Stromatolite research in the Shark Bay World Heritage Area

L B COLLINS [1]* **& R J JAHNERT** [2]

[1] *Department of Applied Geology, Curtin University, GPO Box U1987, Perth 6845, Australia.*

[2] *Petrobras Company, Avenida Chile 65, Rio de Janeiro, 20031912, Brazil.*

* Corresponding author: ✉ L.Collins@curtin.edu.au

Three decades after declaration of World Heritage status for Shark Bay new research findings are being reported on the specialised microbial habitats that characterise its hypersaline settings, the composition of microbial communities, tidal flat evolution, stromatolite geochronology and subtidal microbial systems. In the stable, semiarid and evaporative setting within the intertidal–subtidal environment the microbial ecosystem is trapping, binding and biologically inducing carbonate precipitation within laminated stromatolites, non-laminated thrombolitic forms and cryptomicrobial non-laminated forms. Filamentous microbes constitute the dominant group in the blister, tufted and smooth mat types, and coccoid microbes dominate the pustular, colloform and microbial pavement deposit types. Detailed georeferenced substrate mapping has revealed extensive subtidal microbial deposits occupying ~300 km^2 of the total Holocene 1400 km^2 area of Hamelin Pool. The microbial pavement covers 227 km^2 of the subtidal substrate, which together with columnar structures reveals a subtidal microbial habitat that occupies an area several times larger than the area of the intertidal deposits. Oldest dated stromatolite heads are 1915 ^{14}C years BP, and the overall system was deposited in two stages: the first between 2000 and 1200 and the last from 900 years BP to the present. Slow accretion rates vary from less than 0.1 to 0.5 mm/year. Different internal fabrics were constructed according to their position in relation to the littoral zone by distinct microbial communities, and lateral fabric relations have been established. Evidence of shallowing-upward fabric sequences of microbial origin reflects relative falling sea levels during the late Holocene and is likely useful in ancient environmental interpretation. A new substrate map and depositional history for this distinctive microbial habitat has established the significance of subtidal structures and emphasises the geoscientific importance of Hamelin Pool, especially with respect to early life studies and ancient analogues for understanding microbial activity, deposit characteristics, fenestral fabrics and distribution.

KEYWORDS: **fabrics, geochronology, Holocene, microbial mats, stromatolites, subtidal microbialites.**

INTRODUCTION

Since the existence of stromatolites in Shark Bay first became known in the 1950s there has been a developing interest by researchers in characterising the systems in the unique hypersaline conditions of Hamelin Pool and adjacent embayments (Figure 1), by marine geoscientists, biologists and others. The progress of this work is briefly summarised by Jahnert & Collins (2012 pp. 1-3), Burne & Johnson (2012) and Playford *et al.* (2013).

The purpose of this paper is to summarise the key findings of geoscientific investigations during 2008–2012 that concentrated on several aspects considered important among the wide opportunities for investigations of what is a remarkable occurrence of hypersaline microbial systems. The research was partly driven by a need to broaden the database required for ongoing management of the microbial and related assets of the Hamelin Pool Marine Nature Reserve and nearby areas in the Shark Bay embayments. Some of the questions addressed concern the nature of microbial tidal flats in areas of reduced salinity; the distribution of microbial habitats, substrates and fabrics on the tidal flats of Hamelin Pool; the chronology of stromatolite development; and investigations of the subtidal microbial habitats in Hamelin Pool. This summary draws on

recently published detailed research accounts, particularly Jahnert & Collins (2011, 2012, 2013) and Jahnert *et al.* (2012).

METHODS

Regional mapping using remote sensing and ground-truth transects, shallow coring and sampling, and laboratory analysis were employed to map tidal flats, and marine embayments in order to document microbial habitats (Jahnert & Collins 2012, 2013).

Georeferenced maps were created using ESRI's ArcGIS, high resolution (50 cm/pixel) Shark Bay orthophotos and aerial photos (1:25 000 scale). A Multibeam survey was undertaken with the Department of Transport (DoT), Western Australia, focusing on the measurement of the depth and physical characteristics of the substrate along pre-defined transects. Submarine videos were recorded during marine investigations, and subtidal samples of microbial structures were collected in partnership with the Department of Conservation (now Department of Parks and Wildlife) which managed vessels and divers. A Differential Global Positioning System (DGPS) was used to record transect positions and high-resolution elevations (±5 cm) across tidal flats. Underwater videos were produced using drop-down video-camera, by diving or with cameras attached to the side of the vessel.

Figure 1 Hamelin Pool, L'Haridon Bight and Henri Freycinet embayment at Shark Bay, Western Australia. The image (from Geoscience Australia) shows the locations of Nilemah, Garden Point and Rocky Point.

Sampling involved limited collection of microbial heads from shallow depths by snorkelling and by scuba diving in the deeper portions. A taxonomic study of cyanobacteria was performed in the Microbiology Department at the Federal University of Rio de Janeiro, Brazil. Chemical analysis of microbial sediment and water samples involved X-ray fluorescence spectroscopy (XRF), inductively coupled plasma (ICP) optical emission and mass spectrometry, produced by Ultra Trace Analytical Laboratories, WA, and Petrobras S.A., Research Centre. ^{14}C ages were obtained by the Radiocarbon Dating Centre of the Australian National University. Carbon and oxygen isotopes from sediment samples were analysed by the Federal University of Sao Paulo (USP). X-ray diffraction (XRD) techniques were used to characterise the crystallographic structure and recognise mineralogical constituents of sediment, and were performed at Curtin University. Scanning electron microscopy (SEM) was conducted at Curtin University.

ENVIRONMENTAL AND GEOLOGICAL SETTING

The Shark Bay embayments (Figure 1) are situated on the central west coast of Australia, and are dominated by a semiarid setting and subtropical conditions which are favourable to carbonate secreting organisms and communities. Shark Bay Marine Park is separated into three major embayments: Freycinet, L'Haridon Bight and Hamelin Pool. Freycinet embayment in western Shark Bay maintains the best connection with northerly oceanic waters so that, despite the high evaporation, salinity is metahaline (40–56: Logan & Cebulski 1970). Hamelin Pool, the easterly embayment, has restricted oceanic water influx and hypersaline waters (56–70), and progressively decreases in salinity to the north towards the tidal exchange channels crossing Faure Barrier Bank. L'Haridon Bight embayment contains metahaline conditions in the north and hypersaline waters to the

south. Tidal flats bordering the Shark Bay embayments have low substrate gradients (20–150 cm/km) with shallow and restricted water circulation, resulting in hypersaline conditions and microbial deposits that are widespread as mats or small elongate structures and discrete columns.

Shark Bay has three distinct geomorphic provinces; a western limestone terrain (Edel Province) which includes Dirk Hartog Island; a central Peron Province with characteristic red dune terrain, and an eastern limestone terrain which comprises the hinterland, the Toolonga Province. The geographic features of Shark Bay are controlled tectonically by a regional normal fault system of north–south orientation which intersects a north-northwest–south-southeast oriented fold system responsible for confining the bays to the subsiding tidal-channel, tidal-flat, storm-beach and beach-ridge environments (Hocking *et al.* 1987). Two pre-Holocene marine transgressions are recorded. The Bibra Limestone ('Bibra Formation' of Logan *et al.* 1970; amended by van de Graaff *et al.* 1983), formed during the Bibra marine phase, is estimated to have been deposited during the last Pleistocene interglacial (MIS 5e) high sea-level stand at 120–130ka (van de Graaff *et al.* 1983; Hocking *et al.* 1987).

The Holocene sedimentary sequence was subdivided into five sedimentary units, based on their lithological variation, vertical and lateral relations and mapability: (i) Hamelin Coquina; (ii) Intertidal Veneer; (iii) Sublittoral Sheet; (iv) Bank Unit; and (v) Basal Sheet, which is located on the embayment plain (Logan *et al.* 1974b), where water depth is 10 m maximum. These sediments are dominantly organosedimentary in character and lithotypes in the peritidal zone can be broadly categorised into either microbialites or coquinites. The microbialites have been examined in many studies (Logan 1961, 1968; Davies 1970a, b; Playford & Cockbain 1976; Playford 1979, 1990; Logan *et al.* 1970, 1974b; Burne & James 1986; Burne & Moore 1987; Burne 1992; Burns *et al.* 2004; Dupraz & Visscher 2005; Reid *et al.* 2003; Papineau *et al.* 2005; Burne & Johnson 2012; Jahnert & Collins 2011, 2012, 2013). The most recent review of the Shark Bay microbialites demonstrates that they exist in the form of subtidal pavements, subtidal microbial lithoherms of varying morphotypes and intertidal mats (Jahnert & Collins 2011, 2012, 2013). Their distribution is extensive, occupying nearly half the benthic substrate of Hamelin Pool (Jahnert & Collins 2011, 2012, 2013).

Shark Bay's recent geological past is characterised by three distinct marine transgressions, during the last part of the Quaternary as part of glaciation/deglaciation climate changes (Logan *et al.* 1974b; Jahnert & Collins 2011, 2012). These events are preserved in marine carbonate sequences that outcrop along the Shark Bay shoreline (O'Leary *et al.* 2008). The three drowning events correlate well with the polar ice core records and represent a 100 000 year frequency signal of advance and retreat of the sea. Slowly falling sea level (regression of 2 m) over the last 6000 years has been an important control on salinity increase, decline of seagrass banks (with the exception of the Faure Sill in the metahaline northern Hamelin Pool), stromatolite and tidal flat development, as well as basinward growth (progradation) of coquina coastal ridge systems (Jahnert *et al.* 2012). The spectacular

stromatolite occurrences seen on intertidal surfaces in coastal settings have largely been stranded as sea level has declined, so that subtidal stromatolites (at depths 0–7 m below LWL) comprise much of the present-day microbial habitat.

RESULTS

Tidal flats in contrasting salinity settings

In a comparative study of tidal flat evolution in Shark Bay, three tidal flats (Figure 1) from contrasting salinity settings were evaluated (Jahnert & Collins 2013) to assess the role that salinity has played in their evolution, and to describe any contrasting characteristics in microbial mat and stromatolite occurrence and distribution. Hamelin Pool is a hypersaline embayment surrounded by extensive tidal flats: Gladstone, Hutchinson and the study site at Nilemah. Other nearby tidal flats located in L'Haridon Bight (transitional between hypersaline and metahaline conditions) and Henri Freycinet embayment (metahaline) are Rocky Point and Garden Point, respectively; these were also colonised by microbial communities, but under slightly different environmental conditions and timing. Whereas Nilemah is a north-facing embayment marginal to the Hamelin basin, both Garden and Rocky Point tidal flats are semi-isolated from their embayment waters by coquina barrier ridges.

Falling sea levels during the late Holocene led to establishment of coquina barriers and development of small, semi-barred tidal flats at various sites in the Shark Bay embayments, and establishment of areas suitable for microbial communities (Figures 1, 2). Such spit ridge accretion is usually controlled by south to north wind-driven longshore currents for north–south oriented shorelines which dominate the embayments, but tidally constructed ridges often develop with north to south orientation, depending on coastal facing. The north-facing Nilemah embayment is partially enclosed by storm ridges with southwest and southeast transport directions on opposite shorelines. A combination of shallow conditions, low gradients (frequently 20 cm/km) and microtidal conditions controls the development of elevated salinities favourable for microbial colonisation in these settings.

The tidal flat environment has been colonised by microbial communities specialised in surviving at specific water depths, where a delicate balance between tidal energy, waves, exposure time and water depth results in accretion or erosion (Logan *et al.* 1974a, b) (Figure 3). Low water energy associated with high evaporation rates, sediment pattern and space creation are the key elements for sediment accretion in Shark Bay. Bacteria take advantage of diurnal tidal currents and waves that slowly cover the very flat area, supplying sediments and a habitat for microbes that are still adapting and expanding, producing carbonate by trapping and binding particles, biologically inducing carbonate precipitation and being lithified by aragonite cement. Cyclic tidal fluctuations also play a part in microbial distribution.

Hot summer temperatures (around 40°C) and strong southerly winds (40 km/h) force water out of the tidal
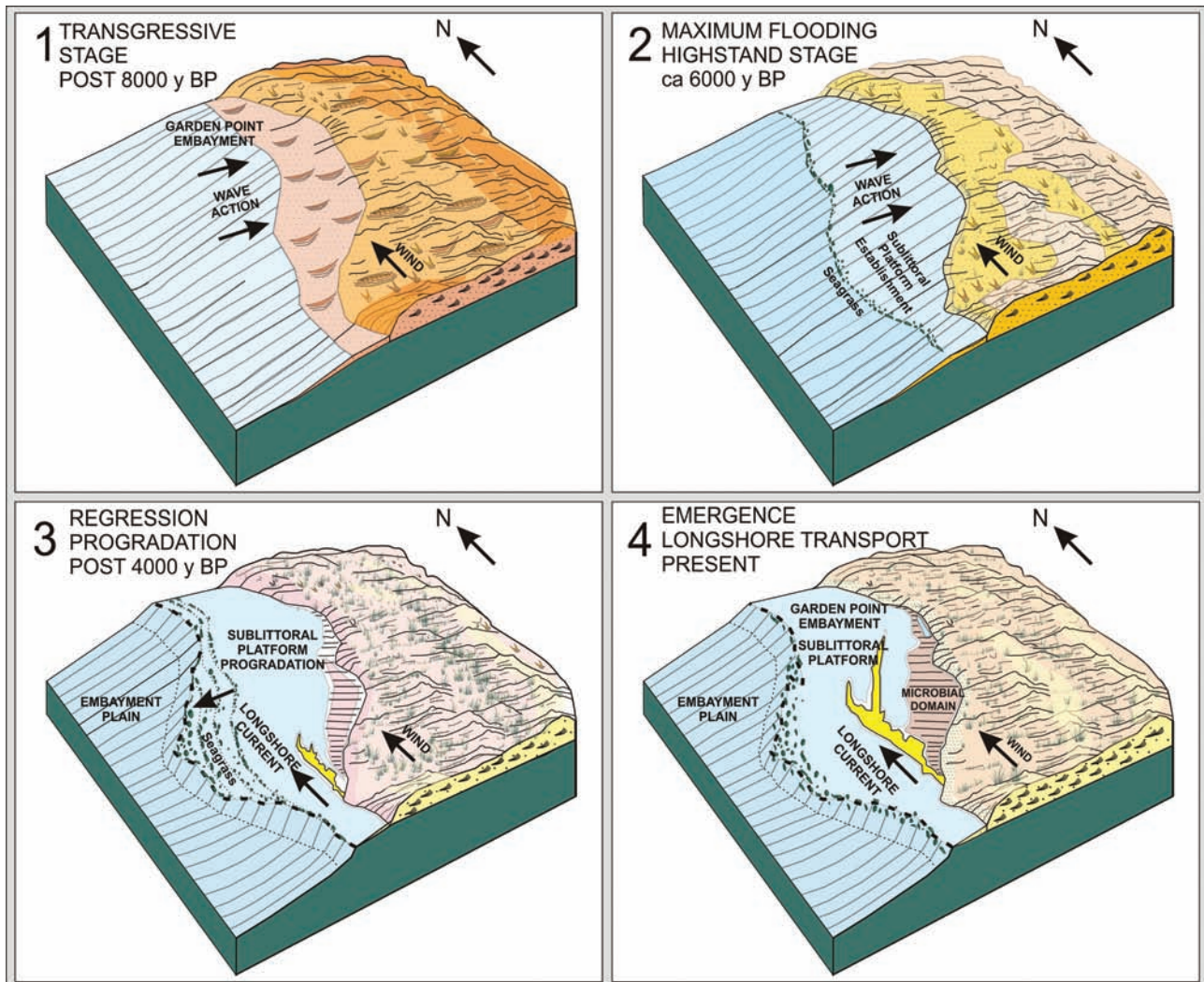
Figure 2 Morphological evolution proposed for the Garden Point embayment. Storm-wave activity was very important during the initial phase, while longshore currents, winds and tides were the morphological drivers during the late stages. Microbial activity started near 2300 years during the fall in sea level. (Jahnert & Collins 2013 figure 5).

flats, causing large areal exposure and desiccation of microbial deposits (pustular mainly), which shed globules of dead microbial mats. The distribution of sediments and microbial types on tidal flats such as at Garden Point reveals a sediment veneer made of carbonate, reflecting recent microbial activity within an environment that is frequently adapting to new conditions.

Six different microbial deposit types were recognised (Figure 4), mapped and sampled. Principal development and occurrence of mats is concentrated in the intertidal zone at Garden and Rocky Point and as additional microbial structures at Nilemah in the subtidal zone (Jahnert & Collins 2013). The supratidal zone does not preserve or generate extensive mats due to strong erosional processes, constant sediment movement and adverse conditions of temperature. Where bacteria survive it is in detached sites receiving a sporadic high-wind-driven water supply or abnormal tides. Microbial deposits in those sites are film and blister mats. Film mats are a black veneer normally covering lithified

surfaces exposed to the sun for long periods of time and belong to a novel type of halophilic archaeon, *Halococcus hamelinensis* sp. (Goh *et al*. 2006; Goh 2007).

Tufted mats occur in the upper intertidal zone, growing in scallops due to long filaments made by *Lyngbya* (Hoffman 1976) that exploit the ability to avoid direct contact with the ground and may block water and sediment inside the created relief. This mat normally develops over shallow muddy substrate where sediment maintains humidity landward of the pustular mat type. The intertidal zone is the growth domain of pustular mat spread as brown dark sheets of small bushes, inhabiting the upper intertidal to the upper subtidal zone. To construct a detailed map (Jahnert & Collins 2013), the term mini-pustular was introduced to refer to small bushes or pustules <1 cm in height and diameter. Pustular mats in the intertidal zone normally reach 3 cm high and >1 cm in bush diameter. In the upper subtidal zone, the high rate of peloid deposition discourages pustular growth that is still small in size (<1 cm high) and sparse, such as mini-pustular mat.
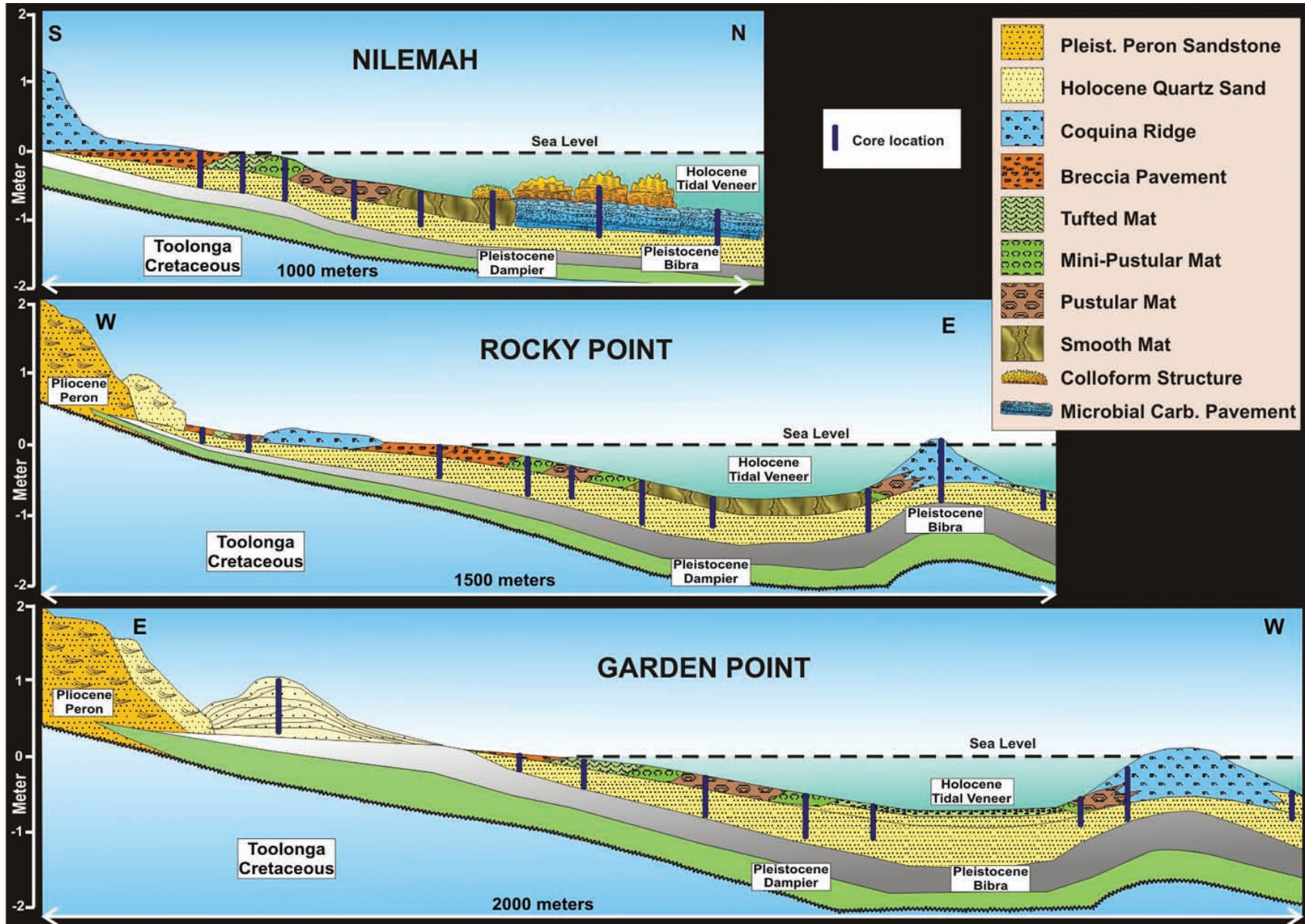
Figure 3 Cross-section of the three tidal flats showing sediment diversity and organofacies distribution and regional stratigraphy for each tidal flat. Pre-Holocene stratigraphy inferred from data in Logan *et al*. 1974b. (Jahnert & Collins 2013 figure 6).
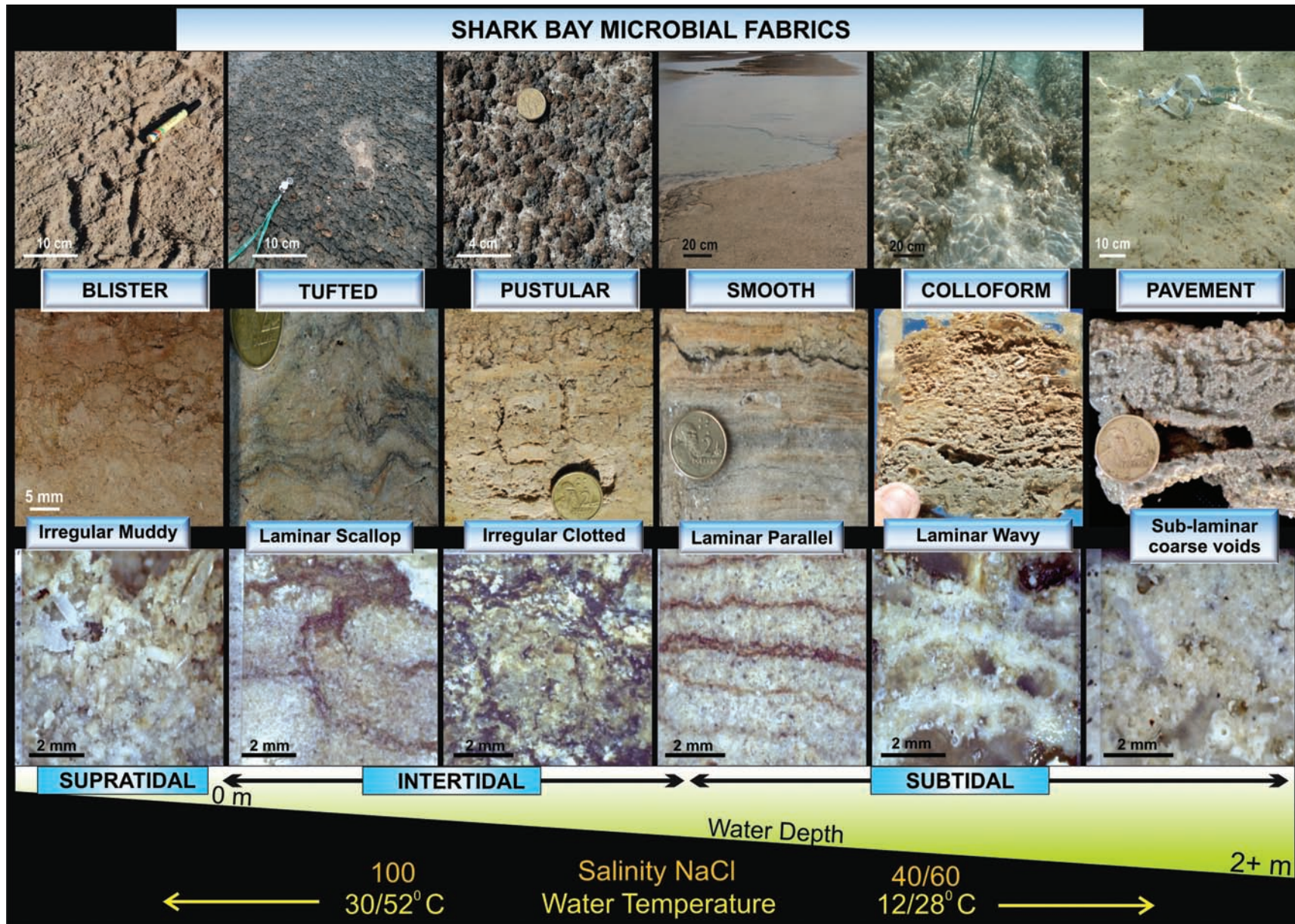
Figure 4 Summary of the principal fabrics and external aspects of the microbial deposits for Nilemah, Rocky and Garden Point tidal flats (coin is 20.5 mm in diameter). (Jahnert & Collins 2013 figure 13).

In the upper subtidal zone, different bacteria such as *Schizothrix friesii* and *Microcoleus* produce a smooth mat composed of fine carbonate grains placed between vertical bacterial filaments that are able to permeate and trap sediments and produce laminar stromatolite fabrics. Garden Point includes a proximal pond where, in very calm water rich in sediment particles, a set of coarse laminar smooth microbial mats has developed. However, Garden Point, in contrast to the other tidal flats, is in the initial phases of establishing bacteria, and only the proximal substrate portion of the subtidal zone is colonised.

In the subtidal zone of Nilemah tidal flat, seaward of the smooth mat terrain, colloform microbial deposits (-0.5 to -1.5 m) develop as elongate structures followed by a tabular microbial carbonate pavement extending to deep subtidal zones (-1.0 to -6.0 m).

The improved knowledge of the nature and distribution of the tidal flat microbial deposits is documented in georeferenced maps (Jahnert & Collins 2013) of the sediments and organodeposits of Garden and Rocky Points. These are characterised by relatively extensive and prolific microbial activity during the last 2300 years, producing microbialites that are exposed in the supratidal zone. These are now subject to erosion, and are progressively colonising the subtidal zone as a consequence of sea level fall, although observations of recolonisation in the intertidal zone provides evidence of a recent short marine transgression (Jahnert & Collins 2013).

TAXONOMIC STUDIES

A taxonomic and phylogenic grouping was established based on microscopic characteristics of the dominant cyanobacteria on the surface of microbial mats or structures (Figure 5) (Jahnert & Collins 2013). Bacterial communities are responsible for the external and internal colours and morphologies of organosedimentary deposits. Sixteen species of cyanobacteria were identified. Ten species that belong to the Class Cyanophyceae, Order Chroococcales, live in coccoid colonies and have small spherical to oval forms arranged in envelopes of jelly-like mucilage, normally yellow to dark orange in colour. Another six species belong to the Class Hormogonae, Order Oscillatoriales; these filamentous bacteria with elongate formats are often surrounded by a sheath that contains many individual cells with colours ranging from dark green to light green and blue. Filamentous bacteria are the dominant group, producing blister mats (*Microcoleus chthonoplastes*), tufted mats (*Lyngbya aestuarii*, *L. fragilis* and *Phormidium willei*) and smooth mats (*Schizothrix friesii* and *Microcoleus chthonoplastes*).
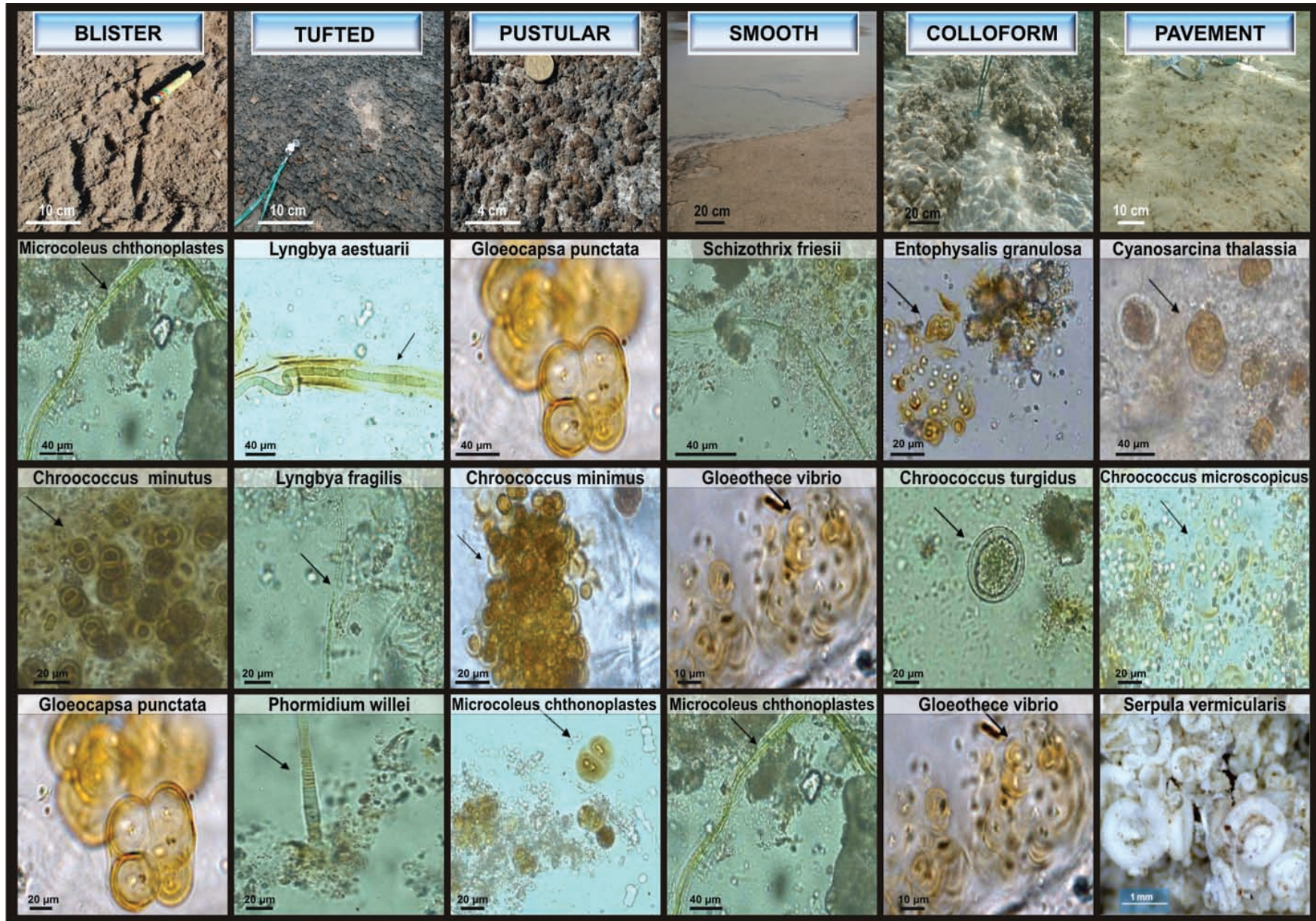
Coccoid bacteria dominate the pustular mats (*Gloeocapsa punctata*, *Chroococcus minimus*, *Entophysalis granulosa*), colloform deposits (*Entophysalis granulosa*, *Chroococcus turgidus*, *Gloeothece vibrio*) and microbial pavement (*Cyanosarcina thalassia*, *Chroococcus microscopicus*, *Entophysalis conferta*). Diatoms including *Navicula* were identified in samples from smooth, colloform and microbial pavement, but despite the thick mucilage around the diatom cells, colonies of bacteria have been seen inside the extracellular polymeric secretions (EPS), and the process of organomineralisation appears to be driven by the bacteria even in diatom domains.

COMPARATIVE EVOLUTION

Table 1 is a summary of the contrasting properties of microbial mats and sediments within the three tidal flats studied (Jahnert & Collins 2013). While the intertidal microbial systems are similar, the destructive effects of bioturbation are more evident at Garden and Rocky Point

Table 1 Comparison between tidal flats, water salinity and the contrasting properties of microbial mats and sediments within the littoral zones (Jahnert & Collins 2013 table 1).

| Tidal flat	Water salinity	Contrasting properties
Garden Point	Metahaline to hypersaline	Microbial mats: pustular mat dominance; smooth mat only in restricted pond. Microbial sediments: carbonate veneer (30 cm max.) with significant influx of quartz sand. Subtidal zone: bioclastic-quartz sand sheets (proximal) and bioclastic seagrass banks (distal). Bioturbation: disturbs and reworks microbial mats. Sediment isotopes: concentrate in less positive values of $\delta^{13}C$ (+3.4 to +5.2) and $\delta^{18}O$ (+2.0 to +3.6) Onset of hypersalinity: coquina storm deposits dated ^{14}C 2050–2150 (±35 years)
Rocky Point	Metahaline to hypersaline	Microbial mats: pustular mat domain intertidal zone and smooth mat in subtidal zone. Microbial sediments: carbonate veneer (50 cm max.) with influx of quartz sand. Subtidal zone: smooth mat (proximal) and bioclastic seagrass banks (distal). Bioturbation: disturbs and reworks microbial mats. Sediment isotopes: concentrate in intermediate values of $\delta^{13}C$ (+3.6 to +5.3) and $\delta^{18}O$ (+2.5 to +3.8) Onset of hypersalinity: coquina storm deposits dated ^{14}C 2420, 2830 and 3160 (±35 years)
Nilemah	Hypersaline	Microbial mats: pustular mat domain intertidal and smooth, colloform and pavement in subtidal zone. Microbial sediments: carbonate layer (1.30 m max.) and low influx of quartz sand. Subtidal zone: smooth, colloform structures and microbial pavement widespread. Bioturbation: limited by hypersalinity. Sediment isotopes: concentrate in more positive values of $\delta^{13}C$ (+4.0 to +5.9) and $\delta^{18}O$ (+3.0 to +3.9) Onset of hypersalinity: coquina storm deposits dated ^{14}C 4630 (±35 years)

Figure 5 Principal microbial deposits and dominant microbial species. Filamentous bacteria dominate the blister, tufted and smooth mat environment and coccoid bacteria dominate the pustular, colloform and microbial pavement. (Jahnert & Collins 2013 figure 17).

than at Nilemah. Also, the subtidal smooth mats give way to seagrass banks offshore, whereas in the hypersaline Nilemah subtidal zone, colloform stromatolites and lithified bioclastic microbial pavement are widespread. The onset and duration of elevated salinities appears to be the driving mechanism for these differences. There is a chronological progression in the ^{14}C age of coquina beach ridges from the least saline to the most saline conditions such that Garden and Rocky Point are relatively youthful, which likely explains the retention of seagrass banks, frequency of bioturbation, and lack of subtidal microbialites relative to the older, more hypersaline Nilemah embayment.

Hamelin Pool substrates and microbial distribution

Whilst previous research has documented specific tidal flats and localised features, the opportunity for a wider mapping of microbial substrates arose from the need for regional data for World Heritage management. The microbial systems and related sediments of Hamelin Pool were mapped (Figure 6) using high-resolution orthophotos, GIS and supporting terrestrial and submarine ground truth information, and classified according to their regional occurrence and distribution within the hinterland, supratidal, intertidal and subtidal domains (Jahnert & Collins 2012) (Figure 7). More
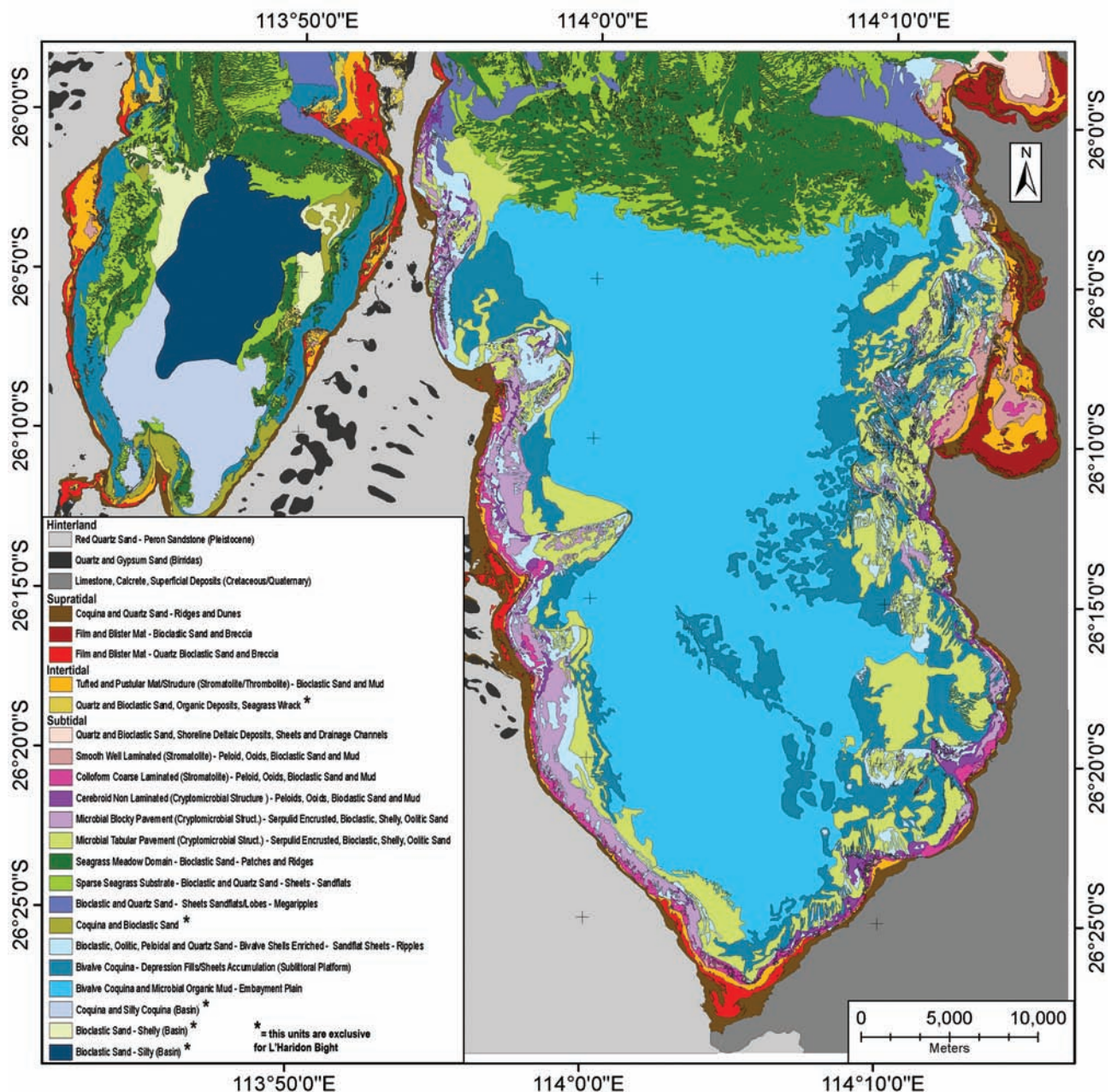
Figure 6 Hamelin Pool and L'Haridon Bight georeferenced sedimentary and organosubstrate map based on numerous coastal and marine ground truth traverses, video transects, aerial surveys, samples and interpretation of digital orthophotos.
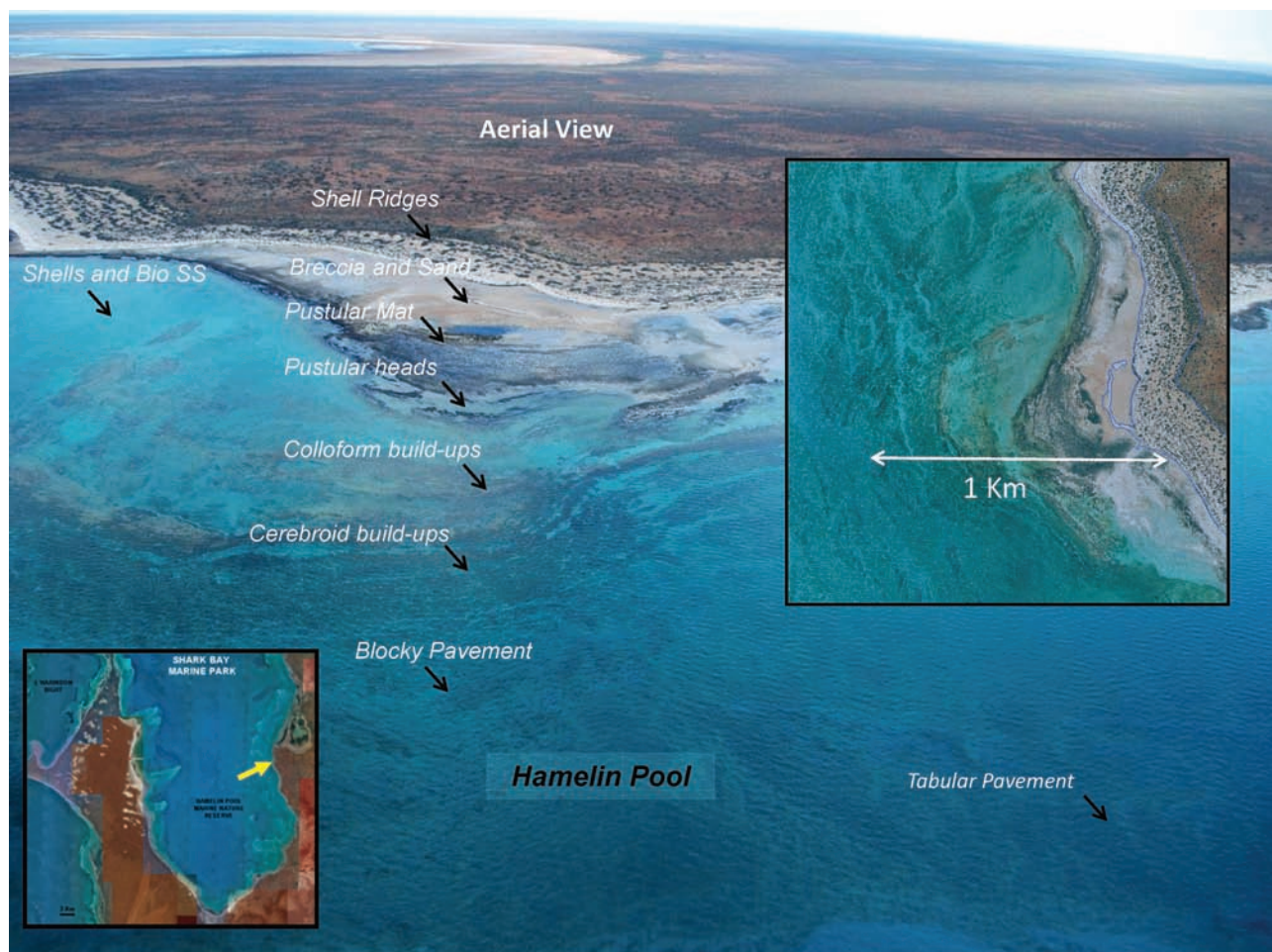
Figure 7 Hamelin Pool microbial substrates.

recently mapping has been extended to cover L'Haridon Bight to the west of Hamelin Pool.

Hinterland deposits are composed of quartz sandstone (Peron Sandstone) that comprises most of the embayment margins. The Peron Sandstone is an eolian Pliocene–Pleistocene deposit generated during glacial phases (Butcher *et al*. 1984). Interdune depressions contain spherical and ellipsoidal depositional basins consisting of granular gypsum and quartz sediment fills, termed birridas. The eastern Hamelin embayment hinterland is dominated by limestone of the Toolonga Calcilutite (Cretaceous) and superficial Quaternary cover that includes calcrete, quartz sand, laterite, alluvial and colluvial deposits. The eastern flank also contains emergent shoals composed of oolitic limestones of the Carbla Oolite (Pleistocene) expressed as elongate bodies parallel to the paleoshoreline which is to landward of the present shoreline.

The supratidal zone is influenced by storms and abnormal tides and thus often exposed to erosional processes. Microbes survive in topographic lows and local depressions as detached sites of ephemeral mats which are only sporadically wet. These microbes are adapted to survive in high substrate temperatures and grow in blister, tuft or pinnacle forms. The supratidal

zone in Hamelin Pool occupies nearly 80 km², and contains two organosedimentary units which are exposed and prograding seaward, as described below.

The Hamelin Coquina, the upper unit of the Holocene system, is a supratidal beach ridge system which overlies thin Pleistocene units and the Pleistocene Bibra Formation and, as a consequence of sea level fall (Logan *et al*. 1974b), prograles toward the centre of the embayment over Holocene supratidal microbial deposits, as shore-parallel ridges above the normal spring high tide level. Bioclastic-oolitic/quartz sand and breccia occupy extensive areas between the coquina deposits and the area reached by normal tides. Breccia pavements (Figure 8H) occur as lithified crusts that developed over older microbial pavements and heads, generated by processes that include desiccation, cementation and disruption by gypsum crystallisation (Logan *et al*. 1974a, b).

Supratidal areas are the domain of film and blister microbial mats. Film mat refers to a black veneer that covers breccia clasts and lithified exposed material in sites that may have a connection with underground water or sites that receive any kind of water spray. Blister mats develop in flat muddy substrates that receive sporadic flooding and maintain humidity.

Intertidal organosediments occupy a relatively small area (22 km²) and accommodate extensive microbial mats and heads in shallow waters. The intertidal is a domain of pustular and tufted microbial deposits. Pustular mats spread as brown dark sheets of small colonies, inhabiting the upper intertidal to the upper subtidal zone and, depending on the substrate gradient, develop mats, ridge-rill or subspherical structures. Tufted mat occurs in the upper intertidal zone, growing in scallops that accumulate water and sediment within the created relief. Tufted mat normally develops over shallow muddy substrate, usually landward of pustular deposits.

Subtidal microbial deposits are extensive, occupying an area of ~300 km² of the total Holocene 1400 km² area of the Hamelin Pool Marine Reserve. Subtidal microbial deposits that grow as structures cover 54 km². Subtidal deposits were classified according to their actual microbial superficial dominance, although many structures were partially constructed in different conditions of sea level presenting internally different fabrics. Areas of Hamelin Pool lacking microbial carbonates are dominated by seagrass and related bioclastic and quartz sand, particularly located near the Faure Bank to the north of the embayment, and bivalve coquina, serpulids and algae with a superficial veneer of organic rich material spread over the 'Embayment Plain'. Mobile sheets of bioclastic and quartz sand occur in areas affected by strong tidal currents, such as the sublittoral platform and over the Faure Bank. The biosedimentary subtidal deposits (Jahnert & Collins 2011) are summarised below.

Laminated microbial smooth stromatolites composed of beige flat surfaces, occur as mats and buildups with internal fabric composed of flat subhorizontal millimetric laminae of fine-grained carbonate sediment interbedded with laminae of microbial organic matter, lithified as micrite laminae. Laminated microbial colloform stromatolites construct buildups of brown/yellow colours externally composed of small (1–5 cm) hemispherical globular shapes rich in fine-grained peloids. Internal layers are composed of ooids/peloids that alternate with thin laminae of lithified micrite generating a coarse laminoid wavy internal fabric with subhorizontal elongate voids. Non-laminated cryptomicrobial cerebroid structures are the deepest subtidal buildups growing as domical, ridge-like or prismatic elongate morphologies of white to cream colours. Cerebroid structures contain superficial cavities with coarse grains/fragments and are often bored by bivalves. Patches of micrite are sparse in a bioclastic/oolitic sediment rich in bivalve shells, serpulids and colonised by algae.

Cryptomicrobial tabular pavement occurs as flat substrates which are being lithified as bioclastic grainstone and includes *Fragum* serpulids, micro-gastropods, foraminifera and algae. Cryptomicrobial blocky pavement is similar to the facies described above but is disrupted/reworked producing partially to wholly disconnected blocks, rich in *Fragum* bivalve shells and colonised by serpulids along basal surfaces.

Bioclastic/oolitic/peloidal sand occurs in the sublittoral region as a result of longshore currents and storm activity producing sand-floored depressions adjacent to microbial deposits. Bivalve coquinas constitute extensive deposits of *Fragum* bivalve shells, which inhabit the

sublittoral platform waters between -1.5 and -6 m. Bivalve shells are abundant in Hamelin Pool. Some of the disarticulated shells are swept into deeper portions of the bay, others fill depressions as gravel and a large number are transported shorewards and deposited in the supratidal zone by storms as exposed beach ridges. Bioclastic sand with variable quartz content comprises the substrate of seagrass domain in channels, patches or as ridges oriented east–west perpendicular to the tidal action. Bioclastic and quartz sand occurs in substrates colonised by seagrass but in disconnected sparse stands such as those found over Faure Bank, and bioclastic and quartz sand also occurs in shallow areas to the north on the Faure Bank where tidal velocity is amplified constructing channel lags, channel bars, subtidal deltas, and sand sheets with sand waves and megaripples. Bivalve coquinas with serpulids, algae and a superficial organic mud dominate the deeper portions in the Embayment Plain.

MICROBIALITES AND INTERNAL FABRICS

Distinct internal fabrics result from microbial processes of trapping and binding, microbially-induced carbonate precipitation, organic matter content, amount and type of sediment input, presence of voids, presence of skeletons, bioturbation and macropore orientation. Subtidal microbial carbonate deposits are designated as pustular, smooth, colloform, cerebroid and microbial pavement (Figures 8, 9). They have distinct internal fabrics, related to the dominant microbial communities (Burns *et al*. 2004; Allen *et al*. 2009; Jahnert & Collins 2012), their growth habits and environmental conditions.

Coccoid bacteria dominate the intertidal environment constructing pustular deposits with non-laminated clotted fabric and are appropriately designated thrombolite (Logan *et al*. 1974a p. 185). Coccoid bacteria also dominate the deep subtidal zone in colloform, cerebroid and microbial pavement, here producing coarse laminated stromatolites in colloform deposits and cryptomicrobial non-laminated carbonate in cerebroid and microbial pavement. Filamentous bacteria are the dominant group in smooth mats and heads in the subtidal zone producing carbonate structures with a fine laminoid fabric and characterised as stromatolite.

The organic matter that constitutes a considerable portion of the sedimentary fabrics is strongly modified when exposed to desiccation and oxidation, mainly by creating volumetric space, producing fenestral porosity (Logan *et al*. 1974a). In many cases, fenestral fabrics remain well preserved in the geologic record and are a distinctive characteristic of many rock sequences and their environments (Riding 1991; Walter 1999; Grammer *et al*. 2004).

Sediment of microbial origin (90 samples) from supratidal to subtidal zones submitted to mineralogic analysis by XRD revealed a predominance of aragonite in the carbonate fraction of 80–98%. Minor amounts of Mg-calcite and calcite and rare dolomite comprise the other carbonate minerals. Quartz is variable (10–40%) and higher in samples from the south and west of Hamelin Pool reflecting its proximity to the Peron Sandstone. Halite is minor (1–10%) and gypsum only occurs in supratidal samples (1–10%).
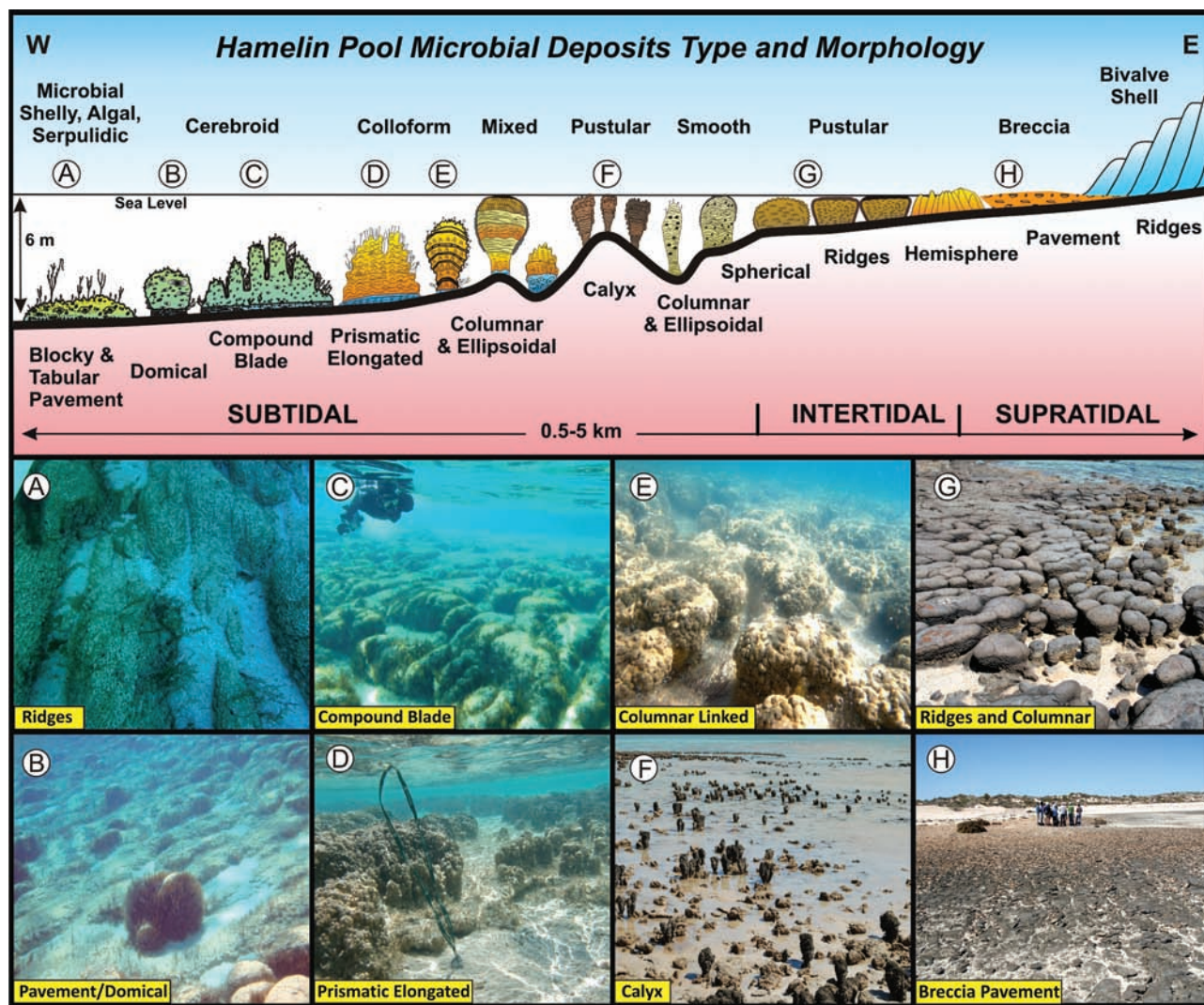
Figure 8 Schematic depositional model for microbial deposits in Hamelin Pool highlighting the distribution, characteristics and morphologies according to the tidal zones. (Jahnert & Collins 2012 figure 5).

Stable isotopes of $\delta^{13}C$ and $\delta^{18}O$ obtained from subtidal microbial carbonate sediment (12 samples) revealed positive values of carbon and oxygen isotopes. The overall $\delta^{13}C$ values vary between +4.46 and +5.88 while the $\delta^{18}O$ varies from +3.06 to +3.88. Smooth and colloform carbonates display the highest $\delta^{13}C$ values (+5.41, +5.67, +5.72 and +5.88). The isotopic relationships suggest that all the samples were deposited in a highly evaporative environment with extensive microbial activity.

GEOCHRONOLOGY

Nine microbial heads were analysed to determine ages and obtain growth rates. The sampling involved a careful selection of heads, collected, as far as possible, to cover the different microbial buildups occurring from the supratidal zone (head 1) to the subtidal zone in water depth of 4 m (head 9). The samples were projected onto a regional single transect (Figure 10) in order to permit a comparison between ages, depths, external morphologies and sizes.

The selected microbial structures display different external morphologies, from columnar to domical and tabular (Figure 10) with external surfaces tending to dark colours in pustular and over shallow-water domains, presumably because of the microbial pigments present. Structures are predominantly composed of carbonate grains, bioclasts and micrite arranged in different fabrics, which likely represent the prevailing conditions at the time and so furnish an evolutionary chronological history when ^{14}C dated. Bivalve shells and other visible coarse skeletal bioclasts (that could contaminate ages) were removed from samples subjected to ^{14}C dating analysis. The samples were composed mostly of fine carbonate particles (mud and silt size), sampled at the top, middle and base of the heads, when possible, to establish a trendline of growth rates.

The high resolution ^{14}C dating age values (Figure 10) for this collection are substantially older (1915–1680 years BP) when compared with the results obtained by Chivas *et al*. (1990), who recognised the interval of 1250–1000 years BP as the time of growth of the first stromatolites. Evidence of an earlier higher sea level than at present can be seen in head 1 (Figure 10) aged 1680 (base), 1300
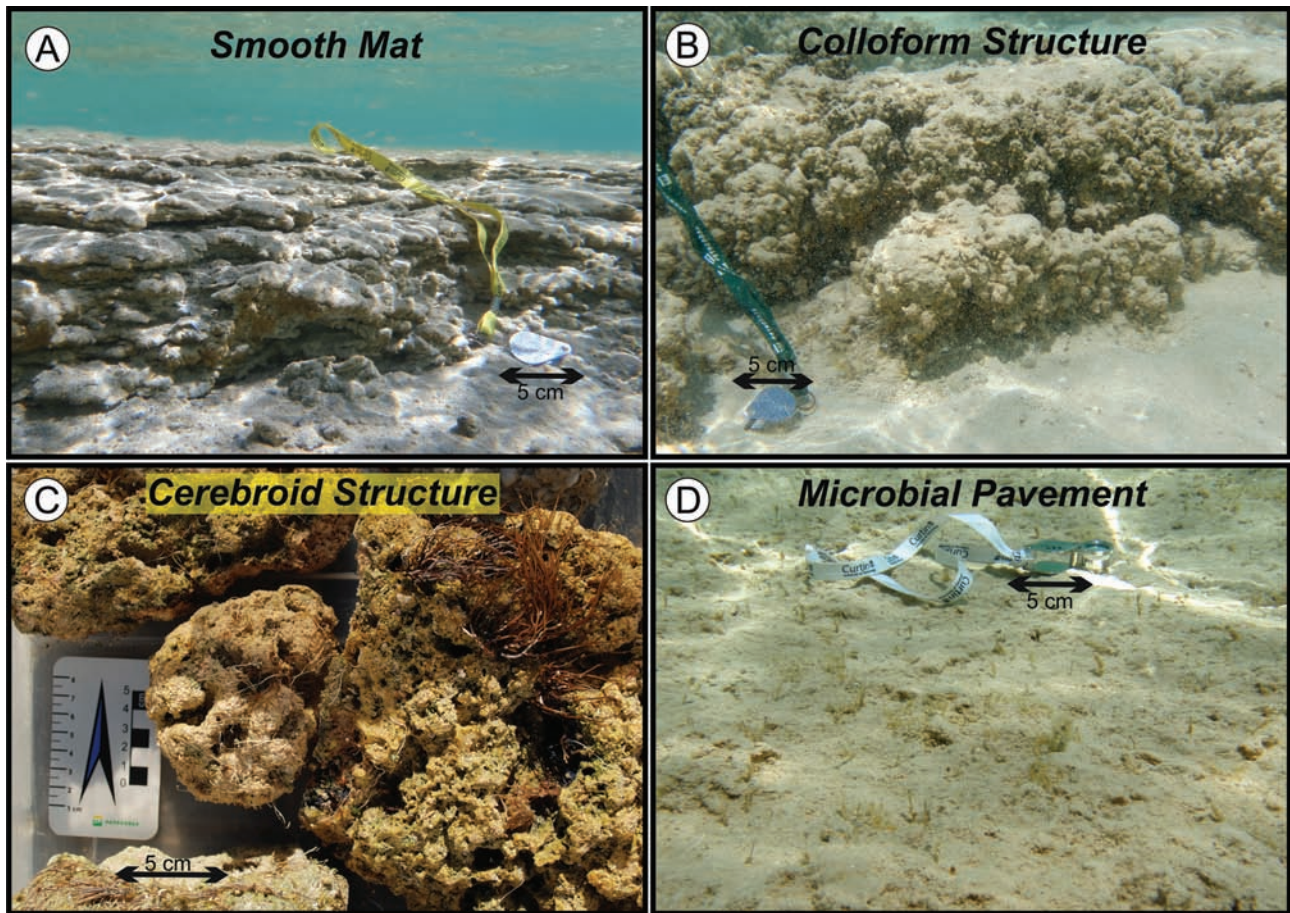
Figure 9 Principal microbial deposits and their external characteristics. (A) Well developed laminar fabric in smooth mat. (B) Colloform structures, external view (globular appearance; rich in fine carbonate particles). (C) Cerebroid structure; note convoluted external form with cavities, and algal ornamentation. (D) Microbial pavement; flat, lithified bioclastic carbonate with abundant bivalve shells, serpulids and soft-bodied algae. Sediment of microbial origin (90 samples) from supratidal to subtidal zones submitted to mineralogical analysis by XRD revealed a predominance of aragonite (80–98%) in the carbonate fraction. Minor amounts of Mg-calcite and calcite and rare dolomite comprise the other carbonate minerals. Quartz is variable (10–40%) and higher in samples from the south and west of Hamelin Pool reflecting Peron Sandstone proximity. Halite is minor (1–10%) and gypsum only occurs in supratidal samples (1–10%). (Jahnert & Collins 2012 figure 9).

and 1120 (top) years, located today in the supratidal zone, exposed 30 cm above mean sea level. Externally it has a columnar morphology characteristic of the subtidal zone and an internal vertical fabric sequence of cerebroid–colloform–smooth (base to top); reflecting a sequence of fabrics generated while submerged in the subtidal zone but at decreasing depths.

Accretion rates obtained from Shark Bay microbial structures are variable from <0.1 mm/year to little more than 0.5 mm/year highlighting how slow the process of stromatolite accretion is and how delicate is the microbial environment. The presence of stromatolite structures 1.5 m in height points to a higher accretion rate of 0.75 mm/year if using the same constructional age period of 2000 years. The relationship between interval accretion rates versus fabrics does not permit establishment of useful trends from the data available: however, the higher overall accretion rate values using trendlines indicate that subtidal colloform and cerebroid heads have faster

development. The ^{14}C accretion rates obtained here (range <0.1–0.54 mm/year) have a greater spread when compared with values obtained by Chivas *et al*. (1990) who determined by ^{14}C dating values between 0.1 and 0.34 mm/year, for microbial structures in Hamelin Pool. Playford & Cockbain (1976) after an investigation period of five years measuring growth rates (with non-corrosive nails) in heads of intertidal and subtidal zones of Hamelin Pool, confirmed that many stromatolites have reached a state of equilibrium, with no accretion but recorded one head with a maximum accretion rate of 1 mm/year.

MICROFABRICS AND CONSTRUCTIONAL MECHANISMS

Internal fabrics preserved in the microbial buildups vary significantly in Shark Bay denoting changes in environment and microbial ecosystems adapted to produce carbonate deposits in different water depths and
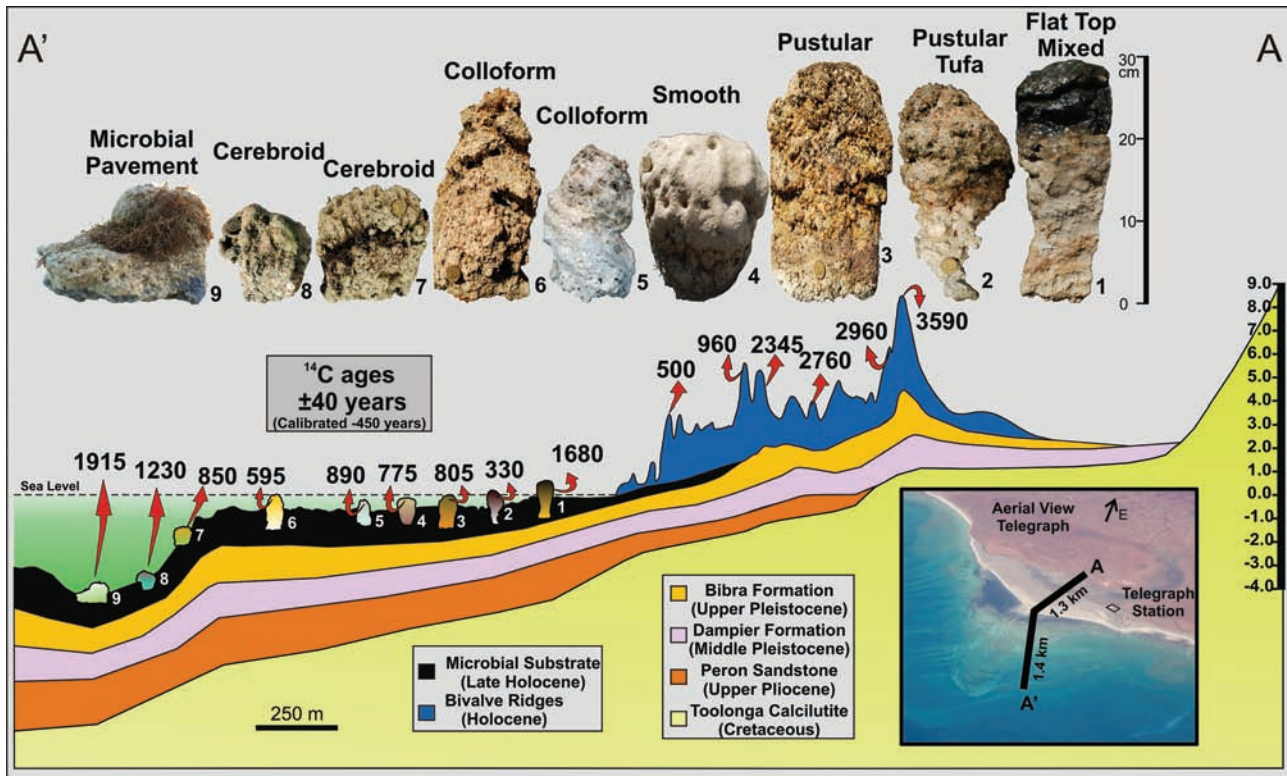
Figure 10 Regional cross-section based on DGPS (land) and multi-beam (water) surveys located north of Telegraph Station area with projected microbial samples and respective ^{14}C ages calibrated by subtracting 450 years from the conventional ages. The stratigraphy is based on boreholes drilled over the ridge system (in blue) and is projected offshore. The supratidal Hamelin Coquina storm ridge transect (morphology and ages) is shown for comparative purposes. Note basinward (upper surface) ages; also relict, emergent head 1 at landward end of transect. (Jahnert & Collins 2012 figure 10).

environmental conditions which are characterised as follows.

Irregular clotted fabric originates from pustular thrombolitic deposits. Pustular deposits are the domain of coccoid cyanobacteria, characterised at the surface by thick brown mucilage produced by the copious amounts of a highly hydrated translucent gelatinous mucilage that undergo organomineralisation after periods of exposure (Golubic 1980, 1982) (Figure 11A). Micrite is generated also by the endolithic activity that fuses and micritises carbonate peloids (SEM images analysis).

Well–laminated (smooth) stromatolites are related to the activity of filamentous cyanobacteria responsible for producing exopolymers that trap sediment producing flat and slippery surface morphology (Figure 11B, 12A). The fabric reveals alternation of grain/bioclast-enriched laminae with peloidal organic-rich laminae generated during storms and subsequent quiescent periods.

Coarse laminoid (colloform) stromatolites develop in subtidal areas deeper than smooth domains, where fine carbonate particles are still available and the ecosystem can develop both vertically and horizontally as adequate space is available. Coccoid cyanobacteria and diatoms produce enough mucilage to trap and bind grains/bioclasts and presumably biologically induced mineralisation producing lithified laminae which are

sustained by vertically constructed lithified columns, leaving horizontal voids (Figure 11C).

Non-laminated cryptomicrobial (cerebroid) structures are the deeper subtidal buildups characterised by external irregular cavities that receive coarse material and are often bored by bivalves. The presence of a significant amount of *Fragum* bivalve shells, ooids and serpulids is a characteristic of these deposits. Lithification results from peloidal grain micritisation and fusion, dark micrite precipitation and fibrous aragonite cementation growing in pore spaces (Figure 11D). Cerebroid structures are a domain of coccoid cyanobacteria.

Microbial pavement refers to light grey cryptomicrobial carbonate deposits with tabular or blocky surface morphologies that are being lithified as bioclastic grainstone and includes skeletons of *Fragum erugatum* bivalves, serpulids, micro-gastropods and foraminifera. It is externally colonised by *Acetabularia* (calcified green algae), Fucales (brown algae) and Gigartinales (red algae).

Coccoid cyanobacteria dominate shallow ecosystems producing pustular deposits, followed by the filamentous cyanobacteria group that produce smooth mat and structures. The permanently submerged buildups, colloform, cerebroid and microbial pavement, represent an ecosystem dominated by coccoid cyanobacteria. In
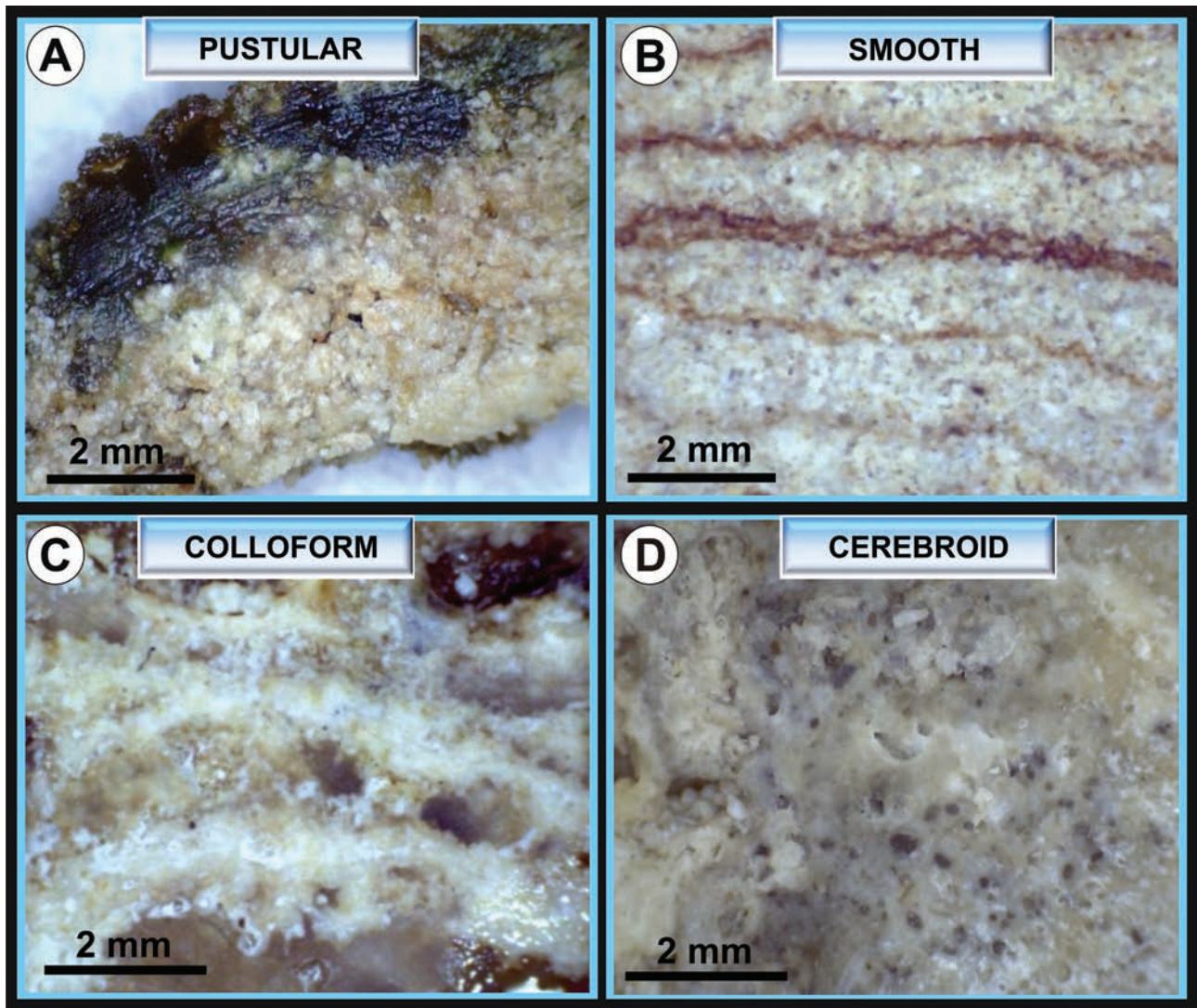
Figure 11 Macrophoto detail of the different fabrics that produce microbial buildups in Shark Bay. (A) Brown dark pustular with thick mucilage and carbonate particles (peloids) trapped. (B) Smooth internal fabric consisting of grain/bioclast-enriched laminae alternating with organic rich laminae with peloids. (C) Colloform coarse laminoid fabric with lithified micritic laminae interbedded with bioclastic and ooidal laminae, sustained by lithified columns constructed vertically, leaving horizontal voids. (D) Cerebroid internal fabric showing non-laminated micrite and bioclastic and ooidal grains. Serpulid exoskeletons are abundant inside the cerebroid fabric. (Jahnert & Collins 2012 figure 13).

water depths of -4 m the filamentous cyanobacteria *Phormidium hypolimneticum* and *Lyngbya fragilis* were detected in the surface of the microbial pavement living within the coccoid domain.

Subtidal microbial structures differ regarding their external morphologies and internal fabrics, which reflect sediment availability, bivalve skeleton supply, substrate morphology and depth, wave activity, tidal runoff, sea level and the microbial community that constructs deposits through different stages and processes of early (synsedimentary) diagenesis which interact as follows.

(1) *Superficial micrite generation* Precipitated micritic carbonate is a characteristic observed in SEM images and occurs within organic gel (EPS) and is related to the microbial communities (Figure 12A–C). Such organic

gels, which are recognised in hand sample and SEM, expand over the surface of structures, connect discrete particles, stabilise sediment and initially sustain the structure. The organic gel also surrounds bacterial filaments, connects material and apparently generates micrite, biologically inducing precipitation (Figure 12A). A detailed image shows a filamentous sheath surrounded by micrite particles generated within the organic gel (Figure 12B), and crystallisation of aragonite that also surrounds bacterial filaments (Figure 12C).

The process of grain accretion is driven by filamentous bacteria in the smooth mat domain and coccoid bacteria in the colloform, cerebroid and microbial pavement domains. Sediment accretion is undertaken mostly by cyanobacteria through photosynthetic production of
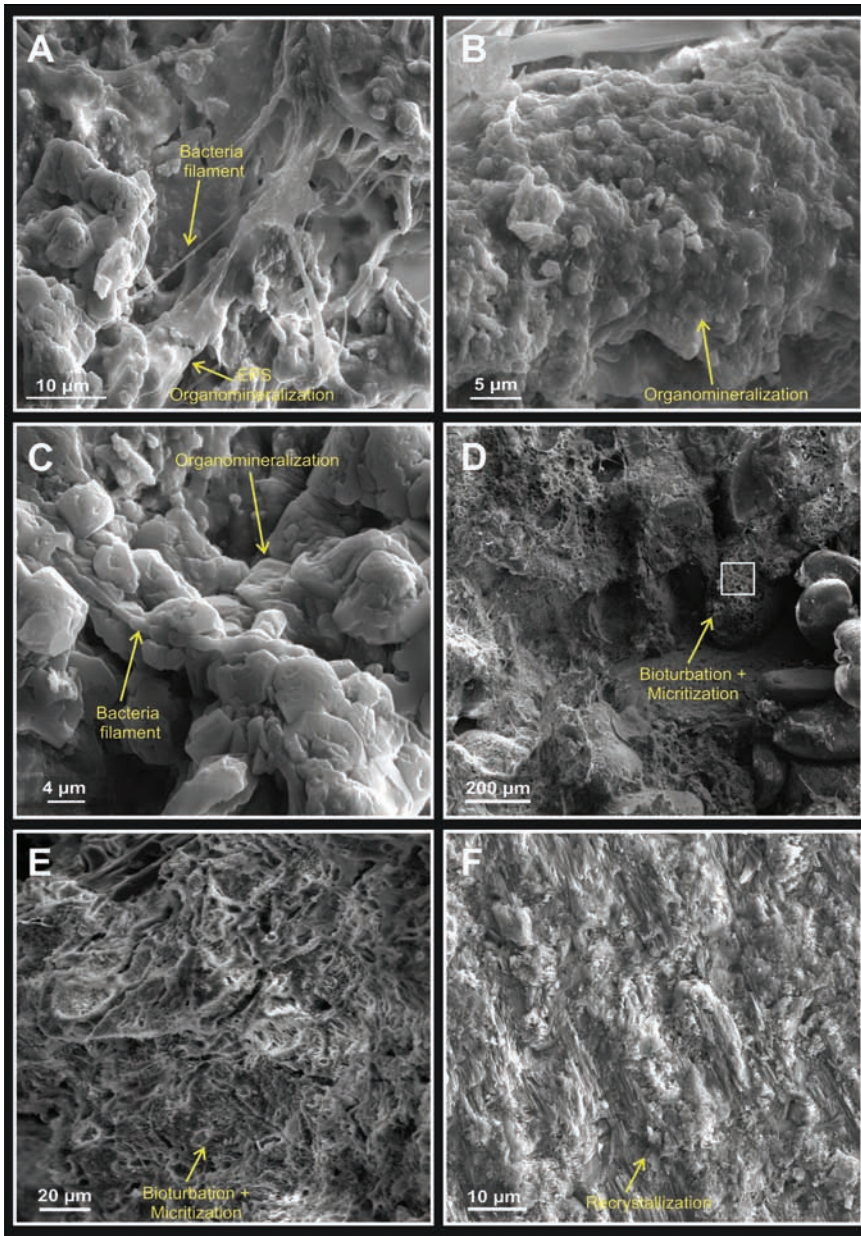
Figure 12 SEM photomicrographs from samples and thin-sections (coated with gold or platinum), showing the sequence of events that involves trapping and binding (stage 1) and organomineralisation in filamentous cyanobacterial domains (A–C) and (stage 2) activity of endolithic microbial bioturbation, micritisation and recrystallisation (D–F); the first stage 1 (A–C) reflects the activity of filamentous bacteria in smooth heads from living (dried) material from Nilemah. (A) The organic gel surrounds bacterial filaments, connects material and apparently is generating micrite. (B) Detail of filamentous sheath surrounded by micrite particles generated within the organic gel (probably EPS). (C) Superficial crystallisation of aragonite that also surrounds bacteria filaments. (D) Carbonate grains severely attacked by microorganisms that produce a honeycomb-like surface in ooids. (E) Detail of rugose surface with tunnels and light-coloured recrystallised microcrystals. (F) Soft peloid grains are micritised and fused obliterating peloid boundaries and producing an extensive new recrystallised micrite. Images from smooth head located at Nilemah and cerebroid heads at Carbla Point and south of Carbla Point. (Jahnert & Collins 2012 figure 14).

exopolymer (Visscher *et al*. 2000; Reid *et al*. 2003; Dupraz & Visscher 2005) that traps and binds grains and particles and also attracts calcium ions to negatively charged sites (Pentecost 1991).

(2) *Bioturbation, micritisation and recrystallisation* Bioturbation, micritisation and recrystallisation (Figure 12D–F) produces grain fusion and recrystallised micritic layers responsible for indurated laminae between soft grainy/bioclastic sand in colloform and smooth heads and produces discontinuous patches of micrite in deeper cerebroid and microbial pavement structures. Carbonate grains are attacked by microorganisms producing a honeycomb-like surface in ooids (Figure 12D) creating a rugose surface with micro-canals and light coloured recrystallised microcrystals (Figure 12E). Soft grains of peloids are micritised and fused producing an extensive new recrystallised micrite (Figure 12F).

These processes are driven by microbial endolithic activity, with an estimated density of 200 000 bacteria/mm^{2} (Golubic 1982), driven by heterotrophic bacteria that penetrate carbonate grains and bioclasts for nutrition and protection (Campbell 1982) producing grain fusion, micritisation (Macintyre *et al*. 2000; Reid *et al*. 2003) and recrystallisation. The most frequent sources of organic carbon for the support of heterotrophic endolithic activity are the primary products of photosynthetic bacteria and organic matrix of skeletons (Campbell 1982).

(3) *Pervasive micrite generation* Occurrence of a last generation of micrite is visible in thin-sections and SEM distributed in all sediment generated, both surficially and within heads in aphotic zones, characterised as a dark cryptocrystalline and microcrystalline micrite, which fills spaces and envelopes grains and skeletons (Figure 13G–J). The micrite is characterised by an amorphous carbonate
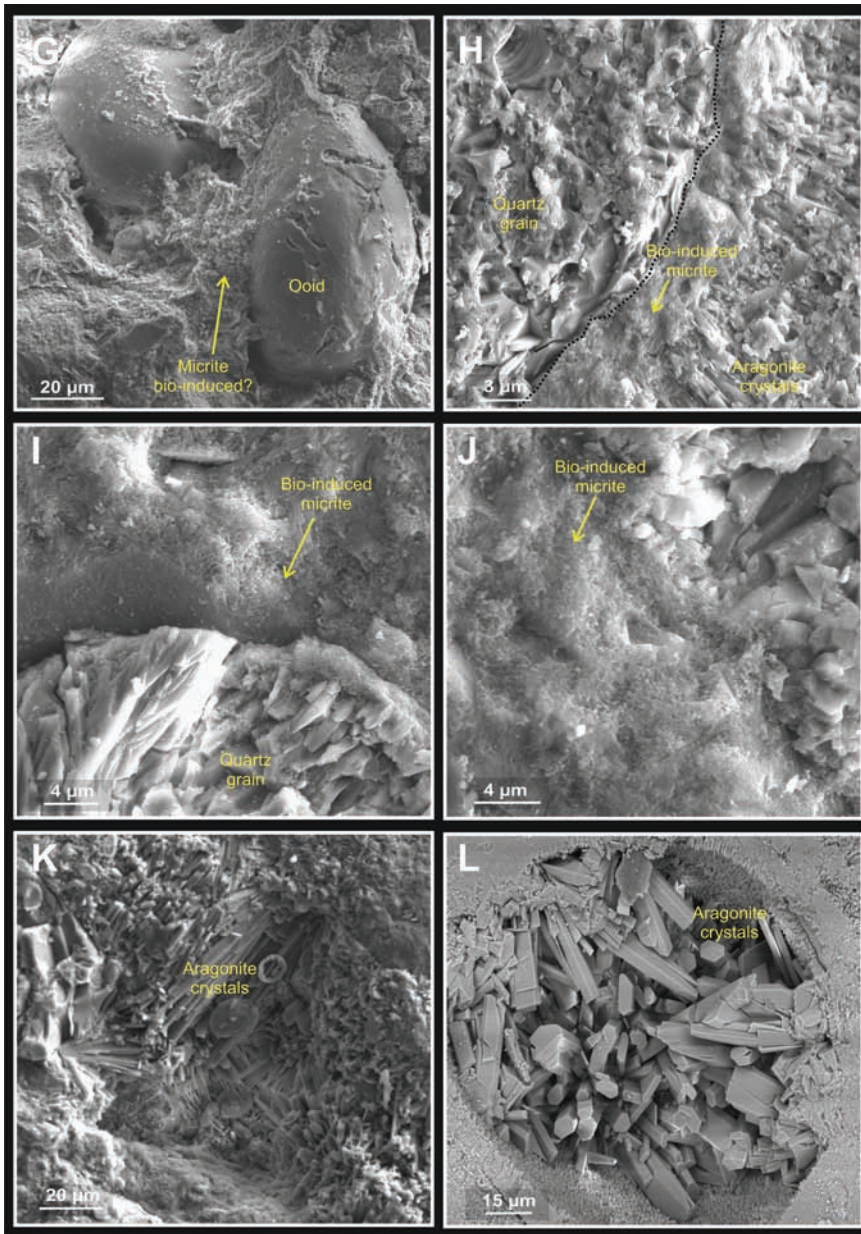
Figure 13 Early diagenetic mechanisms involved in microbial deposits, showing (stage 3) generation of organic micrite enveloping grains and bioclasts (G, H, L, I) and (stage 4) fibrous aragonite precipitation in void spaces (K, L). (G) Ooids grains connected with a fine texture micrite. (H–J) Details of fine texture micrite which precedes the last process of aragonite crystal growth. (K) Aragonite crystals arranged depending on the space available, as a pervasive crystal system or as microcrystals. (L) Well-developed aragonite needles inside larger voids. Images from cerebroid heads located at Carbla and south of Carbla Point. (Jahnert & Collins 2012 figure 15).

which in SEM resembles a texture of fine foam, distinct from other micrite generated by cyanobacteria or endolithic bacterial activity. Grains are connected and stabilised by this kind of micrite (Figure 13G) that reveals in detail (Figure 13H–J) a fine texture that always occurs before the last step of aragonite crystal growth. This micrite is responsible for most of the deeper water source of sediment stabilisation and is deposited presumably as a result of sulfate-reducing bacterial activity (Visscher *et al*. 2005).

(4) *Fibrous aragonite precipitation* Aragonite crystal growth in void spaces is the last diagenetic product during the construction of microbial structures. The process is recognised as an important step for the final stabilisation of sediment in the subtidal cryptomicrobial structures although it is almost negligible in shallow subtidal smooth domains. Aragonite crystals are arranged depending on the space available, as a pervasive crystal system or as microcrystals (Figure 13K) and also well developed needles inside larger voids (Figure 13L).

When the relative abundance of specific microbial substrates is compared it is evident that the subtidal microbial habitat is far more widespread than previously known in Hamelin Pool, for example in comparison to the intertidal microbial substrate, and this will be explored in succeeding sections. The less saline L'Haridon Bight lacks subtidal microbial substrate and has remnant seagrass banks in less saline areas around its margins, a further contrast with Hamelin Pool from which sublittoral seagrass habitat is virtually absent. The Faure seagrass bank forms the northern barrier to both basins. The effect of late Holocene regression is also evident from the laterally extensive intertidal microbial

substrates on low-gradient tidal flats which record shoreline retreat, and the stranding of microbialites as sea level has fallen.

Hamelin Pool: microbial deposits and substrate morphology

The delicate balance between tidal energy, waves, exposure time and water depth results in sediment accretion or erosion in Shark Bay (Logan *et al*. 1974b). Low water energy associated with high evaporation, sediment supply and topography are key elements for sediment accretion. The gross morphology of microbial deposits is related to the interaction of these factors with the embayment coastal morphology and its related substrate gradient. The general coastal morphology of Hamelin Pool can be classified into three different types: headlands, bights and embayment tidal flats (Logan *et al*. 1974a; Hoffman 1976).

Headlands are characterised by steep gradients (Figure 14) of 4 m/100 m, where the substrate favours growth of submerged microbial deposits (up to 1.5 m high) as columnar, domical, conical and club-shaped morphologies. Intense activity of waves and tidal currents is responsible for erosional effects on the microbial structures, which often exhibit basal thin necks, tunnels, and other evidence of erosion. The high energy

of currents also supplies coarse carbonate grains and bioclasts that become trapped by microbial activity. Water depth controls the living microbial communities which respond with distinct communities, internal fabrics, external colours (pigmentation) and growth styles.

Bights are subtle re-entrants with gradients of about 2 m/km with microbial deposits forming mats or elongate structures and tabular microbial pavement in subtidal regions. The structures (about 50 cm height) have their long axes perpendicular to the shoreline and parallel to tidal current direction.

Embayments occur in re-entrants along the coast, normally protected by the presence of coquina barrier ridges. The tidal flats have low gradients of about 30–50 cm/km and produce extensive deposits of microbial mats. Because of sea level fall during the last thousand years the microbial system is adjusting its position seaward, so that landward areas are now exposed and under erosion producing brecciated microbial deposits, often expressed as breccia pavements.

Fluctuating tidal and wave energy controls the amount of carbonate particles available to be deposited and trapped by microbes which, depending on microhabitat, construct laminar or non-laminar fabrics (Figure 14). High-energy water near smooth and
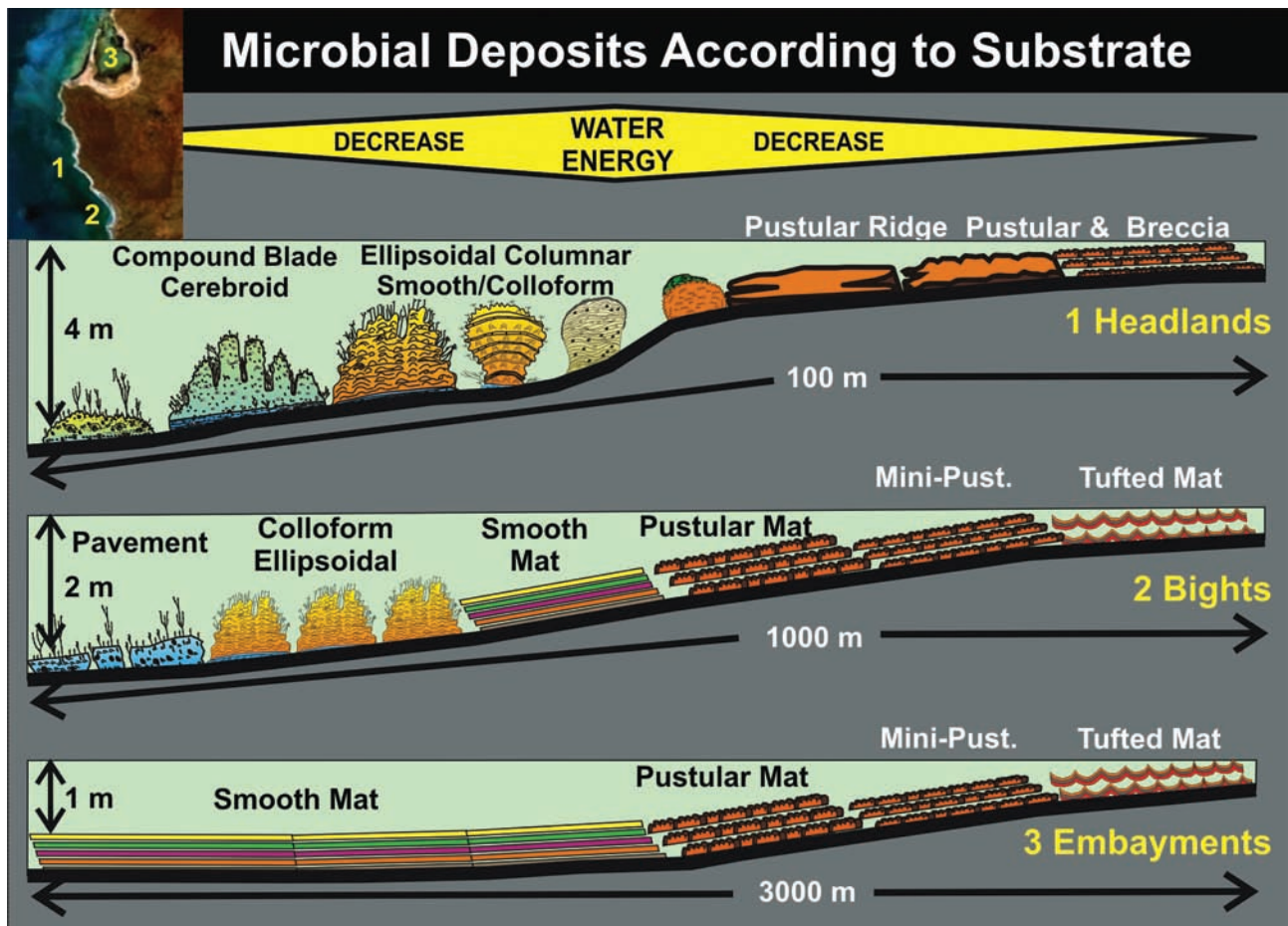
Figure 14 Microbial deposit morphologies and types according to the substrate gradient. Headlands have steep gradients with growing heads while embayments have low gradients and are colonised by widespread mats. (Jahnert & Collins 2012 figure 3).

colloform domains is rich in fine carbonate particles that, after storms, are slowly deposited supplying microbial communities with enough material to produce laminar fabrics. Deeper waters are depleted in fine carbonate particles and microbial communities stabilise sediment by inducing carbonate precipitation and trapping fine grains. Coarse particles such as bivalve shells and fragments, bioclasts and ooids are widely available and are deposited mainly during storms.

Hamelin Pool has an extensive sublittoral platform with a gently sloping top (0.5–3 m/km) and a more steeply sloping margin >4 m/km; this platform extends basinward to water depths as deep as 6 m.

Subtidal realm and subtidal microbial deposits

Submarine videos, photos, samples and bottom substrate profiles have provided substantial material which was used to identify, map and classify the morphology of microbial structures and their distribution in the subtidal areas, supporting the creation of georeferenced organosedimentary maps of Hamelin Pool and supplying accurate substrate elevations for each group of microbial structure type (Figure 7).

Colloform microbial deposits (-0.5 to -1.5 m) occur as beige to brown elongate prismatic, spherical and club-shaped structures (long axis oriented parallel to tidal action) in the subtidal environment. Colloform deposits externally show small (1–5 cm) globular hemispherical forms rich in fine-grained peloids and ooids. Internally layers of grains (2–10 mm) alternate with thin laminae of lithified micrite generating a coarse laminoid internal fabric (Logan *et al.* 1974b) often with weak lamination (Hoffman 1976; Playford 1990). Lithification is promoted by micritic layers of bacterially induced mineralisation, fusion of peloids and aragonite cement. Colloform microbial deposits are the domain of *Entophysalis*, *Chroococcus*, *Gloeothece* cyanobacteria and diatoms (John 1993), that also provide shelter for many living eukaryotes such as *Fragum* bivalves (Logan *et al.* 1974b; Berry & Playford 1997), crustaceans, serpulids, micro-gastropods, foraminifera, *Acetabularia*, Fucales and Gigartinales).

Cerebroid microbial deposits (-1 to -2.5 m) are the deepest subtidal buildups occurring as domical, ridged or prismatic club-shaped morphologies of white to cream colours. The external appearance (Figure 15) resembles a cerebrum in a dorsal view with abundant spherical/elongate dark cavities distributed in a white to grey carbonate mass. Cerebroid structures have superficial cavities that contain coarse material and are often bored by bivalves. Internally pink patches or clots of micrite
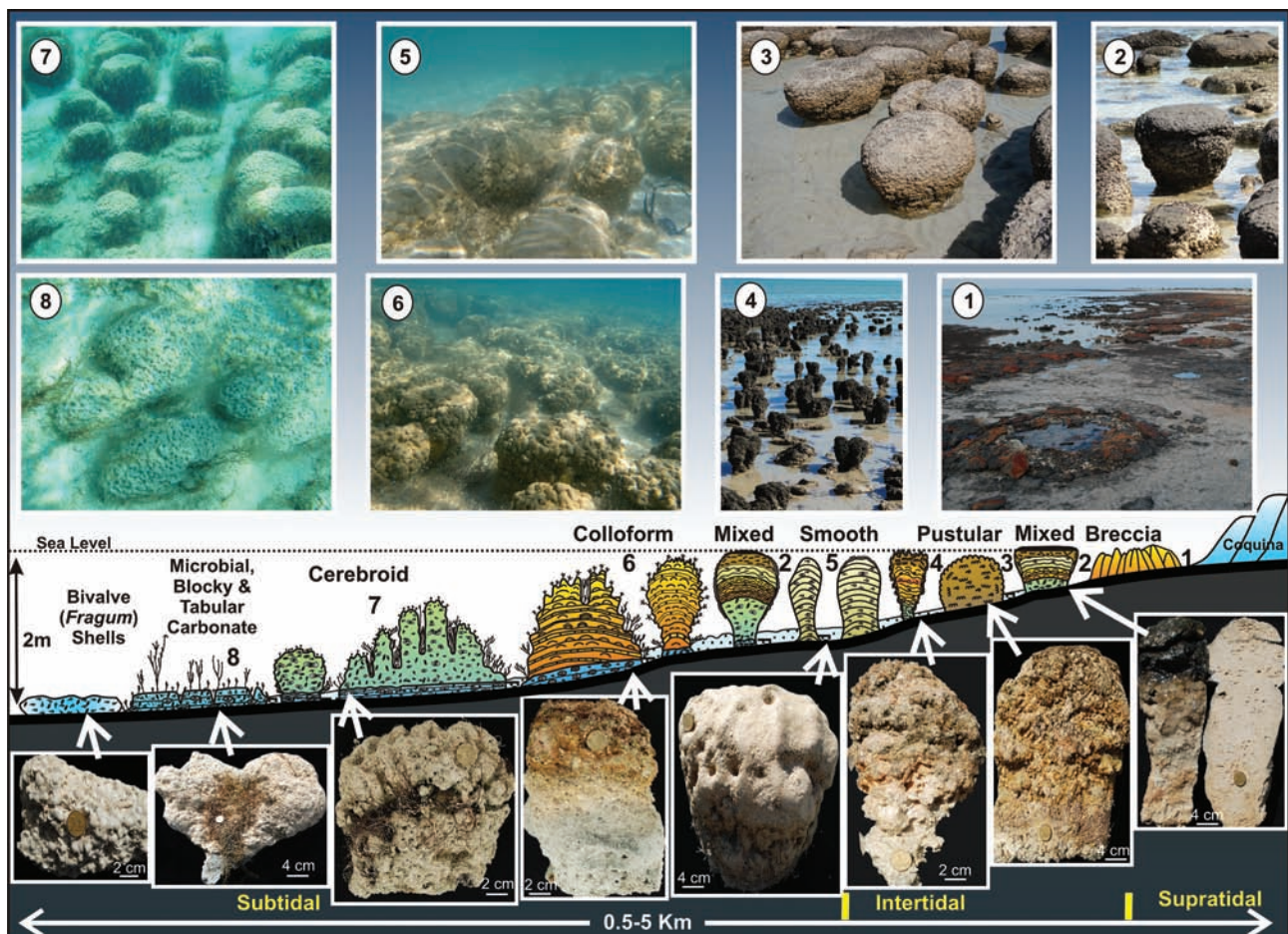
Figure 15 Microbial structure types at base with schematic fabrics and correspondent images taken in the field at Hamelin Pool, Shark Bay. (Jahnert & Collins 2011 figure 2).

occur sparsely around clusters of carbonate sand and shells or within bivalve concavity producing a non-laminated fabric (Figure 16). Bivalve shells of *Fragum erugatum* are abundant in these structures which dominate the subtidal habitat and consist of coccoid cyanobacteria: *Chroococcus microscopicus, C. giganteus, C. ercegovicii* and *Aphanocapsa litoralis* at the superficial photic zone.

Petrographic constituents are ooids, peloids, skeletons, bioclasts and quartz grains. Peloids and ooids are partially fused, micritised and burrowed, producing micrite patches that are sparsely distributed. A dark green late micrite infills cavities and envelopes grains suggesting an important role in sediment stabilisation. Serpulid skeletons, shell fragments and ooids show partial recrystallisation to phosphatic carbonate. Iron-rich carbonate in small amounts (<3%) and pyrite are present in ooids or internally on skeletons. Lithification results from grain micritisation and fusion, dark micrite precipitation and fibrous aragonite cementation growing in pore spaces.

Microbial pavement (-2 to -6 m) is a light grey microbial carbonate deposit with tabular or blocky surface morphologies being lithified to form bioclastic grainstone and includes *Fragum erugatum* bivalves, serpulids, micro-gastropods, foraminifera, *Acetabularia*, Fucales and Gigartinales. The abundance of *Fragum* and serpulid skeletons is characteristic of these deposits that cover extensive areas of the subtidal platform. Dark green micrite as a product of organomineralisation coats grains and skeletons as a fundamental element connecting and stabilising sediment (*sensu* Riding 1991, 2000). Coccoid cyanobacteria *Cyanosarcina thalassia* and *Chroococcus microscopicus* dominate the superficial photic zone.

Based on analysis of data from habitat mapping, subtidal microbial structures from colloform and cerebroid types (Figure 16) are responsible for more than 70% of Shark Bay columnar structures. Colloform structures are as high as 1.5 m, often connected laterally forming extensive kilometric strips 50–500 m wide as reefs parallel to the coast, with cerebroid as the deeper buildups of 1 m maximum height. The microbial pavement is revealed as an important widespread microbialite (*sensu* Burne & Moore 1987) that is colonising and stabilising the substrate over the sublittoral platform of Hamelin Pool in water depths from 2 to 6 m.

MICROBIAL PROCESSES AND PRODUCTS

To produce stromatolites, thrombolites and cryptomicrobial structures in Shark Bay, bacteria take advantage of stressing environmental conditions that limit the attack of predators and competitors. Formation
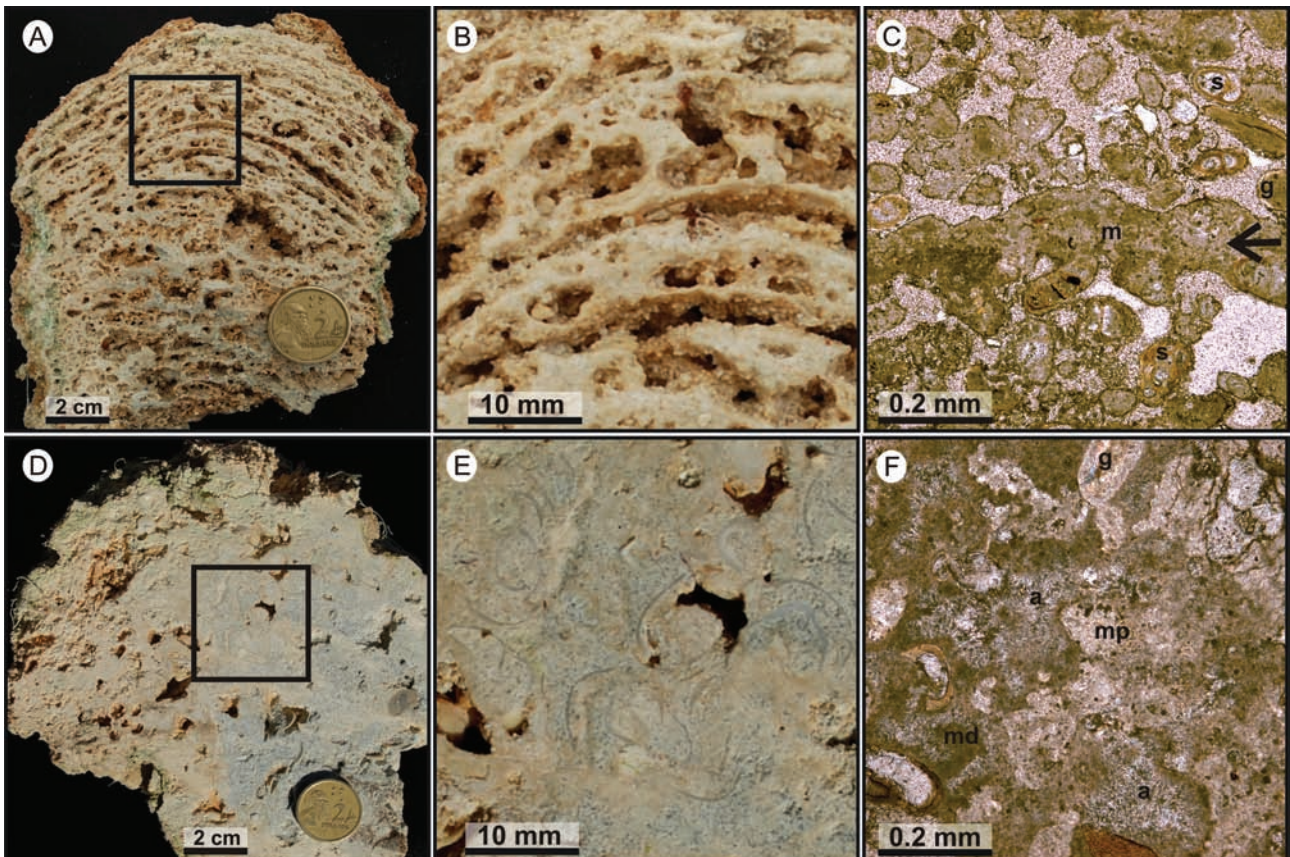
Figure 16 Comparison between the dominant subtidal microbial structures. (A) Colloform structure, with (B) detail of laminoid fabric and (C) photomicrograph showing subhorizontal laminae (arrow) of fused peloids: micrite (m), skeletons (s) and grains (g). (D) Cerebroid structure, with (E) detail of non-laminated fabric and (F) photomicrograph revealing patches of light-pink (mp) and a dark-green micrite (md), grains (g) and aragonite (a). (Jahnert & Collins 2011 figure 3).

of subtidal structures occurs through different stages and processes that interact as follows:

Sediment accretion is conducted mostly by cyanobacteria through photosynthetic production of exopolymer (Visscher *et al*. 2000; Reid *et al*. 2003; Dupraz & Visscher 2005) that traps and binds grains and particles and also attracts calcium ions to negatively charged sites (Pentecost 1985). Grain accretion is driven by filamentous bacteria in the smooth mat domain and coccoid bacteria in colloform and cerebroid domains. These bacterial communities along with diatoms produce volumes of exopolymers sufficient to connect, stabilise sediment and initially sustain the structure. As organic compounds and sulfate/sulfite are present, heterotrophic and phototrophic bacterial activity sponsors a further stage in evolution and growth of heads. Sulfate-reducing bacterial activity (Visscher *et al*. 2000; Dupraz & Visscher 2005; Baumgartner *et al*. 2006; Dupraz *et al*. 2009) is an important source of carbonate precipitation through induced-mineralisation which is also responsible for early lithification of the structures. Sulfate-reducing and sulfur-oxidising bacteria account for 66% of the total population of active bacteria in five samples of Shark Bay submitted to genomic DNA analysis.

Stabilisation of aragonitic micrite in laminae (colloform, smooth) or patches (cerebroid) occurs in peloidal layers submitted to a process of grain fusion and micritisation by endolithic bacterial activity of carbonate mineralisation. In colloform heads these fused micritised levels are responsible for indurated laminae between soft grainy material. In cerebroid heads the process is localised to some mottled portions leaving other patches (2–5 cm) of grainy friable sediment.

Generation of organic micrite, presumably as a result of sulfate-reducing activity produces a dark green microcrystalline micrite which fills spaces and envelopes grains and skeletons and is responsible for most of the deep-water source of sediment stabilisation. Aragonitic cementation subsequently occurs involving fibrous aragonite precipitation in void spaces.

A summary of subtidal morphology and fabrics is presented in Figure 9.

The importance of fusion of micritised grains as responsible for early lithification of microbial structures in Shark Bay has been previously recognised (Reid *et al*. 2003). Those authors have also described a subtidal microbial precipitate of unknown composition which has an originally laminated micrite infilled by an 'entophysalidacean species' that obliterates original lamination producing 'unlaminated stromatolites'. Our findings show cerebroid deposits form as widespread deeper subtidal microbial buildups with unlaminated fabric and patches of micrite, but apparently not as a result of disturbance of lamination. Laminated micrite is a characteristic of shallower waters in colloform and smooth mat domains rich in fine sediment available to be deposited and generate laminar fabric. Cerebroid heads are mostly constructed by coarse sediment forming a non-laminated fabric, because of the irregular surface morphology, intense bioturbation and restricted amount of peloidal particles available in deep subtidal domains.

The abundance of coarse coquina bound into cerebroid heads attests to the high availability of bivalve shells, the dominant sediment type in the subtidal regions and periodic high storm energy to rework and redistribute coquina which is incorporated into these heads, as opposed to quiescent conditions of fairweather waves. In contrast, shallower microbial substrates trap and retain sand-size bioclasts and peloids in lower energy conditions in tidal flats.

The prolific subtidal cementation involves induced microbial mineralisation, grain fusion and aragonite precipitation occurring in a hypersaline setting where both carbonate saturation and microbial activity are significant. Throughout the Hamelin Basin and tidal flats alkalinity, salinity and Ca ion availability is high (pH 7.5–8.6, salinity 60–65 and Ca^{++} 500–1080 mg/L) based on continuous measurements (48 hours) in southern Hamelin Pool. It is likely that these parameters may be related to depth, temperature, wave agitation and CO_2 content of waters, but a firm conclusion awaits future analysis. However, based on DNA/RNA organosediment measurements, the high degree of EPS biomineralisation as seen in SEM photomicrographs of cerebroid heads and relatively high positive values of $\delta^{13}C$ (> +4.2) and $\delta^{18}O$ (> +3.1) recorded in microbial sediment it is clear that microbial activity has a strong imprint on the subtidal facies.

STROMATOLITES, AGE, INTERNAL FABRICS AND REGRESSION

Distinct internal fabrics result from microbial processes of trapping and binding, carbonate-induced precipitation, organic matter content, amount and type of sediment input, presence of voids, presence of skeletons, bioturbation and macropore orientation. Subtidal microbial carbonate deposits are designated as pustular, smooth, colloform, cerebroid and microbial pavement (Figures 8, 9). They have distinct internal fabrics, related to the dominant microbial communities (Burns *et al*. 2004; Allen *et al*. 2009; Jahnert & Collins 2011, 2012, 2013), their growth habits and environmental conditions.

An interpretation of ages versus fabrics and water levels permits recognition of two stages of depositional growth; The first was between 2000 and 1100 years ago, a period when the shoreline shifted landward and buildups were developing as columnar, ellipsoidal, and spherical forms and as large microbial hemispheres (+2 m diameter) in the subtidal zone which remain partially exposed today in the supratidal/intertidal zone around Hamelin Pool. Evidence of this first event can be seen at the observation deck at Telegraph Station, where large microbial hemispheres and some columnar microbial structures are exposed near the shoreline. There is also evidence of old tidal flats exposed in the supratidal zone with microbial mats recognised at Nilemah and Hutchinson, some producing breccia pavements. The second phase of microbial carbonate deposition occurred from 900 years ago to the present day during the falling sea level (on the order of 1.5 m) to present level. During this second phase the microbial domain expanded considerably as the sublittoral platform became shallower and was marked by an increase in fine carbonate particles (peloids) responsible for deposition of the majority of laminated stromatolites. Holocene microbial structures record evidence of changing environmental conditions and water depth producing vertical

depositional sequences, which represent shallowing-up sedimentary sequences.

The relationship between the internal fabric and the water depth where the microbialites are generated has been established. Non-laminated/disrupted cryptomicrobial fabrics with a high content of bivalve shells, ooids, and serpulids are characteristic of 'deep water' (-1 to -6 m) growth as buildups (cerebroid) or microbial tabular or blocky pavement. Coarse and fine laminoid fabrics correlate to shallower waters (-5 cm to -1.5 m) rich in fine carbonate particles developing colloform and smooth structures and the shallow water (0 to -40 cm) is colonised by pustular deposits with internal irregular to clotted fabrics. These relationships (Figure 8) assist identification in columnar forms exposed today in the supratidal zone of distinct internal fabric sequences which are non-laminated at the base (cerebroid) followed by coarse laminated (colloform), well-laminated (smooth) and a flat eroded top with a dark film veneer. These fabric sequences represent a
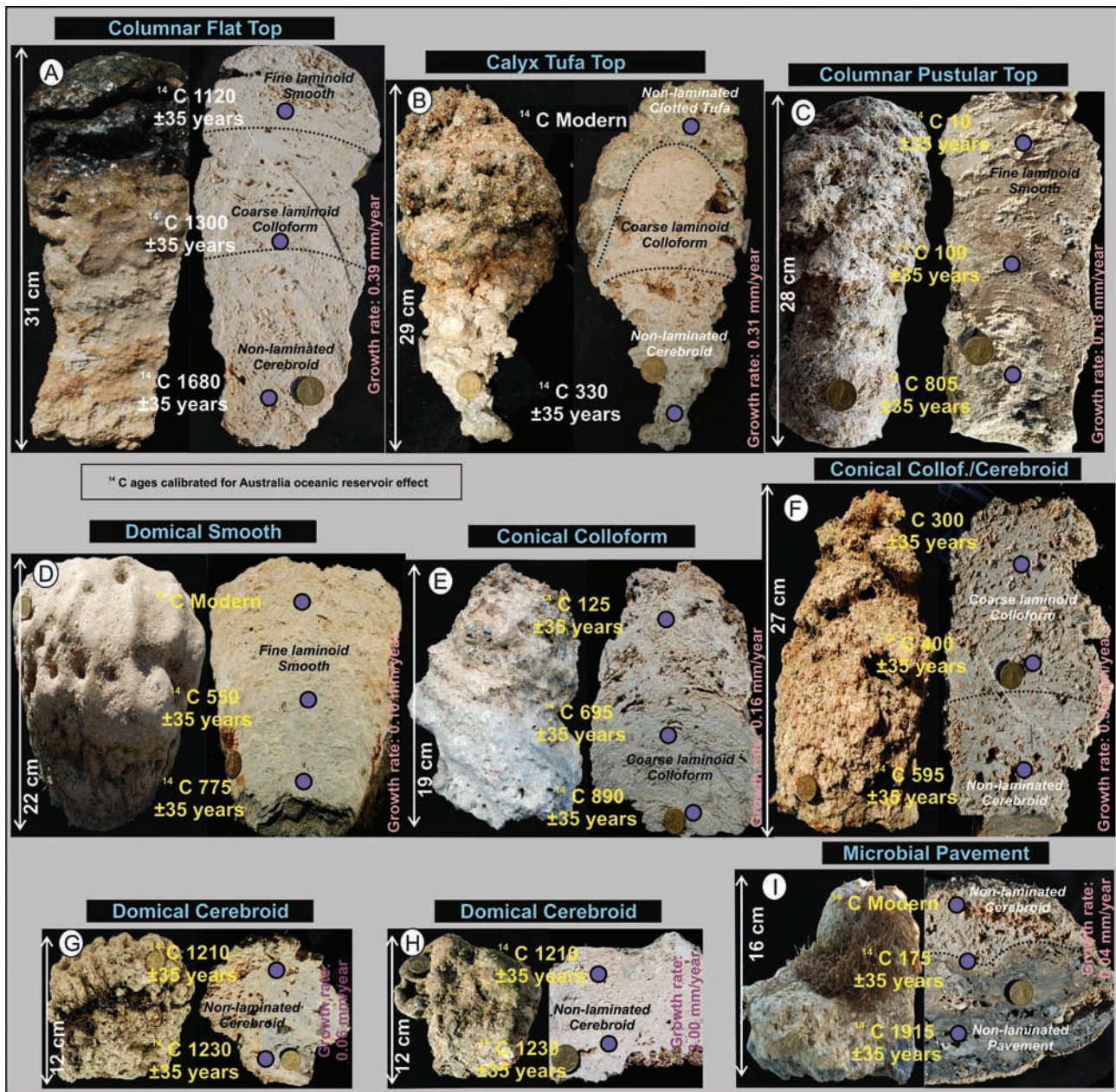
Figure 17 Microbial buildup slices showing internal fabrics, the sampling points and calibrated ^{14}C ages with growth rates. (A) Columnar flat top structure with an internal shallowing-upward carbonate sequence represented by a basal non-laminated fabric passing upward to coarse laminoid and to fine laminoid fabric. (B) Calyx head with ornamented non-laminated fabric at top. (C) Columnar head with internal fine laminoid fabric and colonised by pustular at surface. (D) Domical structure with smooth top and internal fine laminoid fabric. (E) Conical colloform structure with a coarse laminoid internal fabric. (F) Conical structure with non-laminated fabric at base passing upward to a coarse laminoid fabric, (G, H) Domical cerebroid structure with internal non-laminated fabric. (I) Microbial pavement with a non-laminated fabric passing upward to a cerebroid morphology. (Jahnert & Collins 2012 figure 12).
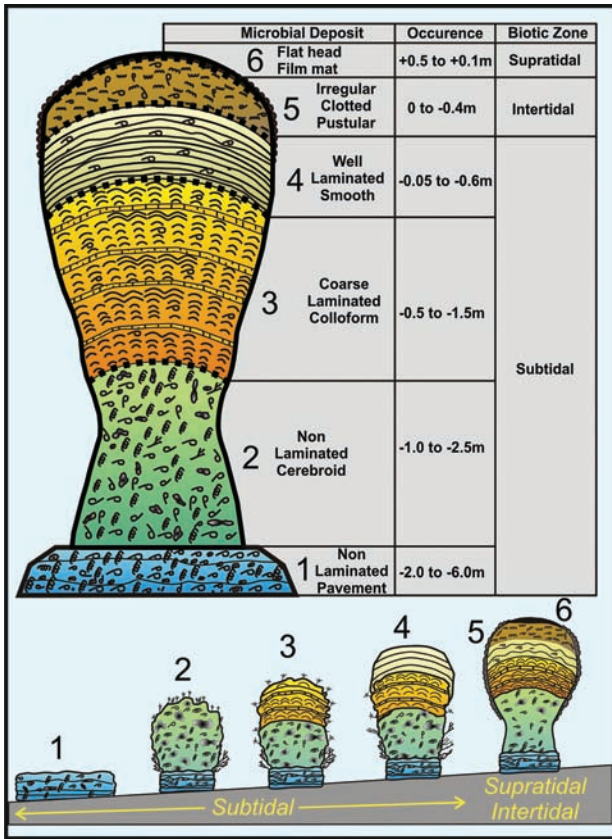
Figure 18 Schematic microbial head with idealised sequence of internal fabrics and their relative water depths. The structures often display a vertical sequence of internal fabrics in shallowing-upward arrangement or show truncated fabric sequences depending on environmental setting and timing of growth history. (Jahnert & Collins 2012 figure 17).

shallowing-upward carbonate system that commenced deposition in waters deeper than 1 m (e.g. see the sample labelled 'columnar flat top' in Figure 17) and support the late Holocene sea level fall inferred from other sea level proxies in Shark Bay.

Some microbial columnar forms exposed today in the supratidal zone consist internally of distinct fabrics that are non-laminated at the base (cerebroid) followed by coarse laminated (colloform), well-laminated (smooth) and a flat eroded top with a dark film veneer, representing a shallowing-up carbonate cycle (Figure 18). This is testimony to the process of sea level fall during the last 6000 years BP (Collins *et al*. 2006), which progressively stranded supratidal microbial deposits, providing an opportunity to study fabrics changing according to water level

Microbialite depositional model

Based on the improved knowledge of the nature and distribution of Shark Bay microbial deposits a revised facies model has been constructed (Figure 19). The last 2000 years are characterised by relatively extensive and prolific activity of microbial communities producing microbialites that are exposed in the supratidal zone and currently undergoing erosion, and intertidal forms. Microbialites are progressively colonising the subtidal zone as a consequence of sea level fall of about 2 m during the last 6000 years. Of particular importance is the significant increase of the known area of subtidal microbial habitat revealed in the mapping and reflected in the idealised cross-section which encapsulates the revised model

DISCUSSION

Tidal flats

The exceptional variety of microbial communities with their specific internal fabrics and their pattern of distribution according to topography and tidal zones identifies Shark Bay as a unique environmental setting.
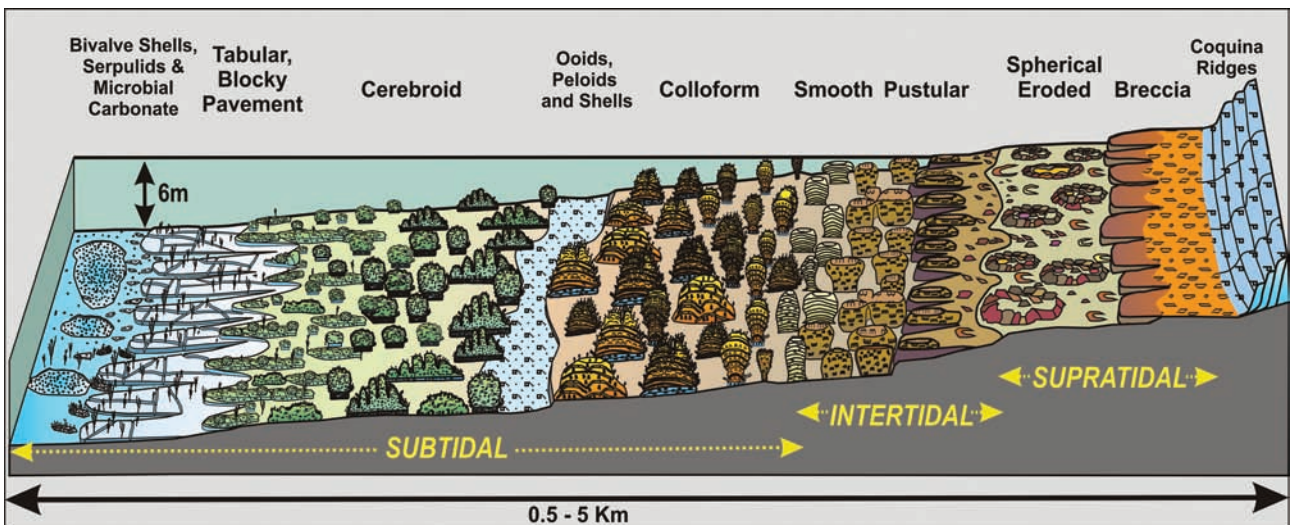
Figure 19 Shark Bay/Hamelin Pool facies model with extensive subtidal deposits. Note the exposed and now eroding supratidal microbial carbonates stranded by sea level fall. (Jahnert & Collins 2011 figure 4).

The modern microbial system is producing internal fabrics with stromatolitic, thrombolitic and cryptomicrobial characteristics laterally arranged within the same environment. Thrombolitic fabrics also occur in shallow intertidal environments with stromatolitic fabrics, in contrast to statements by other authors (Aitken 1967; Kennard & James 1986; Feldman & McKenzie 1998). The widespread nature and distribution of microbialites emphasises the applicability of Shark Bay as an analogue for ancient systems and increases scientific understanding of microbial deposits, which have significance as peritidal environmental markers and reservoir analogues. Table 1 is a summary of the contrasting properties of microbial mats and sediments of the three tidal flats studied.

The main shallow intertidal microbial mat in the tidal flats is the pustular mat which is characterised by a superficial vertical growth style (Golubic 1976a, b) of small mucilaginous pustules that also trap peloidal carbonate particles. After desiccation, this mat produces a mesoclotted fabric that may be designated thrombolitic (Logan *et al.* 1974b). In SEM images, pustular fabric exhibits two types of micrite: (i) a light pink to gold micrite that is apparently a product of mucilage mineralisation from communities of coccoid bacteria (*Gloeocapsa, Chroococcus* and *Entophysalis*), peloid fusion and EPS mineralisation; and (ii) a dark green to black micrite that surrounds grains and is pervasive, occurring as the last generation product of extensive microbial EPS biomineralisation, which is preferentially conducted below the sediment surface, mainly by communities such as sulfate-reducing bacteria and anoxygenic phototrophs (Decho 2000; Reid *et al.* 2000; Dupraz & Visscher 2005; Visscher & Stolz 2005; Vasconcelos *et al.* 2006; Dupraz *et al.* 2009). Microbial sulfide oxidation to elemental sulfur has a positive effect on alkalinity shifting the pH to alkaline, favouring carbonate precipitation (Vasconcelos *et al.* 2006). The microbial pavement is a permanently subtidal microbial deposit that occurs in Nilemah embayment as flat substrate that is being lithified to form a bioclastic grainstone composed of *Fragum*, serpulids, micro-gastropods, foraminifera and algae. The meso-fabric is nonlaminated cryptomicrobial (*sensu* Kennard & James 1986) with open voids and shelter porosity. The microfabric is particularly related to the presence of bioclastic fragments of bivalve shells and ooids that are being lithified by a spongy pervasive micrite (seen in SEM) presumably from sulfate-reducing coccoid bacteria and methanogenic activity.

Communities of dominant cyanobacteria living on the surface of microbial mats and structures indicate correlation of predominantly laminated fabrics (tufted and smooth mats) with filamentous bacterial activity (*Lyngbya, Phormidium, Schizothrix* and *Microcoleus*) while non-laminated fabrics relate to the presence of coccoid bacteria. Within the intertidal zone in the pustular domain coccoid bacteria (Families Entophysalidaceae, Microcystaceae and Chroococcaceae) occur as gelatinous colonies of spherical to sub-spherical cells exhibiting mainly light green-blue colours, cell diameters of 2–20 μm with predominance of sizes of <5 μm. Subtidal colloform structures, despite their weakly laminated fabric, reveal the dominance of coccoid bacteria (Families Chroococcaceae, Entophysalidaceae and Synechococcaceae) which are usually in gelatinous spherical colonies with *Chroococcus turgidus* showing the largest diameters (15–25 μm). Microbial pavement is represented by non-laminated cryptomicrobial fabric with superficial coccoid communities (Families Chroococcaceae and Entophysalidaceae).

A lithified pavement that is commonly found centimetres below the modern surface was described in the tidal flats of Shark Bay and corresponds to an old Holocene surface. This surface was dated at 568, 503 and 490 ± 43 ^{14}C years (calibrated ages) and is presumably related to a small regional sea regression. The ages obtained correspond to a period between 1444 and 1521 AD that is referred to in the literature as dry in the Southern Hemisphere. Lake Malawi's water level (from 1570 to 1850 years AD) was about 120 m lower than during the previous three centuries (Johnson *et al.* 2001) and ice core studies showed that atmospheric circulation intensity increased in the Polar South Pacific and North Atlantic at the beginning (*ca* 1400 AD) of the most recent Holocene rapid climate change known as the Little Ice Age (Kreutz *et al.* 1977). Microbial tidal flats in the Shark Bay World Heritage region occupy a 'niche area' of hypersalinity and alkalinity in the Holocene. Whilst they have apparently thrived during the relative climate stability of the last 6000 years of slowly falling sea level, their future is more uncertain under the predicted climatic change scenarios. Shark Bay tidal flats are reaching a critical moment in their evolutionary history; microbial deposits are highly susceptible to salinity and/or sea level changes. Rapid sea level rise could lead to environmental instability, increased sediment mobility, salinity fall and microbial decline. On the other hand, if sea level falls significantly, microbial survival may also be threatened. A total detachment from the open embayment could generate a shallow evaporitic peritidal environment, and evaporites could progressively restrict microbial and molluscan life, creating a 'sabkha' environment.

In contrast, ancient microbial system analogues of the Phanerozoic and earlier often persisted for long (more than tens of millions of years) periods in stable tectono-eustatic and climatic settings allowing thick (many tens of stacked tidal flat cycles) sequences to accumulate over large areas of entire sedimentary basins recorded as microbial rocks. Examples from the Middle Ordovician of the Canning Basin Nita and Goldwyer Formations, Western Australia (Karajas & Kernick 1984); Ordovician of the central Appalachian Basin, United States (Pope & Read 1998); Permo-Triassic of central European Basins, Zechstein-Buntsandstein Group (Paul & Peryt 2000) and Cretaceous of South America, Santos Basin pre-salt sequence (Formigli *et al.* 2009) reinforce the significant past distribution of these microbial deposits which frequently serve as hydrocarbon reservoirs and sometimes as source rocks.

Hamelin Pool

Microbial activity in Hamelin Pool prospers in response to the unusual environmental conditions in a partially barred basin with restricted water exchange, high evaporation and hypersalinity. The hypersaline environment ensures a restricted diversity of eukaryote species; however the presence of *Fragum erugatum* which

adapted and proliferated early during the first stages of hypersalinity around 4000 years ago, guarantees a large supply of bioavailable carbonate. Whilst the ultimate source of carbonate is yet unknown the linkage between high microbial activity and coquina productivity was established by 2000 years ago, perhaps promoted by sea level fall, reduced storm intensity and water chemistry evolution enriched in calcium ions. Processes of shell abrasion, dissolution and activity of microbial bioturbation might also act as a source of calcium ions which progressively became enriched in the system as the area evolved as an appropriate place for prolific microbial deposits to develop. As observed in fabrics of the oldest microbial deposits (cerebroid and microbial pavement) bivalves were fundamental as a biomass supplier to microbial construction. The extensive colonisation of intertidal and subtidal areas (0 to -2.5 m) by microbial organisms produced changes in aqueous CO_2 partial pressure as a result of consumption during photosynthesis. Also the process of CO_2 degassing (Kerrick 2001) produced by splashing waves, converts the system into a more alkaline environment which facilitates carbonate organomineralisation (Read 1976). Water parameters measured continuously in the south of Hamelin Pool recorded falls in the dissolved oxygen content of about 50% during nights, perhaps due to oxygen consumption, emphasising the high amount of CO_2 consumed during the day by photosynthesis.

Microbial communities also affect conditions by attracting minor amounts of metals (iron, nickel, lithium, strontium, rubidium, molybdenum and lanthanum); these are enriched in microbial samples from Shark Bay, and this process could influence the microenvironment's O_2 partial pressure. Gerdes (2007) reported that the presence of iron in cyanobacterial filaments maintained the partial pressure of oxygen at reduced levels as bacteria used iron to react with oxygen and thereby stabilise excessive oxygen content. Ferric hydroxides also may function as a barrier protecting the cyanobacteria group from the influence of sulfide sourced from deeper anoxic layers (Stal 1994) and used to produce the variety of pigments responsible for the variable colours visible at the surface and within the fabrics of microbial origin.

A summary of the stages producing laminated and non-laminated microbial fabrics is schematically represented in a sequence involving the stages highlighted by SEM and thin-section study (Figure 20). The constructional mechanisms of microbial heads depend on many factors and also on the presence and availability of coarse grains/bioclasts and fine carbonate particles and peloids. During storms coarse material is emplaced in the heads and after storms the deposition of peloids and fine carbonate particles predominates in shallower waters near smooth and colloform domains. Deeper portions are less well supplied by peloids and fine-grained carbonate particles. This is significant when considering microbial activity, which is deficient in micrite produced within fused peloids, and micrite patches are produced rather than laminated fabrics. A dark micrite that envelopes and connects grains and bioclasts, observed in thin-section and SEM (represented in green colour on the diagram in Figure 20) is responsible for a significant deeper water source of sediment stabilisation and is interpreted as a stage in structure construction which occurs presumably as a

result of sulfur-reducing bacterial activity (Riding 2000; Dupraz & Visscher 2005; Reid *et al*. 2000, 2003; Visscher & Stolz 2005; Baumgartner *et al*. 2006).

Microbial deposits in Shark Bay are notable not only because of their abundance and variable external morphologies but in view of the diverse microbial communities involved producing very distinctive internal fabrics. This study analysed a sequence of microbial deposits from shallow to deeper water seeking to advance the knowledge of the relationship between fabrics and water depth (Figure 18). Given the sea level regression in the last 2000 years of ~1.5 m, the fabrics were investigated with respect to what extent such variations are reflected in the resultant deposits. In the relatively small number of heads available for study few heads showed only one fabric type and it was clear that the fabrics often related to those formed in water depths >1 m, which are here termed non-laminated cryptomicrobial structures. They are complex with a significant amount of macroscopic eukaryotes responsible for bioturbation, disruption, skeletal framework and detritus accumulation. Within these fabrics, micrite occurs as bio-induced patches and disconnected clots distributed in coarse grainy sediment, resembling structures described as eukaryote stromatolites in the Bahamas (Feldmann & McKenzie 1998). The microbial structures of Hamelin Pool frequently display vertical sequences of internal fabrics revealing a shallowing-up sedimentary sequence, reflecting late Holocene sea level fall and emergence.

Aitken (1967 pp. 1164, 1171) defined thrombolites as 'non-laminated cryptalgal bodies characterised by a macroscopic clotted or spongy fabric… with microfabric consisting of centimetre-sized patches or clots of microcrystalline limestone (grain-size 8-20 microns) with rare clastic particles…'. Kennard & James (1986 pp. 494, 496) later introduced the term mesoclots as 'discrete colonies or growth forms of calcified, internally poorly differentiated, and coccoid-dominated microbial communities' and also proposed the term cryptomicrobial (a modification of cryptalgal from Aitken) fabrics for 'poorly differentiated, either mottled, patchy, or vague sediment fabrics that are attributable to constructional microbial activities, but that have been largely obscured by other organic and inorganic processes'.

Cerebroid structures and microbial pavement have a non-laminated fabric with micritic patches of mesoclots produced by coccoid bacteria. Also when examined in thin-section and SEM the fabrics reveal two micrite generations: a late micrite occurring as bio-induced micrite that envelopes grains and particles and one early micrite that occurs as patches of micrite resulting from peloid micritisation, fusion and recrystallisation (Jahnert & Collins 2012). Because of the absence of clear evidence of coccoid organomineralisation in the patches of micrite in cerebroid and microbial pavement internal fabrics, it was considered appropriate to describe the fabrics as 'cryptomicrobial non-laminated'. Following Shapiro (2000 p. 169) mesoclots are composed of a variety of microstructures including peloids, grumulous fabric, cement, and calcimicrobes…' and on that definition the deeper subtidal structures and fabrics of Shark Bay (bio-induced patches and disconnected clots; see above)
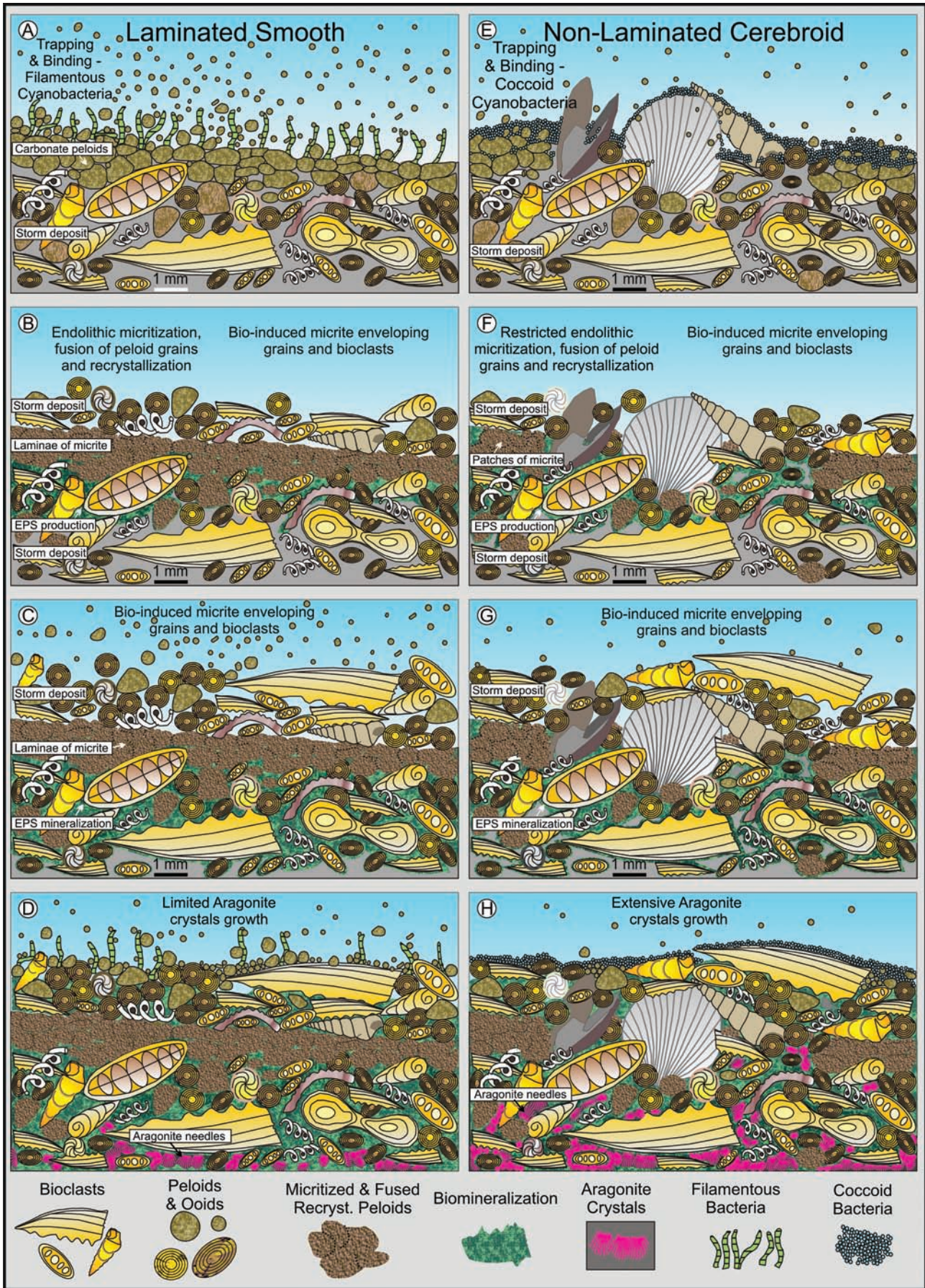
appear suitable to be termed thrombolites, but more investigation and sampling is needed to clarify the matter.

Although the microbial deposits in Shark Bay are referred to as stromatolites (Logan & Chase 1961; Logan *et al*. 1970; Davies 1970a; Playford 1972; Golubic 1973; Logan *et al*. 1974a; Hofmann 1976; Playford & Cockbain 1976; Reid *et al*. 2003 and many others), environmental changes, sea level variation and Bacteria/Archaea and diatoms in diversified communities may provide an explanation for the co-existence of, as reported here, stromatolites, thrombolites and cryptomicrobial deposits growing contemporaneously. Aitken (1967) considered thrombolites as a subtidal phenomenon and stromatolites as intertidal to supratidal deposits. Our investigations have revealed that pustular fabrics are shallow intertidal forms and their vertical growth style produces mesoclotted fabrics and thrombolites; subtidal occurrences have stromatolitic and cryptomicrobial fabrics.

Kennard & James (1986) and Feldmann & MacKenzie (1998) questioned the existence of modern carbonate systems with thrombolites arguing they share calcification with algae or have poorly defined clots which coalesce to form mesoscopic fabric different from the Paleozoic thrombolites. Pustular deposits in Shark Bay are producing mesoclots in an environment controlled by bacteria without any eukaryotic organisms sharing space. Also the modern thrombolite deposits of Lake Clifton and Lake Walyungup located south of Perth, Australia are constructed by classic mesoclots produced by filamentous cyanobacteria. These lacustrine thrombolites occur from shallow to deeper waters, displaying different external morphologies (Moore & Burne 1976), but with the same internal clotted thrombolitic fabric, providing an important example of modern thrombolite deposits.

Logan *et al*. (1974a) recognised that the interaction between microbial mats, sediments and processes of lithification and oxidation affect the deposits creating fenestral fabrics (porosity). Fenestral fabrics constitute an important element with applications in recognition and interpretation of ancient environments. Fenestral fabrics in Shark Bay are irregular within a bushy-like framestone in pustular deposits, a fine to medium subhorizontal laminoid fenestral fabric in smooth deposits and a coarse laminoid porous fabric in colloform deposits. We recognise that subtidal deeper deposits (cerebroid and microbial pavement) will produce an irregular fenestral fabric with voids between skeletal particles and bivalve shells and abundant shelter porosity. The effective

microbial influence and control in some of the subtidal deposits may be difficult to recognise when transformed to rocks because of lack of diagnostic fabrics and the amount of eukaryote skeletons. The presence of *Fragum erugatum,* serpulids, foraminifera, micro-gastropods, crustaceans, *Acetabularia,* Gigartinales, Fucales and bivalve borers living on subtidal buildups obstructs the normal growth of the heads producing irregular surfaces that may cause the head to split into branches, and also disturb and cause disruption of lamination. The peripheral growth of non-calcified algae however protects lower parts of heads from tidal current abrasion and erosion.

CONCLUSIONS

Tidal flats

This study has produced advances in the understanding of the Holocene microbial system and its establishment and development within three distinct tidal flats in Shark Bay (Jahnert & Collins 2013). It provides a new detailed characterisation of the taxonomic grouping of the dominant cyanobacterial consortium whilst describing previously undocumented tidal flat evolution, microbial colonisation and carbonate deposition.

A tentative chronological reconstruction of sea-level events emphasises the late Holocene microbial activity that produces carbonate deposits with distinct macro and microfabrics. These fabrics are related to the different microbial communities inhabiting very specific topographic tidal zones, and their products can be defined as stromatolitic to thrombolitic and cryptomicrobial sediments. Also recognised was the importance of the 'distal' subtidal zone microbial deposits at Nilemah (designated 'microbial pavement') extending to as deep as 6 m. These deposits provide an essential element to the system by consolidating the soft sandy or shelly substrate and thereby providing a hardground as a solid base for microbial head growth.

Environmental differences were recorded between tidal flat waters of different salinity and also in microbial sediments that possess, in permanent hypersaline waters (Nilemah), more positive $\delta^{13}C$ and $\delta^{18}O$ isotopic values and have an older ^{14}C age. In Nilemah's permanently hypersaline domain, extensive subtidal microbial activity and colonisation generated structures (colloform) or spread as cryptomicrobial pavement. In the Garden Point and Rocky Point, tidal flats, where salinity values vary from metahaline to hypersaline, there is incipient colonisation of the subtidal substrate. Smooth mat is

Figure 20 Schematic sequence with the inferred mechanisms involved in the construction of microbial laminated smooth stromatolite (A–D) and non-laminated cryptomicrobial cerebroid (E–H) structures in Shark Bay. Microbial features have been exaggerated in scale for emphasis. In the smooth domain in upper subtidal conditions: (A) After storm activity and carbonate grains/bioclast emplacement, fine material in suspension is deposited creating a layer of peloidal grains with trapping and binding by filamentous microbes; (B) bioturbation, micritisation and fusion of peloids, creating lithified laminae of micrite after recrystallisation; (C) syndepositional processes of micrite generation which envelopes grains (green colour in diagram); (D) the last process is aragonite crystals growing in voids. The constructional process in deeper subtidal heads is: (E) after storms during a limited supply of peloids and over irregular surfaces of heads peloids accumulated in isolated patches, becoming bound by coccoid bacteria; (F) restricted activity of peloid fusion and micritisation; (G) extensive activity of grain/bioclast envelopment by micrite; (H) extensive growth of aragonite crystals filling void spaces. (Jahnert & Collins 2012 figure 16).

present but the subtidal zone does not display any microbial construction and is still receiving sandy influx from offshore (Garden Point) during storm events. In addition, these younger tidal flats are distinguished by seagrass growth at their sublittoral margins. There is also a large amount of quartz sand within the microbial fabrics because of the relatively late onset of microbial activity.

The following processes and findings are fundamental in explaining microbial prosperity in Shark Bay:

(1) Falling sea-levels over the last 6000 years have been responsible for a shallowing in water depth in the embayments and tidal flats, causing a seaward shift of the depositional system. Because of the marine regression, new beach ridges have developed, mainly by longshore currents controlled by southerly winds and high tides in seaward zones. As a result, coastal re-entrances have become protected by north–south-oriented barrier ridges, which restricted water circulation, generating extensive tidal flats exhibiting different stages of evolution and with different stages of microbial colonisation.

(2) A shallowing-up sedimentary cycle was established for the Holocene deposits and correlated with sea-level variations, where microbial sediments aged younger than 2360 (1901 calibrated age) ^{14}C years occupy the upper levels of the sedimentary column. The stressing conditions in the tidal environment were responsible for microbial establishment, trapping and binding or biologically inducing $CaCO_3$ precipitation, and producing laminated stromatolites (tufted, smooth and colloform), non-laminated clotted thrombolites (pustular) and cryptomicrobial non-laminated deposits (blister and pavement).

(3) Tidal flats have low and smooth bottom gradients, varying from 20 to 80 cm/km at Garden Point and Rocky Point and from 20 to 150 cm/km in Nilemah. This low relief is responsible for the restricted tidal influx and well-defined tidal zonation. The intertidal zone occupies 70% of the environment with pustular mat dominance at Garden Point and Rocky Point. At Nilemah, the subtidal environment has significantly more widespread microbial deposits than the intertidal zone. Subtidal microbial deposits at Nilemah grow as mats (smooth) or microbial structures (colloform and microbial pavement) colonising submerged areas (0.5–6.0 m water depth) in the subtidal zone.

(4) Microbial mats living in the supratidal and intertidal zones trap coarse carbonate and quartz grains and bioclastic fragments, in contrast to subtidal systems, which accumulate, after storms, a large amount of very fine to fine grains of carbonate peloids/ooids temporarily suspended by the high-water energy. Filamentous bacteria are the dominant group in the blister, tufted and smooth mats, and coccoid bacteria dominate the pustular, colloform and pavement structures. In the subtidal zone, colloform and microbial pavement structures coexist with other living organisms, such as serpulids, bivalves, diatoms, *Acetabularia*, crustaceans, algae, foraminifera and micro-gastropods, which are responsible for both exoskeleton supply and extensive bioturbation.

(5) Microbial deposits are composed of carbonate grains and quartz, bioclasts, ooids, peloids,

microcrystalline micrite, organic matter and aragonite needles. Fabrics include laminated, sublaminar, scalloped, irregular, cryptomicrobial and clotted, depending on the amount of fine-grained carbonate and bioclasts available, bioturbation intensity, the microbial growth capacity and propensity to trap and bind or induce precipitation of $CaCO_3$.

(6) Relative age and degree of salinity elevation control the contrasting characteristics of the Garden Point–Rocky Point–Nilemah tidal-flat evolutionary sequence. Nilemah tidal flat exhibits the thickest and best-developed microbial system and was established before the other tidal flats, from 2360 years ago, with carbonate sediment composed mineralogically of aragonite with only traces of magnesium-calcite, calcite and gypsum, and revealing more positive values of δ^{13}C and δ^{18}O.

Hamelin Pool

Hamelin Pool is a shallow hypersaline environment with high microbial activity and diversity, and microbial carbonate deposition. The subtidal microbial structures and deposits are in fact, very extensive in the subtidal zone occupying 10 times the area of supratidal and intertidal deposits. More than 80% of microbial deposits occur in the subtidal zone and share space with eukaryotic organisms, especially *Fragum erugatum*. These have developed during the last few thousand years of stable hypersaline conditions and falling sea level. Microbial buildups prosper in water depths to a maximum of 2.5 m, constructing reef framework, although microbial influenced/induced deposits extend as semi-lithified surfaces and hardground to water depths of 6 m. These microbial tabular and blocky pavements occupy more than 220 km².

Subtidal structures are produced by aragonite through processes of trapping and binding particles (agglutination), micritisation, fusion and recrystallisation of peloids as well as presumed biologically-induced carbonate precipitation and lastly aragonite cement filling voids. Microbial structure morphologies consist of ellipsoidal, spherical, calyx, prismatic elongate, ridge-like, compound bladed and domical forms, reaching 1.5 m in height and depending on slope and wave energy or tidal movement, take on varied morphologies or produce widespread underwater pavements. Subtidal microbial structures have a microfabric complex of micritic composition containing ooids, peloids and bioclasts, with bivalves, serpulids, foraminifera, micro-gastropods and secondary quartz grains. *Acetabularia*, Gigartinales, Fucales and some living bivalves are external encrusters on microbial structures.

Subtidal deposits were recognised and mapped based on external organofacies, composition and morphologies as pustular, smooth, colloform, cerebroid, tabular or blocky pavement, bioclastic/peloidal sandflat, subtidal coquina, seagrass domain and bioclastic/ quartz sand. Subtidal structures have distinctive internal fabrics, with aragonitic micrite arranged in millimetric laminae or subspherical micrite patches which have different forms and fabrics such as well laminated (smooth), coarse laminoid (colloform), irregular clotted (pustular) and non-laminated cryptomicrobial (cerebroid and microbial pavement) producing microbial deposits with

stromatolitic fabric (smooth and colloform), thrombolitic fabric (pustular) and cryptomicrobial fabric (cerebroid and microbial pavement).

Finally, this study of microbial system morphogenesis in Hamelin Pool, Shark Bay has redefined the depositional model to include a new subtidal constructional microbial system. The findings emphasise the significance of a Holocene microbial system as one of the most important assets for the interpretation of ancient microbial deposits especially in view of the limited modern examples available to compare with the variety described from the rock record.

ACKNOWLEDGEMENTS

REFERENCES

Aitken J D 1967. Classification and environmental significance of cryptalgal limestones and dolomites with illustrations from the Cambrian and Ordovician of south-western Alberta. *Journal of Sedimentary Petrology* **37**, 1163–1178.

Allen M A, Goh F, Burns B P & Neilan B A 2009. Bacterial, archaeal and eukaryotic diversity of smooth and pustular microbial mat communities in the hypersaline lagoon of Shark Bay. *Geobiology* **7**, 82–96.

Baumgartner L K, Reid R P, Dupraz C, Decho A W, Buckley D H, Spear J R, Przekop K M & Visscher P T 2006. Sulphate reducing bacteria in microbial mats: changing paradigms, new discoveries. *Sedimentary Geology* **185**, 131–145.

Berry P F & Playford P E 1997. Biology of modern *Fragum erugatum* (Mollusca, Bivalvia, Cardiidae) in relation to deposition of the Hamelin Coquina, Shark Bay, Western Australia. *Marine & Freshwater Research* **48**, 415–420.

Burne R V 1992. Lilliput's castles: stromatolites of Hamelin Pool *Landscape* **7**, 34–40.

Burne R V & James N P 1986. Subtidal origin of club-shaped stromatolites, Hamelin Pool. *12th International Sedimentological Congress, Canberra, Abstracts*, p. 49.

Burne R V & Johnson K 2012. Sea-level variation and the zonation of microbialites in Hamelin Pool, Shark Bay, Western Australia. *Marine & Freshwater Research* **63**, 994–1004.

Burne R V & Moore L S 1987. Microbialites: organosedimentary deposits of benthic microbial communities. *Palaios* **2**, 241–254.

Burns B P, Goh F, Allen M & Neilan B A 2004. Microbial diversity of extant stromatolites in the hypersaline marine environment of Shark Bay, Australia. *Environmental Microbiology* **6**, 1096–1101.

Butcher B P, van de Graaff W J E & Hocking R M 1984. Shark Bay–Edel, Western Australia. *Geological Survey* of *Western Australia 1:250 000 Geological Series Explanatory Notes.*

Campbell S E 1982. The modern distribution and geological history of calcium carbonate boring microorganisms. *In*: Westbroek P & De Jong E W (eds) *Biomineralisation and biological metal accumulation*, pp. 99–104. D. Reidel, Dordrecht.

Chivas A R, Torgensen H A & Polach A 1990. Growth rates and Holocene development of stromatolites from Shark Bay, Western Australia. *Australian Journal of Earth Sciences* **37**, 113–121.

Collins L B, Zhao J X & Freeman H 2006. A high-precision record of mid-late Holocene sea-level events from emergent coral pavements in the Houtman Abrolhos Islands, southwest Australia. *Quaternary International* **145/146**, 78–85.

Davies G R 1970a. Carbonate bank sedimentation, eastern Shark Bay, Western Australia. *In:* Logan B W, Davies G R, Read J F & Cebulski D E (eds) *Carbonate sedimentation and environments, Shark Bay, Western Australia*, pp. 85–168. AAPG Memoir **13**.

Davies G R 1970b. Algal-laminated sediments, Gladstone Embayment, Shark Bay, Western Australia. *In:* Logan B W, Davies G R, Read J F & Cebulski D E (eds) *Carbonate sedimentation and environments, Shark Bay, Western Australia,* pp. 168–205. AAPG Memoir **13**.

Decho A W 2000. Microbial biofilms in intertidal systems: an overview. *Continental Shelf Research* **20**, 1257–1273.

Dupraz C & Visscher P T 2005. Microbial lithification in marine stromatolites and hypersaline mats. *Trends in Microbiology* **13**, 429–438.

Dupraz C, Reid R P, Braissant O, Decho A W R, Norman S & Visscher P T 2009. Processes of carbonate precipitation in modern microbial mats. *Earth-Science Reviews* **96**, 141–162.

Feldmann M & McKenzie J A 1998. Stromatolite–thrombolite associations in a modern environment, Lee Stocking Island, Bahamas. *Palaios* **13**, 201–212.

Formigli J M F, Pinto A C C & De Almeida A S 2009. Santos Basin's pre-salt reservoirs development - the way ahead. *Offshore Technology Conference OTC* 19953<http://e-book.lib.sjtu.edu.cn/otc-2009/pdfs/otc19953.pdf>.

Gerdes G 2007. Structures left by modern microbial mats in their host sediments. *In*: Schieber J, Bose P K, Eriksson P J, Banerjee S, Sarkar S, Altermann W & Catenau O (eds) *Atlas of microbial features preserved within the clastic rock record*, pp. 5–38. Elsevier, Amsterdam.

Goh F, Leuko S, Allen M A, Bowman J P, Kamekura M, Neilan B A & Burns B P 2006. *Halococcus hamelinensis* sp. nov., a novel halophilic archaeon isolated from stromatolites in Shark Bay, Australia. *Microbiology* **56**, 1323–1329.

Goh F Q Y 2007. Osmoadaptation mechanisms of cyanobacteria and archaea from the stromatolites of Hamelin Pool, Western Australia. PhD thesis, University of New South Wales, Sydney (unpubl.).

Golubic S 1973. The relationship between blue-green algae and carbonate deposits. *In*: Carr N G & Whitton B A (eds) *Biology of the blue-green algae*, pp. 434–472. Blackwell Scientific Publications, Oxford.

Golubic S 1976a. Organisms that build stromatolites. *In:* Walter M R (ed.) *Stromatolites* (*Developments in sedimentology 20*), pp. 114–126. Elsevier, Amsterdam.

Golubic S 1976b. Taxonomy of extant Stromatolite building Cyanophytes. *In:* Walter M R (ed.) *Stromatolites* (*Developments in sedimentology 20*), pp. 127–140. Elsevier, Amsterdam

GOLUBIC S 1980. Early photosynthetic microorganisms and environmental evolution. *In*: Holmquist R (ed.) *Life Science and Space Research. COSPAR*, 18, pp. 101–107. Pergamon Press, Oxford.

GOLUBIC S 1982. Stromatolites, fossil and recent: a case history. The modern distribution and geological history of calcium carbonate boring microorganisms. *In*: Westbroek P & De Jong E W (eds) *Biomineralisation and biological metal accumulation*, pp. 313-326. D. Reidel, Dordrecht.

GOLUBIC S & HOFMANN H J 1976. Comparison of Holocene and Mid-Precambrian Entophysalidaceae (Cyanophyta) in stromatolitic algal mats; cell division and degradation. *Journal of Paleontology* 50, 1074–1082.

GRAMMER G M, HARRIS P M & EBERLI G P 2004. Overview and examples from the Bahamas. *In*: Grammer G M, Harris P M & Eberli G P (eds) *Integration of outcrop and modern analogs in reservoir modeling*, pp. 1–22. AAPG Memoir 80.

HOCKING R M, MOORS H T & VAN DE GRAAFF W J E 1987. Geology of the Carnarvon Basin Western Australia. *Geological Survey of Western Australia Bulletin* 133.

HOFFMAN P 1976. Stromatolite morphogenesis in Shark Bay, Western Australia. *In:* Walter M R (ed.) *Stromatolites (Developments in sedimentology 20)*, pp. 261–272. Elsevier, Amsterdam.

JAHNERT R J & COLLINS L B 2011. Significance of subtidal microbial deposits in Shark Bay, Australia. *Marine Geology* 286, 106–111.

JAHNERT R J & COLLINS L B 2012. Characteristics, distribution and morphogenesis of subtidal microbial systems in Shark Bay, Australia. *Marine Geology* 303/306, 115–136.

JAHNERT R J & COLLINS L B 2013. Controls on microbial activity and tidal flat evolution in Shark Bay. Western Australia. *Sedimentology* 60, 1071–1099.

JAHNERT R J, DE PAULA O, COLLINS L B, STROBACH E & PEVZNER R 2012. Evolution of a coquina barrier in Shark Bay, Australia by GPR Imaging: architecture of a Holocene reservoir analog. *Sedimentary Geology* 281, 59–74.

JOHN J 1993. Morphology and ultrastructure of the tubes of *Mastogloia cocconeiformis* (Bacillariophyta) from Shark Bay, Western Australia. *Phycologia* 32, 388–394.

JOHNSON T C, BARRY S L, CHAN Y & WILKINSON P 2001. Decadal record of climate variability spanning the past 700 yr in the Southern Tropics of East Africa. *Geology* 29, 83–86.

KARAJAS J & KERNICK C N 1984. A prospective Nita Formation reservoir trend on the Broome Platform. *In*: Purcell P G (ed.) *The Canning Basin, W.A.*, pp. 169–177. Geological Society of Australia and Petroleum Exploration Society of Australia, Canning Basin Symposium, Perth.

KENNARD J M & JAMES N P 1986. Thrombolites and stromatolites: two distinct types of microbial structures. *Palaios* 1, 492–503.

KERRICK D M 2001. Present and past nonanthropogenic CO_2 degassing from the solid Earth. *Reviews of Geophysics* 39, 565–585.

KREUTZ K J, MAYEWSKI P A, MEEKER L D, TWICKLER M S, WHITLOW S I & PITTALWALA I I 1977. Bipolar changes in atmospheric circulation during the Little Ice Age. *Science* 277, 1294–1296.

LOGAN B W 1961. *Cryptozoon* and associate stromatolites from the Recent, Shark Bay, Western Australia. *Journal of Geology* 69, 517–533.

LOGAN B W 1968. Western Australia *In:* Gill E D (ed.) *Quaternary shoreline research in Australia and New Zealand*, p. 110. Australian Journal of Science 31.

LOGAN B W & CHASE R L 1961. The stratigraphy of the Moora Group. *Journal of the Royal Society of Western Australia* 44, 14–31.

LOGAN B W & CEBULSKI D E 1970. Sedimentary environments of Shark Bay, Western Australia. *In:* Logan B W, Davies G R, Read J F & Cebulski D E (eds) *Carbonate sedimentation and environments, Shark Bay, Western Australia*, pp. 1–37. AAPG Memoir 13.

LOGAN B W, DAVIES G R, READ J F & CEBULSKI D E 1970. Carbonate sedimentation and environments, Shark Bay, Western Australia. *AAPG Memoir* 13.

LOGAN B W, HOFFMAN P & GEBELEIN C D 1974a. Algal mats, cryptalgal fabrics, and structures, Hamelin Pool, Western Australia. *In:* Logan B W, Read J F, Haga G M, Hoffman P, Brown R G, Woods P J & Gebelein C D (eds) *Evolution and diagenesis of Quaternary carbonate sequences, Shark Bay, Western Australia*, pp. 140–194. AAPG Memoir 22.

LOGAN B W, READ J F, HAGA G M, HOFFMAN P, BROWN R G, WOODS P J & GEBELEIN C D 1974b. Evolution and diagenesis of Quaternary carbonate sequences, Shark Bay, Western Australia. *AAPG Memoir* 22.

MACINTYRE I G, PRUFERT-BEBOUT L & REI P R. 2000. The role of endolithic cyanobacteria in the formation of lithified laminae in Bahamian stromatolites. *Sedimentology* 47, 915–921.

MOORE L S & BURNE R V 1994. The modern thrombolites of Lake Clifton, Western Australia. *In*: Bertrand-Sarfati J & Monty C (eds) *Phanerozoic stromatolites II*, pp. 3–29. Springer, Netherlands.

O'LEARY M J, HEARTY P J & MCCULLOCH M T 2008. U-series evidence for widespread reef development in Shark Bay during the last interglacial. *Palaeogeography, Palaeoclimatology, Palaeoecology* 259, 424–435.

PAPINEAU D, WALKER J J, MOJZSIS S J & PACE N R 2005. Composition and structure of microbial communities from stromatolites of Hamelin Pool in Shark Bay, Western Australia. *Applied and Environmental Microbiology* 71, 4822–4832.

PAUL J & PERYT T M 2000. Kalkowsky's stromatolites revisited (Lower Triassic Buntsandstein, Hartz Mountains, Germany). *Palaeogeography, Palaeoclimatology, Palaeoecology* 161, 435–458.

PENTECOST A 1991. Calcification processes in algae and cyanobacteria. *In*: Riding R (ed.) *Calcareous algae and stromatolites*, pp. 1–19. Springer-Verlag, Berlin.

PLAYFORD P E 1972. Algal stromatolites in the Devonian of the Canning Basin, Western Australia. *Annales de la Societe geologique de Belgique* 95, 401–402.

PLAYFORD P E 1979. Stromatolite research in Western Australia. *Journal of the Royal Society of Western Australia* 62, 13–20.

PLAYFORD P E 1990. Geology of the Shark Bay area, Western Australia. *In:* Berry P F, Bradshaw S D & Wilson B R (eds) *Research in Shark Bay. Report of the France-Australe Bicentenary Expedition Committee*, pp. 13–31. Western Australian Museum, Perth.

PLAYFORD P E & COCKBAIN A E 1976. Modern algal stromatolites at Hamelin Pool, a hypersaline barred basin in Shark Bay, Western Australia. *In:* Walter M R (ed.) *Stromatolites (Developments in sedimentology 20)*, pp. 389–411. Elsevier, Amsterdam,

PLAYFORD P E, COCKBAIN A E, BERRY P F, ROBERTS A P, HAINES P W & BROOKE B P 2013. The Geology of Shark Bay. *Geological Survey of Western Australia Bulletin* 146.

POPE M & READ J F 1998. Ordovician metre-scale cycles: implications for climate and eustatic fluctuations in the central Appalachians during a global greenhouse, non-glacial to glacial transition. *Palaeogeography, Palaeoclimatology, Palaeoecology* 138, 27–42.

READ J F 1976. Calcretes and their distinction from stromatolites. *In:* Walter M R (ed.) *Stromatolites (Developments in Sedimentology 20)*, pp. 55–71. Elsevier, Amsterdam.

REID R P, JAMES N P, MACINTYRE I G, DUPRAZ C P & BURNE R V 2003. Shark Bay stromatolites: microfabrics and reinterpretation of origins. *Facies* 49, 299–324.

REID R P, VISSCHER P T, DECHO A W, STOLZ J F, BEBOUTK B M, DUPRAZ C, MACINTYRE I G, PAERL H W, PINCKNE J, PRUFERT-BEBOUTK L, STEPPE T F & DESMARAISK D J 2000. The role of microbes in accretion, lamination and early lithification of modern marine stromatolites. *Nature* 406, 989–992.

RIDING R 1991. Classification of microbial carbonate. *In*: Riding R (ed.) *Calcareous algae and stromatolites*, pp. 21–51. Springer-Verlag, Berlin.

RIDING R 2000. Microbial carbonates: the geologic record of calcified bacterial–algal mats and biofilms. *Sedimentology* **47**, 179–214.

STAL L G 1994. Microbial mats: ecophysiological interactions related to biogenic sediment stabilisation. *In*: Krumbein W G, Paterson D M & Stal L G (eds) *Biostabilisation of sediments*, pp. 41–53. University of Oldenburg, Oldenburg.

SHAPIRO R S 2000. A comment on the systematic confusion of thrombolites. *Palaios* **15**, 166–169.

VAN DE GRAAFF W J E, HOCKING R M & BUTCHER B P 1983. Yaringa, Western Australia. *Geological Survey of Western Australia 1:250 000 Geological Series Explanatory Notes*.

VASCONCELOS C, WARTHMANN R, McKENZIE J, VISSCHER P T, BITTERMANN A G & VAN LITH Y, 2006. Lithifying microbial mats in Lagoa Vermelha, Brazil: modern Precambrian relics? *Sedimentary Geology* **185**, 175–183.

VISSCHER P T, REID R P & BEBOUT B M 2000. Microscale observations of sulphate reduction: correlation of microbial activity with lithified micritic laminae in modern marine stromatolites. *Geology* **28**, 919–922.

VISSCHER P T & STOLZ J F 2005. Microbial mats as bioreactors: populations, processes and products. *Palaeogeography, Palaeoclimatology, Palaeoecology* **219**, 87–100.

WALTER M R 1999. *The search of life on Mars*. Allen & Unwin, St Leonards.