Facies and paleoenvironmental setting of Thrombolite-Stromatolite Reefs, Terminal Proterozoic Nama Group (ca. 550-543 Ma), central and southern Namibia

John P. Grotzinger

Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139, grotz@mit.edu

Thrombolite and stromatolite reefs occur at several stratigraphic levels within the terminal Proterozoic Nama Group of central and southern Namibia. The reefs form integral parts of several carbonate platforms within the Nama Group, including the Kuibis platform of the northern Nama Basin (Zaris subbasin) and Huns platform (Witputs subbasin) of the southern Nama Basin. The reefs are composed of both thrombolites (clotted internal texture) and stromatolites (laminated internal texture) that form laterally continuous biostromes, isolated patch reefs and isolated pinnacle reefs ranging in scale from a meter to several kilometers in width. In the majority of cases, the reefs occur stratigraphically as an integral facies within the Transgressive System Tracts of sequences making up the Kuibis and Huns platforms. This suggests that a regime of increasing accommodation was required to form well developed reefs, though reefs occur sporadically in Highstand Systems Tract settings. Within a given TST, a regime of increasing accommodation in time favors the transition from sheet-like biostromal geometries to more isolated patch and pinnacle biohermal geometries. Similarly, increasing accommodation space, such as a transect down depositional dip, shows a similar transition from more sheet-like geometries in updip positions to more isolated geometries in downdip positions. Reefal facies consist of thrombolitic domes, columns and mounds with well developed internal clotted textures, in addition to stromatolitic domes, columns and mounds, with crudely to moderately well developed internal lamination. Stromatolites are better developed in conditions of relatively low accommodation, undip locations under conditions of higher current velocities and greater sediment influx. Thrombolites are better developed in conditions of relatively high accommodation and low sediment influx. Both types of microbialites are intimately associated with the first calcifying metazoan organisms which may have attached themselves or otherwise lived within sheltered depressions within the rough topography created by ecologically complex mats. The appearance of thrombolitic textures during terminal Proterozoic time is consistent with the hypothesis of Feldman and McKenzie (1998) that colonization of cyanobacterial mats by higher algae and metazoans was an important process in generating clotted textures. Fabrics in the Nama thrombolites are well preserved and show evidence of thrombolitic mesoclots being overgrown by fibrous marine calcite, interpreted as former aragonite. This was followed by emplacement of geopetal micrite fills, precipitation of primary dolomite as an isopachous rim cement, followed by occlusion of remaining porosity by blocky calcite spar.

Introduction

Investigations of ancient reefs provide a unique and effective method for assessing the biotic, chemical and physical forces operating on biologic evolution and sediment production on ancient carbonate platforms. Patterns deduced from their long-term development help document the evolution of carbonate-producing organisms, secular changes in the composition of the ocean and atmosphere, the succession of tectonic and subsidence regimes, the mechanisms and magnitudes of eustasy, fluctuations in climate, and the physical conditions in which sedimentation took place. For Phanerozoic reefs, description of facies, formulation of models and analysis of variability have been highly successful in fulfilling these objectives (Heckel, 1974; Wilson, 1975; James, 1983; Tucker and Wright, 1990).

Increasingly, Proterozoic reefs are being considered within the context of the entire depositional system using modern approaches and comprehensive analogues (Grotzinger and James, 2000). The general growth, spatial arrangement of facies and evolution of many Proterozoic reefs is surprisingly similar to younger platforms, although the individual facies are in most cases unique (Grotzinger, 1989, 1994). Today, the most conspicuous gap in our understanding of the first-order, long-term evolution of reefs concerns the transition from the Proterozoic realm of microbial and abiotic carbonates to the Phanerozoic world of metazoan- and metaphyte-dominated sediment production. The explosive diversification in shelly invertebrates and burrowing infauna near the Precambrian-Cambrian boundary (Valentine et al., 1991; Sepkoski, 1992; Bowring et al., 1993) resulted in a dramatic change in the fundamental textures of facies and modes of carbonate production (Grotzinger and James, 2000). A few studies of earliest Phanerozoic carbonates focus on the structure and diversity of lower (but not lowest) Cambrian Archeaocyathid-microbial reefs (e.g. Riding and Zhuravlev, 1995), while others involve studies of upper (but not the uppermost) Proterozoic stromatolite-thrombolite reefs (e.g. Turner et al., 1993, 2000). However, there have been only rare studies of the youngest Proterozoic reefs, where the first well developed, frame-building thrombolites occur (Grotzinger and Khetani, 1994) in direct association with the first calcified invertebrates (Germs, 1972a; Grant, 1990; Grotzinger et al., 1995; Grotzinger et al., 2000) and calcified metaphytes (Grant et al., 1991). Consequently, it is essential to undertake systematic analysis of terminal Proterozoic reefs in order to properly document the first influences of calcified invertebrates and metaphytes on sediment production, platform paleoecology and facies development.

The research reported here involves a detailed investigation of the sedimentological, stratigraphic, paleoenvironmental and paleontological aspects of thrombolite-stromatolite-metazoan reefs developed during terminal Proterozoic time. The reefs described below occur at several stratigraphic levels within the terminal Proterozoic Nama Group of central and southern Namibia.

Geologic Setting of Nama Basin

The geology of southern Namibia, including the distribution of the Nama Group, is shown in Figure 1. The Nama Group has been interpreted as a foreland basin fill (Germs, 1983; Gresse and Germs, 1993) related to convergence along the western and northern margins of the Kalahari craton and overthrusting in the Damara Orogen (Miller, 1983). Flexural subsidence in the Nama foreland basin has been calibrated to continue up to about 543 Ma (J. Grotzinger, unpublished observations) after which the basin was filled with a fluvial molasse that contains coarse-grained detrital white micas with ages of 570-560 Ma (Horstmann et al., 1990) which were derived from the unroofing Damara hinterland (Germs, 1983). Very fine-grained white micas record two subsequent events: folding along the northern and western margins of the basin accompanied by the formation of a slatey cleavage at 530 Ma, and gravity-induced emplacement of the Naukluft Nappe Complex (Korn and Martin, 1959) over the lower Nama succession at 495 Ma (Ahrendt et al., 1977; Horstman et al., 1990).

The general stratigraphy of the Nama Group has been outlined by Martin (1965) and in a series of papers by Germs (1974, 1972b, 1983). Regional isopachs and facies distributions define two subbasins; the Witputs subbasin, located in southern Namibia, thickens toward the Gariep orogenic belt in the west, while the more northerly Zaris subbasin thickens northward toward the Damara orogenic belt. The Osis Arch represents a site of depositional thinning of all Nama units and separates the two subbasins (see Fig. 1). The Nama Group generally consists of a number of marine shelf siliciclastic and carbonate sequences (Kuibis and Schwarzrand Subgroups) overlain by alluvial to shallow marine molasse (Fish River Subgroup) that represents unroofing of the Damara hinterland. Near the subbasin axes,



Figure 1: Geological Map of southern Namibia showing distribution of major tectonic elements, including the Nama Group, referred to in text. thicknesses are on the order of 2-3 km, thinning to less than 1 km further onto the craton toward the Osis Arch (Germs, 1974, 1983). Geochronologic constraints are provided by U-Pb zircon ages on several units. An ash bed within the northern Nama basin yields an age of 548.8 Ma for the middle Kuibis Subgroup; in southern exposures of the Nama, the overlying Schwarzrand Subgroup contains ash beds which yield, in ascending order, ages of 545.1 Ma, 543.3 Ma and 539.4 Ma (Grotzinger *et al.*, 1995). The Precambrian-Cambrian boundary in Namibia is bracketed by the 543.3 Ma and 539.4 Ma ages, although this also includes a significant unconformity; on a global basis the Precambrian-Cambrian boundary is currently regarded to be on the order of 543 Ma (Grotzinger *et al.*, 1995).

Stratigraphic setting of Nama reefs

Thrombolite-stromatolite reefs in the Nama Group are best developed in the Kuibis Subgroup of the Zaris subbasin, and in the Huns platform of the Witputs subbasin (Fig. 2). The reefs discussed here are all constrained to be younger than 548.8 ± 1 Ma and older than 545.1 ± 1 Ma based on direct dating of the ash beds in the succession (Grotzinger *et al.*, 1995). The age of the Kuibis platform is directly constrained by a U-Pb zircon date of 548.8 ± 1 Ma, though its base is probably on the order of 550 Ma and its top somewhat younger, at about



Figure 2: Generalized stratigraphy of Nama Group for Zaris subbasin (north) and Witputs subbasin (south) showing major lithostratigraphic, chemostratigraphic, biostratigraphic and sequence stratigraphic attributes. Note position of thrombolitestromatolite reef complexes above sequence boundaries.

547 Ma. The stratigraphically higher Huns platform is younger and is constrained to be in the order of 546 Ma based on a U-Pb age date of 545.5 ± 1 Ma of strata that occur directly above the top of the Huns platform and on the basis of regional correlations (Grotzinger *et al.*, 1995).

Kuibis Platform

The Kuibis Subgroup is the basal unit of the Nama Group. It is regionally widespread, consisting of a thin, basal, transgressive sandstone that grades upward into a major carbonate platform that ranges in thickness from 150 to 500 meters. Proximal facies are mostly limestone, whereas deep-water facies are mixed with shales and fine sandstones. Outcrops of the Kuibis Subgroup extend from the Gobabis area of west-central Namibia to the Naukluft Mountains of east-central Namibia, continuing southward along the escarpment to southern Namibia and into northeast South Africa (Germs, 1972b, 1974; Gresse and Germs, 1993). The regional lithostratigraphy has been established by Germs (1972b, 1983), the regional sequence stratigraphy by Saylor et al. (1995, 1998), and the regional chemostratigraphy by Kaufman et al. (1991) and Saylor et al. (1995, 1998). Smith (1998) conducted a detailed study of the Kuibis Subgroup in the Zaris subbasin resulting is a high-resolution litho-, sequence-, and chemostratigraphic model.

In the Zaris subbasin (Fig. 1), the Kuibis Subgroup forms a well developed carbonate ramp that thickens from the Osis arch northward to the Naukluft Mountains (Smith, 1998). This change in thickness is accompanied by a gradation from shallow-water facies in the south to deeper water, basinal facies near the Naukluft Mountains. The stratigraphy of the Kuibis platform was first outlined by Germs (1972b, 1974, 1983) who subdivided the platform into two members (Omkyk and Hoogland Members; see Fig. 2) which approximately correspond to stratigraphic sequences (Grotzinger et al., 1995; Saylor et al., 1995, 1998; Smith, 1998). However, the surfaces defining the member boundaries correspond to flooding events rather than sequence boundaries (Smith, 1998). Detailed mapping of these sequences (Smith, 1998) shows that the reefs described here were all nucleated within the Transgressive Systems Tract (TST) to early Highstand Systems Tract (HST) at the base of each sequence (Fig. 2). This implies that the most favorable conditions for reef growth occurred during times of increased accommodation and lowered sediment flux on the platform.

Thrombolite-stromatolite reefs in the Zaris subbasin are found at two stratigraphic levels in the Omkyk Member (Fig. 2). In the first case, a laterally extensive thrombolitic biostrome capping the Omkyk Member (Fig. 3a) occupies a position consistent with an interval of increasing accommodation immediately above a sequence boundary in an initial transgressive position. This placement differs from the interpretation of Saylor et al. (1998) who placed the sequence boundary above the biostrome capping the Omkyk Member. This revised interpretation is based on the subsequent, more detailed study of Smith (1998). The second occurrence of the thrombolitic biostrome facies is at the approximate level of the maximum flooding surface in the middle Omkyk (Fig. 2), again indicating that these reefs are associated with times of increased accommodation. Both biostromes are present depositionally updip as continuous sheets (on the farm Zebra River) but break up into patch-reef bioherms downdip towards and on the farm Donkergange (Figs. 3b, c). The transition from continuous biostrome to discontinuous patch reefs is best exposed within the Zebra River valley, west of the property line between the Donkergange and Zebra River farms. Further downdip, where accommodation was greater, these patch reefs occasionally grew to form large, downslope pinnacle reefs such as that developed at Driedoornvlaagte (Fig. 4).

Huns Platform

The Huns Member in the Witputs subbasin consists of a thick section (0 - 500 meters) of platform carbonates in the middle of the Nama Group (Fig. 2). Designated the "Schwarzkalk Limestone" by Martin (1965), it was later described in more detail by Germs (1972b, 1974, 1983) who recognized the presence of pinnacle reefs (Fig. 5) on the farm Swartkloofberg. Subsequent work (Grotzinger and Khetani, 1994; Saylor and Grotzinger, 1996; Saylor et al., 1998) showed that these reefs are associated with drowning of the platform prior to deposition of the Feldschuhhorn shale. The Huns is interpreted as a broad carbonate ramp divisible into three paleogeographic zones that include inner ramp, ramp crest and a ramp-to-basin transition exposed mostly in a east-to-west transect. The present-day level of erosion has removed the most updip components of the Huns platform west of the Fish River, and it is truncated beneath the sub-Nomstas unconformity between Goageb and Helmeringhausen. It is well exposed from the Huns Mountains west to the Swartpunt and Swartkloofberg farms.

Saylor *et al.* (1995, 1996, 1998) have described the regional facies variations which pass from shallow-water, updip facies in northern and eastern localities to deeper water, downdip facies in southwestern localities, close to the Gariep thrust front. Detailed mapping has shown the presence of several thrust structures which telescope the platform in the Swartpunt and Swartk-loofberg farms, resulting in the tectonic emplacement of deeper water facies over shallow-water facies (Saylor and Grotzinger, 1996).

Small patch reefs occur at several stratigraphic levels in the Huns platform, particularly associated with flooding surfaces in meter-scale cycles which compose much of the platform. However, the only pinnacle reefs discovered so far occur at the top of the platform, above



Figure 3: Reefs of the Zaris subbasin. a) laterally continuous thrombolite-stromatolite biostrome in updip (southeast) location on farm Donkergange. Photograph shows complete section through Omkyk Member of Kuibis Subgroup; basement crops out in far side of river valley. Note lateral continuity of light colored unit (R; reef) at top of Omkyk Member which reflects selective dolomitization of reef facies relative to enclosing dark limestones and shales. Biostrome pinches out downdip (northwest) toward right of photograph and is absent at "A". GS; grainstones within overlying Hoogland Member. b) Further down dip the biostrome at top of Omkyk Member (see Fig. 3a) passes laterally into discrete patch reefs, each indicated by an "R" (R; reef). Reefs are overlain by deepwater shales which in turn pass upward into a grainstone shoal complex. c) Close up of representative patch reef showing stratigraphic position immediately above a sequence boundary which separates reef facies from underlying thick-bedded grainstone facies. Reef passes laterally into relatively thin-bedded shales and fine calcarenites. Note how bedding thickness decreases immediately above sequence boundary indicating a regime of increasing accommodation.



Figure 4: Large pinnacle reef (Driedoornvlagte bioherm) on the farm Driedoornvlagte, Zaris subbasin. a) Landsat TM image showing pinnacle reef developed on platform carbonates (dark blue) and overlain by deep-water shales (orange-red). The platform carbonates unconformably overlie much older quartzites (mauve-grey colors at top of photograph). Color in the TM image maps composition well - reef has grey-lavender color which reflects high dolomite content, whereas dark blue color of shallow-water platform carbonates reflects dominance of limestone. Rocks have structural dip of about 40° toward south. b) Low-altitude, oblique aerial photograph of Dreidoornvlagte bioherm. Note regional structural dip of 40° toward south. Minor folding and a low-displacement thrust fault disrupts eastern part of outcrop. White arrows point to sides of reef which would have been topographically higher than the center of reef (black arrow) suggesting that it may have had a "bucket" geometry with raised rim.



Figure 5: Thrombolite-stromatolite pinnacle reefs at top of Huns platform, Witputs subbasin, southern Namibia. Reefs are formed of a core of coalesced thrombolite mounds overgrown by a stromatolitic mantle. a) Overview of multiple pinnacle reefs formed at top of Huns platform. Reefs have been exhumed by erosion of overlying shales. b) Cross-section of representative pinnacle reef showing foundation of stromatolite sheet facies and remnants of overlying shales which have been eroded to expose reefs. A sequence boundary occurs between the stromatolite sheet facies and pinnacle reef facies; thus, the pinnacle reefs were formed during a time of increasing accommodation space within a Transgressive System Tract.

a sequence boundary and within the overlying flooding interval that defines the TST of the overlying sequence (Grotzinger *et al.*, 1995; Saylor and Grotzinger, 1996). These reefs are 50-70 meters wide at their base and up to 50 meters high (Figs. 5a, b) and are blanketed by enclosing shales, deposited at or below wave base (Fig. 5b).

Reef Facies and Diagenesis

The general makeup of facies within both the Kuibis and Huns platforms indicates that deposition occurred on storm- to wave-dominated ramps. There is little evidence for tidal deposition and most coarser facies show evidence for having accumulated under the influence of episodic, strong flows, often of oscillatory behavior. The reefs constituted part of an inner ramp facies assemblage (*sensu* Burchette and Wright, 1992), representing the shallowest depositional environments which formed above fair-weather wave base and includes sand shoals, thrombolitic/stromatolitic buildups and back-barrier lagoonal and peritidal deposits.

The thrombolite biostrome facies consists of massive thrombolite, stratiform thrombolite and stromatolitic thrombolite forming columns, branching columns, heads and domes of generally decimeter dimensions and relief (Fig. 6). In general, the cores of domes and columns are characterized by a thrombolitic texture (Fig. 6b), whereas the margins become progressively more stromatolitic in nature, exhibiting crude lamination (Fig. 6a). This marginal texture is best described as a stromatolitic thrombolite (Kennard and James, 1986). In the Kuibis reefs, columns are consistently elongated with an azimuth of 270°-310°.

Body fossils are present within thrombolite domes and columns, and the intrachannel fill between domes and columns consists of a trough cross-bedded, fossiliferous packstone and grainstone of simple tubes, goblets, *Cloudina* and their bioclastic detritus (Figs. 6a, 9a, 10c). Fossils range in size from millimeter-scale up to 2 centimeters in width. The thrombolitic cores of domes and columns contain fossils and fossil fragments up to 1 centimeter wide, whereas the stromatolitic rinds of domes and columns contain millimeter-scale fossils and fragments. Data that illustrate the strong relationship between fossil content and thrombolitic textures are shown in Figure 7.

The thrombolite biostrome facies characteristically developed as broad, laterally continuous reef complexes which became discontinuous down depositional dip into isolated bioherms and pinnacle reefs. In updip positions, ambient current velocities were high, demonstrated by the trough cross-bedded intrachannel grainstone, the elongation of the stromatolitic thrombolite columns and the association of this facies with the grainstone facies. The extremely consistent orientation of the thrombolite elongation is similar to other platforms where wave action is inferred to be responsi-



Figure 6: Representative photographs of microbialites and associated textures, a) Stromatolitic thrombolite columns forming laterally continuous biostrome at top of Omkyk Member, Zaris subbasin. Core of each column has dominantly thrombolitic texture, whereas margins have better laminated stromatolitic thrombolite texture. Columns are stongly elongate normal to the trend of the Omkyk carbonate ramp indicating persistent high-velocity, wave-generated flows. Arrows point to goblet and tube-shaped fossils that are abundant within the intercolumn fill sequences but are also trapped within the thrombolitic texture. b) Well preserved thrombolite texture in pinnacle reef at top of Huns platform, Witputs subbasin. Reefal framework is created by dark colored mesoclots; these create shelter pores that are partially filled by light colored geopetal sediment and ultimately filled by fibrous marine and later blocky, burial cements. Inset shows fabric details; T, thrombolite mesoclot; GS, geopetal sediment; SP, shelter porosity filled with cement. Coin is approximately 1.2 cm in diameter. Inset shows enlargement of region near center of photograph. c) Neptunian dike transecting thrombolite mound, Driedoomvlagte bioherm, Zaris subbasin. Dike is infilled with botryoidal fibrous calcite cement interpreted to have replaced primary aragonite. Cements fill fractures within reef providing evidence for early lithification of reef. Coin is approximately 1 cm in diameter. Inset shows enlargement of region below coin.

ble for the elongation of stromatolites (Hoffman, 1969; Cecile and Campbell, 1978; Grotzinger 1986), analogous to the development of "spur and groove" structure in modern coral reefs (Shinn, 1963; Sneh and Friedman, 1980). In downdip positions, ambient current velocities also were high, again demonstrated by the presence of cross-bedded grainstone within thrombolitic buildups.



Figure 7: Distribution of calcified fossils within broadly defined lithologic facies of the Nama Group. Results show that fossils are very strongly correlated with thrombolitic facies. Fossils are less abundant in packstones and grainstones which are composed principally of intraclasts and peloids and are rare in mudstones. The simplest interpretation of this distribution is that the fossil organisms were benthic, with a strong preference for microbially colonized substrates. In addition, the preference for thrombolitic over stromatolitic substrates suggests further paleoecological control on their distribution. See text for discussion.

However, in these latter cases the reefs kept up with relative sea level rise, whereas the inter-reef regions accumulated sediment under much reduced current velocities at greater water depths. Inter-reef water depths are estimated to have been on the order of tens of meters for the Huns pinnacle reefs and over one hundred meters for the Driedoornvlagte bioherm.

This interpretation supports other evidence that the Kuibis ramp was a wave- and storm-dominated system where the dominant currents were induced by strong wave-generated flows. The particular values for the elongation indicate consistent oscillation by waves arriving from the west-northwest, the direction of the Damara-Gariep orogenic belt, and may imply an oro-graphic effect that might have influenced the entire foreland basin (Hoffman and Grotzinger, 1993).

The internal texture of the thrombolite reefs is distinct. It is characterized by mesoclots that range in size from a few millimeters to a few centimeters in diameter (Figs. 6a, 6b, 8b). Curiously, the mesoclots of the Nama reefs do not have the complex digitate or dendriform morphologies that characterize younger thrombolites (e.g. Kennard and James, 1986; Riding and Zhuravlev, 1995) but instead are restricted to simpler ovoid, globular and colliform morphologies are also common in Paleozoic and Mesozoic thrombolites but are the only forms described from older Proterozoic thrombolites (Kah and Grotzinger, 1992; Turner *et al.*, 1993).

Nama mesoclots formed an open framework that resulted in development of abundant cavities (Figs. 6b and 8a-c). Mesoclots typically were overgrown by a synsedimentary crust of fibrous marine cement with botryoidal geometry that now consists of calcite but is interpreted to have replaced former aragonite (Fig. 8a-c). Marine cement crusts were then overlain by a layer of geopetal sediment which partially filled framework pores (Figs. 6b, 8a-c). Remaining porosity was then occluded by a dolomite rim cement followed by infilling with blocky calcite spar (Fig. 8a-c). Mesoclots characteristically are recrystallized to an extent that makes interpretation of growth processes difficult. Figure 8a shows an example of the more poorly preserved mesoclots, whereas Figure 8b shows a well preserved example. Occasionally, mesoclots in the better preserved samples show tentative evidence of having been formed in the presence of coccoid cyanobacteria or algal spores, expressed as poorly preserved spherical objects present only in the cores of mesoclots (Fig. 8c).

Early lithification of thrombolites and stromatolites in Nama pinnacle reefs resulted in development of penetrative networks of neptunian dikes. These are best expressed in the Huns reefs and Driedoornvlagte bioherm as fractures that cut sharply across reefs (Fig. 9b) and are filled with fibrous marine cement which are interpreted as calcite-replaced aragonite (Fig. 6c). Gravitationally induced failure of the larger reefs generated penetrative networks of neptunian dikes; this did not occur in smaller reefs. A related effect includes failure of the sides of the pinnacle reefs which resulted in down slope transport of slide breccias (Fig. 9c). These breccias are composed of angular blocks up to 1 meter in diameter with thrombolite and stromatolite textures. Voids between breccia blocks are filled with massive lime or dolomite mudstones or fibrous marine cements.

Associated Facies

Grainstones are closely associated with thrombolite reefs in the Nama Group. The geometry of grainstone bodies varies with stratigraphic position and occurs in the form of extensive sheets or as local lenses within the reef framework. Grainstones formed in the HST of sequences in the middle and upper Omkyk Member have sheet-like geometry due to their accumulation under conditions of decreasing accommodation. These grainstones commonly form the platform on which the reefal biostromes of the middle and upper Omkyk were built as part of the overlying TST. For example, the major reef at Driedoornvlagte (Fig. 4) was established on a thick interval of grainstone (Smith, 1998), even though this site is the most downdip position preserved in the Nama Group. Careful inspection of Figure 3c reveals the laterally continuous, relatively thick-bedded grainstone deposits beneath the reef.

Grainstones in this stratigraphic setting consist mostly of very fine- to medium-grained calcarenites characterized by planar stratification, quasiplanar stratification (Arnott, 1993), hummocky cross-stratification, wavy bedding, ripple cross-bedding and trough cross-bedding (Fig. 10a). Grains in this stratigraphic position consist dominantly of peloids, small intraclasts, coated peloids (Fig. 10b) and uncommon fossils. These shoal facies are interpreted to have been deposited under moderately high-energy conditions with occasional periods of



Figure 8: Thin section photomicrographs of thrombolite fabrics within pinnacle reef at top of Huns carbonate platform, Witputs subbasin. a) Thin section shows poorly preserved mesoclots (Throm) encrusted with a fringe of fibrous calcite (fibrous marine cement) interpreted to have replaced original aragonite (note square crystal terminations). This was followed by deposition of a layer of siltsized crystals (geopetal sediment). Occlusion of remaining shelter porosity began with precipitation of an isopachous fringe of dolomite rim cement, followed by a final infill of blocky calcite spar. Note that dolomite rim cement is grown in contact with fibrous marine cement or geopetal sediment depending on its location. b) Thin section of thrombolite with well preserved mesoclots (Throm) composed of distinct aggregates of smaller clots. These smallest fabric elements most likely are formed by the early cementation of a complex consortium of mat building cyanobacteria, heterotrophic bacteria and eucaryotic algae. Note the accumulation of geopetal sediment (crystal silt) which smoothes out the rugged relief created by the clots and encusting fibrous marine cements. As in Figure 8a, note presence of isopachous dolomite rim cement and porosity-occluding blocky calcite. c) Magnified view showing textural detail of thrombolite mesoclots. In particular note the mesoclot between the arrow tip and "Throm" which shows several circular cross-sections that may be fossils of coccoid cyanobacteria or eucaryotic algal spores.



Figure 9: Associated reef facies. a) Cloudina packstone forming bioclastic detritus at top of Driedoornvlagte bioherm. Note specimen near center of photograph which shows longitudinal cross-section revealing that Cloudina consists of series of stacked flanges rather than cones. b) Sets of neptunian dikes cross-cutting stromatolitic facies within pinnacle reefs at top of Huns platform, Witputs subbasin. Neptunian dikes are filled with marine cement. The presence of these dikes indicates fracturing of early cemented reefal structures which often collapsed to form piles of breccia within reef (see Fig. 9c). c) Collapse breccia at base of pinnacle reef at top of Huns platform. Angular blocks indicate early lithification of the reef, consistent with evidence for fracturing and infilling with marine cement (Fig. 9b).

quiescence. The presence of quasiplanar stratification and hummocky cross-stratification indicate that these sediments were transported during episodic strong flows, probably of combined unidirectional and oscillatory nature (Southard *et al.*, 1990; Arnott 1993). This evidence points to reworking in the presence of storms; fairweather waves may have been primarily responsible for lower velocity flows leading to development of trough cross-bedding and ripple cross-stratification.

Grainstones forming lenses within reefs have significantly different attributes. First, because of their stratigraphic position within the TST under conditions of increasing accommodation, they form discontinuous lenticular bodies which interfinger with the reefal facies (Fig. 10c). Compositionally, the grains consist dominantly of skeletal fragments representing broken specimens of *Cloudina* (Figs. 10c, 9a) or the new taxa including goblet-shaped (*Namacalathus*) and simple tube-shaped fossils (see Grotzinger *et al.*, 2000).



Figure 10: Associated grainstone facies. a) Cross-bedded, intraclast-peloid-skeletal grainstone near top of Omkyk Member, Zaris subbasin, a few metres below thrombolite-stromatolite biostrome. Cross-beds indicate shallow, high-velocity flows on a wave and storm dominated shoal. The reefal biostrome developed on top of this shoal during accommodation increase and relative sea level rise. b) Close-up of grainstone in Figure 10a, showing individual coarse grains consisting of intraclasts and coated grains. Arrow points to leached intraclast filled with blocky spar. c) Cloudina grainstone-packstone formed at top of Driedoornvlagte bioherm. Inset shows details of skeletal structure and dark, void-filling marine cement. Accumulations of Cloudina are best developed near the tops of the reefs, within the bases of stratigraphic flooding intervals where accommodation greatly out-paced sediment supply. In this stratigraphic position, skeletal debris accumulates between the growing thrombolite-stromatolite mounds.

Discussion

The Nama Group contains the oldest documented assemblage composed of reef-forming microbialites and metazoans. These reefs appear at a critical time in earth history, immediately prior to the dramatic radiation of metazoans in early Cambrian time. Consequently, this motivates discussion of several aspects of this important association, including the significance of thrombolite textures, the paleoecological interactions between metazoans and microbialites and the functional morphology and phylogenetic affinity of the calcified metazoan fossils. Only the first two of these issues is addressed here; the latter two are discussed in Grotzinger *et al.* (2000). The origin of thrombolite textures and the buildups they form have been long debated. Aitken (1967) first coined the term "thrombolite" to refer to rocks with a distinctive class of textures of inferred microbial origin which were distinctly clotted rather than laminated in appearance and thus of potentially different origin than stromatolites.

Thrombolitic textures have been variably interpreted over the years but in all cases it has been recognized that they are very rare in rocks that are older than Neoproterozoic in age (cf. Kah and Grotzinger, 1992) and first appear in abundance at or close to the Precambrian-Cambrian boundary. Thus, most interpretations of thrombolites feature explanations rooted in some aspect of the Cambrian radiation or the environmental state of the earth at that time. For example, the initial interpretation of Aitken (1967), who invoked a microbial origin for the thrombolite clots, was rebuffed by Walter and Heys (1984) who argued that thrombolite clots were the aftermath of burrowing of ordinary stromatolites by organisms that evolved in the late Neoproterozoic time. They linked this to the simultaneous decline of stromatolites during Neoproterozoic time, accounted for in their model by the burrowing and grazing activities of the first macroscopic metazoans. Other models for the decline of stromatolites at this time include changes in ocean chemistry and competitive exclusion by higher algae (summarized in Grotzinger, 1990; Grotzinger and Knoll, 1999).

Following the work of Walter and Heys (1984), it was shown that Paleozoic (Kennard and James, 1986) and even rare Paleoproterozoic (Kah and Grotzinger, 1992) thrombolite textures do not result from the activities of burrowing and grazing metazoans and instead are formed as a primary, likely microbially influenced facies, supporting the original inference of Aitken (1967). Kennard and James argued that the diagnostic clotted fabric of thrombolites is generated by in situ calcification of discrete growth forms of coccoid-dominated microbial communities. Kah and Grotzinger (1992) argued a similar point but invoking encrustation of colloform, coccoid-dominated microbial mats by marine cement, rather than micritic calcification of individual microbes in the manner proposed by Kennard and James (1986). In either case, the point is that coccoid cyanobacteria form very rough, irregular mats (Golubic and Hofmann, 1976) that, if calcified in any manner, will create a clotted texture with only crude lamination. Recent work also supports this interpretation for Neoproterozoic thrombolites (Turner et al., 1997).

Most recently, it has been suggested that Paleozoic thrombolites may result from the participation of higher algae and metazoans in the mat-building consortium (Feldmann and McKenzie, 1998). This inference is based on the observation that procaryotic communities produce well developed lamination in intertidal environments, whereas eucaryotic communities, including green algae produce poorly laminated, thrombolitic textures in open marine subtidal environments. This interpretation is consistent with the many observations of Paleozoic thrombolites that support their growth in subtidal environments (Aitken, 1967; Bova and Read, 1987; Pratt and James, 1986) and that they appear in the historical record at about the same time that macroscopic algae are first preserved (Knoll, 1992). Significantly, the Nama record of thrombolites can be queried as a test of this hypothesis.

Observations of the thrombolites in the Nama Group are consistent with the predictions of the model of Feldmann and McKenzie (1998). Nama thrombolites formed in open marine, wave-swept environments, often associated with grainstone shoals and set within a stratigraphic position consistent with accommodation increase and sea level rise. Well laminated stromatolites are rare in the Nama group but so are intertidal facies. Nevertheless, the best stromatolites are developed as columns within the sheet-like biostromal unit at the top of the Omkyk Member (Figs. 3, 6a) which is interpreted to have formed in a very shallow subtidal environment. Interestingly, the margins of the columns are much better laminated than the cores, suggesting that sediment abrasion may have influenced the column texture. Feldmann and McKenzie (1998) indicate that high sediment bombardment restricts the distribution of eucaryotic mat components, favouring procaryote-dominated communities and better lamination. Eucarvotes tend to colonize sites with lower sediment flux, including the lee sides of columns and their tops. This is consistent with the relationships seen in Figure 6a where the cores would have been paleotopographically higher (clotted texture) than the margins (laminated texture) based on tracing laminae that define synoptic profiles.

Significantly, thrombolite textures are most abundant and best developed within the Nama pinnacle reefs at the top of Huns platform and at Driedoornvlagte. The reefs are composed of large mounds which are rarely elongate; where elongation is developed it is defined by a low length-to-width ratio consistent with low current velocities in deeper water subtidal settings. The thrombolite textures developed in this setting (Figs. 6b, 8) are extremely similar to those of Paleozoic age (compare Fig. 6b of this paper with Fig. 2b in Kennard and James, 1986) and at the same time somewhat different from those illustrated by Feldmann and McKenzie (1998) from the eucaryote-dominated columns of the Bahamas.

Some of the differences between the Nama thrombolites and Bahamian thrombolites include the lack of cylindrical voids created by boring metazoans and the larger size of mesoclots. The absence of borings along the margins of Nama thrombolites is most simply related to the absence of organisms during terminal Proterozoic time that had the capacity to form tubes comparable in size to that seen in the Bahamian thrombolites (1-2 mm; see Fig. 8 of Feldmann and McKenzie, 1998). However, it has been noted that microboring organisms may have been present in rocks of this age, as shown by the presence of possible predation holes in *Cloudina* shells (Bengtson and Zhao, 1992).

Mesoclots in the Nama thrombolites (up to 1.5 cm in diameter) are distinctly larger than those in the Bahamian thrombolites (a few mm in diameter). Accounting for this size difference must lie in elucidating the mechanism by which clots are formed. Kennard and James (1986) invoke calcification of coccoid-dominated microbial communities but Feldmann and McKenzie (1998) emphasize the limited evidence from modern mats which supports that interpretation. Instead, they argue that a consortium of procaryotes, algae and their spores, and metazoans including sponges, could have triggered precipitation of micrite within an organic framework to form irregularly shaped mesoclots. This is attractive in accounting for the Nama thrombolites in that it is almost certain, on the basis of the fossil record, that green and brown algae (Knoll, 1992), and possibly sponges (Brasier et al., 1997), were present at that time. However, the exact roles that these organisms had in inducing carbonate secretion remain vague at this time.

A final point concerns the role of the Nama calcified metazoans in reef development. Cloudina, Namacalathus and simple tube-shaped fossils have a strong affinity for thrombolitic substrates. On the basis of their very restricted facies distribution, these organisms must have been benthic in origin, with a very strong preference for firm, relatively sediment-free substrates that built thrombolites. However, they did not participate in any substantial way in reef building, either as framebuilders or sediment bafflers. They are best interpreted to have lived as solitary individuals, apparently attached by the closed end in the case of *Cloudina* and the stem end in the case of Namacalathus (see Grotzinger et al. (2000) for detailed discussion of fossil morphologies). In this mode it is straightforward to visualize a paleoecological reconstruction in which the calcified organisms were loosely attached to the accreting thrombolitic substrate, much in the same way that sponges and green algae do in the Bahamian thrombolites. Somewhat paradoxically, however, if they were attached to the thrombolite substrate, it has been very difficult to find individuals preserved in growth position. In one or two cases there are some hints of this but nothing compelling has been discovered so far. One would presume that under the condition of progressive accretion of the thrombolitic substrate that at least occasional individuals would be trapped and accreted in growth position. In fact, calcified fossils in general are not abundant in the Nama thrombolite columns and where they do occur they are not preserved in growth position (Fig. 6a). Consequently, an alternative interpretation of their growth habit and fossil distribution can be accounted for by allowing for attachment, as epibionts, to the green and or brown algae that likely inhabited the thrombolitic substrate. Upon death or dislocation of the algal components the calcified organisms would have

collapsed to the sea floor as detrital particles and been simply swept into the depressions between thrombolite columns and mounds, or occasionally trapped in random positions within the accreting mats. This interpretation also provides a mechanistic basis for understanding the locally great abundance of randomly scattered fossils in thin (a few cm) beds of thrombolitic laminates that form spatially extensive sheets within deeper subtidal facies. Indeed, before the radiation of predating metazoans, it is possible to envision broad expanses of the terminal Proterozoic seafloor which would have been best characterized as microbial-algal "carpets" with these earliest calcified metazoans inhabiting a forest of kelp.

Whatever the current uncertainties in understanding the environmental and phylogenetic affinities of these fossils, it is clear that the Nama Group holds the potential, distributed over more than 10,000 sq. km of some of the world's best outcrop, for answering these important questions. The broad expanse of the Nama Group has just started to be tapped. It is certain that the next decade of work will provide important additional discoveries that will test the various hypotheses for the origin of thrombolitic textures, their significance as recorders of earth evolution and in providing important habitats for the earliest biomineralized metazoans.

Acknowledgments

The Geological Survey of Namibia is gratefully acknowledged for providing a field vehicle and logistical support for ten years of research in Namibia. Wolf Hegenberger, Charlie Hoffman and Roger Swart are thanked for help in providing an introduction to the geology of Namibia and for providing helpful guidance and advice. Roger Swart and NAMCOR are thanked for providing the Landsat TM image in Figure 4. Special thanks go to Rob and Marianne Field and Roy Magson for access to their farms, Zebra River and Donkergange, and for their hospitality. Support for this research was provided by NSF grant EAR-9628257. Mark Feldman and Noel James reviewed the final manuscript and provided helpful comments.

References

- Ahrendt, H., Hunziker, J.C. and Weber, K. 1977. Age and degree of metamoprhism and time of nappe emplacement along the southern margin of the Damara Orogen/Namibia (SW-Africa). *Geol. Rdsch.*, 67, 719-742.
- Aitken, J.D. 1967. Classification and environmental significance of cryptalgal limestones and dolomites, with illustrations from the Cambrian and Ordovician of southwestern Alberta. *J. sedim. Petrol.*, **37**, 1163-1178.
- Arnott, R.W.C. 1993. Quasi-planar-laminated sandstone beds of the Lower Cretaceous Bootlegger Member, north-central Montana: Evidence of combined-flow

sedimentation. J. sedim. Petrol., 63, 488-494.

- Bengtson, S. and Zhao, Y. 1992. Predatorial borings in late Precambrian mineralized exoskeletons. *Science*, 257, 367-369.
- Bova, J.P. and Read, J.F. 1987. Incipiently drowned facies within a cyclic peritidal ramp sequence, Early Ordovician Chepultepec interval, Virginia Appalachians. *Bull. geol. Soc. Am.*, 98, 714-727.
- Bowring, S.A., Grotzinger, J.P., Isachsen, C.E., Knoll, A.H., Pelechaty, S.M. and Kolosov, P. 1993. Calibrating rates of Early Cambrian evolution. *Science*, 261, 1293-1298.
- Brasier, M., Green, 0. and Shields, G. 1997. Ediacaran sponge spicule clusters from southwestern Mongolia and the origins of the Cambrian fauna. *Geology*, 25, 303-306.
- Burchette, T.P. and Wright, V.P. 1992. Carbonate ramp depositional systems. *Sedim. Geol.*, **79**, 3-57.
- Cecile, M.P. and Campbell, F.H.A. 1978. Regressive stromatolite reefs and associated facies, middle Goulburn Group (Lower Proterozoic) in Kilohigok Basin, N.W.T.: an example of environmental control on stromatolite forms. *Bull. Can. Petrol. Geol.*, 26, 237-267.
- Feldmann, M. and McKenzie, J. 1998. Stromatolitethrombolite associations in a modern environment, Lee Stocking Island, Bahamas. *Palaios*, **13**, 201-212.
- Germs, G.J.B. 1972a. New shelly fossils from the Nama Group, South West Africa. *Am. J. Sci.*, **272**, 752-761.
- Germs, G.J.B. 1972b. The stratigraphy and paleontology of the lower Nama Group, South West Africa. *Bull. Precamb. Res. Unit, Univ. Cape Town*, **12**, 250 pp.
- Germs, G.C.B. 1974. The Nama Group in South West Africa and its relationship to the Pan African Geosyncline. J. Geol., 82, 301-317.
- Germs, G.J.B. 1983. Implications of a sedimentary facies and depositional environmental analysis of the Nama Group in South West Africa/Namibia, 89-114. *In*: Miller, R.McG. (ed.) *Evolution of the Damara Orogen*, Spec. Publ. geol. Soc. S. Afr., **11**, 515 pp.
- Golubic, S. and Hofmann, H.J. 1976. Comparison of modern and mid-Precambrian Entophysalidaceae (Cyanophyta) in stromatolitic algal mats: cell division and degradation. *J. Paleont.*, **50**, 1074-1082.
- Grant, S.W.F. 1990. Shell structure and distribution of *Cloudina*, a potential index fossil for the terminal Proterozoic. *Am. J. Sci.*, **290-A**, 261-294.
- Grant, S.W.F., Knoll, A.H. and Germs, G.J.B. 1991. Probable calcified metaphytes in the latest Proterozoic Nama Group, Namibia. J. Paleont., 65, 1-18.
- Gresse, P.G. and Germs, G.J.B. 1993. The Nama foreland basin: sedimentation, major unconformity bounded sequences and multisided active margin advance. *Precambr. Res.*, **63**, 247-272.

- Grotzinger, J.P. 1986. Evolution of early Proterozoic passive-margin carbonate platform, Rocknest Formation, Wopmay Orogen, N.W.T., Canada. *J. sedim. Petrol.*, 56, 831-847.
- 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. and Read, J.F. (eds) *Controls on Carbonate Platform and Basin Development*. Spec. Publ. Soc. econ. Paleont. Mineral., 44, 79-106.
- Grotzinger, J.P. 1990. Geochemical model for Proterozoic stromatolite decline. Am. J. Sci., 290-A, 80-103.
- Grotzinger, J.P. 1994. Trends in Precambrian carbonate sediments and their implication for understanding evolution. *In*: Bengtson, S. (ed.) *Early Life on Earth*. Columbia University Press, New York, 245-258.
- Grotzinger, J.P. and James, N.P. 2000. Carbonate Sedimentation and Diagenesis. *In: The Evolving Precambrian World*. Spec. Publ. Soc. econ. Paleont. Mineral., 65.
- Grotzinger, J.P. and Khetani, A. 1994. Facies and diagenesis of late Vendian thrombolite-shelly (*Cloudina*?) invertebrate pinnacle reefs, Nama Group, Namibia. *In: Abstracts with Programs (Northeast Section).* Boulder, Geol. Soc. Am., 56.
- Grotzinger, J.P. and Knoll, A.H. 1999. Stromatolites in Precambrian carbonates: Evolutionary Mileposts or Environmental Dipsticks? *Ann. Rev. Earth Planet. Sci.*, 27, 313-358.
- Grotzinger, J.P., Bowring, B.Z., Saylor, B.Z. and Kaufman, A.J. 1995. Biostratigraphic and geochronologic constraints on early animal evolution. *Science*, **270**, 598-604.
- Grotzinger, J.P., Watters, W. and Knoll, A.H. 2000. Diversity, paleoecology and evolutionary significance of thrombolite-stromatolite-metazoan reefs, Terminal Proterozoic Nama Group, Namibia. *Paleobiology*, In Press.
- Heckel, P.H. 1974. Carbonate buildups in the geologic record: a review. In: Laporte, L.F. (ed.) Reefs in Time and Space. Spec. Publ. Soc. econ. Paleont. Mineral. 18, 90-154 pp.
- Hoffman, P.F. 1969. Proterozoic paleocurrents and depositional history of the east arm fold belt, Great Slave Lake. *Can. J. Earth Sci.*, **6**, 441-162.
- Hoffman, P.F. and Grotzinger, J.P. 1993. Orographic precipitation, erosional unloading and tectonic style. *Geology*, **21**, 195-198.
- Horstmann, U.E., Ahrendt, H., Clauer, N. and Porada,
 H. 1990. The metamorphic history of the Damara Orogen based on K/Ar data of detrital white micas from the Nama Group, Namibia. *Precambr. Res.*, 48, 41-61.
- James, N.P. 1983. Reef environment. In: Scholle, P.A., Bebout, D.G. and Moore, C.H. (eds) Carbonate

Depositional Environments. Mem. Am. Assoc. Petrol. Geol., **83**, 345-440.

- Kah, L.C. and Grotzinger, J.P. 1992. Early Proterozoic (1.9 Ga) thrombolites of the Rocknest Formation, Northwest Territories, Canada. *Palaios*, 7, 305-315.
- Kaufman, A.J., Hayes, J.M., Knoll, A.H. and Germs, G.J.B. 1991. Isotopic compositions of carbonates and organic carbon from upper Proterozoic successions in Namibia: stratigraphic variation and the effects of diagenesis and metamorphism. *Precambr. Res.*, 49, 301-327.
- Kennard, J.M. and James, N.P. 1986. Thrombolites and stromatolites: Two distinct types of microbial structures. *Palaios*, 1, 492-503.
- Knoll, A.H. 1992. The early evolution of eucaryotes: A geological perspective. *Science*, **256**, 622-627.
- Korn, H. and Martin, H. 1959. Gravity tectonics in the Naukluft Mountains of South West Africa. *Bull.* geol. Soc. Am., 70, 1047-1078.
- Martin, H. 1965. The Precambrian geology of South West Africa and Namaqualand. *Precambr: Res. Unit, Univ. Cape Town*, 159 pp.
- Miller, R.McG. 1983. The Pan-African Damara Orogen of South West Africa/Namibia, 431-515. *In:* Miller, R.McG. (ed.) *Evolution of the Damara Orogen.* Spec. Publ. geol. Soc. S. Afr., **11**, 515 pp.
- Pratt, B.R. and James, N.P. 1986. The St. George Group (Lower Ordovician) of western Newfoundland: tidal flat island model for carbonate sedimentation in shallow epeiric seas. *Sedimentology*, **33**, 313-343.
- Riding, R. and Zhuravlev, A.Y. 1995. Structure and diversity of oldest sponge-microbe reefs: Lower Cambrian, Aldan River, Siberia. *Geology*, **23**, 649-652.
- Saylor, B.Z. and Grotzinger, J.P. 1996. Reconstruction of important Proterozoic-Cambrian boundary exposures through the recognition of thrust deformation in the Nama Group of southern Namibia. *Communs geol. Surv. Namibia*, **11**, 1-12.
- Saylor, B.Z., Grotzinger, J.P. and Germs, G.J.B. 1995. Sequence stratigraphy and sedimentology of the Neoproterozoic Kuibis and Schwarzrand Subgroups (Nama Group), southwest Namibia. *Precambr. Res.*, 73, 153-171.
- Saylor, B.Z., Kaufman, A.J., Grotzinger, J.P. and Urban, F. 1998. A composite reference section for terminal Proterozoic strata of southern Namibia. *J. sedim. Res.*, 66, 1178-1195.

- Sepkoski, J.J. 1992. Proterozoic-Early Cambrian diversification of metazoans and metaphytes. *In*: Schopf, J.W. and Klein, C. (eds) *The Proterozoic Biosphere*. Cambridge University Press, Cambridge, 553-561.
- Shinn, E.A., 1963. Spur and groove formation on the Florida reef tract. J. sedim. Petrol., **33**, 291-303.
- Smith, O.A. 1998. Terminal Proterozoic Carbonate Platform Development: Stratigraphy and Sedimentology of the Kuibis Subgroup (ca. 550-548 Ma), Northern Nama Basin, Namibia. Unpubl. MSc. thesis, Massachusetts Institute of Technology, 132 pp.
- Sneh, A. and Friedman, G.M. 1980. Spur and groove patterns on the reefs of the northern gulfs of the Red Sea. *J. sedim. Petrol.*, **50**, 981-986.
- Southard, J. B., Lambie, J. M., Federico, D. C., Pile, H. T. and Weidman, C. R. 1990. Experiments on bed configurations in fine sands under bidirectional purely oscillatory flow, and the origin of hummocky cross-stratification. *J. sedim. Petrol.*, **60**, p. 1-17.
- Tucker, M.E. and Wright, V.P. 1990. Carbonate Sedimentology. Blackwell Scientific Publications, Oxford, 482 pp.
- Turner, E.C., James, N.P. and Narbonne, G.M. 1997. Growth dynamics of Neoproterozoic calcimicrobial reefs, Mackenzie Mountains, northwest Canada. J. sedim. Petrol., 67, 437-450.
- Turner, E.C., Narbonne, G.M. and James, N.P. 1993. Neoproterozoic reef microstructures from the Little Dal Group, northwestern Canada. *Geology*, 3, 259-262.
- Turner, E.C., Narbonne, G.M. and James, N.P. 2000. Framework composition of early Neoproterozoic calcimicrobial reefs and associated microbialites, Mackenzie Mountains, N. W. T. *In*: Grotzinger, J.P. and James, N.P. (eds) *Carbonate Sedimentation and Diagenesis in the Evolving Precambrian World*. Spec. Publ. Soc. econ. Paleont. Mineral., 65.
- Valentine, J.W., Awramik, S.M., Signor, P.W. and Sadler, P.M. 1991. The biological explosion at the Precambrian-Cambrian boundary. *Evol. Biol.*, 25, 279.
- Walter, M.R. and Heys, G.R. 1984. Links between the rise of the metazoa and the decline of stromatolites. *Precamb. Res.*, **29**, 149-174.
- Wilson, J.L. 1975. Carbonate facies in geologic history. Springer Verlag, New York, 470 pp.