

Seawater chemistry, coccolithophore population growth, and the origin of Cretaceous chalk

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ABSTRACT

The magnesium/calcium ratio (Mg/Ca) and calcium (Ca) concentration of seawater have oscillated throughout geologic time; our experiments indicate that these variables have strongly influenced biomineralization and chalk production by coccolithophores. The high Mg/Ca ratio of modern seawater favors precipitation of high-Mg calcite and/or aragonite. In contrast, the low Mg/Ca ratio of imputed Cretaceous seawater favored precipitation of low-Mg calcite. We have discovered that some coccolithophore species today secrete skeletal elements of high-Mg calcite, rather than low-Mg calcite, as conventionally believed. These species incorporated less Mg when the ambient Mg/Ca ratio was lowered, secreting low-Mg calcite in imputed Cretaceous seawater. Calcification stimulates coccolithophore population growth by contributing CO₂ to photosynthesis. Three extant coccolithophore species multiplied much faster as the composition of ambient seawater was shifted toward that estimated for Cretaceous seas. Two of these species secreted high-Mg calcite in ambient seawater having Mg/Ca > 1, and incorporation of Mg in a calcite crystal inhibits growth. Calcification of the third species, which secreted low-Mg calcite at all ambient Mg/Ca ratios, is hindered by the high Mg/Ca ratio and low absolute concentration of Ca of modern seawater. We conclude that the ionic composition of Cretaceous seawater enabled coccolithophores to produce massive chalk deposits, and conversely, that the ionic composition of modern seawater inhibits population growth for most extant coccolithophore species, which occupy nutrient-poor waters and fail to respond to fertilization by nitrate, phosphate, or iron.

Keywords: coccolithophore, limestone, chalk, calcite, high-Mg calcite.

INTRODUCTION

Coccolithophores (calcareous nannoplankton) are unicellular, spheroidal planktonic algae that play a significant role in food webs of the modern ocean. These algae secrete coccoliths, which are shield-like elements of calcite, typically 1–10 μm in diameter, that are produced in the Golgi body and extruded to cover the cell surface. Coccolithophores are classified as nannoplankton because of their small size (mostly <20 μm). They were much more productive during Late Cretaceous time than today, producing the voluminous chalk deposits that gave the Cretaceous Period its name. We have conducted experiments that support the hypothesis (Stanley and Hardie, 1998, 1999) that the composition of Cretaceous seawater permitted coccolithophores to flourish, whereas the composition of modern seawater retards their productivity.

There have been three intervals during the Phanerozoic Eon when shallow-marine nonskeletal carbonate precipitates have consisted of aragonite and high-Mg calcite, and two intervals when they have consisted of low-Mg calcite (Sandberg, 1985). Oscillations in the Mg/Ca ratio of seawater have produced these mineralogical shifts (Hardie, 1996). Laboratory experiments indicate that low-Mg calcite (<4 mol% Mg substituting for Ca) precipitates from seawater when the Mg/Ca

mole ratio is <1, high-Mg calcite precipitates when this ratio is >1, and aragonite precipitates along with high-Mg calcite when the ratio is >2 (Füchtbauer and Hardie, 1976, 1980). Furthermore, marine hydrothermal brine/river flux mass-balance calculations (Hardie, 1996), fluid inclusions (Lowenstein et al., 2001), and bromine concentrations in halite (Siemann, 2003) indicate that transitions between aragonite and calcite seas have coincided with shifts in the Mg/Ca ratio of seawater to above or below 2, as predicted from experiments. Calcifying marine organisms exemplify the same pattern. Most biologically simple taxa that have functioned as major carbonate reef builders or producers of carbonate sediment have secreted skeletons consisting of minerals favored by ambient seawater chemistry (Stanley and Hardie, 1998, 1999).

COCCOLITHOPHORE CALCIFICATION AND PRODUCTIVITY

The molar Mg/Ca ratio (≤1) and absolute concentration of Ca (~25–30 mM) in Late Cretaceous seawater were close to their minimum and maximum values, respectively, for the Phanerozoic Eon. We have hypothesized that these conditions accounted for the unique formation of massive, widespread Upper Cretaceous chalk deposits through the accumulation of calcitic coccoliths (Stanley and Hardie, 1998, 1999). Such chalks are present in North America, Europe, the Middle East, and Australia (Hattin, 1988). Despite existing at high taxonomic diversity, coccolithophores failed to form comparable chalk deposits in the Early Cretaceous or post-Cretaceous time. Nearly 300 coccolithophore species exist today (Winter and Seisser, 1994). Late Cretaceous chalk accumulated at estimated depths of 100–500 m in warm epicontinental seas (Scholle, 1977). Such seas persisted in Europe and the Middle East throughout Paleogene time, but accumulated moderate volumes of chalk only during the Paleocene, when Mg and Ca concentrations in seawater remained close to Cretaceous levels.

Emiliania huxleyi is an exceptional extant coccolithophore species that blooms in cool seas, even though low temperatures hinder calcification (Brand, 1994). This species is extremely proficient at pumping Ca²⁺, being saturated with this ion at its modern seawater concentration of ~10 mM (Nimer and Merritt, 1996). Its cells produce unusually large coccoliths at a high rate and shed about half of them (Balch et al., 1992). *Emiliania* is not only atypical in its high rate of calcium secretion, but it is also unusual in having arisen only 268 k.y. ago (Thierstein et al., 1977). *Gephyrocapsa oceanica*, an extant species that blooms rampantly in the tropics (Brand, 1994), belongs to the same clade as *Emiliania* and is also of Pleistocene origin (McIntyre, 1970). Today the highest species diversity of coccolithophores is in the nutrient-depleted central regions of subtropical and/or tropical oceanic gyres (Hulbert, 1983). Unlike the recently evolved *Emiliania* and *Gephyrocapsa*, the more typical oligotrophic forms do not respond to experimental nitrate, phosphate, or iron enrichment (Brand, 1991, 1994).

Calcification promotes population growth of calcareous algae; it generates CO₂ that radiocarbon tracer studies have shown to fertilize photosynthesis in both codiaceans (Borowitzka and Larkum, 1976) and coccolithophores (Sikes et al., 1980): Ca²⁺ + 2HCO₃⁻ → CaCO₃ + H₂O + CO₂. In contrast, elevated ambient CO₂ retards coccolitho-

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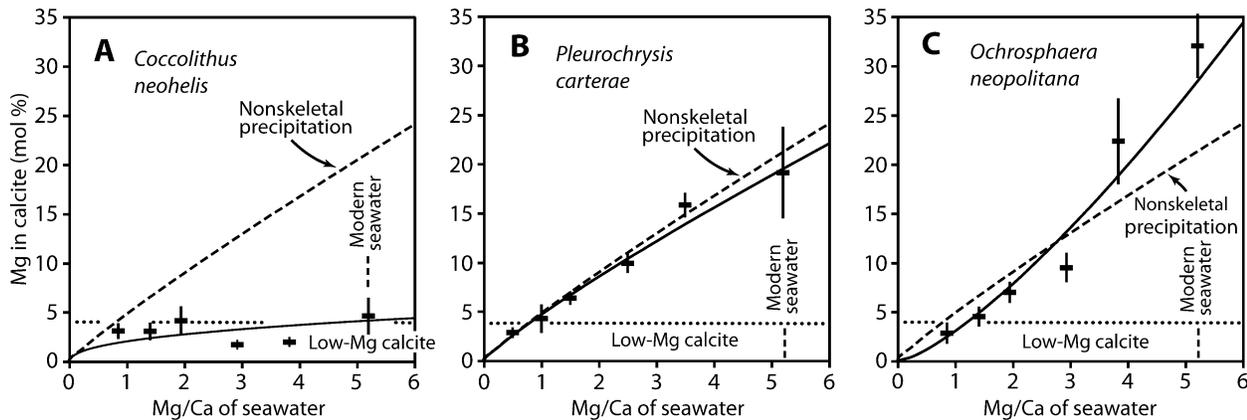


Figure 1. Magnesium in calcite (mol%) secreted by three species of coccolithophores as function of molar Mg/Ca ratio of artificial seawater in which they were grown. Error bars are standard deviations of five measurements. Fitted curves are power functions. Dashed lines depict pattern for inorganic precipitation (Füchtbauer and Hardie, 1976, 1980).

phores' calcification and therefore inhibits population growth (Riebesell et al., 2000).

Given the importance of CO_2 fertilization from calcification, we hypothesized that the high Mg/Ca ratio and low calcium concentration of modern seawater limit population growth rates of most coccolithophore species in the modern ocean—species that may not pump calcium as effectively as the newly evolved *Emiliania* and *Gephyrocapsa*.

EXPERIMENTS ON THE EFFECTS OF SEAWATER CHEMISTRY

We conducted experiments to test the effects of the Mg/Ca ratio and absolute concentration of Ca in seawater on the population growth rate of three coccolithophore species that represent a variety of ecological adaptations: *Pleurochrysis carterae*, a nearshore species that blooms in the presence of abundant nutrients, although less prolifically than *E. huxleyi* (Brand, 1991); *Coccolithus neohelis*, a nearshore species that does not bloom; and *Ochrosphaera neopolitana*, an oceanic species that is confined to low-nutrient oceanic environments where it cannot bloom.

Our experiments employed Mg/Ca ratios and absolute concentrations of Ca for Cretaceous and post-Cretaceous intervals produced by marine hydrothermal brine/river flux mass-balance calculations (Hardie, 1996; Stanley and Hardie, 1998).

Changes in Mineralogy with Changes in Seawater Chemistry

Although the conventional view is that coccolithophores secrete low-Mg calcite in modern seawater (Siesser, 1977), *Coccolithus neohelis* was the only one of our experimental species to secrete low-Mg calcite in all seawater treatments (Fig. 1A). In contrast, *Pleurochrysis carterae* and *Ochrosphaera neopolitana* secreted high-Mg calcite in seawater of modern composition. Like coralline algae (Stanley et al., 2002), echinoids, crabs, shrimp, and serpulid worms (Ries, 2004), these species incorporated progressively less Mg in their skeletons as the ambient Mg/Ca ratio was reduced from that of modern seawater. They departed only slightly from the fractionation pattern for nonskeletal calcite, secreting low-Mg calcite in imputed Cretaceous seawater (Figs. 1B, 1C).

Population Growth Rates and Chalk Production

Coccolithus neohelis would be expected to calcify and multiply progressively more rapidly as the ambient Mg/Ca ratio is lowered because it secretes low-Mg calcite at all Mg/Ca ratios and this mineral is favored by low ratios. Although *Pleurochrysis carterae* and *Ochrosphaera neopolitana* secrete calcite with Mg percentages that are more compatible with ambient seawater chemistry, they too would be

expected to secrete coccoliths more effectively and multiply more rapidly with a decrease in the ambient concentration of Mg, because incorporation of Mg reduces the rate of step growth in a calcite crystal (Davis et al., 2002). In addition, reduction of the absolute concentration of Ca when seawater is shifted from Cretaceous to modern composition would be expected to retard population growth for all coccolithophore species, because Ca is the dominant cation even in high-Mg calcite. In other words, regardless of whether a given coccolithophore species incorporated more Mg in its calcite as the Mg/Ca ratio of seawater rose after Cretaceous time and the absolute concentration of Ca declined, it should have calcified and multiplied more slowly.

As predicted, stepwise reduction of the ambient Mg/Ca ratio and concomitant increase in the absolute concentration of Ca from modern seawater values to Cretaceous values resulted in a marked increase in population growth rates for all three of our experimental species (Figs. 2 and 3). These results are robust in that the higher growth rates were

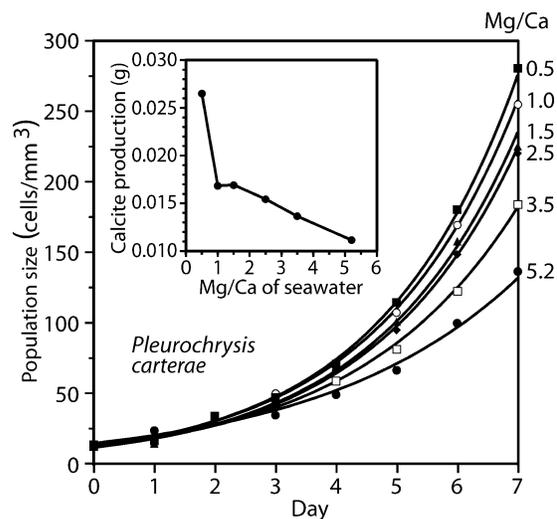


Figure 2. Exponential population growth and chalk production for *Pleurochrysis carterae* as function of ambient Mg/Ca molar ratio and Ca concentration of seawater. For modern seawater, Mg/Ca molar ratio is 5.2 and absolute concentration of Ca is 0.2 mM; for imputed Late Cretaceous seawater, Mg/Ca molar ratio is between 0.5 and 1, and absolute concentration of Ca is between 42.2 and 25.3 mM. Inset displays total calcite production for each culture of *P. carterae* after 7 days. Spearman rank correlation (r_s) = 0.99 for both growth rates and calcite production.

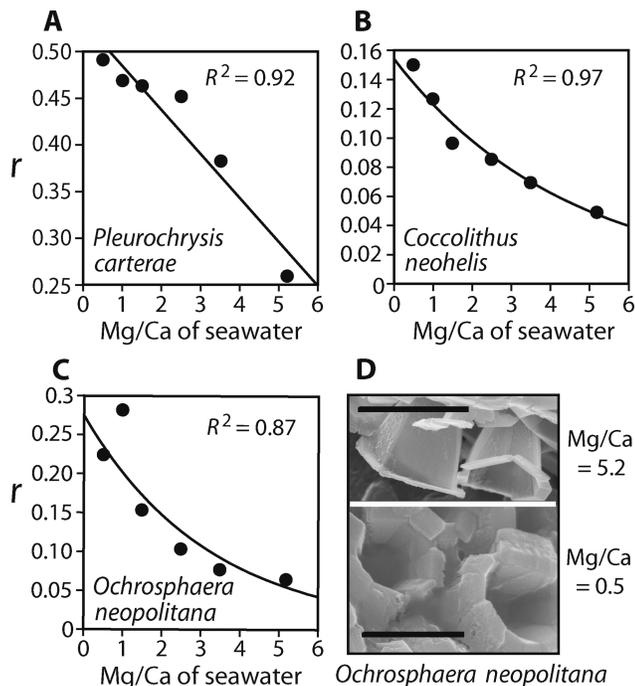


Figure 3. Effects of ambient Mg/Ca ratio on growth of three coccolithophore species. A–C: Exponential rates of population growth (r) for species as function of Mg/Ca molar ratio and absolute concentration of Ca in ambient seawater. Fitted curves in B and C are exponential, whereas that in A is linear. For all three sets of data, Spearman rank correlation (r_s) = 0.99. D: Increase in size and robustness of coccoliths of *Ochrosphaera neopolitana* when grown in seawater of Cretaceous composition (scale bar = 1 μm).

in unfamiliar media. Even *P. carterae*, which blooms in the modern ocean, exhibited a substantial acceleration of the initial exponential phase of population growth; its chalk production also increased substantially (Fig. 2). *C. neohelis* and *O. neopolitana* responded even more strongly, exhibiting exponential growth rates three to four times as high in Cretaceous seawater as in modern seawater (Figs. 3B, 3C). In addition, *O. neopolitana* secreted larger and more heavily constructed coccoliths in Cretaceous seawater (Fig. 3D).

We tested the independent effects of the ambient Mg/Ca ratio and the absolute concentration of Ca on population growth for *P. carterae* and *C. neohelis* by holding each variable constant while varying the other. Both variables influenced population growth rate for these species in the ways that were predicted (Fig. 4). These results support the hypothesis that both the low Mg/Ca ratio and the high concentration of Ca in Cretaceous seawater were responsible for the high growth rates of coccolithophores that produced massive Cretaceous chalk deposits (Stanley and Hardie, 1998, 1999) at a time when the high concentration of atmospheric CO_2 (Royer et al., 2001) would have retarded precipitation of calcium carbonate in the ocean.

Population Growth and Paleoclimatology

Phytoplankton fractionate carbon isotopes as a function of the concentration of CO_2 in the upper ocean, which is equilibrated with atmospheric CO_2 . Alkenones, which are secreted by some coccolithophores, are refractory organic compounds that are valuable indicators of changes in atmospheric CO_2 during Neogene time (Pagani et al., 1999a, 1999b). Coccolithophores also fractionate carbon isotopes as a function of their population growth rate (Bidigare et al., 1997). For this reason, paleoclimatic studies have focused on the alkenones of subtropical and/or tropical species, for which population growth rates are relatively low (Pagani et al., 1999a, 1999b). Our experiments in-

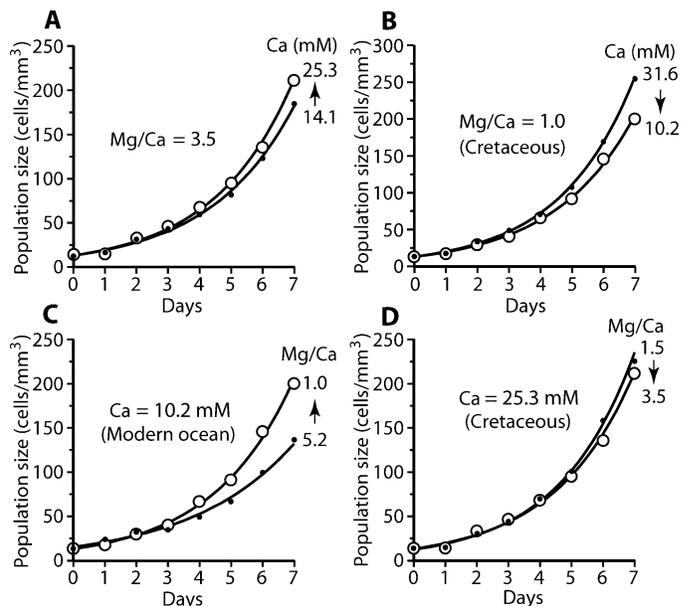


Figure 4. Dependence of population growth rate of *Pleurochrysis carterae* on both Mg/Ca ratio and absolute concentration of Ca in ambient seawater. A: With Mg/Ca molar ratio held constant at 3.5, elevation of Ca concentration from 14.1 mM to 25.3 mM produced faster population growth. B: With Mg/Ca molar ratio held constant at 1.0 (Late Cretaceous level), reduction of absolute concentration of Ca from Late Cretaceous level of 31.6 mM to modern seawater level of 10.2 mM produced slower population growth. C: With Ca held constant at 10.2 mM (concentration in modern seawater), reduction of Mg/Ca molar ratio from 5.2 (ratio for modern seawater) to 1.0 (Late Cretaceous ratio) produced faster population growth. D: With absolute concentration of Ca held constant at 25.3 mM (Early Cretaceous level), elevation of Mg/Ca molar level from Early Cretaceous level of 1.5 to aragonite sea level of 3.5 produced slower population growth. Experiments with *Coccolithus neohelis* yielded similar results.

dicating that population growth rates for these species should have been higher earlier in the Cenozoic Era than they are today. Thus, additional experiments will be needed to adjust estimates of past atmospheric CO_2 concentrations from alkenones.

LIMITING FACTORS FOR POPULATION GROWTH IN THE MODERN OCEAN

Our results imply that the high Mg/Ca ratio and low absolute concentration of Ca in modern seawater are limiting factors for the majority of extant coccolithophore species, i.e., those that occupy warm, nutrient-poor waters. *Ochrosphaera neopolitana* is one of these oligotrophic species; therefore, we grew it exclusively at low nutrient levels (see Appendix) and found that, when transferred to seawater with the imputed Cretaceous Mg/Ca ratio, its exponential rate of population growth approximately quadrupled (Fig. 3C).

Unlike concentrations of iron, silica, nitrate, and phosphate, which serve as limiting factors for other groups of phytoplankton (Brand, 1991, 1994; Martin et al., 1994), those of Ca and Mg vary little from place to place in the ocean. We conclude that the unfavorable concentrations of Ca and Mg in modern seawater prevent all but a few coccolithophore species from blooming when conventional nutrients are in abundant supply. Most coccolithophore species are restricted to nutrient-deficient subtropical and/or tropical gyres of the ocean, where they exist at relatively low abundance in what amounts to a refugium.

APPENDIX. METHODS

Coccolithophore strains (CCMP645, CCMP2119, CCMP298) were obtained from the Provasoli-Guillard National Center for Culture

of Marine Phytoplankton (P-G CCMP). Artificial seawaters were prepared according to the formula of Bidwell and Spotte (1985), but with the Mg/Ca molar ratio varying from 5.2 to 0.5; the molar sum of Mg and Ca was held constant at the level of modern seawater. Cultures were grown in 500 mL of seawater in 1000 mL beakers that were partially covered to reduce evaporation but permit some air circulation. Each beaker was illuminated by a single 120 V, 25 W aquarium lamp at an elevation of 15 cm above the water surface. The beakers sat in a large bath of fresh water maintained at 25 °C by electrical heaters and kept in circulation by aeration. In cultures of *Pleurchrysis carterae* and *Coccolithus neohelis*, concentrations of nitrogen (as nitrate), phosphorus (as phosphate), and iron (as Fe³⁺) were, respectively: 8.8×10^{-4} , 2.3×10^{-4} , and 1.4×10^{-5} mol/L (P-G CCMP culture medium f/2). In cultures of *Ochrosphaera neopolitana*, the corresponding concentrations were lower: 3.5×10^{-5} , 9.2×10^{-6} , and 5.8×10^{-7} , as specified by P-G CCMP (culture medium f/50) for growth of this oceanic species. The pH of all cultures remained at 8.15 (± 0.1) without any secular trend.

Experiments were carried out over 6–7 d during the initial exponential phase of population growth. Cell concentrations in cultures were measured daily by removing 15 mL of water after homogenizing the upper part of the culture by gentle stirring with a sterile glass rod. Cell density was measured with a Hach 2100P turbidimeter, after which the sample was returned to the culture. The turbidimeter was calibrated by relating measured values linearly to cell concentrations measured with a hemocytometer. Scanning electron microscopic images of culture residues showed that nearly all coccospheres remained intact throughout experiments. Because coccoliths were small relative to cell size and infrequently lost, we are confident that cells constituted nearly all of the suspended material. Percentage of Mg substituting for Ca in calcite was determined by means of the energy-dispersive spectrometry analytical method of a JEOL 8600 Superprobe microprobe with a beam current of 0.02 μA , accelerating potential of 15 kV, counting time of 15 s, and beam diameter of 1–2 μm .

ACKNOWLEDGMENTS

We thank the Provasoli-Guillard National Center for Culture of Marine Phytoplankton for providing cultures. Elma Gonzalez provided helpful information on culturing procedures. This research was supported by the National Science Foundation (grant EAR-0202849) and the Petroleum Research Fund (AC2-38468).

REFERENCES CITED

Balch, W.M., Holligan, P.M., and Kilpatrick, K.A., 1992, Calcification, photosynthesis and growth of the bloom-forming coccolithophore, *Emiliania huxleyi*: Continental Shelf Research, v. 12, p. 1353–1374, doi: 10.1016/0278-4343(92)90059-S.

Bidigare, R.R., Fluegge, A., Freeman, K.H., Hanson, K.L., Hayes, J.M., Hollander, D., Jasper, J.P., King, L.L., Laws, E.A., Milder, J., Millero, F.J., Pancost, R., Popp, B.N., Steinberg, P.A., and Wakeham, S.G., 1997, Consistent fractionation of ¹³C in nature and in the laboratory: Growth rate effects in some haptophyte algae: Global Biogeochemical Cycles, v. 11, p. 279–292, doi: 10.1029/96GB03939.

Bidwell, J.P., and Spotte, S., 1985, Artificial seawaters: Formulas and methods: Boston, Massachusetts, Jones and Bartlett, 349 p.

Borowitzka, M.A., and Larkum, A.W., 1976, Calcification in the green alga *Halimeda*, 3. The sources of inorganic carbon for photosynthesis and calcification and a model of the mechanism of calcification: Journal of Experimental Botany, v. 27, p. 879–893.

Brand, L.E., 1991, Minimum iron requirements of marine phytoplankton and the implications for biogeochemical control of new production: Limnology and Oceanography, v. 36, p. 1756–1771.

Brand, L.E., 1994, Physiological ecology of marine coccolithophores, in Winter, A., and Siesser, W.G., eds., Coccolithophores: Cambridge, Cambridge University Press, p. 39–49.

Davis, K.J., Dove, P.M., and De Yoreo, J.J., 2002, Resolving the controversial role of Mg²⁺ in calcite biomineral formation: Science, v. 290, p. 1134–1137.

Füchtbauer, H., and Hardie, L.A., 1976, Experimentally determined homogeneous distribution coefficients for precipitated magnesian calcites: Appli-

cation to marine carbonate cements: Geological Society of America Abstracts with Programs, v. 8, p. 877.

Füchtbauer, H., and Hardie, L.A., 1980, Comparison of experimental and natural magnesian calcites: International Association of Sedimentologists Abstract, p. 167–169.

Hardie, L.A., 1996, Secular variation in seawater chemistry: An explanation for the coupled secular variation in the mineralogy of marine limestones and potash evaporites over the past 600 m.y.: Geology, v. 24, p. 279–283, doi: 10.1130/0091-7613(1996)0242.3.CO;2.

Hattin, D.E., 1988, Cretaceous shelf-sea chalk deposits: A global synthesis: American Association of Petroleum Geologists Bulletin, v. 72, p. 195–196.

Hulbert, E.M., 1983, Quasi K-selected species, equivalence, and the oceanic coccolithophorid plankton: Bulletin of Marine Science, v. 33, p. 187–212.

Lowenstein, T.K., Timofeeff, M.N., Brennan, S.T., Hardie, L.A., and Demicco, R.V., 2001, Oscillations in Phanerozoic seawater chemistry: Evidence from fluid inclusions: Science, v. 294, p. 1086–1088, doi: 10.1126/science.1064280.

Martin, J.H., and 43 others, 1994, Testing the iron hypothesis in ecosystems of the equatorial Pacific Ocean: Nature, v. 371, p. 123–129.

McIntyre, A., 1970, *Gephyrocapsa protohuxleyi* sp. n.: A possible phyletic link and index fossil for the Pleistocene: Deep-Sea Research, v. 17, p. 187–190.

Nimer, N.A., and Merritt, M.J., 1996, Inorganic carbon transport in relation to culture age and inorganic carbon concentration in a high-calcifying strain of *Emiliania huxleyi* (Prymnesiophyceae): Journal of Phycology, v. 32, p. 813–818, doi: 10.1111/j.0022-3646.1996.00813.x.

Pagani, M., Arthur, M.A., and Freeman, K.H., 1999a, Miocene evolution of atmospheric carbon dioxide: Paleoceanography, v. 14, p. 273–292, doi: 10.1029/1999PA900006.

Pagani, M., Freeman, K.H., and Arthur, M.A., 1999b, Late Miocene atmospheric CO₂ concentrations and the expansion of C₄ grasses: Science, v. 285, p. 876–879, doi: 10.1126/science.285.5429.876.

Riebesell, U., Zondervan, I., Tortell, P.D., Zeebe, R.E., and Morel, F.M.M., 2000, Reduced calcification in marine plankton in response to increased atmospheric CO₂: Nature, v. 407, p. 364–367.

Ries, J.B., 2004, Effect of ambient Mg/Ca ratio on Mg fractionation in calcareous marine invertebrates: A record of the oceanic Mg/Ca ratio over the Phanerozoic: Geology, v. 32, p. 981–984, doi: 10.1130/G20851.1.

Royer, D.L., Berner, R.A., and Beerling, D.J., 2001, Phanerozoic atmospheric CO₂ change; evaluating geochemical and paleobiological approaches: Earth Science Reviews, v. 54, p. 349–392.

Sandberg, P.A., 1985, Nonskeletal aragonite and pCO₂ in the Phanerozoic and Proterozoic: American Geophysical Union Geophysical Monograph 32, p. 585–594.

Scholle, P.A., 1977, Chalk diagenesis and its relation to petroleum exploration: Oil from chalks, a modern miracle?: American Association of Petroleum Geologists, v. 61, p. 982–1009.

Siemann, M.G., 2003, Extensive and rapid changes in seawater chemistry during the Phanerozoic: Evidence from Br contents in basal halite: Terra Nova, v. 15, p. 243–248, doi: 10.1046/j.1365-3121.2003.00490.x.

Siesser, W.G., 1977, Chemical composition of calcareous nanofossils: South African Journal of Science, v. 73, p. 283–285.

Sikes, C.S., Roer, R.D., and Wilbur, K.M., 1980, Photosynthesis and coccolith formation: Inorganic carbon sources and net inorganic reaction of deposition: Limnology and Oceanography, v. 25, p. 248–261.

Stanley, S.M., and Hardie, L.A., 1998, Secular oscillations in the carbonate mineralogy of reef-building and sediment-producing organisms driven by tectonically forced shifts in seawater chemistry: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 144, p. 3–19, doi: 10.1016/S0031-0182(98)00109-6.

Stanley, S.M., and Hardie, L.A., 1999, Hypercalcification: Paleontology links plate tectonics and geochemistry to sedimentology: GSA Today, v. 9, p. 1–7.

Stanley, S.M., Ries, J.B., and Hardie, L.A., 2002, Low-magnesium calcite produced by coralline algae in seawater of Late Cretaceous composition: National Academy of Sciences Proceedings, v. 99, p. 15,323–15,326, doi: 10.1073/pnas.232569499.

Thierstein, H.R., Geitenhauer, K.R., and Molino, B., 1977, Global synchronicity of late Quaternary coccolith datum levels: Validation by oxygen isotopes: Geology, v. 5, p. 400–404, doi: 10.1130/0091-7613(1977)52.0.CO;2.

Winter, A., and Siesser, W.G., 1994, Atlas of living coccolithophores, in Winter, A., and Siesser, W.G., eds., Coccolithophores: Cambridge, Cambridge University Press, p. 107–159.

Manuscript received 20 November 2004

Revised manuscript received 22 March 2005

Manuscript accepted 25 March 2005

Printed in USA