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Cenozoic coccolith size changes—Evolutionary and/or ecological controls?

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ABSTRACT

Size is one of the most important characteristics of any organism and can readily be used in quantitative analyses of patterns in physiology, ecology, and evolution. One of the best archives for the history of organism evolution are deep-sea sediments, because (1) microfossils are one of their major constituents, (2) they can be accurately dated, and (3) they are available from almost all areas of the world. We present new data on size variations of entire oval to circular coccolith assemblages during the last 65 million years from a number of globally distributed deep-sea cores. We document the generally decreasing size patterns of these assemblages from the early Cenozoic to the Holocene and show that higher size variability and thus largest sizes can be observed in high latitudes. However, the documented size trends are not directly related to available proxies for paleoenvironmental conditions. Taxonomic investigations of the measured assemblages indicate that the evolution, abundance, and extinction of large-sized species in different lineages, such as *Calcidiscus*, *Coccolithus*, *Chiasmolithus*, *Cruciplacolithus*, *Helicosphaera*, and *Reticulofenestra*, and the newly developed small-coccolith producing taxa in the Neogene, such as *Emiliania*, *Gephyrocapsa*, *Reticulofenestra haqii*, *R. minutula* and *Umbilicosphaeraceae*, are responsible for the observed assemblage size variations during the last 65 million years.

1. Introduction

Biological evolution is generally defined as change in the characteristics of descendant populations of organisms. Theories of biological evolution were developed to explain today's diversity among organisms, the history of diversity as documented by fossils, and the natural processes that may have influenced them (Skelton, 1993). Paleontological investigations provide data on the age, distribution, as well as morphological and chemical characteristics of extinct taxa. Such data form the basis of any interpretation of tempo and mode of evolutionary transitions (e.g. Jablonski et al., 1997 and references therein). A unique attribute examined in paleontological studies is body size, respectively size of the fossilized remains of organisms. Size, as a geometric and thus objective parameter to characterize any organism, is a significant, but hitherto rather poorly known parameter across scales of time and hierarchical levels. In general nearly every aspect of the biology of an organism is influenced by its size, e.g. metabolism, reproduction, and differential survival (Calder, 1984).

One of the major topics in current nannoplankton research is the importance of genetic versus environmental factors for the evolution of coccolithophores. Two active fields of research have contributed heavily to this fundamental question: (1) the biology (including genetics and culturing) of living coccolithophores, and (2) the fossil record. Within the latter, the traditionally defined species successions, based on qualitative morphology, have recently been succeeded by attempts to quantify morphology, including measures of size and shape. In particular the marine plankton remains of single-celled organisms (coccolithophores and planktic foraminifera) represent one of the best documented archives of any organism group, both geographically and stratigraphically, because they are the major contributors of marine carbonate sequences covering the world's ocean floor. Studies of these sediments have generally shown that, since the first appearance of coccolithophores in Upper Triassic sediments (~225 Ma; Bown et al., 2004), their species richness has varied significantly (for a recent summary see Bown et al., 2004). Several, rather gradual diversity increases were interrupted by rapid diversity reductions usually associated with known events of rapid environmental change pointing to a correlation of environmental factors and evolutionary trends in coccolithophores. Based on several regional studies, the morphology of coccoliths has been shown to vary over the Cenozoic Era, with a gradual reduction of coccolith sizes from a maximum of about 26 μm during the Paleocene/Eocene (about 50 Ma, e.g. *Chiasmolithus* (Romein, 1979)) to <12 μm maximum size by the Miocene/Pliocene time (about 20 Ma, Backman, 1980; Young, 1990). Whether observed shorter-term fluctuations, overprinting this general size decrease, are local or global features has remained unclear (Backman and Hermelin, 1986; Kameo and Bralower, 2000). A reproducible stratigraphic size decrease in placoliths of *Watznaueria* across

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the Jurassic–Cretaceous boundary has been identified in various Deep-Sea Drilling holes of the North Atlantic (Bornemann et al., 2003). Cenozoic size changes at the genus, species and morphotype level were documented in *Calcidiscus* (Knappertsbusch, 2000), where coccolith sizes and number of elements increased from 23 to 11 Ma associated with changes in oceanographic conditions. The variations in size were explained by changing morphotypes within the genus (Knappertsbusch, 2000). Henderiks and Pagani (2008) observed large *Reticulofenestra* coccoliths in the Eocene and early Oligocene (up to 16 μm) and medium sized specimens until the late Oligocene (6-13 μm). Henderiks and Pagani (2008) described relatively small *Reticulofenestra* coccolith sizes (around 4 μm) before 21 Ma, which subsequently evolved into several larger morphospecies (with mean sizes of 5 to 6.5 μm) from 19.7 Ma onward. They speculate that size of reticulofenestrids is related to environmental parameters. Henderiks (2008) furthermore discussed coccolithophore size rules for the dominant Cenozoic genera *Reticulofenestra*, *Cyclicargolithus* and *Coccolithus*, based on the observation of a constant correlation of coccolith size with coccosphere and cell diameter driven by changes in their environment.

All these lineage and species investigations point to several questions considering the entire coccolith assemblage: How do all these size changes in morphotypes or lineages influence the overall coccolith assemblage size? Is the overall coccolith assemblage size driven by one or more environmental factors? How does the evolution within different coccolithophore lineages influence the entire assemblage size signal?

To answer these questions, we collected and interpret size information on a higher taxonomic level by investigating size trends of all circular to oval coccoliths in generally well preserved deep-sea carbonate samples, a measure that we call coccolith assemblage size (CAS).

In a previous study we investigated CAS of 51 globally distributed core top samples covering the Holocene and compared them with environmental parameters of the overlying photic zone (Herrmann et al., 2012). We found that CAS generally increases from the tropics polewards. The CAS trend is caused by relative abundance variations among various genera. Size changes within single genera (including abundance changes among sister-group species and size variabilities within sister-groups) have only a minor impact on total coccolith assemblage size changes.

Here we report on the long-term size changes of entire coccolith assemblages over the last 65 million years. We have selected samples from well-preserved deep-sea records from high to low latitudes and from the major ocean basins. Key points that we aim to investigate are:

a) Did the Holocene CAS pattern of larger sizes at high latitudes, persist throughout the Cenozoic?
b) Holocene CAS variability is caused by changes in the relative abundance of two genera producing large coccoliths, namely *Coccolithus* and *Helicosphaera*. Are abundance changes of genera producing large versus those producing small coccoliths also the major factor driving CAS variations throughout the Cenozoic?
c) To what extent did the development of new species within genera and/or new genera producing especially large or small coccoliths influence CAS in the Cenozoic. Specifically, the known Eocene and Miocene dominance of large species in the lineages of *Reticulofenestra* and *Cyclicargolithus* (e.g. Henderiks and Pagani, 2008) should be recognizable as CAS variations in our records.

2. Materials and methods

2.1. Sites and samples analyzed

A total of 289 Cenozoic samples from 11 DSDP or ODP drill sites and one gravity core were chosen for our study (Fig. 1, Table 1, Appendix A). They are from three major ocean basins and cover low to high latitudes. These records were selected for the following reasons:

(1) Previous investigations on coccoliths had already shown the presence of diverse coccolith assemblages of generally good preservation (e.g. Thierstein and Woodward, 1981; Haq et al., 1990; Siesser and Bralower, 1992; Curry et al., 1995; Knappertsbusch, 2000). The sample sequences investigated here are from locations of less than 4 km waterdepth. A maximum paleodepth estimate for our samples is 3500 m for the late Cretaceous at North Atlantic DSDP site 384 (Table 1). In most of our sites chosen stable isotope analyses had been carried out previously (Table 2) indicating that microfossils were generally well preserved.

(2) The most significant trend in Holocene CAS (Herrmann et al., 2012) is the general increase in coccolith size from low latitude warm waters to high latitude cold waters. The trend is the result of changes in the relative abundance of genera with species producing large coccoliths versus genera with species producing small coccoliths. The selected Cenozoic records cover a significant latitudinal gradient and should enable us to test the Holocene pattern back in time to the early Cenozoic/latest Cretaceous.

Eight of our 11 sites analyzed represent the core data base (221 samples) for the long-term observations with a time resolution of at least 0.5–1 m.y. In two additional sites a detailed investigation during the final closure of the Isthmus of Panama in the Pliocene (around 2–5 Ma) was performed with 100 samples from the ODP site 999 A (Caribbean Sea, average resolution of 0.02–0.05 m.y.) and 29 samples from DSDP site 548 (North Atlantic, average resolution of 0.02–0.4 m.y.). To test the assumption of macroevolutionary stasis during the last 5 million years, we compared our size results of Pliocene coccolith assemblages with the late Pleistocene records of site GeoB 1710-3 and ODP site 723 A, both located in upwelling areas. For that we investigated 17 samples with an average time resolution of about 0.0–0.047 m.y. Results from our 51 globally distributed Holocene samples (Herrmann et al., 2012), covering a depth range of 200 m to 4670 m, are included in the discussion to compare the past with the present coccolith size variabilities.

The age models used are listed in Table 1. The absolute ages are taken from the calibration of Berggren et al. (1995). Within the framework of our investigations, we also considered important paleogeographic changes over time. The most prominent change occurred for the Indian Ocean sites, where the Australian plate, originally attached to Antarctica, drifted northward. For the Ontong Java Plateau records (ODP sites 806 B/C and 807 C, Fig. 1) the paleodepths were similar to today's since the late Eocene (Resig et al., 1976), because distinct collision and subduction periods formed its present shape (Kroenke et al., 1991; Yan and Kroenke, 1993). The permanent position above the lysocline, as evidenced by exceptionally good nannofossil preservation, qualifies this region as suitable for our investigations. The Exmouth Plateau (ODP site 762 B/C) moved from a temperate to a subtropical position from the Paleogene to the early Oligocene (Haq et al., 1990) and subsided over the Cenozoic from a paleodepth of about 800 m to its present depth of 1360 m (Haq et al., 1992). Consequently, potential differences in size variations between records from the western Pacific/subtropical Indian Ocean (ODP sites 762 B/C, 806 B/C /807 C) and tropical Atlantic (ODP site 925 A/B) during the Paleogene might in part be caused by these latitudinal drifts. The well-preserved early Miocene to Holocene record of DSDP site 251 (A) (SW Indian Ridge) has previously been investigated by Thierstein (1974) and Knappertsbusch (2000). Another long-term record investigated in this study is from the Ontong Java Plateau (ODP sites 806 B/C, 807 C; 2500–2800 m waterdepth), with Cenozoic paleo-waterdepths estimated to have always been