Extensive metazoan reefs from the Ediacaran Nama Group, Namibia: the rise of benthic suspension feeding

R. WOOD AND A. CURTIS

Grant Institute, School of GeoSciences, University of Edinburgh, Edinburgh, UK

ABSTRACT

We describe new, ecologically complex reef types from the Ediacaran Nama Group, Namibia, dated at ~548 million years ago (Ma), where the earliest known skeletal metazoans, Cloudina riemkeae and Namacalathus, formed extensive reefs up to 20 m in height and width. C. riemkeae formed densely aggregating assemblages associated with microbialite and thrombolite, each from 30 to 100 mm high, which successively colonised former generations to create stacked laminar or columnar reef frameworks. C. riemkeae individuals show budding, multiple, radiating attachment sites and cementation between individuals. Isolated Namacalathus either intergrew with C. riemkeae or formed dense, monospecific aggregations succeeding C. riemkeae frameworks, providing a potential example of environmentally mediated ecological succession. Cloudina and Namacalathus also grow cryptically, either as pendent aggregations from laminar crypt ceilings in microbial framework reefs or as clusters associated with thrombolite attached to neptunian dyke walls. These reefs are notable for their size, exceeding that of the succeeding Lower Cambrian archaeocyath-microbial communities. The repeated colonisation shown by C. riemkeae of former assemblages implies philopatric larval aggregation to colonise limited favourable substrates. As such, not only were skeletal metazoans more important contributors to reef building in the Ediacaran, but there were also more variable reef types with more complex ecologies, than previously thought. Such an abundance of inferred suspension feeders with biomineralised skeletons indicates the efficient exploitation of new resources, more active carbon removal with a strengthened energy flow between planktic and benthic realms, and the rise of biological control over benthic carbonate production. These mark the prelude to the Cambrian Explosion and the modernisation of the global carbon cycle.

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Corresponding author: R. Wood. Tel.: +44 131 650 6014; fax.: +44 131 668 3184; e-mail: Rachel.Wood@ed.ac.uk

INTRODUCTION

While metazoans may have had an origin around ~780 Ma, they did not come to ecological dominance as manifest in the geological record until the Ediacaran–Cambrian transition (Erwin et al., 2011). The first appearance of metazoan fossilizable hard parts in the latest Ediacaran (~550–541 Ma) and the subsequent radiation of skeletons in the early Cambrian mark a profound transition in Earth’s history. Calcareous biomineralization changed carbonate sediment production from one of the inorganic and microbially mediated precipitation driven by evaporation to a system under considerable biological control. Today, nearly all calcium carbonate leaves the oceans as skeletons, which form in a wide range of both shallow marine and open oceanic settings. As such, the rise of marine metazoans and the onset of biomineralization marked a step change in the workings of the global carbon cycle.

Most modern shallow calcium carbonate is produced by reefs and their associated carbonate platforms. The evolution of the reef-building habit is a significant ecological innovation, involving close aggregating growth, permanent fixture to a hard substrate and the creation of topographic relief with internal complexity on the seafloor. Reefs are an important focus of biodiversity in modern ecosystems and have been since their inception (Wood, 1999).

Metazoan hard parts in the Ediacaran are represented by non-mineralised and mineralised tubes (Hahn et al., 1982;
Grant, 1990; Ivantsov, 1990), possible siliceous sponge spicules (Reitner & Worheide, 2002) and supportive calcareous skeletons, including Cloudina (Germs, 1972; Grant, 1990), Namacalathus (Grotzinger et al., 2000) and Namapoikia (Wood et al., 2002). These calcified taxa are of uncertain affinity, but were probably stem group Eumetazoa, Cnidaria and Bilateria, or Cnidaria (Wood, 2011). All were sessile benthos and grew in equatorial, shallow marine carbonate settings. Far more diverse assemblages appeared later in the early Cambrian (Fortunian to ‘Stage 2’), including univalved and bivalved shells, tooth-like structures, arthropodtype exoskeletons, spicules, sclerites, tubes, cones and ossicles (Bengtson, 2004). Many consider that the rise of predation pressure as a result of the radiation of bilateria, particularly in the early Cambrian, promoted the first appearance of hard parts (Bengtson, 1994, 2004; Knoll, 2003; Wood, 2011; Wood & Zhuravlev, 2012).

The ecology and affinity of Ediacaran skeletal metazoa is not well understood. Cloudina is a globally distributed cylindrical fossil (~550–541 Ma) built of incremental, funnel-like, apically flaring tubes of originally high-Mg calcite. The ecology and affinity of Ediacaran skeletal metazoa is problematic, with some preferring an annelid affinity, evidence for dichotomous, asexual budding, as well as microstructure and a closed-tube organisation (Grant, 1990; Cortijo et al., 2010; Vinn & Zaton, 2012), suggests a broadly cnidarian affinity. The Cloudina animal is thought to have occupied only the uppermost cones and has been interpreted as a sessile and gregarious suspension feeder with an epibenthic mode of life associated either with microbial substrates (Warren et al., 2011; Wood, 2011) or forming freestanding framework reefs (Penny et al., 2014). The apical part of the tube (or cone) may have served as an attachment site (Cai et al., 2011, 2014; Penny et al., 2014).

Namacalathus is a thin-walled, stalked, goblet-shaped fossil (~550–541 Ma) of up to 35 mm cup diameter (Wood, 2011) and probable original high-Mg calcite mineralogy, although an aragonitic mineralogy remains a possibility (Grotzinger et al., 2000; Zhuravlev & Wood, 2008). Namacalathus has been described from thrombolitic reefs and shallow, platform carbonates in Namibia (Grotzinger et al., 2000; Wood, 2011), thrombolitic reefs in Canada (Hofmann & Mountjoy, 2001) and Oman (Ansthor et al., 2003), and undetermined ecology in Russia (Kontorovich et al., 2008). Namacalathus is problematic, but the morphology is suggestive of a cnidarian affinity, and the absence of pores but presence of large symmetrical lacunae in the cup walls do not support a poriferan origin. Namacalathus has also been interpreted as an aggregating, sessile suspension feeder with an epibenthic mode of life, attached to either microbial surfaces or embedded within soft substrate (Grotzinger et al., 2000; Wood, 2011).

Namapoikia is currently known only from the Nama Group (~548 Ma). Namapoikia has a robust basal suspensivé skeleton with a domal or laminar, modular and encrusting habit. This fossil resembles chaetetid sponges or simple colonial cnidarians and reaches up to 1 m in diameter (Wood et al., 2002). An original aragonitic skeleton is inferred on the basis of preservation as coarse spar mosaic-filled moulds and epipastial, synsedimentary radiating fans of calcitic, neomorphosed aragonitic cement (Zhuravlev & Wood, 2008). Namapoikia encrusts the walls of vertical synsedimentary fissures within thrombolitic reefs, which formed perpendicular to bedding, and more rarely on open reef surfaces (Wood et al., 2002).

While Cloudina, Namacalathus and, locally, Namapoikia are all known to be associated with reefs, Ediacaran metazoan reef ecosystems are believed to be small, of limited biodiversity and variety, and generally of simple ecologies compared to Phanerozoic examples. By contrast, here, we describe new, ecologically complex and notably extensive metazoan reef types from the Nama Group, Namibia, built by the inter- or alternating growth of the smaller Cloudina species, C. riemkeae and Namacalathus. An accurate understanding of ecosystem functioning during the Ediacaran is vital, as ecosystem function is acknowledged to be one of the major drivers of the Ediacaran to Cambrian transition, even though its precise role is debated (e.g. Butterfield, 2009; Erwin et al., 2011). Such extensive metazoan reef systems also provide the first direct evidence that benthic suspension feeders were abundant in the late Ediacaran, which also has implications for the exploitation of new resources by evolving metazoan body plans, as well as for the workings of the global carbon cycle.

**GEOLOGICAL SETTING**

The terminal Ediacaran Nama Group (~550 – ~541 Ma) was deposited in a foreland basin on the Kalahari Craton that developed during convergence along the Damara and Gariep compressional belts (Gems, 1974, 1995; Gresse & Gems, 1993; Grotzinger & Miller, 2008). The Osis basement arch separated the northern Zaris and southern Witputs sub-basins during the deposition of the lower Nama Group (Fig. 1; Grotzinger & Miller, 2008; Gems, 1983; Saylor et al., 1998). The Ediacaran Kuibis and Ediacaran to Cambrian Schwarzrand Subgroups were deposited in settings ranging from upper shoreline/tidal...
flats to below-wave-base lower shoreface (Germs, 1995; Saylor et al., 1995, 1998; Grotzinger & Miller, 2008).

Large metazoan reefs are here described from the Omkyk Member of the Kuibis Subgroup of the Nama Group, at the Driedoornvlagte pinnacle reef complex, near Rietoog, Namibia (23° S, 51.50° E, 39.38°) (Fig. 1). The Nama Group is a series of interbedded shallow marine carbonates and siliciclastics deposited in a storm-dominated ramp setting (Saylor et al., 1998). The Omkyk Member, at the base of the succession, is a carbonate unit containing a series of microbial reefs, as well as the fossils of the earliest skeletal metazoans. An ash bed that immediately overlies the Omkyk Member has been dated as 548.8 ± 1 Ma (Grotzinger et al., 1995), revised to 547.32 ± 0.31 Ma by Schmitz (2012).

The Driedoornvlagte reef complex is up to 500 m thick and 7–10 km long, and formed down-dip in a deepening, mid-ramp setting during the transgressive systems tract of the Upper Omkyk (or OS2) Member (Grotzinger et al., 2000; Adams et al., 2004). The reef complex is interpreted to represent an isolated platform with two well-defined margins that flanked the platform interior, which attained compacted syndepositional relief from 25 m to about 100 m (Adams et al., 2004).

The reefs described here are found in the platform margin of the final (third) accommodation cycle of reef growth (Unit 3M) which grew under increasing accommodation (Adams et al., 2004). The platform margin grew in shallow waters subject to waves and currents and kept up with rising sea level where complex pinnacle reefs formed. Reefs consist of fused and coalesced thrombolite mounds, which increase in size up-section, and were associated with bioclastic grainstones in the lower parts and collapse breccias towards the top as mound relief grew and water depth increased (Adams et al., 2004). Unit 3M mostly aggraded, resulting in a platform relief of up to 50–100 m, and is enclosed by outer ramp and basal shale of the Urikos Member, interpreted to indicate the final stage of the carbonate platform before drowning (Grotzinger et al., 2000).

Diverse reef types have been described, including large (up to 20 m in diameter and 5 m in height) microbial (thrombolite and stromatolite) reefs mounds with subvertical margins and entrapped Cloudina and Namacalathus (Grotzinger et al., 2000; Adams et al., 2004) and abundant syndepositional fissures, some with encrusting Namapoikia (Wood et al., 2002), and smaller (up to 2 m in diameter and 1 m in height) Cloudina reefs formed by the larger species C. hartmannae (Penny et al., 2014). Here, we describe a further, and by far the most extensive, metazoan reef community.

### Cloudina and Namacalathus reefs

The reefs described are up to 20 m in height and width. *Cloudina riemkiae* formed extensive series densely intergrown and aggregating assemblages from 30 to 100 mm high, which repeatedly colonised former generations to form either extensive stacked laminar biostromes (Fig. 2A, B) or small mounds (Fig. 2C,E), or isolated columnar reef frameworks (Fig. 2D). Free-standing mounds were often encrusted by stromatolitic laminae (Fig. 2E). These laminae, and onlapping or enveloping sediments reveal the coeval topographic relief of each small mound assemblage to have been up to 0.5 m (Fig. 2C).

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Fig. 1 Location and stratigraphic setting of Driedoornvlagte reef complex. (A) Location of Namibia in Africa. (B) Landsat TM image showing outcrop expression of Driedoornvlagte reef complex. Outcrop dips 40 degrees to the south. Reef is underlain by shelf facies of Omkyk Sequence 1 (OS1) and consists of a lower unit dominated by stromatolitic reefs (SR), overlain by a capping unit of mostly thrombolitic reef (TR). Stratigraphically younger shales of the Urikos Member (Kuibis Subgroup) form the poorly exposed plain south of the reef. (C) Stratigraphy of the northern Nama Group (Zaris Subbasin) illustrating the position of major sequences, ranges of Ediacaran fossils, Cloudina and Namacalathus, and the position of Driedoornvlagte bioherm and Namapoikia. Arrow indicates the stratigraphic position and age of the dated volcanic ash bed. Modified from Wood et al., 2002; after Grotzinger et al., 2000.

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Cloudina riemkeae was present as sinuous or straight individuals, which were dominantly horizontally or subhorizontally orientated, but sometimes subvertical (Figs 3A, 4A and 5A). Individual tube width varies from 0.25 mm to 2 mm, with an average of ~0.8 mm, and length is up to 10 mm, but this is likely to represent a minimum. These assemblages are associated with diffuse thrombolitic clots, where clots either encrusted C. riemkeae (Fig. 4B) or individuals were directly attached to clots (Fig. 4C). Remaining void space between aggregated individuals and within individual skeletal elements is filled with large botryoids up to 10 mm in radius that represent early marine aragonite cements now neomorphosed to calcite (Fig. 4C). There is limited geopetal micrite sediment, often dolomitised, but some late burial calcite spar filled remaining pore space. C. riemkeae skeletons are also often preferentially dolomitised (Figs 3B, 5A and 6A).

Each C. riemkeae assemblage initiated on an undulating sheet of intergrown microbialite and thrombolite 5–25 mm thick, in which grew isolated C. riemkeae individuals (Fig. 4A,F). Vertically, thrombolitic clots become more diffuse as the density of C. riemkeae aggregations increases. Cement botryoids increase in size and abundance towards the top of each assemblage until they dominate (Figs 2B, 4A,F and 6A).

Cloudina riemkeae individuals show budding (Fig. 4B) and multiple, radiating attachment sites from either each other (Fig. 3A) or thrombolitic clots (Fig. 4C). Cementation between individuals is by patch, or meniscus-like, skeletal features now preserved neomorphic calcite (Fig. 4D) to form chains or rings of multiple attachments, as noted in C. hartmannae reefs by Penny et al. (2014). There is some possible indication of preferred oriented growth (Fig. 4E).

Namacalathus individuals are occasionally intergrown with C. riemkeae (Figs 3B, 4A and 6B). But, they more often occur as densely aggregating layers of single individuals that succeed C. riemkeae assemblages (Fig. 3C,D). Namacalathus is often very densely packed and shows almost tessellate growth (Figs 3C,D and 5C), and there is possible evidence for attachment of adjacent cups (Fig. 5B). The cup diameter, averaging 5 mm, is consistent within communities over a decimetre scale (Fig. 3C,D), but there are patches of larger individuals up to 14 mm in cup diameter (Fig. 5C). The Namacalathus skeleton is
often preferentially dolomitised with further multiple generations of early encrusting dolomite and other cement (Fig. 5C).

*Cloudina riemkeae* and *Namacalathus* also grew cryptically. Extensive (up to 0.5 m in length and 10 mm high), undulose, laminar crypts are present in some reefs where the reef framework was constructed by microbialite and thrombolite (Fig. 7A). *C. riemkeae* and *Namacalathus* grew pendent from crypt walls and ceilings (Fig. 7B,C) as well as upwards from the floor of crypts (Fig. 7B), intergrowing with clotted microbialite. A cryptic habit is also noted within neptunian dykes, where similar *Cloudina*, *Namacalathus* and microbialite/thrombolite intergrowths grew as clusters from dyke walls (Fig. 2F). Further cryptic growth is noted within mm to cm-scale framework crypts within thrombolitic sheets. Here, *Cloudina* grew as clusters associated with thrombolite to form crypt ceilings and floors, where the crypt floors are covered with geopetal sediments and remaining pore space filled with early cement botryoids (Fig. 7D).

**DISCUSSION**

The presence of these extensive metazoan reefs demonstrates not only that skeletal metazoans were more important contributors to reef building in the Ediacaran, but there were also more variable reef types, with more complex ecologies, than previously thought. We may now add these extensive, alternating *C. riemkeae* and *Namacalathus* communities, as well as their cryptic habit within thrombolitic reefs, to other documented styles of Ediacaran metazoan reef ecology, including free-growing, reef-building *Cloudina bartmannae*, thrombolite-associated *Cloudina* and *Namacalathus*, and thrombolitic reefs with fissure-dwelling *Namapoikia* (Grotzinger *et al.*, 2000; Wood *et al.*, 2002; Wood, 2011; Penny *et al.*, 2014). The metazoan reefs described here are notable for their size, exceeding that of the succeeding Lower Cambrian archaeocyath–microbial communities, which commonly are 1–2 m and rarely exceed 5 m in height and width (Wood, 1999).
Modern suspension feeding communities are highly efficient feeders because of their ability to self-organise to form complex structures (Gili & Coma, 1998). *Cloudina riemkeae* was highly aggregating and gregarious. In modern marine habitats, available substrates for colonisation are often a limiting resource, and as a result, solitary (aclonal) metazoans show many adaptations to gain substrate, including rapid colonisation, high growth rates and short life cycles, and an aggregating habit (Jackson, 1983). Aggregation also protects all individuals from high-energy events, overgrowth from competitors, larval invasion and infestation, and attack by predators. Mutually cemented, skeletal individuals also gain further stability by producing topographic relief to create a reef, and as such, this biologically controlled substrate is important for the successful fostering of future generations (Wood, 1999).

Aggregating individuals of *Cloudina riemkeae* showed mutual cementation and no competitive incompatibility.
Benthic suspension feeders form communities that organise into patches or clusters by means of asexual reproduction or dispersal of larvae over short distances. This could imply that assemblages of *C. riemkeae* represent substrates colonised by a limited number of larval spat falls. There are no intermediate individuals between the size ranges of *C. riemkeae* and *C. hartmannae*, which suggests, in the absence of any other indications, that *C. riemkeae* and *C. hartmannae* were distinct species, each growing as separate and distinct monospecific stands.

Likewise, *Namacalathus* often occurred as laterally extensive monospecific aggregations that succeeded *C. riemkeae* aggregations forming a single layer of closely packed individuals, often with a locally consistent clustering of size. This suggests that *Namacalathus* also grew from a single spat fall that synchronously colonised large areas of substrate.

The preferential colonisation of former *Cloudina* assemblages rather than other substrate types is notable (Fig. 2D): as such, we see a clear separation of microbial- and metazoan-dominated communities. This behaviour is found in both laminar and columnar reef types and implies philopatric larval aggregation (where larval offspring settle close to parents) to colonise favourable available substrates. Cloudinids are, however, globally dispersed, suggesting that larvae were also long-lived and capable of wide dispersal. Indeed, species of *Cloudina* appears to have ecological preferences other than reefs in shallow carbonate settings (Cai *et al.*, 2011, 2014; Warren *et al.*, 2011; Wood, 2011).

Isolated *Namacalathus* individuals are occasionally found associated with *Cloudina* aggregations. As such, these metazoans shared the same habitat, as noted also in Paraguay where the problematic skeletal metazoan *Corumbella* occurs in close association with *in situ* *Cloudina* (Warren *et al.*, 2011). Multiple species often co-occur in modern suspension-feeding communities where sufficient food is available. Active and passive suspension feeders are able to share the same resource, or partition resources based on particle size: species that trap smaller particles require
higher flow velocities but can coexist with other species that feed on larger prey but require a smaller volume of water, so making efficient use of all energy available under the same hydrodynamic conditions (Lesser et al., 1994). Erect forms require higher flow rates compared to modular encrusting forms (Sebens & Johnson, 1991). This may explain the ecological segregation seen in Ediacaran reefs of dense aggregations of solitary Cloudina growing in energetic shallow waters, with the preferential growth of modular Namapokia in lower energy reef fissures.

The alternation of Cloudina and Namacalathus assemblages repeats many times and suggests the operation of environmentally mediated ecological succession, a process by which a community undergoes an orderly and predictable change following initial colonisation or repeated disturbance. In general, communities in early succession will be dominated by fast-growing, well-dispersed species (with possible opportunist life histories) where laminar flow dominates. But, as succession proceeds, such species tend to be replaced by more locally superior competitor species and the hydrodynamic regime becomes more heterogeneous enhancing energy retention so favouring the development of more biodiverse communities (Gili & Coma, 1998). Indeed, these Cloudina and Namacalathus assemblages may be an example of cyclic succession, perhaps in response to a repeating environmental trigger, such as minor changes in water depth, temperature, nutrient availability or disturbance.

Soft-bodied Ediacaran biota (~579–541 Ma) have poorly constrained ecologies, but may represent a diversity of osmotrophs or chemotrophs, algal mat grazers, suspension feeders, as well as potential deposit-feeders (Laflamme et al., 2013). Aggregating, tubular forms that were attached to the sea floor via narrow, conical ends, and which show elevated, incremental growth via serial elements, were a common body plan in the Ediacaran. Examples include the soft-bodied Funisia dorothea (Droser & Gehling, 2008), an annulated tubular fossil reported from Siberia (Grazhdankin et al., 2008), Wutubus annularis (Chen et al., 2014) and Palaeopascichnus (Antcliffe et al., 2011). Other skeletal forms include Conotubus (Cai et al., 2011), Sinotubulites (Chen et al., 2007) and Corumbella (Hahn et al., 1982). Many of these metazoaos are inferred to represent benthic suspension feeders.

By exploiting the plankton, suspension feeders link the benthic and planktonic systems. Modern suspension feeding communities remove large amounts of energy (in the form of organic particles) from the water column and so may be responsible for a major share of the biomass and energy transport in marine ecosystems (Bonsdorff & Blomqvist, 1993). As such, suspension-feeding populations exert a major impact on ecosystems as they can have a direct role in decreasing the concentration of plankton, increasing the retention time on suspended particles on the seafloor, sharply reducing primary production in the water column and so creating a strong energy flow from the pelagic to the benthic system. This may in turn create feedbacks that regulate primary production directly and secondary production indirectly (Kimmerer et al., 1994).
role of suspension feeders in energy transfer in the marine carbon cycle is thus far more important than would be expected on the basis of their size and abundance alone.

While the Cryogenian is often characterised as a passive ecosystem, these findings establish direct evidence for a greater ecosystem role for more active modes of feeding by the late Ediacaran. Where environmental conditions were conducive, Ediacaran skeletal benthic metazoans could appear in profusion. Such an abundance of inferred benthic suspension feeders has implications for the exploitation of new resources as the prelude to the Cambrian Explosion. Many have argued that the Ediacaran–Cambrian transition and subsequent radiation is an unfolding of evolutionary innovation to acquire new resources (summarised in Erwin & Valentine, 2013). Metazoan trophic structures had to be constructed from the bottom up, presumably through the innovation first of filter and suspension feeding, then deposit feeding, to small herbivores, and finally to primary, secondary, and tertiary carnivores (Butterfield, 2001). All this may have been accompanied by increasing standing biomass of suspension feeders, as well as an increase in individual size and longevity.

The rise of benthic suspension-feeding metazoans is likely to have led to more active carbon removal: faster sinking fluxes of organic carbon, an increase in the removal of DOC and smaller phytoplankton from the water column, and more efficient transport and burial of organic carbon to depth (Lenton et al., 2014). As a result, this coupling causes animals to excrete dissolved inorganic and organic waste back into the water column, so becoming major components in the cycling and feedback of essential elements.

It has further been argued that the presence of a faster biological pump would have contributed to the ventilation of shelf seas, so shifting oxygen demand over a greater depth of the water column and to shelf sediments. In turn, this would have reduced total phosphorus recycling from sediments, so reinforcing the shift to a more oxygenated ocean state (Lenton et al., 2014). Indeed, some have suggested that the appearance of Edimetazoa triggered co-evolutionary feedbacks facilitating the rise of higher oxygen-demanding mobile and predatory animal forms, without the need for any increase in atmospheric oxygen (Butterfield, 2009; Lenton et al., 2014). We note that the rise of skeletal metazoan suspension feeders was synchronous with the oldest documented predation borings (Hua et al., 2003) and large trace fossils (Jensen, 2003; Macdonald et al., 2014).

In sum, we have established that calcareous skeletal metazoans were abundant by the late Ediacaran, marking an increase in the biological control of carbonate production even though it has been suggested previously that a quantitatively important skeletal sink for carbonate may not have been established until Middle Ordovician time (Pruss et al., 2010). Not only were reef and suspension-feeding ecosystems more diverse, but the more active carbon removal facilitated by abundant suspension feeders would have created a close-coupling of the planktic and bentic metazoan realms with potential for the much-debated consequences for bottom water oxygenation and nutrient cycling.

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