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Stromatolite branching in the Neoproterozoic of the Centralian Superbasin, Australia: an investigation into sedimentary and microbial control of stromatolite morphology

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ABSTRACT

The extensive and well-preserved Neoproterozoic *Acaciella australica* Stromatolite assemblage of Australia is ideal for examining the relative roles of microbial and environmental influences on stromatolite branching and stromatolite macrostructure across a wide geographical area. Detailed sedimentological analyses indicate that the basal hemispheroidal section of bioherms contains abundant sediment. By contrast, the columnar sections of bioherms are composed almost exclusively of micritic laminae. These micritic laminae display little evidence for environmental, especially sedimentary, control over stromatolite morphology. The change from a hemispheroidal morphology to branching morphology is linked to variations in the relative contributions of sediment and framework growth. The shift to columns appears to be closely linked to a decrease in sediment supply that resulted in a more stable environment in which microbially mediated framework growth began to control stromatolite morphology. Branching in the *A. australica* assemblage stromatolites appears to be caused by shifting sedimentary and microbial control on stromatolite morphology.

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INTRODUCTION

Stromatolites are abundant and widespread throughout the Proterozoic. However, many fossil stromatolites show significant differences from most modern examples in both macroscopic and microscopic characteristics. For instance, there is a far greater variation in the gross morphology of Proterozoic stromatolites than is seen in modern stromatolites. Notably, many Precambrian stromatolites display multiple stages of branching and well-defined branching patterns. Modern stromatolites rarely branch, and if there is branching, it is simple in pattern and typically poorly defined (e.g. Grey *et al.*, 1990; Dupraz *et al.*, 2006). The lack of an appropriate modern analogue for most Precambrian stromatolite branching has hindered understanding of the branching process (Southgate, 1989). The abundance of factors involved in stromatolite accretion, and thus the complexity of the process, prevents concurrence on many basic aspects of stromatolite formation. Some of the factors that influence stromatolite morphogenesis include the involved microbial community, ambient geochemical conditions, amount of sediment input, current conditions, amount of wave energy, underlying substrate, climate, depth of formation, light abundance, and levels of nutrient availability. Proposed models for branching are almost as numerous as the factors that can affect stromatolite accretion (e.g. Hofmann, 1969; Walter, 1972; Logan *et al.*, 1974; Haslett, 1976; Monty, 1976; Horodyski, 1977; Pratt & James, 1982; Monty *et al.*, 1987; Southgate, 1989, 1991; Grey *et al.*, 1990; Grotzinger & Knoll, 1999; Dupraz *et al.*, 2006). The main area of contention between the various models is the relative contribution made by environmental and biotic factors to the branching process. This is unsurprising since debate about the degree of biological control on stromatolite formation is one of the most commonly addressed and contentious issues in the study of stromatolites (Semikhatov & Raaben, 2000).

Modeling of stromatolite growth has provided a new and valuable tool for grappling with factors involved in stromatolite accretion (Grotzinger & Knoll, 1999; Dupraz *et al.*, 2006). The theoretical approach has allowed for a refinement of loosely based morphogenesis models and has provided discrete models that can be tested using fossil stromatolites.

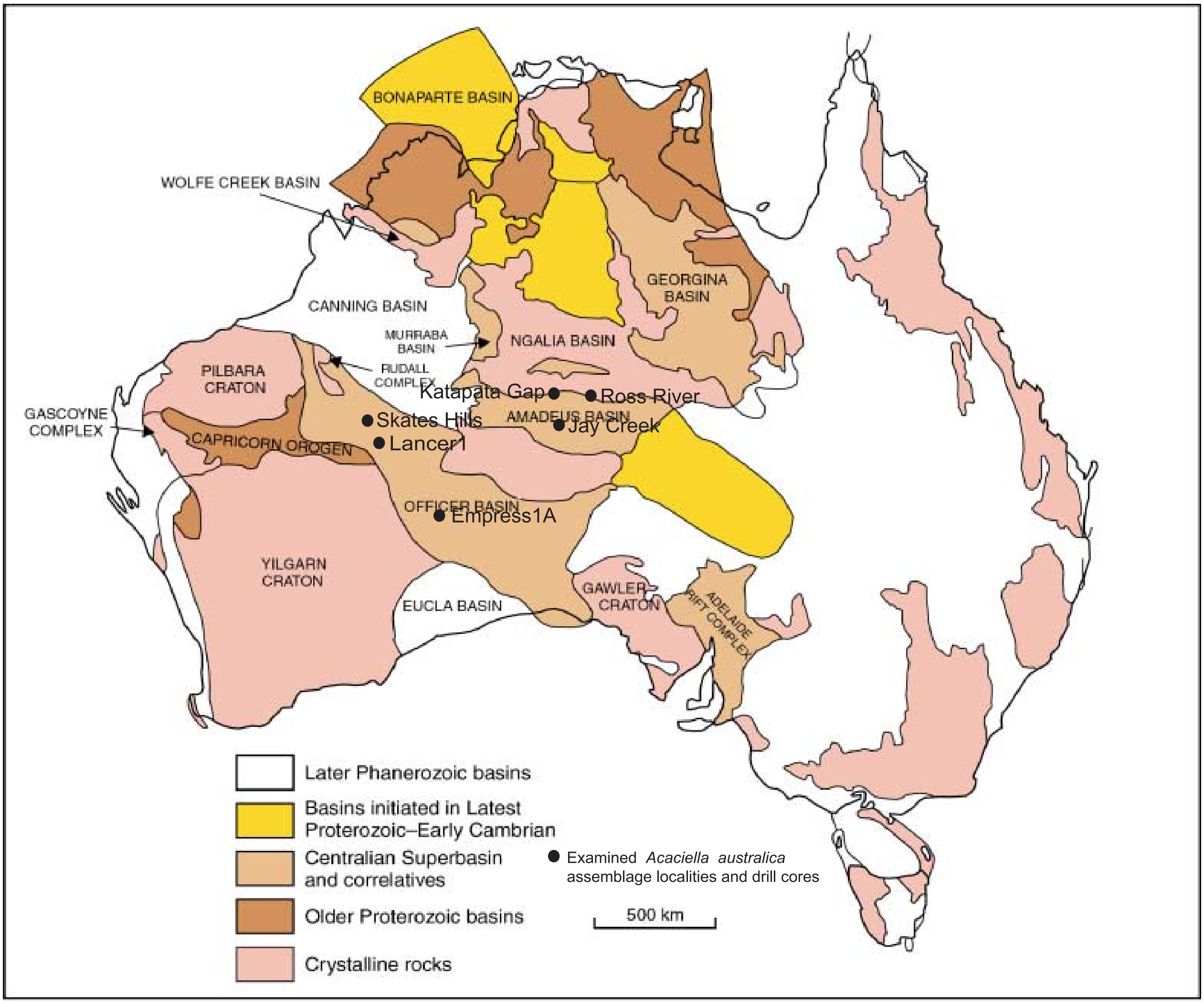

Fig. 1 Location of examined Centralian Superbasin stromatolite outcrops and drill cores (modified from Grey *et al*., 2005).

Notably, theoretical models suggest that complex stromatolite morphologies and branching patterns can arise from variations in the relative contributions of sediment and framework growth to the stromatolite structure (Grotzinger & Knoll, 1999).

In this study, we present a sedimentological examination of the Cryogenian *Acaciella australica* Stromatolite assemblage from Australia (Stevens & Grey, 1997; Hill *et al*., 2000) with the goal of elucidating the effect that sedimentation has on stromatolite branching and macrostructure. Examined stromatolite features include lamina shape and stacking, branching style, degree of fabric disruption, and percentage and distribution of detrital material. The *A. australica* assemblage is well sampled, well documented, and extends across a wide geographical area of Australia including the Centralian Superbasin, the Adelaide Rift Complex and Kimberley area (Fig. 1) (e.g. see Walter, 1972; Walter *et al*., 1995; Hill *et al*., 2000). In addition to being geographically widespread, many of the localities are exceptionally well preserved, and some contain a distinguishable siliciclastic-rich detrital component. This combination of features makes the *A. australica* Stromatolite assemblage ideal to directly test the applicability of previously proposed stromatolite branching models and try to disentangle factors influencing stromatolite morphology.

MATERIAL, METHODS, AND DEFINITIONS

The *A. australica* Stromatolite assemblage is known from more than 100 localities across Australia. One of us (K.G.) has examined most of these localities, together with specimens (including type specimens) housed in the South Australian Museum Collection (previously the University of Adelaide Collection), the Primary Industry and Resources of South Australia Collection, and the Commonwealth Palaeontological Collection of Geoscience Australia. More than 150 specimens from the *A. australica* assemblage are held in the Geological Survey of Western Australia (GSWA) collection. The specific study described here is based on selected hand specimens, polished slabs, serial sections, and thin sections from the GSWA collection; two drill core sections (Empress 1A and Lancer 1), and on-field observations conducted at several localities in the Ross River area of the Amadeus Basin, Northern Territory, Australia.

Probably the best-known outcrops of the *A. australica* assemblage are at two localities near Ross River homestead in the Amadeus Basin, Northern Territory. Other previously collected Amadeus Basin specimens examined came from near Jay Creek and Katapata Gap. Previously collected specimens from the Officer Basin are from 15 localities in the Skates Hills Area. In addition, two continuous core sections (GSWA Empress 1A and GSWA Lancer 1, stored in the GSWA Core Library) were examined. Full locality details and stratigraphic information for illustrated specimens are given in Appendix S1.

Many specimens were previously described and illustrated as part of taxonomic and biostratigraphic studies (Walter, 1972; Preiss, 1973a,b, 1976a, 1987; Grey, 1995; Walter *et al.*, 1979). For these, and as yet unpublished studies, selected specimens were serially slabbed in vertical orientation and reconstructed three-dimensionally. Petrographic examination was carried out using thin sections (30 µm and 90 µm) and acetate peels. The thicker thin sections display stromatolite fabric details not normally visible in standard petrographic thin sections.

Stromatolite terminology follows that of Krylov (1959, 1963), Hofmann (1969, 1976), Walter (1972), and Preiss (1976b). Linnean (binominal) nomenclature is adopted for stromatolite names, and the terms 'Group' and 'Form' are used (capitalized to distinguish between the taxonomic and general use of the terms) instead of 'genus' and 'species' in recognition that the named entities do not represent individual species (Semikhatov *et al.*, 1979). Full taxonomic names and author citations are listed in Appendix S2 rather than in the main body of the text. There is no generally accepted definition for stromatolites. The Awramik and Margulis (in Walter, 1976) genetic definition, which infers a biogenic origin, and the descriptive definition of Semikhatov *et al.* (1979) are the most commonly used. For the purposes of this paper, we follow the descriptive definition and specifically address the roles of the microbial played in the stromatolites' formation.

Acaciella australica *assemblage*

Early Cryogenian stromatolites of the Australian Centralian Superbasin form a distinctive assemblage. The stromatolites were originally described and correlated based on taxonomic characteristics (Walter, 1972; Preiss, 1973a; 1976a,b; Grey, 1978, 1995; Walter *et al.*, 1979). Initial correlations have been supported by carbon isotope chemostratigraphy, sequence stratigraphy, event stratigraphy, biostratigraphy, and lithostratigraphy (Fig. 2) (Preiss, 1987; Walter *et al.*, 1995; Hill & Walter, 2000; Hill *et al.*, 2000; Grey *et al.*, 2005). The most conspicuous Cryogenian stromatolite taxon is *A. australica*. This taxon was initially defined by basic macro- and mesostructural (in the sense of Dupraz *et al.*, 2006) characteristics in which a stromatolite that contains hemispheroids or very broad coalescing columns shifts into narrow columns by α parallel branching (Fig. 3) (Walter, 1972). *A. australica* is often found associated with similar stromatolite Forms, such as *Jurusania nisvensis*, *Inzeria intia*, and more rarely with *Kulparia alicia*, which are defined by different branching patterns, column characteristics (Fig. 3), and microstructures (see Walter, 1972, for detailed discussion). The association of about 12 taxonomic Forms, including those mentioned above, was defined as the *A. australica* Stromatolite assemblage (Stevens & Grey, 1997; Hill *et al.*, 2000). Although taxonomic descriptions (Walter, 1972; Walter *et al.*, 1979; Grey 1978, 1995; Grey & Blake, 1999) and general sedimentological studies (Southgate, 1989, 1991) have been well documented in the literature, to date there has never been an extensive study of stromatolite morphogenesis.

General geological background and stratigraphy

The Centralian Superbasin is a Neoproterozoic intracratonic basin that is estimated to have covered approximately 2 000 000 km^2 (Walter *et al.*, 1995) and contains sedimentary rocks ranging in age from the early Cryogenian to the Devonian. Initial basin formation probably occurred in an extensional setting. Subsequent extensional and compressional events formed several separate structural basins (Amadeus, Georgina, Officer, and Ngalia) and sub-basins. One of the essential features of the Centralian Superbasin is a common depositional history, especially in the early stages of formation (Walter *et al.*, 1995; Grey *et al.*, 2005). At the same time, deposition was taking place in a rift setting in the Adelaide Rift Complex. The recognition of common stratigraphic successions led to the designation of four supersequences that span the depositional history of the basin (Walter *et al.*, 1995). The examined stromatolites are found in Supersequence 1, which was deposited in the early Cryogenian between about 850 and 750 million years ago, well before the Sturtian glaciation in Australia (Fig. 2). The narrow stratigraphic time range, broad geographical distribution, and variety of lithologies and depositional environments in which the *A. australica* assemblage is present provide a suitable selection of material for examining branching controls.

The selected stromatolites examined from the Amadeus Basin stromatolites are from the Loves Creek Member, unit II of the Bitter Springs Formation. The basal, subtidal, evaporitic Gillen Member of the Bitter Springs Formation shallows upwards into the regressive Loves Creek Member. Thin-bedded dolo-mudstone in Loves Creek Member unit I is overlain by up to 200 m of stromatolite-dominated carbonate

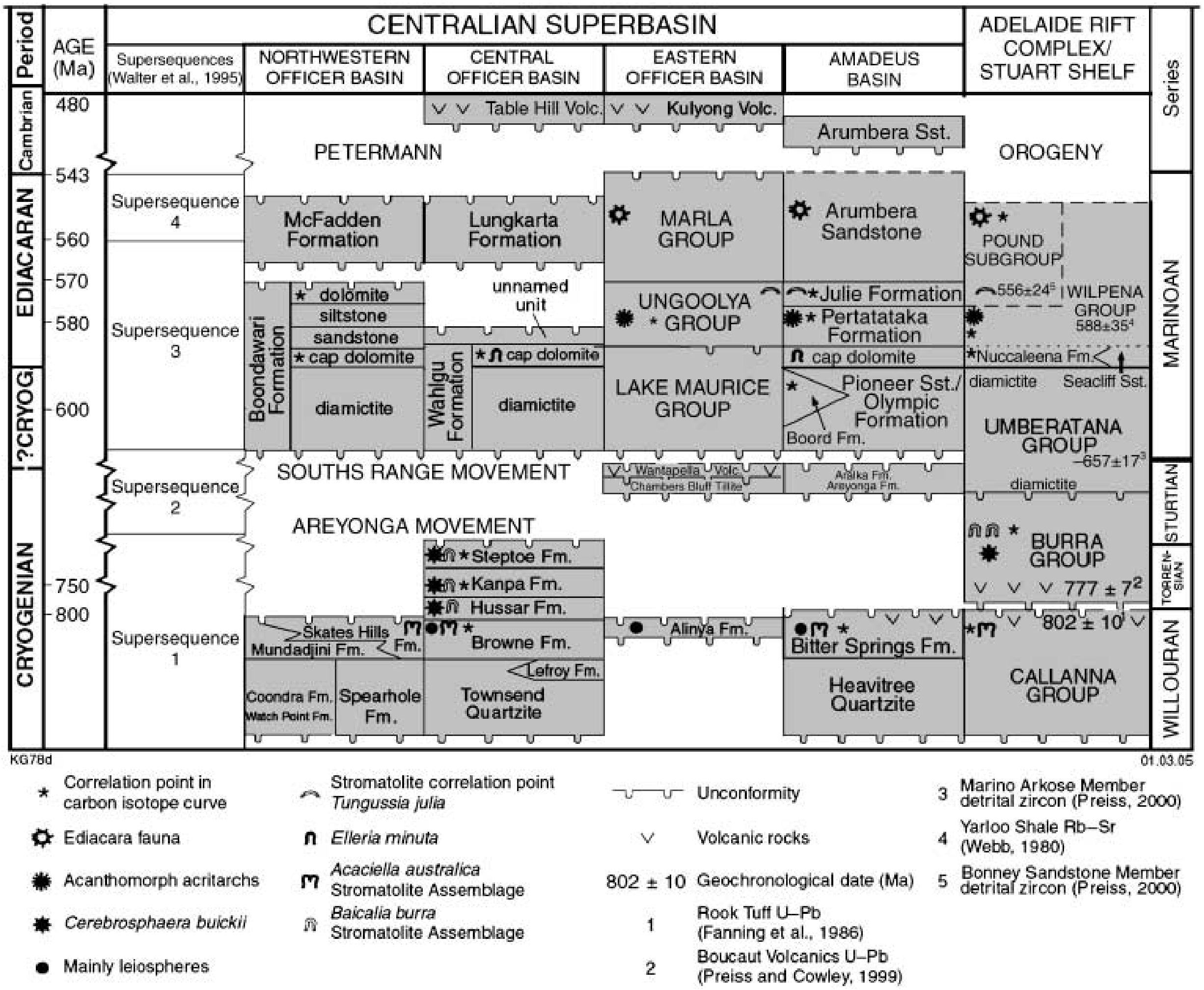

Fig. 2 Generalized sections and stratigraphic correlations in the Centralian Superbasin (after Grey *et al*., 2005).

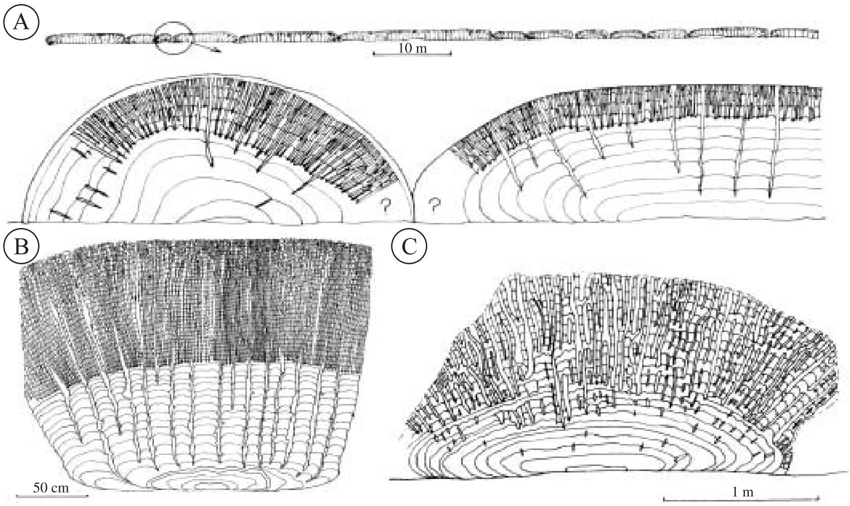

Fig. 3 Idealized reconstructions of examined branching stromatolite taxa: (A) *Acaciella australica*, (B) *Inzeria intia*, and (C) *Jurusania nisvensis* (after Walter, 1972).

of Loves Creek Member unit II (Southgate, 1989, 1991). Unit II is overlain by up to 400 m of interbedded redbeds and lacustrine carbonate (unit III). The stromatolite-dominated member shallows upwards and eventually forms a seasonal, possibly lacustrine environment, which contains the Bitter Springs microfossil assemblage (Schopf, 1968; Southgate, 1986, 1989).

In the Officer Basin, drill holes GSWA Lancer 1 and GSWA Empress 1A contain a thick Neoproterozoic sedimentary succession ranging from early Cryogenian to Ediacaran in age (Stevens & Apak, 1999; Haines *et al.*, 2004; Mory & Haines, 2005). The *A. australica* assemblage is present in the early Cryogenian Browne Formation in these two drill-holes as well as in the laterally equivalent Skates Hills Formation in the northwestern Officer Basin (Grey, 1995). The Browne and Skates Hills Formations are equivalent to the Bitter Springs Formation of the Amadeus Basin (Fig. 2) (Grey *et al.*, 2005).

In unit II of the Loves Creek Member, in the Amadeus Basin, the *A. australica* assemblage lies in a regressive–transgressive succession within the sequence-stratigraphic framework proposed by Southgate (1989, 1991). The deepest facies consist of thin-bedded lensoidal dolostone and limestone beds that contain rare, poorly laminated, hemispheroidal and stratiform stromatolites. The shallowest facies are characterized by desiccation cracks and extensive evaporite deposits (Southgate, 1989). The stromatolite-dominated interval shows a vertical progression of stromatolite Forms that can be traced laterally over considerable distances and between outcrops (Southgate, 1989, 1991). There is, however, a large amount of minor variation from the generalized macrostructural progression in various measured sections. For instance, near Ross River, one to six separate horizons of columnar stromatolites are present within the transgressive cycle in a series of partially scree-covered cliffs (Fig. 4) that extend for about 2.5 km. Similar stacked horizons of *A. australica* assemblage bioherms are present in other parts of the Amadeus, Georgina, and Officer Basins and in the Peake and Denison Ranges of the Adelaide Rift Complex (Walter, 1972; Preiss, 1973a, 1987; Walter *et al.*, 1979; Freeman & Woyzbun, 1986; Grey, 1995, 1999, 2005; Stevens & Grey, 1997; Hill *et al.*, 2000; Grey *et al.*, 2005) but have not been fully documented. However, the same general association of stromatolite Forms and morphological progression is found at Skates Hills, and in the two drill cores.

Description of stromatolite branching

Branching in *A. australica* (and associated Cryogenian taxa, *Kulparia alicia*, *Jurusania nisvensis* and *Inzeria intia*) is generally characterized by a transition from broad hemispheroids to narrow columns. Branching usually occurs at a uniform horizon that is equidistant from the point of origin of the bioherm, although, as previously noted (Walter, 1972), branching can be poorly developed on the basal sections of the hemispheroids. After branching, the columns are inclined at varying angles depending on the convexity of the underlying hemispheroid (Fig. 5). In vertical view, columns near the center of the bioherm are perpendicular; those near the margins are inclined, so that branches fan out in a pattern of regularly increasing inclination the greater the distance from the center of the bioherm. Lateral branches eventually curve and become perpendicular so that all of the columns become vertical at the tops of the bioherms.

Basic attributes of the underlying hemispheroids and the columns vary widely. The underlying hemispheroids vary from small (less than 1 m in diameter) to broad (between 1 and 2 m in diameter). The hemispheroids are typically isolated but there are horizons of laterally linked hemispheroids. There is no consistency in column length at any of the examined localities. A maximum column length of 2.1 m was observed in the Ross River area. No elongation in plan view, as seen at

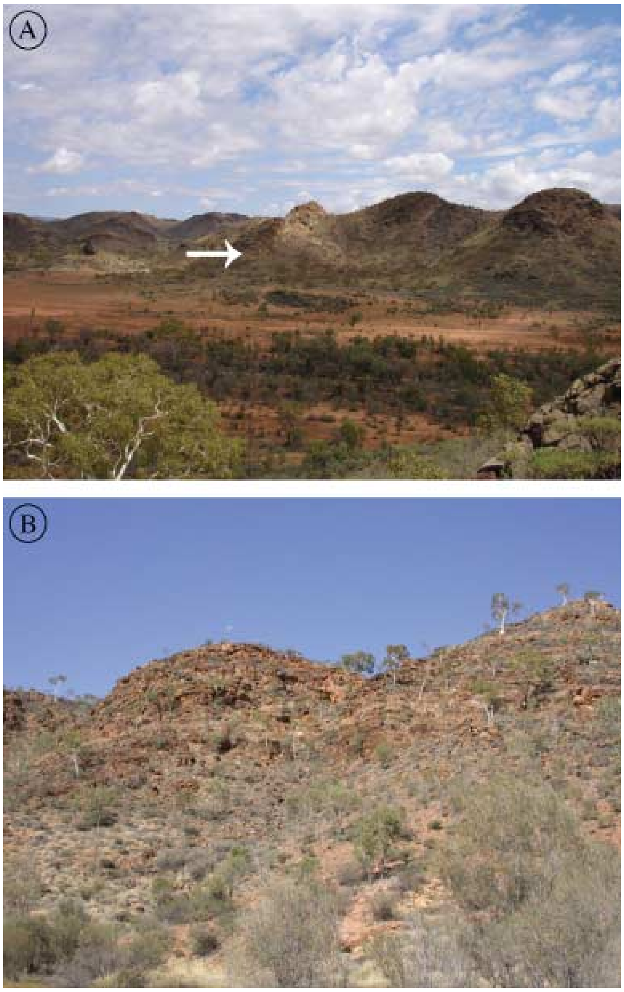

Fig. 4 Type of outcropping present in Loves Creek unit II stromatolite horizon in the Bitter Springs Formation, Ross River area. (A) General view; (B) detail of unit II showing showing several horizons composed almost exclusively of stromatolites.

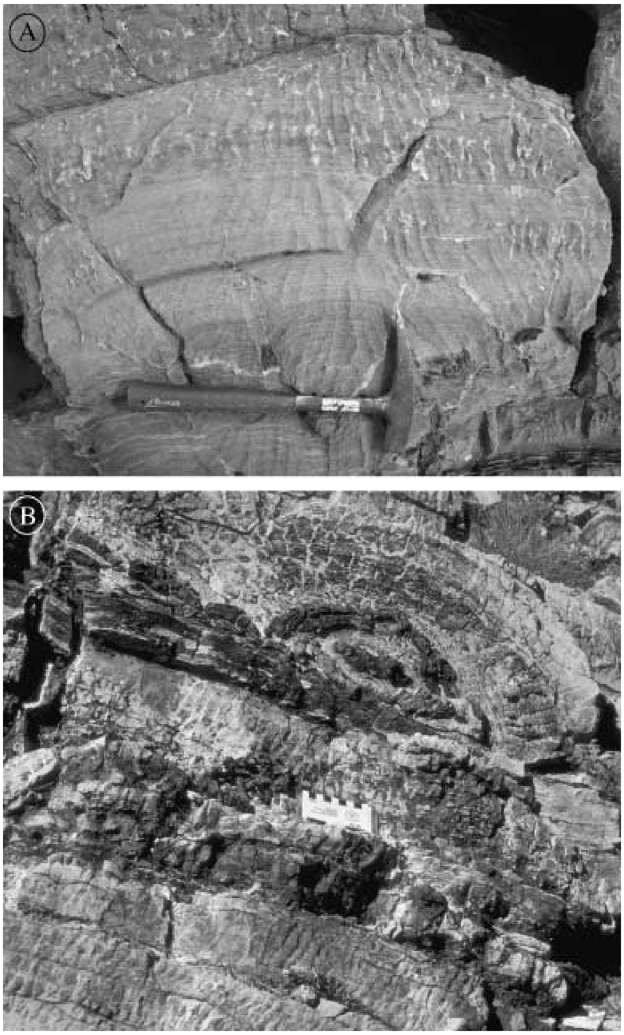

Fig. 5 (A) *Acaciella australica* bioherm, Bitter Springs Formation, Ross River area. Hammer for scale. (B) *A. australica* bioherm from the Skates Hills Formation, Skates Hills. Scale bar in centimeters.

some modern and Precambrian localities (Hoffman, 1974, 1976), was observed in either the hemispheroids or the overlying columns. Individual columns are rounded to lobate in plan view.

The lower section of each bioherm is a hemispheroid composed of micritic laminae but characterized by a high input of detrital material and disruption of the lamina couplets (Fig. 6). It is not always possible to differentiate carbonate detrital material from micritic laminae and cement, especially where carbonate textures are not well preserved because of recrystallization and stylolitization. However, in better-preserved stromatolites, especially those with a quartz sand and dolomite-rich silt component, the micritic laminae can be easily distinguished from the coarser allochthonous component. In general, detrital lenses flatten out upwards rather than following the convexity of the hemispheroids or the micritic laminae (Fig. 6B,C). In the lowest section of the hemispheroids, the detrital grains fill in topographic lows created by scouring (Fig. 6D), or are completely draped over lenses of lamina couplets. Neither the micritic laminae nor the detrital material in this section are laterally continuous, giving rise to a mesostructure with a lensoidal appearance. Lensoidal areas in the hemispheroids contain the highest amounts of detrital material.

The middle section of each bioherm, the uppermost part of the hemispheroid, contains smaller quantities of detrital material and has a significantly different fabric from the lower, lensoidal section. The micritic laminae in this part of the bioherm develop a waviness, which expands into small, linked hemispheroids (Fig. 7). The hemispheroids attain heights of several centimeters. Detrital material is most commonly found in the spaces between the small, linked hemispheroids of micritic laminae. The development of pseudocolumnar stromatolites (*sensu stricto* Walter, 1972) is common in the Empress 1A drill core. Pseudocolumnar stromatolites consist of small, stacked, linked hemispheroids of micritic laminae. The hemispheroids appear to have been periodically completely covered by detrital material allowing for the repeating, or stacking, of the hemispheroids without separation into distinct columns. In areas with higher amounts of detrital grains, second-order curvature is not commonly present, and there is an undulatory, rather than pseudocolumnar, mesostructure (Fig. 7D). Many of the laminae have a ragged appearance and appear to have undergone minor amounts of scouring and fabric disruption (Fig. 7B). Detrital substrates are normally overlain by flat-lying micritic laminae, which develop a constant curvature upwards in the bioherm. Although detrital material is an important component of this fabric type, it is not consistently intermixed with micritic laminae as it is in the lower, lensoidal section of the bioherm.

Branching in all examined Forms from the *A. australica* assemblage (*A. australica*, *K. alicia*, *J. nisvensis*, and *I. intia*) occurs where there is undisturbed development of hemispheroids of micritic laminae from the underlying bioherm. The curvature of the lamina at the point of branching changes from flat-lying to convex where they form linked hemispheroids. Such laminae generally develop several centimeters of synoptic relief above the first order of curvature hemispheroid surface. Persistent, or at least periodic, synoptic relief is indicated by the well-defined wall structure on the margins of two burgeoning columns (Fig. 8). Bridges (laminae occurring between two columns) are prevalent near the branching point (Fig. 9B), but otherwise are not a significant feature in either *A. australica* or *I. intia*. The columns are composed almost entirely of micritic laminae. Laminae at the branching point and in the overlying columns show only limited, if any, evidence of disruption. Small-scale scouring or sediment-reworking features, like those seen in the underlying hemispheroids, are absent in the overlying columns. Once branching has occurred, there is typically little or no change in the

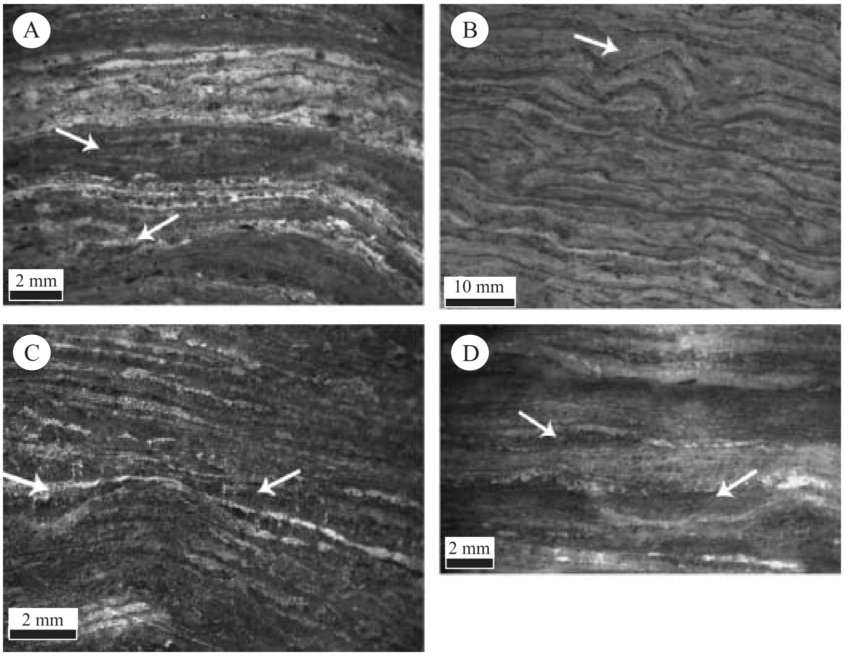

Fig. 6 Bottom, lensoidal section of bioherms. (A) *Acaciella australica* from the Skates Hills Formation, Skates Hills. (B) *A. australica* from the Browne Formation in GSWA Lancer1 drill core. (C, D) *A. australica* from Bitter Springs Formation at Katapata Gap. Note the presence of numerous local increases in lamination convexity that are covered by detrital material and topped by low convexity laminations. Arrows note lens of detrital material. All photos in reflected light (RL).

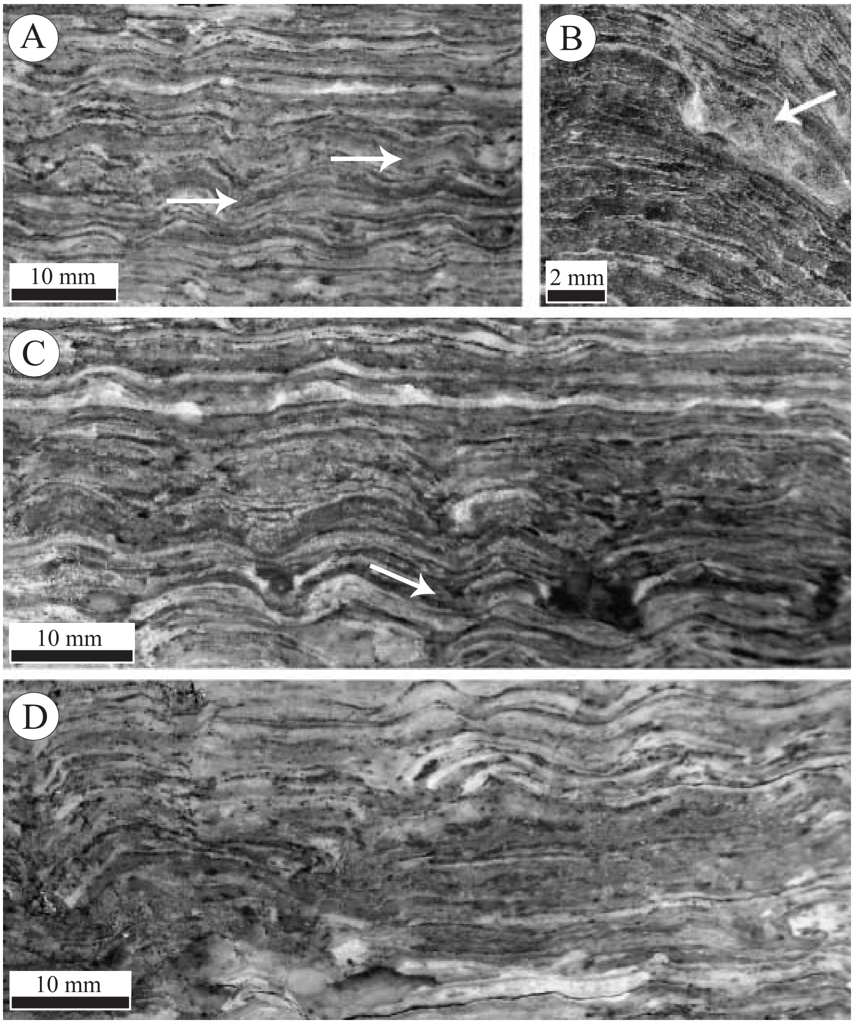

Fig. 7 Middle, undulatory section of bioherms. (A) *Acaciella australica* from Browne Formation in GSWA Lancer1 drill core. Arrows indicate incipient columns that develop from flat laminations. (B) *Inzeria intia* hemispheroid from Bitter Springs Formation, Ross River area. Arrow indicates an example of coarse quartz and dolomite rich detrital infill. (C) *A. australica* from Browne Formation in GSWA Lancer drill core. (D) *A. australica* from Browne Formation in GSWA Empress 1A drill core. Arrow indicates a detrital lens between two incipient columns. Note the numerous examples of incipient columns that are covered by upward flattening detrital material. All photos in reflected light (RL).

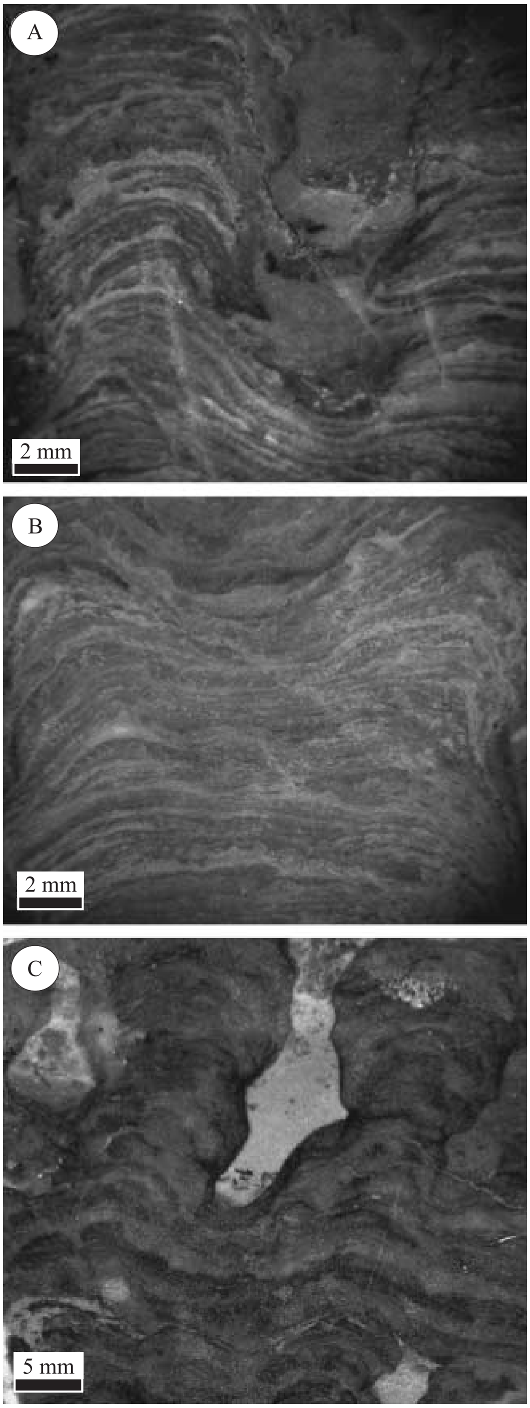

Fig. 8 (A, B) Branching point in *Acaciella australica* from the Skates Hills Formation, Skates Hills. (C) Branching point in a *Kulparia alicia* bioherm from Bitter Springs Formation, Jay Creek area. Note the continuity of laminations during the branching process and the gentle increase in lamination convexity underlying the branching point. All photos in RL.

morphology of the columns. Laminae within the columns generally maintain the same degree of convexity (Fig. 9). Columnar sections of the bioherms, in stark contrast to the lower and middle sections of the bioherm, contain minimal amounts of detrital material. This trend is most clearly seen at the Ross River localities where the siliciclastic-rich detrital material can be readily distinguished.

The most common progression of features in branching stromatolites of the *A. australica* assemblage is described above, but other progressions are present. The vertical change from lensoidal to pseudocolumnar hemispheroids dominates, but there are several variations on this pattern. In the Ross River area, lensoidal and pseudocolumnar hemispheroids may alternate over several centimeters. *I. intia* often branches into irregular columns that display a faintly pseudocolumnar or undulatory mesostructure (*I. intia* parts 2 and 3; Walter, 1972) before branching into typical columnar structures. In the deepening sequences at Ross River, columns are sometimes underlain by stratiform stromatolites and peloid-rich sandstones. The columns often formed directly from the grainstone. The columns in the deepening sequence appear to have developed without the well-defined branching pattern seen in the shallowing upwards sequence and, therefore, are not further considered here in the discussion of branching.

Stromatolite branching is mostly a phenomenon of gross morphology, but several microstructural observations are pertinent in discussing the branching process. In general, lamination in the examined taxa consists of alternating light and dark laminae. The thinner, darker laminae have a mean thickness of 0.11 mm and the thicker light laminae have a mean thickness 0.24 mm ($n = 80$). The dark laminae are faintly autofluorescent. Given that the change in autofluorescence does not appear to be associated with variations in crystal size or structure, the laminae are probably composed of alternating organic-rich and organic-poor layers. The presence of a combustible residue after acid dissolution of sections of the stromatolites confirms the presence of residual organics. Both the upper and lower boundaries between light and dark laminae are gradational (Fig. 10).

In most cases, *in situ* calcification seems to be the predominant mode of lamina formation. The compositional disparity between micritic laminae and intercolumnar material and the lack of any intermixed siliciclastic material in the majority of micritic laminae (e.g. Fig. 10B) are unlikely to be caused by extremely selective trapping and binding. The composition of micritic laminae therefore suggests autochthonous accumulation. However, in places, detrital material may have been trapped and bound. Even given the exceptional state of preservation, recrystallization limits the potential for definitively determining the relative contribution of *in situ* precipitation versus trapping and binding of the fine-grained fraction of the detrital load. Interestingly, there does not appear to be evidence of the trapping and binding of coarse grains similar to that observed in modern Bahamian stromatolites (Dill *et al.*, 1986) or the Western Australian Shark Bay stromatolites (Logan *et al.*, 1974), despite the abundance of peloids or coarse siliciclastic sediment in the stromatolite interspaces.

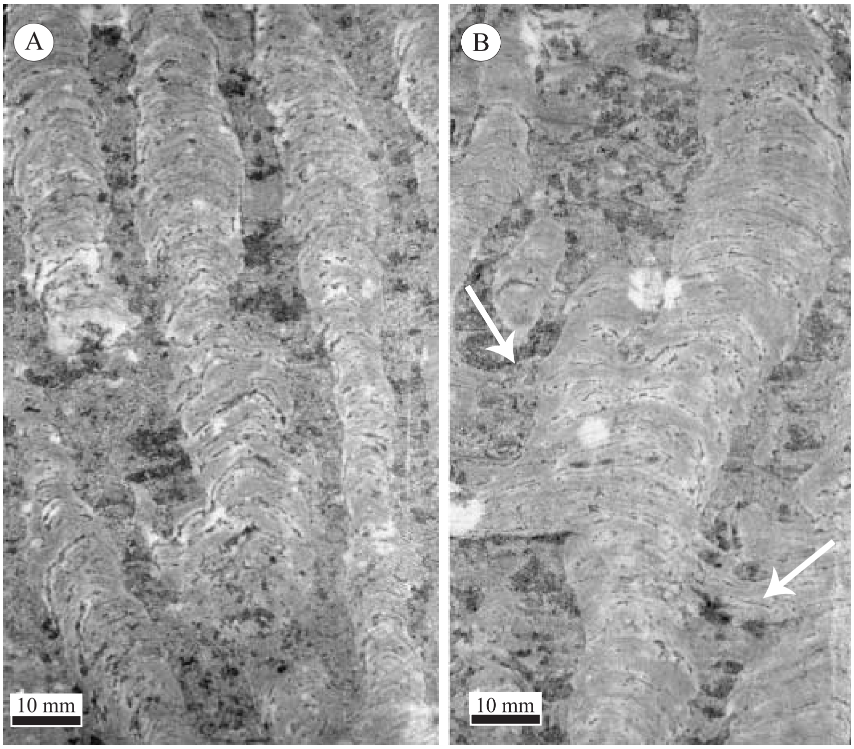

Fig. 9 Columnar section of the *Acaciella australica* bioherm from Browne Formation in GSWA Lancer1 drill core. (A) Upper part of the bioherm with non linking columns that maintain a continuous width. (B) Columns near the branching point, which have variable widths and common linkages and bridges. Example of a bridge is indicated by the arrow. Photos in reflected light (RL).

As previously noted, detrital material is locally abundant and forms a third type of lamina, which consists of detrital material showing a tendency to flatten upwards in scours and former topographic lows. The detrital material most commonly consists of silty or coarsely recrystallized dolomite with varying amounts of siliciclastic sediment, predominantly quartz grains. It is not clear whether the dolomite in the detrital laminae originated from preferential diagenesis or if the dolomite was transported in the detrital load. Higher depositional porosity in detrital lenses could have promoted preferential dolomitization. Further work, however, is needed to constrain the origin of the dolomite associated with detrital lenses.

DISCUSSION

This study has identified several sedimentological factors that are important in controlling stromatolite branching. The most obvious factor controlling the distribution of branching is the abundance of detrital sediment input. In all *A. australica* assemblage stromatolites examined, there is a much higher amount of detrital sediment in the fabric of the lower hemispheroidal stromatolite than in the overlying columns. This is clearly demonstrated at localities where detrital material contains siliciclastic grains. The regularity of sediment input also appears to have an effect on branching. The non-detrital laminae in the lower section of a bioherm are consistently intermixed with detrital material. In the middle section of a bioherm (upper part of the hemispheroid), several laminae develop before there is any significant detrital input. This suggests that the middle-undulatory and upper-columnar sections of the bioherm experienced more episodic sediment input along with reduced total sediment supply. This trend could also reflect differing rates of lamina growth. It appears that stromatolite branching takes place during a transition from high, regular sediment supply to low, irregular sediment input. Observations from this study on the link between sediment supply and branching are similar to trends observed in Mesoproterozoic stromatolites from the Belt Supergroup (Horodyski, 1977).

The variation in sedimentological regimen has a noticeable effect on lamina morphology. Many individual lamina appear to be reworked or disrupted and show little variance in mesostructure from the detrital material (Fig. 6). The lensoidal fabric in the lowermost section of bioherms developed under a high sedimentation rate and an apparently high-energy regime. In the lower and middle sections of the bioherms, small, lamina-scale topographies, created by localized upward growth, are covered and smoothed out by accumulation of detrital material. Branching in *A. australica* begins with a gentle increase in the convexity of the laminae until a stasis point is reached and column morphology becomes consistent. Distinguishable columns develop when the surface topography produced by lamina growth is not regularly covered by detrital sediment. The lateral continuity of laminae during the branching process provides compelling evidence that branching is a growth process and is not created by an extrinsic process, such

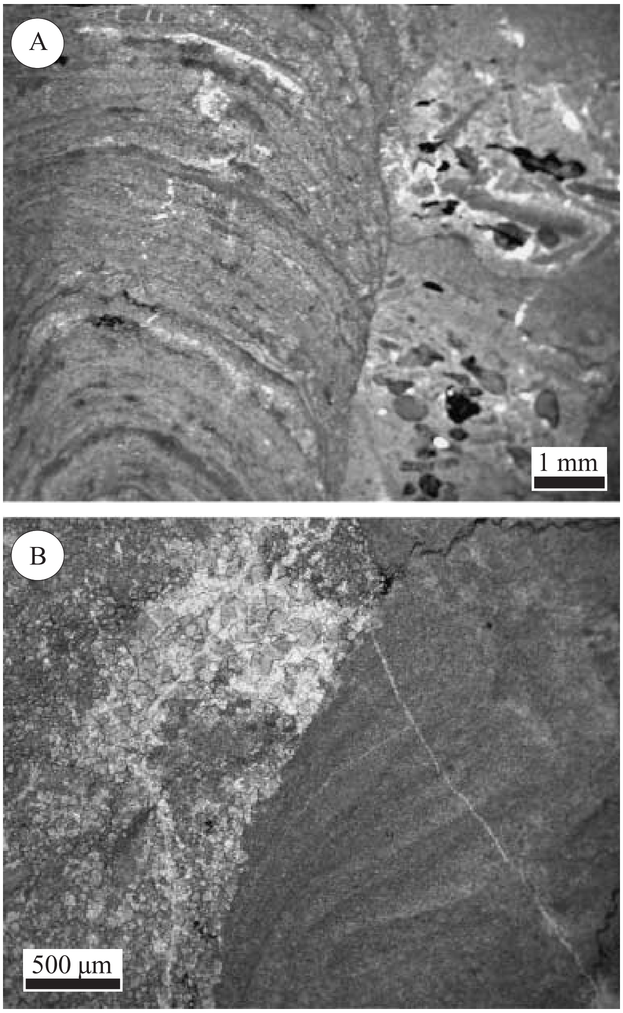

Fig. 10 (A) Microstructure of columnar section of *Acaciella australica* from the Skates Hills Formation, Skates Hills. (B) Microstructure of columnar section of *Inzeria intia* from Bitter Springs formation, Ross River area. Photos in plain polarized light (PPL).

as scouring, as was previously suggested for the *A. australica* assemblage stromatolites (Southgate, 1989). Once columns are established, column diameter remains constant, often over meter-scale vertical successions, implying that laminae growth and sedimentation are in near equilibrium.

As in modeling studies (Grotzinger & Knoll, 1999), changing stromatolite morphology can be largely explained through variation in the relative contributions of two basic parameters: upward growth and sedimentation. *A. australica* branching (α parallel branching) appears to develop when sedimentation decreases and ceases to fill in topographic lows while still allowing upward growth on the highs. High sediment input at the base of the *A. australica* bioherm smothers out any topography created by framework growth. *A. australica* branching therefore appears to be distinct from *Baicalia* branching morphologies, which may be related to increasing sedimentation rates (Dupraz *et al.*, 2006).

Shifts in sedimentological regimes within stromatolite bioherms are commonly linked to sea-level change. The shift from a hemispheroidal to columnar morphology in some of the bioherms examined in this study is linked with a shallowing-upward sequence (Southgate, 1989). A change in sea level could result in a dramatically different depositional environment and promote morphological change. Alternatively, the growth of the bioherm could promote a change in the amount of sediment available for stromatolite growth, which would also prompt a change in stromatolite morphology. In many of the *A. australica* assemblage bioherms, branching can be directly linked to changes in synoptic relief – that is, in the relief of the stromatolite above the seafloor. Many of the hemispheroids had at least a period during which relief was greater than a meter. It appears that as the stromatolites grew through *in situ* precipitation and developed higher levels of synoptic relief, less detrital sediment became incorporated. Stromatolite accretion can be assumed to have been directly responsible for the change in the amount of detrital sediment available for growth. Stromatolite accretion may be another process, besides the natural amplification of mirror irregularities (discussed in detail by Grotzinger & Knoll, 1999), that could lead to branching or dendritic structures without requiring exceptional conditions. An intrinsically promoted branching mechanism would produce considerable along-strike variation in the vertical progression of stromatolite morphologies. Such variation would not occur if morphological change was exclusively dictated by sea-level change. At the Ross River localities there are large along-strike variations in the vertical development of stromatolite morphologies.

The *A. australica* assemblage stromatolites have been used as a classic example of microbially controlled stromatolite growth (Walter, 1972; Southgate, 1989), but what specific role did the microbial community play in shaping stromatolite morphology? The predominance of gradational laminae, rich in finely particulate carbonaceous matter of probable biogenic origin, suggests accretion by a microbially mediated lamina. It is often possible to distinguish laminae produced by sedimentary processes from those produced as a result of biogenic activity by examining the nature of the laminar boundaries and the gradation and uniformity of the matrix within a lamina. Most sedimentary laminae observed in the field, as well as experimentally produced sedimentary laminae (Makse *et al.*, 1997) and modeled abiogenic stromatolite laminae (Grotzinger & Rothman, 1996; Grotzinger & Knoll, 1999), contain distinct lamination boundaries with sharp contacts. Laminations in numerous microbial mats, caused by minor changes in the abundance of organic material and microbial community stratification, are commonly gradational and have highly variable lamina boundaries (e.g. Monty, 1976). These laminar features are present in the *A. australica* assemblage stromatolites and are not found in thin-bedded sedimentary laminae at the same outcrops. Gradational, irregular lamination boundaries and laminations defined by varying levels of organic matter suggest microbial mediation, especially in the *A. australica* stromatolites, which have high levels of synoptic relief and laminations that formed through *in situ* precipitation.

There are few stromatolite morphologies that can be directly attributed to microbial growth. The thickening of laminae across a convexity peak, however, appears to be one feature that is difficult to explain through abiogenic processes (Grotzinger & Knoll, 1999; Batchelor *et al.*, 2004). Many *A. australica* assemblage columnar stromatolites display such crestal thickening (e.g. Fig. 8B), further suggesting microbial control on stromatolite morphology and accretion. No single feature by itself is diagnostic of a biogenic origin, but when these features are observed in combination and with a high degree of frequency, they usually indicate a biogenic origin. As noted above, the lack of any signs of lamina disruption and minimal amounts of coarse detrital material in the columnar and undulatory section of the bioherms suggests low levels of environmental, particularly sedimentological, control on stromatolite morphology.

By contrast, the lower part of a bioherm has high levels of fabric disruption and contains abundant detrital material. Micritic laminae that appear to have formed by microbially mediated precipitation display little variation from laminae composed of detrital material. There is no direct or indirect evidence for trapping and binding of the sediment. The high amounts of allochthonous material, however, suggest microbial stabilization. Colonization of a loose substrate by a microbial community would stabilize detrital material and, along with *in situ* precipitation, promote accretion of a structure with positive synoptic relief. Thus, a microbial community was involved in the accretion of the lower parts of the bioherms, but it does not appear to have had direct control over stromatolite morphology.

A gradation of microbial control over stromatolite morphology can be recognized in *A. australica* assemblage bioherms. Branching occurred as sediment supply decreased, as the environment became more stable, and as the microbial community began to have a stronger influence on stromatolite morphology. The tendency of microbially influenced micritic laminae to consistently form a convex hemispheroidal shape of similar dimensions resembles the tendency of some modern microbial mats to assume a consistent morphology (e.g. Golubic & Focke, 1978). Although microbial mat morphology can be controlled by intrinsic factors, such as the motility of the constructing microbial communities (e.g. Walter, 1976), external factors, such as currents and the underlying substrate, will also influence the morphology of the microbial mat. Factors such as nutrient levels, carbon dioxide partial pressures, and ambient carbonate chemistry will all affect microbial mat morphology. The style and timing of calcification acts as a final control on stromatolite morphology because it controls what features are preserved.

Further controlled studies on microbial mats similar to those of Shepard *et al.* (2005) are necessary to estimate the degrees to which intrinsic (notably individual bacterium motility and quorum sensing) and extrinsic factors (notably the ambient chemical conditions and energy regimen) affect microbial mat morphology. Currently, the importance that extrinsic (compared to intrinsic) factors have in controlling microbial mat morphology is not clear. However, because branch formation takes place in an interval of apparently undisturbed microbially mediated carbonate accretion, we interpret the ultimate control of the branching process to be essentially microbial. A branching process nearly identical to that described in this study has been interpreted as being essentially environmental (Grotzinger & Knoll, 1999, p. 342). The differing perspectives invite us to question whether much of the disagreement over the dominance of microbial or environmental factors in stromatolite formation is interpretive rather than substantive. Accordingly, the detailed description of *A. australica* stromatolites presented here provides an example of stromatolite morphology forming through the interplay of microbial and environmental factors.

CONCLUSIONS

There is a wide range of hypotheses about factors that control stromatolite morphology, but there are few detailed descriptive studies on stromatolites that allow proposed models to be tested. This study presents a detailed analysis of stromatolite morphology and branching in the *A. australica* Stromatolite assemblage from a variety of localities across Australia. At widely spaced geographical localities, the stromatolites in this assemblage show consistent patterns of gross morphology: the formation of narrow undisturbed columns from an underlying broad hemispheroid. There is consistently less detrital material integrated into the base of the *A. australica* stromatolites than is present in the upper columnar section. The amount of detrital material controls the levels of surface topography and, therefore, has a clear effect on stromatolite morphology. This study provides support from a specific group of fossil stromatolites for theoretical models that suggest that complex stromatolite morphologies can arise from variations in the relative contribution of sediment and stromatolite framework growth (Grotzinger & Knoll, 1999).

Description of stromatolite components has also allowed an estimate to be made on the level of microbial influence on stromatolite morphology. The microstructure, composition, and morphology of the micritic laminae suggest a strong microbial influence, particularly in the upper parts of bioherms where columnar bioherms grew in a stable environment. The change from a hemispheroidal to a columnar morphology composed almost exclusively of micritic laminae reflects a shift from a sedimentary control to a strong microbial control over stromatolite morphology. This study applies specifically to a group of Neoproterozoic stromatolites that are *c.* 0.85–0.8 billion years old. However, there are stromatolites throughout the Precambrian that show similar morphological patterns (e.g. Raaben *et al.*, 2001) and which may have been subject to similar shifting microbial and sedimentary controls of the stromatolites' morphology.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1. Sample identification, stratigraphic information and locality details.

Appendix S2. Full references for cited stromatolite taxa.

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