

Microbial carbonate abundance compared with fluctuations in metazoan diversity over geological time

Robert Riding

School of Earth, Ocean and Planetary Sciences, Cardiff University, Cardiff CF10 3YE, UK

Abstract

Secular variation in microbial carbonate abundance may be reflected by stromatolite morphotype diversity and reefal microbial carbonate abundance. These datasets reveal long-term changes over the past 3000 Myr that include a peak of abundance 1250 Myr ago, Late Proterozoic decline, Cambrian resurgence, and fluctuating decline during the remainder of the Phanerozoic. It is conceivable that Proterozoic metazoan diversification coincided with inception of stromatolite decline ~1250 Myr ago, but microbial carbonate increase during Cambrian metazoan radiation together with failure of microbial carbonates to increase in the aftermaths of the End-Ordovician, End-Triassic and End-Cretaceous Mass Extinctions suggest that factors in addition to metazoan competition significantly influenced long-term changes in microbial carbonate abundance.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Competition; Mass extinction; Phanerozoic; Proterozoic; Stromatolite

1. Introduction

The contrast between carbonate platforms dominated by microbial deposits in the Precambrian and those dominated by algal and invertebrate skeletons and their debris in the Phanerozoic, is a conspicuous reminder of long-term changes in processes of carbonate sediment accumulation. It also reflects major changes in marine biotas through time (Awramik and Sprinkle, 1999). Although benthic microbial carbonates persisted in marine environments throughout the Phanerozoic (Pratt, 1982), present-day examples are much less abundant than during the acme of microbial carbonates in the Proterozoic, and a widely considered explanation for the long-term decline of microbial carbonates is eukaryote competition and interference, including predation, competition for space, substrate modification

and other effects (Fischer, 1965; Awramik, 1971, 1992). This view is prompted in the first instance by the observations that present-day microbial mats can be heavily grazed by herbivores, such as cerithid gastropods (Garrett, 1970), and that large domical microbial carbonates broadly resembling those that were widespread in the Early Palaeozoic and Precambrian are noticeably restricted to locations, such as Shark Bay, Australia (Logan, 1961) and Lee Stocking Island, in the Bahamas (Dill et al., 1986), where competitors may be reduced by seasonal hypersalinity and mobile sediment in current-swept channels. This possibility that competition, particularly from metazoans, has reduced microbial carbonates and progressively relegated them to ecological refuges, is supported by their broad pattern of distribution in the geological record (Fischer, 1965; Awramik, 1971). Microbial carbonates dominated marine carbonate platforms during the late Archaean and Proterozoic (Beukes, 1987; Grotzinger, 1989), prior to the origin of metazoans. As metazoans appeared and

E-mail address: Riding@Cardiff.ac.uk.

diversified in the late Proterozoic, microbial carbonates underwent dramatic decline (Awramik, 1971) that continued during the Phanerozoic (Fischer, 1965) as metazoans continued to diversify.

If the primary factor influencing microbial carbonate abundance has been metazoan competition, then it follows that temporary reduction in metazoans should favour similar temporary increase in microbial carbonates. In addition to overall long-term diversity increase, metazoans episodically underwent major extinction events, at least five of which during the Phanerozoic can be designated Mass Extinctions (Sepkoski, 1996). Similarly, in spite of overall decline, microbial carbonates at times temporarily recovered some of their former abundance; e.g., in the Late Devonian and Early Triassic (Riding, 1992). Schubert and Bottjer (1992, 1995) interpreted Early Triassic stromatolites as ‘post-mass extinction disaster forms’: ‘long-ranging opportunistic generalists that briefly proliferate in the aftermath of mass extinctions, invading vacant ecospace until forced to return to more marginal settings through competition with specialist taxa returning from refugia’ (Rodland and Bottjer, 2001). Thus, the concept of stromatolite decline resulting from algal–metazoan diversification (Fischer, 1965; Garrett, 1970; Awramik, 1971) has also given rise to that of stromatolite resurgence in the aftermaths of Mass Extinctions (Schubert and Bottjer, 1992, p. 885).

These approaches to the secular distribution of microbial carbonates by competitive exclusion by eukaryotes in general, and metazoans in particular, link major patterns of biodiversity over long time-scales and have been a powerful stimulus to research for several decades. These evaluations rely on comparisons with microbial carbonate abundance through time. In the Proterozoic, in particular, this has been derived by compiling diversity of stromatolite morphotypes (Awramik, 1971; Walter and Heys, 1985). However, in the Phanerozoic there has been little attempt to comprehensively distinguish stromatolites in terms of morphotype (Awramik and Sprinkle, 1999). This would, in any case, be complicated by complex intergrowth resulting from the tendency for stromatolites to co-exist in reefs with skeletal algae and invertebrates (Riding, 2000). Paucity of data has therefore hampered attempts to recognize patterns of Phanerozoic secular abundance (Riding, 2000). However, this situation changed with compilation of reefal microbial carbonate abundance data (Kiessling, 2002). In conjunction, stromatolite morphotype (Awramik and Sprinkle, 1999) and reefal microbial carbonates abundance (Kiessling, 2002) data provide a comprehensive view of changes in microbial carbonate

abundance for the past 3000 Myr. Here I compare these datasets with marine metazoan generic diversity (Sepkoski, 1992, 1997). The aim is to evaluate whether changes in microbial carbonates abundance coincide with changes in metazoan diversity. This straightforward comparison reveals some significant discrepancies. In particular, it draws attention to increase in microbial carbonates as metazoans radiated during the Cambrian, and to instances where microbial carbonates did not increase in Mass Extinction aftermaths. These observations cast doubt on the likelihood that competitive exclusion by metazoans can offer a general explanation for the long-term secular distribution of microbial carbonates.

2. Data

Benthic microbial carbonates are essentially accumulations of carbonate minerals, such as aragonite, calcite and dolomite, localized by microbial mats composed of bacteria, and also algae and fungi (Awramik and Margulis, 1974; Burne and Moore, 1987). Grain-trapping can be locally important, but the key processes are microbially mediated precipitation (Riding, 2000). The resulting deposits commonly have heterogeneous and complex microfabrics reflecting the diversity of organisms and processes involved, and the overprinting that occurs as mat sediments accumulate. In contrast, discrimination between macrofabrics is relatively straightforward and recognizes major categories, such as stromatolite (laminated), thrombolite (clotted), dendrolite (dendritic) and leiolite (aphanitic), that constitute large domes and columns that aggregate into reefal masses (Riding, 2000). In the Phanerozoic, these forms commonly intermingled with skeletal organisms to construct complex algal–invertebrate–microbial reefs (Pratt, 1982; Soja, 1994; Webb, 1996).

2.1. Stromatolite abundance and diversity

Precambrian benthic microbial carbonates are dominated by stromatolites (Walter, 1994) and two categories of abundance data have been compiled for Proterozoic stromatolites. Morphotype diversity data counts numbers of stromatolite form taxa through time. Forms are based on macroscopic features such as external shape and internal lamina arrangement (Awramik, 1971; Walter and Heys, 1985; Awramik and Sprinkle, 1999; Semikhatov and Raaben, 2000). Qualitative abundance data measures number of rock units dominated by stromatolites through time (Grotzinger, 1990; Walter et al., 1992a; Schopf, 1992). While

it is generally agreed that stromatolite abundance and diversity reduced from a peak in the Proterozoic, there has been considerable debate concerning when decline actually commenced. Initial study of stromatolite morphotype diversity data suggested that this was relatively late, ~675 Myr ago (Awramik, 1971). As more data became available, estimates increased to ~1000 (Walter and Heys, 1985) and then ~1250 (Awramik and Sprinkle, 1999) Myr ago. In contrast, in the case of qualitative abundance data, estimates of the age of commencement of decline have become younger. Initial study suggested that decline commenced ~2000 Myr ago (Grotzinger, 1990), but subsequent evaluations reduced this to 1100–700 Myr ago (Walter et al., 1992a) and 870 Myr ago (Schopf, 1992). Thus, the more recent estimates based on both diversity and abundance place inception of decline in the time range ~1250–700 Myr ago (Walter et al., 1992a; Schopf, 1992; Awramik and Sprinkle, 1999). The most recent and most extensive compilation of stromatolite morphotype data, showing changes in taxonomic diversity for 1187 forms from ~3000 Myr ago to the present-day, indicates decline from a peak that occurred 1350–1000 Myr ago (Awramik and Sprinkle, 1999, fig. 2) (Fig. 1).

2.2. Reefal microbial carbonate abundance

Kiessling (2002, fig. 16) used comprehensive information concerning Phanerozoic reef components in the Paleoreefs Database, based on 3050 reef sites (Kiessling and Flügel, 2002), to compile relative abundance of nine

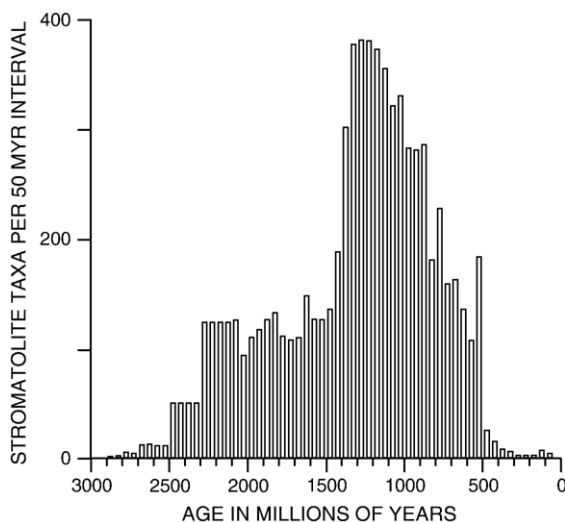


Fig. 1. Numbers of stromatolite morphotype taxa per 50 Myr interval for the past 3000 Myr. Redrawn from Awramik and Sprinkle (1999, fig. 2).

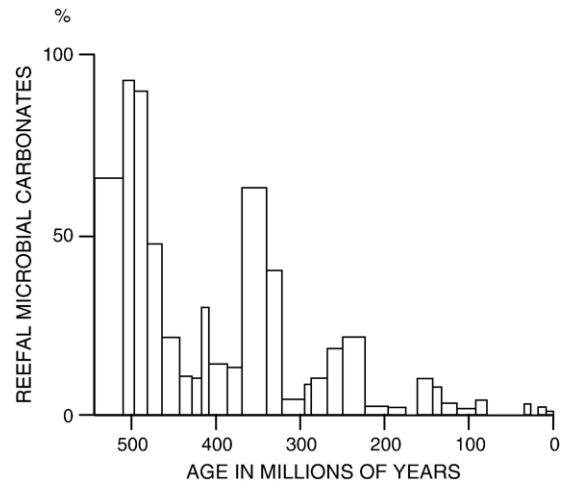


Fig. 2. Relative abundance of microbial carbonates in reefs during Phanerozoic supersequences; data replotted from Kiessling (2002, fig. 16) using Golonka and Kiessling's (2002, fig. 1, pp. 13–18) time intervals for each supersequence (Riding, 2005).

reef-builder categories, one of which is marine microbial carbonates, in thirty-two Phanerozoic 'supersequence' time-slices (Kiessling, 2002, fig. 16). These microbial carbonate reef data are replotted using time ranges for each supersequence based on Golonka and Kiessling's (2002) absolute ages (Riding, 2005) (Fig. 2).

2.3. Combined datasets

Evaluation of controls on secular variation in microbial carbonates has been hampered by lack of data concerning abundance patterns. Awramik and Sprinkle's (1999, fig. 2) and Kiessling's (2002, fig. 16) datasets shows variation in microbial carbonate abundance over geological time at probably the best resolution currently available. However, since these datasets use differing measures they cannot be merged. Their juxtaposition here (Fig. 3) relies merely on the Cambrian increase shown by both trends. Furthermore, neither dataset represents absolute abundance. Awramik and Sprinkle (1999) compiled numbers of stromatolite morphotypes, 'roughly equivalent to form species', per 50 Myr interval from 3500 to 0 Myr ago. It is not established that these data reflect volumetric abundance. Furthermore, since morphotype data are much scarcer for Phanerozoic stromatolites (Awramik and Sprinkle, 1999) they are likely to be under-represented. This may have exaggerated apparent stromatolite decline. Kiessling's (2002) data represent relative abundance of dominant reef builders in Phanerozoic supersequence timeslices and therefore are directly influenced by secular changes in the abundance of other reef-forming

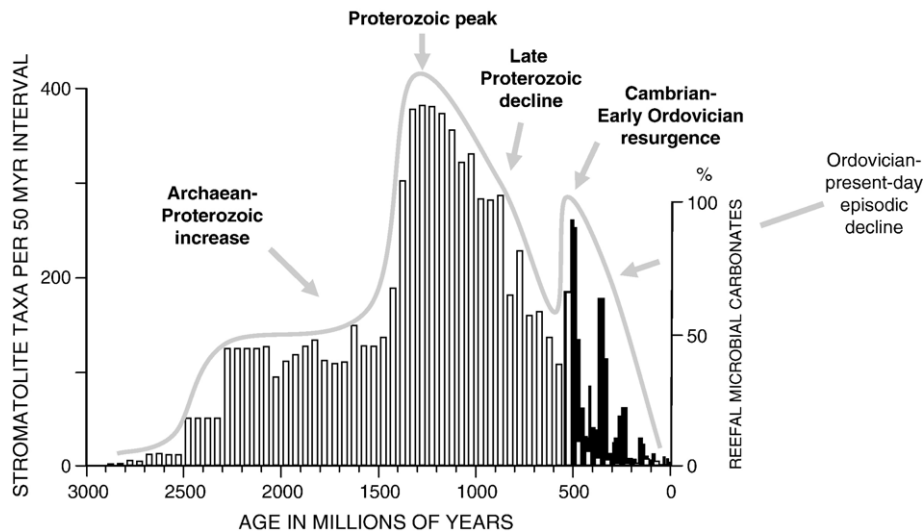


Fig. 3. Stromatolite diversity (white columns, from Fig. 1) (Awramik and Sprinkle, 1999, fig. 2) and reefal microbial carbonate abundance (black columns, from Fig. 2) (Kiessling, 2002, fig. 16) datasets juxtaposed. These differing measures of microbial carbonates are combined in this figure simply by matching the Cambrian values of the two datasets. Major elements of the overall trend are arrowed.

organisms. Nonetheless, Kiessling's (2002) data support earlier generalized recognition that microbial carbonates have markedly oscillatory Phanerozoic abundance, with peaks in the Cambrian–Early Ordovician, Late Devonian, and Triassic (Riding, 1992).

Schubert and Bottjer (1994) stressed their view that Disaster Form stromatolites are 'a phenomenon in the level-bottom subtidal environment'. Kiessling's (2002) data are reefal. However, the Paleoreef Database arguably "includes not only microbial carbonates within algal–metazoan reefs, but also microbial domes and horizons of the type referred to as Disaster Forms by Schubert and Bottjer (1992)" (Riding, 2005). If this is correct then Paleoreef data can be used to assess the secular abundance of stromatolites generally, not only those within algal–metazoan reefs.

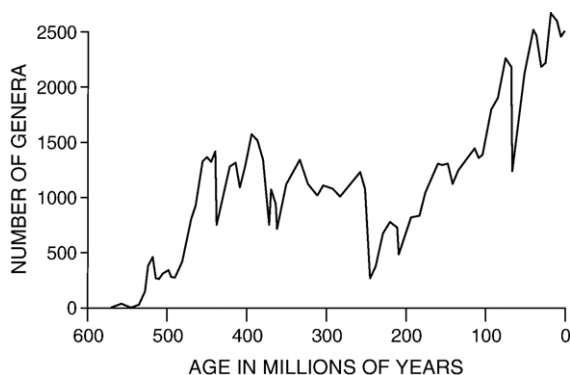


Fig. 4. Marine metazoan generic diversity for the past 600 Myr (from Sepkoski, 1992, 1997).

2.4. Metazoans and mass extinction events

Sepkoski (1992, 1997) compiled numbers of genera of marine metazoans for the Vendian–Cambrian and Phanerozoic, respectively (Fig. 4). These show rapid early Palaeozoic increase, stability in the general range 1000–1500 genera for the remainder of the Palaeozoic, and Mesozoic–Cenozoic increase from ~200 to 2500 genera. Marked fluctuations superimposed on this overall pattern include relatively brief ~50–80% reductions in number of genera that mark major Mass Extinctions (Sepkoski, 1996). According to these data, the largest Mass Extinction Events were End-Ordovician (60% of genera extinct), Late Devonian (57%), End-Permian (82%), End-Triassic (50%), and End-Cretaceous (47%) (Sepkoski, 1996, table 1).

3. Secular patterns of microbial carbonates

Stromatolites increased in abundance from the late Archaean to ~2250 Myr ago, remained at this level until ~1450 Myr ago and then rapidly increased to a peak 1350–1100 Myr ago (Fig. 3). Irregular decline from this peak occurred until 550 Myr ago. This declining trend was reversed immediately prior to the Cambrian Period, ~550 Myr ago. Awramik and Sprinkle (1999, fig. 2) attributed increase in morphotypic diversity at 550–500 Myr to grouping of Vendian and Cambrian data. However, reefal microbial carbonate relative abundance data (Kiessling, 2002) also show progressive Cambrian–Early Ordovician increase. Stromatolites,



Fig. 5. Late Cambrian (Late Franconian–Early Trempealeuan) stromatolite (Cryptozoon), transverse section. Hoyt Limestone, Petrified Gardens, Saratoga Springs, New York, USA. Coin diameter ~3 cm.

together with other microbial carbonates such as dendrolites and thrombolites, became abundant throughout the Cambrian (543–490 Myr ago) and Early Ordovician (490–473 Myr ago) (Pratt, 1982; Kennard and James, 1986; Kiessling, 2002; Webby, 2002). Stromatolites were especially abundant and diverse, and show increase relative to other microbial carbonates in the Mid- and early Late Cambrian, 511–497 Myr ago (Zhuravlev, 1996; Rowland and Shapiro, 2002, pp. 107–8) (Fig. 5). The result of these increases was a peak of microbial carbonate abundance in the Mid-Cambrian to Earliest Ordovician, 511–482 Myr ago (Fig. 3).

In the Mid–Late Ordovician, microbial carbonates in general, and especially stromatolites (Webby, 2002), declined abruptly to a low 443–418 Myr ago (Early–Late Silurian), that included the aftermath of the End-Ordovician Mass Extinction. This was followed successively by slight increase 418–409 Myr ago (Latest Silurian–Earliest Devonian), decline 409–370 Myr ago (Early–Late Devonian), marked increase 370–323 Myr ago (Latest Devonian–Early Carboniferous), and then marked decline 323–296 Myr ago (Late Carboniferous). Progressive Mid-Permian to Mid-Triassic increase, 269–225 Myr ago, was followed by decline 225–163 Myr ago (Late Triassic–Mid-Jurassic) to the lowest point since the beginning of the Phanerozoic. Recovery 163–135 Myr (Late Jurassic–Earliest Cretaceous) was followed by Cretaceous decline, after which reefal microbial carbonates never regained their Late Jurassic level of abundance. Cenozoic levels were substantially less than those of the Mesozoic, and present-day levels are lower than at any time prior to the Jurassic.

Overall decline during the past 1250 Myr since the all-time acme of the Proterozoic has thus been patterned by considerable fluctuation (Fig. 3). The highest point of the Phanerozoic, ~500 Myr ago, was followed by

successively diminishing peaks of relative abundance ~350, 240 and 150 Myr ago. During the Phanerozoic, the largest decline occurred in the Ordovician (Fischer, 1965).

4. Comparisons with metazoan diversity

4.1. Decline ~1250–550 Myr ago

There is no direct evidence for grazing or disturbance of stromatolites by metazoans in the Proterozoic (Walter et al., 1992a,b), and inference of competitive exclusion relies on comparison of the timing of metazoan origins with the inception of stromatolite decline. Uncertainty concerning the timing of metazoan origins hinders assessment of this possible link. Both relatively early and late origins have been suggested for the Metazoa. Evidence of possible metazoan fossils 1000 Myr ago and earlier (e.g., Seilacher et al., 1998; Fedonkin and Yochelson, 2002) is consistent with molecular studies that estimate that metazoans originated ~1250 Myr ago (Wray et al., 1996). An early, ‘slow burn’ (Conway Morris, 2000), origin for metazoans, such as this, could therefore coincide with inception of stromatolite decline. On the other hand, no confidently identified metazoan body fossils much older than 600 Myr are known (Knoll and Carroll, 1999) and revised molecular estimates suggest that bilaterians diverged ~650–575 Myr ago (Aris-Brosou and Yang, 2003; Peterson et al., 2004). This is consistent with the successive timings of the low diversity Doushantuo fauna (600 Myr) and the higher diversity Denying fauna (560 Myr) (Xiao et al., 2002). It is therefore conceivable that bilaterian phyla diversified in the Early Cambrian relatively soon after the origin of crown-group Bilateria (Knoll and Carroll, 1999; Peterson and Takaes, 2001; Butterfield et al., 2003). A late origin for metazoans, such as this, would not support metazoan competition as a factor in stromatolite decline (Grotzinger, 1990). Furthermore, prior to ~600 Myr ago laminated sediments are widespread, indicating that metazoans, if present, were either scarce or very small (Knoll and Carroll, 1999) and had no noticeable affect on stromatolitic fabrics. Nonetheless, the timing of metazoan origins remains uncertain (Blair and Blair Hedge, 2004).

In contrast, there is agreement that other eukaryotes such as algae diversified prior to 1500 Myr ago (Falkowski et al., 2004) and are likely to have been incorporated into stromatolite communities from that date (Walter et al., 1992b, p. 336). Monty (1973) argued against metazoan competition as a factor controlling stromatolite abundance, but echoed Fischer (1965) in

considering that algal competition may have been significant. However, again, there is no direct evidence that this development contributed to stromatolite decline (Walter et al., 1992a, p. 260). Furthermore, algae themselves underwent major decline commencing ~850 Myr ago (Schopf, 1992, p. 551). Major glaciations ~700–570 Myr ago (Walter et al., 2000) may have created evolutionary bottlenecks that could have affected algae as well as any metazoans that may have been present (Hoffman and Schrag, 2002). It is therefore conceivable that climatic deterioration in the late Neoproterozoic affected both stromatolites and eukaryotes and could have been a factor in the late origin of metazoans (Harland, 1964; Riding, 1994; Peterson and Takacs, 2001; Xiao et al., 2002). These possibilities remain to be elucidated. At present there is no clear evidence that eukaryotes in general, or metazoans in particular, influenced stromatolite decline during the Proterozoic; but this possibility cannot be ruled out.

4.2. Resurgence 550–482 Myr ago

Microbial carbonates are major components of shallow marine carbonates throughout the Cambrian and Early Ordovician (Copper, 1974; Fagerstrom, 1987; Wood, 1999; Webb, 1996; Rowland and Shapiro,

2002; Webby, 2002; Kiessling, 2002) (see Secular patterns of microbial carbonates, above). Microbial carbonates were also arguably at their most diverse at this time, with dendrolites and thrombolites as well as stromatolites (Kennard and James, 1986; Armella, 1994; Kennard, 1994; Zhuravlev, 1996; Riding, 2000). This recovery of microbial carbonates is all the more striking because it coincided with metazoan radiation. During a relatively short interval of ~15 Myr in the latter part of the Early Cambrian, crown-group Bilateria and sponges underwent rapid diversification that introduced twelve phyla (Sepkoski, 1992; Knoll and Carroll, 1999; Valentine et al., 1999). A number of factors may have contributed to the proliferation of microbial carbonates during the Cambrian (Rowland and Shapiro, 2002), but coincidence between their increase and major animal radiation would conflict sharply with the view that metazoan competition significantly limited development of either microbial carbonates in general or stromatolites in particular at this time.

4.3. Mid–Late Ordovician decline and Silurian minimum

Microbial carbonate decline from latest Cambrian to earliest Silurian, reflected in both Awramik and Sprink-

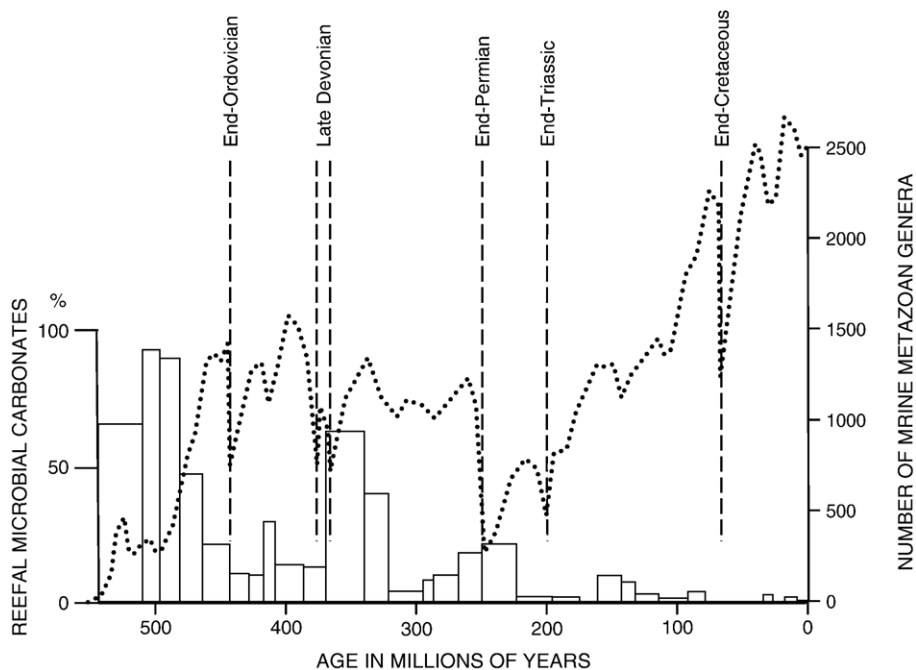


Fig. 6. Relative abundance of microbial carbonates in reefs during Phanerozoic supersequences (Kiessling, 2002, fig. 16) (see Fig. 1), compared with marine metazoan Phanerozoic generic diversity (from Sepkoski, 1997) (see Fig. 4). Five major Mass Extinction events (Sepkoski, 1996) are indicated by vertical lines. Reefal microbial carbonates increased in Late Devonian and End-Permian aftermaths; they did not increase in End-Ordovician, End-Triassic and End-Cretaceous aftermaths (Riding, 2005).

le's (1999) and Kiessling's (2002) data, was the largest of the Phanerozoic (Fig. 3), supporting Fischer's (1965) view that stromatolite decline occurred from the Mid-Ordovician onwards. The Mid–Late Ordovician was a time of continued significant metazoan radiation (Sepkoski, 1997; Webby, 2002), and it would therefore be reasonable to consider that metazoan competition may have contributed to marked microbial carbonate decline. This is possible. However, if competition were the primary factor then some recovery of microbial carbonates would be expected in the aftermath of the End-Ordovician Mass Extinction (Schubert and Bottjer, 1992, p. 885). Sheehan and Harris (2000, 2004) proposed that earliest Silurian (Rhuddanian) stromatolites in Nevada and Utah do reflect temporary recovery by stromatolites following End-Ordovician metazoan extinctions. However, this pattern is not shown by Kiessling's (2002) data which instead indicate that the level of reefal microbial carbonate abundance during the Silurian (443–419 Myr ago) was the lowest of the entire Early–Middle Palaeozoic (Fig. 6). Absence of microbial carbonate recovery in the End-Ordovician extinction aftermath, indicated by Kiessling's (2002) extensive data compilation, suggests that abundance was determined by factors other than metazoan competition.

4.4. Late Devonian and End-Permian Mass Extinctions

Reefal microbial carbonates increased 370–323 Myr ago (Latest Devonian–Early Carboniferous) and 269–225 Myr ago (Mid-Permian to Mid-Triassic). The first of these peaks was an abrupt increase following Late Devonian extinctions. In contrast, the Early–Mid-Triassic peak was not substantially larger than that of the Late Permian. Nonetheless, these patterns generally support Schubert and Bottjer's (1992, 1995) contention that microbial carbonates did increase in some Mass Extinction aftermaths (Fig. 6).

4.5. Post-Triassic to present-day patterns

Apart from the Early to Mid-Triassic, Mesozoic–Cenozoic abundances of reefal microbial carbonates were generally low, and the Late Jurassic–earliest Cretaceous (163–135 Myr ago) was the last substantial peak of reefal microbial carbonate abundance (Fig. 3). The Triassic–Palaeocene interval included two Mass Extinction events, End-Triassic and End-Cretaceous. At neither of these did reefal microbial carbonates show increase. Following the End-Triassic there was slight decline in microbial carbonate abundance. At the

End-Cretaceous there was no change, and Kiessling's (2002) data show no measurable contribution by microbial carbonates to reef construction either immediately before or after the Cretaceous–Tertiary boundary, 65 Myr ago (Fig. 2). Based on Kiessling's (2002) data, overall percentage changes in reefal microbial carbonate abundance following the following five major Mass Extinction Events were: End-Ordovician, 50% decrease; Late Devonian, 370% increase; End-Permian, 17% increase; End-Triassic, 17% decrease; End-Cretaceous, no change (Riding, 2005). These data therefore indicate that, whereas microbial carbonates increased in the Late Devonian and End-Permian aftermaths, they did not increase in the End-Ordovician, End-Triassic or End-Cretaceous aftermaths (Fig. 6).

5. Conclusions

Increases and decreases in metazoan competition over time have been considered as possible factors influencing microbial carbonate abundance. For example, Proterozoic decline of stromatolites (Awramik, 1971, 1992), overall Phanerozoic decline (Fischer, 1965), and resurgence in Mass Extinction aftermaths (Schubert and Bottjer, 1992). Marine metazoan generic diversity (Sepkoski, 1997) and datasets of stromatolite morphotype diversity (Awramik and Sprinkle, 1999) and reefal microbial carbonate abundance (Kiessling, 2002) can be used to roughly compare secular variation in microbial abundance with that of metazoan diversity.

Proterozoic stromatolite diversity declined from a peak 1350 to 1000 Myr ago to 550 Myr ago. A relatively early origin for metazoans, e.g., ~1250 Myr ago, would therefore indicate that metazoan diversification coincided with stromatolite decline. On the other hand, a relatively late origin for metazoans, e.g., ~650 Myr ago, would not. Further information concerning the timing of metazoan origins is required to establish whether either of these origination dates is correct. At present, it remains conceivable, but not established, that stromatolite decline coincided with metazoan diversification.

The relationship between metazoan diversity and microbial carbonate abundance may be more clearly revealed in the Phanerozoic record. This commenced with marked Cambrian–Early Ordovician increase in microbial carbonate abundance that coincided with important metazoan radiation. Subsequently, microbial carbonate abundance shows an overall pattern of long-term decline, patterned by marked resurgences. However, these fluctuations do not always coincide with opposing changes in metazoan diversity. Follow-

ing a peak in the Late Cambrian, reefal microbial carbonates show successively diminishing peaks of relative abundance in the Late Devonian–Early Carboniferous, Early Triassic, and Late Jurassic. Two of these correspond with the aftermaths of Mass Extinctions (Late Devonian, End-Permian), but there is no increase in reefal microbial carbonates immediately following three other Mass Extinctions (End-Ordovician, End-Triassic, End-Cretaceous). In short, resurgence of microbial carbonates during the Cambrian metazoan radiation and failure to recover in the aftermaths of three Mass Extinctions, raises doubts that metazoan competition can be invoked as a general explanation for fluctuations in microbial carbonate abundance.

The data used here may be the best currently available to assess these significant questions, but they are undeniably limited. Furthermore, the assumption that metazoan diversity can be used to represent competition is simplistic. The possibilities outlined here must therefore be regarded as tentative. Nonetheless, it appears necessary to reconsider the factors that are likely to have influenced microbial carbonate abundance through time (Fischer, 1965; Awramik, 1971; Monty, 1973; Serebryakov and Semikhatov, 1974; Gebelein, 1976; Grotzinger, 1990; Riding, 1997; Awramik and Sprinkle, 1999; Grotzinger and Knoll, 1999). The comparisons presented here do not show that metazoan competition was unimportant, rather they suggest that a variety of factors must have operated that each changed through time.

Acknowledgements

I am grateful to reviewers Stanley M. Awramik and Gregg Webb for helpful suggestions, and to Gilbert Camoin for expert editorial guidance.

References

- Aris-Brosou, S., Yang, Z., 2003. Bayesian models of episodic evolution support a late Precambrian explosive diversification of the Metazoa. *Mol. Biol. Evol.* 20, 1947–1954.
- Armella, C., 1994. Thrombolitic–stromatolitic cycles of the Cambro-Ordovician boundary sequence, Precordillera Oriental Basin, western Argentina. In: Bertrand-Sarfati, J., Monty, C. (Eds.), *Phanerozoic Stromatolites II*. Kluwer, Dordrecht, pp. 421–441.
- Awramik, S.M., 1971. Precambrian columnar stromatolite diversity: reflection of metazoan appearance. *Science* 174, 825–827.
- Awramik, S.M., 1992. The history and significance of stromatolites. In: Schidlowski, M., Kimberley, M.M., McKirdy, D.M., Trudinger, P.A. (Eds.), *Early Organic Evolution: Implications for Energy and Mineral Resources*. Springer, Berlin, pp. 435–449.
- Awramik, S.M., Margulis, L., 1974. *Stromatolite Newsletter*, vol. 2, p. 5.
- Awramik, S.M., Sprinkle, J., 1999. Proterozoic stromatolites: the first marine evolutionary biota. *Hist. Biol.* 13, 241–253.
- Beukes, N.J., 1987. Facies relations, depositional environments and diagenesis in a major early Proterozoic stromatolitic carbonate platform to basinal sequence, Campbellrand Subgroup, Transvaal Supergroup, Southern Africa. *Sediment. Geol.* 54, 1–46.
- Blair, J.E., Blair Hedge, S., 2004. Molecular clocks do not support the Cambrian radiation. *Mol. Biol. Evol.* 22, 387–390.
- Burne, R.V., Moore, L.S., 1987. Microbialites: organosedimentary deposits of benthic microbial communities. *Palaeos* 2, 241–254.
- Butterfield, N.J., Jensen, S., Budd, G.E., 2003. Reassessing the record of Proterozoic eukaryotes; implications for the Cambrian explosion. *Geol. Soc. Amer., 2003 Annual Meeting, Abstracts with Programs*, vol. 35, p. 384.
- Conway Morris, S., 2000. The Cambrian ‘explosion’: slow-fuse or megatonnage. *Proceed. Natl Acad. Sci. USA*, vol. 97. National Academy of Sciences, Washington, pp. 4426–4429.
- Copper, P., 1974. Structure and development of Early Paleozoic reefs. *Proceedings of the Second Intern. Coral Reef Symp.*, vol. 1. Great Barrier Reef Committee, Brisbane, pp. 365–386.
- Dill, R.F., Shinn, E.A., Jones, A.T., Kelly, K., Steinen, R.P., 1986. Giant subtidal stromatolites forming in normal salinity waters. *Nature* 324, 55–58.
- Fagerstrom, J.A., 1987. *The Evolution of Reef Communities*. John Wiley and Sons, New York.
- Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O., Taylor, F.J.R., 2004. The evolution of modern eukaryotic phytoplankton. *Science* 305, 354–360.
- Fedonkin, M.A., Yochelson, E.L., 2002. Middle Proterozoic (1.5 Ga) *Horodyskia moniliformis* Yochelson and Fedonkin, the oldest known tissue grade colonial eukaryote. *Smithson. Contrib. Paleobiol.* 94, 1–29.
- Fischer, A.G., 1965. Fossils, early life, and atmospheric history. *Proceed. Natl Acad. Sci. USA*, vol. 53. National Academy of Sciences, Washington, pp. 1205–1215.
- Garrett, P., 1970. Phanerozoic stromatolites: noncompetitive ecological restriction by grazing and burrowing animals. *Science* 169, 171–173.
- Gebelein, C.D., 1976. The effects of the physical, chemical and biological evolution of the earth. In: Walter, M.R. (Ed.), *Stromatolites, Developments in Sedimentology*, vol. 20. Elsevier, Amsterdam, pp. 499–515.
- Golonka, J., Kiessling, W., 2002. Phanerozoic time scale and definition of time slices. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic Reef Patterns*, Soc. Econ. Paleont. Mineral. Special Publication, vol. 72, pp. 11–20. Tulsa.
- Grotzinger, J.P., 1989. Facies and evolution of Precambrian carbonate depositional systems: emergence of the modern platform archetype. In: Crevello, P.D., Wilson, J.L., Sarg, J.F., Read, J.F. (Eds.), *Controls on Carbonate Platform and Basin Development*, Soc. Econ. Paleont. Mineral. Special Publication, vol. 44, pp. 79–106. Tulsa.
- Grotzinger, J.P., 1990. Geochemical model for Proterozoic stromatolite decline. *Am. J. Sci.* 290-A, 80–103.
- Grotzinger, J.P., Knoll, A.H., 1999. Stromatolites in Precambrian carbonates: evolutionary mileposts or environmental dipsticks? *Annu. Rev. Earth Planet. Sci.* 27, 313–358.
- Harland, W.B., 1964. Evidence of Late Precambrian glaciation and its significance. In: Nairn, A. E. M. (Ed.), *Problems in Palaeoclimatology*. Interscience, John Wiley and Sons, London, pp. 119–149, 180–184.
- Hoffman, P.F., Schrag, D.P., 2002. The snowball Earth hypothesis: testing the limits of global change. *Terra Nova* 14, 129–155.

- Kennard, J.M., 1994. Thrombolites and stromatolites within shale-carbonate cycles, Middle–Late Cambrian Shannon Formation, Amadeus Basin, central Australia. In: Bertrand-Sarfati, J., Monty, C. (Eds.), *Phanerozoic Stromatolites II*. Kluwer, Dordrecht, pp. 443–471.
- Kennard, J.M., James, N.P., 1986. Thrombolites and stromatolites; two distinct types of microbial structures. *Palaos* 1, 492–503.
- Kiessling, W., 2002. Secular variations in the Phanerozoic reef ecosystem. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic Reef Patterns*, Soc. Econ. Paleont. Mineral. Special Publication, vol. 72, pp. 625–690. Tulsa.
- Kiessling, W., Flügel, E., 2002. Paleoreefs — a database on Phanerozoic reefs. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic Reef Patterns*, Soc. Econ. Paleont. Mineral. Special Publication, vol. 72, pp. 77–92. Tulsa.
- Knoll, A.H., Carroll, S.B., 1999. Early animal evolution: emerging views from comparative biology and geology. *Science* 284, 2129–2137.
- Logan, B.W., 1961. Cryptozoon and associated stromatolites from the Recent, Shark Bay, Western Australia. *J. Geol.* 69, 517–533.
- Monty, C.L.V., 1973. Precambrian background and Phanerozoic history of stromatolitic communities, an overview. *Ann. Soc. Géol. Belg.* 96, 585–624.
- Peterson, K.J., Takacs, C., 2001. Fossils, molecular clocks and the Cambrian explosion. *Geol. Soc. America*, 2001 Annual Meeting, Abstracts with Programs, vol. 33, p. 430.
- Peterson, K.J., Lyons, J.B., Nowak, K.S., Takacs, C.M., Wargo, M.J., McPeck, M.A., 2004. Estimating metazoan divergence times with a molecular clock. *Proceed. Natl Acad. Sci. USA*, vol. 101. National Academy of Sciences, Washington, pp. 6536–6541.
- Pratt, B.R., 1982. Stromatolite decline — a reconsideration. *Geology* 10, 512–515.
- Riding, R., 1992. Temporal variation in calcification in marine cyanobacteria. *J. Geol. Soc. London* 149, 979–989.
- Riding, R., 1994. Evolution of algal and cyanobacterial calcification. In: Bengtson, S. (Ed.), *Early Life on Earth*, Nobel Symposium, vol. 84. Columbia University Press, New York, pp. 426–438.
- Riding, R., 1997. Stromatolite decline: a brief reassessment. In: Neuweiler, F., Reitner, J., Monty, C. (Eds.), *Biosedimentology of Microbial Buildups*. IGCP Project 380, Proceedings of 2nd Meeting, Göttingen, Germany, Facies, vol. 36, pp. 227–230.
- Riding, R., 2000. Microbial carbonates: the geological record of calcified bacterial–algal mats and biofilms. *Sedimentology* 47 (Supplement 1), 179–214.
- Riding, R., 2005. Phanerozoic reefal microbial carbonate abundance: comparisons with metazoan diversity, Mass Extinction events, and seawater saturation state. *Rev. Esp. Micropal.* 37, 23–39.
- Rodland, D.L., Bottjer, D.J., 2001. Biotic recovery from the end-Permian Mass Extinction: behavior of the inarticulate brachiopod *Lingula* as a disaster taxon. *Palaos* 16, 95–101.
- Rowland, S.M., Shapiro, R.S., 2002. Reef patterns and environmental influences in the Cambrian and earliest Ordovician. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic Reef Patterns*, Soc. Econ. Paleont. Mineral. Special Publication, vol. 72, pp. 95–128. Tulsa.
- Schopf, J.W., 1992. Patterns of Proterozoic microfossil diversity: an initial, tentative, analysis. In: Schopf, J.W., Klein, C. (Eds.), *The Proterozoic Biosphere; a Multidisciplinary Study*. Cambridge University Press, Cambridge, pp. 529–552.
- Schubert, J.K., Bottjer, D.J., 1992. Early Triassic stromatolites as post-mass extinction disaster forms. *Geology* 20, 883–886.
- Schubert, J.K., Bottjer, D.J., 1994. Significance of Silurian stromatolite–sphinctozoan reefs: comment and reply. *Geology* 22, 1051.
- Schubert, J.K., Bottjer, D.J., 1995. Aftermath of the Permian–Triassic mass extinction event; paleoecology of Lower Triassic carbonates in the western USA. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 116, 1–39.
- Seilacher, A., Bose, P.K., Pflüger, F., 1998. Triploblastic animals more than 1 billion years ago: trace fossil evidence from India. *Science* 282, 80–83.
- Semikhatov, M.A., Raaben, M.E., 2000. Proterozoic stromatolite taxonomy and biostratigraphy. In: Riding, R., Awramik, S.M. (Eds.), *Microbial Sediments*. Springer-Verlag, Heidelberg, pp. 295–306.
- Sepkoski Jr., J.J., 1992. Proterozoic–Early Cambrian diversification of metazoans and metaphytes. In: Schopf, J.W., Klein, C. (Eds.), *The Proterozoic Biosphere; A Multidisciplinary Study*. Cambridge University Press, Cambridge, pp. 553–561.
- Sepkoski Jr., J.J., 1996. Patterns of Phanerozoic extinction: a perspective from global databases. In: Walliser, O.H. (Ed.), *Global Events and Event Stratigraphy in the Phanerozoic*. Springer, Berlin, pp. 35–51.
- Sepkoski Jr., J.J., 1997. Biodiversity; past, present, and future. *J. Paleontol.* 71, 533–539.
- Serebryakov, S.N., Semikhatov, M.A., 1974. Riphean and recent stromatolites: a comparison. *Am. J. Sci.* 274, 556–574.
- Sheehan, P.M., Harris, M.T., 2000. Early Silurian stromatolites and thrombolites: successful disaster forms after the Late Ordovician mass extinction. *Abstr. Programs* 32 (7), 367–368 (Geological Society of America National meeting).
- Sheehan, P.M., Harris, M.T., 2004. Microbialite resurgence after the Late Ordovician extinction. *Nature* 430, 75–78.
- Soja, C.M., 1994. Significance of Silurian stromatolite–sphinctozoan reefs. *Geology* 22, 355–358.
- Valentine, J.W., Jablonski, D., Erwin, D.H., 1999. Fossils, molecules and embryos: new perspectives on the Cambrian explosion. *Development* 126, 851–859.
- Walter, M.R., 1994. Stromatolites: the main geological source of information on the evolution of the early benthos. In: Bengtson, S. (Ed.), *Early Life on Earth*, Nobel Symposium, vol. 84. Columbia University Press, New York, pp. 270–286.
- Walter, M.R., Heys, G.R., 1985. Links between the rise of the Metazoa and the decline of stromatolites. *Precambrian Res.* 29, 149–174.
- Walter, M.R., Grotzinger, J.P., Schopf, J.W., 1992a. Proterozoic stromatolites. In: Schopf, J.W., Klein, C. (Eds.), *The Proterozoic Biosphere; A Multidisciplinary Study*. Cambridge University Press, Cambridge, pp. 253–260.
- Walter, M.R., Bauld, J., Des Marais, D.J., Schopf, J.W., 1992b. A general comparison of microbial mats and microbial stromatolites: bridging the gap between the modern and the fossil. In: Schopf, J.W., Klein, C. (Eds.), *The Proterozoic Biosphere; A Multidisciplinary Study*. Cambridge University Press, Cambridge, pp. 335–338.
- Walter, M.R., Veevers, J.J., Calver, C.R., Gorjan, P., Hill, A.C., 2000. Dating the 840–544 Ma Neoproterozoic interval by isotopes of strontium, carbon, and sulfur in seawater, and some interpretative models. *Precambrian Res.* 100, 371–433.
- Webb, G.E., 1996. Was Phanerozoic reef history controlled by the distribution of non-enzymatically secreted reef carbonates (microbial carbonate and biologically induced cement)? *Sedimentology* 43, 947–971.
- Webb, B., 2002. Patterns of Ordovician reef development. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), *Phanerozoic Reef Pat-*

- terns, Soc. Econ. Paleont. Mineral. Special Publication, vol. 72, pp. 129–179. Tulsa.
- Wood, R., 1999. Reef Evolution. Oxford University Press, Oxford.
- Wray, G.A., Levinton, J.S., Shapiro, L.H., 1996. Molecular evidence for deep Precambrian divergences. *Science* 274, 568–573.
- Xiao, S., Hua, H., Chen, Z., Zhang, L., 2002. In the wake of a snowball Earth and in the dawn of animal radiation; terminal Proterozoic evolution of multicellular eukaryotes. Geological Society of America 2002 Annual Meeting, Abstracts with Programs, vol. 34, p. 169.
- Zhuravlev, A. Yu., 1996. Reef ecosystem recovery after the Early Cambrian extinction. In: Hart, M.B. (Ed.), Biotic Recovery from Mass Extinction Events, Geol. Soc. London, Spec. Publ., vol. 102, pp. 79–96.