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Ediacaran metazoan reefs from the Nama Group, Namibia

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Abstract

Reef-building in metazoans represents an important ecological innovation, whereby individuals collectively enhance feeding efficiency and gain protection from competitors and predation. The appearance of metazoan reefs in the fossil record therefore indicates an adaptive response to complex ecological pressures. In the Nama Group, Namibia, we found evidence of reef-building by the earliest known skeletal metazoan, the globally-distributed but problematic *Cloudina*, ~548 million years ago. These *Cloudina* reefs formed open frameworks with no microbial component but with mutual attachment and cementation between individuals. Orientated growth implies a passive suspension-feeding habit into nutrient-rich currents. The characteristics of *Cloudina* support the view that metazoan reef-building was promoted by the rise of substrate competitors and predators.

Main Text

The appearance and rapid diversification of metazoans with fossilizable hard parts around the Precambrian-Cambrian boundary [541 million years ago (Ma)] records one of the most dramatic events of evolution (1, 2). Biomineralization, which first occurred in metazoans in the Ediacaran, went on to mark a step change in biodiversity, in the complexity of marine ecosystems, and in the workings of the global carbon cycle. Metazoan hard-parts from late Ediacaran (terminal Proterozoic) strata (~552-541Ma) are represented by mineralized and non-mineralized tubes (3), possible siliceous microfossils (4, 5), and supportive calcareous skeletons (3, 6, 7).

These calcified taxa were sessile benthos and grew in equatorial, shallow marine carbonate settings, raising the possibility that they formed reefs. The evolution of the reef-building habit represents a significant ecological innovation, involving close aggregating growth, permanent fixture to a hard substrate, and the creation of topographic relief on the seafloor. Reefs are an important focus of biodiversity in modern ecosystems, and have been since their inception. Previously, the oldest known metazoan reefs were the archaeocyath sponge reefs of the Lower Cambrian (Tommotian), around 530 Myr (8).

With the exception of *Namapoikia*, which is found within fissures in microbialite reefs (7), Ediacaran skeletal forms have only generally constrained ecological preferences (3, 6, 9). The oldest and most widely described of these is *Cloudina*, a genus characterized by stacked funnel-shaped elements which form a distinctive cone-in-cone exoskeleton. *Cloudina* was first described from the Nama Group of southern Namibia (10), and has subsequently been reported globally from late Ediacaran carbonates (3, 11, 12). *Cloudina* has been interpreted previously as a sessile and gregarious filter feeder of possible Cnidarian affinity (11) with an epibenthic mode of life associated with, or attached to, microbial mats or thrombolitic reefs (3, 11-17). Various growth

habits have been reported: *Cloudina* may have grown either vertically from or within microbial surfaces (11, 12) where the apical part of the tube (or cone) may have served as an attachment site (16), or embedded either vertically or sub-horizontally within thrombolites (17), or recumbent attached to the upper surfaces of thrombolitic heads (17).

We present the first evidence for in-situ, reef-building growth in *Cloudina* (Fig. 1). We found reef-building *Cloudina* are found in the Omkyk Member of the Nama Group, Namibia (Fig. S1A). The Nama Group is a series of interbedded shallow marine carbonates and siliciclastics deposited in a storm-dominated ramp setting (18-20) (Fig. S2). 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 recently as 547.32 ± 0.31 Ma (21). The dominant reef-building *Cloudina* species is the larger *C. hartmannae*, but the smaller *C. riemkeae* is also noted in reef settings, where it may play an accessory role.

Cloudina reefs grew associated with larger thrombolitic and stromatolitic reefs within the Driedoornvlagte pinnacle reef complex, near Rietoog (23° S, 51.50'; 16° E, 39.38') (Fig. S1B). The reef complex is over 300 m thick and at least 7 km long (18, 22). Here microbial reefs individually form elliptical mounds that reach up to 20 m in diameter, 5 to 10 m in width, and 5 m in height, but coalesce to produce near-continuous structures with their long axes displaying a strong orientation parallel to the inferred paleoshoreline (now about northeast-southwest). Microbial reef cores were constructed by massive thrombolites, often with entrapped *Cloudina* and the skeletal metazoan *Namacalathus*; the outer (younger) layers often consist of stromatolites up to 0.75 m thick. A further skeletal metazoan, *Namapoikia* encrusts the walls of vertical syndimentary fissures, which formed perpendicular to bedding, and more rarely open reef surfaces (Fig. 2).

At Driedoornvlagte, *Cloudina* reefs grew in highly aggregating clusters, either as smaller coalescing thickets to create reef framework cavities (Fig. 1B), as single bioherms up to 1 – 1.5 m in diameter (Fig. S3A), or in sheets upon microbial bioherms (Figs. 1I and S3I). Some bioherms show intermittent colonisation by stromatolitic laminae, and are subsequently encrusted by thick layers of stromatolite (Fig. S3A). These laminae reveal the topographic relief of these bioherms to be up to 0.2m.

It is noteworthy that *Cloudina* reefs grew in the absence of any internal microbial component. Remaining void space between aggregated *Cloudina* individuals (Fig. 1D), within individual skeletal elements (Fig. 1C), and within primary reef framework cavities between coalescing clusters (Fig. 1B) is dominantly filled with large botryoids up to 50 mm in radius that represent early marine aragonite cements now neomorphosed to calcite (Fig.1H). These cements can fill framework cavities up to 0.15m in diameter (Fig. 1B). There is limited geopetal micrite sediment but some late burial calcite spar filled remaining pore space (Fig. 1D), and *Cloudina* skeletons are often preferentially dolomitised (Fig. 1E).

We infer that colonising *Cloudina* attached to a hard microbial substrate, initially sub-vertically (Fig. 1I). Most *Cloudina* individuals, however, show horizontal or sub-horizontal, sinuous growth. Some individuals show bifurcation to form two sub-horizontal tubes 60 to 90 degrees apart (Fig. 1D, 1G and S3B). Previously, variable orientation of growth in *Cloudina* has been suggested to be a strategy to ensure high feeding efficiency (12) in settings of variable or limited food availability or living space, or inter-population competition. But here we note that growth orientation is consistent and regular within communities (23) (Figs. S3D and S4).

Cloudina individuals are attached to each other in two ways. Colonising individuals settle on the outer walls of older individuals where the apical part of the tube (or cone) served as an attachment

site (Fig. 1F), where subsequent growth is often perpendicular to the orientation of the host tube (Figs. 1F and S3C) and shows an increase in tube diameter for the first 5 mm of extensional growth (Fig. 1F). Attachment appears to have been facilitated by some further precipitation of skeletal material, which is now preserved as neomorphosed calcite (Fig. 1F). Although this occurrence is observed rarely, such colonisation may in fact be a frequent occurrence. Similarly, *Cloudina* tubes in close proximity are also commonly cemented together by patch, or meniscus-like, cement features also now neomorphic calcite (Fig. 1A). These are interpreted as skeletal material between horizontally-growing tubes, as cement botryoids are noted to nucleate upon them or grew abutted against these features (Fig. 1C); testament to their presence prior to the onset of lithification. Similar early patch-like cements both between shell layers and within the central cavity of the tubes have been noted previously (3), suggested to be inorganic precipitation of calcareous cements between shell laminae that occurred during the lifetime of the organism conveying robustness to the *Cloudina* tubes. Others have also noted the fusing of adjacent tubes during the life of *Cloudina* (11), though the cement present was interpreted as inorganic. Given their formation prior to any inorganic cementation, we suggest rather that these features were skeletal structures produced by *Cloudina*, similar to the mutual cementation of adjacent vermetid gastropods or calcareous polychaetes in formation and structure.

Many consider that the rise of predation-pressure as a result of the radiation of bilaterians, particularly in the early Cambrian, promoted the first appearance of hard-parts (1, 17, 24). The presence of metazoan on metazoan predation (carnivory) by the Ediacaran is in part corroborated by the finding of predatory boreholes in *Cloudina* individuals from China (25). Although most of these borings appear to have successfully penetrated the shell, the eccentrically stacked funnel-in-funnel structure of *Cloudina* may have been a defence strategy, and rugged shells with varying

thickness have been shown to be more effective in hindering access to prey tissue (26). In addition, the relatively uniform distance of the borings from the shell apertures may indicate an avoidance response by the predator to protective measures located near the aperture (13), where soft-tissue was located.

Cloudina was clearly aggregating and gregarious. An aggregating habit in solitary organisms assists the acquisition of favourable substrate for growth to maturity, affords protection from currents or high-energy events, and reduces susceptibility to overgrowth from competitors, larval invasion and infestation, and to attack by predators (27). The aggregating habit has also been noted in the Ediacaran skeletal *Namacalathus* (17) and soft-bodied *Fusinia dorothea* (28).

Reef-building is facilitated by the ability to attach to a hard substrate and mutual cementation of individuals, enabling the formation of a stable, rigid reef framework and topographic relief so creating a biologically-controlled substrate for the successful fostering of future generations (27, 29). Permanent, stable, attachment also confers a selective advantage by inhibiting manipulability by predators, although drilling predation, which involves minimal manipulation, might not be hindered by attachment. Here we note that the rarity of associated sediment and the abundance of early marine cements indicating that *Cloudina* grew elevated above a substrate, with further rigidity imparted by the presence of skeletal structures connecting adjacent individuals. Such a feature suggests that, as in many non-related modern and Phanerozoic reef benthos (29), aggregating individuals showed no competitive incompatibility. This could imply that the clusters of *Cloudina* represent substrates colonised by a limited number of larval spat falls. The aligned growth of horizontal tubes also suggests a passive suspension feeding mode of life with tubes orientated into nutrient-rich currents.

Ediacaran reefs had been thought to be ecologically simple and of low biodiversity (6, 29) but the presence of free-growing, reef-building *Cloudina*, as well as thrombolite-associated *Cloudina* and *Namacalathus*, and fissure-dwelling *Namapoikia*, suggests a far more common metazoan component to these otherwise microbial communities, as well as a clear differentiation of metazoans into the distinct open surface and cryptic biotas so characteristic of Phanerozoic and modern reefs (Fig. 2). *Cloudina* possessed additional features such as the ability for inter-individual skeletal cementation that enabled elevated growth above a substrate, and mutual support to form an open framework with high mechanical strength and potential resistance to predation. These paleoecological characteristics are all consistent with competitive strategies and anti-predation traits, and support the view that both skeletonization and reef-building in metazoans was promoted by the rise of substrate competitors and bilaterian predators, and that such a selective pressure was a strong driving evolutionary force by the Ediacaran.

Figure captions

Figure 1. *Cloudina* from the Omkyk Member, Nama Group, Namibia. **A)** Transverse section across a number of *Cloudina* individuals showing meniscus-like calcite structures joining tubes together laterally (white arrows); **B)** Coalescing thickets enclose primary reef cavity (white arrow); **C)** Photomicrograph of thin section showing cementation of adjacent *Cloudina* by patch, meniscus-like neomorphosed calcite structures. Early marine cement botryoids abut against these; arrow shows nucleation of early marine botryoids upon one example; **D)** Abundant, aggregating *Cloudina* showing horizontal arrangement of tubes parallel to bedding, surrounded by early marine botryoidal fan cements. Internal void of tubes are filled by early marine botryoidal fan cements or late burial spar. Bifurcating individual is arrowed; **E)** Early marine botryoidal fan cements nucleating upon

Cloudina individuals. Some *Cloudina* skeletons are dolomitised; **F**) Two *Cloudina* individuals attached to each other (at point indicated by white arrow). The shorter of the two tubes is interpreted as nucleating on a pre-existing individual; **G**) Aggregating *Cloudina* showing horizontal arrangement of tubes parallel to bedding, surrounded by botryoidal fan cements. Bifurcating individual showing marked growth reorientation is arrowed; **H**) Neomorphosed early marine botryoidal fan cements infilling primary reef framework cavity between *Cloudina* clusters; **I**) Growth of *Cloudina* from a microbial substrate.

Figure 2. Reconstruction of a late Ediacaran reef. **1**, Thrombolite, **2**, Neptunian dyke, **3**, Stromatolite, **4**, *Cloudina*, **5**, *Namapoikia*, **6**, *Namacalathus*, **7**, Cement botryoids, **8**, trapped *Namacalathus*, **9**, Sediment. Copyright: J. Sibbick.

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