# Rates and pattern of evolution among Cretaceous radiolarians: relations with global paleoceanographic events

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**ABSTRACT:** We present a new approach for analyzing the turnover rates of Cretaceous radiolarians recorded in pelagic sequences of western Tethys. The analysis of major extinction-radiation events and the fluctuation of diversity are compared with major paleoceanographic events and variation of diversity in dinoflagellates, calcareous nannoplankton and ammonites. There is an extraordinary correlation between biotic changes and sea level changes, temperatures, O, C and Sr isotopes, phosphorus accumulation rates and anoxic episodes. This reveals a predominantly abiotic control on the evolution of radiolarians. The rate of turnover and the diversity through time of two major orders of radiolarians (nassellarians and spumellarians) exhibits (1) the quasi-parallelism of their diversity curves, excluding a direct competition between them, (2) greater resistance of spumellarians to extinction during the early stage of extinction intervals and (3) a stronger post-extinction recovery of nassellarians. Evolutionary rates of radiolarians can be a good means of monitoring global environmental changes and allowing us to understand more clearly the relationship between plankton evolution, climate and paleoceanographic processes.

## INTRODUCTION

Several recent textbooks are devoted to the study of problems related to extinctions (e.g. Chaloner and Hallam 1994; Larwood 1988; Donovan 1989; Kauffman and Walliser 1990; Lawton and May 1995; Hart 1996). Most authors who have worked on extinction and origination descriptions have studied the variations of those two parameters separately. Such approaches do not allow a precise discussion of the relationships between sub-contemporaneous extinctions and originations in the fossil record.

The aim of the present paper is twofold: firstly, we attempt to describe a new and different approach for analyzing the radiolarian faunal turnover rates discernible in the fossil record and, secondly, to analyze the paleobiologic and paleoceanographic reasons for such turnovers.

## DATA AND METHODS

The methodological approach followed is to make a quantitative study of the relationship between extinctions and originations occurring within the shortest biochronological intervals defined by concurrent ranges within very precise biostratigraphic data sets (see Guex 1991 and below). Our method allows us to make a distinction between extinction and diversity minima, which are generally used to define extinction events in the recent literature. We will demonstrate that Cretaceous radiolarian extinction events precede the diversity minima peaks during major crisis periods.

The data analyzed here cover the stratigraphic distribution of Tithonian to Turonian radiolarians in western Tethys, a time interval of about 50 My. These data have been published in two very detailed monographs concerning the Tithonian to Barremian (Jud 1994) and Aptian to Turonian (O'Dogherty 1994) intervals. More than 430 radiolarian species are described in these monographs and the two biostratigraphic data sets have been merged in the present paper with minor revisions to homogenize the taxonomy around the stratigraphic interval where the two studies overlap.

Two complementary zonations (Tithonian-Barremian by Jud 1994 and Aptian-Turonian by O'Dogherty 1994) were established from these data by means of Unitary Associations (UAs; Guex 1991) and using the BioGraph computer program (Savary and Guex 1991) which allows us to construct the UAs. This method is well-known to radiolarian specialists thanks to the work of Baumgartner (1984), Baumgartner et al. (1995), Gorican (1994), O'Dogherty (1994), Jud (1994), Carter (1993), Carter et al. (1998) and has also been used to construct biochronological scales in micromammals (Martinez and Guex 1996), dinoflagellates (Edwards and Guex 1996), nannoplankton (Boulard 1993), and ammonites (Dommergues and Meister 1987).

This biochronological method is designed to construct a sequence of inter-species coexistence intervals of shortest duration. All such intervals are strictly distinct from each other and the sequence itself is used as a biochronological referential to assign relative ages to the fossiliferous stratigraphic levels (see Guex 1991 for more theoretical details).

A synthesis of our biochronological results is presented in text-figure 1. The range chart consists of 53 Unitary Associations, which are calibrated to the standard geological time scale and stages on the basis of works of Jud (1994) and O'Dogherty (1994).

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# *Mendacastrum* n. gen. and *Domuzdagia* n. gen., two Jurassic spherical Spumellaria (Radiolaria) with hagiastrid medullary shell

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**ABSTRACT:** Two new spumellarian radiolarian genera, *Mendacastrum* and *Domuzdagia*, are described from the lower Tithonian and lower Pliensbachian respectively. Both have a spherical cortical shell of actinommid type and a spherical or subspherical double medullary shell with the inner medullary shell of hagiastrid s.l. type. The inner medullary shell of *Mendacastrum* is of dactyliosphaerid or higumastrid s. str. type, whereas that of *Domuzdagia* is of angulobracchiid type. Since they cannot be assigned to any described Mesozoic pylonioccan families, they are considered as type genera of two new families: Mendacastridae and Domuzdagiidae respectively.

## INTRODUCTION

In a series of contributions, the senior author has insisted upon the fact that the natural systematics of spumellarian and entactinarian Radiolaria at the generic and suprageneric level must be based primarily upon the structure of the innermost skeleton; this skeleton is built first and is the most conservative. The new Jurassic genera, *Mendacastrum* and *Domuzdagia*, described in the present paper are good examples of this premise.

The genus *Mendacastrum* n. gen. comes from a rich sample (Mue 22) collected by the junior author from a lower Tithonian cherty limestone of the Mühlheim Member of the Mörnsheim Formation (*Hybonoticeras hybonotum* Zone of ammonites) outcropping in the old Schaudiberg quarry. The quarry is 1km south of Mühlheim, a small village about 4km south of the town of Solnhofen, southern Germany (text-fig. 1) (Zügel 1997, Dumitrica and Zügel 1998). The sample was taken from the topmost 5cm of a partly silicified limestone bed 28cm thick, about 2m above the base of the Mühlheim Member. The limestone bed is distinctly laminated and contains coarse debris with abundant sponge spicules at its base. Radiolarians are restricted to three levels of this bed, each one about 2cm thick. Silicification is strongest in the radiolarian-bearing levels, but still allows isolation of radiolarian tests by using hydrochloric acid.

The radiolarian fauna is very well preserved at this level and contains about 500-600 species, most of them new. It is a peculiar fauna that contains many radiolarian species and genera unknown until present in the Tithonian faunas of Tethys. By its character it is a low or middle latitude fauna lacking *Parvicingula* Pessagno, but containing also very rare *Ristola* Pessagno and Whalen and pantanelliids. The most abundant radiolarians are spumellarians (*Triactoma* and groups of species related to it, diverse spherical forms, and hagiastrids) and several tens of entactinarian genera; nassellarians are relatively rare.

The genus *Mendacastrum* n. gen. is one of the most frequent spumellarians. Externally, or at least superficially, it could be considered an actinommid having three concentric shells: a cortical shell with three-bladed or needle-shaped main spines and by-spines, and a double medullary shell, both connected by a large number of radial bars, some aligned with the main spines. However, if we look in detail and from different positions at the innermost medullary shell we see that it is not spherical, as is the case of most Actinommidae, but flat in lateral view and square in axial view (pl. 1-4). More detailed examination of the shell proves that it represents the first system of girdles of a hagiastrid test consisting of a typical microsphere, or first girdle, with two opposite four-pillared cupolas and four primary beams in the equatorial plane (pl. 1, figs. 1, 4); a cross-shaped second girdle built in horizontal and vertical planes in the directions of the four primary beams (pl. 1, fig. 2); and a third girdle built in the equatorial plane (pl. 1, fig. 3). This construction leaves four gates or large pores (G) on either face of the first system (pl. 1, fig. 3). In this genus the four gates are partly obscured by a less regular construction representing the first girdle of the second system.

The genus *Domuzdagia* n. gen. was found in the lower Pliensbachian sample 1662D collected by A. Poisson from the Domuz Dag Massif, Turkey, and partly studied by Pessagno and Poisson (1981) and De Wever (1981a, 1981b, 1982). The sample is from the lower member (Radiolaria limestones) of the Sögütlüdere Formation, an alternating sequence of 10-20cm thick limestones beds and 1-10cm thick marls. This member is overlain by the upper member (the Ayiburnu tepe limestones), a condensed "ammonitico rosso" facies whose oldest level is middle Domerian in age (*Margaritatus* Zone of ammonites) (Pessagno and Poisson 1981).

Sample 1662D contains an extremely diverse radiolarian fauna with several hundred species of which only a very small number were described in the papers mentioned above. The genus *Domuzdagia* is very rare, but very interesting by its structure

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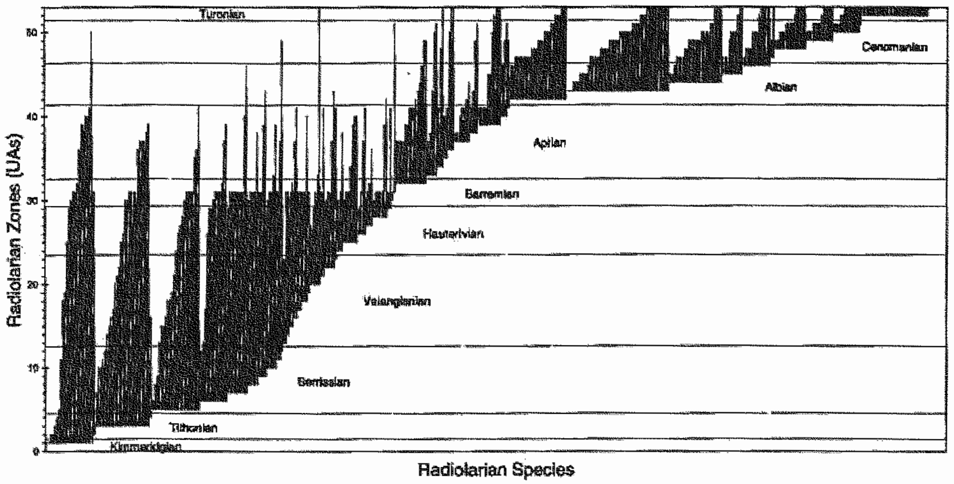


TEXT-FIGURE 1
Range chart showing the distribution of 431 radiolarian species in the Tithonian-Turonian of western Tethys. Output of the BioGraph computer program (Savary and Guex 1991).

**Faunal turnover rates in the western Tethyan Cretaceous**

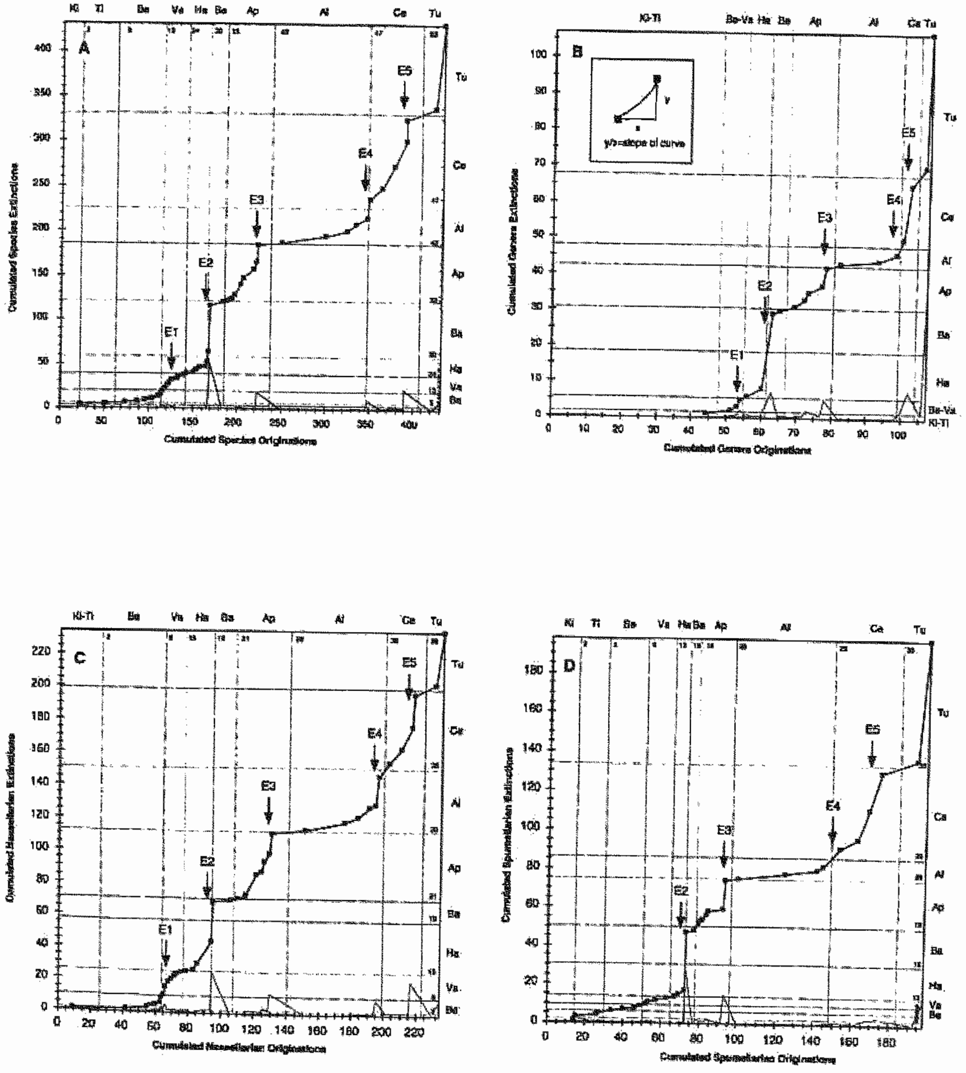
From the range chart (text-fig. 1) we construct a bivariate graph relating the number of species originating and disappearing in each UA. Such a graph expresses the variation in faunal turnover rates and the succession of high diversification phases (great cumulated number of appearances versus low number of disappearances) following high extinction phases (great cumulated number of disappearances versus low number of appearances) during the interval of time studied (text-fig. 2, redrawn from O'Dogherty et al. 1997). In text-figure 2 horizontal parts of the curve indicate high origination rates and the vertical parts indicate high extinction rates. In other words, our extinction events are identified by the steep parts of the curve and the diversification episodes are indicated by the flat parts of the curve.

Variations in the slope of the global curve are expressed by calculating the number of disappearances divided by the number of originations in each UA (see bottom of text-fig. 2A). These variations show peaks which correspond to extinction palliates in the original range chart; five major extinction events are recognized throughout the interval. For example, 52 extinctions and only one origination occur in UA 31: that extinction event (noted as E2 in text-fig. 2A) appears as a peak in the curve illustrated at the bottom of the curve (slope of the curve).

The beginning and the end of such a curve are biased by the fact that the base and the top of the original range chart only record truncated originations and disappearances, respectively. These parts of the curve must obviously be ignored. The curves illustrated here show five extinction events followed by diversification periods. These events are named E1 to E5 and will be discussed below (text-fig. 2). We note that the turnover curve made for radiolarian genera alone (text-fig. 2B) is almost identical to the general curve where all species are taken into consideration (text-fig. 2A). This implies great taxonomical homogeneity of the data used in the present paper, as well as a validation of the extinction amplitude not only at species but also at generic level.

Before proceeding we recall that radiolarians are classically subdivided into two main groups based on their growth pattern and initial spicules: nassellarians and spumellarians. Nassellarians consist of forms, which are generally conical-shaped with an egg-shaped central capsule, and a single pore located at one pole. Spumellarians are considered to be among the most primitive radiolarians (Dumitrica et al. 2000), and are generally spherical or multi-armed and possess a finely perforated spheroidal central capsule. To facilitate the evolutionary interpretation, we have calculated separately the sequences of UAs generated respectively by nassellarians (235 species) and by spumellarians (196 species). The calculation produces a sequence of 40 nassellarian UAs and a sequence of 34 spumellarians UAs (text-figs. 2C and 2D). (NB: the difference in the number of UAs is produced by the difference in the number of species; correlation amongst the three scales and former radiolarian zonations for the western Tethys is given in text-figure 3).

In order to analyze the fluctuation of radiolarian diversity during the radiation-extinction intervals we have also plotted variations of the slope of the global curve (i.e. ratio of number of disappearances to number of originations in each UA; see text-fig. 2A) against the temporal variation of the total diversity (number of species per UA) (text-fig. 4A). These parameters are plotted separately for the nassellarians and spumellarians (text-figs. 4B-4D).



TEXT-FIGURE 2
Bivariate plots showing the rates of radiolarian faunal turnover during the Tithonian-Turonian interval in western Tethys; extinction events are indicated (E1 to E5) and unitary associations defining stage boundaries are shown along the top of the figure, e.g. 2, 5, 13, etc. A) Total radiolarian species (redrawn from O'Dogherty et al. 1997). B) Radiolarian genera only. C) Nassellarian species only. D) Spumellarian species only. Box at top left of text-figure 2B: the ratio y/x expresses the slope of the faunal turnover curve. Numerical output of the BioGraph computer program, tool BG-T05.

| Stages | Radiolarian Zones for the Western Tethys | | | | |
|---|---|---|---|---|---|
| | All species | Nassellarians | Spumellarians | Zones | |
| Turonian | 53 | 40 | 34 | Superbum | |
| | 52 | 39 | 33 | | |
| Cenomanian | 51 | 38 | | Biacuta | |
| | 50 | 37 | 32 | | |
| | 49 | 36 | 31 | Spica | |
| | 48 | 35 | 30 | | |
| | 47 | | 29 | Anisa | |
| Albian | 46 | 33-34 | | | |
| | 45 | 32 | 28 | Missilis | |
| | 44 | 31 | 27 | | |
| | 43 | 30 | 26 | Romanus | |
| | 42 | 29 | 25 | | |
| Aptian | 41 | 28 | | Costata | |
| | 40 | 27 | | | |
| | 39 | | 23-24 | | |
| | 38 | 25 | 22 | | |
| | 37 | 24 | 20-21 | Berbeeki | |
| | 36 | 23 | | | |
| | 35 | 22 | | | |
| | 34 | | 19 | | |
| | 33 | 21 | 17-18 | Asseni | G2 |
| Barremian | 32 | 20 | | | |
| | 31 | 19 | | | G1 |
| | 30 | | 16 | F3 | |
| Hauterivian | 29 | 18 | | | |
| | 28 | | 15 | F2 | |
| | 27 | | 14 | | |
| | 26 | 17 | | | |
| | 25 | 16 | 13 | F1 | |
| | 24 | 15 | | | |
| Valanginian | 23 | 14 | | | |
| | 22 | | 12 | | |
| | 21 | 13 | 11 | E2 | |
| | 20 | 12 | | | |
| | 19 | | 10 | | |
| | 18 | 10-11 | | | |
| | 17 | | | E1b | |
| | 16 | | 9 | | |
| | 15 | | | | |
| | 14 | 8-9 | | | |
| | 13 | | | | |
| Berriasian | 12 | 7 | | E1b | |
| | 11 | | 6-8 | | |
| | 10 | 6 | | | |
| | 9 | 5 | | | |
| | 8 | | | D2 | |
| | 7 | 3-4 | | | |
| | 6 | | 5 | | |
| | 5 | 2 | | | |
| Tithonian | 4 | | 4 | D1 | |
| | 3 | | 3 | | |
| | 2 | | 2 | C2 | |
| Kimmeridgian | 1 | 1 | 1 | | |

TEXT-FIGURE 3
Correlation between the 3 UA scales discussed in the text correlated with the western Tethys radiolarian zonation (Jud 1994 and O'Dogherty 1994) and standard geological stages. Left-hand column shows standard geological stages; all species column = UA calculated using all species in radiolarian zonations of Jud (1994) and O'Dogherty (1994); Nassellarian column = UA calculated using nassellarians alone; Spumellarians column = UA calculated using spumellarians alone; right-hand column = radiolarian zones from western Tethys (Jud 1994; O'Dogherty 1994).

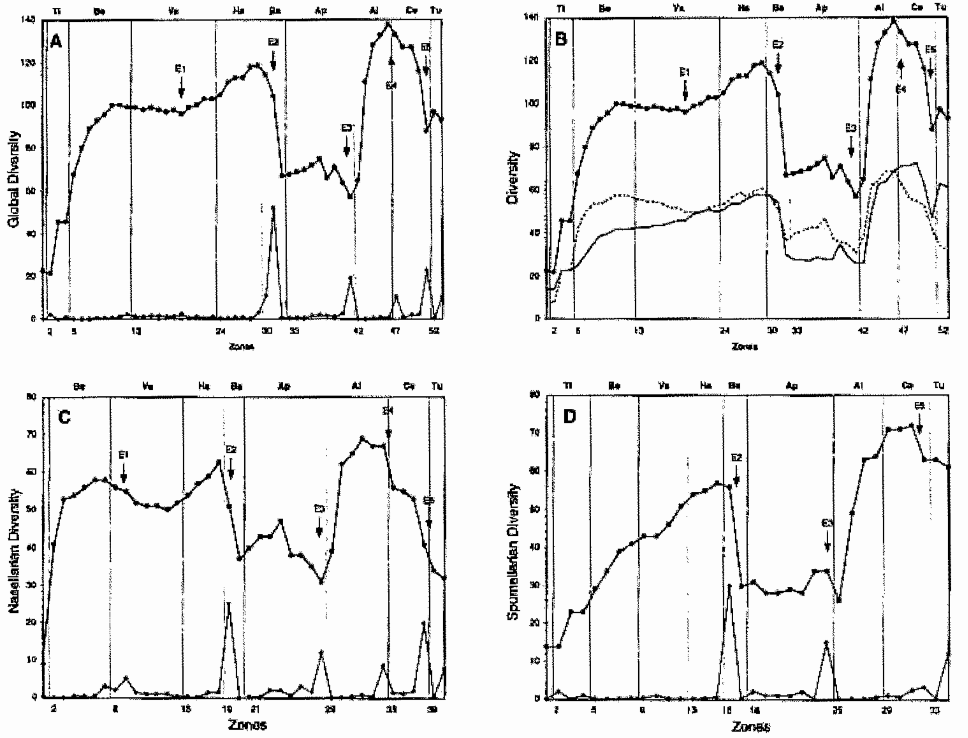
Before analyzing the means of such extinction episodes and diversity fluctuation, it is interesting to note that extinction and minimum of diversity do not coincide in any of the extinction events; the diversity always reaches a minimum following the initial extinction peak (text-fig. 5, curves 1-2 and 10).

### Radiolarian extinction events, variations in the diversity and paleoceanographic signals during Cretaceous radiolarian faunal turnovers

In the past two decades much discussion has focused on diversity fluctuation in pelagic systems, as well as its origin and ecological significance (see Haq 1973; Tappan and Loeblich 1973; Lipps 1986; Roth 1987; Knoll 1989; Collom 1990; Hart 1990; Bown et al. 1991; Swain 1992). All these papers stressed the role of abiotic factors versus biotic ones in the evolution of marine plankton and its importance in the paleobiology of the extinction episodes. Since the work of Tappan (1968) and Tappan and Loeblich (1973) a model for the evolution of pelagic systems in which biota are intimately related with continental physiography, sea-level fluctuations, climatic changes, availability of nutrients, atmospheric oxygen and $CO_2$ levels has acquired great acceptance. In this model global tectonics ultimately control the evolutionary changes. The analysis of these parameters in the sedimentary record is a keystone which enables us to make paleoceanographic and paleoenvironmental interpretations through geological time and leads us to better understanding of the evolution of oceanic plankton. Here we synthesized the main stratigraphic correlation of radiolarian diversity and extinction events with other marine biotic events: diversity of dinoflagellates, ammonites and nannoplankton; abundance of planktonic foraminifers, radiolarians etc., as well as the correlation between faunal changes and major paleoceanographic events: sea level fluctuation, anoxic events, isotopic variations and stratigraphic and sedimentological crisis (text-figs. 5 and 6). The relationships between isotopic variations ($^{87}Sr/^{86}Sr$, $\delta^{13}C$, $\delta^{18}O$), the phosphorus content of sediments, sea level fluctuations and episodes of anoxia in the Cretaceous have been discussed at length in recent publications (Hallam 1984; Arthur et al. 1990; Arthur and Sageman 1994; Föllmi 1996; Hallam and Wignall 1997). The correlations between these parameters and their paleoenvironmental meaning are as follows:

1) There is a coincidence between anoxia and positive $\delta^{13}C$ peaks generated by the burial of organic carbon (Jenkyns 1980; Scholle and Arthur 1980; Schlanger et al. 1987; Weissert and Channell 1989). Carbon is a fundamental requirement for the support of life anywhere on the earth, but the availability of dissolved carbon is not a limiting factor in biological production. Nevertheless, the carbon isotopic ratio has provided the most relevant information about the primary productivity of past oceans. A positive shift in $\delta^{13}C$ is an indicator of sequestration of isotopically light organic matter (depleted in $^{13}C$). However, a negative shift of $\delta^{13}C$ in carbonate deposits should not necessarily be interpreted as a decline in surface productivity, but as showing a net flux of carbon from the total organic reservoir to the total carbonate reservoir (Hallam and Wignall 1997).

2) Oxygen isotopes have been widely used for paleotemperature analysis where a negative shift in $\delta^{18}O$ indicates warmer temperatures. However, interpretation of $\delta^{18}O$ frequently remains difficult due to (a) the uncertainty of the $\delta^{18}O$ of Cretaceous sea water, (b) modification of the original $\delta^{18}O$ during diagenesis, and (c) the fact that $\delta^{18}O$ can reflect local instead of global temperature changes. Other methods for estimating paleotemperatures, such as pollen and facies analysis, are necessary to corroborate the results. Relatively low species diversity has commonly been associated with lower temperatures, because it may be involved as a disturbance factor in the energy flow and community function; however temperature per se is not the basic cause of extinction in the marine biota (Lipps 1986; Clarke 1993).



TEXT-FIGURE 4
Extinction peaks (bottom curve) and variation of the diversity through time. A) Global curves; B) Radiolarian diversity plotted against nassellarian and spumellarian diversities from range chart in text-figure 1: upper curve = overall radiolarian diversity, lower curve (solid) = spumellarian diversity, lower curve (dotted) = nassellarian diversity; C) Nassellarian diversity curve, same data as used in text-figure 2C and D) Spumellarian diversity curve, same data as used in text-figure 2D. From the numerical output of the BioGraph computer program, tool BG-T05.

3) A correlation also exists between transgressive events and widespread anoxic layers (Schlanger and Jenkyns 1976; Scholle and Arthur 1980; Hallam 1984; Hallam 1987; Arthur and Sageman 1994; Wignall 1994). There are many black shale deposits in the initial stages of the transgression on top of erosive or hiatal surfaces (Hallam 1984; Jenkyns 1988), but black shales also occur at the maximum of transgression and represent condensed section associated with basin starvation during high stand of sea level (Arthur et al. 1987; Leckie et al. 1992).

4) There is a relationship between the widespread development of anoxic-dysoxic episodes and most marine extinction events (Hart and Leary 1991; Hallam and Wignall 1997). The correlation of mid-Cretaceous radiolarian extinction events with oceanic anoxic events has been established and discussed by O'Dogherty (1994; see also Lambert and DeWever 1996; Erbacher and Thurow 1997).

5) There is also a correlation between eustatic variation and major bio-events in the biosphere. Periods of sea level fall correlate with episodes of endemicity and extinctions in the marine biota (Hallam 1984; Hallam 1989; Kauffman and Hart 1996), whereas times of sea level rise are associated with episodes of expansion and diversification of favorable ecospace and major evolutionary radiation in the history of the earth (Hallam 1984; Taylor and Larwood 1990). It is important to recognize that the general sea level rise of the mid-Cretaceous seems to have occurred through changes in the volume of the ocean basins (variation due for example to mid-oceanic flood basalts or to the closure of the Alpine Tethys), which were generally more im-

portant than glaciation and deglaciation in controlling pre-Quaternary sea-level. The volume variation of these basins was also extremely important, as it was responsible for the oceanographic dynamic of water masses in the absence of authentic cold polar waters during the Cretaceous (Hallam 1984).

6) Strontium is less sensitive to short term paleoenvironmental changes than carbon or oxygen isotopic curves and the correlation between the trend of $^{87}Sr/^{86}Sr$ sea-water content and sea level is difficult, at least, during the Cretaceous. Classically the $^{87}Sr/^{86}Sr$ ratio of sea-water is used as an indicator of uplift rates and continental weathering since the late Cretaceous (Hallam 1984; Veizer 1989; Bralower et al. 1997; Veizer et al. 1997) (there exists a reverse correlation between the trend of $^{87}Sr/^{86}Sr$ and long term sea level changes). The $^{87}Sr/^{86}Sr$ curves reflect the changing balance between radiogenic strontium delivered from continental weathering (higher $^{87}Sr/^{86}Sr$ ratios) and relatively non-radiogenic strontium injected by mid-oceanic ridge hydrothermal fluids into oceans (lower $^{87}Sr/^{86}Sr$ ratios). Well marked short-term excursions towards lower values during the Cretaceous are interpreted as important pulses of sea-floor hydrothermal activity (Jones et al. 1994).

7) Phosphorus is an essential nutrient for organic productivity in the marine biosphere; its relative abundance in sea water correlates specifically with a time of relative sea level rise (Hallam 1984; Föllmi 1996). Although carbon is a fundamental requirement, more important constraints are the intensity of illumination, the supply of oxygen and the availability of nitrate, phosphate and silica. The availability of biolimiting constituents (such as phosphates, nitrates and silica) controls the biological primary production in surface waters, where nutrients are most heavily utilized. Continental weathering is the most important original source of phosphate, although the location of the most important reservoir of phosphate is found below the photic environment. Approximately 95% of phosphorus is re-introduced to the photic zone by upwelling processes and hence re-utilized by marine ecosystems ensuring photosynthetic primary production (Föllmi 1996). There is also a correlation of the Cretaceous OAE's with brief periods of decrease in phosphorus burial rates. This is substantially lowered during widespread oceanic anoxia due to the decreased capacity of sediments to hold back phosphates (Ingall et al. 1993; Van Cappellen and Ingall 1994). Such postulates have also been used to support arguments for a general negative correlation of the phosphorus and carbon cycles (Arthur and Jenkyns 1981; Delaney and Filippelli 1994).

Text-figure 6 shows a tendency towards an inverse long-term correlation between the $\delta^{13}C$ curve and the phosphorus burial curve during the Cretaceous. There is a correlation between phases of incipient drowning of helvetic platforms (eutrophication, platform destruction, condensation, and phosphogenesis) and several periods of relative sea level rise ranging from late Valanginian to earliest Albian (Föllmi et al. 1994; Föllmi 1996). These phases of widespread breakdown in shallow-water carbonate production appear to coincide with phases of increased organic-carbon burial and with positive excursion of $\delta^{13}C$ record (Föllmi et al. 1994; Weissert et al. 1998). A causal link has also been observed between widespread oceanic anoxia and Cretaceous platforms drowning (Schlager and Philip 1990). The same episodes of platform drowning have been also reported in the late Albian (Schlager 1981) and late Cenomanian (Jenkyns 1991) of the northern European margin.

A distinct change in the radiolarian fauna, not analyzed in this paper, takes place in the early Tithonian and has been discussed in other studies (Baumgartner 1987; Jud 1994). This change involves the transition from Jurassic to Cretaceous radiolarian morphotypes and coincides approximately with the appearance of calpionellids. During the latest Jurassic, calcareous nannoplankton become abundant and hence for the first time planktonic limestones replace radiolarites in western Tethys; this is the transition from radiolarian chert to Maiolica limestone type facies (Baumgartner 1987). This major paleoceanographic change is related to changes in surface water productivity from high to low-medium fertility, probably controlled by fluctuation in atmospheric $CO_2$ concentrations and by the transition from a Jurassic monsoonal climate to a Cretaceous zonal climate (Weissert and Mohr 1996).

The synthesis presented in text-figures 5 and 6 confirms these classical correlations and illustrates some new relationships between variations in diversity and radiolarian faunal turnover related to major paleoceanographic events during Cretaceous time. We will first discuss the extinction events (E1 to E5) and the variations in the diversity in relation to the major paleoceanographic changes during this period (text-figs. 5 and 6).

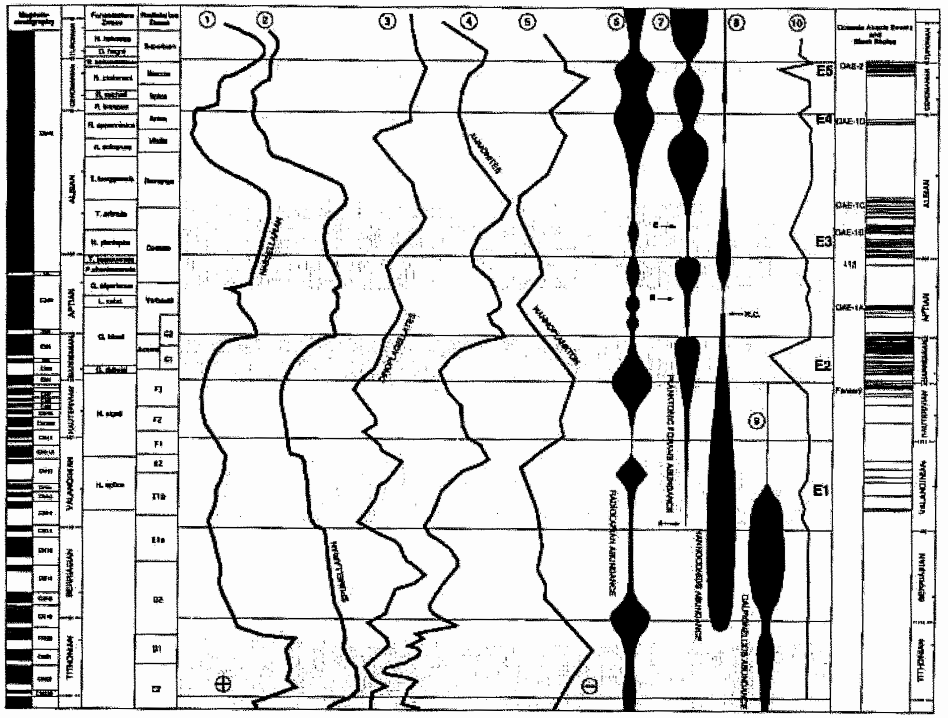
### Extinction event E1 (early Valanginian)

Extinction event E1 occurs during the early Valanginian to early late Valanginian. It starts with a drop in diversity in the nassellarian fauna, but is not observed in spumellarians (text-fig. 5, curves 1 and 2). The extinction event correlates with a major regression of shallow epicontinental seas, as can be traced by the progradation of the carbonate platform in western Tethys. This drop in diversity is correlated with the beginning of thin and discrete laminated organic-rich sediments and also coincides with a temperature minimum as indicated by pollen analysis (cold period of supercycle A, Kemper 1987) and by paleotemperatures based on oxygen isotopes (Polsak 1976). This fall in diversity preceded the climatic turnover towards warmer and more humid climates characteristic of late Valanginian-Hauterivian times (Weissert and Lini 1991, van der Schootbrugge et al. 2000). Recently, Stoll and Schrag (1996) argued in favor of rapid glacio-eustatic control of the main Early Cretaceous variations in sea level (in spite of the generally warm climate) as indicated by $\delta^{18}O$ of bulk carbonates. These authors analyzed the high-frequency variations of $\delta^{18}O$ PDB values (0.5 to 1.7‰) in several DSDP sites of the Early Cretaceous and found good correlation between periods of low temperature (high ice volume) recorded by increased $\delta^{18}O$ values and episodes of low sea level (reflected by high Sr concentrations).

The spumellarian turnover was less striking than that of nassellarians during the fall in diversity displayed by the progressive increase in the spumellarian/nassellarian diversity ratio. Minimum radiolarian diversity coincides with maximum values in $\delta^{13}C$ (3.2‰) in the late Valanginian (CM11 polarity chron). Then diversity increases between the latest Valanginian-Hauterivian, in parallel with enhanced atmospheric and oceanic temperatures (Douglas and Savin 1975; Polsak 1976). This increase is concomitant with a transgressive sea level trend, a major increase in the phosphorus burial record, decreases of $\delta^{13}C$, and the development of a better-oxygenated environment.

The cessation of platform-carbonate progradation during the late Valanginian-earliest Hauterivian in several areas of western Tethys seems to have been diachronous and related to various rapid episodes of relative third-order sea-level rise (peri-Vocontian platforms Arnaud-Vanneau et al. 1982; Helvetic platforms Föllmi et al. 1994). During this episode of platform drowning (incipient phase D1 in Föllmi et al. 1994) the period of maximum phosphogenesis coincides with the highest $\delta^{13}C$ values and is synchronous with a major biotic crisis observed in deep and shallow-water environments. This phosphogenic episode is also documented in pelagic swells of the Betic Cordillera by phosphatic microcrusts and oncoids encrusting the discontinuity surface in a thin condensed bed of latest Valanginian-early Hauterivian age (Vera and Martín-Algarra 1994).

The late Valanginian-early Hauterivian has been considered as an episode of significant carbon burial as indicated by the highest values of the $\delta^{13}C$ (3.0-3.2‰) and represents the beginning of a major turnover in the Cretaceous climate (Weissert and Lini 1991; Lini et al. 1992). The simultaneous positive excursion in $\delta^{13}C$ values of carbonate and organic matter was interpreted as a major perturbation of the global carbon cycle to elevated atmospheric $CO_2$ concentrations, where the response of the biota was the acceleration of carbon export from oceanic to burial reservoir (Lini et al. 1992). This large emission of $CO_2$ has been related to an important pulse of sea-floor spreading in the Valanginian (Larson 1991), which in turn, forced the climate toward a greenhouse mode during the late Valanginian. Evidence for this is the progressive increase of $^{87}Sr/^{86}Sr$ ratio of sea water during the late Valanginian-earliest Aptian, which is related to intense continental weathering as a response to the acceleration of water cycling during a greenhouse climate (Weissert and Mohr 1996). Another indication of intensified weathering is the increasing frequency of laminated organic-rich deposits of terrestrial origin found in Maiolica-type facies of the North and South Atlantic margins during the late Valanginian-Hauterivian



TEXT-FIGURE 5

Correlation of radiolarian diversity and extinction events (E1 to E5, horizontal gray bands) with other biotic events. Magnetostratigraphy zones adapted from Berggren et al. (1996), Channell et al. (2000); Planktonic foraminifera zones adapted from Bralower et al., (1996), Erba et al. (1999); radiolarian zones for western Tethys from (Jud 1994) and O'Dogherty (1994). 1. Nassellarian diversity; 2. Spumellarian diversity; 3. Dinoflagellate diversity (from Bujak and Williams 1979; Powell 1992); 4. Ammonite diversity (from Collom 1990); 5. Nannoplankton diversification rates (Roth 1987); 6. Radiolarian abundance; 7. Planktonic foraminifer abundance; A. occurrence of early small planktonic forms (Hedbergellidae); B. occurrence of normal-size morphotypes; C. re-appearance of small planktonic forms; 8. Nannoconid abundance (Roth 1978); 9. Calpionellid abundance (Roth 1978; Remane 1985); 10. Extinction events E1 to E5, curve represents slope of faunal turnover diagram for nassellarians from text-figure 2C. Stratigraphic position of Oceanic Anoxic events (OAE) in the area studied with location of other episodes of black shale deposition (see Jud 1994 and O'Dogherty 1994 for a more detailed information). Cretaceous anoxic levels: Faraoni Level; OAE-1a; 113 Level or Niveau Jakob, OAE-1b; OAE-1c; OAE-1d; OAE-2.

(Stein 1991; Lini et al. 1992). This has been related in the North Atlantic area to intensified continental runoff under a warm and humid climate, as signified by the presence of bauxites, coals, and abundant fluvial deposits (Hallam 1987).

### Extinction event E2 (late Hauterivian-Barremian)

Radiolarian extinction event E2 occurs at the boundary between the Hauterivian and Barremian and is located immediately preceding the first major Cretaceous anoxic event in western Tethys (known as the "Faraoni level" in Italian sections, *Angulicostata* ammonite Zone, Channell et al. 1993; Coccioni et al. 1998). Throughout the latest Hauterivian-Barremian, the widespread deposition of thin laminated organic-rich shales coincides with a period of relatively high sea level and the start of a short-term positive $\delta^{13}C$ excursion that precedes the strong positive values of the late early Aptian excursion (Weissert and Lini 1991; Lini et al. 1992). The extinction phase E2 is extremely strong in both groups of radiolarians, as well as in dinoflagellate and ammonite fauna (text-fig. 5, curves 1-4), and led to the most dramatic decrease in diversity in the Cretaceous. This interval is characterized by the extinction of several radiolarian genera, mostly inherited from the Jurassic, and the disappearance of seventy species (diversity falls by ca. 60%); in addition, an extremely poor faunal replacement occurs progressively up to the Barremian-Aptian boundary (only 4 new taxa). It is interesting to note that although 51 radiolarian species cross this boundary, approximately 95% go extinct between the Aptian and early Albian. The spumellarian/nassellarian diversity ratio stays relatively balanced at the Barremian-Aptian boundary, related probably to the special nature of the extinction (gradual disappearance of taxa during a relatively long interval). Here we note that the huge and very slow drop in diversity is not an artifact due to the fossil record because preservation before, during and after the extinction event is excellent (Jud 1994, O'Dogherty 1994). This extinction occurs essentially within the upper part of the Maiolica Formation (e.g. standard levels 821 to 895 of Gorgo a Cerbara; 580 to 617 of Fiume Bosso in Jud 1994 and O'Dogherty 1994) and is not correlated with a change in lithology. Therefore we can conclude that the drop in diversity is a direct consequence of the extinction and can not be related to preservational problems.

Open ocean-dwelling planktonic foraminifers initially became established in the early Valanginian, but an explosive development of very small and simple planktonic foraminiferan individuals (mostly Hedbergellidae) occurred in the Barremian. The loss of radiolarian diversity is concomitant with this proliferation of surface-dwelling morphotypes, which probably opportunistically occupied the ecological niche left by the gradual elimination of radiolarians under the progressive environmental deterioration.

The dramatic drop in diversity in this extinction event is tentatively correlated with a more continuous input of shales into the basins, which could be related to a cooling of the climate during the low stand of sea level in the Barremian-early Aptian. Evidence for this relative sea level fall is the increase in terrigenous input recorded in some deep-sea basins due to the re-activation of numerous turbiditic systems in western Tethys (Subbetic basin, Vera 1988; Martín-Algarra et al. 1992); at the same time progradation and platform-carbonate production were intensified (Helvetic domain, Föllmi et al. 1994). Moreover the extremely sharp fall of ocean-crust production must have played a major role in global eustasy (Larson 1991), which in turn led to a relative increase in the $^{87}Sr/^{86}Sr$ ratio. The high abundance of thin black shale containing type III kerogen in this interval is characteristic of black shales dominated by terrestrial organic matter (Stein 1991). An exception is the Faraoni level (CM4 polarity chron, late Hauterivian) where black shales contain type II kerogen (Coccioni et al. 1998) and record a positive $\delta^{13}C$ (2.4-2.5‰, Lini et al. 1992). These values can be used as an indicator of elevated productivity, as has been observed in other Cretaceous OAE's developed during early stages of transgression. Concomitant with the onset of this early oceanic anoxic event, another incipient phase of platform drowning and phosphogenesis occurs in the Helvetic realm (phase D3 of Föllmi et al. 1994), which correlates well with the early stage of our extinction event. Similar synchronicity has been found between biotic and sedimentological crisis of carbonate platforms in SE France (Arnaud-Vanneau et al. 1982). This phase of platform destruction is interpreted as a probable result of several transgressive phases (Föllmi et al. 1994; Weissert et al. 1998).

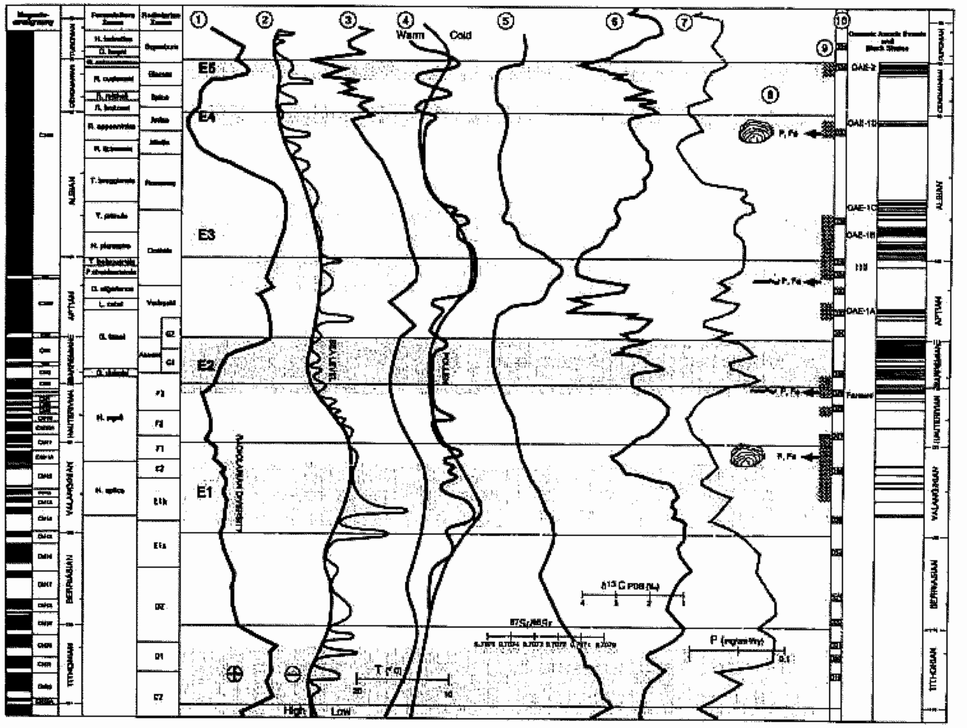
The latest Hauterivian-Barremian recorded the transition towards cooler sea water temperatures (Kemper 1987; Frakes and Francis 1990). The radiolarians have a serious drop in nassellarian and spumellarian diversity, which reaches a minimum during the latest Barremian (text-fig. 5). Other groups such as ammonites and large benthic foraminifers also record a major turnover in the late Barremian (Arnaud-Vanneau et al. 1982; Collom 1990). The deterioration observed above in the structure of pelagic ecosystems denotes important changes in the marine environment around the Barremian/Aptian boundary (Kemper 1995), which is also manifested in a major change in the stratigraphic record i.e. the disappearance of the Maiolica-type facies in Mediterranean areas during the earliest Aptian (i.e. Vera 1988; Coccioni et. al. 1992). This synchronicity of biotic events seems not casual, but may correspond to the predicted Barremian mass extinction event in Raup and Sepkoski's extinction curves (1986).

Finally, the recovery of the radiolarian fauna starts with a slight increase in diversity within the M0 polarity chron (earliest Aptian, Channell et al. 2000) up to the latest early Aptian and reaches a maximum prior to the OAE-1a.

### Extinction event E3 (late early Aptian-early Albian)

Recently Kauffman and Hart (1996) have considered the late Aptian-early Albian as a mass extinction episode and place the beginning of this extinction near the end of OAE-1a. Among major faunal turnovers that have been well documented in the marine ecosystems are: ostracods (Whatley 1986; Swain 1992), dinoflagellates (Bujak and Williams 1979; Powell 1992), ammonites (Kemper 1987; Collom 1990) and planktonic foraminifers (Jarvis et al. 1988; Bréhéret and Delamette 1989); the observations presented below support this consideration.

The decline in diversity in this extinction shows some different steps: a very weak initial drop in OAE-1a ("Selli level" in Italian sections, Coccioni et al. 1990, Coccioni et al. 1992 or "Niveau Goguel" in SE France, Vocontian basin, Weissert and Bréhéret 1991), a second falling within the *G. algerianus* Zone, and a third which becomes maximal in the latest Aptian-early Albian around OAE-1b ("Urbino level" in Italian sections, Coccioni et al. 1990). The stepwise decline in diversity is probably related to drastic rhythmic changes in the environment, from well-oxygenated to hypoxic or even anoxic conditions recorded throughout this interval.



TEXT-FIGURE 6
Correlation of radiolarian diversity and extinction events E1 to E5 with paleoceanography. 1. Radiolarian diversity; 2. Global sea level changes curve (Haq et al. 1988); 3. Composite smoothed oxygen isotopic temperature curve from the Early Cretaceous of Dinarids and the Slovenian Alps (Polsak 1976) and the mid-Cretaceous of the Northern Apennines (Corfield et al. 1991; Jenkyns et al. 1994, Stoll and Schrag 1996, 2000); 4. Climatic curve based on pollen (Kemper 1987); 5 $^{87}Sr/^{86}Sr$ isotopic curve (Jones et al. 1994; Bralower et al. 1997); 6. Carbon isotopic curve $\delta^{13}C$ (‰) for the Italian Apennines (after Weissert and Channell 1989; Weissert and Lini 1991; Lini et al. 1992; Jenkyns et al. 1994; Erbacher et al. 1996; Weissert and Mohr 1996; Stoll & Schrag 2000); 7. Marine phosphorus accumulation curve from synthesis of various DSDP-ODP sites (Föllmi 1996); 8. Stratigraphic position of pelagic stromatolites in the Betic Cordillera (Vera and Martín-Algarra 1994); 9. Periods of platform drowning in the Helvetic platforms (late Valanginian to early Albian, from Föllmi et al. 1994; Weissert et al. 1998), Eastern Alps platforms (late Albian, from Schlager 1981; Grötsch et al. 1993) and Dinarid Platform (late Cenomanian, from Jenkyns 1991); 10. Stratigraphic position of major Cretaceous discontinuities in the Betic Cordillera.

The cumulative effect of these successive drops in diversity alternating with minor radiations led to the almost complete renewal of the radiolarian fauna (only 7 species originating prior to the Barremian still occur in the late Albian). This may be considered a major transition between the important late Barremian extinction and the huge radiation of the middle Albian. This period together with the late Cenomanian records two of the major Cretaceous turnovers of marine taxa (Jarvis et al. 1988; Bréhéret and Delamette 1989; Hart and Leary 1991; Kemper 1995) that coincide with: (1) major changes in sea level (Haq et al. 1988), (2) development of an expanded oxygen minimum zone in the world ocean (Schlanger and Jenkyns 1976; Jenkyns 1980; Arthur et al. 1987; Arthur et al. 1990) and (3) high values in $\delta^{13}C$ (Arthur et al. 1987; Hart and Leary 1991; Weissert and Lini 1991, Hochuli et al. 1999).

Subsequent to the Barremian faunal crisis (extinction of more than half of the species), the earliest Aptian is characterized by a moderate and slow recovery (only 30% of the fauna is renewed). During this interval the recovery is much more pronounced in nassellarians as indicated by the diversity ratio of spumellarians to nassellarians (text-fig. 7). The initial extinction event is practically undifferentiated both in the general diversity curve and in the nassellarian one, only being observed as a minor drop in the spumellarian diversity curve (text-fig. 5, curve 2). However, the importance of this initial decline in diversity is justified by its location shortly before OAE-1a, which precedes the long crisis that occurred through the late Aptian-early Albian interval. The most striking biotic aspect is the apparent absence of radiolarian extinctions within OAE-1a; only 7 species (of a total 68) become extinct immediately before or during the anoxic event. In spite of the great similarity to the late Cenomanian OAE-2 (identical sedimentological and chemostratigraphic characteristics, similar stratigraphic sequence, thickness, fossiliferous content, etc.) the absence of major extinctions within OAE-1a is puzzling, inasmuch as in the former most planktonic foraminifers and radiolarians disappear. The only explanation may be the relatively low rate of radiolarian faunal turnover close to OAE-1a (3 extinctions against 8 originations) which cannot be regarded as artifact due to preservational problems (68 species survive OAE-1a). Planktonic foraminifers are represented near OAE-1a by large number of small-sized morphotypes (globigerinelloids and hedbergellids) which increase in abundance and diversification. This is probably related to the opportunistic occupation of the niche left open by the extensive elimination of numerous genera and species of radiolarians in the latest Barremian.

The weak initial decrease of spumellarian diversity occurs at the top of the *Globigerinelloides blowi* Zone of planktonic foraminifers and seems synchronous with the nannoconid crisis (Erba 1994). This latter group of nannofossils went through a drastic production crisis in the early Aptian immediately preceding the OAE-1a (Mutterlose 1992; Erba 1994). The nannoconid crisis may reflect a competition between phytoplankton groups for nutrients or more likely, competition between different calcareous nannoplankton (Erba 1994). This could result in a change in the structure of the surface waters caused by the superplume volcanic episode proposed by Larson (1991).

Early Aptian sediments in OAE-1a display a high content of organic matter of marine origin (type II kerogen, Coccioni et al. 1992; Erbacher et al. 1996). These sediments were probably deposited during the initial stage of the transgression, postdating the major sea level fall of the earliest Aptian (text-fig. 6, curve 2). Spumellarian diversity decreases during OAE-1a and correlates with the beginning of a strong positive $\delta^{13}C$ shift (1.8 to 4.2‰) located in the upper part of the *Globigerinelloides blowi* Zone (Weissert and Lini 1991; Weissert and Bréhéret 1991, Erbacher et al. 1996; Erba et al. 1999). The marine origin of the organic matter and the strong positive shift of $\delta^{13}C$ recorded in OAE-1a suggest an intensified productivity, which in turn triggered the accumulation of organic matter.

The OAE-1a seems also to coincide with an incipient episode of platform drowning on the basis of the highly condensed succession resulting from relative sea level rise. The time span estimated for this drowning unconformity is the equivalent of a supersequence, but highly condensed (Föllmi et al. 1994). The phosphorus burial curve (text-fig. 6, curve 7) shows a relatively high ratio during the earliest Aptian, which decreases to reach a relative minimum during the development of the anoxic sediments.

Non-anoxic sediments abruptly succeed OAE-1a in the Northern Apennines ranging between the *Leupoldina cabri* and the middle part of the *Ticinella bejaouensis* zones. In this interval radiolarian diversity increased following OAE-1a to reach a relative peak in both groups of radiolarians within the *Globigerinelloides algerianus* Zone of planktonic foraminifers in parallel with decreasing $\delta^{13}C$ values (down rapidly from 4.2 to 1.0‰). Simultaneously, the first occurrence of normal-size morphotypes of planktonic foraminifers is recorded. Coincidentally, the proliferation and radiation of these morphotypes is again determined by the drop in radiolarian diversity, as occurred in late Barremian time. It seems obvious that during extinction event E3 the biotic interactions between planktonic foraminifers and radiolarians were decisive in the evolution of both groups but were ultimately modulated by progressive environmental deterioration.

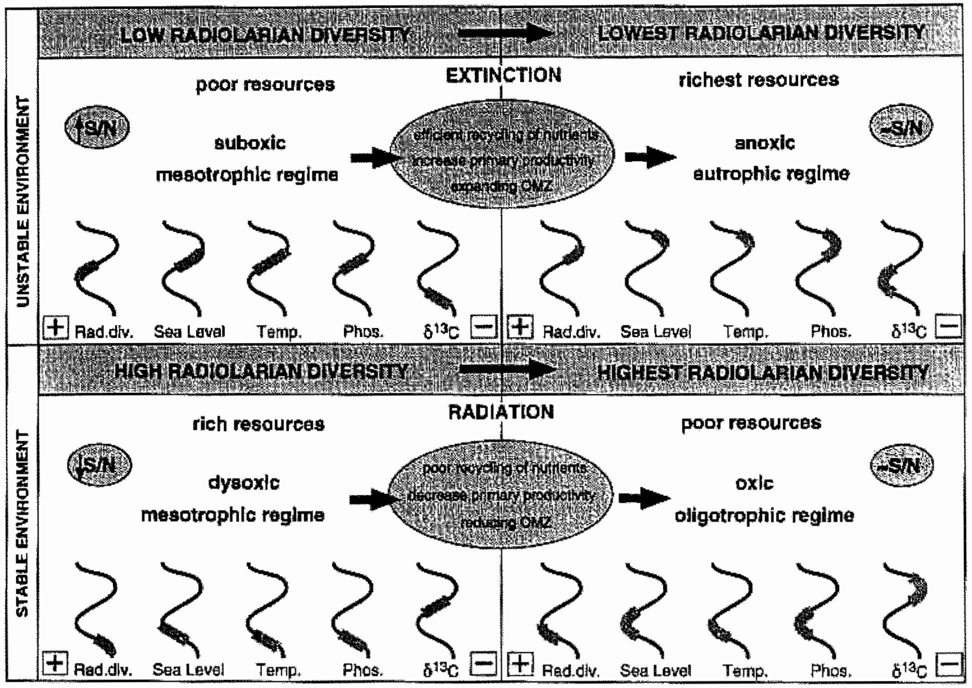
In the Northern Apennines a characteristic clay level within the *Ticinella bejaouensis* Zone (Coccioni et al. 1990) marks the return to anoxic conditions and the beginning of the long late Aptian-early Albian anoxic episode. The biotic response seems to occur shortly before this time, as shown by the general fall in radiolarian diversity (text-fig. 5, curve 2). We note the spectacular rise of the spumellarian/nassellarian diversity ratio as the frequency of anoxic levels increases up to the *Ticinella breggiense* Zone (text-fig. 7), where black shales hold a high content of organic matter of marine origin (type II kerogen). This is interpreted as indicative of increased fertilization and productivity during initial transgression. Simultaneous with the drop in radiolarian diversity, a major positive excursion of $\delta^{13}C$ (3.3-4.2‰) occurs, which was directly calibrated with planktonic foraminifers (*Planomalina cheniourensis-Ticinella bejaouensis* zones) by Weissert and Lini (1991) in the Southern Alps and Northern Apennines (Erbacher et al. 1996) or in its counterpart anoxic event "Niveau Jacob" in the Vocontian basin (Weissert and Bréhéret 1991).

Among planktonic foraminifers, this fall in radiolarian diversity is recognized when *Ticinella* and normal-sized forms of *Hedbergella* disappear and only minute hedbergellids survive (Bréhéret and Delamette 1989). This foraminiferal decline in the Northern Apennines represents an extreme scarcity of planktonic forms ranging exactly from the 113 level to the following anoxic level OAE-1b. The planktonic crisis correlates with cold temperatures (text-fig. 6, curves 3-4) as indicated by palynomorphs (Kemper 1987) and oxygen-isotopes.

Radiolarian faunal change seems to be coincident with OAE-1b of Jenkyns (1980), which records relatively high values of $\delta^{13}C$ (2.3-2.7‰, Weissert and Bréhéret 1991; Erbacher et al. 1996). This turnover is remarkable for the great number of extinctions (32 species), and the origination of a few important genera and species from which new phyletic lineages develop.

The spumellarian/nassellarian diversity ratio attains a maximum (text-fig. 8) within OAE-1b. This black shale interval is located within the *Ticinella primula* Zone and is approximately equivalent to the "Niveau Paquier" in the Vocontian basin (Weissert and Bréhéret 1991). The deposition of organic-rich facies during OAE-1b is linked to the transgressive phase characterized by high $\delta^{13}C$ values (Jenkyns 1980). During this part of extinction event E3, the radiolarian fauna has the lowest diversity of the Cretaceous, which could be correlated with the transition to warmer temperatures as deduced from $\delta^{18}O$ values (Douglas and Savin 1975; Polsak 1976; Corfield et al. 1991) and palynomorphs (Kemper 1987).

The top of the late Aptian-early Albian anoxic episode corresponds to OAE-1c (known as "Amadeus segment" in the Northern Apennines, Coccioni et al. 1998, equivalent to Niveau Breistroffer in SE France, Bréhéret and Crumière 1989). During OAE-1c $\delta^{13}C$ attains values of 2.2-2.3‰ (Erbacher et al. 1996; Stoll and Schrag 2000), radiolarians attain minimum diversity and planktonic foraminifers become progressively more abundant and diverse. This anoxic episode is characterized by thin black shales with a high content of terrestrial organic matter (type III kerogen) interpreted as leaching of lowland areas during either a maximum flooding surface or high stand of sea level.



TEXT-FIGURE 7
Summary sketch of the main paleoceanographic controls in radiolarian evolution during the Early-Mid Cretaceous. Key: S/N = spumellarian/nassellarian diversity ratio; Inverted "S" curves = Radiolarian diversity; Sea level; Temperature; Phosphorus; and $\delta^{13}C$.

A final phase of platform destruction in the Helvetic domain occurred in the latest Aptian-earliest Albian (phase D5 of Föllmi et al. 1994) after a brief period of platform regeneration that coincides approximately with the brief non-anoxic interval in which radiolarian diversity increased. The phosphorus burial curve (text-fig. 6, curve 7) shows relatively low values during this phase of condensation which coincides approximately with the initial development of the long late Aptian-early Albian anoxic episode, and is tentatively situated prior to OAE-1b.

Throughout extinction interval E3 (late early Aptian-early Albian) a decrease in $^{87}Sr/^{86}Sr$ ratio is recorded, which is related to the increased rates of hydrothermal activity associated with enhanced rates of oceanic crust production (Jones et al. 1994). The large production of mid-plate volcanic plateaus and increased ridge-crest crustal production could have resulted from a superplume episode, which coincides with a period of constant magnetic polarity during the mid-Cretaceous (Larson 1991; Larson and Erba 1999). The paleoceanographic consequence of this large superplume is the rapid decrease of $^{87}Sr/^{86}Sr$ values in seawater by an accelerated oceanic ridge crustal production associated with large emissions of $CO_2$. It is likely that the emission of large volumes of $CO_2$ may be the most damaging inherited consequence of the intense volcanism that occurred during the superplume episode (Caldeira and Rampino 1991; Larson 1991; Larson and Erba 1999). Higher $CO_2$ in the mid-Cretaceous atmosphere led to a natural greenhouse effect and then to global warming (Caldeira and Rampino 1991; Weissert and Lini 1991). The onset of the short-term excursion towards lower $^{87}Sr/^{86}Sr$ correlates well with the deposition of organic-rich sediments of OAE-1a (Bralower et al. 1994), suggesting the existence of a possible link among extinctions, anoxic events, decrease in $^{87}Sr/^{86}Sr$ ratio and volcanism (Bralower et al. 1994; Jones and Jenkyns 1995; Wignall and Twitchett 1996).

Finally, the middle-late Albian radiolarian radiation is shown by the long flat part of the faunal turnover curve (text-fig. 2) at either generic or specific level, and the diversity curve shows a progressive tendency to higher values reaching a maximum peak within the *Rotalipora ticinensis* Zone of planktonic foraminifers (text-fig. 6, curve 1). This diversification period coincides with low $\delta^{13}C$ values, high marine phosphorus burial rates, non-anoxic waters, and the major Albian transgression.

### Extinction event E4 (late Albian)

During the long period of progressive sea level rise of the middle-late Albian, the major Cretaceous radiolarian radiation occurred (165 new species arose and 75% of the fauna completely renewed). The marked tendency of sea level rise is well monitored by the strontium sea water curve, which shows higher, but constant, values of $^{87}Sr/^{86}Sr$ during the middle Albian-Cenomanian, however there is no common explanation due to elevated oceanic crust production at this time (Larson 1991; Bralower et al. 1994). It seems most probable that the effect of hydrothermal activity was balanced by a constant fluvial weathering flux with minimal variations in runoff input (Jones et al. 1994). A period of a progressive sea level rise (Haq et al. 1988; House 1989) and higher temperatures are compatible with the long negative excursion of $\delta^{18}O$ (-2.5 to -3.5‰, Jenkyns et al. 1994; Stoll & Schrag, 2000). It seems evident that this steady scenario favored the rapid development of new niches in a well-oxygenated environment, which were of extreme importance in the diversification of new genera and families of radiolarians during most of the Albian. Planktonic foraminifers also recorded a major evolutionary radiation with the appearance of keeled morphotypes characteristic of progressively deeper-dwelling environments as a consequence of increased ecospace (Hart 1990). In general, the mid-Cretaceous is an interval when one of the most spectacular and explosive diversifications among fossil groups took place. This coincides with the largest sea level rise recorded since the mid-Paleozoic (Hallam 1984). Soon after, the major radiation that gave rise to the origination of new phyletic lineages of Radiolaria was suddenly reversed.

Extinction event E4 is linked with late Albian post-regressive anoxia. The drop in diversity shortly precedes the OAE-1d anoxic event (also called "appenninica event", Grötsh et al. 1993), which is located at the base of an important drop in nassellarian diversity (text-fig. 5, curve 1). This relative diversity minimum is well correlated with the positive excursion of $\delta^{13}C$ (2.5-2.7‰) which occurred within the *Rotalipora appenninica* Zone (Jenkyns et al. 1994; Erbacher et al. 1996; Gale et al. 1996). After the anoxic event, nassellarian diversity falls rapidly throughout the early Cenomanian, but spumellarian diversity remains stable. Diversity displays a similar nassellarian-pattern diminishing up to the middle Cenomanian, then is stabilized prior to the late Cenomanian crisis. From the beginning of this crisis the carbon isotope curve displays a progressive tendency to heavy values, coinciding with the gradual drop in radiolarian diversity throughout the late Albian-Cenomanian (text-fig. 6, curves 1 and 6). This short anoxic episode occurs in a whitish-gray limestone succession having thin black shales with considerable levels of marine organic matter (type II kerogen) and moderate values of $\delta^{13}C$; both signals may indicate moderate productivity during the initial phases of sea level rise.

The drop in faunal diversity could be related to a second-order relative sea-level fall during the latest Albian-Cenomanian (Haq et al. 1988; House 1989). In pelagic swells of the Betic Cordillera a discontinuity surface located within the *Rotalipora ticinensis* Zone has been correlated to one of these regressions (text-fig. 6, curves 1 and 6). The basal sequence boundary is characterized by a striking paleokarstic surface covered by an important phosphatic stromatolite belt concurrent with most of the *Rotalipora appenninica* Zone (Vera and Martín-Algarra 1994). This phosphogenic episode has been described in several areas of the Alps and may be also related to a major episode of platform drowning in carbonate sequences of the Austroalpine domain. This drowning episode is concomitant with widespread anoxic conditions (OAE-1d) in pelagic deposits (Grötsch et al. 1993). Throughout the latest Albian-Cenomanian the phosphorus burial record curve displays a relative long-term decrease (text-fig. 6, curve 7).

Around the traditional division between the Early and Late Cretaceous the existence of an abrupt change in the marine biotas is widely accepted (Kauffman and Hart 1996). The late Albian-Early Cenomanian interval in Italian sections records a positive excursion of $\delta^{18}O$, indicating lower temperatures in the *R. brotzeni-R. richly* planktonic foraminifera zones (Cornfield et al. 1991; Jenkyns et al. 1994; Stoll and Schrag 2000). This temperature decline seems to be at least concurrent with, if not the origin of, the abrupt decrease in diversity of radiolarians.

### Extinction event E5 (late Cenomanian)

Extinction event E5 is characterized by an accelerated decrease in the number of species and illustrates the transition of radiolarians from the Cenomanian to Turonian, with the consequent drastic radiolarian faunal change that takes place around this boundary. This serves as the starting point for several typical Late Cretaceous radiolarian lineages (O'Dogherty 1994).

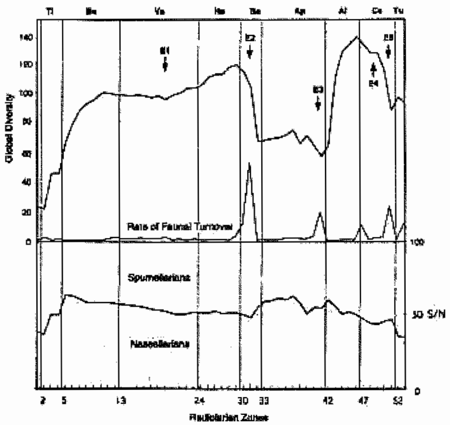
Extinction event E5 occurs during the transgressive anoxia of the topmost Cenomanian and is clearly correlated to OAE-2. A typical characteristic of this level as in other Cretaceous OAE's, is the occurrence of alternating laminated black shales and radiolaritic levels (blackish radiolarites rich in marine organic matter, known as phtanites) which are generally thought to be the result of high planktonic productivity (De Wever and Baudin 1996). The Cenomanian-Turonian interval is widely accepted as one of the most important high stands of sea level in earth history, although detailed sequence stratigraphy has placed the stage boundary within a transgressive phase (Haq et al. 1988). Therefore the deposition of black shales is related to the initial stage of transgression following a minor sea level fall occurring in the upper part of the *Rotalipora cushmani* Zone. Carbon and oxygen isotope curves have been used in the stratigraphic definition of this oceanic anoxic event. The $\delta^{13}C$ shows a rapid and strong positive shift (from 2.5 up to 4.5‰) at the top of the *Rotalipora cushmani* Zone (Jarvis et al. 1988; Jenkyns et al. 1994) and a decrease of 2‰ in the *Dicarinella hagni* Zone. The same positive excursion has been well documented in the Northern Apennines (Scholle and Arthur 1980; Jenkyns et al. 1994; Erbacher et al. 1996) and in SE France ("Niveau Thomel", Bréhéret and Crumière 1989). Oxygen isotope analysis estimates the temperature reached a peak of 28°C (negative excursion $\delta^{18}O$ PDB of -2.9 to -3.7‰) within the anoxic interval (Jenkyns et al. 1994).

Analysis of the radiolarian fauna reveals that after a brief period of stability during the middle Cenomanian, diversity falls again simultaneous with the beginning of a strong positive carbon isotope excursion (text-fig. 6, curves 1 and 6). This drop in diversity represents the start of this important extinction event that led to the disappearance of 60% of the radiolarian fauna. Although the majority of Cenomanian extinctions occur beneath OAE-2, faunal turnover occurs within this anoxic interval (O'Dogherty 1994) with the recovery being relatively important: 23 species fade out within the lower part of OAE-2 and 35 new taxa arise within the upper part. It is worth noting that out of a total of 65 species of radiolarians crossing OAE-2 approximately 75% are spumellarians (47 species). Although the most severe extinctions occurred prior to or during the anoxic episode, a few meters immediately above the anoxic interval 20% of species become extinct and this seems to coincide with a relative decrease in temperatures (a decrease of 5°C, Jenkyns et al. 1994). Finally, a small recovery follows the major nassellarian-spumellarian diversity minimum (text-fig. 5, curves 1 and 2).

The beginning of OAE-2 coincides with the maximum values of $\delta^{13}C$, the start of the major transgression, and approximately with the disappearance of the planktonic foraminifer genus *Rotalipora* (Piergiovanni 1989; Hart and Leary 1991), although in other areas this genus becomes extinct precisely within the anoxic event (Jarvis et al. 1988). We postulate that the faunal turnover undoubtedly occurs within OAE-2 but the drop in radiolarian diversity proceeded stepwise earlier, at the same time as the first occurrence of discrete laminated hemipelagic black shales, in the middle Cenomanian.

Simultaneous with the widespread occurrence of the late Cenomanian anoxic event, a drowning of the Dinarid platform has been related to a rapid relative sea level rise (Jenkyns 1991). A similar link between faunal crisis and dysoxia during a drowning episode is summarized by frame-building corals and rudists, which were seriously damaged during the rapid change of sea level that exceeded the rate of upward reef framework accretion. The late Cenomanian extinction affected not only shallow-water taxa, such as corals or rudists, but also caused a crisis for many deeper water groups such as radiolarians, dinoflagellates and planktonic foraminifers.

The late Cenomanian OAE-2 was due to strong intensification and expansion of the oxygen minimum zone, as a result of intense coastal upwelling at times of enhanced primary productivity along the shelf margins and preferentially in mid-water settings. This scenario led to the deposition of laminated black shales containing II type kerogen (marine organic matter) and showing a positive $\delta^{13}C$ (Jenkyns et al. 1994, Erbacher and Thürow 1997). These chemical signals exclude riverine input as a source for the large supply of nutrients and hence alternative paleoceanographic models were presented to explain the origin of this elevated primary productivity. Arthur and Premoli-Silva (1982) proposed that the intense evaporation in low-latitude platforms favored the development of warm-saline bottom waters as transgression evolved. This current system intensified the upwelling and favored highly productive surface waters (widespread radiolarian and dinoflagellate blooms). Recently, Kerr (1998) proposed that the anomalous volcanism that occurred during the late Cenomanian-Turonian played a decisive role in worldwide environmental disturbance. The extensive melting of hot mantle plumes and the development of vast oceanic plateaus in the Pacific and Indian oceans resulted in the emission of large quantities of $CO_2$ into the atmosphere, leading to greenhouse effect and global warming. Indirect support for this volcanogenic hydrothermal input is found in the short-term decrease in $^{87}Sr/^{86}Sr$ seawater ratio around the Cenomanian-Turonian boundary (Jones et al. 1994; McArthur et al. 1994; Bralower et al. 1997). In short, the eruption of these large igneous provinces was responsible for the disturbance of the biosphere, directly, due to sea level transgression (increasing shallow water evaporation) and disrupted circulation patterns (generating warm-saline bottom waters), and indirectly, due to large emission of $CO_2$ to the atmosphere (increasing temperatures). The intensification of upwelling systems, as well as the increased $CO_2$, led to enhanced primary productivity up to eutrophic levels in the open oceans and hence increased organic carbon burial rates. Anoxia plus eutrophication triggered the ecological stress forcing the stepped mass extinction of the late Cenomanian.



TEXT-FIGURE 8
Bivariate diagram showing diversity and rate of radiolarian faunal turnover plotted against the spumellarian/nassellarian diversity ratio. Note that immediately post extinction, recovery capacity is stronger in nassellarians than in spumellarians.

### Radiolarian turnover related to other biotic events occurring in the planktonic realm

A first glance at text-figure 5 reveals a strong correlation among the diversity curves of different fossil groups. The comparison between the nassellarian-spumellarian diversity curves and the nannoplankton diversification rate shows an inverse correlation (text-fig. 5 curves 1, 2, 5). High rates of nannoplankton speciation coincide with widespread black shales and when radiolarian diversity drops the nannoplankton reaches a maximum peak in diversification. This inverse correlation may be explained by nutrient availability in the oceanic surface waters. In this sense planktonic blooms in the oceanic structure would depend on the position of the nutricline within the photic zone. This mechanism was argued by Erba (1994) to explain the possible competition occurring between nannoconids and coccolithophorids during the Cretaceous. It is suspected that radiolarians and their dinoflagellate symbionts had the same preferences for the lower euphotic zone between 80-150m (see Petrushevskaya 1971, Casey et al. 1979; Takahashi 1991) as nannoconids, whereas coccolithophorids and other nannoplankton were restricted to the upper euphotic zone. The abrupt increase in nutrient availability in the surface waters (shallow position of nutricline) induced a rapid bloom of coccolithophorids having low speciation, and a decreased production of nannoconids. This mechanism may have had the same result in the radiolarian-dinoflagellate couple, their diversities being severely reduced during periods of nannoplankton diversification. It seems probable that a shallow nutricline favors the rapid speciation of radiolarians while a deeper position of the nutricline increases the speciation of coccolithophorids. These adaptive strategies pursued by planktonic organisms faced with different trophic resource regimes seem to have played a major role in their diversity regulation; periods of diversification may be associated with lower resource levels, whereas pelagic extinction are linked with higher resource levels (Casey and Sloan 1971; Valentine 1971). In this sense radiolarian diversification seems to have occurred during periods of constant food source in oligotrophic conditions in a stable physical environment.

We also note that the calpionellid extinction and the progressive diminution in the abundance of nannoconids (Roth 1978) occur during the radiolarian diversity minimum in the late Valanginian. This fall in nannoconid diversity ends in the nannoconid crisis (Erba 1994), which occurs after the radiolarian diversity minimum observed at the lowermost Aptian.

The first occurrence of Cretaceous "primitive" and small planktonic foraminifers, the Hedbergellidae, occurs near extinction event E1 (early Valanginian) and the explosive development of these small forms is concomitant with radiolarian extinction event E2 (late Hauterivian, text-fig. 5, curves 6, 7). The origination of the first Cretaceous large planktonic foraminifers coincides with the diversity minimum which occurred in the early Aptian and the explosion of these forms (mainly hedbergellids and ticinellids) immediately follows the E3 extinction event. Small primitive planktonic morphotypes reappear during the early Albian. The subsequent diversification of these forms in the middle-late Albian coincides with the highest diversity of the radiolarian fauna during Cretaceous time. In strata immediately adjacent to, and within, OAE-1b, only small primitive hedbergellids are found. According to Bréhéret and Delamette (1989) this is due to a major expansion of the oxygen minimum zone restricting planktonic foraminifers to the surface waters, which triggers an unstableness in marine environments. In the opinion of Guex (1992, 1993) periods of increased ecological stress favor the repetitive appearance of simplified forms of small size and of very primitive aspect. Some of these end-forms can generate, in extreme cases, new simplified groups which are often at the origin of new evolutive lineages. The pressure of environmental stress is manifested in the late Albian by a general decrease in hedbergellid size and simplification in morphology (reduction of chambers, globigerinelloids-type). This hypothesis may explain the iterative occurrence of small planktonic foraminifers probably throughout the Cretaceous.

At the Cenomanian-Turonian boundary we note that the major foraminiferal and radiolarian E5 extinctions are simultaneous. Jarvis et al. (1988) recorded a bloom of small planktonic forms in OAE-2 (late Cenomanian) which is exactly parallel to that described above.

Finally it is interesting to note that the Berriasian, late Valanginian and late Hauterivian-Barremian radiolarian abundance peaks coincide with episodes of low diversity within this group. In other words, the periods of radiolarian low diversity are exceedingly rich in individuals.

### Evolutionary pattern of radiolarians in the Cretaceous

In general, patterns of evolution can be considered in terms of successive extinction and radiation periods. An excellent example of this is the evolution of the radiolarians throughout the Cretaceous. The importance of biotic interactions in the structure of planktonic communities and the simultaneity of biotic crises during the Cretaceous point to a first-control by the physical environment. In this sense, the high sensitivity of radiolarians to external change enables us to analyze their paleoceanographic and paleoclimatic meaning during episodes of radiolarian turnover.

Following detailed analysis of text-figures 5 and 6, the extinction-radiation pattern of the radiolarian faunal turnover can be sequenced in four successive phases which are summarized in text-figure 7. This evolutionary process occurred several times throughout the Cretaceous period following approximately the same pattern as that described below:

### Phase 1. Radiolarian extinction event

Times of relative sea level fall mean times of restriction and deterioration of the neritic habitat, such as the increase in temperature and salinity gradients (Hallam and Wignall 1997). During falls of sea level the thermal gradients become sharper as inferred from climatic deterioration observed in fauna and floras. The relative cooling trend observed in particular episodes during the Cretaceous seems to correspond to periods of decreased volcanic degassing (deceleration in oceanic crustal production) and hence lower atmospheric $CO_2$ concentrations. During sea level falls platforms are subaerially exposed, sediments are redistributed and in turn, there is a moderate increase in the nutrient supply to the open ocean. This distribution leads to a decrease in the productivity of epicontinental seas (as nutrient transfer in these areas decreases), whereas productivity in the open ocean (helped by reactivating deep sea system currents) is slightly enhanced. Consequently, the pelagic environment may reach mesotrophic water conditions. The combination of these components in a progressively narrower neritic habitat leads to a gradual increase in ecological stress. We observe that diversity falls during a period of platform progradation and a decrease in the marine phosphorus burial rates.

The abrupt drop in biodiversity coincides with the beginning of positive $\delta^{13}C$ excursions. Some discrete short anoxic episodes may occur in hemipelagic and pelagic environments as indicated by organic matter of terrestrial origin. Thereafter, radiolarian diversity falls rapidly, but intraspecific variability is progressively enhanced. During these initial periods of environmental instability, the strong extinction resistance of spumellarians leads to a noticeable increase in the diversity ratio of spumellarians to nassellarians (text-fig. 8). The progressive environmental deterioration has important consequences in other planktonic taxa like planktonic foraminifers or calcareous nannoplankton. In this way the ecological niche left by the gradual elimination of radiolarians induces the opportunistic proliferation of small planktonic foraminifers several times during the mid-Cretaceous. Simultaneously, we observe a progressive increase in nannoplankton diversity. It seems likely that the association between poor to moderate resources and unstable environment constitutes a causal link with the observed decline of diversity.

### Phase 2. Lowest radiolarian diversity

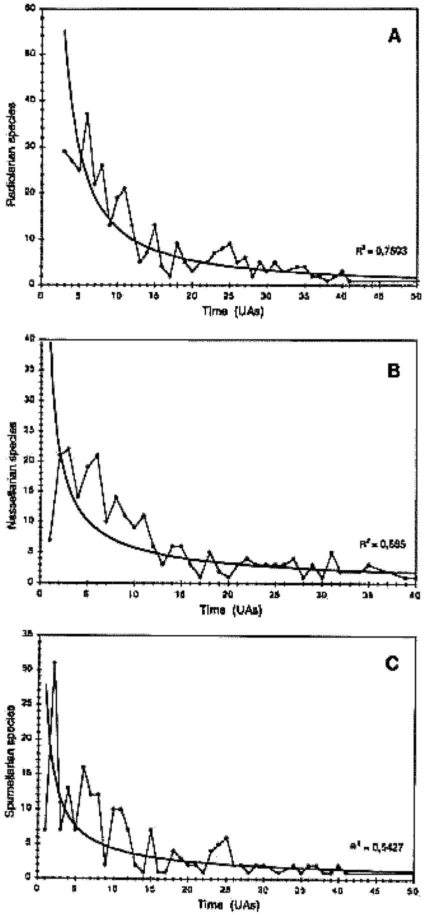
Lowest radiolarian diversity is reached at times of a low stand of sea level and the initial stages of transgression. The progressive decline in diversity is seriously deteriorated by the development of anoxic water during the initial stages of transgression. We observe that minimum diversity peaks correlate well with oceanic anoxic events. The strong alliance between sea level change and oceanic anoxic phases is the most reliable mechanism for radiolarian extinction in the Cretaceous. The deposition of laminated organic-rich shales of OAE's occurs during an early stage of the transgressive cycle when warm saline bottom waters enhance deep water renewal and allow the transit of organic matter from productive surface to bottom sediments and hence carbon preservation.

Another interesting observation is the coincidence of lowest radiolarian diversities and maximum values in $\delta^{13}C$ (text-fig. 6). There is general agreement that strong positive $\delta^{13}C$ excursions are indicators of high primary productivity in the oceans; this is attributed to the increased preservation of $^{12}C$ in organic matter during anoxia in periods of rapid warming.

Caldeira and Rampino (1991) have signaled the importance of episodes of intense flood-basalt volcanism as mechanisms leading to large degassing rates of $CO_2$. The huge amount of volcanic $CO_2$ and $SO_2$ originating in such events leads to episodes of rapid global warming and humid climate. In this scenario intensified water cycling is triggered by elevated $CO_2$ concentrations in the atmosphere (Weissert and Mohr 1996). This warm and humid climate intensified the chemical weathering, increasing runoff and nutrient transfer. In fact, the disappearance of nutrient barriers (lowland river plains and estuaries) during rapid transgression led to most nutrients being transported directly into the ocean and advected far along platform margins (Föllmi et al. 1994).

The faunal turnover also occurs at time of drowning in neighboring carbonate platforms (platform destruction, condensation and phosphogenesis). The elevated $^{87}Sr/^{86}Sr$ ratio of sea-water indicates intense continental weathering during these periods, favoring strong continental input and the consequent leaching of many nutrients to the basin (basically phosphate, nitrate and silica). As a consequence, an important nutrient mobilization starts in the oceanic water masses characterized by a homogeneous water column (poorly stratified). The surface water becomes well-mixed and deeper (due to relative cooling of the surface) with high turbulence, probably wind-induced by heavy rainfall and coastal upwelling. The organic matter must have partially decomposed in these relatively shallow and turbulent waters, thus encouraging plankton blooms (Ittekkot et al. 1992). However most organic matter produced by phytoplankton photosynthesis is rapidly stored. The origination of biogenic particle aggregates (fine particles and freshly photosynthesized organic matter) facilitate rapid removal. These biogenic aggregates possess rapid sinking speeds, which make their dissolution in the water column difficult (poor recycling of nutrients). The intensity of vertical mixing (flow of nutrients into the photic zone) is largely a function of atmospheric and oceanic circulation, and strong upwelling during the transition from low stand to transgressive periods, triggers primary and secondary producers. The explanation may be found in the drastic overturn occurring in the oceanic circulation induced by intense evaporation during warm and humid periods, increasing the generation of warm saline bottom waters (Arthur and Premoli-Silva 1982).

This anomalous input of nutrients leads to eutrophic conditions, in which the amount of plankton production increases linearly to a level where some of the essential nutrients become limiting; after this point the productivity gradient fades and the planktic ecosystem becomes highly unstable. In these circumstances diversity falls and favors the emergence of opportunistic species. These environments are highly productive in terms of the amount of organic matter produced by photosynthesis, but when the phytoplankton bloom exhausts essential nutrients, the bacterial decomposition of large amounts of organic matter depletes the available oxygen and generates widespread anoxic conditions. These periods coincide with a short decrease in marine phosphorus burial rates.



TEXT-FIGURE 9
Survivorship curves showing the relative life duration of Cretaceous radiolarian species. Y-axis = number of species. X-axis = life duration expressed in terms of number of UAs. A) Global curve; B) Nassellarian curve; and C) Spumellarian curve.

To summarize, periods of lowest diversity coincide with high nutrient concentrations in surface water and consequently are highly productive of organic matter produced by phytoplankton photosynthesis. This high biological production and poor nutrient recycling favored the storage of organic matter in the deep ocean. This scenario obviously favored the expansion and intensification of the oxygen minimum zone (OMZ) and hence the widespread oceanic anoxic episode. This represents the final stage in radiolarian faunal turnover and gives rise to a subsequent radiation episode.

Periods of maximum ecological stress, in which the dramatic increase in fertilization collapses primary productivity, are characterized by: a) lowest radiolarian diversity; b) increased radiolarian and dinoflagellate abundances (high number of opportunistic individuals); c) a balanced ratio of spumellarians to nassellarians, as spumellarian diversity progressively declines; and d) high rates of nannoplankton speciation. Basically, radiolarian faunal turnover events occur at times of rich resources and extreme environmental stress resulting in assemblages of the lowest diversity.

### Phase 3. Radiolarian radiation event

The radiolarian radiation event starts within the transgressive sea level rise immediately after the anoxia, i.e. during well-oxygenated periods where the recovery of neritic habitat is favored by an increase in speciation. Slow rates of deep sea circulation lead to a drastic reduction of the oxygen minimum zone and CCD falls enhance deposition of carbonate in hemipelagic settings. Marine circulation becomes less intense during the radiation of new taxa as inferred from paleobiogeographic patterns; a noticeable disappearance in the provincialism of pelagic microfossils is observed during these episodes favored by the weakening of oceanic thermal gradients (climatic amelioration).

During transgressive sea level change the re-activation of surficial system currents takes place, favoring a constant flow of nutrients which, by efficient recycling, leads to a consequent decrease in carbon export from the oceanic to the sedimentary reservoir, and to progressively lower $\delta^{13}C$ values. This moderate productivity, as inferred by the carbon signal, is indicative of mesotrophic to oligotrophic water regimes in the open ocean. The slow rate of deep-sea circulation and the surface-reduced OMZ favor the widespread development of well-oxygenated conditions through the water column biasing the storage of organic matter in the deep ocean. At this time, phosphorus accumulation rates display a progressive increase probably due to the efficient oxidation of organic marine matter in the deep-sea environment.

Periods of radiation of this planktonic biota also coincide with periods of regeneration in adjacent carbonate platforms and are characterized by a progressive increase in radiolarian diversity (as well as dinoflagellates); concomitantly the diversification rate of calcareous nannoplankton drops. The rapid decrease in the spumellarian/nassellarian diversity ratio is noticeable due to the effectiveness of nassellarian recovery. Radiolarian diversity increases but intraspecific variability is relatively weak to moderate (typical for stable environments). To sum up, a constant flux of resources together with a stable environment leads to an increase in diversity.

### Phase 4. Highest radiolarian diversity

Phases of high radiolarian diversity correspond with periods of a relatively high stand in sea level (i.e. early late Albian, see text-fig. 6). These occur during climatic transition from warmer to cooler periods. At such times, a poor and debilitated deep oceanic circulation leads to a well-stratified water column with poorly mixed surface waters. The minimized runoff and nutrient supply together with the probable inflow of nutrient-poor low salinity waters leads to more rapid nutrient depletion of surficial waters, resulting in low primary production. These layers are gravitationally stable and nutrients below the surficial layers have low sinking speeds, which favor their dissolution in the water column. This ensures rapid and effective recycling of nutrients in oligotrophic regimes. The poor preservation of organic matter leads to relatively low $\delta^{13}C$ and the deceleration of the oceanic biological $CO_2$ pump (increase in the ratio of organic carbon to carbonate carbon).

Relative high sea level is the transition period for carbonate platform aggradations and for the restoration of oligotrophic regimes. The highest radiolarian diversity coincides with relatively high values of phosphorus burial rates or in the shift toward lower values.

In the open ocean oligotrophic regimes are characterized by a low concentration of essential nutrients and therefore low primary productivity; but from an ecological point of view they represent stable environments. At such times, radiolarian diversity reaches maximum values and a balanced spumellarian to nassellarian ratio is obliterated. Simultaneously, calcareous nannoplankton show low rates of speciation. The combination of very poor resources and stable environment leads to highest radiolarian diversity.

### Radiolarian evolution: Relative extinction resistance of spumellarians versus nassellarians

The spumellarian/nassellarian diversity ratio does not vary considerably throughout the interval studied. The quasi-parallelism observed between diversity curves of the two groups during most of the Cretaceous (text-figs. 4B and 5, curves 1-2) means that there was no direct competition between them. However, we note that post-extinction recovery capacity is stronger in nassellarians than in spumellarians. Text-figure 4B shows a very strong increase in nassellarian diversity following extinction events E1 to E4.

Text-figures 2 and 4 illustrate that spumellarians are more resistant to extinction than nassellarians. For example, extinction events E1, E3 and E4 are clearly discernible in the extinction/recovery diagram of nassellarians (text-figs. 2B and 2C) but are indistinguishable in the diagram concerning spumellarians (text-figs. 2B and 2D). An identical conclusion can be drawn by examining the diversity and extinction peak diagrams of the two groups (text-figs. 4C and 4D): the five extinction peaks E1 to E5 are obvious in text-figure 4C (nassellarians) but only E2, E4 and E5 are discernible in text-figure 4D (spumellarians). The Tithonian-Barremian interval corresponds to a more oxic oceanic environment, except for very limited and thin levels of black shales (Lini et al. 1992; Jud 1994). Text-figure 4B demonstrates that the late Valanginian nassellarian extinction (E1) is clearly marked in the stratigraphic record but the same event is indiscernible in spumellarians. In contrast, the Aptian-Turonian period is punctuated by large and widespread anoxic events which are clearly responsible for extinctions E3 to E5 and show clearly that nassellarians are much more affected by the anoxic events OAE-1a to OAE-2 (extinction events E3 to E5) than spumellarians.

Another way of demonstrating extinction-resistance of spumellarians is to plot the rate of radiolarian faunal turnover against the spumellarian/nassellarian diversity ratio (text-fig. 8). The two curves in this text-figure show that high S/N diversity ratios coincide with typical periods of lower nassellarian diversity following extinction event peaks. In contrast, during the initial stages of radiation, nassellarian recovery is noticeably stronger than spumellarian recovery (lowest S/N diversity ratios), but as global diversity increases, radiolarian diversity rapidly balances.

It is interesting to recall that nassellarians probably derived from spumellarians during the Early-Middle Triassic. In the Late Triassic nassellarians were very diverse. However, most radiolarians surviving the Triassic-Jurassic boundary crisis were spumellarians (Carter 1994; Hori 1997). Our own observations show that spumellarians are more opportunistic than nassellarians. For example in the Jurassic it is well known that spumellarian genera such as *Pantanellium* Pessagno (Pessagno et al. 1987) and *Vallupus* Matsuoka (Matsuoka 1996) are opportunistic. From the beginning of the Jurassic, nassellarians developed very high taxonomic diversity and during the Jurassic and Cretaceous they are numerically equal with their ancestral group (about the same number of species in both groups). This observation shows that the evolutionary rate of nassellarians was greater than that of the spumellarians following extinction periods. The nassellarians have a mean relative life span of 11 UAs (Unitary Associations) compared with that of 12 UA's for the spumellarians (about 10% more).

The greater evolutionary potential of nassellarians is strongly correlated with a high sensitivity to external events generating extinctions. This is confirmed by the survivorship curves shown in text-figure 9 where the time component is expressed in number of UAs (each UA has a mean estimated duration of about 1 million years). Survivorship curves plot the number of radiolarian species surviving for different times; most still survive after a short time, but as time passes the members of the original sample drop out one by one. The slope of the survivorship curves measures the evolution rates for the group (curves fall rapidly for groups evolving quickly). These curves are similar but show that short-lived nassellarians (text-fig. 9B) are more abundant than short lived spumellarians (text-fig. 9C). The general curve (text-fig. 9A) shows that about half our Cretaceous radiolarian species have quite a short life; therefore this group of microfossils has an excellent biochronological power of resolution.

We disagree with the common belief that abundant spumellarians are diagnostic of shallow waters and abundant nassellarians are characteristic of deep waters (e.g. Casey 1971, 1993; McMillen 1979; Takahashi and Honjo 1981; Premoli Silva et al. 1999). According to Hollande and Cachon-Enjumet (1963), living spumellarians are commonly found at a depth of 1000 meters. As another example, the deep water sediments of the major mass extinction at the Triassic-Jurassic boundary contain up to 95% spumellarians (Carter 1994; Hori 1997). Koutsoukos et al. (1989) have shown the good ecophenotypic adaptation of the planktonic foraminifers *Favusella* to high salinity and shallow water environments during the mid-Cretaceous. Some samples from shallow environments contain abundant specimens of this disaster foraminifer and are also very rich in spongy spumellarians (O'Dogherty, personal data). In other words we believe that the spumellarian/nassellarian abundance ratio is more likely a potential indicator of ecological stress than of living depth. The spumellarian/nassellarian ratio is highly varied in radiolarite samples; this is certainly due to preservational factors such as selective dissolution in the water column during postmortem sinking and in the sediment. Such differences in preservation could be generated by variations in robustness, chemistry of the skeletons, and dissolution during acid processing (Blome and Reed 1993).

Nassellarians start from a very simple initial spicule and apparently have a large degree of freedom to diversify following extinction periods. The initial structures of spumellarians are usually much more complex and they may lack such freedom. This is probably why the taxonomic diversification rate of nassellarians is higher than that of spumellarians following extinction episodes.

## CONCLUSION

Our new paleontological approach to analyzing faunal turnover rates of Cretaceous radiolarians leads us to several new paleobiological conclusions. We observe that under conditions of ecological stress, the biotic response of the group seems to be different in nassellarians and spumellarians. The spumellarians are much more extinction-resistant during episodes of critical environmental deterioration. However, we observe that nassellarians possess a relatively higher evolutionary rate than spumellarians during periods of radiation, i.e. immediately after the group attains lowest diversity values. These two points mean that nassellarians have a relatively higher biochronological power of resolution than spumellarians. In addition, the diversity ratio between spumellarian/nassellarian can be used as an indicator of climatic deterioration or an index of ecological stress.

Correlations of Cretaceous radiolarian extinction and diversity events with paleoceanography and other biotic events (text-figs. 5-7) tend to confirm several conclusions of authors working on other groups of fossils. The different diversity curves show that the largest biotic response usually occurred during the early stages of climate change, as indicated by the coincidence of radiolarian diversity minima, heavy $\delta^{13}C$ values, overturn of temperature, and widespread oceanic anoxia. In general, there exists a long-term correlation between sea level, temperature, carbon isotopes, the phosphorus burial curve, and faunal diversity.

The extinction mechanism involves the succession of two major paleoceanographic controls in the evolution of the radiolarians during the Cretaceous: 1) the sea level regression, probably induced by tectonic reorganization, leads to a drastic drop in diversity as a response to changes in ocean water circulation; and 2) the reduction in habitat caused by the widespread development of oceanic anoxic water masses during post-regressive periods leads to diversity minima and triggers faunal turnover. From an evolutionary point of view, enhanced environmental stress ultimately produces assemblages of the lowest diversity and large population size, in which new simplified morphotypes may be generated that frequently represent the source of a new evolutionary lineage.

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