Radiolarians decreased silicification as an evolutionary response to reduced Cenozoic ocean silica availability

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It has been hypothesized that increased water column stratification has been an abiotic “universal driver” affecting average cell size in Cenozoic marine plankton. Gradually decreasing Cenozoic radiolarian shell weight, by contrast, suggests that competition for dissolved silica, a shared nutrient, resulted in biologic coevolution between radiolaria and marine diatoms, which expanded dramatically in the Cenozoic. We present data on the 2 components of shell weight change—size and silicification—of Cenozoic radiolarians. In low latitudes, increasing Cenozoic export of silica to deep waters by diatoms and decreasing nutrient upwelling from increased water column stratification have created modern silica-poor surface waters. Here, radiolarian silicification decreases significantly ($r = 0.91$, $P < 0.001$), from ≈ 0.18 (shell volume fraction) in the basal Cenozoic to modern values of ≈ 0.06 . A third of the total change occurred rapidly at 35 Ma, in correlation to major increases in water column stratification and abundance of diatoms. In high southern latitudes, Southern Ocean circulation, present since the late Eocene, maintains significant surface water silica availability. Here, radiolarian silicification decreased insignificantly ($r = 0.58$, $P = 0.1$), from ≈ 0.13 at 35 Ma to 0.11 today. Trends in shell size in both time series are statistically insignificant and are not correlated with each other. We conclude that there is no universal driver changing cell size in Cenozoic marine plankton. Furthermore, biologic and physical factors have, in concert, by reducing silica availability in surface waters, forced macroevolutionary changes in Cenozoic low-latitude radiolarians.

evolution | microfossils | micropaleontology | morphometrics | Ocean Drilling Program

The evolution of ocean plankton has played an important role in the development of the earth’s climate system, and changes in ocean plankton may affect future changes in climate (1). The deep-sea microfossil record of protist plankton provides an unusual opportunity to understand how plankton evolution and environmental change mutually affect each other. Recently, it has been proposed that Cenozoic changes in upper ocean water column stratification have influenced the evolution of cell size in a variety of marine protist plankton groups, including planktonic foraminifera (2), diatoms (3), and dinoflagellates (4), and it has been suggested that these patterns are indicative of a “universal driver” of size change in Cenozoic plankton (4). The polycystine radiolarians are an important marine protist zooplankton group abundant as fossils in Cenozoic and Mesozoic deep-sea sediments. Their general size, feeding ecology, and distribution patterns are similar to those of the better-known planktonic foraminifera (5, 6), although radiolarians are more diverse and, at least since the Oligocene (7), possess distinct, diverse endemic high-latitude faunas. Radiolarians are most diverse in low latitudes and most abundant in near-surface waters, although some species inhabit very deep waters. These general patterns appear to have persisted throughout at least the Cenozoic (6). As zooplankton, they are less dependent than phytoplankton for

various dissolved nutrients for growth but do require, as do the siliceous-shelled diatom phytoplankton, dissolved silica to build their opaline shells (5, 6). Silica is highly undersaturated in modern marine waters and is frequently a limiting nutrient to siliceous plankton growth (8). In sharing a need for dissolved limiting nutrients with phytoplankton, radiolarians thus differ from the carbonate shelled planktonic foraminifera, the other main marine zooplankton group available for study in the Cenozoic fossil record.

Radiolarians intriguingly show a trend toward lower shell weights in tropical faunas over the Cenozoic (9). This was interpreted (10) as radiolarians using silica more efficiently in response to gradually decreasing silica availability in Cenozoic ocean waters. The silica decrease was inferred to have been caused by increasing abundances of Cenozoic planktonic marine diatoms. This hypothesis, which invokes biologic interactions, provides an alternative explanation to the physical mechanism of water column stratification-driven size change in plankton. These 2 hypotheses thus appear, at first glance, to present an straightforward opportunity to compare the roles of biologic interactions vs. physical environmental change in large-scale patterns of evolution [e.g., the Red Queen hypothesis vs. Stationary Model (11, 12)]. However, the situation in radiolarians is rather more complex. First, the published shell weight evidence is ambiguous because shell weight is a function of both size and the efficiency of silica use (“silicification”: volume shell silica per unit shell volume). Furthermore, in this article, we argue that biologic vs. physical change hypotheses may be a false dichotomy and are not mutually exclusive. Silica availability in ocean water is affected by many factors, including not only silica removal by diatoms but also the intensity of surface–deep ocean water mixing due to the strength of water-column stratification and the rate of silicate weathering on land. Here, we document size and silicification trends for Cenozoic radiolarian faunas and compare these results both to those obtained previously for other plankton groups and to the 2 proposed causal factors: change in ocean water column stratification and the rise to ecologic dominance of diatoms.

Strategy

We present data from both low- and high-latitude environments, because these environments show quite different values for silica availability for plankton and for water column stratification today: Tropical surface waters are both highly stratified and

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Fig. 1. Location of samples used in study, with distribution of dissolved silica in modern ocean surface waters at 50 m, the water depth where radiolarian abundances are most often at a maximum. Silica map from http://www.nodc.noaa.gov/OC5/WOA05/pr_woa05.html.

highly silica limited, but high (southern) latitude environments are only weakly stratified and are often not silica limited for plankton growth (8, 13) (Fig. 1). If changing silica availability has affected the evolution of Cenozoic radiolarians, we would expect a significantly reduced trend toward more efficient use of silica by radiolarians in silica-rich high latitudes than in the more strongly silica-limited low latitudes. To determine which factor(s) are responsible for any trends seen, we compare our results with the differing histories of silica availability as indicated by the history of diatoms and water stratification as summarized in refs. 2 and 4.

A total of 29 samples from Deep Sea Drilling Program (DSDP) and Ocean Drilling Program (ODP) drill sites with well-preserved radiolarian faunas were analyzed. Age determinations are from the primary literature and are generally accurate to ± 1 my. Detailed sample information including age models is given in the [supporting information \(SI\) Text](#). Samples from low-latitude environments come from all major ocean basins and include some samples from different ocean regions of approximately the same age. These temporally overlapping but geographically separated samples were used to confirm the geographic robustness of results for our low-latitude data. High southern-latitude samples are from the Atlantic sector only but are thought to be representative of the full south polar fauna because of circumpolar faunal distributions for Cenozoic radiolarians (14, 15). The early Neogene and Paleogene locations of high-latitude samples were, due to subsequent plate motion, significantly further south and within the Antarctic radiolarian province. Poor preservation of silica in early Paleogene Antarctic sediments provides only a single temporally isolated sample with sufficient quality for measurement. Results from this sample are shown but not interpreted in this study.

Results

Radiolarian size and silicification values for both low- and high-latitude samples are given in Fig. 2. Radiolarian size shows

a high degree of variability within some but not all samples, as reflected in the standard error bars of Fig. 2 and in [Table S1](#). Although there are significant changes in mean radiolarian size between samples, there is no significant net trend in size over the Cenozoic in either low- or high-latitude data ($r \approx 0.1$, $P \approx 0.5$ for both time series). Although limited by the small number of available data points and within-sample variability, there is also no obvious correlation in shorter-term size trends between low- and high-latitude radiolarian faunas.

Radiolarian silicification values, by contrast, show a clear, highly significant ($r = 0.91$, $P < 0.001$) trend vs. geologic age toward lower silicification over the Cenozoic in low-latitude faunas. This trend is not due to the geographic location of samples in low latitudes, because samples from the same time interval but different ocean basins yield similar results ([SI Text](#) and [Table S1](#)). High-latitude faunas, by contrast, show only a very weak, statistically insignificant trend with geologic age ($r = 0.58$, $P = 0.1$) for the mid-Eocene–Recent time interval. In the mid-Eocene radiolarian silicification values were similar in both low and high latitudes but diverged soon afterward, particularly because of a relatively large reduction ($\approx 1/3$ of the total Cenozoic shift) in low-latitude silicification in the latest Eocene, between ≈ 36 and 33 Ma. Fig. 3 illustrates how different the silicification values are for pre- and post-shift populations in low-latitude data: Mean, mode, and range of Oligocene to Recent silicification values in low-latitude faunas are only approximately half those of older Paleogene low-latitude faunas. These results thus confirm the existence of the trend in low-latitude radiolarian shell morphologies first reported in shell weight data by Moore (9) and show that the trend is primarily due to increased efficiency in silica use and not to any major trend in cell size.

Discussion

Radiolarians do not show a significant trend in mean size over the Cenozoic, nor do low- and high-latitude faunas show any

Fig. 4. Trends in Cenozoic radiolarian silicification for low- and high-latitude samples compared with trends in low-latitude ocean water column stratification (4) and rough proxies for the increase in abundance of diatoms: 2 estimates of diversity (31, 37) and evolutionary turnover (first and last appearances of species combined) plotted vs. latitude (32). Evolutionary turnover patterns are based on first and last occurrence events, estimates of which vary only slightly beyond a minimum sample size (38) and are, in our opinion, the most robust of these metrics, whereas within-bin diversity estimates (e.g., ref. 37) are more likely to be affected by sampling and reporting variations in the primary deep-sea drilling diatom reports. The gray vertical bar in both plots marks the Southern Ocean formation time interval (15, 30).

evolutionary turnover equal to, or exceeding, that seen in low latitudes (Fig. 4B). These patterns, thus, cannot be explained by single factors acting in isolation but can be interpreted as due to the interaction of 2 causal factors—water column stratification and diatom abundance—and their combined effect on silica availability in Cenozoic low- and high-latitude ocean waters.

Evolution of Cenozoic Ocean Circulation, Diatom Abundance, and Silica Availability in Ocean Waters. Modern ocean dissolved silica concentrations represent a balance between input from rivers and sea-floor basalt weathering and removal by biologic, primarily diatom, activity (8, 20). Dissolved silica is extremely low in low-latitude surface waters, being higher only at subthermocline depths (more than ≈ 300 m) and in a few highly local regions of upwelling or in coastal waters immediately adjacent to river input of silica to surface waters. This is due to the combined effect of strong, primarily thermally created, density stratification of low- to mid-latitude oceans, which prevents nutrients in deep waters from being mixed back to the surface, and extremely rapid stripping of silica from surface water to deep ocean water by growth and export of diatoms in geographically localized areas of strong upwelling/deep mixing. In high latitudes, water column stratification is weak, and the ocean's deep waters are

mixed to the surface, providing surface waters with high levels of dissolved nutrients including silica (13).

Ocean distributions of silica, however, are thought to have undergone a long-term Phanerozoic trend from high-silica oceans to low, due to the increasing “capture” of the marine silica cycle by biologic activity, in particular the evolution and expansion of diatoms between the late Cretaceous and late Paleogene (10, 21, 22) (Fig. 4). Although no generally available geochemical proxies exist to directly determine past ocean water silica concentrations, indirect geochemical arguments suggest that ocean silica concentrations were an order of magnitude higher than modern values in the Paleozoic–early Cretaceous (23) but declined, presumably due to the expansion of diatoms, in Late Cretaceous to Recent times. These geochemical estimates match qualitative trends inferred from past distributions of siliceous sediments and arguments from knowledge of the oceanic silica cycle. Marine diatoms first become locally abundant in late Cretaceous neritic or coastal sediments and locally common in open ocean pelagic sediments in the later Paleocene but only begin to form significant volumes of deep-sea pelagic ooze in the mid-Eocene (21, 24–26). This gradual increase in occurrences is mirrored by gradually increasing Paleocene–mid Eocene chert (19), much of which may have been diagenetically derived from diatom shells.

Early Cenozoic ocean silica concentrations, however, were apparently quite different from those seen today. The ocean silica system can be viewed via the “conveyor belt” analogy first used to describe global deep circulation. A set of geographically limited upwelling regions bring silica to the surface, from where it is transported horizontally over relatively long distances while being gradually extracted and exported to deep water again by diatom growth and the sinking of diatom shells to subsurface depths. The extent of geographic distribution of silica in sediments, thus, represents a balance between rates of supply and removal.

Geographically widespread silica in ocean sediments in the Paleogene suggests either higher absolute concentrations of silica in ocean waters (19, 22) and/or more gradual removal of silica from horizontally circulating surface waters by less-efficient diatom export. Either would imply higher silica availability in most surface waters compared with the modern situation. Equally, early Paleogene ocean circulation was different, most notably in the absence of a circumpolar Southern Ocean and much warmer (≈ 6 – 12 °C) deep-ocean waters (27). The resulting reduced early Paleogene vertical water stratification in low to mid latitudes (2, 4) (Fig. 4) would also help maintain higher silica levels in larger regions of the ocean's surface waters via geographically widespread vertical water mixing. These patterns suggest decreasing availability of dissolved oceanic silica over the Cenozoic and highlight the importance of Cenozoic changes in diatom abundance and ocean stratification, because geochemical budgets suggest a general global increase in weathering and input of dissolved nutrients to the oceans over Cenozoic time (28).

The ocean silica cycle is likely to have undergone its most profound change in the Cenozoic as a consequence of the cardinal event of Cenozoic ocean history: the development of the Southern Ocean and the associated deep, cold-water global circulation during the late Eocene. These circulation changes effectively replaced the early Paleogene ocean with a largely modern one (27). Low-latitude vertical water column stratification substantially increased (2, 4), reducing silica supply to surface waters, while simultaneously, high-latitude stratification decreased, and upwelling and nutrient availability, including silica, in high-latitude ocean waters increased (27, 29). The timing of this event, which is independently estimated as occurring within the late Eocene $\approx 35 \pm 1$ Ma (15, 30) matches well the timing of the shift in silicification in low-latitude radiolarians and

the divergence of low- and high-latitude radiolarian faunas seen in our data. Thus, it is likely that both causal factors—stratification increase and increased diatom silica removal—were closely linked in the development of the Cenozoic ocean silica cycle and the evolutionary response of low-latitude radiolarians toward greater silica efficiency. The major increase in diatom diversity in the mid-late Eocene and the dramatic increase in diatom species turnover, particularly in high southern latitudes, are also presumed to be a response to this circulation-driven repartitioning of surface water silica availability (18). However, because low-latitude radiolarian silicification decreased in the early Paleogene, even as stratification was weakening, in the early Paleogene, change in water column stratification was apparently not the predominant factor affecting radiolarian silicification. We suggest that decreased radiolarian silicification in the early Paleogene was primarily in response to decreasing silica availability because of the gradual increase in abundance of diatoms in the early Cenozoic (18, 19, 21, 22, 31, 32) (Fig. 4B). Last, despite a doubling of the surface to deep thermal gradient in the last ≈ 20 my, radiolarian silicification in low-latitude faunas has declined only slightly. This may possibly reflect the increasing concentration of marine silica cycling into the modern pattern of production and rapid removal of silica primarily within restricted regions of upwelling, particularly in the circumpolar Southern Ocean. Silica availability to low-latitude surface-water radiolarian faunas would increasingly be controlled by upwelling dynamics in these regions and patterns of upper subsurface water flow [e.g., transport of potentially silica-rich Antarctic Intermediate water to lower latitudes (13)] rather than the globally averaged open-ocean density contrast between surface and deep waters in low to mid latitudes, as summarized in the low-latitude water column stratification curve (4) (Fig. 4).

Coevolution of Diatoms and Radiolarians? Coevolution has traditionally been difficult to document in evolutionary research, or indeed even to define, and published neontologic studies often have difficulty distinguishing between possible alternate causes because the historical development of observed characters is not available (33). In principle, the fossil record should provide such historical evidence but is normally too incomplete (temporally, geographically and in preserved biologic characteristics) to provide much help at the level of individual species interactions. Paleontologic data have been used instead to suggest the predominance of biologic interactions over physical environmental control in the evolution of larger clades [e.g., the Red Queen Hypothesis (11)], although this has proved controversial (12), and most studies of fossil marine microplankton have suggested primarily physical mechanisms as regulators of macroevolutionary change (2, 4, 34, 35). The results of this study suggest that, at least for radiolarians and diatoms, both factors may have played a role, and indeed, both may have been necessary to have produced the patterns of change in silicification seen in our data. This conclusion is tentative and will require more information to fully test. These include better knowledge of the limiting effects of low dissolved silica concentrations on living diatoms and radiolarians, controls on size in living radiolarians, and more direct data on Cenozoic changes in the magnitude of diatom export and the concentration of dissolved ocean silica.

In principle, decreasing silica availability in the Cenozoic

should also have affected diatom shell morphology. In addition to decreasing size (3); at least anecdotal evidence for decreasing average shell thickness in Cenozoic diatoms has also been reported (36). Barron and Baldauf (36) have interpreted this as a macroevolutionary trend because of Red Queen-style competition between diatom species for rapid growth in geographically restricted upwelling areas. Our results from radiolarians, whose ecology depends less on rapid growth than the phytoplanktonic diatoms, suggest that Cenozoic decreases in diatom valve robustness may reflect reductions in the general level of silica availability as well.

Conclusions

Radiolarian assemblages in low latitudes show a Cenozoic trend toward decreased silicification of their shells, with latest Cenozoic faunas using only approximately a third as much silica per unit shell volume as early Cenozoic assemblages. In particular, radiolarian silicification in low latitudes decreases substantially in the late Eocene (≈ 35 Ma). High southern-latitude radiolarian faunas in the mid/late Eocene show silicification values similar to those of coeval low-latitude assemblages but do not show a similar large decrease in silicification values at 35 Ma and show little change over the remainder of the Cenozoic. Both the overall Cenozoic trend and the more abrupt shift at ≈ 35 Ma in low-latitude radiolarian silicification are interpreted as an evolutionary response to inferred decreases in ocean silica availability, due both to increasing low-latitude ocean stratification and the Cenozoic spread of silica-sequestering diatoms. Both factors are inferred to have increasingly removed silica from low-latitude ocean surface waters, with the effect becoming more pronounced with the development of the Southern Ocean and deep cold-oceanic psychrosphere at ≈ 35 Ma. Local environments in high southern latitudes would not have experienced the same degree of reduction in silica availability because of reduced high-latitude vertical stratification and upwelling of silica-rich deep waters, and, indeed, radiolarian faunas there did not, in contrast to those in low latitudes, adjust their use of silica to the same extent.

Methods

Standard radiolarian extraction methods were used and [unlike in the prior study of Moore (9)] the full $>45\text{-}\mu\text{m}$ fraction was retained for study to ensure capture of sometimes numerous specimens of smaller species. Radiolarians are randomly oriented on prepared slides and are too small to manipulate or image fully in a single focal plane, and, thus, measurements were taken manually by using a point-digitization system. We measured an average of 126 specimens per sample (total of 3,657 specimens) and for each specimen, measured length, width, average shell thickness, and average shell porosity (the latter 2 being based on repeat measures of several parts of the shell). All radiolarians that preserved the majority of characters were measured. Because Cenozoic radiolarians mostly are modifications of spherical or conical shapes, raw measurements were converted to overall volume and fractional volume of shell material by using appropriate geometric formulas. For full details of measurement methods and calculations, as well as summary values for each measurement in each sample see *SI Text* and *Figs. S1–S3*.

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