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Autor(en): **Wever, Patrick de / O'Dougherty, Luis / Gorian, Špela**

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The plankton turnover at the Permo-Triassic boundary, emphasis on radiolarians

PATRICK DE WEVER[1], LUIS O'DOGHERTY[2] & ŠPELA GORIČAN[3]

Key words: Permian, Triassic, extinction, radiation, protists, Radiolaria
Mots clés: Permien, Trias, extinction, radiation, protoctistes, radiolaires

ABSTRACT

The examination of plankton biodiversity through Permian-Triassic period seems to display different patterns of evolution depending of the scale of study (taxonomy stratigraphy or biogeography). In this paper we present the state of the art of the plankton turnover at the Permo-Triassic and we review more precisely the pattern of extinction and recovery of radiolarians during such period, because at that time, plankton was essentially represented by radiolarians. At a global scale the end-Permian to early Triassic period is marked by several strong extinctions in the marine realm, and in the radiolarians they occur progressively as exemplified by two orders of radiolarians: Albaillelaria and Latentifistularia. Nevertheless, this period is marked by a tremendous post-crisis diversification in both at family and generic level, more than extinction; an actualized revision of the diversity at the family level is also offered in our review. At a moderate scale (i.e. genera and in a region) the modifications appear impressive while at specific and regional domain the message is not so clear, one can wonder if some crisis manifestation results from a taxonomic accident or from preservative conditions. In fact, strangely enough more the number of studies is, more the diversity is high, and oppositely less they are, more the provincialism is evoked.

RESUME

L'examen de la biodiversité du plancton au passage Permien-Trias semble montrer différents types de manifestation selon l'échelle d'observation aussi bien en terme de stratigraphie que de taxonomie ou de géographie. A cette époque, le plancton était surtout représenté par les radiolaires. A une échelle globale cette période est certes marquée par des extinctions mais elles sont progressives comme le prouvent les deux ordres de radiolaires: les *Albaillelaria* et des *Latentifistularia*. Néanmoins cette période est surtout marquée par une énorme diversification post-crise, plus encore que par l'extinction. A une échelle moyenne (ex. niveau générique et celui d'un pays) les renouvellements de faune semblent impressionnants, alors qu'à l'échelle des espèces et de bassins particuliers, on est conduit à se demander si des modifications résultent de réelles crises biologiques ou de problèmes de conservation. Il est amusant de constater que plus le nombre d'études est élevé, plus la diversité apparaît grande et à l'opposé, plus elles sont rares, plus le provincialisme est évoqué.

1. Introduction

Mesozoic deep-sea sedimentary rocks are widespread, the successions are relatively complete and little altered, and they have been sampled extensively. Undoubtedly, the appearance of evolutionary innovation among the plankton is enhanced by these circumstances, furthermore, many of the best preserved Paleozoic sedimentary rocks were deposited in shallow, epicontinental seaways where open-ocean plankton might not be present or abundant. The minute calcite plates of calcareous nannoplankton, delicate opaline silica tests (radiolarians) and frustules (diatoms) might well be destroyed in more highly altered sediments, and if early dinoflagellates lacked archeopyles, their affinities would not be recognizable. Nonetheless, the spectacular diversity changes recorded after the Permo-Triassic crisis within the sedimentary successions containing well-preserved fossils indicate that during the Early Mesozoic a genuine radiation of microplankton took place, one that included heterotrophic as well as photoautotrophic protists. Undoubtedly, the radiolarians are the most important and dominant group among the microplankton after the Permo-Triassic crisis. This is the reason why we analyse in this paper the changes that occurred in this group.

1.1 Bioevents concept and faunal turnover

The idea of global bioevents is under discussion since the very beginning of the science of Earth history. Georges Cuvier (1769–1832) already recognized that most intervals occurred in Earth history from time to time, each of them with a strong

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Correspondance: Patrick De Wever
[1] Muséum National d'Histoire Naturelle, 43 Rue Buffon, F-75005 Paris, France. Email: pdewever@mnhn.fr
[2] Facultad de Ciencias del Mar, Universidad de Cádiz, 11510 Puerto Real, Spain. Email: lodogher@uca.es
[3] Paleontoloski Institut Ivana Rakovca ZRC SAZU, Novi trg 2, SI-1000 Ljubljana, Slovenia. Email: spela@zrc-sazu.si

Table 1. Effects of the main crisis of biodiversity on families and genera with indication of calculated species loss (simplified from Jablonski 1996)

	Families		**Genera**	
	Observed extinction (%)	**Calculated species loss (%)**	**Observed extinction (%)**	**Calculated species loss (%)**
End Ordovician	26	84	60	85
Late Devonian	22	79	57	83
End Permian	51	95	82	95
End Triassic	22	79	53	80
End Cretaceous	16	70	47	76

faunal turnover, later called catastrophe, extinction event, faunal change, bio-event, and so on. The concept of catastrophe seems somewhat exaggerate as described and emphasized later by d'Orbigny, but one should set this idea in its proper context: at that time the Earth was supposed to be approximately 6000 years old only.

Bioevents, often in connection with a significant change in lithology, were used by d'Orbigny and most scientists concerned in the first three quarters of the 19th century in order to subdivide the Phanerozoic. The result of these works is the stratigraphic scale. Nevertheless, three decades ago the fact of bio-event was disputed and even if these have now been accepted, the global synchronicity of the events has often been doubted, and the question as to causation has been discussed very controversially. If we still use the term catastrophism, we are not using it in its original meaning (Cuvier's definition), but accepting his valid observation of the existence of bioevents. According to the main phases these bioevents are named extinction-radiation or faunal turnover sequence.

1.2 Scale of time

Some supposed catastrophes were in fact only the result of a lack of record and they are no more considered as catastrophic events. One should also be aware of global *vs.* regional catastrophes. If the distinction is quite easy in theory, practically it is not so obvious, as it will be discussed later herein.

Biotic crises and events are sometimes distinguished. Differentiating from an event, a crisis spans a relatively long time interval. This is the case where over a relatively long period the extinction rate exceeds the origination rate. Crises do not only occur in times of long-term environmental changes or fluctuations, but also as a terminal phase of a taxon, when the diversity of a group of organisms decreases, sometimes towards to zero.

1.3 Crisis: at which taxonomic level?

Biodiversity changes in the paleontological record show that mass extinctions and recoveries occurred during some relatively short time intervals. These events are named and analysed as "evolutionary crises". When considering crisis one might discuss the taxonomic level involved, the message can vary according to the category. Plots of generic turnover should provide a better indication of morphological innovation than those of species, because genera are erected according to major features of morphology.

The problem of estimating the importance of extinctions and recovery depends upon the involved taxonomic level and the way the counting is conducted. Sepkoski's family and genus level (1989) summaries have allowed the species-level extinction intensities of the five major extinctions to be calculated (Table 1).

The fossil record of planktonic life has the advantage of abundant specimens, good stratigraphic control, closely spaced samples, and broad geographic distribution. The quality, however, varies substantially from group to group on the one hand, and is largely dependent on the desired stratigraphic level of precision on the other hand.

At a global scale, the Permian-Triassic boundary was characterized by the extinction of 50% of invertebrate families and 90% of invertebrate species; extinction of fusulinids, rugose and tabulate corals (orders), 2 orders of bryozoans, productids (order) and several orders of articulate brachiopods, trilobites (class), euryperids (orders), blastoids (sub-phylum) and several subclasses of attached echinoderms (mostly crinoids).

1.4 Estimation and counting: how variations can be illustrated

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, advantageous if the counting of taxa is done by one or several specialists with practice in the respective group and after a thorough taxonomic review.

1.5 Recovery

A study by David Jablonski (1996) shows that recovery from mass extinctions differs from one geographical region to another. Regions differ greatly from each other not only in terms of which and how quickly species diversified, but also in the ratio of surviving local species to foreign invaders. In general, Phanerozoic patterns of phytoplankton radiation and extinction parallel those documented for skeletonized marine invertebrates, both augmenting and constraining thought about evolution in the oceans. Plants and animals may be the most conspicuous fossils in Phanerozoic rocks, but planktonic protists are the most abundant.

Much of our ability to discriminate among various hypotheses explaining the evolutionary changes within geologic times not only depends on careful and detailed comparisons of evolutionary patterns, recognised in trophically, ecologically, reproductively, and developmentally different groups of organisms, but also is essential to know how the earth system climate drives the evolutionary process during critic periods of the past.

The time for recovery in the earliest Triassic was also highly variable depending on marine oxygen levels, like it has been recently shown (Twitchett et al. 2004). These authors observed a faster recovery in well-oxygenated environments (seamounts) after the P-T extinction in the middle Griesbachian. An apparent delay in recovery after the end-Permian extinction event was observed in deeper-marine settings due to widespread and prolonged benthic oxygen restriction.

2. The Permo-Triassic Setting: Scenario for a crisis

2.1 Environmental constraints

According to the classic Permian paleogeography, only one continent (Pangea) was present at that time and surrounded by only one super-ocean (Panthalassa). In this land-sea distribution, the concomitant drastic decrease of shelf surface added by the Carboniferous-Permian glaciation (Scheffler et al. 2003) resulted in a drastic dynamic change of the global ocean circulation (Fluteau et al. 2001).

An important event, occurring over a very brief span of geological time (initiated by 251.7 ± 0.4 Ma and terminated by 250.2 ± 0.3 Ma; Kamo et al. 2003) took place in this scenario: the Siberian flood volcanism. A comparatively extensive flood volcanism occurred somewhat earlier in China (Emeishan traps, about 259 ± 3 Ma old; Courtillot & Renne 2003). The large amount of volcanic gases played a primary role in the Permo-Triassic extinction (Wignall 2001) but the rapid and strong negative $\delta^{13}C$ excursion (c.a. 4–6‰), (Benton & Twitchett 2003) is too great to be explained solely by the catastrophic collapse of ocean primary productivity in the late Changxingian (Wang et al 1994; Hallam & Wignall 1997). In this scenario and an additional source of C^{12} to the ocean-atmosphere system is required, but the causes of the isotopic excursion seem to be complex and multiple (Korte et al. 2004). In this sense, the Siberian volcanism triggered an initial global warming at the P-Tr boundary, which in turn melted clathrate bodies, releasing a large input of methane into the atmosphere causing more warming (Heydary & Hassanzadeh 2003). The process continued in a positive feedback spiral that has been termed the 'runaway greenhouse' phenomenon (Benton & Twitchett 2003) leading to the most dramatic extinction known.

In this palaeogeographic reconstruction, the Late Permian was characterized by falling sea levels (Ross & Ross 1988) exposing large areas in the northern high latitudes. But superimposed on this longer trend a large-scale transgressions is record in China, Iran, western Tethys, and in central Europe. This transgression became even more pronounced in the latest Permian (Wignall et al. 1998), just before the Permo-Triassic transition, and reached its maximum in the Early Triassic, with flooding of many areas of the Tethys and North America. In fact the Permo-Triassic boundary interval was a time of second order highstand of sea-level. This reinforces the fact that the end-Permian mass extinction cannot, in any regard, be considered as the product of sea-level fall (Hallam & Wignall 1999). Increasing values of $^{87}Sr/^{86}Sr$ since the latest Permian-Early Triassic time (Korte et al. 2003) are related to enhanced continental weathering under humid climatic conditions in the latest Permian and the lack of a dense land vegetation in the Early Triassic, prior to the Spathian, which are in agreement with the observed sea-level trend. A consequence of this flooding was the spread of anoxic bottom waters into the shallow marine habitat during the early stages of transgression, which in turn may have played an important role during the aftermath of the P-Tr extinction event (Hallam 1989).

In order to establish the duration of the Permo-Triassic extinction several attempts were made and estimates for the duration of the extinction vary according to different inclinations in fixing relevance to particular fossil groups or sampling locations. Holser & Magaritz (1992) suggest a duration of 5–10 Ma for the crisis, whereas Hallam & Wignall (1997) prefer a rapid but not instantaneous mass extinction, although unfavourable climatic and environmental conditions prevailed during most of Early Triassic (Wignall & Hallam 1992; Bottjer et al. 1996). Radiometric ages point to a duration of 0.7–0.3 Ma for the extinction interval, or at least for the interval between the $\delta^{13}C$ decline and the P-Tr boundary (Bowring et al. 1998). Other studies using estimates of sedimentation rates suggest more rapid rates of ecosystem collapse, about 10–30 kyr for marine extinctions (Twitchett et al. 2001; Rampino & Alder 1998). However, analysis of terrestrial flora (Looy et al. 2001) gives a different picture. The time lag between terrestrial ecosystem collapse and plant extinction had a duration of 0.5–0.6 million years, showing also a temporary diversity increase after the negative $\delta^{13}C$ excursion.

2.2 For various groups: real extinctions or incompleteness of the fossil record?

Early Mesozoic radiating protists include taxa characterized by both siliceous and calcareous skeletons, as well as unmineralized groups. Possibly the break up of continents and the partitioning of the world's oceans, including strengthened circulation and upwelling of nutrients, contributed to the ecologic opportunities for diversification of planktonic organisms. After the Permian crisis during the Mesozoic, planktonic protists underwent remarkable evolutionary innovations and radiations.

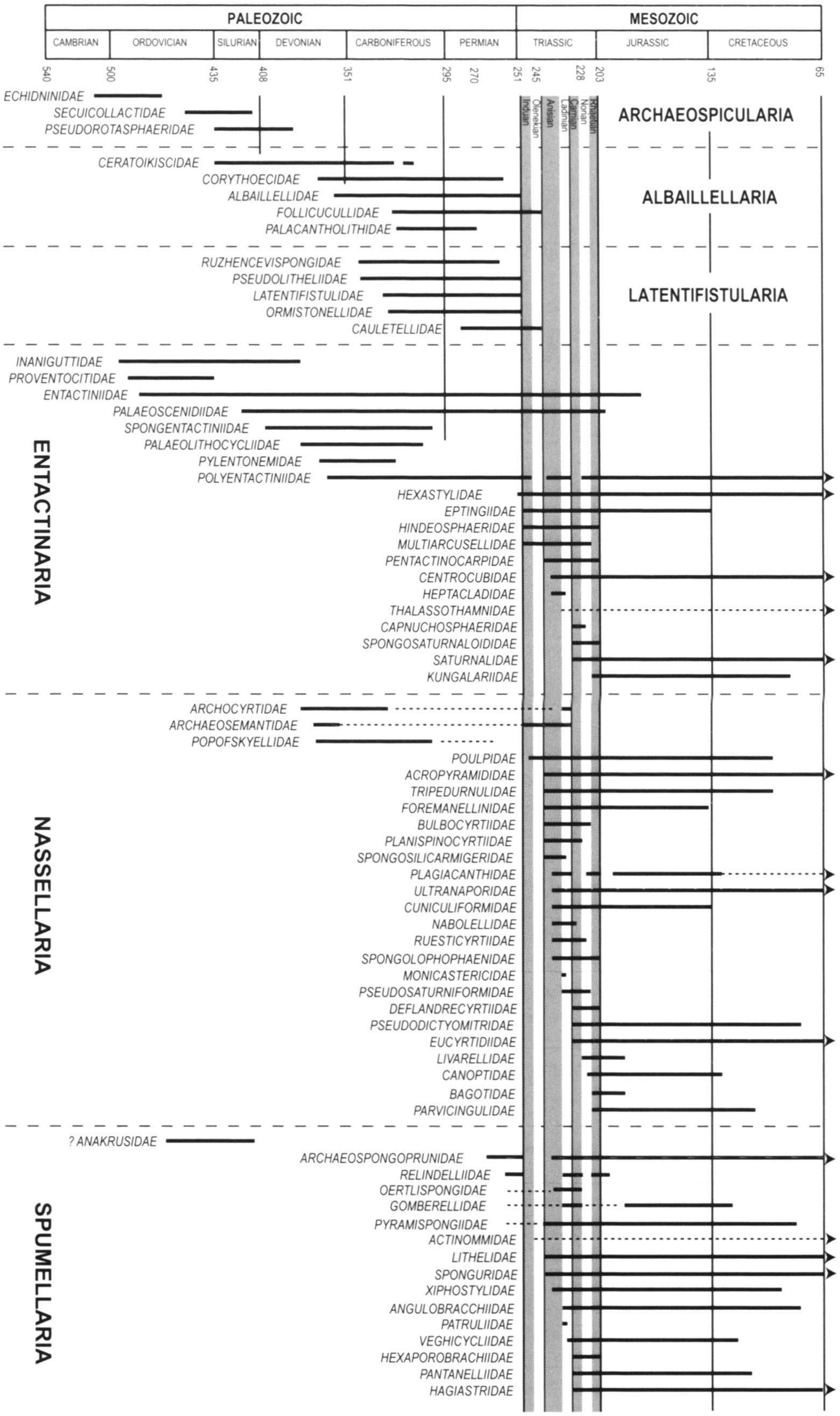

Fig. 1. Stratigraphic ranges of radiolarian families through time (Redrawn from De Wever et al. 2001).

Radiolarians, dinoflagellates, calcareous nannoplankton, diatoms, silicoflagellates, and planktonic foraminifers either appeared and radiated for the first time, or diversified from preexisting forms into a greater variety of new types. The causes of the early Mesozoic plankton revolution remain uncertain; probably they are as complex as the factors that promoted the radiation of skeleton metazoans and protists at the beginning of the Paleozoic. The fluctuations of diversity in planktonic protists have been suggested many times to be a function of variations in primary productivity and heterogeneity of water masses. During intervals of strong heterogeneity of water masses and high productivity, the oceans can support many specialized species that live effectively, at least for a part of their life-cycles, within a narrow range of environments. When productivity drops and oceanic water masses become less structured and more homogeneous, narrowly adapted species disappear. Obviously, as it has been shown by paleontology, petrography and geochemistry, the oceans' physical structure provides opportunities for plankton speciation and the biologic inter-actions of constituent populations. Unfortunately, such biologic interactions are not understood, even for living plankton, and so explanations concentrate on types of oceanographic changes that are known to correlate with stratigraphic changes in diversity.

The fossil record indicates that recovery of ecosystems affected by the crisis needs about 5 Ma (Bottjer et al. 1996; Schubert & Bottjer 1995), which seems to be achieved during Anisian time (Gall et al. 1998). The apparently low recovery together with the poor quality of the fossil record characterizing the interval aftermath the P-Tr extinction modifies the perception of the magnitude of the end-Permian extinction, as well as, it masks the paths undergone by the recovery. These particular patterns have led to explain the recovery in terms of recolonization of damaged Early Triassic environments by the so-called "Lazarus taxa", that is, super-specialized taxa that migrate to "unknown" refuges during extinction periods and that reappear "unchanged" after millions of years when adequate environmental conditions are re-established. One may wonder if it is just the simple variation in the quality of fossil record which masks our perception of the extinction event magnitude and hides devlopments during the recovery phase.

According to Twittchett (2001) the incompleteness of the fossil record in the Early Triassic was caused by a sharp decrease in productivity at the end of the Permian. The drop of productivity during the crisis in turn lead to a reduction of the biomass, which must be readjusted by decrease in abundance (but retaining body size) or decrease in body size (but with similar population size). Those forms that reduce their population sizes play a "Lazarus role" giving an apparent extinction, because they reduce in number so much that they are below paleontological detection levels (Wignall & Benton 1999). Only when the primary productivity returns to pre-crisis normal levels, Lazarus taxa seem to "reappear". Obviously, those taxa that reduce their body size, but retain or even increase their population size would be the best candidates to become fossilized. In this sense the picture displayed by the fossil record is biased. We will show later how this mechanism is illustrated in the radiolarian record at the Permo-Triassic crisis.

Among Paleozoic 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. We therefore focus hereafter on radiolarians, undoubtedly the dominant plankton fossils in the Paleozoic and Triassic oceans. They first occurred in the Cambrian (Won & Below 1999) and became morphologically complex through time (like Foraminifera) with the number of species increasing significantly in the Ordovician and Devonian.

3. The radiolarian record

3.1 Diversity of radiolarian families at a global scale

Some evaluation of biodiversity for the Phanerozoic was attempted several years ago for all fossil groups at the family level and these included radiolarians (Benton 1993). This tentative analysis, however, does not present a correct image of the radiolarian world: only 35 families are referred to the whole geologic period whereas more than 130 are known (De Wever et al. 2001, 2003). Some analyses were also done at the Permo-Triassic (Erwin 1993; Yao & Kuwahara 1997; Kozur 1998) but these curves also show contradictory results. In order to give a realistic picture we present herein curves of radiolarian diversity following the recent work of De Wever et al. (2001) who have homogenised the taxonomic criteria used for the Paleozoic, Mesozoic and Cenozoic, and updated the stratigraphic ranges for all families known. At a global scale (Figs. 1, 2), rapid changes in the biodiversity of radiolarian assemblages appear to be fairly rare throughout the geological record except during the Early to Middle Triassic, after the major mass extinction event which occurred at the Permian/Triassic boundary. During this time interval of nearly 20 Ma a large number of families occurred for the first time (Fig. 2).

Among the six radiolarian orders occurring in Paleozoic-Mesozoic deposits (Fig. 1), three were more or less extinct at the Late Paleozoic crisis (Albaillellaria, Archaeospicularia and Latentefistularia). Only one order clearly crossed the event (Entactinaria), and two (Nassellaria, Spumellaria) sporadicaly occured before, but clearly diversified after the crisis.

Representatives of the **Archaeospicularia** are the oldest radiolarian order and the only one that clearly became extinct before the Permo-Triassic crisis. The **Entactinaria** had a continuous and regular diversification during the Paleozoic, and crossed the Permian/Triassic boundary to be rather common and diversified in the Mesozoic.

Evolution within the **Albaillellaria** seems to have been continuous and regular during the Paleozoic. During the Carboniferous and the Permian, the Albaillellidae underwent a great and biostratigraphically important diversification. In the Late Carboniferous, simplifications of the internal spicule gave

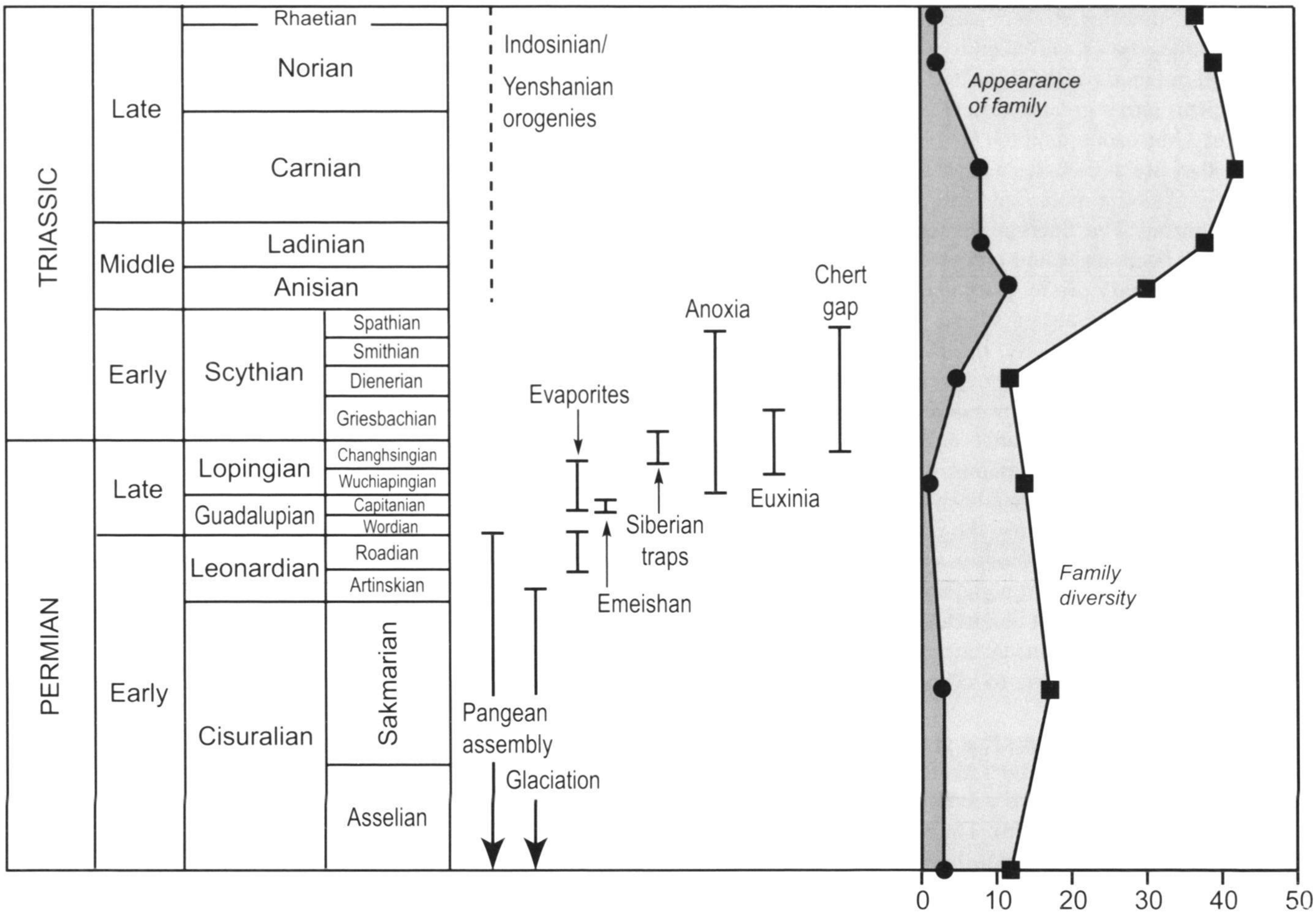

Fig. 2. Radiolarian diversity at the family level facing the main events of the Permo-Triassic boundary. The number of appearance of new families clearly corresponds to the periods of main stresses; modified after Kidder & Worsley (2004).

rise to the last Albaillellaria (Follicucullidae and Palacantholitidae). During the Late Permian the evolution of some albaillellarians underwent two different directions: one was to build a complex shell (*Neoalbaillella*), the other was to simplify this shell (*Follicucullus*); only the latter crossed the boundary (Bragin 1991; Sugiyama 1992, 1997; Yao & Kuwahara 1997). It is known that under environmental stresses, some radiolarian species seem to be able to adopt a regressive/primitive character. Often this process happens along with a reduction or even loss of skeleton (Guex 1981, 2001; De Wever et al. 2003).

The evolution of **Nassellaria** was very slow during the Late Paleozoic and they practically disappeared during the Permian so that one can say that the main nassellarian groups appeared during the Triassic. The oldest Triassic nassellarians are morphologically similar and possibly related to Paleozoic Archaeosemantidae.

The Permian is not marked by the appearance of new orders of radiolarians, although some representatives of probable spumellarians occur together with the last Latentifistularia (Cauletellidae). Some representatives of Latentifistularia (*Ishigaum* and *Cauletella*, *cf.* Takemura et al. 2003) seem to cross the P/T crisis, and then the order became extinct in the Early Triassic. The presence of Spumellaria in the Paleozoic is still uncertain; in fact, many of the Paleozoic spherical radiolarians, previously considered to be Spumellaria contain the remains of an inner spicule, indicative of Entactinaria (De Wever et al. 2001). Since their identification depends on the study of the innermost skeleton, and in most cases this 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 general morphology. One could consider, for example, that they are represented by some many-layered spongy skeletons occurring in the Permian assigned to the Relindellidae and Archaeospongoprunidae. Nevertheless, studies in Oregon and South China (Blome & Reed 1992; Shang et al. 2001) show that true spumellarians (Pantanelliidae-like forms) seem to be already present before the P/T boundary. More recently some representative of several families were reported from uppermost Permian from China (Feng et al. in progress); they are respectively Pyramispongidae

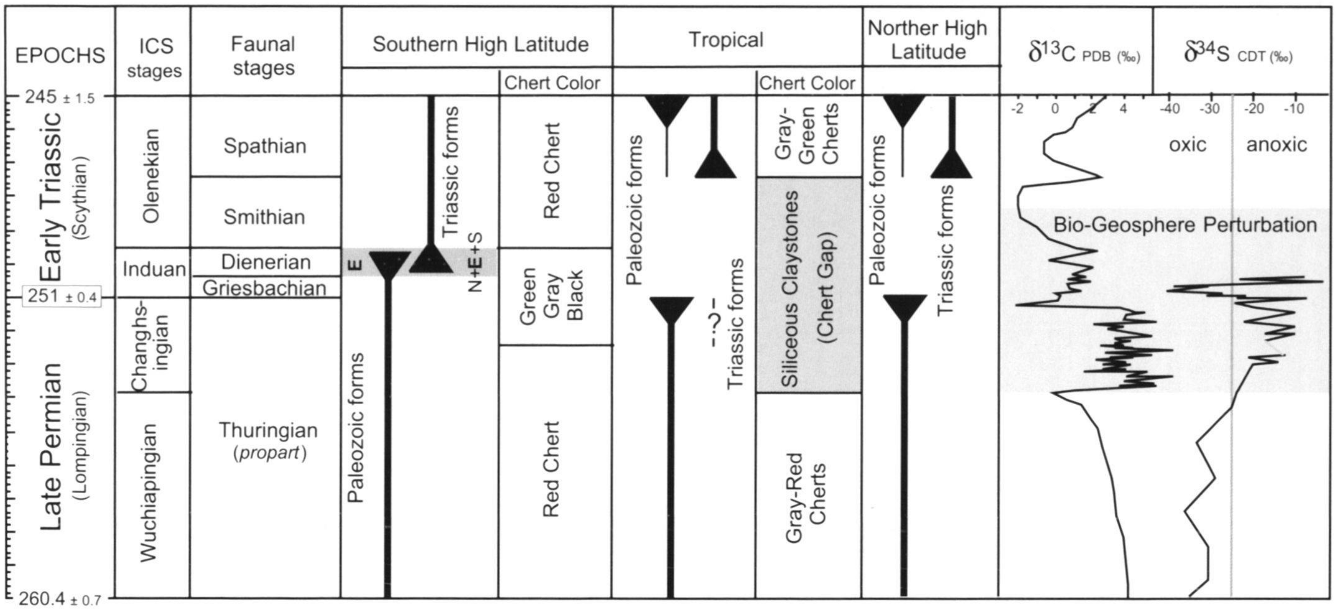

Fig. 3. Stratigraphy of events according to their geographic (latitudinal) position. It points out the lack of information for the critical levels; Carbon isotopes from Benton & Twitchett (2003) and Atudorei (1998), Sulfur isotope from Kato et al. (2002).

(*Tetrapaurinella, Paurinella*), Gomberellidae (*Tamonella*) and Oertlispongidae (*Paraoertlispongus*). Since these genera extent upward, but have not been yet mentioned in the Lower Triassic, they are considered as Lazarus taxa by these authors.

According to the data reviewed above, no new orders of radiolarians appeared after the Permian-Triassic crisis. The only exception might be Nassellaria, if we consider that Mesozoic nassellarians are not direct descendants of Paleozoic representatives, all of which disappeared by the end of the Carboniferous. The existing lineages of radiolarians, nevertheless, produced an impressive number of new morphotypes grouped into new families. Of the 14 families known in the Permian, 9 continued to exist in the Mesozoic and among the 55 families known in the Triassic, 25 appeared during the Early and Middle Triassic. The Middle Triassic was undoubtedly the main epoch for radiolarian radiation; more than a third of the total number of radiolarian families, recognized from the Cambrian to the Present originated during this important period of plankton radiation (Figs. 1, 2).

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 ocean modelling, and induced up-welling of nutrients (De Wever et al. 1994). It is known that during the Early Mesozoic, modern oceanic basins began to form (Neotethys spreading) and new oceanic current systems appeared. Numerous microplates began their separation in the Tethys Ocean, creating new seaways in the western Tethys and modifying oceanic circulation. (De Wever & Baudin 1996).

In the aftermath of the mass extinction, when the last representatives of the orders Albaillellaria and Latentifistularia completely disappeared, with the exception of some genera: *Follicucullus, Ishigaum, Cauletella* which are mentioned till the Early Triassic, (Sugiyama 1997; Takemura et al. 2002), the Early Triassic faunas were characterized by extremely low diversity and poor preservation (Hori et al. 2003; Sashida 1983, 1991; Sugiyama 1992, 1997; Suzuki et al. 2002). These faunas mostly contain entactinarians (*Cryptostephanidium, Entactinia, Hegleria, Parentactinia, Pseudostylosphaera, Tiborella*), some sparse mono- and dicyrtid nassellarians (*Archaeosemantis, Hozmadia, Poulpus, Spongosilicarmiger?*), and rare spumellarians with inner spicule (*Glomeropyle, Plafkerium?*). In addition to this extremely low diversity, the poor preservation and the scarcity of good outcrops, limit the information that is now available about Early Triassic faunas (Fig. 3). Furthermore, we stress the importance played by the apparent abrupt disappearance of radiolarian cherts that were common in the deep-marine sections of South China, Japan, and Western Canada in the Late Permian (Fig. 4). They reappeared only in the Spathian after a "chert gap" of 7 to 8 Ma (Isozaki 1994; Kakuwa 1996). This is, in part, the reason why the abrupt change in radiolarians is amplified after this long period of instability. For the reasons mentioned above the current information available for the radiolarians during the Early Triassic should be considered quite incomplete and the evolutionary pattern undergone by the group at this interval remains poorly known.

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. For example, the extinction of radiolarians between the

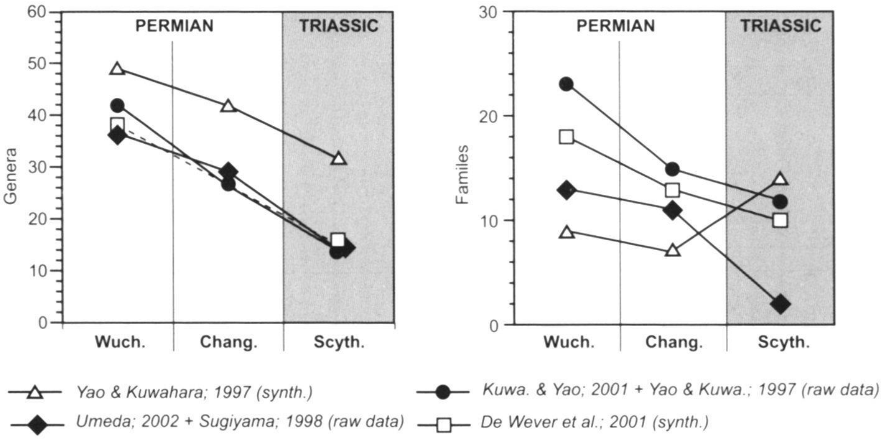

Fig. 4. Numbers of quoted families and genera near the Permian-Triassic Boundary according to several authors, and from raw data (Umeda 2002 + Sugiyama 1997 and Kuwahara & Yao 2001 + Yao & Kuwahara 1997) and from synthetic data (Yao & Kuwahara 1997 and De Wever et al. 2003). For genera all curves follow the same trend, they decrease from Wuchiapingian to Scythian. For families appears a discrepancy between curves. In fact information from Yao & Kuwahara (1997) have been complied but not previously homogenised. Data treatment influences the conclusions.

Permian and Triassic (Fig. 1) seems to have been a slow progressive and important phenomenon. But, the most distinctive feature for this event is not the diminishing number of taxa at both family and generic levels near the P/T boundary, but rather an important diversification that followed it, during the Triassic: nine families cross the P/T boundary (six of these Paleozoic families became extinct by the end of the Triassic) and 45 new families originated during the Triassic; in other words the fauna is almost completely renewed. The Figure 4 displays a similar tendency between family and generic curves, but a reverse tendency is observed in the data from Yao & Kuwahara (1997). The differences can be explained because the supra-generic assignments into families followed by these authors is different from that we have used for our curves (De Wever et al. 2001). Like it was mentioned in the foreword of this article, Figure 4 well-displays how the biodiversity (especially at family level) is strongly biased by the taxonomy employed in the analysis of faunal turnovers. Irrespective to this correlation, the Middle Triassic is a period of unprecedented blooming and accelerated evolution of Entactinaria, Nassellaria and Spumellaria (Fig. 1). This figure clearly shows that Entactinaria represent the most numerous radiolarian group that survived both, the P/T boundary and the Early Triassic crisis, however, the nassellarians represent the group with the most rapid evolution and diversification during the Triassic and later. This fact well illustrates how the nassellarians display a powerful recovery during post-extinction periods as has been signalled for the Mesozoic time (O'Dogherty & Guex 2002) Since the Anisian the entactinarians, nassellarians and spumellarians diversified simultaneously resulting in new families that will become the base for the spectacular radiation at generic and species level.

Usually under anoxic environments radiolarian diversity minima occur simultaneously with the $\delta^{13}C$ positive excursion (O'Dogherty & Guex 2002). During the Changxingian a minor positive peak is concomitant with the end Permian extinction (cf. Holser et al. 1991), but just before the Permo-Triassic boundary a conspicuous negative carbon isotopes excursion (5–6‰) is recorded (Hallam & Wignall 1997; Benton & Twitchett 2003; Korte et al. 2004). The available data for the diversity at generic or family level are insufficient to correlate to the carbon isotope curve. We can only observe that extinction (and the drop on diversity) at family or generic level during the end-Permian (cf. Fig. 3) seems to be linked with decreasing values of $\delta^{13}C$. But, it seems obvious that any interpretation of the $\delta^{13}C$ signal without taking into account other geoindicators and a detailed correlation has actually not much paleobiological significance.

3.2 P-T radiolarian diversity at a detailed scale

Available data

Only 21 years of investigation covers all our information on Early Triassic radiolarians; a rather moderate period of research, and with still few data. Table 2 reports the available taxonomic data for the Early Triassic: 19 papers from the circum-Pacific region and only 12 papers from the Tethyan area (South China, Thailand and Turkey) (Fig. 5). It is also interesting to note that the majority of publications deal with Spathian radiolarians. The earliest Triassic (Griesbachian) radiolarians, on the other hand, are known from New Zealand only and were first described in 2002. The review clearly shows the weakness of our knowledge about the radiolarian stratigraphy during this phase of recovery, and the number of taxa identified at genera or species level is extremely low. It is now known how poor preservation can influence the apparent composition of the fauna (O'Dogherty et al. 2003). The small number of species illustrated or described by publication (Table 2) also strongly contributes to an unrealistic vision about the taxonomic re-organization and the radiation of radiolarians during the Early Triassic. This insufficiency of data, evidently, can be, in some cases, provisionally translated into a wrong interpretation about the paleobiogeography and phylogeny at both order and family levels.

All these papers report the presence of highly abundant

Table 2. Synthesis of published papers concerning Early Triassic radiolarians with respectively: Age, author(s), number of recorded genera/number of species and nov. sp. This table underlines how new study implies new taxa, as a result of the very poor knowledge of these fauna of that precise period.

Faunal stage	Author	Gen./Sp.	n.sp
Griesbachian	Takemura et al. 2002, 2003 (Waipapa, New Zealand)	5/?	
Dienerian	Kozur et al. 1996 (Karakaya, Turkey)	2/2	2
	Sashida et al. 1998 (Phatthalung, Thailand)	5/5	
	Feng et al. 2001 (Hunan, China)	2/2	
	Kamata et al. 2003 (Waipapa, New Zealand)	7/?	
Smithian	Blome & Reed 1992 (Oregon, USA)	4/4	
	Yao & Kuwahara 1997 (Inuyama, Japan)	4/7	
	Yao & Kuwahara 1999 (Ziyun,China)	2/2	
Spathian	Sashida 1983, 1991 (Kanto, Japan)	7/13	8
	Zhang et al 1999 (Nadanhada, China)		
	Bragin 1991 (Shikote Alin, North Eastern Russia)	4/4	
	Sashida & Igo 1992, Sashida et al. 1993 (Phatthalung, Thailand)	6/7	1/4
	Feng 1992 (Southwest China)		
	Feng & Liu 1993 (Yunnan, China)		
	Sugiyama 1992, 1997 (Gifu, Japan)	22/26	19
	Nagai & Mizutani 1993 (Gifu, Japan)	11/14	
	Kusunoki & Imoto 1996 (Kyoto, Japan)		
	Yao & Kuwahara 1997 (Inuyama, Japan)	7/17	
	Isogawa et al. 1998 (Ashio, Japan)	12(17)	60
	Kamata 1995, 1999 (Tochigi, Japan)	16/30	5
	Feng et al. 2000 (Yunnan, China)	12/27	
	Sashida et al. 2000 (Northern Thailand)	38/50	4
	Yao & Kuwahara 2000 (Guizhou,China)	11/14	
	Suzuki et al. 2002 (Ashio, Japan)	15/30	
	Hori et al. 2003 (Kaka Point, New Zealand)	7/15	3

Entactinaria along with rare Nassellaria and undeterminable Spumellaria. The Late Permian extinction undoubtedly played an important role in the evolutionary history of Radiolaria. A quasi-complete renovation took place during the aftermath of the Permian crisis at generic level (only a few genera belonging to 10 families), although at order level all the groups seems to cross the critical boundary (Fig. 1). It is interesting to note the presence of some radiolarians with Triassic affinities (i.e.: pantanelliids) in the uppermost Paleozoic strata (Shang et al. 2001), as well as some Paleozoic forms (Fig. 3) which have been recorded in the Early Triassic (Sugiyama 1992, 1997; Yao & Kuwahara 1997, 1999).

Discussion

Evoking a crisis requires precise definition of the involved level (taxonomic, geographic or stratigraphic) because a phenomenon may appear sharp at one scale but not at a different one. That is why at the family level and global scale radiolarians did not seem to be strongly affected by the Permo-Triassic crisis, but seems very sharp at specific level (i.e. 96% of species disappeared, *cf.* Kozur & Mostler 1982). Other authors (Suzuki et al. 2002) from a database of published data propose at least three distinct turnovers during the Early Triassic time, the most conspicuous turnover being that of the Late Olenekian-Anisian boundary (143 species disappearing and 118 new species appearing).

The small quantity of data is undoubtedly related to the scarcity of localities with a complete record for the Permo-Triassic boundary. As was mentioned earlier, the preservation of radiolarian faunas were so strongly affected by the end Permian environmental collapse that a conspicuous "radiolarite gap" has been described (Isozaki 1994, 1997; Kakuwa 1996) from the uppermost Permian (*Clarkina iranica* Zone of conodont) until the end of the lower Olenekian (top of the Smithian) lasting about 10 Ma. But recent investigations show that this gap, spread over the world, does not exist in high southern latitudes (New Zealand) where radiolarites have been recently described (Kamata et al. 2003; Takemura et al. 2002, 2003).

At the family level and global scale, we have seen that the number of radiolarian families was not affected (Figs. 1, 4). But, oppositely, radiolarian species (and genera) were strongly affected at low latitudes but not in high southern latitudes (Kozur 1998). This discrepancy has been interpreted by Kozur (op. cit) as a differential effect of extinction in southern high latitude with respect to low or northern latitudes due to a huge volcanic activity in northern hemisphere (Siberia and China). The long phase of recovery would be due to immigration from the southern high latitude cold water (less affected than those of high northern and low latitudes) rather than from tropical waters, which would be a faster process (Kozur 1998, Kozur et al. 1996). For this author, this process would be slow (c.a. 5 Ma; late Scythian to early Anisian) because it would require at first the adaptation of some elements of the cold water fauna to warm tropical conditions. In addition, the recovery of the radiolarians, for this author, started at the base of the Spathian where, however, not yet a distinct radiation of Triassic elements occurred but mainly Paleozoic (Late Devonian-Missis-

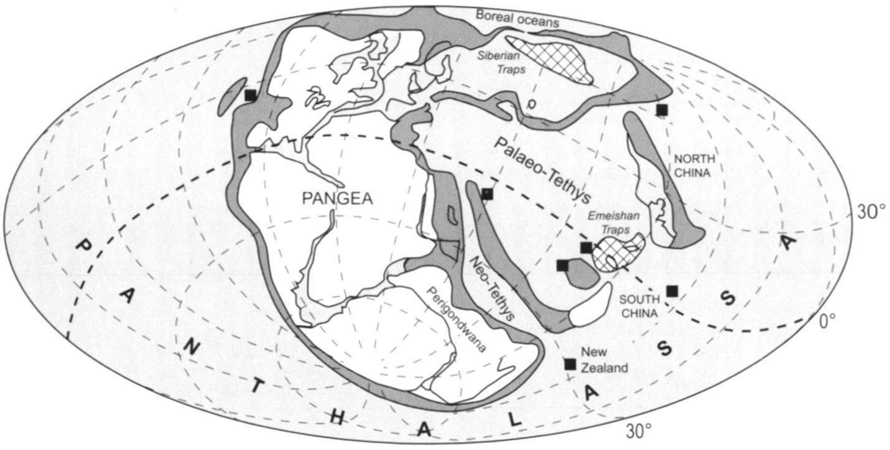

Fig. 5. Paleogeographic map for the Early Triassic (adapted from Hallam & Wignall (1997), displaying the heterogeneous distribution of studied sites for radiolarians. The number of publication for each region is as follow: Oregon: 1; Turkey: 1, Thailand: 4; S.China: 7; Japan: 13; NE Russia:1; New Zealand: 4.
It clearly reveal that besides tropical western Panthalassa almost nothing is known (only 1 locality for Oregon, Turkey, New Zealand and NE Russia). It is therefore difficult to have a representative scope of events which happens at that time. Note the type of projection (with a sigmoid equator) which seems to locate New Zealand close to south pole while it is at 30°S, as mentioned on figure.

sippian) "Lazarus taxa" reappeared from "unknown refuges", which are the origin for some phylogenetic connection at family or even at order level. The proposed "Lazarus recovery" is very big, about 50% of the genera that disappeared at the P/Tr boundary re-appeared only in the Olenekian-Middle Triassic interval. As shown here above, real data neither support nor contradict this interpretation, they are just insufficient at present time.

From a paleobiogeographic point of view, some paleolatitudinal differences were mentioned for Anisian radiolarians, where stratigraphic and taxonomic data are quite abundant and consistent (Bragin 1991; Sugiyama 1997; Kozur & Mostler 1994). In this sense, Aita & Bragin (1999) established the genus *Glomeropyle* for a large, thick-walled form occurring exclusively in high (south and north) latitudes, where other non-Tethyan species co-occur with well known Tethyan representatives (Hori et al. 2003). The same type of reconstruction using a compilation of the published data for the late Early Triassic (Olenekian) has been presented (Suzuki et al. 2002). These authors find a strong provinciality between the radiolarian faunas of the western Panthalassa and the eastern Tethys. Nevertheless, the non-homogeneous data used in the comparison (4 studies for the eastern Tethys against 14 papers for the western Panthalassa) and different stratigraphic levels led them to consider that radiolarian provinces were significantly distinct during late Olenekian because there is only a 5% of coincidence at specific level. Comparing the same data at a generic level rises up the coincidence to 50%. Such differences, in our opinion, probably derived from an inhomogeneous taxonomy (mostly open nomenclature assignations) in the utilised synthesis, partly at least due to the bad preservation recorded in this interval worldwide.

Alternative explanation

It is clear that the plankton response to the adverse environment of the Late Permian is complex and unfortunately badly documented. Forms with thin skeletons have not been preserved, being more fragile, so some may have appeared and evolved during this time of environmental crisis without any fossil record. The strong reduction of biomass at time of the crisis is undoubtedly related to the collapse of the primary productivity. In order to equilibrate the global biomass reduction, some strategies can be drawn (Fig. 6). Like in several groups (e.g. Foraminifera, Leven & Korgachin 2001) radiolarians may strongly decrease their population but maintain their body size, as it is the case of some Paleozoic relict forms (some albaillellids belonging to the genus *Follicucullus*) that could be considered to be "Lazarus forms" (in the sense of scarce record due to a poor preservation rate). Also some forms that reduce the complexity of their skeleton by partial loss of the outer components (=proteromorphosis *sensu* Guex 2001), but moreover having a more delicate skeleton, are more susceptible to be dissolved, and therefore reinforce the Lazarus effect (i.e. Latentifistulidae). On the other hand, other forms reduce their body size under environmental stress by, i) reducing the size of the entire skeleton (as is the case of large spherical spumellarian-type forms of the late Permian (Shimizu et al. 2004), or ii) by losing the external skeleton (proteromorphosis, i.e. Entactinaria forms); the population size being not necessarily reduced. It seems likely that many spicular forms belonging to entactinids in the earliest Triassic in the aftermath of the crisis are the result of a severe loss of the outer skeleton. This simple and economic architecture is a potential source for new phylogenetic developments and would explain also the sudden appearance of so many new groups (families, genera and species) since the beginning of the Middle Triassic when the preservation of radiolarian skeletons improved dramatically. The strong diversification also coincides with the rising values of strontium isotope ratios (Korte et al 2003), interpreted as the consequence of Early Triassic sea level rise and the return to normal geo-biosphere conditions.

It is interesting to note that in spite of the low diversity assemblages displayed in the earliest Triassic, all the information available shows a clear domination by Entactinaria, with many spicular forms, some Spumellaria and mono- or dicyrtid Nas-

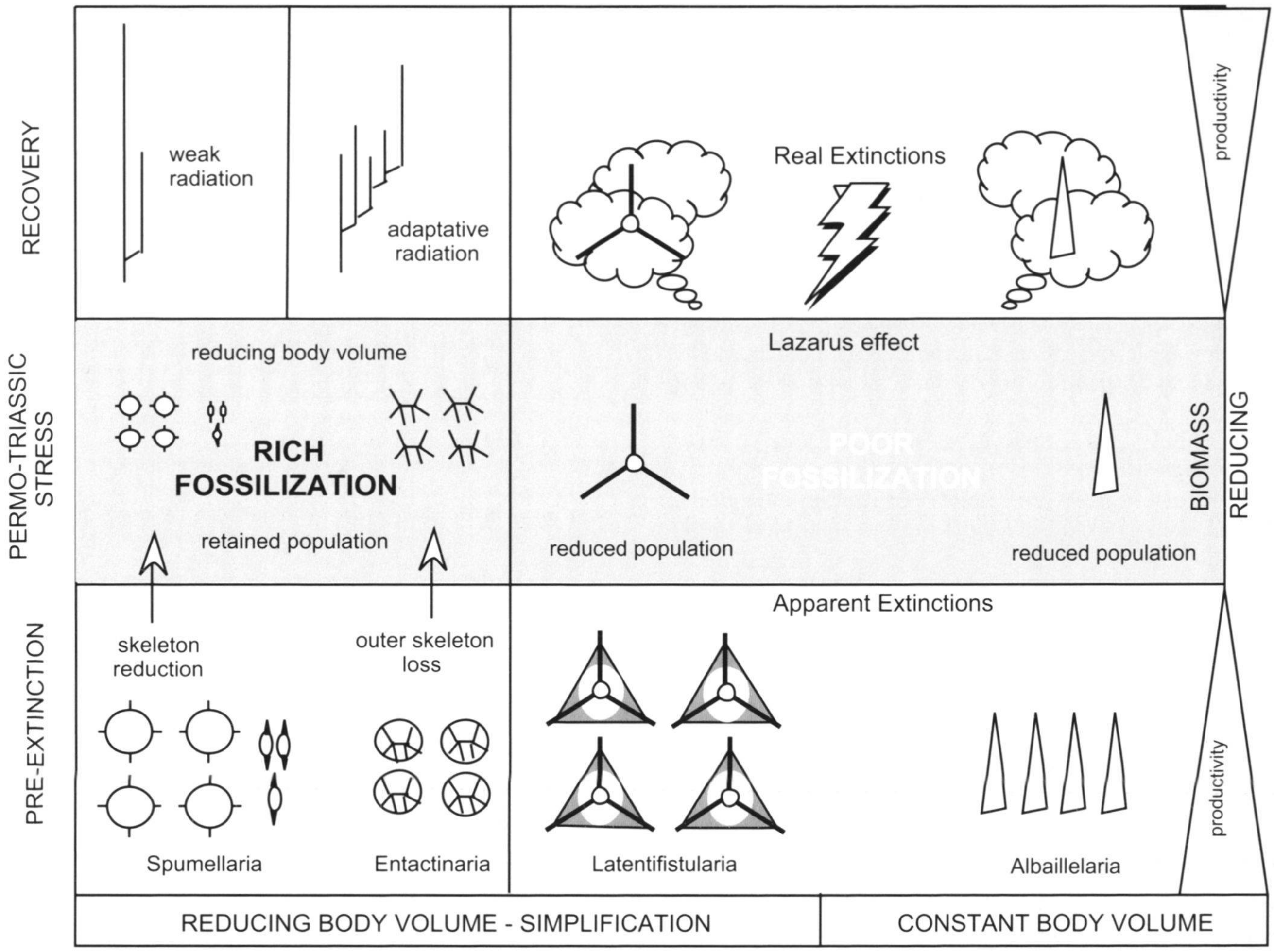

Fig. 6. Stress effects on radiolarian populations (see explanation in text)

sellaria. Multicycrtid Nassellaria do not occur before the Anisian. These shapes fit perfectly with the ability of some species to adopt a regressive/primitive character such as spicular forms and monocyrtids (De Wever 1982, De Wever et al. 2003).

All the data available today show that the picture we have for Early Triassic radiolarian fauna is very far from being complete. We agree with Wignall & Benton (1999) who emphasize that the abundance of Lazarus taxa (largely favoured by Kozur 1998, in the aftermath of the Late Permian extinctions is most probably the reflection of the extreme rarity of these organisms at this time, as well as, the incompleteness of the stratigraphic record (radiolaritic gap) and its poor preservation.

Final consideration

The low diversity displayed by the currently available data reflects the poor quantity of the pelagic fossil record at the Early Triassic, and can be due to the extremely low abundances of planktonic fauna (basically radiolarians) but it could also be a result of exceptionally poor preservation. Both phenomena are undoubtedly connected. For this reason, the apparent faunal dissimilarity displayed between some local studies, actually can not be considered as a solid argument for discussing an early and high provincialism because it would lead to an unrealistic paleobiogeography model for the group at Early Triassic time. A supplementary problem is that larger the interval lacking data is, smaller the probability is to illustrate the origin of the phylogenetic lineages. Indeed, the main period of diversification (Spathian) corresponds to the period for which the number of publications is the highest (2 for Griensbachian, 4 for the Dienerian, 2 for Smithian and 17 for Spathian). This coincidence reminds that of Sheehan (1977) who showed that the highest specific diversity of Phanerozoic marine invertebrate per Ma corresponds to the largest areal exposure of rocks of a given age.

4. Conclusion

We can summarize that the biodiversity of radiolarian families increased constantly throughout the Paleozoic and decreased only slightly towards the end of the Permian. While during the Late Paleozoic time primitive nassellarians appeared, with their characteristic internal spicules, and with skeletons still having some entactinarian characteristics, Spumellaria seem to have appeared only during the latest Permian. 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. The most distinctive feature for the Permian-Triassic event is, not the diminishing number of taxa, but also the especially important diversification that followed it, during the Triassic especially at family level.

Bad record, scarcity of complete outcrops, preservational problems related to silica dissolution or remobilization during diagenesis, and the extremely low diversity "observed" after the P-T boundary extinction, limit our actual knowledge on radiolarian radiation during the aftermath of the Permo-Triassic extinction. Even if some information is available (strong stress leading to diminishing diversity, more fragile or scarcer forms, etc;) the number of data remains too few to be representative and significant, therefore hypotheses are possible, but they should be considered as somewhat speculative guess.

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