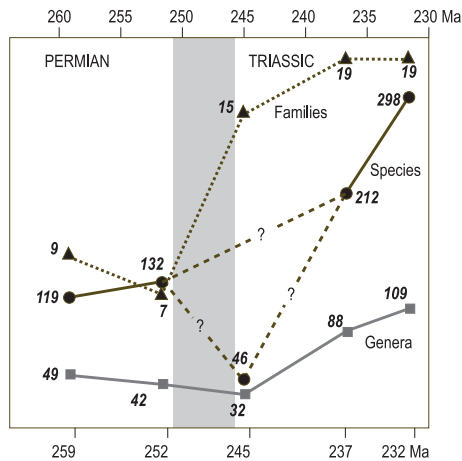


FIG. 7. – Families, genera and species evolution during the Permian-Triassic period.

Triangles indicate family numbers. Corresponding numbers for each triangle are reported. The number of genera (squares) and species (circles) are also reported for each interval. The light grey zone represents a biostratigraphic zone barren of information.

All curves follow the same trend, except for one point (46) on the species curve. This low value point is attributed to poor preservation because it is easier to assign a specimen to a family than to a species in poorly preserved material as is the case for the Spathian [Yao and Kuwahara, 1997].

FIG. 7. – Variation du nombre de familles, genres et espèces au passage Permien-Trias.

Les triangles indiquent le nombre de familles. Le nombre correspondant à chaque donnée est mentionné. Les nombre de genres (carrés) et d'espèces (cercles) sont aussi reportés pour chaque échantillon. La zone en gris clair représente un intervalle dépourvu d'information.

Toutes les courbes indiquent la même tendance, sauf pour un point (46) de la courbe des espèces. Cette faible valeur est attribuée à une pauvre conservation, car il est plus aisé d'assigner un spécimen à une famille plutôt qu'à une espèce dans un matériel mal conservé, comme c'est le cas de ce Spathian [Yao et Kuwahara, 1997].

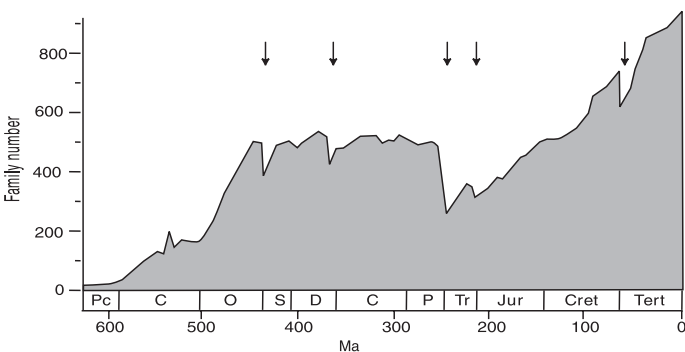


FIG. 8. – Marine family diversity during the Phanerozoic showing the long-term increase punctuated by diversity crashes caused by the “big five” mass extinction events (arrows). Diversity decreases correspond to the following percentage losses of families : Silurian : 12 %, Devonian : 14 %, Permian-Triassic : 52 %, Triassic-Jurassic : 12 %, Cretaceous-Tertiary : 11 % (modified after Raup and Sepkoski [1982]).

FIG. 8. – Diversité des organismes marins, au niveau familial, au cours du Phanérozoïque montrant une augmentation générale du nombre, interrompue par quelques baisses brutales : les “cinq grandes” extinctions en masse (soulignées par des flèches). Les chutes de diversité correspondent aux pourcentages suivants : Silurien : 12 %, Dévonien : 14 %, Permian-Trias : 52 %, Trias-Jurassique : 12 %, Crétacé-Tertiaire : 11 % [modifié d'après Raup et Sepkoski, 1982].

characteristic that it allows instant recognition of the Triassic period. Several scenarios, based on genomic modifications, have been proposed [De Wever *et al.*, 2001] to explain the puzzling coincidence of this morphological character in different groups belonging to the orders Entactinaria and Spumellaria.

1) Since slightly twisted spines exist in different orders of radiolarians from the Palaeozoic to the present, it may be that this phenotypic character occurs within the genetic pool of all radiolarians, at least as a latent gene. When a genome is accidentally altered by environmental factors (cosmic rays, strong chemical or thermic changes ; an unusual increase of the global temperature of 6 °C was recorded at the end-Permian, cf. Thompson and Newton [1989] the organism tries to repair it as completely as possible, but not with immediate success, and in such a case, some unusual phenotypic characters can be expressed. In the case of the twisted spines, such an alteration (producing strongly twisted spines) may have occurred during the “chert gap” interval that is related to the strong environmental changes at the Permian/Triassic boundary. It is also possible that if only one protein is altered (e.g. a heat-shocked protein), for the same reason as previously mentioned, some phenotypic modifications may appear, even if the genome remains unaffected. Such modifications are known to be effective for temperature differences restricted to a few degrees [from 18 to 23 °C as indicated by Rutherford and Lindquist [1998]. These authors also mentioned that some proteins could be the cause of rapid morphological radiations in the fossil record (fig. 9).

2) The strongly twisted spines could be related to the arrival of a gene in the cell, either by contamination with a virus or by a gene transfer from a symbiont or any other flagellates. Such a hypothesis is supported by the fact that different taxa are affected by a similar phenomenon possibly due to the bloom of a specific organism. This interspecies recombination (or horizontal gene transfer) has been recognised in many organisms [Page and Holmes, 1998]. According to these authors transposable elements make up a substantial portion (more than 50 %) of the genomes of many eukaryotes. Transposable elements are also found in bacteria where they are referred to as insertion sequences or transposons. Endogenous retroviruses are important components i.e. they make up to about 1 % of the mammalian genome. These are copies of retroviruses which have integrated as their DNA form (known as the provirus) into the germ-line of eukaryotes and which are now inherited along with the host genomic DNA. Although these elements were originally derived from infectious viruses, they have since acquired so many mutations that they are transcriptionally silent and so are non-infectious. Transposons, as well as jumping around genomes, are sometimes able to move between species and can affect the phenotype of their host organism [Page and Holmes, 1998]. Transposable elements can influence host biology in other ways, for example, elements inserted into host genes can inactivate them, or lead to other major mutations.

**Triassic-Jurassic boundary**

Transition between Triassic and Jurassic radiolarian assemblages is not well known because only two appropriate stratigraphic sequences are known, one in Japan and one in

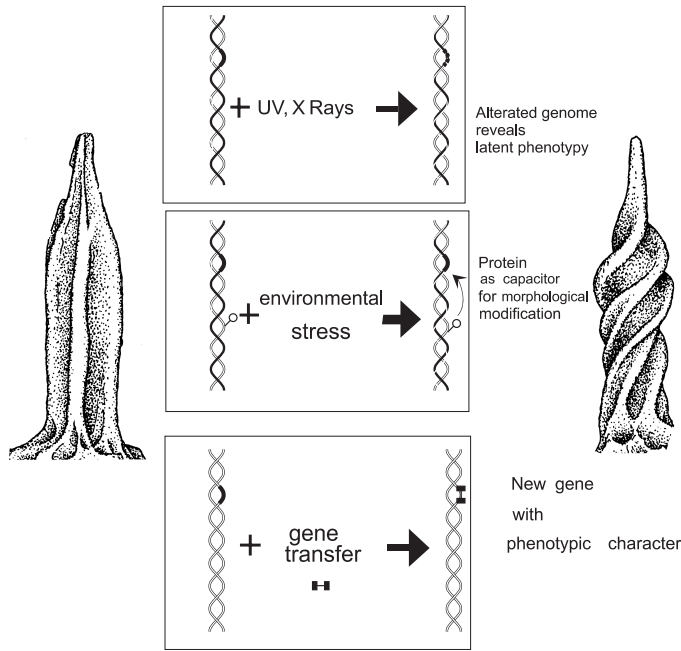


FIG. 9. – Hypothetical scheme using genetic modifications explaining the abundance of twisted spines during Triassic times [from De Wever *et al.*, 2001].

FIG. 9. – Schéma des possibilités de modifications génétiques qui expliqueraient la fréquence d'épines vrillées pour de nombreux taxons au Trias [d'après De Wever *et al.*, 2001].

Canada. The Japanese sections are complete and without any change of facies according to Hori [1992]. The transition from Triassic to Jurassic radiolarian fauna spans a range of about 7 m.y.

In Canada, a detailed study of the transition reveals a clear change at different taxonomic levels, from families to species [Tipper *et al.*, 1994 ; Carter *et al.*, 1998 ; Ward *et al.*, 2001]. These authors reported that the Upper Norian is particularly rich, with over 90 radiolarian species and more than 35 genera being recognised. These diverse faunas contain many architecturally complex, short-ranging forms, a number of which continue to evolve almost until their apparent demise. The most diverse and abundant genera are : *Betraccium*, *Canoptum*, *Ferresium*, *Mesosaturnalis*, *Plafkerium*, and *Squinabolella*. In these faunas, spumellarians outnumber nassellarians, both in genera and species, by a ratio of two to one, but at the family level, they are almost equivalent (20 Spumellaria *vs.* 22 Nassellaria families). In the earliest Hettangian the radiolarian fauna is of very low diversity and consists mainly of latticed or spongy spumellarians with irregular meshwork and simple spines and very few nassellarians. These radiolarians are primitive in appearance, and possess little definable organised structure. The diversity increases markedly toward the end of the Hettangian when new genera appear along with surviving Triassic genera, but rarely more than one or two species per genus are observed. The fauna becomes more diverse in the Sinemurian, and nassellarians (especially multicyrtyd) become increasingly dominant. The genera that survive the end of the Triassic crisis include *Archaeocenosphaera*, *Gorgansium*, *Pantanellium*, *Paronaella*, *Citriduma*, some saturnalids, cannoptids,

eptingiids, etc. It is interesting to note that most of these taxa are not recorded in the basal Hettangian. They reappear later in the Hettangian and Sinemurian as the fauna gradually rebuilds and diversifies. This suggests that the Triassic/Jurassic crisis was not so dramatic for radiolarians as was formerly believed. It could have been a regional event since many of the genera and species considered extinct at the Triassic/Jurassic boundary could have survived and evolved in some other areas of the world ocean that were more favourable to radiolarian development. From these areas they could have migrated later into the areas from which they had disappeared, as a favourable environment was re-established (Lazarus effect [Jablonski, 1986]). It is also possible that these genera and species are lacking due to scarcity or poor preservation in the stratigraphic record (only two sections display a continuous record suitable for radiolarian studies)

### Cretaceous events

One of the earliest and most fascinating discoveries of the Deep Sea Drilling Project was several levels of the Cretaceous characterised by widespread organic-rich deposits [Schlanger and Jenkyns, 1976]. These intervals were considered to be evidence of oceanic anoxic events (OAEs) of which three have been identified : OAE1, a prolonged Aptian-Albian event ; OAE2, a much shorter event at the late Cenomanian-Turonian stage boundary ; and OAE3, during the Coniacian-Santonian interval. The second oceanic anoxic event has been generally identified as corresponding to a mass extinction event.

Reefs, calcareous algae and benthic foraminifers suffered a late Aptian crisis, at least in the carbonate platforms of southern Europe. Losses of tropical taxa were matched by numerous extinctions reported from close oceanic regions, and planktonic populations underwent a rapid change in composition [Hallam and Wignall, 1997]. A minor foraminiferal extinction around the Aptian/Albian boundary (called OAE1b) was marked by the loss of a few radially elongated planispiral species [Leckie, 1989]. Another foraminiferal event in the late Albian (OAE1c) is characterised by the disappearance of a few species of *Ticinella* [Caron and Homewood, 1983]. The Aptian-Turonian was a period of major changes in the ocean-atmosphere system. An increase in ocean spreading, documented in the Atlantic and the Pacific, coupled with opening of new seaways, and a global transgressive period modified the palaeogeography to a broad extent. These modifications were paralleled by major faunal and floral changes in the marine biosphere [Sanfourche and Baudin, 2001].

Taxonomic investigations have shown that the evolution of early/late Cretaceous radiolarians is dominated by several extinction/radiation events. Extinction events correlate well with the Oceanic Anoxic Events : OAE1a in the latest early Aptian, OAE1b in the earliest Albian, the *Appenninica*-Event at the late Albian, and OAE2 at the Cenomanian/Turonian-boundary (figs 10, 11). A less pronounced extinction event in the late Albian can be recognised in a few different sites [O'Dogherty, 1994 ; Lambert and De Wever, 1996 ; Erbacher and Thurow, 1997]. Organic matter and stable isotope investigations of early/late Cretaceous sections at several localities in the western Tethys and North Atlantic have shown that major



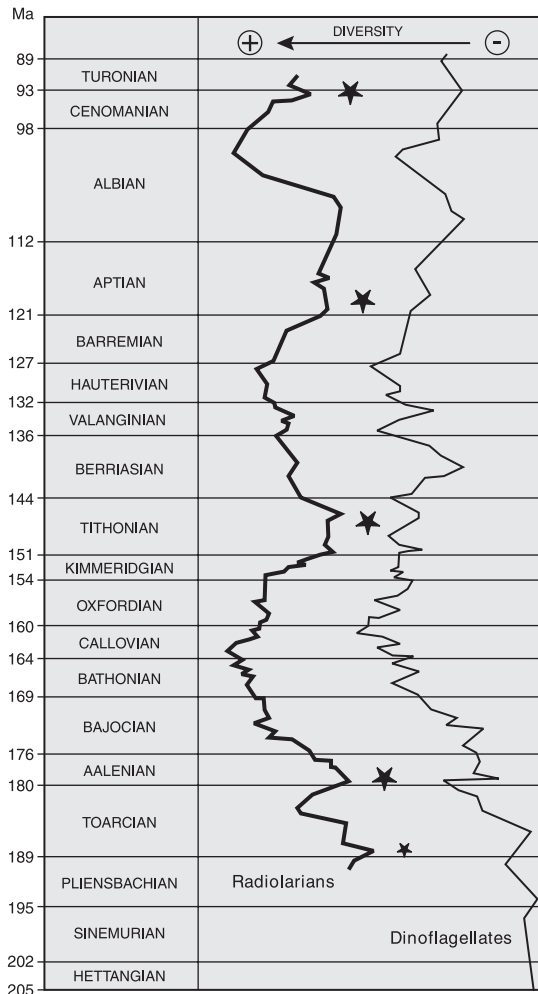


Fig. 10. – Species biodiversity of radiolarians and dinoflagellates during the Jurassic and Cretaceous : radiolarian data from O'Dogherty, unpublished ; dinoflagellate data from Bujak and Williams [1979] and Powell [1992], adapted). Stars represent minima of diversity.

This diagram indicates that following a period of radiolarian diversification during the Aalenian-Bajocian, a maximum diversity is reached during late Bathonian-early Callovian. A lower diversity is visible in the Tithonian, when the radiolarite facies disappears from Tethyan countries. A slight increase is visible up to the late Hauterivian. While less precisely documented, the Aptian – early Albian period is also a period of low diversification. It corresponds to oceanic anoxic events (OAE1). The Cenomanian – Turonian boundary is also a period of anoxia (OAE2). One can observe that the variations of diversity are of the same order of magnitude (60 to 120 sp.) and that periods of depletion are shorter than periods of high diversity.

On the other hand, periods of low diversity occurs at 93 Ma, 121 Ma, 147 Ma and 178-180 Ma, with intervals of 26 m.y., 26 m.y. and 32 m.y. respectively. These numbers are comparable to the general cyclicity evoked by Sepkoski [1989].

Secondarily, there is a good match between the radiolarian and dinoflagellate diversities. This correspondence is probably due to similar environmental needs of these organisms, or some other association.

Fig.10. – Variation de la biodiversité, au niveau spécifique, des radiolaires et des dinoflagellés au Jurassique et Crétacé [données pour les radiolaires de O'Dogherty, non publié, et pour les dinoflagellés de Bujak et Williams, 1979 ; Powell, 1992]. Les étoiles représentent des minima de diversité.

Les courbes montrent une période de diversification au cours de l'Aalénien-Bajocien, un maximum atteint au Bathonien supérieur-Callovien inférieur. Une diversité moindre se note au Tithonien, quand le faciès radiolaritique disparaît dans la Téthys. Une légère augmentation est visible jusque dans l'Hauterivien supérieur. Bien que moins précisément documenté, la période Aptien-Albien inférieur est aussi une période de faible diversité ; elle correspond aux événements anoxiques (OAE1). La limite Cénomano-Turonien est aussi une période anoxique (OAE2). On note que les variations de diversité des radiolaires et des dinoflagellés sont du même ordre de grandeur (de 60 à 120 espèces) et que les périodes de faible diversité sont plus courtes que les périodes de grande diversité. En outre les faibles diversités se trouvent à 93, 121, 147 et 178-180 Ma avec des intervalles respectifs de 26, 26 et 32 Ma. Ces chiffres sont comparables à ceux de la cyclicité générale évoquée par Sepkoski [1989].

Accessoirement, il y a une bonne concordance entre la biodiversité de ces deux groupes d'organismes planctoniques. Cette correspondance est probablement due à des besoins environnementaux équivalents, ou à un autre type d'association (symbiotique pour certains).

radiolarian extinction events did happen during time intervals characterised by elevated  $\delta^{13}\text{C}_{\text{org}}$  values [Jud, 1994 ; Weissert and Lini, 1991]. These high values co-occur with the deposition of black shales that are dominated by marine organic matter (type II kerogen). Oceanic Anoxic Events, that are characterised by positive  $\delta^{13}\text{C}_{\text{org}}$  excursions and deposition of marine black shales are believed to be caused by an increased flux of marine organic matter due to enhanced surface productivity. Some authors [Erbacher *et al.*, 1996 ; Erbacher and Thurow, 1998] have suggested that major transgressive phases resulting in a spatial extension of the oxygen minimum zone (OMZ) were responsible for concomitant radiolarian extinctions. The leaching of nutrients from flooded soils and the enhanced nutrient cycling resulting from an accelerated water mass circulation would result in an increasing exported marine productivity, and thus to an extension of the OMZ. Deeper dwelling taxa loose their habitats and disappear. The onset of the contraction of the OMZ at the end of the high sea-level stand and its following fall would create new habitats inducing radiolarian radiation. This radiation would presumably be forced by a decrease in marine productivity. This scenario would explain the faunal changes observed during OAE1b, OAE1d and OAE2. Other interpretations are however suggested by recent data [Lambert,

1999] where radiation is directly tied to an increase in sea level. Recent studies have shown that different scenarios are needed to explain each of these events [Erbacher *et al.*, 1996]. Nevertheless, similarities between OAEs can be observed. It is worth noting, however, that in the Upper Jurassic and Lower Cretaceous, radiolarian genera and species numbers are changing correlatively [O'Dogherty and Guex, 2002].

### Cretaceous-Tertiary boundary

At the end of the Cretaceous, a famous mass extinction occurred in the oceanic plankton, reef biota, and some shallow-water benthic biota, as well as among terrestrial plants and animals [Hallam and Wignall, 1997]. Good examples of this faunal extinction and related ecological changes are recorded in marine deposits containing protist microfossils. These sections provide a record of continuous sedimentation across the K/T boundary, large fossil populations, and millimetre-scale stratigraphic resolution. Some microplankton groups show rapid and almost total extinction at the Cretaceous/Tertiary boundary [Keller *et al.*, 1995]. For example, the diverse, ecologically and biogeographically stable flora of late Cretaceous calcareous nannoplankton collapsed at the Cretaceous-Tertiary bound-



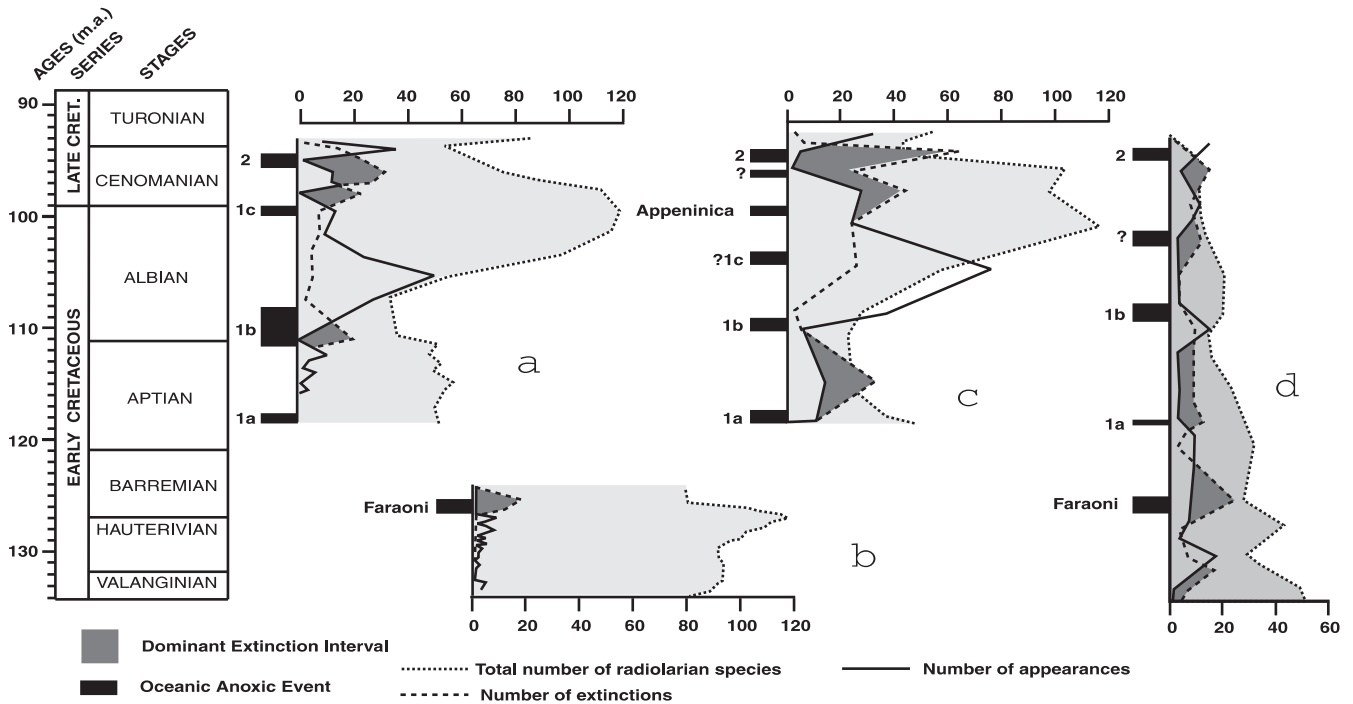


FIG. 11. – Variations of radiolarian species during the late Cretaceous of the western Tethys. Data from : a– O’Dogherty [1994] ; b– Jud [1994], c– Erbacher [1994] and d– Gorican [1994].

Dotted line = total number of species ; dashed line = number of species extinctions ; continuous line : number of originations. When the number of disappearing species is higher than appearing species the diversity decreases ; these zones are marked by grey zones. It is noticeable that periods of crisis fit well with periods of Oceanic Anoxic Events (OAE) positioned by black rectangles [adapted from Lambert and De Wever, 1996].

FIG. 11. – Variation du nombre d’espèces au Crétacé supérieur en Téthys occidentale. Données de : a– O’Dogherty [1994], b– Jud [1994], c– Erbacher [1994] et d– Gorican [1994].

Ligne en pointillé : nombre total d’espèces, ligne en tirets nombre d’espèces éteintes, ligne pleine : nombre de nouvelles espèces. Quand le nombre d’espèces qui disparaissent est plus grand que le nombre d’espèces qui apparaissent, la biodiversité diminue, ces périodes sont marquées par un grisé. Il est remarquable que les périodes de crises correspondent bien avec les périodes d’anoxie océanique (OAE) repérées par un rectangle noir [d’après Lambert et De Wever, 1996].

ary, although limited populations of some Cretaceous species persisted for up to several tens of thousands of years into the Palaeocene [Pospichal, 1996].

In the late Cretaceous and early Paleocene interval, Radiolaria had a gentle decline : 8 families (minor since they were already rare in the Maastrichtian) became extinct as compared to 5 between the Triassic-Jurassic and Jurassic-Cretaceous eras.

Although many oceanic sections crossing the K/T boundary were recovered during ocean drilling programs, no continuous radiolarian oceanic sequence crossing the boundary has ever been described. The single continuous record of radiolarian faunas evolving through this boundary was recovered and described from a land based section in New Zealand [Hollis, 1993]. The author observed that “no evidence is found for mass extinction at the end of the Cretaceous” but instead the K/T event appears to have promoted a prolonged (1-2 m.y.) siliceous plankton bloom. Interpretations of previous data [Hollis, 1996 ; Hollis *et al.*, 1995 ; MacLeod *et al.*, 1997] have been speculative because of limited knowledge of Cretaceous-early Tertiary radiolarian fauna. It was inferred that there was no radiolarian evolutionary crisis precisely at the K/T boundary. Recent works on radiolarian fauna recovered from late Cretaceous and early Palaeocene intervals confirm this con-

tinuous evolution of radiolarians through the K/T boundary [Hollis *et al.*, 2000] : representatives of a total of 28 radiolarian families cross the K/T boundary while only 8 families become extinct and 10 place their first occurrence close to boundary (fig. 2).

At a more detailed level (genera and species) there is a change in the composition of the population. A shift from nassellarian to spumellarian dominance occurs within 3 mm, with the base of the boundary clay containing essentially a Cretaceous fauna (15 % Spumellaria) and the upper part of the clay consisting of 60 % Spumellaria, half of which are the lowest Palaeocene index species *Amphisphaera aotea*. This transition is accompanied by a decrease in radiolarian abundance and diversity indicating that, although the K/T event favoured some actinomids, and did not cause significant radiolarian extinctions, it did adversely affect the radiolarian population [Hollis *et al.*, 2000]. Keller *et al.* [1995] distinguished three major categories of biotic changes at the K/T boundary : the first are strongly affected (benthic and planktic foraminifera and calcareous nannofossils), the second records relatively minor gradual changes in species richness (pollen, spores, ostracods) and the third shows increasing species richness (dinoflagellates). Radiolarians would belong to the second category.

More important than this extinction is the general trend of diversification : the number of radiolarian families had been increasing since the beginning of the Mesozoic, but that number began to decrease after the Cretaceous/Tertiary boundary. We do not know the real cause of this general diminution, but one can imagine that it may be related to the developing diversity and resulting competition of other silica-producing organisms such as diatoms at that time [Harper and Knoll, 1975 ; Racki, 1999], or it is an artefact of the broad taxonomic concepts applied to Cenozoic families.

### Eocene-Oligocene boundary

The Eocene was an epoch of pronounced speciation, resulting in diverse, morphologically complex mid to late Eocene faunas characterised by marked latitudinal provinciality. The transition from Eocene to Oligocene faunas was not abrupt but rather took place through several million years of late Eocene and early Oligocene time through a series of discrete events that appear to have been climatically and oceanographically induced [Lazarus and Caulet, 1994]. In Barbados, several radiolarian extinction events roughly correlate with a series of extraterrestrial impacts recorded in the sedimentary record as microtektite horizons [Sanfilippo *et al.*, 1985]. This is also the case in North America [Glass and Zwart, 1979]. Nevertheless radiolarian extinctions in Barbados predate the microtektite layer and the highest iridium concentrations apparently coincide with the extinctions. On the other hand, while some Eocene-Oligocene extinctions and population fluctuations correlate with microtektite horizons, others do not. The Eocene-Oligocene boundary has long been recognised as a period of climatologic and oceanographic changes inducing a significant biologic turnover [Prothero and Berggren, 1992]. Calcareous nannoplankton, dinoflagellates, silicoflagellates, and ebridians, presented higher diversities in the Eocene than in the Oligocene. The details of this big turnover are, however, not identical among the various taxonomic groups. The timing of last appearances, population fluctuations, degree of latitudinal diachroneity of events, and degree of correlation to microtektite distributions or isotopic events vary within and among major groups. At least in part, these differential responses appear to reflect the biologic and biogeographic differences among major groups of microplankton. Also, most of the Eocene extinctions were followed quickly by the first appearances of new species.

The diversity decline of late Eocene to early Oligocene radiolarian assemblages appears to be related to major climatic, palaeoceanographic and sea-level changes. Many of the biologic changes that occurred near the Eocene/Oligocene boundary appear to be the culmination of trends heralded by an interval of major plankton turnover at the mid to late Eocene boundary, probably related to the onset of the production of deep cold Antarctic bottom-water [Lazarus and Caulet, 1994]. On a more diffuse level, a Cenozoic trend of decreasing test weight in radiolarians [Moore, 1969] parallels the pronounced radiation of marine diatoms, and the two patterns may be linked through the mutual dependence of radiolarians and diatoms on silica. If the metabolic cost of precipitating a skeleton is at all proportional to ambient  $\text{SiO}_2$  concentrations, then the exceptional effectiveness of diatoms in depleting oceanic silica should have exerted a continuing

selective pressure in favour of radiolarians able to form functional tests using less  $\text{SiO}_2$ . One prediction of this hypothesis is that radiolarian species living in surface waters should show far more pronounced test diminution than forms inhabiting deeper waters.

In summary, Eocene-Oligocene changes in radiolarian assemblages cannot be characterised as mass extinction events because they do not involve rapid extinctions. In fact, the Eocene-Oligocene radiolarian turnover is almost non-existent at the family level. Ongoing late Eocene rates of extinction continue into the Oligocene. The early Oligocene interval is unusual in that it is characterised by a low rate of species origination. In general, the Eocene/Oligocene transition featured moderate rates of extinction amongst marine plankton that were not simultaneous among appreciable numbers of species, no great expansion of surviving plankton, and low rates of speciation. This is consistent with the fossil records of continental groups, especially land plants and vertebrates, which suggest that dominant factors controlling the evolutionary turnovers at the Cretaceous-Tertiary and Eocene/Oligocene boundaries intervals were different.

### CONCLUSIONS

The biodiversity of radiolarians increased constantly throughout the Palaeozoic and decreased slightly towards the end of the Permian. The appearance of representatives of all orders of radiolarians can be successively recognised in the Palaeozoic. During this period primitive nassellarians appeared, with their characteristic internal spicules, but with skeletons still having some entactinarian characteristics. Spumellaria seem to have appeared only during the latest Permian. They diversified enormously during the Jurassic and Cretaceous. Mesozoic pyloniaceans practically disappeared at the end of the Cretaceous and during the Tertiary diversified again giving rise to new families. During the Mesozoic existing lineages of radiolarians produced an impressive number of new morphotypes grouped into new families. The Middle Triassic especially is a period of unique blooming and accelerated evolution of Entactinaria, Nassellaria and Spumellaria. Nassellarians represent the group of radiolarians with the most rapid evolution and diversification during the Triassic and later. Radiolarians were abundant and widespread in the oceans throughout the Cenozoic, but their diversity was comparatively reduced.

Drastic changes in the biodiversity of radiolarian assemblages appear to be fairly rare throughout the geological record except during the Lower to Middle Triassic. The most distinctive feature for the Permian-Triassic event is, not only the diminishing number of taxa, but also the especially important diversification that followed it during the Triassic. The Triassic/Jurassic crisis was not so dramatic for radiolarians as was formerly believed. The K/T event favored some actinommids, but did not cause significant radiolarian extinctions ; it did adversely affect radiolarian population. The Eocene-Oligocene radiolarian turnover is insignificant at the family level.

In the Phanerozoic diversity pattern of radiolarians the most important trend is the diversification of the number of families especially since the beginning of the Mesozoic, but a slight decrease after the Cretaceous/Tertiary boundary

may be related to the expansion of other planktonic organisms, notably diatoms.

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## References

- AMARAL-ZETTLER L.A., ANDERSON R.O. & CARON D.A. (1999). – Towards a molecular phylogeny of colonial spumellarian Radiolaria. – *Mar. Micropaleont.*, **36**, 67-79.
- AMARAL-ZETTLER L.A., SOGIN M.L. & CARON D.A. (1997). – Phylogenetic relationships between the Acantharea and the Polycystinea : a molecular perspective on Haeckel's Radiolaria. – *Proc. Natl. Acad. Sci.* **94**, 11411-11416.
- ANDERSON O.R. (1983). – Radiolaria. – Springer-Verlag, New York, 365 p.
- ANDERSON O.R. & SWANBERG N.R. (1981). – Skeletal morphogenesis in some living collosphaerid Radiolaria. – *Mar. Micropaleont.*, **6**, 385-396.
- ATUDOREI V. & BAUD A. (1997). – Carbon isotope events during the Triassic. – *Albertiana*, **20**, 45-49.
- BARRON J. A. [1996]. – Diatom constraints on the position of the Antarctic Polar Front in the middle part of the Pliocene. – *Mar. Micropaleont.*, **27**, 195-216
- BARTOLINI A., BAUMGARTNER P.O. & GUEX J. (1999). – Middle and late Jurassic radiolarian palaeoecology versus carbone-isotope stratigraphy. – *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, **145**, 43-60.
- BENGTSON S. (1986). – Siliceous microfossils from the Upper Cambrian of Queensland. – *Alcheringa*, **10**, 195-216.
- BENTON M.J. (1993). – The fossil record 2. – Chapman & Hall, 845 p.
- BRAGIN N.Y. (1991). – Radiolaria and lower Mesozoic units of the U.S.S.R. east regions. – *Geol. Inst. Transactions*, **469**, 126 p.
- BUJAK J.P. & WILLIAMS G.L. (1979). – Dinoflagellate diversity through time. – *Mar. Micropaleont.*, **4**, 1-12.
- CARON M. & HOMEWOOD P. (1983). – Evolution of early planktonic foraminifers. – *Mar. Micropaleont.*, **7**, 453-462.
- CARTER E.S. (1993). – Biochronology and paleontology of uppermost triassic (Rhaetian) radiolarians, Queen Charlotte Islands, British Columbia, Canada. – *Mémoires de Géologie (Lausanne)*. Vol.11, 175p.
- CARTER E.S., CAMERON B.E.B. & SMITH P.L. (1988). – Lower and Middle Jurassic radiolarian biostratigraphy and systematic paleontology, Queen Charlotte Islands, British Columbia. – *Geol. Surv. Canada Bull.*, **386**, 1-109.
- CHENG Y.-N. (1986). – Taxonomic studies on Upper Paleozoic Radiolaria. Upper Paleozoic (Upper Devonian and Carboniferous) Radiolaria from the Ouachita Mountains, Oklahoma and Arkansas, 1. – *Nat. Mus. nat. Sci., Taiwan, Sp. Publ.*, 1-310.
- CLARKSON E.N.K. (1998). – Invertebrate palaeontology and evolution. 4th ed. – Blackwell Science, Univ. Press, Cambridge, 452 p.
- COTTEREAU N. (1992). – Reconstitutions paléobathymétriques de la Téthys au Jurassique terminal – Méthodes et conséquences sur les courants océaniques. – Thèse Université, Paris, 245 p.
- DANELIAN T. (1999). – Taxonomic study of Ordovician (Lanvirn-Caradoc) Radiolaria from the southern Uplands (Scotland, U.K.). – *Geodiversitas*, **21**, **4**, 625-635.
- DE WEVER P. (1982). – Radiolaires du Trias et du Lias de la Téthys (Systématique, Stratigraphie). – *Pub. Soc. Géol. Nord*, **7**, Lille, 599 p.
- DE WEVER P., AZEMA J. & FOURCADE E. (1994). – Radiolaires et radiolari-tes : production primaire, diagenèse et paléogéographie. – *Bull. Centres rech. Expl. - Elf Aquitaine*, **18**, **1**, 315-379.
- DE WEVER P., DUMITRICA P., CAULET J.-P., NIGRINI C. & CARIDROIT M. (2001). – Radiolarians in the sedimentary record. – *Gordon & Breach*, 524 p.
- DONG X., KNOLL A.H. & LIPPS J.H. (1997). – Late Cambrian Radiolaria from Hunan China. – *J. Paleontology*, **71**, 753-758.
- DUMITRICA P., CARIDROIT M. & DE WEVER P. (2000). – Archaeospicularia, ordre nouveau de radiolaires : une nouvelle étape pour la classification des radiolaires du Paléozoïque inférieur. – *C.R. Acad. Sci., Paris*, **330**, 563-569.
- DUMITRICA P. & ZÜGEL P. (2003). – Lower Tithonian mono- and dicyrtid Nassellaria (Radiolaria) from the Solnhofen area, southern Germany. – *Geodiversitas*, Paris, **25**, **1**, 5-72.
- ERBACHER J. (1994). – Entwicklung und Paläoozeanographie mittelkretazischer Radiolarien der westlichen Tethys (Italien) und des Nordatlantiks. – *Tübinger Mikropaläont. Mitt.*, **12**, 1-160.
- ERBACHER J. & THUROW J. (1997). – Influence of oceanic anoxic events on the evolution of mid-Cretaceous Radiolaria in the North Atlantic and western Tethys. – *Mar. Micropaleont.*, **30**, 139-158.
- ERBACHER J. & THUROW J., (1998). – Mid-Cretaceous radiolarian zonation for the North Atlantic : an example of oceanographically controlled evolutionary processes in the marine biosphere ? *In* : CRAMP A., MACLEOD C.J., LEE S.V. & JONES E.J.W. Eds, Geological evolution of ocean basins : Results from the Ocean Drilling Program. – *Sp. Pub. Geol. Soc. London*, **131**, 71-82.
- ERBACHER J., THUROW J. & LITKE R. (1996). – Evolution patterns of Radiolaria and organic matter variations : A new approach to identify sea-level changes in mid-Cretaceous pelagic environments. – *Geology*, **24**, 499-502.
- FLUTEAU F., BESSE J., BROUTIN J. & RAMSTEIN G. (2001). – The late Permian climate. What can be inferred from climate modelling concerning Pangea scenarios and Hercynian range altitude ? – *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, **167**, 39-71.
- GINGERICH P.D. (1985). – Species in the fossil record : concepts, trends, and transitions. – *Paleobiology*, **11**, 27-41.
- GLASS B.P. & ZWART M.J. (1979). – North American microtektites in Deep Sea Drilling Project cores from the Caribbean Sea and Gulf of Mexico. – *Geol. Soc. Amer. Bull.*, **90**, 595-602.
- GORICAN S. (1994). – Jurassic and Cretaceous radiolarian biostratigraphy and sedimentary evolution of the Budva Zone (Dinarides, Montenegro). – *Mém. Géol., Lausanne*, **18**, 1-120.
- GUEX J. (1981). – Associations virtuelles et discontinuités dans la distribution des espèces fossiles : un exemple intéressant. – *Bull. Soc. Vaud. Sci. Nat.*, **359**, 179-197.
- HAECKEL E. (1887). – Report on the Radiolaria collected by H.M.S. Challenger during the years 1873-1876. – *Report on the Scientific Results of the Voyage of the H.M.S. Challenger. – Zoology*, **18**, clxxxviii + 1803p.
- HALLAM A. & WIGNALL P.B. (1997). – Mass extinctions and their aftermath. – Oxford Univ. Press, 320 p.
- HARPER H.E. & KNOLL A.H. (1975). – Silica, diatoms and Cenozoic radiolarian evolution. – *Geology*, **3**, **4**, 175-177.
- HART M.B. & WILLIAMS C.L. (1993). – Protozoa. *In* : BENTON M.J. Ed., The fossil record 2. – Chapman & Hall., 43-70.
- HOLDSWORTH B.K. (1977). – Paleozoic Radiolaria : stratigraphic distribution in Atlantic borderlands. *In* : SWAIM F.M. Ed., Stratigraphic micropaleontology of Atlantic basin and borderlands. – *Elsevier*, 167-184.
- HOLLIS C.J. (1993). – Latest Cretaceous to late Paleocene radiolarian biostratigraphy : A new zonation from the New Zealand region. – *Mar. Micropaleont.*, **21**, 295-327.



- HOLLIS C.J., (1996). – Radiolarian faunal change through the Cretaceous-Tertiary (K-T) transition of eastern Marlborough, New Zealand. *In* : MAC LEOD N. & KELLER G. Eds, Cretaceous Tertiary mass extinction : biotic and environmental changes. – W.W. Norton, London, 173-204.
- HOLLIS C.J., (1997). – Cretaceous-Paleocene Radiolaria from eastern Marlborough, New Zealand. – *Institute of Geological & Nuclear Sciences*, monograph **17**, 152 p.
- HOLLIS C.J., RODGERS K.A. & PARKER R.J. (1995). – Siliceous plankton bloom in the earliest Tertiary of Marlborough, New Zealand. – *Geology*, **23**, 835-838.
- HOLLIS C., FIELD B., ROGERS K., STRONG P. & WILLUMSEN P. (2000). – Radiolarian faunal changes across the K/T boundary in a southern high-latitude neritic-bathyal transect : an integrated approach. – INTERRAD 2000, *Ninth meeting of the International Association of Radiolarian Paleontologists* (Blairsdon, California), Program with Abstracts, 34.
- HOLSER W.T., SCHÖNLAUB H.P., BOECKELMANN K., MAGARITZ M. & ORTH C.J. (1991). – The Permian-Triassic of the Gartnerkofel-1 core (Carnic Alps, Austria) : synthesis and conclusion. – *Abhandlungen der Geologischen bundesanstalt*, **45**, 213-232.
- HORI R. (1992). – Radiolarian biotratigraphy at the Triassic/Jurassic period boundary in bedded cherts from the Inuyama area, Central Japan. – *J. Geosci.*, Osaka City Univ., **35**, 53-65.
- ISOZAKI Y. (1994). – Superanoxia across the Permo-Triassic boundary ; record in accreted deep-sea pelagic chert in Japan. *In* : A.F. EMBRY Ed., Pangea : global environments and resources. – *Canad. Soc. Petrol. Geol.*, 805-812.
- JABLONSKI D. (1986). – Causes and consequences of mass extinctions : a comparative approach. *In* : D.K. ELLIOT, Ed., Dynamics of extinction. – Wiley-Interscience Publ., New York, 183-229.
- JUD R. (1994). – Biochronology and systematics of early Cretaceous Radiolarian of the western Tethys. – *Mém. Géol.*, Lausanne, **19**, 1-147.
- KELLER G., LI L. & MACLEOD N. (1995). – The Cretaceous/Tertiary boundary stratotype section at El Kef, Tunisia : how catastrophic was the mass extinction ? – *Palaeogeogr. Palaeoclimatol., Palaeoecol.*, **119**, 221-254.
- KISSLING W. & TRAGELEHN H. (1994). – Devonian radiolarian faunas of conodont-dated localities in the Frankenwald (Northern Bavaria, Germany). – *Abh. geol. Bund. in Wien*, **50**, 219-255.
- KOZUR H.W., MOSTLER H. & REPETESKI J.E. (1996a). – Well-preserved Tremadocian primitive radiolarian from the Windfall Formation of the Antelope Range, Eureka County, Nevada, USA. – *Geol. Paläont. Mitt.*, Innsbruck, **21**, 245-271.
- KOZUR H., KRAINER K. & MOSTLER H. (1996b). – Radiolarians and facies of the Middle Triassic Loibl Formation, south Alpine Karawanken mountains (Carinthia, Austria) – *Geol.-Paläont.Mitt.*, Innsbruck, Vol.4, 195-269
- LAMBERT E. (1999). – Les radiolaires crétacés du bassin Vocontien : stratigraphie, paléoenvironnements. – Unpublished Thesis Mus. Nat. Hist. Nat., Paris, 237 p.
- LAMBERT E. & DE WEVER P. (1996). – Événements biologiques chez les radiolaires au cours des phases kénoxiqes du Crétacé. – *Rev. Micropaléont.*, **39**, 283-292.
- LAZARUS D. & CAULET J.P. (1994). – Cenozoic southern Ocean reconstructions from sedimentologic, radiolarian, and other microfossil data. *In* : J.P. KENNETT & D.A. WARNKE, Eds, The Antarctic paleoenvironment : A perspective on global change. Part 2. – *Antarct. Res. Ser.*, 145-174.
- LECKIE R.M. (1989). – An oceanographic model for the early history of planktonic foraminifera. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **73**, 107-138.
- LETHIERS F. (1998). – Evolution de la biosphère et événements géologiques. – Gordon and Breach, Paris, 321 p.
- MACLEOD N., RAWSON P.F., FOREY P.L., BANNER F.T., BOUDAGHERFADEL M.K., BOWN P.R., BURNETT J.A., CHAMBERS P., CULVER S., EVANS S.E., JEFFERY C., KAMINSKI M.A., LORD A.R., MILNER A.C., MILNER A.R., MORRIS N., OWEN E., ROSEN B.R., SMITH A.B., TAYLOR P.D., URQUHART E. & YOUNG J.R. (1997). – The Cretaceous-Tertiary biotic transition. – *J. Geol. Soc. London*, **154**, 265-292.
- MARCOUX J., BAUD A., RICOU L.E., GAETANI M., KRYSSTYN L., BELLION Y., GUIRAUD R., MOREAU C., BESSE J., GALLET Y. & THEVENIAUT, H. (1993). – Late Anisian. *In* : J. DERCOURT, L.E. RICOU & B. VRIELYNCK (Eds.), Atlas Tethys palaeoenvironmental maps. – Gautier-Villars, Paris, 21-33.
- MOORE T.C. (1969). – Radiolaria : change in skeletal weight and resistance to solution. – *Geol. Soc. Amer. Bull.*, **80**, 2103-2108.
- NAGAI H. & MIZUTANI H. (1993). – Early Triassic radiolarians from Tsuzuya, Minokamo City, Gifu Prefecture, central Japan. – *Bull. Nagoya Univ. Furukawa Mus.*, **9**, 1-23.
- NAZAROV V.V. & ORMISTON A.R. (1985). – Evolution of Radiolaria in the Paleozoic and its correlation with the development of other marine groups. – *Senckenb. Lethaea*, **66**, 203-216.
- NAZAROV V.V. & ORMISTON A.R. (1986). – Trends in development of Paleozoic Radiolaria. – *Mar. Micropaleont.*, **11**, 3-32.
- O'DOGHERTY L. (1994). – Biochronology and paleontology of Mid-Cretaceous radiolarians from northern Apennines (Italy) and Betic Cordillera (Spain). – *Mém. Géol. Lausanne*, **21**, 1-415.
- O'DOGHERTY L. & GUEX J. (2002). – Rates and pattern of evolution among Cretaceous radiolarians : relations with global paleoceanographic events. – *Micropaleontology*, **48**(1), 1-22.
- PAGE R.D.M. & HOLMES E.C. (1998). – Molecular evolution, a phylogenetic approach. – Blackwell, London, 345 pp.
- PETRUSHEVSKAYA M. G. (1977). – On the origin of Radiolaria. – *Zoologicheskii Zhurnal (Zoological Journal)*, **56**, 10.
- POSPICHAL J.J. (1996). – Calcareous nannoplankton mass extinction at the Cretaceous/Tertiary boundary : an update. – *Geol. Soc. Amer. Spec. Paper* **307**, 335-360.
- POWELL A.J. (1992). – A stratigraphic index of Dinoflagellates cysts. – Chapman and Hall, London, 290 p.
- PROTHERA D.R. & BERGGREN W.A. (1992). – Eocene-Oligocene climatic and biotic evolution – Princeton University Press, Princeton, 568 p.
- RACKI G. (1999). – Silica-secreting biota and mass extinctions : survival patterns and processes. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **154**, 107-132.
- RAUP D.M. & SEPKOSKI J.J. Jr. (1982). – Mass extinction in the marines fossil record. – *Science*, **215**, 1501-1503.
- RUNNEGAR B. & BENGSTON S. (1990). – Origin of hard parts – early skeletal fossils. *In* : BRIGGS D.E.G. & CROWTHER P.R. Eds, Palaeobiology, a synthesis. – Blackwell, London, 24-29.
- RUTHERFORD S.L. & LINDQUIST S. (1998). – HSP90 as a capacitor for morphological evolution. – *Nature*, **396**, 336-342.
- SANFILIPPO A., RIEDEL W.R., GLASS B.P. & KYTE F.T. (1985). – Late Eocene microtektites and radiolarian extinctions on Barbados. – *Nature*, **314**, 613-615.
- SANFOURCHE J. & BAUDIN F. (2001). – La genèse des événements anoxiques de la période moyenne du Crétacé. Examen de l'hypothèse du méromictisme océanique. – *Ann. Soc. Géol. du Nord*, Lille, **8**, 107-119.
- SASHIDA K. (1983). – Lower Triassic Radiolaria from the Kanto Mountains, Central Japan. Part 1 : Palaeoscenediidae. – *Trans. Proc. Palaeont. Soc. Japan*, new ser., **131**, 168-176.
- SASHIDA K. (1991). – Early Triassic radiolarians from the Ogamata Formation, Kanto Mountains, central Japan. Part 2. – *Trans. Proc. Palaeont. Soc. Japan*, new ser., **161**, 681-696.
- SASHIDA K. & IGO H. (1992). – Triassic radiolarians from a limestone exposed at Khao Chiak near Phatthalung, southern Thailand. – *Trans. Proc. Palaeont. Soc. Japan*, new ser., **168**, 1296-1310.
- SCHLANGER S.O. & JENKYN H.J. (1976). – Cretaceous oceanic anoxic events : causes and consequences. – *Geol. Mijnb.*, **55**, 179-184.
- SCOTESE C.R. & LANGFORD R.P. (1995). – Pangea and the paleogeography of the Permian. *In* : P.A. SCHOLLE, T.M. PERYT & D.S. ULMER-SCHOLLE Eds, The Permian of northern Pangea : I, Paleogeography, paleoclimates, and stratigraphy. – Springer-Verlag, Berlin, p. 3-19.
- SEPKOSKI J.J. Jr. (1989). – Periodicity in extinction and the problem of catastrophism in the history of life. – *J. Geol. Soc. London*, **146**, 7-19.
- SHANG Q., CARIDROIT M. & WANG Y. (2001). – Radiolarians from the uppermost Permian Changhsingian of southern China. – *Acta Micropaleontol. Sinica*, **18**, **3**, 229-240.
- STANLEY S.M. & YANG X. (1994). – A double mass extinction at the end of Paleozoic Era. – *Science*, **266** (5189), pp.1340-1344.



- SUGIYAMA K. (1992). – Lower and Middle Triassic radiolarians from Mt. Kinkazan, Gifu Prefecture, Central Japan. – *Palaeont. Soc. Japan*, New Ser., **167**, 1180-1223.
- SUGIYAMA K. (1997). – Triassic and Lower Jurassic radiolarian biostratigraphy in the siliceous claystone and bedded cherts Units of the southeastern Mino Terrane, Central Japan. – *Bull. Mizunami Fossil Mus.*, **24**, 79-193.
- SWANBERG N.R. (1979). – The ecology of colonial radiolarians : their colony morphology, trophic interactions and associations, behavior distribution, and the photosynthesis of their symbionts. – *Woods Hole Oceanogr. Inst.*, PhD Thesis, WHOI 79-79, 202p.
- THOMPSON J.B. & NEWTON C.R. (1989). – Late Devonian mass extinction : episodic climatic cooling or warming. In : N.J. MCMILLAN, A.F. EMBRY & D.J. GLASS (Eds.), *Devonian of the world*. – *Canad. Soc. Petrol. Geol. Mem.*, **14**, pp. 29-34.
- TIPPER H.W., CARTER E.S., ORCHARD M.J. & TOZER E.T. (1994). – The Triassic-Jurassic boundary in Queen Charlotte Islands, British Columbia defined by ammonites, conodonts and radiolarians. – *Géobios, mém. spec.* **17**, 485-492.
- UMEDA A. (1998). – Upper Silurian to Middle Devonian radiolarian zones of the Yokokurayama and Konomori areas in the Kurosegawa Belt, Southwest Japan. – *The Island Arc*, **7**, 637-646.
- UMEDA A. (2003). – Paleozoic radiolarian extinction events – A new attempt at radiolarians classification and zonation. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, (in press)
- VISHNEVSKAYA V.S. & KOSTYUCHENKO A.S. (2000). – The evolution of radiolarian biodiversity. – *Paleont. J.*, **34**, 124-130.
- VRIELYNCK B. & BOUYSSÉ P. (2001). – Le visage changeant de la Terre. – Commission for the Geological Map of the World, Paris, 32 p.
- WANG K., GELDSETZER H.H.J. & KROUSE H.R. (1994). – Permian-Triassic extinctions : organic  $\delta^{13}\text{C}$  evidence from British Columbia, Canada. – *Geology*, **22**, 580-584.
- WARD P.D., HAGGART J.W., CARTER E.S., WILBER D., TIPPER H.W. & EVANS T. – Sudden productivity collapse associated with the Triassic-Jurassic boundary mass extinction – *Science* (May 11, 2001)
- WEISSERT H. & LINI A. (1991). – Ice Age interludes during the time of Cretaceous greenhouse climate ? In : D.W. MÜLLER, J.A. MCKENZIE & H. WEISSERT Ed., *Controversy in modern geology*. – Academic Press, London, 173-191.
- WON M.Z. & BELOW R. (1999). – Cambrian Radiolaria from the Georgina Basin, Queensland, Australia. – *Micropaleont.*, **45**, 325-363.
- YAO A. & KUWAHARA K. (1997). – Radiolarian faunal change from Late Permian to Middle Triassic times. In : A. YAO Ed., *Proceeding of the Fifth Radiolarian Symposium*. – News of Osaka Micropaleontologists, Spec. vol., 1087-1096.

