Eve of biomineralization: Controls on skeletal mineralogy

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ABSTRACT

Carbonate mineralogies have oscillated between aragonite and calcite seas through geological time, proposed to be due mainly to secular variation in the magnesium/calcium ratio driven by changing rates of ocean crust production. A quantitative compilation of inorganic and biominerals from the onset of biomineralization (late Ediacaran–Middle Ordovician) reveals a correspondence between seawater chemistry and the first adopted mineralogy of skeletal clades. Ediacaran–Tommotian skeletons and inorganic precipitates were composed exclusively of aragonite or high-Mg calcite, but these were replaced by low-Mg calcite mineralogies during the early Atdabanian, implying the onset of a calcite sea. This transition is empirically constrained by fluid inclusion data. Late Atbadanian–Botoman inorganic precipitates returned to aragonite, with high-Mg calcite echinoderms and solitary tabulaconids and massive aragonitic tabulaconids originating during this interval. Middle Cambrian–Ordovician inorganic precipitates were low-Mg calcite, and the Ordovician radiation in skeletal expression was due mostly to groups with low-Mg calcite mineralogies. These short-lived transitions can be most parsimoniously explained by minor oscillations of mMg:Ca around ~2 during this period, possibly combined with the progressive onset of greenhouse conditions during the mid-Late Cambrian.

INTRODUCTION

It is now widely accepted that both inorganic and biogenic carbonate mineralogies have oscillated between aragonite + high-Mg calcite (HMC) (>4 mol% Mg) and low-Mg calcite (LMC) through the Phanerozoic, and probably before (Sandberg, 1983; Stanley and Hardie, 1998). Skeletal mineralogies are usually considered to be conserved within phylogenetic lineages; representatives of some Early Cambrian taxa still exist and appear to have retained the same mineralogy throughout their history. However, compilations of fossil data (Wood, 1991; Dickson, 2004; Smith et al., 2006; Porter, 2007) as well as in vivo experiments on organisms grown in artificial seawaters (e.g., Ries, 2006; Checa et al., 2007) have shown that some groups exhibit nonlinear relationships between skeletal and ambient Mg/Ca ratios, and are able to change their mineralogy from HMC to LMC, and from aragonite to LMC (Stolarski et al., 2007).

The intervals of aragonite and calcite seas are thought to be caused by a secular variation in molar magnesium/calcium ratio (mMg:Ca) of seawater, with aragonite and HMC forming at mMg:Ca >1, and LMC forming at mMg:Ca <1. This phenomenon has been attributed to either secular variations in pCO_2 (Sandberg, 1983; Opdyke and Wilkinson, 1990), or seawater mMg:Ca (Hardie, 1996; Stanley and Hardie, 1998; Lowenstein et al., 2001).

To assess the relationship between seawater chemistry and skeletal mineralogy, we present here quantitative data on biogenic and inorganic carbonates from the eve of biomineralization, the Ediacaran–Ordovician interval, for which both seawater chemistry (Hardie, 1996) and pCO_2 (Berner and Kothavala, 2001) are poorly constrained.

DATA

The distribution of major biominerals (LMC, HMC, aragonite, and calcium phosphate) at the onset of biomineralization of a group, together with the carbonate mineralogy of synsedimentary marine cements and ooids from the late Ediacaran (ca. 550 Ma) to early Middle Ordovician (ca. 460 Ma) is given in Figure 1 (see Tables DR1–DR3 in the GSA Data Repository[1]). Data are collected from all principal basins and derived from temporally well constrained units only.

The bulk distribution of biogenic LMC, HMC, and aragonite through this interval was assessed using the number of genera per zone per mineralogy. We considered 3395 genera in total from a global database of 4122 genera (Zhuravlev, 2001) (Fig. 2; see Data Repository). As the majority of these genera are monotypic, this analysis provides a reasonable quantification of biomineralization trends.

Biomineral Distribution

Cambrian trilobites and *Salterella* (agmatan) have skeletons with a low (1–2 mol%) magnesium carbonate ($MgCO_3$) content and without detectable iron and neomorphic alterations (James and Klappa, 1983). Lower Paleozoic trilobites probably also possessed LMC carapaces, which are encrusted by equant calcite cements and preserve an isotope composition similar to coeval unaltered rhynchonellid brachiopods (Wilmot and Fallick, 1989). Unlike aragonite, calcitic prisms tend to be nonfibrous and are commonly preserved by a single crystal. In addition, coral-like hydroconozoans, rhynchonellid and kutorginate brachiopods, and stenothecoids all show well-preserved, probably pristine LMC shell fabrics. Hydroconozoan skeletons show only minor Mg content compared to archaeocyath species and synsedimentary cements from the same samples. Some helcionelloid mollusks secreted shells with foliated calcite microstructure later in the Middle Cambrian (Runnegar, 1985).

An HMC mineralogy is suggested for archaeocyaths (calcified sponges) and renalcids (a problematic group commonly attributed to calcified cyanobacteria), because they display microgranular skeletal microstructure retaining some primary features, often with microdolomite that formed in a closed system during conversion to LMC, and common encrustation by fibrous synsedimentary marine cement also containing microdolomite (James and Klappa, 1983). The same fabrics characterize problematic cribricyaths and earliest coralomorphs (khasaktiids and low modular tabulaconids). An aragonitic or HMC mineralogy is also suggested for *Cloudina* and some other late Ediacaran shelly fossils (Grotzinger et al., 2000; Zhuravlev et al., 2007).

Cambrian echinoderm plates and calcarean sponge spicules are preserved as single calcite crystals with iron-rich and iron-poor phases containing from 2–3 to 10–12 mol% $MgCO_3$; epitaxial Mg-calcite and microdolomite inclusions are common, indicating primary HMC composition (James and Klappa, 1983). This has been confirmed by a direct measurement of the $MgCO_3$ content of Botoman (Lower Cambrian) echinoderms, which show 10.3–10.6 mol% Mg (Dickson, 2004).

Namapoikia, chancelloriids (coeloscleritomorphs), orthothecimorph hyoliths, helcionelloid
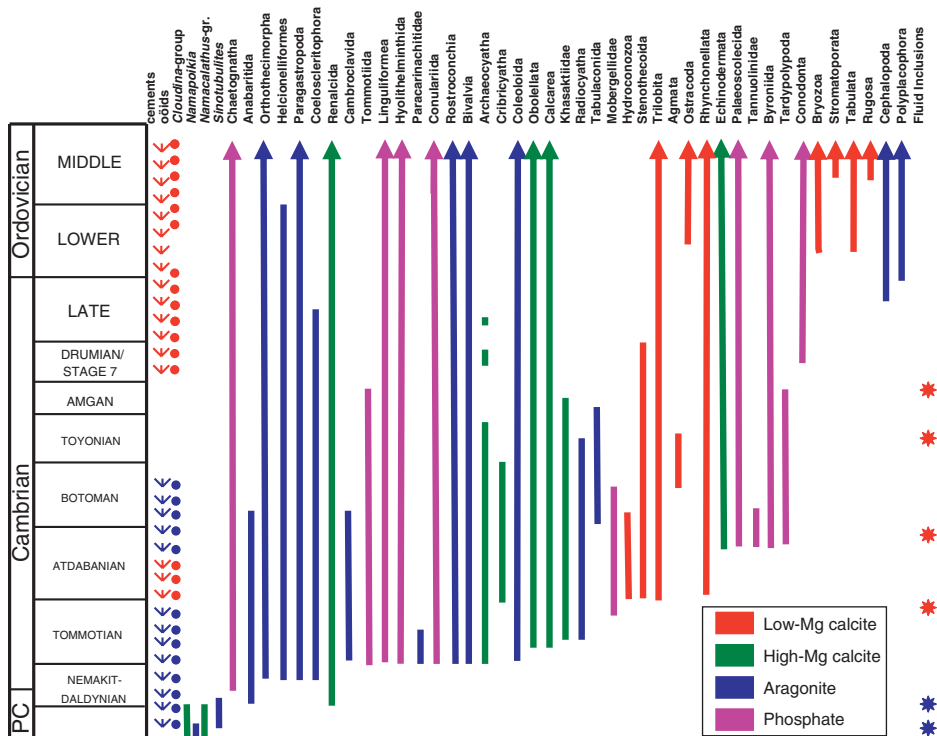
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Figure 1. Distribution of major skeletal taxa and carbonate inorganic precipitates (ooids and synsedimentary marine cements) from upper Ediacaran to Middle Ordovician (see footnote 1). Phyogenetic relationships are not shown and independent acquisition of skeletons in all clades is not implied. Fluid inclusion data are from Lowenstein et al. (2001) and Petrychenko et al. (2005). 7—Cambrian Stage 7. PC—Precambrian.

mollusks, obolellate brachiopods, and *Labyrinthus* (coralomorph) are represented by skeletons preserved as coarse mosaic spar-filled molds indicative of the dissolution of primary aragonite fabrics (James and Klappa, 1983; Wood et al., 2002). The same type of preservation is typical of radiocyaths and other Early Cambrian mollusks, whose skeletons are epitaxially encrusted by botryoids of acicular aragonite synsedimentary cement (Wood et al., 1993). Massive modular tabulaconids display similar preservational characteristics (see the Data Repository).

The abundance of phosphatic skeletons in the Early Cambrian is now accepted to be a secondary diagenetic phenomenon (Porter, 2004). Thus in phosphatic facies, coelosclertomorph, orthothecimorph hyolith, mollusk, radiocyath, as well as anabaritid, coleolid, and carinachitid skeletal fabrics are replicated in phosphate retaining submicron-scale features of typical aragonite microstructures, including prismatic, nacreous, and lamello-fibrillar fabrics (Runnegar, 1985). Although some mollusks produce low Mg-calcite fabrics possessing overall similarities with aragonitic ones, these fabrics differ by crystal size and morphology due to the primary organic matrix structure (Kobayashi and Samata, 2006).

Inorganic Precipitate Distribution

Widespread aragonitic cements and ooids have been recorded from Nemakit-Daldynian to earliest Cambrian (Tommotian) sediments (Tucker, 1992). Ooids of LMC original mineralogy have been documented from the lower Atdabanian of Australia, Morocco, and the Siberian platform (Tucker, 1992). The oolitic Churan Member of the Siberian platform has well-preserved LMC ooids in the lower part (dated as lower Atdabanian), but ooids with microdolomite crystals suggestive of an original HMC composition within the upper part (dated as upper Atdabanian).

Aragonite and HMC cements as well as open-marine HMC ooid shoals have been recorded from all principal Early Cambrian carbonate settings spanning the entire late Atdabanian–late Botoman interval (James and Klappa, 1983; Wood et al., 1993).

The late Middle to Late Cambrian interval records the mass precipitation of LMC equant marine cements instead of HMC fibrous calcite and acicular aragonite. This interval also records the first appearance of unequivocal hardgrounds cemented by LMC. LMC ooids and cements are widely recorded from Ordovician sediments (Sandberg, 1983; Opdyke and Wilkinson, 1990).

CAMBRIAN ARAGONITE TO CALCITE SEAS

By the end of the Ediacaran, skeletal animals were already abundant and relatively diverse (Grotzinger et al., 2000; Wood et al., 2002). These earliest, as well as Tommotian, skeletons are characterized exclusively by either aragonite or HMC, contrary to previous compilations that show the delayed appearance of both LMC and HMC polymorphs (Porter, 2007). Aragonite inorganic precipitates dominate this interval.

LMC skeletons are first known from the following early Atdabanian interval, and appeared synchronously in several independent groups, i.e., hydroconozoans, stenothecoids, rhynchonellid, and kutorginate brachiopods, and trilobites. Only two species with inferred LMC skeletons (*Hydroconus* and brachiopod *Khasaktina*) are known from the uppermost Tommotian strata (Fig. 1). LMC inorganic precipitates also appear during the early Atbadanian.

Aragonite and HMC inorganic precipitates reappear globally during the late Atdabanian. The two significant groups that appeared at the end of the Atdabanian and the beginning of the Botoman had either HMC (echinoderms and solitary tabulaconids) or aragonite mineralogy (massive tabulaconids). Both were already represented by several different and geographically isolated taxa that may have independently acquired skeletons. A single LMC genus, *Salterella*, appeared around the Botoman-Toyonian boundary. This, however, possessed an unusual agglutinated conch and was restricted to Laurentia.

The first probable aragonitic cephalopods and polyplacophorans are known from the uppermost Upper Cambrian. Both these groups, however, were probably derived from skeletonized ancestors rather than having acquired shells independently. The Ordovician radiation in its skeletal expression is due mostly to groups with supposed LMC mineralogies (stromatoporoid sponges, tabulate and rugosan corals, bryozoans, and ostracodes).

Quantitative data on the abundance of carbonate biominerals show a similar notable shift from exclusively aragonitic + HMC mineralogies in the late Ediacaran–Tommotian to their successive replacement by LMC mineralogies from the early Atdabanian onward. By the end of the Early Cambrian, only ~20% of skeletal biota was of aragonitic + HMC mineralogy, coinciding with the appearance of LMC inorganic precipitates (Fig. 2).

In general, late Ediacaran–Ordovician inorganic and biogenic carbonate precipitates show a marked synchronicity. They reflect an oscillation from a late Ediacaran–late Tommotian aragonite sea characterized by aragonite and HMC polymorphs to an early Atdabanian
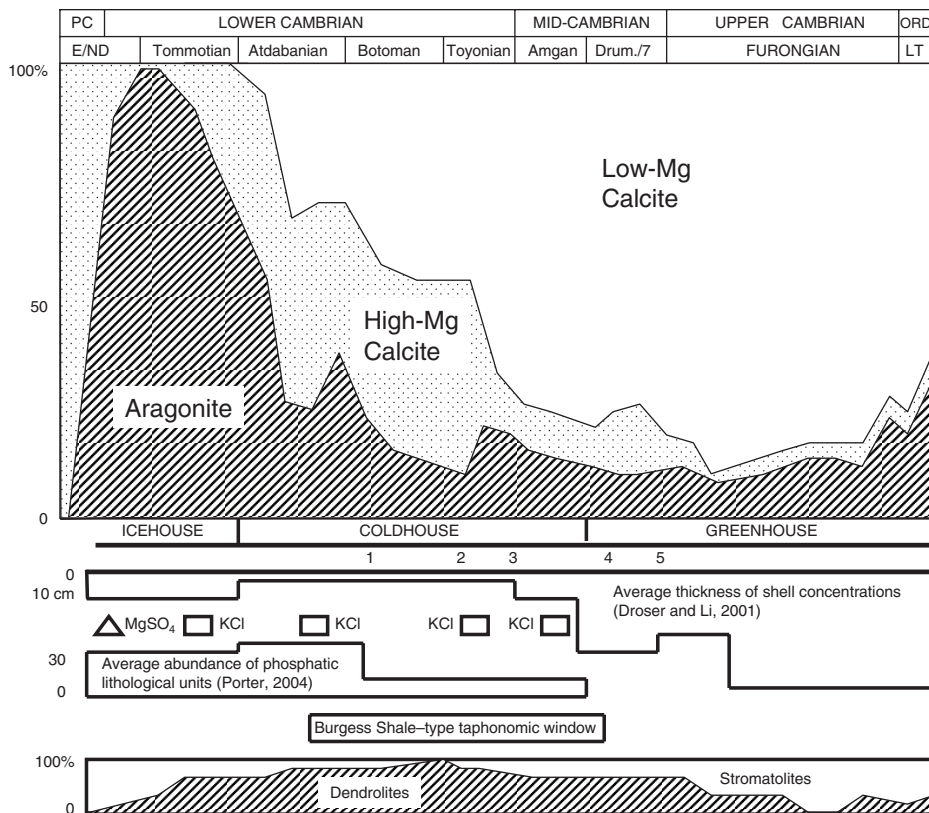
Figure 2. Distribution of skeletal carbonate mineralogies expressed as percentage of number of genera per zone (see footnote 1), from upper Ediacaran to Lower Ordovician (lower Tremadocian). Stromatolites and dendrolites diversity data are from Zhuravlev (1996). Climatic intervals are from Tucker (1992). 1—Sinsk global anoxic event and mass extinction (Zhuravlev and Wood, 1996). 2—Hawke Bay global regression (Zhuravlev and Wood, 1996). 3—Kalkarindji flood basalt (Hough et al., 2006). 4—Decline in acritarch species diversity (Zhuravlev, 2001); appearance of hardgrounds and carbonate tempestites cemented by low-Mg calcite (LMC; see the Data Repository [see footnote 1]); major echinoderm diversification. 5—Loss of renalcids, increase in stromatolites and thrombolites (Zhuravlev, 1996). Data on evaporites are after Lowenstein et al. (2001) and Petrychenko et al. (2005). PC—Precambrian; E—Ediacaran period; ND—Nemakit-Daldynian Stage; ORD.—Ordovician Period; LT—lower Tremadocian Series; Drum./7—Drumian Stage (Stage 6) and Cambrian Stage 7.

calcite sea, which facilitated the appearance of groups precipitating LMC skeletons. The data are also suggestive of a reappearance of a short-lived aragonite sea in the late Atdabanian–late Botoman, followed by a return to calcite seas during the Middle Cambrian to Ordovician.

DISCUSSION

The widely accepted model of Hardie (1996) proposes that secular variation in seawater chemistry has been controlled primarily by fluctuations in the mid-ocean ridge hydrothermal brine flux, which in turn have been driven by changes in the rate of ocean crust production. For the late Ediacaran–Tommotian interval, this model is supported by potashevaporites ($MgSO_4$ to KCl) secular variation and fluid inclusions trapping primary surface brines (Hardie, 1996; Stanley and Hardie, 1998; Lowenstein et al., 2001). The overall trend in the quantitative distribution of biogenic and inorganic carbonate polymorphs observed here is also consistent with this model.

However, the pronounced biomineralogical switch to LMC mineralogies from the Tommotian to early Atdabanian, and the less pronounced shift back to HMC + aragonite mineralogies from the late Atdabanian to Botoman, is not reflected in the fluid inclusion data: mMg:Ca from Tommotian, late Atdabanian, Toyonian, and Amgan formations all show the same values of ~1, which predicts the presence of calcite seas through the entire Cambrian (Lowenstein et al., 2001; Petrychenko et al., 2005) (Fig. 1). Late Ediacaran and Tommotian evaporites also differ, but carbonate precipitates remain the same (Fig. 2). The Mg:Ca of 3.3 reported from Botoman echinoderm plates is similar to values found from the late Paleozoic to early Mesozoic aragonite sea and so also contradicts both model and fluid inclusion data (Dickson, 2004). The strontium isotope ($^{87}Sr/^{86}Sr$) secular trend

likewise does not support the suggestion of a marked increased ocean-crust growth rate that could drive changing mMg:Ca during the Cambrian: the only pronounced negative excursion, which may be indicative of such a process, is revealed in the Amgan (Montañez et al., 2000).

Several explanations are possible for these contradictory data. The most parsimonious is that mMg:Ca underwent minor oscillations around ~2, enabling short-term switches from calcite to aragonite seas. Alternatively, some observed Mg:Ca values may reflect basinal-scale rather than global-scale processes, such as the dolomitization of extensive carbonate platforms during periods of high sea level. This is probably the case for the Siberian platform, from which the entire data set on Cambrian evaporites and fluid inclusions was obtained. The data presented here on carbonate precipitates, however, were collected globally, from all principal Cambrian basins.

A further explanation may be in a model that couples mMg:Ca ratio oscillations with secular variations in pCO_2 and, thus, with global climatic cycles during the Neoproterozoic–Cambrian. As atmospheric CO_2 concentration and temperature increase, the average composition of carbonate sediments may change in favor of minerals with lower Mg content and higher stability (Kleypas and Langdon, 2006; Morse et al., 2006). In the absence of pelagic carbonate production, all these processes were directly linked to shallow-marine settings in the Cambrian.

The Botoman–Amgan interval records a series of notable events compatible with the onset of a greenhouse epoch from the Tommotian icehouse via a coldhouse interval (Tucker, 1992), driven by a rise in pCO_2 rather than a decline in mMg:Ca ratio (Fig. 2). These include global anoxic events (Zhuravlev and Wood, 1996; Saltzman et al., 2004), positive $\delta^{13}C$ excursions (Montañez et al., 2000), and a sharp increase of ^{34}S values in seawater sulfates (Hough et al., 2006). These all imply a reduced ocean circulation typical of greenhouse epochs (Tucker, 1992). Eruption of the ca. 510 Ma Kalkarindji continental flood basalts may also have promoted oceanic greenhouse conditions (Hough et al., 2006).

More evidence for emergent greenhouse conditions appeared after the Drumian, including the almost complete replacement of HMC reefs by stromatolites and nonskeletal thrombolites (Zhuravlev, 1996), and a threefold increase in average shell bed concentration thickness dominated by LMC biota (Fig. 2) (Droser and Li, 2001). Also noteworthy is the marked increase of carbonate flat-pebble conglomerates (tempestites) during the Cambrian (Kim and Lee, 1995; Table DR4) and the closure of the Burgess Shale–type taphonomic window at the end of the Amgan (Butterfield, 2003) (Fig. 2; see the Data

Repository), both of which have been attributed to increased storm and/or hurricane intensity and duration as a result of the onset of a greenhouse epoch (Emanuel, 2006). Finally, a change in the weathering regime with the commencement of a greenhouse epoch might have led to a nutrient supply exhaustion, as expressed in the synchronous cessation of significant phosphogenic events, complete closure of the phosphatization window (Cook, 1992; Porter, 2004), and decline in acritarch (phytoplankton) species diversity and triaromatic dinosteroid frequency (Moldowan et al., 2001; Zhuravlev, 2001).

REFERENCES CITED

Berner, R.A., and Kothavala, Z., 2001, Geocarb III: A revised model of atmospheric CO_2 over Phanerozoic time: American Journal of Science, v. 301, p. 182–204.

Butterfield, N.J., 2003, Exceptional fossil preservation and the Cambrian explosion: Integrative and Comparative Biology, v. 43, p. 166–177, doi: 10.1093/icb/43.1.166.

Checa, A.G., Jiménez-López, J., Rodríguez-Navarro, A., and Machado, J.P., 2007, Precipitation of aragonite by calcitic bivalves in Mg-enriched marine waters: Marine Biology, v. 150, p. 819–827, doi: 10.1007/s00227–006–0411–4.

Cook, P.J., 1992, Phosphogenesis around the Proterozoic-Phanerozoic transition: Geological Society of London Journal, v. 149, p. 615–620, doi: 10.1144/gsjgs.149.4.0615.

Dickson, J.A.D., 2004, Echinoderm skeletal preservation: Calcite-aragonite seas and the Mg/Ca ratio of Phanerozoic oceans: Journal of Sedimentary Research, v. 74, p. 355–365, doi: 10.1306/112203740355.

Droser, M.L., and Li, X., 2001, The Cambrian radiation and the diversification of sedimentary fabrics, in Zhuravlev, A.Y., and Riding, R., eds., The ecology of the Cambrian radiation: New York, Columbia University Press, p. 137–169.

Emanuel, K.A., 2006, Climate and tropical cyclone activity: A new model downscaling approach: Journal of Climate, v. 19, p. 4797–4802, doi: 10.1175/JCLI3908.1.

Grotzinger, J.P., Watters, W.A., and Knoll, A.H., 2000, Calcified metazoans in thrombolite-stromatolite reefs of the terminal Proterozoic Nama Group, Namibia: Paleobiology, v. 26, p. 334–359, doi: 10.1666/0094–8373(2000)026<0334:CMITSR>2.0.CO;2.

Hardie, L.A., 1996, Secular variations in seawater chemistry: An explanation for the coupled secular variation in the mineralogies of marine limestones and potash evaporites over the past 600 m.y.: Geology, v. 24, p. 279–283, doi: 10.1130/0091–7613(1996)024<0279:SVISCA>2.3.CO;2.

Hough, M.L., Shields, G.A., Evins, L.Z., Strauss, H., Henderson, R.A., and Mackenzie, S., 2006, A major sulphur isotope event at c. 510 Ma: A possible anoxia-extinction-volcanism connection during the Early-Middle Cambrian transition?: Terra Nova, v. 18, p. 257–263.

James, N.P., and Klappa, C.F., 1983, Petrogenesis of Early Cambrian reef limestones, Labrador, Canada: Journal of Sedimentary Petrology, v. 53, p. 1051–1096.

Kim, J.C., and Lee, Y.I., 1995, Flat-pebble conglomerate: A characteristic lithology of Upper Cambrian and Lower Ordovician shallow-water carbonate sequence, in Ordovician Odyssey, Short papers, International Symposium on the Ordovician System, 7th, Fullerton, California: Pacific Section, SEPM (Society for Sedimentary Geology), p. 371–374.

Kleypas, J.A., and Langdon, C., 2006, Coral reefs and changing seawater chemistry, in Phinney, J.T., et al., eds., Coral reefs and climate change: Science and management: American Geophysical Union Geophysical Monograph 61, p. 73–110.

Kobayashi, I., and Samata, T., 2006, Bivalve shell structure and organic matrix: Materials Science and Engineering C, v. 26, p. 692–698, doi: 10.1016/j.msec.2005.09.101.

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.

Moldowan, J.M., Jacobson, S.R., Dahl, J., Al-Hajji, A., Huizinga, B.J., and Fago, F.J., 2001, Molecular fossils demonstrate Precambrian origin of dinoflagellates, in Zhuravlev, A.Y., and Riding, R., eds., The ecology of the Cambrian radiation: New York, Columbia University Press, p. 475–493.

Montañez, I., Osleger, D., Banner, J.L., Mack, L.E., and Musgrove, M., 2000, Evolution of Sr and C isotope composition of Cambrian oceans: GSA Today, v. 10, p. 1–5.

Morse, J.W., Andersson, A.J., and Mackenzie, F.T., 2006, Initial responses of carbonate-rich shelf sediments to rising atmospheric pCO_2 and "ocean acidification": Role of high Mg-calcites: Geochimica et Cosmochimica Acta, v. 70, p. 5814–5830, doi: 10.1016/j.gca.2006.08.017.

Opdyke, B.N., and Wilkinson, B.H., 1990, Paleolatitude distribution of Phanerozoic marine ooids and cements: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 78, p. 135–148, doi: 10.1016/0031–0182(90)90208-O.

Petrychenko, O.Y., Peryt, T.M., and Chechel, E.I., 2005, Early Cambrian seawater chemistry from fluid inclusions in halite from Siberian evaporites: Chemical Geology, v. 219, p. 149–161, doi: 10.1016/j.chemgeo.2005.02.003.

Porter, S.M., 2004, Closing the phosphatization window: Testing for the influence of taphonomic megabias on the pattern of small shelly fossil decline: Palaios, v. 19, p. 178–183, doi: 10.1669/0883–1351(2004)019<0178:CTPWTF>2.0.CO;2.

Porter, S.M., 2007, Seawater chemistry and early carbonate biomineralization: Science, v. 316, p. 1302, doi: 10.1126/science.1137284.

Ries, J., 2006, Aragonitic algae in calcite seas: Effect of seawater Mg/Ca on codiacean biomineralization: Journal of Sedimentary Research, v. 76, p. 515–523, doi: 10.2110/jsr.2006.051.

Runnegar, B., 1985, Shell microstructure of Cambrian molluscs replicated by calcite: Alcheringa, v. 9, p. 245–257, doi: 10.1080/03115518508618971.

Saltzman, M.R., Runkel, A.C., Cowan, C.A., Runnegar, B., Stewart, M.C., and Palmer, A.R., 2004, The Upper Cambrian SPICE ($\delta^{13}C$) event and Sauk II-Sauk III regression: New evidence from Laurentian basins in Utah, Iowa and Newfoundland: Journal of Sedimentary Research, v. 74, p. 366–377, doi: 10.1306/120203740366.

Sandberg, P.A., 1983, An oscillating trend in nonskeletal carbonate mineralogy: Nature, v. 305, p. 19–22, doi: 10.1038/305019a0.

Smith, A.M., Key, M.M., Jr., and Gordon, D.P., 2006, Skeletal mineralogy of bryozoans: Taxonomic and temporal patterns: Earth-Science Reviews, v. 78, p. 287–306, doi: 10.1016/j.earscirev.2006.06.001.

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.

Stolarski, J., Meibom, A., Przenisosło, R., and Mazur, M., 2007, A Cretaceous scleractinian coral with a calcitic skeleton: Science, v. 318, p. 92–94, doi: 10.1126/science.1149237.

Tucker, M.E., 1992, The Precambrian-Cambrian boundary: Seawater chemistry, ocean circulation and nutrient supply in metazoan evolution, extinction and biomineralization: Geological Society of London Journal, v. 149, p. 655–668, doi: 10.1144/gsjgs.149.4.0655.

Wilmot, N.V., and Fallick, A.E., 1989, Original mineralogy of trilobite exoskeletons: Palaeontology, v. 32, p. 297–304.

Wood, R.A., 1991, Problematic reef-building sponges, in Simonetta, A.M., and Conway Morris, S., eds., The early evolution of Metazoa and the significance of problematic taxa: Cambridge, UK, Cambridge University Press, p. 113–124.

Wood, R.A., Zhuravlev, A.Y., and Chimed Tseren, A., 1993, The ecology of Lower Cambrian buildups from Zuune Arts, Mongolia: Implications for early metazoan reef evolution: Sedimentology, v. 40, p. 829–858, doi: 10.1111/j.1365–3091.1993.tb01364.x.

Wood, R.A., Grotzinger, J.P., and Dickson, J.A.D., 2002, Proterozoic modular biomineralized metazoan from the Nama Group, Namibia: Science, v. 296, p. 2383–2386, doi: 10.1126/science.1071599.

Zhuravlev, A.Y., 1996, Reef ecosystem recovery after the Early Cambrian extinction, in Hart, M.B., ed., Biotic recovery from mass extinction events: Geological Society of London Special Publication 102, p. 79–96.

Zhuravlev, A.Y., 2001, Biota diversity and structure during the Neoproterozoic-Ordovician transition, in Zhuravlev, A.Y., and Riding, R., eds., The ecology of the Cambrian radiation: New York, Columbia University Press, p. 173–199.

Zhuravlev, A.Y., and Wood, R.A., 1996, Anoxia as the cause of the mid-Early Cambrian (Botomian) extinction event: Geology, v. 24, p. 311–314, doi: 10.1130/0091–7613(1996)024<0311:AATCOT>2.3.CO;2.

Zhuravlev, A.Y., Gámez Vintaned, J.A., and Liñán, E., 2007, Skeletal Precambrian: XXIII Jornadas de la Sociedad Española de Paleontología, Caravaca de la Cruz, Spain, Libro de Resúmenes, p. 229–230.