EDIMENTOLOGY

Modelling Ediacaran metazoan-microbial reef growth

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ABSTRACT

Throughout the Phanerozoic, sessile metazoans grew in close association with various microbial carbonates to form reefs. The first metazoans with calcareous hard-parts appeared in the terminal Ediacaran, ca 550 million years ago, and these also commonly grew associated with microbial mats, thrombolites and stromatolites, to form the oldest known metazoan-microbial reefs. These hardparts also formed the first skeletal (bioclastic) carbonate sediments, which increased to dominate shallow marine carbonate sedimentary production during the Phanerozoic. Here the growth dynamics and sedimentary interactions between Ediacaran microbial-metazoan reefs and their bioclastic products are described based on reef complexes from the Nama Group, Namibia (ca 547 Ma), and the first three-dimensional numerical models are constructed to parametrize these dynamics. These reefs are observed to form large domal mounds and columns neighbouring locally high rates of bioclastic sediment accumulation, and commonly evolve to flat-topped surfaces overlain by sediment. This model is parsimonious, embodying a single dynamic rule: metazoans attach to microbialite mounds which grow radially into free space shedding bioclasts in proportion to metazoan production. Models evolve mounds into columns due to spatial competition, and produce an oscillating interplay between mound expansion and smothering that results in an interfingering of microbialite mound and detrital sediment. This dynamic is shown to be non-linear in the proportion of bioclastic sediment produced. Smothering by bioclastic sediment is also demonstrated to both reduce the rate (by volume) of subsequent mound growth, and to overwhelm the growing mat surfaces of stromatolites: after a threshold is reached in the rate of bioclastic sediment deposition, sediment terminates all stromatolite growth. These models show that the general characteristics of field observations can be explained by a single dynamic rule, and that reef-sourced bioclasts may make an important local contribution to Ediacaran to Cambrian microbial-metazoan reef dynamics - a contribution that remains important throughout the Phanerozoic.

Keywords Bioclasts, Ediacaran, metazoan, microbialite, modelling, reefs.

INTRODUCTION

Reefs are biogenic carbonate structures that form topographic relief on the seafloor (Wood, 1999).

Most reefs have variable contributions from both skeletal components (either metazoan or algal) and microbially-mediated carbonate, as well as inorganic cements, which are often synsedimentary. The ecological consortium between skeletal material and microbial-mediated precipitates, although varying in relative contributions, shows a persistent association throughout the Phanerozoic. Yet the origins of this association are found in the terminal Ediacaran.

Prior to the rise of skeletal metazoans, carbonate platforms were dominated by stromatolites (lithified laminated organosedimentary deposits produced by the sediment trapping, binding, and/or precipitation activities of microbial communities) and increasingly in the terminal Ediacaran, thrombolites (macroscopically-clotted microbial carbonate) (Grotzinger & Knoll, 1999). Quantitative analyses suggest that after reaching a peak of abundance in the Proterozoic where microbialites (organosedimentary deposits produced by benthic microbial communities (modified from Burne & Moore, 1987) formed widespread reefs on shallow marine carbonate platforms (Grotzinger & James, 2000), microbialites declined in both abundance and diversity, first during the early Neoproterozoic, and then dramatically at the end of the Proterozoic (e.g. Awramik, 1971; Grotzinger & Knoll, 1999). This may have occurred over a protracted interval from 700 to 541 Ma (Peters et al., 2017), or more abruptly (Awramik & Sprinkle, 1999). Many of the changes in stromatolite growth style, and in carbonate sedimentology in general, which accompany the Proterozoic/Phanerozoic transition, have been proposed to be the consequence of metazoan and metaphyte evolution, including the evolution of biomineralization (Knoll & Swett, 1990).

The first known metazoans with calcareous hard-parts appear globally in the terminal Ediacaran, ca 550 to 540 Ma. This was coincident with the widespread appearance of thrombolites (Grotzinger & Knoll, 1999). Skeletal metazoans often grew associated with microbial carbonates to create the first metazoan reefs, and also formed the first documented skeletal carbonate (bioclastic) sediments (Wood, 2011; Warren et al., 2013). These taxa essentially colonized pre-existing stromatolitic and particularly thrombolitic reef structures, but little is known about the sedimentary dynamics of the oldest known examples of this important system: metazoan-microbialite reefs with self-sourced bioclastic sediment. Here these dynamics are explored through new field observations and novel three-dimensional (3D) numerical modelling.

Microbial carbonate modelling to-date

The fundamental parameters of microbialite (stromatolite, thrombolite or other microbial precipitate) growth are the balance of microbial growth processes, rates of early lithification, aspects of the hydrodynamic regime such as scour, and rates of sedimentation. When sedimentation rates exceed a (currently unknown) critical threshold, sediment accumulation will overwhelm microbial mat growth (Grotzinger & Knoll, 1999; Johnson & Grotzinger, 2006). It has been suggested that the rise of bioclasts and pellets in the latest Proterozoic increased rates of carbonate sedimentation so restricting the habitat of stromatolite growth, particularly in tidal settings (Pratt, 1982). Yet, little is currently known as to either the specific response times or the relevant timescales for the interaction of these microbial-precipitation-sediment processes (Grotzinger & Knoll, 1999).

Most stromatolite models implement a set of rules in an attempt to explain observed growth relations (e.g. Drummond & Dugan, 1999) or to recreate certain physical processes of either sedimentation or stromatolite growth (Grotzinger & Rothman, 1996; Batchelor et al., 2000). Microbialites grow elevated away from a point or limited surface of initiation (Grotzinger & Knoll, 1999). Models show that an initially rough surface grows with constant velocity normal to all local surfaces; over time and with continued sedimentation larger domes overtake smaller domes leading to a smoother interface with a reduced number of broader domes (Grotzinger & Rothman, 1996). Branching in stromatolites can occur where topographic lows are preferentially filled by sediment, leaving only high points free for continued growth (Grotzinger & Knoll, 1999). Scour by moving sediments can prevent mat growth between individual stromatolite columns, and the characteristic convex-upward form of columnar stromatolites may be due, at least in part, to the reduced abrasion on topographic highs (Bosak et al., 2013).

Simulations of generic microbial mound growth in 3D were used to quantify the distribution of internal primary porosity and permeability using the stratigraphic forward modelling (SFM) program Sedsim (Griffiths *et al.*, 2012). Two-dimensional numerical simulations have been used to explain the internal growth dynamics of a single columnar thrombolite–stromatolite reef from the Nama Group (Johnson & Grotzinger, 2006) where the thrombolite–stromatolite inter-fingers with carbonate mudstones, grainstones and fine-grained terrigenous sediments. Here two stromatolite growth rules were used: (i) that growth preferentially occurs on broad topographic highs, because topographic lows preferentially accumulate sediment; and (ii) growth only occurs on carbonate sediment, not on siliciclastic mud (i.e. now shale). Lateral and vertical growth rules for the reef facies were also added, including that when stromatolites abut against carbonate sediments then lateral reef growth occurs as one horizontal grid spacing per timestep over those carbonates, which forces active stromatolite growth and sediment to be the same elevation. These models demonstrated how the input of different sediment types correlates with changes in reef growth, in particular column width and individual reef thickness. Stromatolite columns that grew during siliciclastic mud deposition are narrower and more widely spaced than columns grown during carbonate deposition, and the ratio of stromatolite column width to fill width tends to increase with carbonate sedimentation. Reef bed thicknesses are also larger during carbonate deposition than siliciclastic mud deposition.

Aims of this study

To date, no models exploring the interaction of microbialite mound growth and surrounding sediment have been produced in 3D, nor do they consider the impact of reef-sourced, bioclastic sediment. Modelling geological phenomena in three dimensions is critical for the study of natural processes: the space-filling properties of geometries such as domes and columns change significantly between two and three-dimensional domains, and so also does the surface area available for metazoan colonization and the volume of space available for sediment accumulation.

While some conclusions from simulations in 2D might mirror those produced from 3D models, the geometrical spreading (and hence rate of volumetric increase) of each microbial mound over time is very different in 2D versus 3D, as are the mound geometries generated. For example, in 2D one mound may abut others on either side and so be precluded from lateral growth; in 3D that same mound might grow continuously in the other horizontal dimension from the start to the end of the simulation. This in turn radically changes the amount of bioclastic sediment shed by that mound in 2D and 3D simulations, and hence whether and when this and other mounds are smothered. Since the real world exists in 3D, it therefore only makes sense to examine the non-linear relationship between bioclastic sediment production rate and emergent mound and sediment geometries in 3D simulations.

The aims of this work are four-fold. First, to present new field evidence that attests to: (i) the principal 3D growth patterns of microbialite mounds; (ii) the metazoan colonization of these mounds; and (iii) the corresponding bioclastic sedimentary accumulation between mounds, in a terminal Ediacaran reef system from the Nama Group, Namibia.

Second, the hypothesis is tested that the general character of local mound geometry and sedimentary accumulation patterns can be reproduced using a parsimonious (Occam's razor) approach, specifically that a single dynamic rule can explain the observed relationships between mat growth, metazoan colonization and bioclastic sediment accumulation.

Third, the nature of the relationship between the proportion of reef metazoans that contribute bioclastic sediment, the background sedimentation rate, and the local geometry of mounds produced, is explored.

Finally, these enable testing of the hypothesis that self-sourced reef bioclastic sediment had no impact on the geometry of mounds observed in this period of the geological record. This hypothesis is disproved.

GEOLOGICAL SETTING

The Nama Group, Namibia

The Nama Group (*ca* 550 to 539 Ma) is a terminal Ediacaran to Cambrian ramp succession of mixed clastics and carbonates deposited in supratidal to subtidal, inner to outer ramp settings under varying hydrodynamic conditions (Grotzinger & Miller, 2008). The Nama Group was deposited across the Zaris and Witputs subbasins separated by the tectonic Osis Arch (Fig. 1A), and strata have been correlated over many hundreds of kilometres using sequence stratigraphy, chemostratigraphy and dated ash beds (Saylor *et al.*, 1995; Grotzinger *et al.*, 1995; Saylor *et al.*, 1998).

Here, observations are made at the Driedoornvlakte reef complex from the far north of the Zaris sub-basin (Fig. 1A), which formed during deposition of the Omkyk Member within the



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Fig. 1. Location and stratigraphic setting of the Nama Group, Namibia. (A) Simplified map showing geological setting, subgroups and sub-basins of the late Ediacaran to early Cambrian Nama Group of southern Namibia, with the location of Driedoornvlakte reef complex. (B) Stratigraphic log of the Omkyk Member at the Driedoornvlakte isolated carbonate platform showing concurrent slope and basinal shale and overlying shale of the Urikos Member (after Adams *et al.*, 2004) with metazoan fossil distribution: B = Boundstone; G = Grainstone; P = Packstone; M = mud/clay. (C) Geological map of the Driedoornvlakte isolated carbonate platform with farm boundaries and road numbers, showing position (yellow boxes) of studied areas 1 and 2 in Unit 3M (after Adams *et al.*, 2004). Modified from Wood *et al.* (2018).

Kuibis Subgroup (Fig. 1B). Driedoornvlakte is an isolated reef complex with a tectonic dip ca 40 degrees to the south, which hosts the oldestknown stromatolitic and thrombolitic (henceforth termed microbialite) mounds associated with skeletal metazoans - Cloudina. Namacalathus and Namapoikia (Fig. 2A to C; Wood et al., 2002; Grotzinger et al., 2005; Wood, 2011; Penny et al., 2014; Wood & Curtis, 2015). Cloudina and Namacalathus colonized the surfaces of microbialites, and their bioclastic debris accumulated between mounds: Namapoikia encrusted the walls of synsedimentary reef fissures (Neptunian dykes) (Fig. 2D).

Driedoornvlakte is an isolated carbonate platform approximately 10 km in length and ca 500 m thick (Figs 1C, 3A and 3B) that grew in a generally high-energy, mid-ramp setting (Adams et al., 2004). Uranium-lead dating of an ash bed in the immediately overlying lower Hoogland Member from the Zaris sub-basin yields an age of 547.32 ± 0.65 Ma (Bowring *et al.*, 2007). Driedoornvlakte records deposition during the Lower Omkyk (OS1) and Upper Omkyk (OS2) members, but the stratigraphic thickness of OS2 is markedly expanded relative to up dip sections, inferred to be due to foreland basin subsidence as a result of proximity to the Damara orogen (Grotzinger & Miller, 2008). Driedoornvlakte carbonate platform growth kept up with a trend of increasing subsidence and hence relative sea-level rise during deposition of OS2, and can be divided into three cycles (Units 1 to 3) which each represent successively expanded stratigraphic thicknesses (Fig. 1B and C) (Adams et al., 2004).

Microbial-metazoan reefs at Driedoornvlakte grew in association with coalesced thrombolitestromatolite (microbialite) mounds of the final cycle of reef growth (Unit 3M; Figs 1B, 3A, 3C and 3D), representing a *ca* 50 m thick transgressive succession which formed in an energetic, shallow subtidal setting immediately prior to drowning (Grotzinger *et al.*, 1995; Adams *et al.*, 2004). The inferred accommodation increase during deposition of Unit 3M is based upon an observed increase in size and relief of coalesced microbialite mounds (Fig. 3A, C and D), and the formation of synsedimentary fissures and collapse breccias as a result of frequent reworking by currents and waves (Adams *et al.*, 2004). Driedoornvlakte was eventually drowned by the fine, basinal siliciclastics of the Urikos Member, equivalent to carbonate production of OS2 Units 4 and 5 in shallower sections to the south (Smith, 1998; Adams *et al.*, 2004, 2005; Dibenedetto & Grotzinger, 2005).

METHODS

First, the growth dynamics of in situ microbialmetazoan (Cloudina and Namacalathus) reefs is documented as revealed in 2D outcrops on the south-east flank (study area 1) of the reef complex on Farm Driedoornvlakte, and in an isolated reef (study area 2), both within the *ca* 50 m thick mixed microbial-metazoan Unit 3M (Fig. 1C). Second, these microbialite-sediment interactions are modelled numerically to understand the dynamic interaction between microbialite growth, metazoan contribution to microbialite growth, and the effects of surrounding bioclastic sediment accumulation. These models are now explained in more detail.

Modelling three-dimensional microbialite and bioclastic sediment interactions

The model was coded in MATLAB®, and the source code is provided as Supplementary Material. Both the uppermost sediment height and the radius of each growing microbial mound take arbitrary real values which evolve during each simulation. The model output is parameterized on a regular, square, three-dimensional grid of cells, each of which is assigned the value of sediment or mound number once the majority of



Fig. 2. Terminal Ediacaran reef-associated skeletal metazoans: (A) *Cloudina*; (B) *Namacalathus*; (C) *Namapoikia*. Scale bars = 20 mm. (D) Reconstruction of a late Ediacaran microbialite-metazoan reef: 1 – thrombolite; 2 – Neptunian dyke; 3 – stromatolite; 4 – *Cloudina*; 5 – *Namapoikia*; 6 – *Namacalathus*; 7 – cement botryoids; 8 – trapped *Namacalathus*; 9 – sediment. From Penny *et al.* (2014); Copyright John Sibbick.



Fig. 3. Field photographs, Driedoornvlakte reef complex: (A) view looking westward along ridge which marks the youngest part of the complex from Unit 31 and 3M; (B) interior of complex looking west along ridge to *ca* 3 km; (C) study area 1, Unit 3M of coalesced microbialite mounds, geologists for scale, *ca* 1.8 m tall; (D) drone image of study area 2, Unit 3M showing an isolated large reef composed of coalesced microbialite mounds.

that cell volume is filled with the respective product.

Dynamics

A parsimonious approach to geological process modelling is followed, where microbialite growth is assumed to be subject to only one dynamic rule: *metazoans attach to microbialite mounds which grow radially into free space shedding bioclasts in proportion to metazoan production.* The models also allow for additional *background* sedimentation at a constant rate.

Ediacaran skeletal fauna attach to algal mats, thus they are both incorporated within microbialite mounds and observed to contribute *bioclasts* to sediment (Wood & Curtis, 2015). The relative proportion of skeletal material that remains bound within mounds compared to its contribution to bioclastic sediment is unknown, so here the *bioclastic* contribution is modelled as a constant proportion of the rate of total microbialite accumulation, where the latter is defined to include incorporated bioclasts. The overall volume of available sediment is distributed in topographic lows up to a constant height across the model, thus neglecting topographic effects due to sedimentary redistribution.

The model is thus governed by a dynamic rule that produces kinematic effects: it describes emergent changes in the geometrical form of microbialite and sediment which can partially be observed. It is not designed to model specific,

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observed microbialites because this would require knowledge of nucleation sites that lie outside of 2D field exposure planes. This study does not include the effects of strong currents which might redistribute sediment and impose significant directivity on the flow of nutrients, but does allow background sedimentation of more mobile sediments contributed from elsewhere. Despite such limitations, it is shown that these simple controls can explain a variety of observed large-scale Ediacaran microbialite reef topologies and bioclast distribution.

Implementation

The model is discretized spatially as a regular grid of cuboid cells, the base of which consists of square cell faces oriented horizontally. Time is represented at constant intervals of length equal to the time to produce one microbialite growth increment. Neither the spatial nor temporal discretization is given physical units so the model can be scaled to any spatiotemporal interval. Mound nuclei are initially distributed randomly in space (with an equal probability of nucleation at any location) on horizontal seafloor topography, and have randomly chosen initial sizes with radii between one and 10 spatial cells to create an undulating initial topography. All results reported herein are found to be robust to changes in these initial conditions provided that at least *ca* 10 mounds are initiated.

The growth rate of mound surfaces, the proportion of mound growth that contributes as bioclasts, and the background sedimentation rate are modelled as spatiotemporally constant and these are the only remaining free parameters. Erosion is assumed to be negligible over the period modelled, and additional mounds are not nucleated dynamically during model runs as the controls on nucleation on Ediacaran substrates are not known.

The model builds 3D structures iteratively, simulating a fixed total number of time steps. If the time step is given specific dimensions, this corresponds to simulating a given interval of geological time.

In each time step, mound surfaces grow radially from their nuclei at the specified growth rate, and only into free space. The radius of each mound in turn is incremented, and each cell additionally spanned by the current mound is tested: if it is already filled with either sediment or material from another mound then no new mound growth extends to that cell. If the cell is currently unassigned (more than 50% of its volume was free space in the previous iteration), and as a result of radial increment the current mound spans more than 50% of its volume, that cell is assigned to the current mound. The total volume of microbialite growth in the current iteration is calculated.

In each time step, background sediment is contributed at the specified rate, and bioclastic sediment is contributed at the specified proportion of the total microbialite growth volume. The latter effectively incorporates two numbers: the volume of mound growth attributable to attached metazoans, and the volumetric proportion of those metazoans that contributed bioclastic material to sediment rather than to the mound. Since these are confounded in 2D field observations (from which no proportion of incorporated versus detrital skeletal matter can be calculated), only their product is used in the model.

The total budget of additional sediment is then distributed into topographic lows created by mound surfaces and pre-existing sediment. The top surface of existing sediment is parametrized by a single number – the height of the horizontal sedimentary surface (which may be a fraction of a cell height). Given the total top-sediment surface area available, the height is increased so as to accommodate the sedimentary budget for the current iteration, taking care to adjust for changes in horizontal surface area with height due to mound topography.

RESULTS

Field observations of Ediacaran microbialitemetazoan growth

Microbialites in Unit 3M form elliptical mounds up to 10 m high and 20 m in diameter, and columns from 5 to 50 cm wide. Individual mounds may have an internal structure of columns (Fig. 4A). Microbialites can coalesce to produce near-continuous structures with their long axes displaying a strong orientation parallel to the inferred palaeoshoreline (now about north-east/ south-west) (Wood *et al.*, 2002).

Cloudina and *Namacalathus* debris can locally form extensive bioclastic packstone and grainstone sediments, which often surround microbialite structures (Fig. 4A and B). Individual beds can reach 0.5 m thick and form stacked packages many metres in thickness. Skeletal debris is mainly whole, with clasts usually ranging from 10 to 70 mm long (*Cloudina*), and 7 to



Fig. 4. Field photographs of study area 1, Driedoornvlakte reef complex, Ediacaran Nama Group, Namibia. (A) Columnar microbialites ('C') at top of microbialites mound, smothered by bioclastic sediment ('S'). (B) Columnar microbialites ('C') surrounded by bioclastic grainstone sediment ('S') dominated by large *Cloudina*. (C) Microbialites columns ('C') with bioclastic sediment ('S'). Black arrows show *in situ Cloudina* within columns. White arrow indicates growth direction. (D) Black arrows showing *in situ Cloudina* within microbialite mound. White arrow indicates growth direction.

35 mm long (*Namacalathus*), which show limited evidence of significant transport.

Cloudina and *Namacalathus* also grow *in situ* attached to, or within, stromatolite mounds and other microbial surfaces, often also in significant quantities and volumes (Fig. 4C and D). *Cloud-ina* and *Namacalathus* may also have lived as dense thickets on the sea floor, perhaps attached to microbial mats, but this ecology remains unproven (e.g. Cai *et al.*, 2014; Mehra & Maloof, 2018).

Some key dynamic features of the relationship between the microbialite mounds and bioclastic sediment are noted. Mounds can grow over other mounds to coalesce, appearing to truncate growth of the latter to produce near-continuous structures. Domes and mounds are commonly steep-sided and separated by narrow, shallowsediment filled depressions (Fig. 4C). At Driedoornvlakte, mounds are separated by packages of often bioclastic deposits that form either columnar-shaped accumulations (Figs 4C and 5A), or cover large areas to create laterally extensive beds (Fig. 5A). At least in the plane of exposure, bioclastic sediment can be deposited over mounds, which appears to truncate mound growth (Figs 5A and 6C); and vice versa – microbialite mounds can encroach over sediment forming successive laminae that create stacked sedimentary packages (Fig. 5B). Where microbialite growth effectively inter-fingers with the intervening depression containing bioclastic



Fig. 5. (A) Drone image of field outcrop surface of study area 1 approximately perpendicular to bedding. Driedoornvlakte reef complex, Ediacaran Nama Group, Namibia. Showing nucleating hemispherical microbialite mounds, boundaries denoted by dashed lines. Mounds are composed of microbialite columns, some inclined to vertical, with intervening packages of sediment between columns and mounds, and some forming laterally extensive sheets. (B) Steeply-dipping edge of hemispherical microbialite mound ('M'), packages of bioclastic sediment ('S'), and microbialite column bounded by sediment packages ('C'). Dotted lines trace timelines between microbialite column laminae and bioclastic sediment, study area 2. Width of foreground = $ca \ 0.5 \ m$. (C) Top of hemispherical microbialite mounds ('M'), covered by bioclastic sediment ('S'), study area 2. Width of foreground = $ca \ 2 \ m$.

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Fig. 6. Example 3D model initiated with 100 random mounds. Grey scale differentiates different mounds, and all free space represents sediment: although the volume is a solid $60 \times 60 \times 100$ unit block only microbialite are displayed. All microbialite die at a height of around 92 units, so the upper eight units are filled with sediment. Arrow 1: transition from domal to sub-horizontally layered. Arrow 2: demise of the mound at extreme right. Arrow 3: demise of all remaining mounds.

inter-mound sediment, microbialite laminae can be traced from the sides of adjacent steep mound walls into the growing depression (Fig. 5B). In many examples noted, the inter-reef sediment thickness between successive laminae far exceeds the equivalent mound growth (Fig. 5B). The relative growth rates of the microbialite versus bioclastic inter-reef sediment can thus be measured, yielding a mound to bioclastic sediment rate ratio of up to 1 : 1.8.

Three-dimensional modelling outputs

The numerical model was run for a number of different scenarios initiated with between 10 and 100 mounds across a grid of cells of dimension 60×60 in the horizontal plane. The results presented here are robust features of all runs other than pathological cases in which all mounds are initiated very close together in one sector of the plane. Such cases are almost guaranteed never to occur by random chance: for example, the probability that all of *n* mounds are located within a 30×30 sub-area of the 60×60 grid is less than (900/3600)^{*n*} which even for only 10 mounds is *ca* 10^{-6} . Therefore, the results presented here are regarded as representative.

The model always produces both mound and columnar reef geometries, depending on the time since nucleation (Fig. 6). Mounds initially grow as dome-like forms due to the dominance of radial growth processes but after a while (Fig. 6, arrow 1) their sphericity becomes irrelevant as competition for free space limits lateral expansion; exposed surfaces then all become sub-horizontal (observable at arrows 2 and 3). Thereafter, all growth is essentially sub-vertical creating columnar reef structures.

Mounds are surrounded by background and self-sourced bioclastic sediment. If the total sedimentary volume exceeds inter-mound space, residual sediment laps over mounds. This decreases the total exposed mound surface area and hence subsequent mound and bioclastic production. It is also possible that one or more mounds is entirely smothered after which growth ceases since it can no longer expand into free space (Fig. 6, arrow 2). The rates of total sedimentary deposition relative to mound and metazoan skeletal growth dictates whether mounds remain emergent or are submerged by sediment.

An oscillating interplay is noted between mound expansion and smothering that results in an inter-fingering of microbialite mound and

Fig. 7. Vertical cross-sections through a typical 3D model. Top: grey scale represents different mounds and white represents sediment. Bottom: contours of time step of deposition, of either sediment or microbialite.

detrital sediment (Fig. 7), as observed in the field (Fig. 5B). After a certain point, mound growth and bioclastic sediment deposition reach some kind of apparent dynamic equilibrium where growth and deposition approximately balance, during which stable growth leads to columnar structures. This process nevertheless retains some potential to become unstable over longer timescales within which mounds are occasionally smothered. This is because the bioclastic production rate is proportional to the available (emergent) mound surface area, and so varies temporally with mound-surface production rates. The resulting subtle variations in detrital deposition rates over time, combined with close to horizontal topography, leads to the occasional submergence of an entire mound surface, after which the growth of that mound is irrecoverable (Fig. 6, arrows 2 and 3).

The exact timing of mound demise is non-linearly related to the proportion of bioclastic sediment produced per unit volume of microbialite: as shown in Fig. 8 (arrows), the indicated mound survives longer if the proportion is increased from 0.2 to 0.3, yet is submerged very

Fig. 8. Six 3D models with identical parameters other than the proportion of preserved microbialite volume that was deposited as bioclastic sediment (in addition to the constant background sedimentation rate), which increases from 0 to 0.5 (shown beneath each panel). Arrow indicates a particular mound submerged under sediment at different times in each panel.

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early if the proportion increases to 0.4. This can be explained as follows. At proportion 0.2 certain other mounds survive for longer, generating bioclastic sediment which smothers the indicated mound. At proportion 0.3 those other mounds are wholly or partially smothered; this reduces their associated bioclastic sediment production, allowing the indicated mound to survive for longer. At proportion 0.4 the indicated mound is overwhelmed and smothered much earlier in the simulation. Thus it is deduced that the growth of every mound depends materially on the evolution of every other mound in the system, and that this dependence is manifest physically through the process of sediment generation and deposition.

The absolute timescale for production of a single observable lamina in ancient microbialite mounds is unknown; each time step in the models here may therefore represent any period, and rates are necessarily specified in terms of thickness of deposition per time step. Absolute background deposition rates are unknown ('background' refers to all sedimentary material arriving into the modelled area from elsewhere). Additionally, while the proportion of microbialite volume that comprises preserved skeletal material in growth position may be observed, the original proportion of associated or attached skeletal metazoans may have been far greater; the rate at which their skeletal material was removed and deposited as bioclastic detritus is therefore also unknown. Nevertheless, conclusions can be drawn on the *relative* rates of mound growth versus total sedimentary deposition since this balance must control the apparent dynamic equilibrium reached by the system. The term accumulation is used to denote the aggregate deposition from bioclastic and background sedimentation.

For any given background sedimentation rate and initial mound geometry, there is always a mound-growth rate which outstrips the sedimentary accumulation rate to ensure continued emergence and hence survival of one or more mounds for the time period simulated. However, for mound-growth rates that are similar to rates of accumulation, the addition of detritus from mound-attached metazoans increases the sedimentary accumulation rate, leading to increased pressure on mound survival. If that additional bioclastic material is too great, this mechanism leads to the submergence of all mounds (Fig. 6, arrow 3) and hence to their demise. All future microbialite or microbialite-attached skeletal

contributions to the local sedimentary record then stops.

The threshold at which sedimentary accumulation causes the demise of the entire reef system varies strongly with the specific reef geometry. Figure 8 shows a case where complete demise of the reef occurs at a threshold value of skeletal detritus of between 0.4 and 0.5 of the volume of microbialite growth; changing only the random locations of 100 mound nuclei causes the threshold to vary between 0.2 and 0.8. Since the initial 2D topography and set of nucleation sites of any field area are usually impossible to infer, conclusions are only drawn about properties of the models which remain robust to variations in the random initial conditions.

DISCUSSION

Bioclastic debris can locally be abundant in the terminal Ediacaran, even though total local and global metazoan skeletal biodiversity was limited to very few taxa. As such, local sedimentological analysis of the impact of bioclasts may provide greater insight into the dynamics and controls on stromatolite growth than metrics of global metazoan biodiversity, which have been evoked to explain the decline of stromatolites (e.g. Garrett, 1970; Awramik, 1971; Walter & Heys, 1985).

Models used here do not attempt to represent complex branching of microbialite columns, nor sedimentary redistribution and anisotropies in stromatolitic geometry that may be caused by persistent current orientations, since these are not necessary in order to support the conclusions herein. These models show that a single dynamic rule successfully reproduces the oscillating behaviour observed between mound growth and inter-mound sediment. The exact timing of mound demise is related non-linearly to the proportion of bioclastic sediment (Fig. 8). Modelling also shows that any mound-like. microbialite structure will evolve into a sub-horizontal surface due to the decrease in spherical curvature with mound radius. The models therefore successfully reproduce the field observation of mound coalescence to produce near-continuous structures. This is consistent with the first hypothesis of this study, that the parsimonious model adopted here is sufficient to represent large-scale features of mound geometries observed in the field.

While the relationships are non-linear, there are no clear trends. Of course the rate of

sedimentary production is linear with the actively-growing mound surface area (by definition of the model). Other than that, clearly parameterizable relationships are not observed. The total volume varies non-linearly over time and this is clear from Fig. 6: at around a height of 15 units there is a mass demise of the near-side mounds and hence sedimentary production decreases (linearly) with the removal of those mounds; from then on the mound surface area increases overall with small oscillations (again due to the oscillations in mound surface area visible in the figure), until at a certain point in time, coinciding with height of 91 units, there is complete demise of all mounds so bioclastic sedimentary production decreases to zero. As the mounds grow away from their nucleation point, the particular location of that point becomes less and less important, and (fairly rapidly) the key to continued growth is to outstrip sedimentary deposition rates, hence the flat tops noted in outcrop as the mounds are simply competing with the sedimentary deposition rate (Fig. 4A). Overall, this represents very non-linear behaviour.

Once all surviving mounds reach this state, mounds become vulnerable to being submerged by sediment for almost any appreciable sedimentary accumulation rates. Indeed, when left to evolve for sufficiently long, these models often show that all microbialite mounds are eventually swamped (for example, Fig. 6). This is because at some point in time, all mounds will have an essentially flat top surface at similar heights, and will always grow to fill available accommodation space. At that point, any local accumulation of sediment that is greater than the available intermound volume will be distributed over all of the mounds at once. While mound growth must have been robust to some amount of sediment accumulation, to-date there are no estimates of the threshold at which mounds would have ceased to grow for given mat types or settings. So, in the models, this overlying layer of sediment leads to demise of the mounds.

Mound-shaped reef structures become significantly more vulnerable to sedimentation once they have developed a sub-horizontal surface topology. This may explain the present field observations of truncated mound top surfaces, overlain by sediment, sometimes followed by nucleation of other mounds. In any case, the extreme sensitivity of the demise of mounds to bioclast production in this evolved state disproves the second hypothesis herein: models show that even a modest rate of bioclastic sediment production eventually affects mound growth and evolved geometries, if the simulation is continued over a sufficiently long time interval. Model outputs show that some mounds die at around five units of height (Fig. 6), and are clearly still hemispherical; others die later after they have developed flat tops. Flat-topped mounds can be seen to have terminated at a range of different times throughout the simulation.

This study has shown that the growth of each mound depends on the sedimentary production from all other mounds. This inter-mound relationship is affected by sedimentary transport between the mounds. The authors deduce that transport processes are key to being able to predict or analyse further details of observed realworld mound geometries, so adding transport processes other than the homogeneous sedimentary redistribution hypothesis implemented in the current model would be informative.

Given the general increase in bioclastic sediment accumulation rates in carbonate platforms from the terminal Ediacaran onward, unless reef mound growth rates also increased so as to outstrip accumulation rates, the present modelling suggests that such mounds could only continue to grow in particular hydrodynamic settings where a proportion of loose sediment could be removed to leave mounds sediment-free space into which to grow. Thus it would be expected not only that the abundance of closely-spaced microbial mounds would decrease in the Cambrian–Ordovician, but also that they would become geographically restricted rather than covering the extensive areas observed prior to the Ediacaran. Such a habitat contraction has been noted, as Archean and Proterozoic stromatolites grew across a range of marine environments where stromatolites and mats generally seldom persist today (Bosak et al., 2013). It is an explicit outcome of the models presented here, that where skeletal metazoan growth is locally prolific, presumably controlled by factors such as nutrient availability and/or carbonate saturation, these assemblages can locally overwhelm the substrates upon which some may attach.

With all the facets and feedbacks of the Cambrian Explosion, the environmental and biological landscape must have changed fundamentally. The addition of skeletal metazoans to a pre-existing microbial reef ecosystem, which in turn could locally produce large volumes of reef-sourced bioclastic debris, was part of that revolution, and appears to have changed the local growth dynamics of reefs.

CONCLUSIONS

Field evidence demonstrates a complex interplay between the growth of terminal Ediacaran microbial mounds or columns, and local bioclastic sediment depositions. Skeletal material is incorporated within the mounds which thus contributes to their volume, and likewise bundant bioclasts to the inter-mound volume of loose sediment. Complex inter-fingering is observed between microbialites on the flanks of mounds and the surrounding sediments.

A numerical model with a single dynamic rule is sufficient to represent the above observations. The model demonstrates that mounds become columns due to competition for space, that the interplay between mounds and sediments is highly dynamic, and that both growth of mounds and timing of their demise are nonlinearly dependent on the proportion of skeletal metazoan bioclasts contributed to sediment. Once the system has evolved over sufficient time, columnar top-surfaces become essentially flat, and occupy sufficient volume that sediment is almost exactly level with those surfaces. At this point the system becomes highly susceptible to small variations, such that any change in sedimentary input rate due to timevarying changes in top-surface area and hence metazoan production may submerge the reef surface in sediment, halting further reef buildup. This demonstrates that skeletal debris from mound-attached metazoans may change mound growth rates and geometries with dramatic effect.

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DATA AVAILABILITY STATEMENT

The model code used in this study is supplied in the Supplementary Information.

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Supporting Information

Additional information may be found in the online version of this article:

Supplementary Information. Microbialite model source code.