

# Problems with proxies? Cautionary tales of calcareous nannofossil paleoenvironmental indicators

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**ABSTRACT:** Many studies relating to long-term global change and climate variability rely on proxy data from fossils and geochemistry to reconstruct paleoenvironments. Such data can also contribute to our understanding of biodiversity through time. In this respect, calcareous nannofossils are an excellent proxy resource, with a number of taxa having become established as indices of paleotemperature and/or paleofertility. However, although the majority of the original works that identified these nannofossil proxies are basically sound, the application of the proxies to a widening range of scenarios, in differing paleoenvironmental situations and time-intervals, is beginning to challenge some of our original assumptions. Consequently, there is a growing need for more precise evaluations of the status of these proxies. In addition, there are a number of nannofossil taxa which have proxy potential but which require focused study to determine the extent of their utility.

Here, we point to the problems associated with some of the most commonly used Mesozoic nannofossil proxy taxa (*Watznaueria* spp., *Biscutum constans*, *Zeugrhabdotus erectus*, *Nannoconus* spp.), and introduce the taxon *Micula* as a potential fertility proxy, by virtue of its high abundance in particular environments. Further to this, we outline a program that is in progress, involving geochemical 'finger-printing' of individual taxa combined with nannofossil statistical data, that should enable us to better understand the paleoecological preferences of these taxa and so help in restoring confidence in these proxies and provide a better understanding of their potential limitations.

## INTRODUCTION

The surface ocean plays a major role in climate change, transporting heat, sinking or sourcing greenhouse gases, and influencing the lower atmosphere. With implications for future climate change, it is supremely important that we gain a greater understanding of the role and response of the surface ocean to greenhouse forcing, CO<sub>2</sub> drawdown and changing nutrient/productivity flux. To achieve this, we need to study past intervals of global warmth and/or high atmospheric CO<sub>2</sub>, and the paleoproductivity record. Proxy data from fossils and geochemistry provide us with balanced models for these intervals. Calcareous nannoplankton (unicellular algae that inhabit the photic zone) offer several great advantages. First, they have possibly the best-preserved, globally distributed Mesozoic-Cenozoic fossil record. Second, they are intimately associated with the carbon cycle and thus with climate. Third, they occupy the base of the marine food chain, thus supporting most other marine life. Fourth, they are empirically responsive to nutrification events. In addition, in order to understand the early history and long-term diversity patterns of coccolithophores, we need to gain information on the specific effects of photic zone environments on nannoplankton. It is particularly important to be informed on the Mesozoic (an interval of high atmospheric CO<sub>2</sub> and reduced thermal gradients) because the Cretaceous/Tertiary (K/T) boundary, and succeeding global change, so fundamentally altered the world, and possibly the way in which nannoplankton could respond to environmental change. For instance, it appears that the nannoplankton responded to cooling in Mesozoic greenhouse climates by diversifying. The consequence of this was enhanced biogeographical differentiation

between the poles and the tropics (Bown et al. 2004; Bown this volume). In the Cenozoic, however, cooling resulted in diversity decrease, perhaps because nannoplankton were unable to compete with diatoms in colder surface-water environments (note that the diatom group radiated only after the K/T boundary events, so Mesozoic nannoplankton were not in competition with this group) (Bown et al. 2004; Bown this volume).

Although certain species of planktonic foraminifera are widely used as marine biological proxies, from which carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotope ratios provide valuable information on C<sub>org</sub> burial rates, paleotemperature and depth habitat, the data derived is frequently questioned, due to concerns over preservation and vital effects related to vertical migration of species in the water-column (e.g. Pearson et al. 2001). Moreover, planktonic foraminifera only became common in the sedimentary record in the mid-Cretaceous. Consequently, there is a need for additional proxy data with which to test the foraminiferal proxy data and to independently inform on surface-water conditions. Calcareous nannoplankton are/were restricted to the photic zone of the world ocean (similarly to planktonic foraminifera), and record geochemical signals that can be related to temperature and productivity. They therefore constitute a useful proxy resource. Furthermore, especially relevant to future climate change scenarios, the productivity of these, the only calcifying primary producers in the Mesozoic-Cenozoic oceans, affects climate through both positive and negative feedbacks (Burnett et al. 2000), and so the proxy information they supply constitutes a gauge of the general condition of the marine environment.

Thus, to better understand large-scale patterns of biodiversity, the causes and consequences of global oceanographic/climatic change, and to test current interpretations, we need the kind of information that can be uniquely provided by nannoplankton. Their potential to provide information on surface-water conditions is severely hampered, however, by the widely variable degrees of confidence associated with the paleoecological signals provided by species that are currently used as proxies, for which there are no living analogues.

This paper was prompted by an invitation (of JAL and PRB) to participate in the 'Assessment of Mesozoic Calcareous Nannoplankton Diversity and Evolution' Workshop held at Rutgers University in December, 2003. Consequently, we set out here some examples of Mesozoic nannofossil proxies currently in use, and some with potential. We highlight interpretive problems arising from the overall assumption that they can be applied to all paleoenvironmental situations, and question the proxy status of those where there is too little supporting data, or where data from different sources are conflicting. In conclusion, we outline our ongoing research program, which was designed to address the limitations of these, among other, taxa *via* geochemical 'finger-printing'.

### CALCAREOUS NANNOFOSSILS AS PROXIES

Changes in percent-abundance, specimens per unit area, or absolute abundance of certain taxa in a nannofossil assemblage can be assumed to indicate changing environmental conditions, of local to global significance, since this is true of time-series observations of modern assemblages (e.g. Cortés et al. 2001). In fossil material, these relative abundances are generally calculated from counts of 300 specimens or more on a smear-slide (see Bown and Young (1998) for a summary of preparation techniques and justification for the methodology). Techniques to establish absolute abundance of nannofossils per gram of rock are increasingly being used (e.g. Backman and Shackleton 1983; Flores et al. 1995; Williams and Bralower 1995; Geisen et al. 1999 and references therein; Herrle 2002; Mattioli and Pittet 2002). Gross changes in relative abundance, used in association with the presence or absence of endemic taxa, can be related to the latitudinal distribution of water-masses, as demonstrated for the present day by McIntyre and Bé (1967) and Okada and Honjo (1973). This is essentially a proxy for broad climatic zones (e.g. Haq 1980; Aubry 1992, 1998; Mutterlose and Kessels 2000; Street and Bown 2000; Lees 2002; Kahn and Aubry 2004), and changes in the distribution of these through time can be used as a proxy for global change, mainly related to paleotemperature (e.g., Lees 2002).

Increasingly in the last decade, nannofossil abundance changes have been plotted against geochemical proxy data, commonly generated from either individual, picked planktonic foraminifera or the <63µm bulk-carbonate fraction (the latter comprising mainly coccolith calcite but also juvenile planktonic foraminifera, pieces of larger organisms, along with potentially non-biogenic carbonate). The commonly-used geochemical proxies are  $\delta^{18}\text{O}$  (from foraminifera or bulk) with, latterly, Ca/Mg and Sr/Ca ratios (from foraminifera) for paleotemperature, and  $\delta^{13}\text{C}$  (from foraminifera or bulk) and, latterly, Sr/Ca ratios (from fractionated nannofossils) for paleo-productivity. Henderson (2002) provided an overview and discussion of the utility of these geochemical proxies, among others. Note that Sr/Ca ratios, depending on the source, can be used as a proxy for both temperature and productivity; nannoplankton and foraminiferal Sr/Ca ratios record different

ecological signals, because the former precipitate the calcite intracellularly (e.g. Stoll and Schrag 2000).

Certain nannofossil species have become established, and others are being postulated, as indicators of fertility/productivity and/or temperature in a variety of situations, but particularly in relation to Milankovitch cycles, oceanic anoxic events (OAEs) and the Paleocene/Eocene Thermal Maximum (PETM) (e.g. Watkins 1989; Aubry 1992; Erba 1991, 1992; Erba et al. 1992; Windley 1995; Eshet and Almogi-Labin 1996; Gale et al. 2000; Street and Bown 2000; Mutterlose and Kessels 2000; Bralower 2002; Bucefalo Palliani et al. 2002; Herrle 2002; Lees 2002; Pittet and Mattioli 2002; Stoll and Bains 2003; Erba 2004; Lees et al. 2004, submitted.; Mattioli and Pittet 2004; Mattioli et al. 2004; Tremolada and Bralower 2004). Although the arguments for the proxy status of many of these taxa in particular situations are generally sound, it is becoming apparent that taxa may not be consistently reliable, and that their sensitivity to changing paleoenvironmental parameters is more complex than originally understood, leading to contradictory interpretations between different settings. Consequently, claims for the global significance of certain proxies may be being overstated (see the section on problematic nannofossil proxies below). Furthermore, there are several taxa that have enigmatic signals, which may have potential as environmental proxies (e.g. see Lees 2002, table 4 for a summary of the postulated paleoenvironmental affinities of Late Cretaceous taxa). This situation may have serious ramifications, affecting the interpretation of, for example, putative high-productivity scenarios such as OAEs and the PETM, and the determination of global surface-water-mass dynamics in a greenhouse world, all of which are linked to natural, global climate change. Since calcareous nannoplankton suffered a 93% species extinction at the K/T boundary (Bown et al. 2004), there are no modern representatives of most Mesozoic taxa, and also the functional morphology of the calcareous parts of this group is, in any case, enigmatic (Young 1994), so direct analogies cannot be made with living taxa, unlike the case for certain foraminifera proxies. We *can* still assume, however, that the general distribution of calcareous nannoplankton in the photic zone of the Mesozoic (and Cenozoic) oceans was governed by nutrient concentration/availability and temperature, as is the case for modern nannoplankton, and that certain environmentally-sensitive taxa change in relative abundance in response to changes in nutrient concentration/availability and/or temperature.

One final point to note about potential problems with nannofossil paleoenvironmental analysis is that of taxonomic ambiguity, as described in the following section. Since individual species evolved to fill particular ecological niches, taxonomic rigor should be viewed as an essential part of paleoenvironmental reconstruction.

### PROBLEMATIC NANNOFOSSIL PROXIES

A few of the most often cited Mesozoic nannofossil proxies are discussed here to highlight the potential problems associated with their broad usage, and/or to suggest the need for caution when applying them as proxies in situations in which they may not have been rigorously proved, and to urge re-evaluation of their utility. All taxa are fully authored and referenced in Bown (1998).

#### Species of *Watznaueria*

*Watznaueria* species are ubiquitous in Mesozoic sediments, and generally abundant to dominant in Cretaceous nannofloras, in-

dependent of palaeoenvironment or preservational effects. However, because it is one of the most solution-resistant Mesozoic coccolithophore taxa (e.g. Thierstein 1980), Cretaceous nannofloras with low species diversity and high abundances of *Watznaueria barnesiae* have often been dismissed as poorly-preserved. Recent data from Lees et al. (2004, unpublished manuscript) have shown, however, that extraordinarily low species diversity, and predominance of *Watznaueria fossacincta/barnesiae* (members of a morphological continuum), is a primary palaeoenvironmental feature of pristinely-preserved, laminated assemblages in the English Kimmeridge Clay Formation (KCF) coccolith stone bands; *Watznaueria britannica* and *Cyclagelosphaera margerelii* also dominate in certain laminae. (Note that Thomsen (1989) also found *Watznaueria*-dominated laminae in the similarly pristinely-preserved Lower Cretaceous Munk Marl Formation of the North Sea.) Some of the KCF laminae also bear seasonal bloom abundances (Lees et al. 2004). The inference drawn from this data, and the general ubiquity of the taxon, is that *Watznaueria fossacincta/barnesiae* is likely to have been eurytopic and ecologically r-selected for rapid reproduction in heightened-nutrient (but perhaps sometimes otherwise bioinhibiting) environments. Consequently, analogy has been made between this taxon and the Cenozoic Noelaerhabdaceae, and especially to the extant, similarly ubiquitous (especially in atypical marine environments) *Emiliania huxleyi* (Mutterlose and Kessels 2000; Street and Bown 2000; Lees et al. unpublished manuscript).

The dark mudrocks of the remaining KCF, although not so well preserved, arguably record primary proportions of the different *Watznaueria/Cyclagelosphaera* taxa; because their morphologies are essentially similar, their preservation potential is also likely to be the same (Pittet and Mattioli 2002; Lees et al. submitted). In these, *Watznaueria britannica* is generally the dominant species. Clearly, the different species of *Watznaueria* had differing ecological strategies, although they all appear to display r-selected characteristics. Both the shales and limestones of the KCF were deposited in an anoxic basin, the major difference between the two lithologies being that the latter were deposited in better oxygenated (stormy) conditions (e.g. Pearson 2000; Pearson et al. 2004). *Watznaueria britannica* gave way to *Watznaueria barnesiae* dominance at the end of the Jurassic, only ever appearing abundantly again in Cretaceous sediments in proximity to OAE1a, before extinction in the earliest Cenomanian (Bown et al. 1998; Bown in press). Since there is evidence that *Watznaueria fossacincta/barnesiae* bloomed in turbulent conditions (when nutrients were recycled to the surface-waters from a deep nutricline which only supported *Watznaueria britannica*?; when (micro)nutrients were refreshed through terrestrial runoff into the basin as a result of hypothesized storminess?; when CO<sub>2</sub>/O<sub>2</sub> became available in the surface-waters allowing increased biomineralisation?), it has been suggested by Lees et al. (2004) that this taxon occupied the more eutrophic end of a trophic continuum than *Watznaueria britannica* or *Cyclagelosphaera margerelii* (note that nannofossils as a group fall within the mesotrophic region of the trophic resource continuum of Margalef 1997).

The results of these latest studies have profound ramifications for the use of *Watznaueria* as a proxy. Based on its depressed abundances at putative mid-Cretaceous paleo-upwelling locations, Roth and Bowdler (1981) interpreted *Watznaueria barnesiae* as an index of low fertility/oligotrophy. Its commonly-observed negative correlation with relative abundances of *Biscutum constans* and *Zeugrhabdotus erectus* (both previ-

ously interpreted as high-fertility indices; see below) has corroborated this assumption in numerous studies of the predominantly North Atlantic-centric mid-Cretaceous (e.g. Roth and Krumbach 1986; Erba 1991; Erba et al. 1992; Williams and Bralower 1995; Fisher and Hay 1999; Herrle 2002, 2003; Erba 2004), although this may simply reflect a closed sum effect. Indeed, other studies (e.g. Watkins 1989) have shown no such correlation, nor any correlation with diversity.

In a Late Oxfordian shelf environment (SW Germany), the coccoliths *Lotharingius hauffii*, *Watznaueria britannica*, *Cyclagelosphaera margerelii*, *Watznaueria barnesiae*, *Watznaueria manivittiae* and the *incertae sedis* *Schizosphaerella* spp. display their highest relative abundances sequentially, in stratigraphic order (Pittet and Mattioli 2002). This succession of nannofossil taxa parallels a gradual increase in allochthonous carbonate-mud accumulation on the deep-shelf, as well as a gradual decrease in clay input to the adjacent shallow platform. This similar, linked sedimentary evolution of the shallow platform and deep-shelf suggests a climatic control, likely through humidity/aridity cycles, on shallow-platform carbonate production and basinwards export, and on nutrient availability in deep-shelf surface-waters. Nutrient concentration in turn controlled the nannoplankton assemblage composition. Therefore, the described succession, of sequential highest relative abundance of different nannofossil taxa, can be interpreted as representing a trophic preference continuum from more eutrophic to oligotrophic conditions. Pittet and Mattioli (2002) thus determined *Watznaueria barnesiae* to be more mesotrophic than *Watznaueria britannica*, which they interpreted as more eutrophic, in this Late Oxfordian shelf environment. This is contrary to the interpretations of Lees et al. (2004) for the younger KCF, but in agreement with the hypothesis of Lees et al. (submitted), who argue that the mudrocks containing *Watznaueria britannica* represent the more eutrophic environment! The observation that the absolute abundance of *Watznaueria barnesiae* fluctuates very little in Jurassic and Cretaceous sediments, while its relative abundance displays fluctuations because of the decrease or increase in abundance of the other species (Pittet and Mattioli 2002; Giraud et al. 2003), supports the idea that *Watznaueria barnesiae* is an ecologically robust taxon, able to adapt to fluctuating and/or more extreme environmental conditions more efficiently than other species (e.g. Mutterlose 1991).

*Watznaueria britannica* displays a high morphological plasticity, with specimens showing small (<5.5µm), intermediate (5.5 to 8µm) and large sizes (>8µm) (Olivier et al. 2004). Although the taxonomic and/or ecophenotypic significance of these different-sized morphotypes is still under study (Giraud et al. 2004), it appears that their paleoecological preferences are slightly different. In Oxfordian marl-limestone alternations of SW Germany, the small morphotypes are observed in higher abundances in clay-rich lithologies, where small, but probably significant, increases of *Biscutum dorsetensis*, *Biscutum dubium*, *Discorhabdus rotatorius* and *Zeugrhabdotus erectus* are also recorded. This assemblage potentially corresponds to high mesotrophic conditions (but see below). Conversely, the large morphotypes of *Watznaueria britannica* are more abundant in carbonate-rich sediments, as well as the large *Watznaueria manivittiae*, possibly indicating more oligotrophic environments (EM personal observation 2003; Olivier et al. 2004). Thus, different paleoecological strategies may have been employed by different morphotypes of *Watznaueria britannica*, which may indicate that these should actually be considered as

distinct species. Precise taxonomic concepts are therefore key to paleoenvironmental interpretation.

Obviously, these examples indicate that watznaueriacean paleoecological signals are complex, with variations in abundance in high-diversity and high-productivity assemblages more likely a result of ecological interaction with taxa such as *Biscutum ellipticum* and *Zeugrhabdotus erectus*, rather than a signal of surface-water fertility, although in certain, but not all, scenarios this may amount to the same thing. *Watznaueria* percent-abundance may well be a measure of the success, or otherwise, of other species, rather than a direct response to environmental change, since *Watznaueria* appears to have been quite capable of successfully inhabiting virtually all Mesozoic marine environments. However, *Watznaueria* did have (or evolved) ecological limits; in the Late Campanian-Early Maastrichtian, there is evidence to suggest that the minimum temperature-tolerance of *Watznaueria barnesiae* was over-reached with a withdrawal from polar regions having been documented in numerous studies (Bukry 1973; Thierstein 1981; Huber and Watkins 1992; Watkins et al. 1996; Lees 2002).

A further point of paleoecological interest, in connection with the KCF, is that *Cyclagelosphaera margerelii*, a potential proxy that formed a significant component of nannofossil assemblages only at certain enigmatic stratigraphical levels through the Jurassic and Cretaceous, survived the K/T boundary extinction event. It has been hypothesized (e.g. Bown et al. 1998, 2004; Street and Bown 2000) that such survivors were likely neritic taxa. High-abundance, low-diversity assemblages of *Cyclagelosphaera margerelii* and *Watznaueria britannica* (= *Ellipsagelosphaera communis* in Busson et al. 1992) have been reported by Busson et al. (1992, 1993) from a Late Jurassic restricted-lagoon environment that possibly received fresh-water influxes. High accumulations of *Cyclagelosphaera margerelii* also form the pale-coloured laminae in Kimmeridgian bituminous laminites of the French Jura, interpreted as being deposited in a lagoonal environment with significant salinity variations (Tribovillard et al. 1992). Both of these assemblages are poorly-preserved, and it is possible that these unusual nannofloras simply represent the most robust elements of the original assemblages, although it is interesting to note the absence of *Watznaueria fossacincta/barnesiae* from these unusual assemblages.

Clearly, watznaueriaceans have potential as proxies in a variety of paleoenvironmental settings, and their abundance in nannofloras will allow them to be individually geochemically tested, but their ecological status requires re-evaluation. Questions to be addressed include: under precisely which situations (excluding poorly preserved assemblages) were *Watznaueria* dominant in Mesozoic nannofloras? Is *Watznaueria* analogous to *Emiliana huxleyi* in being the supreme opportunist nannofossil taxon, in which case, does it, like *Emiliana huxleyi*, have several ecophenotypes, and can we identify these based on physical parameters, e.g. size? What are the differentiating ecological conditions that determine which species of *Watznaueria/Cyclagelosphaera* was dominant in the Jurassic to Early Cretaceous?

#### ***Nannoconus* and *Assipetra* (incorporating *Rucinolithus terebrodentarius*)**

*Nannoconus* is a relatively large, solution-resistant, conical nannolith, rather than a plate-like coccolith. It is a well-documented Cretaceous, predominantly low-latitude, carbonate-

shelf/carbonate-dominated epicontinental basin taxon (Berger and Roth 1975; Thierstein 1976; Roth and Bowdler 1981; Roth and Krumbach 1986; Busson and Noël 1991; Mutterlose 1992; Street and Bown 2000), which has periodically formed monospecific assemblages in apparently bloom abundances (indicating potential ecological r-selection) at low paleolatitudes (e.g. Bréhéret 1983). One or two endemic species (*Nannoconus abundans*, *Nannoconus borealis*) also achieved short-lived high-abundances at higher paleolatitudes (e.g. Mutterlose 1989; Thomsen 1989), associated with putative warming. It has further been noted that nannoconids occur in lesser abundances in sediments with a significant clay component (Busson and Noël 1991). Busson and Noël (1991) suggested that nannoconids were meroplanktonic calcareous dinoflagellates, with water-depth restrictions imposed by cyst viability, and the potential to develop toxic, bioinhibiting blooms.

Nannoconids evolved towards the end of the Jurassic, and became extinct in the Late Campanian. Their extinction was most likely primarily a result of cooling at low latitudes (e.g. Kolodny and Raab 1988) and concomitant oceanographical adjustments, although they never reached high abundances in the Late Cretaceous (JAL personal observations 1984-2005) although localized elevated abundances have been reported (e.g. Aubry 1970). This combination of ecological clues - high nannoconid abundance in warm, low-latitude, shelfal, possibly stratified, waters with arid hinterlands - alludes to environments in which oligotrophy may have been a more-or-less permanent feature of the surface-waters, and in which salinity may also have been a significant control. Their apparent 'distaste' for clayey over more-carbonatic sediments (as noted by Busson and Noël 1991) may indicate that water-clarity played a role in their distributions.

The so-called 'nannoconid crises' (several have been recorded since Erba (1994) coined the term for that which preceded OAE1a in the Early Aptian) potentially occur after nitrification events, but before anoxic sediment deposition, in relation to OAEs (e.g. Erba 1994; PRB and JAB unpublished data 2003), further suggesting a more oligotrophic habitat for this taxon. This genus is virtually never found in (ostensibly oligotrophic) open-ocean sediments, however, even at low paleolatitudes (e.g. Lees 2002 - Indian Ocean; Bown in press; Lees and Bown in press; Lees, unpublished data 2003 - Pacific Ocean), although it can occur abundantly on certain low-latitude structural highs where there is evidence of underlying subaerial limestone, i.e. in warm, shallow environments (e.g. DSDP Site 463, western Mid-Pacific Mountains; see illustrations in Erba 1994). Erba (1994) suggested that *Nannoconus* may be analogous to the extant genus *Florisphaera*, which lives in the deep photic zone of modern oceans, where it proliferates in low light conditions at a deep nutricline, in temperatures >10°C (e.g. Molfino and McIntyre 1990), with water transparency being paramount in more marginal settings (Ahagon et al. 1993). Consequently, Erba (1994) hypothesized that the OAE1a-related nannoconid crisis may have been the result of nitrification of oligotrophic surface-waters (through major volcanic activity), leading to an upper photic zone productivity increase, which essentially starved the nannoconids (living at depth) of nutrients. However, the analogy is debatable, since *Florisphaera* is found almost exclusively in oligotrophic, open-oceanic regions (Reid 1980; Venrick 1982). It thus seems that temperature and water-depth/light are major controls on nannoconid distribution, and there is still a question over whether they lived at depth. Despite observations that may indicate that nannoconids were r-se-

lected/high-nutrient-exploiting taxa, they have also been interpreted as oligotrophic (Coccioni et al. 1992) and mesotrophic (Scarparo Cunha and Shimabukuro 1997).

An aside to the nannoconid debate, but possibly environmentally-related, is the nannolith, *Assipetra*. Erba (1994, fig.4) illustrated an acme of this taxon through and above the Livello Selli (OAE1a), during the nannoconid crisis (postulated high coccolithophore productivity). The abundance of *Assipetra* declined as nannoconids returned. This apparent replacement perhaps indicates a shared ecological niche, especially as both *Assipetra* and *Nannoconus* are bulky forms, and *Assipetra* became extinct in the Pacific Ocean at about the same time as nannoconids became extinct in shallower environments (Lees and Bown in press). If the nannoconids did live at depth, then the occupation of the niche by *Assipetra* would imply that there were still nutrients at depth and that some other circumstances than competition with coccolithophores caused the nannoconid crises, possibly related to water-depth/light and/or temperature. Additionally, if nannoconids were deep-dwellers, influenced by nutricline depth, then during upwelling their absolute abundances should not decrease (although their relative abundance could decrease due to increases in coccolith taxa) because nutrients would have been available to both the upper and lower photic zones. Furthermore, if it is true that high-productivity environments favour very small- to small-sized coccoliths/coccolithophores, which require less calcification, potentially related to a limitation on their rate of biomineralisation (as hypothesized by, for example, Tremolada and Erba 2002), then how could we explain high abundances of bulky *Assipetra* nannoliths through such intervals? Our interpretations are hampered because we don't know whether nannoconids were produced intracellularly, and, therefore, if their calcification was similar to that of coccoliths. However, we do not subscribe to the hypothesis that *Nannoconus* and *Assipetra* are bacterial precipitates (e.g. Tremolada 2002) for the reasons given below.

Questions remain to be answered, for example: Did nannoconids really exploit a deep nutricline? Were the surface-waters above proliferating nannoconids necessarily oligotrophic or did salinity limit coccolithophore diversity? Was light/water-clarity the limiting parameter that kept nannoconids in shallower environments? If they occupied similar ecological niches, why do nannoconids not occur, and *Assipetra* occur, in low-latitude oceanic sediments? Did *Assipetra* occupy a niche nannoconids were unable to fill because of water-depth or temperature constraints? And, if nannoconid crises are related to biomineralisation crises in high  $p\text{CO}_2$  environments, then why is *Assipetra* so calcite-heavy? The paleoecology of *Nannoconus* is clearly still debatable.

***Biscutum constans* (= *Biscutum ellipticum* of some authors) and *Zeugrhabdotus erectus* (= small *Zeugrhabdotus* spp. (<5 $\mu\text{m}$ ) of some authors)**

It is worth mentioning, in the context of this paper, that poor application of taxonomic concepts can lead to meaningless paleoenvironmental interpretation, through merging of species with differing paleoecologies (e.g. see the implications discussed in connection with *Watznaueria britannica*, above). A prime example is the Cenozoic to modern *Coccolithus pelagicus*, which has discrete sub-Arctic and temperate upwelling morphotypes/subspecies (e.g. Ziveri et al. 2004). In the case of *Biscutum constans*, two names (*constans* and *ellipticum*) have been used interchangeably for ostensibly the same species, however Bornemann and Mutterlose (submitted) have deter-

mined that these are probably ecophenotypic varieties, the smaller types possibly being related to reduced temperatures.

The use of the name *Zeugrhabdotus erectus* for the small (<5 $\mu\text{m}$ ) Cretaceous zeugrhabdotids with a highly-birefringent, simple bar bearing a spine(-base), has been disputed (hence the use of *Zeugrhabdotus* spp. (<5 $\mu\text{m}$ ) by some authors). This species was described from the Oxfordian by Deflandre (in Deflandre and Fert 1954). Although the Jurassic specimens are generally larger than the Cretaceous specimens (~5 $\mu\text{m}$  compared to ~3 $\mu\text{m}$ ), the structure appears similar. However, there is some ambiguity as to whether it is actually only this taxon (i.e. Burnett 1998, pl.6.2, fig.30c; Herrle 2002, pl.7, figs 13-17) that is being used to interpret Cretaceous paleoenvironments, as some authors combine it with other zeugrhabdotids. Since the genus name of a fossil taxon with no living counterparts is a somewhat artificial grouping based on gross morphological characteristics, this lumping of similar taxa (i.e. those with short-ellipse bars) could lead to erroneous interpretation. Consequently, there may also be some taxonomic problems underlying ambiguous distributions of this species.

Since Roth (1981) labelled *Biscutum constans* and *Zeugrhabdotus erectus* as "High-productivity/high-surface-water-fertility ('upwelling') forms" as well as "Restricted sea" forms (op. cit., p. 480), these taxa have been used extensively as high-fertility indices in the Aptian-Turonian (e.g. Roth and Krumbach 1986; Watkins 1989; Erba 1992; Erba et al. 1992; Williams and Bralower 1995; Fisher and Hay 1999; Gale et al. 2000; Herrle 2002), although Erba (1992, p. 194) admitted that "...discrepancies in their distribution" had been noted by various authors. Negative correlation of high abundances of these taxa with diversity and equitability data (e.g. Watkins 1989; Fisher and Hay 1999) and their co-occurrence with radiolaria and/or hedbergellid planktonic foraminifera (indicators of high fertility; Erba 1991) have lent support to their proxy usage. However, as Gale et al. (2000) highlighted, and Erba (2004) remarked upon, there is an abundance decrease of *Biscutum constans* associated with OAE2 at Eastbourne (Kent, SE England), despite the fact that *Zeugrhabdotus erectus* is present throughout the event (i.e. probably not a preservational signal). At Gubbio (central Italy), '*Zeugrhabdotus*' (including *Zeugrhabdotus erectus* and *Zeugrhabdotus* spp.) does not show any significant increase in abundance below OAE2, is absent during the event, and reappears above, whilst *Biscutum constans* abundances decrease sharply from ~7% well below the event, and the taxon is then absent during and above the event (Erba 2004, fig.6).

Clearly, there is a relationship between these taxa and high-productivity, at least at intermediate to low paleolatitudes in the mid-Cretaceous. However, Thierstein (1981) and Lees (2002) observed high abundances of *Biscutum constans* only at high-latitudes in the post-Turonian Upper Cretaceous in well-preserved material, but no high abundances of *Zeugrhabdotus erectus*. Conversely, Eshet and Almogi-Labin's (1996) study of a Campanian-Maastrichtian upwelling system in Israel also revealed high abundances of *Biscutum constans* but no *Zeugrhabdotus erectus* in assemblages which otherwise contained delicate and solution-prone taxa. This, and the fact that Erba (1992) found both taxa in samples taken from between (virtually) barren horizons, indicates that preservation is not the factor for *Zeugrhabdotus erectus*'s absence from these paleoenvironmental scenarios. Erba (1992, fig.11) suggested that *Zeugrhabdotus erectus* occupied a more eutrophic ecological niche than *Biscutum constans*, but this is usually manifested by its abundance reaching a peak only after that

of *Biscutum constans*, not usually its absence from/rarity in nutrient-rich waters. So, it appears that there is some ecological factor which limits one but not the other, possibly related to temperature and/or water-depth, which is being overlooked in current paleoenvironmental assessments. Furthermore, Erba's (1992) suggestion that *Zeugrhabdotus erectus* indicated higher fertility in more eutrophic environments, whilst *Biscutum constans* reacted positively to high fertility in mesotrophic environments was disputed by Fisher and Hay (1999), who determined the opposite.

On Shatsky Rise (NW Pacific Ocean), radiolarian cherts dominate pre-Lower Campanian deposits, at which point there is a switchover to predominantly nannofossil carbonate sediments (Bralower, Premoli Silva, Malone et al. 2002; Lees and Bown in press). These chert accumulations have been postulated as indicating high-fertility conditions associated with a wide tropical oceanic divergence belt, wherein radiolaria were providing high phytoplankton productivity, analogous to modern scenarios wherein the siliceous diatoms dominate in similar environments where silica is available. However, this is a controversial interpretation (e.g. see Bown in press and references therein). Erba (1992) linked increases in relative abundances of *Biscutum constans* and *Zeugrhabdotus erectus* at Sites 800 and 801 (south of Shatsky Rise), which coincided with increases in radiolarian abundances, to movement of these sites into the Pacific equatorial upwelling region, from 10°S to 5°S, with nannoplankton being replaced by radiolaria from 2°S. The wider nannofossil picture seems not to support this interpretation, however. Erba (1992) suggested there was a time-lag between the abundance increases between the two sites, in support of the idea that the sites moved progressively into the upwelling zone from the Late Albian to Early Cenomanian. This time-lag, however, cannot be precisely demonstrated from the data presented. More widespread data from the Pacific region (ODP/DSDP Sites 1207 and 1213 on Shatsky Rise to the north of 800 and 801; Kanungo 2005; PRB unpublished data 2004; 463 on the mid-Pacific Mountains to the east, and 464 and 465 on the Hess Rise to the north-east; Roth 1981) show that large increases in abundance of *Biscutum constans* occurred *simultaneously* at these locations in the latest Albian/earliest Cenomanian interval (these sites occupying a region covering ~30° of latitude). This leaves Erba's (1992) interpretation in question, since this appears to be an ocean-wide phenomenon. Furthermore, *Biscutum constans* is an abundant to common component of nannofossil assemblages of Albian to Cenomanian age in even more widely dispersed locations (e.g. the Naturaliste Plateau, paleolatitude >60°S, DSDP Site 258, SE Indian Ocean; Lees 2002; SE England, paleolatitude ~40°N, The Warren, Folkestone, Dover; JAL unpublished data 2001). This implies that high abundances of this age were a phenomenon related to global climatic/oceanographic conditions.

Shatsky Rise carbonates also record OAE1a and possibly OAE1b (Bralower, Premoli Silva, Malone et al. 2002; Robinson et al. 2004). However, *Biscutum constans* and *Zeugrhabdotus erectus* do not show high/peak abundances in relation to these events and are indeed absent for much of the interval (Kanungo 2005; PRB unpublished data 2004). Comparatively, at Site 1049 (Blake Nose, NE Atlantic), *Biscutum constans* and *Zeugrhabdotus erectus* reach high abundances well before (several tens of kyr) the OAE1b black shale, in proximity to a peak in Sr/Ca ratios, proposed as representing the initial OAE1a nitrification trigger (Kanungo 2005; PRB and JAL unpublished data 2003; D. Gröcke unpublished data 2003).

Thus, although it seems apparent that high abundances of both taxa relate to high fertility in particular situations, neither the ecological relationship between the taxa, nor the environmental extent to which we can reliably use either of them, is clear. What is the differentiating ecological parameter that distinguishes the abundant occurrences of these taxa? Is there a temperature or water-depth control on producing high abundances of either taxon, and is this related to upwelling? What is the ecological relationship between these taxa and *Discorhabdus*, identified as another high-fertility taxon, but with an unpredictable distribution, by Premoli Silva et al. (1989), Erba (1991), Coccioni et al. (1992) and Herrle (2002)?

## POTENTIAL NANNOFOSSIL PROXIES

### Species of *Micula*

This nannolith taxon is typically cubic, composed of eight pyramidal elements, early in its evolutionary history, evolving morphological modifications to this structure towards the end of the Cretaceous. The idea (Tremolada 2002) that this genus (along with the nannolith genera *Nannoconus* and *Assipetra*) is a bacterial precipitate, supported by the lack of 'coccospheres', is refuted: (a) *Micula* and *Nannoconus* have a complex architecture; (b) evolutionary change in *Micula* and *Nannoconus* can be clearly demonstrated (e.g. Deres and Achéritéguy 1980; Perch-Nielsen 1985; Burnett 1988) and (c) extant coccolithophores produce non-coccolith calcareous structures that do not form spheres but which are of similar size and structure to fossil nannoliths, e.g. ceratoliths (Young et al. 2003), whilst coccospheres of most Mesozoic taxa have never been found.

It has so far been overlooked as an environmental proxy (it did not evolve until the Coniacian, so is not associated with the mid-Cretaceous OAEs), and is included here as one illustration of the wider potential of currently unused taxa as proxies. *Micula staurophora* (= *Micula decussata* of some authors) is a major constituent of Coniacian to Maastrichtian assemblages, in some situations displacing *Watznaueria barnesiae* in abundance, and in others forming virtually monospecific assemblages (e.g. the Shefala Basin, Israel; Eshet and Almogi-Labin 1996). It also is a solution-resistant taxon (e.g. Thierstein 1981; Eshet and Almogi-Labin 1996). This species has been shown to be less abundant at intermediate than at high and low paleolatitudes (Thierstein 1976; Lees 2002), and shows abundance changes relative to uniform *Watznaueria barnesiae* abundances in a high-productivity situation (Eshet and Almogi-Labin 1996).

In the Maastrichtian, *Micula staurophora/swastica* began to diversify, most notably by shrinking and rotating one of its cycles of elements. A likely reason for this diversification is environmental change (morphological changes are also observable in a number of other Maastrichtian taxa), and so perhaps morphological change within a defined lineage could hold some exploitable proxy meaning. Aside from the potential proxy value of *Micula* on its own, an understanding of its paleoenvironmental value could potentially shed light onto the paleoecological relationships between nannoliths and coccoliths.

## A NEW APPROACH TO PROXY RESEARCH

In order to address concerns over the precise utility of nannofossil paleoecological (paleotemperature, paleofertility/paleoproductivity) proxies, and to enhance our precision in interpreting paleoenvironments, we describe here a research strategy that is in progress, and the rationale behind it. This

approach combines specifically-chosen, well-preserved, well-dated sediments, biogeographical information, and geochemical data ( $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ , Sr/Ca ratios), all generated together with nannofossil statistical data, to provide the most unambiguous results. Our aim is to produce geochemical fractionation signatures of around 18 taxa (13 Mesozoic, five Cenozoic), comprising both established and potential proxies for productivity or temperature. The status of some of these taxa as proxies has so far been based on their elevated abundances (arbitrarily >15%) in nannofossil assemblages, and the correlation of such abundance increases with changes in bulk-carbonate  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  isotope and Sr/Ca ratio curves.

### Preparation technique

In the last few years, the need for an effective separation technique to constrain nannofossil geochemical data has been appreciated and, after much experimentation, Stoll and Ziveri (2002) developed a non-quantitative, density-stratified, settling-based method, as part of the CODENET project ([www.nhm.ac.uk/hosted\\_sites/ina/CODENET/index.html](http://www.nhm.ac.uk/hosted_sites/ina/CODENET/index.html)). Independently, Minoletti et al. (2001) developed a different system, based on repeated microfiltration using ion-etched polycarbonate filters in an ultrasonic bath. The ultrasonic bath inhibits clogging of the filter, allowing filtration of significant volumes of sediment at much lower pore-sizes (<10 $\mu\text{m}$ ) than is possible with conventional wet-filtration. This technique has subsequently been applied to detailed analysis of K/T boundary sections (Minoletti et al. 2004).

We are employing the fine-filtration protocol, rather than the settling technique, so as to avoid any suspicion that the chemicals used in filtration might have a deleterious effect on the nannofossils (see, e.g., Stoll and Bains 2003, fig.1; JAL personal observation 2003; although it is presently unclear if this etching is a diagenetic feature of the assemblages used). Near-monospecific assemblages (>80%) can be achieved using the Minoletti et al. (2001) protocol, allowing investigation of the geochemistry, and especially isotope fractionation, of virtually individual taxa. This subdivision of samples is quantitative and, in conjunction with counting the assemblages in each split and estimating the mass of each species, the proportional contribution of the different components to each geochemical value can be calculated. The sediments from which we are producing our splits are very well preserved.

### The rationale - a summary of geochemical fractionation in nannofossils

Various studies have directly linked increases in relative abundance of certain nannofossil species to changes in bulk-carbonate (usually <63 $\mu\text{m}$ )  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values (as broad proxies for productivity and temperature, respectively). The carbonate components responsible for such shifts in geochemical values are usually identified only as the 'nannofossil' fraction. However, nannofossils generally fall into the 20-3 $\mu\text{m}$  size-range, and so this 'nannofossil' fraction actually contains juvenile forms of other microfossil groups (e.g. planktonic foraminifera), along with fine carbonate (the so-called 'micarb', comprising unidentifiable broken parts of larger organisms, bacterial precipitates, cryptogenic platform carbonates, etc.), and up to ~60 nannofossil species that may have lived at a variety of depths in the photic zone, as is true of modern assemblages. As such,  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  data from bulk-carbonate provide, at best, a blended signal only partially related to any changes in the nannofossil assemblages. Consequently, this

type of geochemical data does not contribute to our understanding of nannofossil paleoecology.

Differential depth habitats have long been recognized in modern planktonic foraminifera, and have been elucidated in the fossil record using single-species  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  isotopes (e.g. Huber and Watkins 1992; Pearson et al. 1993). Using size separation techniques, we can now investigate nannofossils in a similar way. Dudley and Goodney (1979) and Dudley et al. (1980, 1986) first demonstrated that a number of modern nanoplankton species grown in culture fractionated  $\delta^{18}\text{O}$  isotopes. These effects have been confirmed by Ziveri et al. (2003), who also demonstrated strong fractionation of C isotopes and Sr/Ca ratios, both in culture and in the wild. These values can be correlated with productivity (P. Ziveri personal communication 2004) and, for example, using the known ecology of *Florisphaera profunda* as a deep-dwelling species (Molfinio and McIntyre 1990), also indicate differential water-depth/temperature habitats for the species. In addition, it has been shown that the bulk fine-fraction, representing an averaged value of not only nannofossils but also possibly benthic organisms and cryptogenic material, obscures such environmental information, and does not allow for interpretation of individual biological signals (P. Ziveri personal communication 2004). It is these signals that have the potential to reveal so much new, and more accurate, information about the photic zones of past environments.

### What can we learn from nannofossil isotope signatures?

The most routinely used proxy for paleotemperature is  $\delta^{18}\text{O}$ , commonly determined from individual planktonic foraminifera species. By determining the range of fractionation values for our selected nannofossil species, we can determine if these change in relation to time, preservation and environment. Differential values between species may allow us to hypothesize relative depth-habitats.

$\delta^{13}\text{C}$ , commonly derived from planktonic foraminifera or bulk fine-fraction carbonate, is routinely used to measure changes in the rate of  $\text{C}_{\text{org}}$  burial, therefore constituting a proxy for productivity. Again, we can aim to determine the range of fractionation values of selected species, and record changes vs time, preservation and environment. Pearson et al. (2001, fig.1) used cross-plots of  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  to interpret foraminiferal depth-habitats, and we will be able to attempt something similar for selected nannofossils for which depth-related hypotheses already exist (e.g. *Discoaster* and *Nannoconus* - deep-dwellers: Aubry 1992; Erba 1994). Furthermore, we can use this data in conjunction with Sr/Ca ratios to provide an indication of relative productivity.

The use of Sr/Ca ratios as a proxy for nanoplankton species productivity is a new development. Studies of calcareous nanoplankton cultures by Ziveri et al. (2000, 2003) revealed physiological changes in certain species related to ecological changes, expressed as non-equilibrium effects on the carbonate chemistry of the nanoplankton species (i.e. minor element partitioning). Variability of the Sr/Ca offsets between different taxa were found not to be the result of biological vital effects but were overwhelmingly influenced by coccolith calcification and growth rates (Stoll and Schrag 2000, 2001). Note that Stoll et al. (2002) found that the Sr/Ca ratio in cultured coccoliths increased with temperature but that the productivity signal was dominant, and that our measurements of  $\delta^{18}\text{O}$  will allow us to monitor paleotemperature in relation to the Sr/Ca. We will be

able to use Sr/Ca data, in conjunction with the  $\delta^{13}\text{C}$  data, to test hypothesized high-productivity taxa, for example *Biscutum* and *Toweius/Coccolithus* (e.g. Erba 1992; Bralower 2002).

## CONCLUSIONS

Nannofossil environmental proxy data is invaluable to a wide range of globally-significant studies because the group (a) has one of the best Mesozoic to modern fossil records, covering a wide range of marine photic-zone environments, (b) was intimately linked with the carbon cycle (through photosynthesis and biomineralization), (c) supported virtually all other marine life, (d) was demonstrably responsive to nitrification fluxes and temperature changes, and (e) has arguably better preservation potential than foraminifera. By exploiting the proxy potential of the group, we can shed light onto the causes and effects of global change of the surface ocean, explain the long-term diversity of the group, and provide a test for foraminiferal proxy data, which suffers from its own drawbacks.

Although many of the established nannofossil paleoecological determinations for the proxies in use are probably more-or-less correct (e.g. *Biscutum constans*, *Zeughrabdotus erectus* as high-fertility indicators), recent application of these nannofossils as proxies to a broader range of environmental scenarios (e.g. *Nannoconus*), and in differing time-intervals (*Watznaueria*), suggests that our original assumptions require more precise evaluation, or in a few cases, possibly a complete reappraisal.

There are a number of potential nannofossil proxies waiting to be evaluated and tested, including those which show morphological responses to changing environments (e.g., in the Maastrichtian).

In order to gain reassurance, or in some cases to regain some lost confidence, in the established nannofossil proxy taxa, a dedicated program has been designed, aiming to geochemically characterize individual taxa. This should enable us to more precisely constrain the paleoecologies of disputed taxa, and also to identify further, potentially useful, nannofossil proxies.

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