Evolution and Extinction in the Marine Realm: Some Constraints Imposed by Phytoplankton [and Discussion]

A. H. Knoll and J.-J. Jaeger

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Evolution and extinction in the marine realm: some constraints imposed by phytoplankton

By A. H. Knoll

Botanical Museum, Harvard University, Cambridge, Massachusetts 02138, *U.S.A.*

The organic and mineralized remains of planktonic algae provide a rich record of microplankton evolution extending over nearly half of the preserved geological record. In general, Phanerozoic patterns of phytoplankton radiation and extinction parallel those documented for skeletonized marine invertebrates, both augmenting and constraining thought about evolution in the oceans. Rapidly increasing knowledge of Proterozoic plankton is making possible the recognition of additional episodes of diversification and extinction that antedate the Ediacaran radiation of macroscopic animals. In contrast to earlier phytoplankton history, the late Mesozoic and Cainozoic record is documented in sufficient detail to constrain theories of mass extinction in more than a general way. Broad patterns of diversity change in planktonic algae show similarities across the Cretaceous–Tertiary and Eocene–Oligocene boundaries, but detailed comparisons of origination and extinction rates in calcareous nannoplankton, as well as other algae and skeletonized protozoans, suggest that the two episodes were quite distinct. Common causation appears unlikely, casting doubt on monolithic theories of mass extinction, whether periodic or not. Studies of mass extinction highlight a broader class of insights that palaeontologists can contribute to evolutionary biology: the evaluation of evolutionary change in the context of evolving Earth-surface environments.

1. Introduction

Palaeontologists seeking to understand evolution from the evidence of the fossil record are a bit like astronomers who rely on Earth-based telescopes to study the heavens. The atmosphere is transparent or nearly so to radiation in some spectral regions, but opaque for others. Thus there are some astrophysical phenomena that the astronomer can observe clearly and others about which he or she can infer nothing at all. Because of the selective information loss attendant on fossilization, the palaeontological record is similarly 'transparent' to some evolutionary phenomena, permitting one to document palaeobiological pattern and draw reasonable inferences about process, whereas it is 'opaque' for others. Complicating interpretation and the search for evolutionary generality is the fact that the several major fossil records – those of terrestrial animals, land plants, marine invertebrate animals, benthic protists and microplankton – have different regions of evolutionary 'opacity' and 'transparency'. Thus palaeobotanical patterns permit inferences about the importance of resource competition in tracheophyte evolution but shed relatively little light on the evolutionary role of herbivory (see, for example, Knoll 1986; Knoll & Niklas 1987; Lidgard & Crane 1988; but see Wing & Tiffney 1987), whereas for the marine invertebrate record, much the opposite appears to be true (see, for example, Benton 1987; but see Jackson 1988; Vermeij 1987). This, of course, does not necessarily indicate that plant and marine invertebrate evolution are driven primarily by competition and predation, respectively. It means that the nature of plants and animals and the differing properties of their fossil records make such comparisons extremely difficult.

Studies of evolutionary responses to environmental change are attractive, in part, because they provide a focus for the direct palaeobiological comparison of disparate taxonomic and ecological groups of organisms. In this context, the fossil record of phytoplankton assumes particular significance. The distinctive ecology, life cycles and metabolism of planktonic algae provide useful counterpoint to often zoocentric discussions of evolution and extinction in the marine realm. Further, phytoplankton are widely distributed in sedimentary rocks and have a long evolutionary record; plants and animals may be the most conspicuous fossils in Phanerozoic rocks, but planktonic protists are the most abundant. Particularly important, the calcareous tests of at least some photosynthetic and heterotrophic microplankton species preserve isotopic indications of the relative depth, temperature and productivity of the water masses in which they formed (Douglas & Savin 1978; Boersma *et al.* 1987). Thus planktonic microfossils can provide sensitive and stratigraphically precise indications of change in physical environments. In so far as mass extinctions are widely viewed as the consequences of environmental change or perturbation, phytoplankton, then, can do much to constrain thinking about these signal evolutionary events.

2. The earliest record: Proterozoic microplankton

Prokaryotes undoubtedly colonized marine water columns early in Earth history, but the oldest fossils reasonably interpreted as plankters are spheroidal Problematica found in *ca.* 2000 Ma old rocks from Canada (Hofmann 1976; Knoll *et al.* 1978). The oldest probable eukaryotic microplankton are assemblages of acritarchs from 1400–1800 Ma old successions in China (Zhang 1986), the Soviet Union (Keller & Jankauskas 1982), Australia (Peat *et al.* 1978), and the United States (Horodyski 1980). All consist of morphologically simple, spheroidal cysts of limited apparent diversity; at least in Australia, this morphological record is complemented by abundant steranes, biomarker molecules that independently confirm the role of eukaryotes in Middle Proterozoic ecosystems (Jackson *et al.* 1986).

The patchy stratigraphic coverage and limited morphological complexity of these early remains preclude statements about radiation and extinction, but it is clear that by 850–950 Ma ago, a significant morphological radiation of phytoplankton had begun. The plankton record of this era has long been known to include spheroidal acritarchs with modestly sculptured walls (see, for example, Vidal 1976; Jankauskas 1982), but discoveries over the past decade indicate that a wide variety of acanthomorphic and otherwise complexly ornamented forms also evolved, many of them unusually large relative to Palaeozoic taxa (see, for example, Timofeev *et al.* 1976; Knoll 1984; Yin 1985, 1987; Butterfield *et al.* 1988; Zang 1988; Zang & Walter 1989). Critical data on stratigraphic distribution remain limited, but on present evidence it appears that the Proterozoic acritarch biota reached its zenith in both diversity and morphological complexity during the Vendian interval (*ca.* 600 Ma ago) (Zang 1988; Zang & Walter 1989). The youngest assemblages that contain distinctively Proterozoic, large, process-bearing cysts occur in rocks stratigraphically above Varangian glacial deposits but below Ediacaran metazoans (see Awramik *et al.* 1985; Yin 1985, 1987; Zang 1988; Knoll & Ohta 1988). Latest Proterozoic biotas are dominated by simple leiosphaerid acritachs and small, spiny micrhystrids (Volkova 1972; Vidal & Knoll 1983). Thus by the time large animals first diversified, planktonic protists had already undergone at least one protracted radiation and one or more episodes of major extinction (Vidal & Knoll 1983; Zang 1988; Zang & Walter 1989). The early phytoplankton record effectively doubles, and with work may treble, the span of geological history through which palaeontological patterns of extinction can be studied.

3. Increasing diversity and turnover: the Palaeozoic record

Prasinophyte green algae and other cyst-forming phytoplankton diversified markedly during the early Cambrian, and an even more pronounced radiation followed during the Ordovician (Volkova *et al.* 1979; Tappan 1980; Vidal & Knoll 1983). Skeletonized microplankton – the siliceous radiolaria and problematic scale-forming protists – also appeared during this interval (Nazarov & Ormiston 1985; Allison & Hilgert 1986). Recently, it has been established that phytoplankton experienced a brief but pronounced extinction episode at the end of the Ordovician period (Colbath 1986; Martin 1988). Recovery was rapid, as previously subordinate as well as newly evolved genera diversified to establish a diverse but distinctively Silurian phytoplankton biota (Downie 1973; Dorning 1981). Widespread extinctions again reduced acritarch diversity markedly near the end of the Devonian Period, and, curiously, the diversity of organic-walled phytoplankton remained low throughout the remainder of the Palaeozoic era (Downie 1973; Tappan 1980). The precise timing of this diversity collapse is not clear, but judging from recent publications (see, for example, Martin 1984; Wicander & Playford 1985), many late Devonian extinctions may have occurred within the Famennian or close to the Devonian–Carboniferous boundary, rather than being concentrated at the Frasnian–Fammenian boundary, the point most commonly inferred to have been a time of abrupt ecosystem collapse (see, for example, McGhee 1988). Because some extant microalgae do not produce preservable cysts, and some form them only under particular environmental conditions, the absence of an obvious post-Devonian rebound in acritarch diversity does not necessarily mean that planktonic algae remained depauperate for the remainder of the era. It is equally possible that late Palaeozoic oceans teemed with phytoplankton, but that the dominant taxa did not produce fossilizable cysts. (Although this confounding feature of organic-walled microplankton fossils is particularly pertinent to discussions of late Palaeozoic phytoplankton, it must, of course, be kept in mind in all considerations of acritarch and dinoflagellate diversity.) According to Tappan (1982), acritarchs suffered further extinctions at the close of the Permain.

The major intervals of radiation (early Cambrian, Ordovician) and extinction (end Ordovician, late Devonian, late Permian) seen in Palaeozoic phytoplankton clearly parallel those documented for skeletonized marine invertebrates (Sepkoski 1982) (figure 1). Benthic calcareous algae also approximate this pattern: lightly calcified Problematica diversified early in the Cambrian and more-heavily skeletonized red and green algae radiated during the Ordovician, whereas major extinctions mark the ends of the Devonian and Permian (Chuvashov & Riding 1984; Flügel 1985). At the very least, these parallels constrain thinking about Palaeozoic evolution by indicating that the major episodes of diversification, extinction, and innovation in biomineralization documented for marine invertebrates were not limited to animals, but were ocean-wide in extent. Hypotheses advanced to explain any one of these events must apply to photoautotrophs as well as heterotrophs, single-celled protists as well as developmentally complex animals, and plankton as well as benthos.

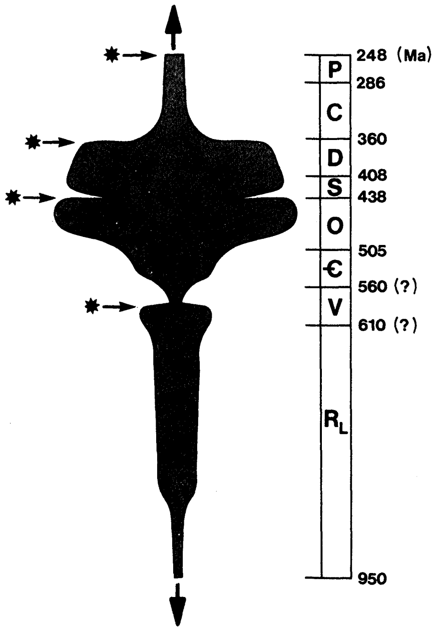

Figure 1. Diagram showing major patterns of change in phytoplankton cyst diversity during the late Proterozoic and Palaeozoic eras. Much remains to be accomplished in the taxonomic description of early phytoplankton; thus the figure is drawn to convey only general patterns of diversification and extinction, and a diversity scale for the diagram has been omitted intentionally. Asterisks with arrows indicate times of major extinction. Stratigraphic intervals are indicated by initials as follows: R_L, Late Riphean; V, Vendian; €, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian. The timescale is that of Harland *et al.* (1982), except for the beginning and end of the Vendian interval. Question marks denote uncertainties in those dates.

4. MESOZOIC AND CAINOZOIC RADIATIONS AND EXTINCTIONS

The Mesozoic era was a time of major morphological and physiological innovation among pelagic phytoplankton. At least some Palaeozoic acritarchs may have dinoflagellate affinities, but dinoflagellates that produce cysts unambiguously attributable to that group first became diverse and abundant during the late Triassic, with notable Jurassic and, especially, mid- to late Cretaceous radiations. Calcareous nannoplankton (largey attributable to the Coccolithophyceae, but also including the extinct discoasters and nannoconids, as well as – in some treatments – a few calcareous dinoflagellates) also have a scattered and sometimes questioned Palaeozoic record, but they, too, rose to ecological abundance in the Jurassic and diversified markedly during the second half of the Cretaceous. Diatoms and silicoflagellates similarly show Mesozoic origins and notable late Cretaceous increases in abundance and diversity.

Modern ocean basins date from this same time, providing the geological advantage of thick, often relatively complete and little-altered sedimentary sequences, as well as a much improved record of palaeogeography and palaeoceanographic circulation. (Undoubtedly, this circumstance contributes to the *perception* of Mesozoic phytoplankton radiations. The minute calcite plates of calcareous nannoplankton and delicate opaline silica frustrules produced by diatoms might well be destroyed in older, more highly altered sediments, and if early dinoflagellates lacked archaeopyles, their affinities would not be recognizable. None the less, the clear diversity changes recorded within Mesozoic sedimentary successions containing well-preserved fossils indicate that during the late Mesozoic, a genuine radiation of microplankton took place, one that included heterotrophic as well as photoautotrophic protists.) Carbon, oxygen and strontium isotopic ratios in microplankton tests themselves contribute to a refined understanding of climatic, oceanographic, and biogeochemical change over the last 100 Ma. Thus, compared with those of earlier eras, late Mesozoic and Cainozoic sediments not only contain a much expanded and improved record of phytoplankton evolution; they also provide a far better documentation of the environmental context in which that evolution took place.

Arguments for cyclicity in mass extinction (Raup & Sepkoski 1984), with their implied unity of causation, rest largely on the timing and nature of events during this interval. At first glance, the Mesozoic–Cainozoic phytoplankton record, like that of Palaeozoic acritarchs, appears to corroborate palaeozoological data on the timing and severity of mass extinctions. For example, dinoflagellates show significant decreases in diversity during the Norian, Tithonian, Cenomanian, Campanian–Maastrichtian, late Eocene, and Middle Miocene ages (Bujak & Williams 1979). Calcareous nannoplankton also show diversity drops during the late Jurassic, Cenomanian, Maastrichtian, and late Eocene (Haq 1973; Roth 1987). However, closer examination of these diversity changes, especially the relatively well documented events at the Cretaceous–Tertiary and Eocene–Oligocene boundaries, reveals a more complex picture that places sharp constraints on our general thinking about these events. In the following paragraphs, I briefly review the much scrutinized record of phytoplankton extinctions across the Cretaceous–Tertiary (K–T) and Eocene–Oligocene (E–O) boundaries and then record a few observations about the less frequently discussed patterns of phytoplankton originations associated with the same events.

Pelagic ecosystems experienced a profound disruption at the end of the Cretaceous period. Among calcareous nannoplankton and planktonic foraminifera, rates of extinction increased sharply at the K–T boundary, resulting in nearly total devastation of the diverse biotas that had populated late Cretaceous oceans (Bramlette & Martini 1964; Percival & Fischer 1977; Perch-Nielsen *et al.* 1982; Smit & Romein 1985; Jiang & Gartner 1986; Brinkhuis & Zachariasse 1988). Arguments persist as to whether the extinctions occurred instantly, in rapid pulses, or gradually through 10000 to 100000 years, but there is no question that the terminal Cretaceous event must be considered abrupt on any save perhaps the finest of geological timescales.

This is not to say that the terminal Cretaceous event was visited upon an evolutionarily static world. Several marine invertebrate groups declined in diversity though part or all of the Maastrichtian, and a similar pattern can be seen in the calcareous nannoplankton (Roth 1987) (figure 2).

The dinoflagellate record also shows a major late Cretaceous diversity reduction, but extinctions do not cluster at the K–T boundary. After a Santonian peak in species diversity, dinoflagellate extinctions reduced diversity more or less continuously throughout the Campanian and Maastrichtian (Bujak & Williams 1979). Detailed analyses of dinoflagellate assemblages in K–T boundary sections show changes in relative abundance but few if any extinctions at or near the boundary (Hultberg 1986; Brinkhuis & Leereveldt 1988; Brinkhuis & Zachariasse 1988). Diatoms and prasinophytes also appear to have weathered the K–T event relatively well (Tappen 1982; Fenner 1985; Kitchell *et al.* 1986). A characteristic common to many species within these three groups is the capacity to form a non-planktonic resting stage during periods of nutrient deprivation or other ecological stress (see, for example, Tappan 1980; Kitchell *et al.* 1986).

Extinction patterns across the Eocene–Oligocene boundary contrast with those seen at the end of the Cretaceous. As in the Maastrichtian, late Eocene to Early Oligocene phytoplankton extinctions took place throughout an interval of several million years. However, the younger episode is not terminated by a sudden dramatic rise in extinction rates. Phytoplankton do not show uniquely high or, in some groups, even notable increases extinction rates at the E–O boundary (Corliss *et al.* (1984); Perch-Nielsen (1986), and other papers in Pomerol & Premoli-Silva (1986)) (see figure 2). Last appearances among species are not synchronous (see Beckman *et al.* 1981; Corliss *et al.* 1984; Saunders *et al.* 1984), and even within species last appearances at different latitudes may be diachronous by as much as 500000 years (see, for example, Beckman *et al.* 1981). With some justification, Corliss & Keigwin (1986) have questioned whether the E–O event should be called a mass extinction at all. Calcareous nannoplankton, among other groups, experienced equally high or higher rates of extinction several times earlier in the Palaeogene (figure 2).

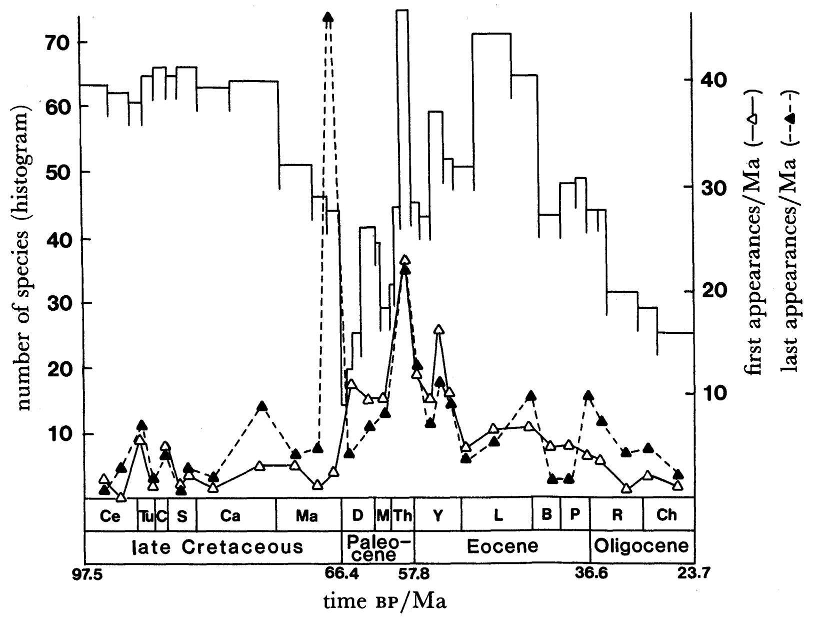

FIGURE 2. Taxonomic richness, first appearances per million years, and last appearances per million years for Late Cretaceous and Palaeogene calcareous nannoplankton species. Not all living species leave readily preservable coccoliths in sea-floor sediments. Therefore the fossil record probably provides an incomplete sampling of coccolithophorid diversity at any one time, a problem well known to invertebrate palaeontologists and palaeobotanists. In terms of the present discussion, which simply seeks to ascertain whether or not first and last appearances are clustered at or near stratigraphic horizons perviously identified as times of mass extinction, the data are considered adequate to the task. Species are defined palaeontologically as discrete morphological entities; palaeospecies do not necessarily correspond to biological species recognized in the living biota (see, for example, Aubry 1988). Data are plotted by nannoplankton zone, with the exception of origination and extinction data for zones shorter than one million years. In those cases, first and last appearances have been combined with those of the shorter adjacent zone. Cretaceous data are replotted from Roth (1987); Palaeogene data were compiled from Perch-Nielsen (1985*a*). The timescale follows Berggren *et al.* (1985) and Kent & Gradstein (1985). Ages indicated by initials are as follows: Ce, Cenomanian; Tu, Turonian; C, Coniacian; Ca, Campanian; Ma, Maastrichtian; D, Danian, M, Montian; Th, Thanetian; Y, Ypresian; L, Lutetian; B, Bartonian; P, Priabonian; R, Rupelian; Ch, Chattian. See Roth (1987) for a discussion of how such data are assembled, their advantages and disadvantages.

Inspection of origination rates highlights additional distinctions between the K–T and E–O boundaries. Immediately after the K–T extinction episode, so-called 'disaster plankton', especially the calcareous dinoflagellate *Thoracosphaera*, bloomed throughout depopulated oceans (Perch-Nielsen 1985*a*). Subsequent early Paleocene origination rates were quite high in calcareous nannoplankton (Perch-Nielsen 1985*a*) (figure 2), as well as in foraminifera. In contrast, the most interesting feature of turnover at the E–O boundary are the unusually low rates of origination characterizing early Oligocene phytoplankton. This can be seen in figure 2, and additionally characterizes silicoflagellates, ebridians and dinoflagellates (Bujak & Williams 1979; Tappan 1980). In many phytoplankton groups, the relative abundances of species change at several points during late Eocene and early Oligocene time, including at or near the epoch boundary (see, for example, Fenner 1985); however, unlike the aftermath of the K–T extinction, there is no spike of 'disaster' forms.

Thus, to judge from the marine phytoplankton record, the K–T and E–O events appear to be quite different. The K–T boundary is characterized by truly high rates extinction through a very short interval followed by expansion of 'disaster' species and, shortly thereafter, high rates of diversification. This pattern is consistent with hypotheses favouring ecological catastrophy, in particular the physical, chemical, climatic and/or productivity effects of a bolide impact (Alvarez *et al.* 1980). Despite the presence of microtektites and an iridium anomaly near the E–O boundary (Alverez *et al.* 1982; Ganapathy 1982), this transition is characterized by moderate rates of extinction spread through several million years followed by unusually low rates of origination, a pattern consistent with other data indicating a complex series of climatic and oceanographic changes that reduced both productivity and water-mass heterogeneity, eliminating the habitats of narrowly adapted species and simultaneously limiting the oceanographic opportunities for continued diversification (Corliss *et al.* 1984; Lipps 1986). My intent here is not so much to advocate particular causal explanations as to emphasize that the two best-known episodes widely characterized as mass extinctions were in fact very different events. This casts doubt on any monolithic theory of mass extinction, whether periodic or not.

5. Discussion

The phytoplankton record highlights several general and unresolved issues in the biology of diversification and extinction. First, there is the question of how mass extinctions relate to biological innovation. It has been proposed that mass extinction is a major force in the generation of evolutionary novelty, breaking the 'stagnation [of long running macroevolutionary régimes] by clearing ecospace for the radiation of new lineages' (Sepkoski 1985, p. 230). This appears to be the case for many animal groups, but phytoplankton present a more complicated picture. Morphological and physiological innovation are not obviously tied to mass extinction events. Microplanktonic species that proliferate after major extinctions look tolerably like those that disappeared; indeed the zooplanktonic foraminifera are famous for their patterns of iterative evolution (Lipps (1986) and papers cited therein). Figure 3 illustrates patterns of origination and extinction for late Cretaceous and Palaeogene calcareous nannoplankton genera. Plots of generic turnover should provide a better indication of morphological innovation than those of species, because genera are erected according to major features of morphology. High rates of origination follow the K–T boundary, but they also characterize other intervals of late Cretaceous and Palaeogene time. These latter bursts of diversification precede rather than follow extinctions and appear to reflect palaeoceanographic changes that promoted opportunities for diversification (see, for example, Roth 1987). Indeed, the most dramatic phytoplankton radiation of the Cainozoic era, the Miocene diversification of

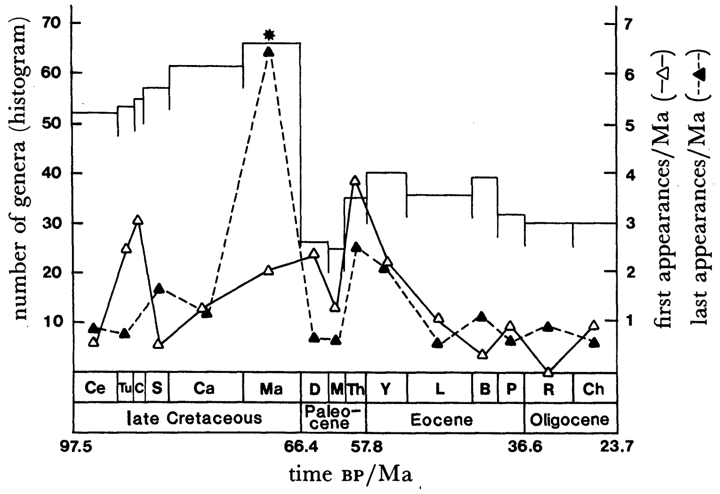

FIGURE 3. Taxonomic richness, first appearances per million years, and last appearances per million years for calcareous nannoplankton genera, plotted by age. The asterisk draws attention to the fact that the severity of the terminal Cretaceous event is underestimated because the Maastrichtian extinction rate was determined by dividing total extinctions by the 8 Ma duration of the age, whereas many last appearances are actually concentrated at or near the boundary. Data are compiled from Perch-Nielsen (1985*a*, *b*). Timescale as indicated in figure 2.

diatoms (Tappan 1980), cannot be related to the clearing of ecospace by mass extinction. In that there are long-term evolutionary trends in phytoplankton, these probably reflect continuing selection pressures of organism–organism interactions and, possibly, directional changes in the marine environment.

Another observation whose generality is challenged by the phytoplankton record is Jablonski's (1986*a*, *b*) hypothesis that characters selected for during 'normal' macroevolutionary régimes are distinct from those that promote survival during catastrophic mass extinctions. In theory, one might expect that an exception to this would be adaptations that facilitate survival during periods of ecological stress. Such features may be rare in marine invertebrates, but they are characteristic features of the life cycles of many bacteria, protists and plants. As Kitchell *et al.* (1986) have suggested for diatoms, patterns of differential phytoplankton survival across the K–T boundary may reflect just such adaptations.

Seeking another type of generalization, one can, perhaps optimistically, ask whether the details of phytoplankton origination and extinction that shed such useful light on terminal Cretaceous and Tertiary extinctions might prove equally valuable in constraining hypotheses about earlier episodes of mass extinction. Colbath (1986), working on the terminal Ordovician extinction, has made important strides in this direction, but much remains to be learned. Also, can the palaeoceanographic insights that isotopic geochemistry has provided for late Mesozoic and Cainozoic oceans be applied more fruitfully to older systems? Surely, the dearth of earlier calcareous plankton and deep-ocean sedimentary records limits direct extension of Cainozoic techniques, but can we recognize physical, chemical or sedimentological correlates of oceanographic change in shelf or epicratonic sediments that will improve our understanding of the palaeoenvironmental context of Proterozoic or Palaeozoic radiations and extinctions?

Finally, let me suggest that the study of mass extinctions represents a special case of a broader class of inquiry through which palaeontologists can make important contributions to evolutionary biology. The fundamental question is, how do populations and communities respond to environmental change? Earth history is marked by repeated changes in climate, oceanographic circulation, productivity, tectonic activity, geography and atmospheric composition of an order that lies outside of the range of ecological observation or experiment. If Cainozoic palaeoceanography provides any indication, such change is a continuing feature of the Earth's surface (see, for example, Boersma *et al.* 1987). On the geological timescales on which evolution is played out, the physical development of our planet may be a major engine of evolutionary change. In making this statement, I do not wish to minimize the importance of the biological component of the environments of the organisms (for microplankton, see Kitchell (1983) and other papers discussed in Knoll (1987)); nor do I deny that evolutionary change is itself a significant contributor to the development of Earth-surface environments. The context of biological history is the interplay between non-directional environmental perturbations of varying magnitude and directionally changing features of the biological and physical environment. Depending on the timescale, spatial dimensions and magnitude of environmental change, population responses may include migration, the evolution of broad tolerances or plastic responses or both, new adaptations, or extinction. The important point is that we can no longer assume in theory or practice that evolution continues for long periods of time under conditions of environmental constancy. Rapidly growing sophistication in our understanding of the historical development of Earth-surface environments provides a rich new framework for the interpretation of palaeobiological pattern, including extinctions.

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Discussion

J.-J. Jaeger (*Department of Vertebrate Palaeontology, Pierre and Marie Curie University, Paris, France*). Would it be possible to relate the increase of the diversity of the phytoplankton through time with an increase in its biomass?

A. H. Knoll. The short answer to Dr Jaeger's question is probably 'no', but given the importance of the question, let me explain briefly why I hold this view. The first problem is that we have no direct way of estimating phytoplankton biomass for ancient oceans. In that chlorophyll concentration (a parameter related to phytoplankton biomass) provides a useful indication of primary production for water masses in the present-day oceans, estimates of palaeoproductivity drawn from vertical oceanic $\delta^{13}C$ gradients recorded in calcareous microfossil tests might provide indirect insights into secular variations in biomass. For the Cretaceous and Tertiary periods, palaeoproductivity estimates do show a positive correlation with diversity in phytoplankton fossils, as suggested years ago by Tappan, Lipps, Fischer and Arthur, and others. However, the relation is not simple and is complicated by the effects of radiations and mass extinctions: it is doubtful, for example, whether the observed doubling of phytoplankton diversity from the Cambrian to the Ordovician reflects a comparable change in algal biomass. I have no confidence that phytoplankton diversity itself can be used as an index of biomass in pre-Cretaceous rocks. This leads me to the second problem, which is that many algae that contribute in important measure to marine productivity and biomass are not represented in the geological record by recognizable fossils. This further confounds efforts to relate ancient biomass and diversity in any predictive way. I hope, by the way, that my pessimism is misplaced.