Flexible and responsive growth strategy of the Ediacaran skeletal Cloudina from the Nama Group, Namibia

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ABSTRACT

The Ediacaran skeletal tubular putative metazoan *Cloudina* occurs globally in carbonate settings, which both provided lithified substrates and minimized the cost of skeletonization. Habitat and substrate preferences and the relationship of *Cloudina* to other metazoans have not been fully documented, so we know little as to its ecological demands or community dynamics. *In situ Cloudina* from the Nama Group, Namibia (ca. 550–541 Ma), formed mutually attached reefs composed of successive assemblages in shallow, high-energy environments, and also communities attached to either stromatolites in storm-influenced deep inner-ramp settings or thin microbial mats in lower-energy habitats. Each assemblage shows statistically distinct tube diameter cohorts, but in sum, *Cloudina* shows an exponential frequency distribution of diameter size. In reefs, we document a periodicity of size variation, where mean, minimum, and maximum tube diameters vary together and show a systematic increase toward the top of each assemblage. We conclude that most Nama Group *Cloudina* represent one ecologically generalist taxon with highly variable size, that size was environmentally mediated, and that *Cloudina* could respond rapidly to periodic environmental changes. While Nama Group skeletal metazoans coexisted with soft-bodied biota, there was no apparent ecological interaction, as they were segregated into lithified carbonate and non-lithified clastic microbial mat communities, respectively. We infer that ecological flexibility allowed *Cloudina* to form varied communities that colonized diverse carbonate substrates under low levels of interspecific substrate competition. This is in notable contrast to the earliest Cambrian skeletal epibenthos that formed biodiverse reef communities with specialist niche occupancy.

INTRODUCTION

The oldest metazoans are known from the Ediacaran (ca. 575–541 Ma), but not only are the affinities of many Ediacaran metazoans poorly constrained, but so are the ecological dynamics of the communities they formed. Given the importance of key innovations such as biomineralization, reef-building, new trace fossil behavioral types, and predation as well as ecosystem engineering in fueling the Cambrian radiation, documentation of the terminal Ediacaran ecological landscape is fundamental to understanding the rise of metazoans.

The non-uniformitarian Ediacaran marine world was characterized by a heterogeneous redox landscape (e.g., Wood et al., 2015), and carbonate and clastic seafloors were covered by extensive microbial mats in the absence of deep bioturbation (Droser et al., 2005). All known Ediacaran biomineralized metazoans were exclusively benthic and found in carbonate settings where the physiological cost of skeletonization may have been minimized by both high carbonate supersaturation and the low metabolic demand of an immobile habit (Wood, 2011).

Here we consider the *in situ* distribution of the putative metazoan *Cloudina* in the Nama Group, Namibia (ca. 550–541 Ma) (Fig. 1). While *Cloudina* has been documented to have occupied diverse carbonate habitats globally (e.g., Grotzinger et al., 2005; Hua et al., 2005; Warren et al., 2011), we know little as to its environmental distribution, substrate preferences, and community dynamics, even though these are critical elements in the survival and success of benthic metazoans. Here, we use size data and ecological associations to explore the environmental controls on *Cloudina* within the context of these early metazoan life habits and ecosystems.

MORPHOLOGY AND GROWTH OF CLOUDINA

Cloudina individuals were built of repeating funnel-like, adapically flaring tubes or cones set
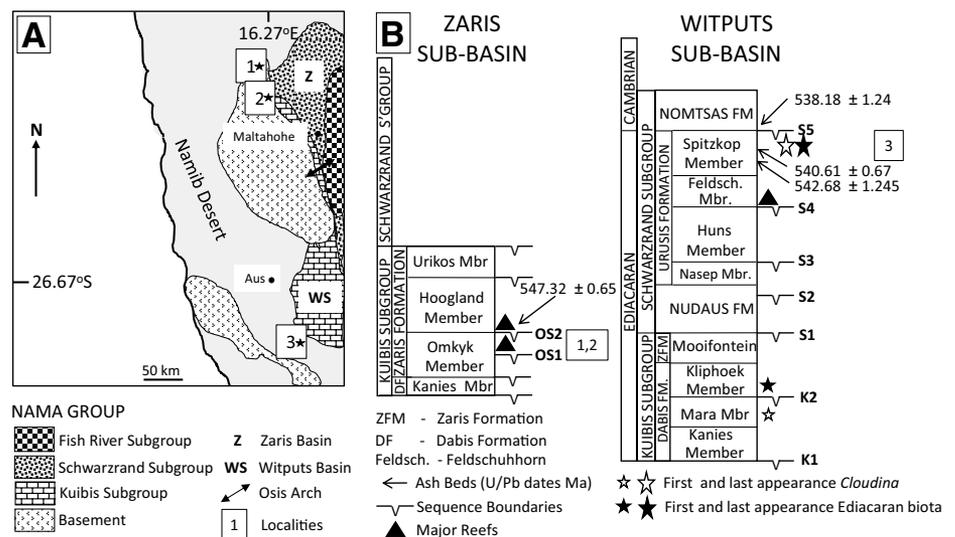

Figure 1. Locations and stratigraphic setting of Nama Group, Namibia. A: Simplified map showing geological setting, subgroups, and sub-basins of late Ediacaran to early Cambrian Nama Group of southern Namibia (modified after Grotzinger and Miller, 2008). Locations: 1—Driedoornvlagte; 2—Zebra River; 3—Swartpunt. B: Stratigraphy of northern Zaris and southern Witputs sub-basins with major sequences, dated ash beds, first and last appearances of *Cloudina* and Ediacaran biota, and major reefs (modified after Wood et al., 2015).

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one within the next to form a distinctive cone-in-cone, eccentrically built skeleton (Germs, 1972). *Cloudina* may have been a filter or suspension feeder of possible Cnidarian affinity, where soft parts probably occupied the youngest cones only (Wood, 2011). *Cloudina* was capable of multiple reproductive modes, including aggregation and episodic larval settlement (Wood and Curtis, 2015), and clonal reproduction (Hua et al., 2005). From the ancestral cone (Fig. 2F), *Cloudina* shows a variety of growth modes where cones may have been added at variable intervals, commonly manifest as external annular ridges, and could grow in size (diameter and height) to varying degrees. Growth mode A has densely stacked cones with rapid early cone size increase to achieve maximum diameter, which then remains constant. Growth mode B shows densely stacked cones with continuous cone size increase through the lifetime of the individual. Growth mode C has a constant cone size with widely spaced cones. Some *Cloudina* assemblages show directional orientation, which may indicate preferential growth into a nutrient-rich current as might be expected of passive suspension feeders (Penny et al., 2014).

Two species are described from the Nama Group (Germs, 1972): *Cloudina hartmanae* and *C. riemkeae*. Support for two species was provided by the disjunct distribution of tube diameter based on 200 individuals of *C. hartmanae* and *C. riemkeae* showing a mean tube diameter of 4.18 mm and 0.82 mm, respectively. *C. hartmanae* was also suggested to show growth modes A and B, but *C. riemkeae*, which commonly grew attached to *C. hartmanae*, showed growth modes A, B, and C (Germs, 1972).

GEOLOGICAL SETTING OF THE NAMA GROUP

The Nama Group (ca. 550–541 Ma) is a terminal Ediacaran succession of highly fossiliferous mixed clastics and carbonates ranging from supratidal to outer ramp settings with varying hydrodynamic conditions (Grotzinger and Miller, 2008). The Nama Group was deposited across the Zaris and Witputs sub-basins (Fig. 1A), which have been correlated using sequence stratigraphy, chemostratigraphy, and dated ash beds. The base of the Nama Group is estimated at ca. 550 Ma, and the youngest dated ash bed 130 m below the top of the Nama Group yields a U-Pb date of 540.61 ± 0.67 Ma (Grotzinger et al. [1995] as 543.3 ± 1 Ma; recalculated by Schmitz [2012]). *Cloudina* is found in most carbonate units of the Nama Group (Fig. 1B).

Assemblages from three localities are considered in this study: Driedoornvlagte reef complex, Zebra River, and Swartpunt (Fig. 1). Iron speciation, Fe/Al, and cerium anomalies show these assemblages to have grown under stable, well-oxygenated conditions (Wood et al., 2015; Tostevin et al., 2016). Localites span ≥6
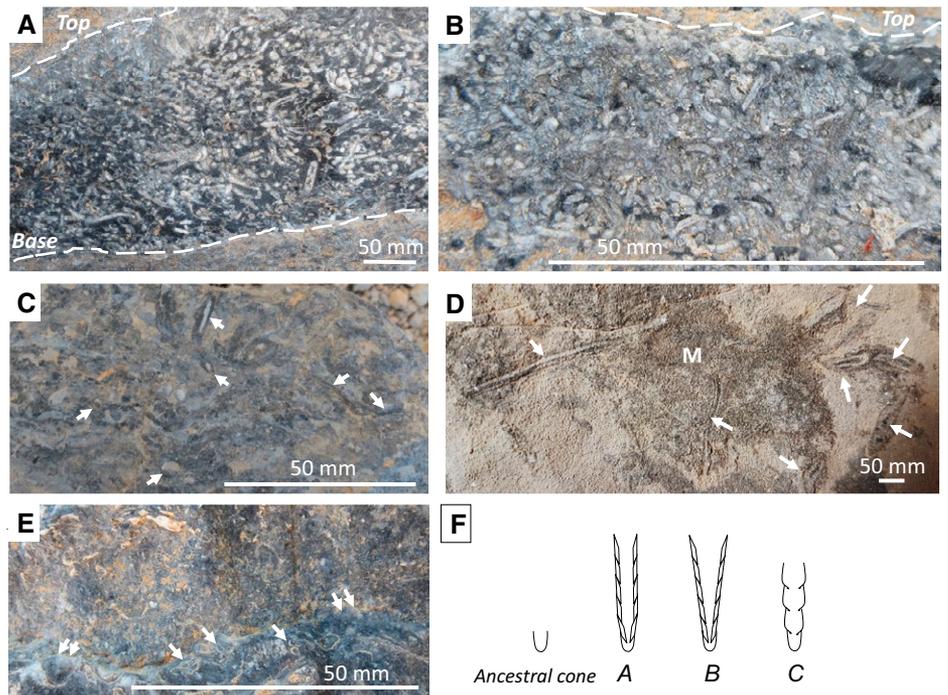

Figure 2. *In situ Cloudina* ecological associations from Nama Group, Namibia. **A,B:** Reefs ascribed to *Cloudina hartmanae* (A) and *C. riemkeae* (B) from upper Omkyk Member, Driedoornvlagte. Base and top of each assemblage is shown. **C:** Variously oriented, including recumbent and sinuous, *Cloudina* individuals (arrowed) attached to elongate stromatolite heads, from upper Omkyk Member, Zebra River. **D:** Many individuals (arrowed) attached horizontally to thin, patchy microbial mats (M) in Spitzkop Member, Swartpunt. **E:** Clusters of small individuals (arrowed) and truncation surface (double arrows) in reefs ascribed to *C. hartmanae*, Driedoornvlagte. **F:** Growth modes of *Cloudina*. From ancestral cone, *Cloudina* can show either rapid early cone size increase (diameter and height) to achieve maximum diameter which then remains constant (mode A), continuous cone size increase through lifetime of individual (mode B), or widely spaced cones (mode C).

m.y. from the upper Omkyk Member (>547 Ma) to the top of the Spitzkop Member (ca. 541 Ma).

METHODS

Cloudina fossils were identified as *in situ* on the basis of attachment either to each other or to a substrate. Common sinuous growth makes measurement of maximum length rarely possible, so tube diameter was used as a size indicator. Measurements were taken as either minimum diameter on bedding planes, or maximum diameters in longitudinal section via both counting within measured areas and through central reef transects approximately perpendicular to bedding (see Table DR1 in the GSA Data Repository[1]). Data are presented in 1 mm increment size bins where the limit of visual detection is taken to be ~0.25 mm. Data were normalized by dividing frequencies within size bins by number of specimens, and Shapiro-Wilk statistical tests were then used to determine whether data were normally distributed. Kolmogorov-Smirnov tests were used to determine significant differences

in distribution between localities (see the Data Repository).

RESULTS

Cloudina Ecological Associations

Three types of *in situ Cloudina*-dominated communities with different substrate preferences are noted:

(1) Shallow-water *Cloudina* reefs from the mid-ramp, high-energy platform margin associated with coalesced thrombolite mounds of the final cycle of reef growth of the upper Omkyk Member at Driedoornvlagte reef complex. Large *Cloudina* (*C. hartmanae*) reefs grew by mutual attachment (Fig. 2A), commonly via additional extra-tubular patches or meniscus-like features (Penny et al., 2014). Individuals of small *Cloudina* (*C. riemkeae*) formed reefs via attachment either to each other or to diffuse, microclotted thrombolite (Wood and Curtis, 2015) (Fig. 2B). Early botryoidal cements are abundant, and *Cloudina* has a variable but dominantly subhorizontal orientation. Both reef types are composed of many repeated units or assemblages (Figs. 2A and 2B). These are 10–30 cm in height and laterally lens-shaped and up to 3 m in length. The upper part of these units grades into a layer

5–32 mm thick, which is preferentially dolomitized, composed of an increasing density of micro-thrombolitic clots, sediment, and microbial laminae with *Cloudina* (Figs. 2A and 2B). The final microbial laminae commonly mark a sharp boundary before growth of the succeeding unit. More rarely a unit may be erosionally truncated (Fig. 2E). We noted at least 20 such units within one large *C. hartmanae* reef. The density of individuals within the *C. hartmanae* reefs has a mean of 48.34 per 100 mm^2 (range = 27–87 per 100 mm^2; n = 435), and *c. riemkeae* a mean of 482 per 100 mm^2 (range = 465–500 per 100 mm^2; n = 193). Smaller individuals commonly cluster in groups (Fig. 2E). Individuals ascribed to *C. hartmanae* are dominated by growth mode A, but B is also present. *C. riemkeae* shows all growth modes A, B, and, more rarely, C.

(2) Elongate stromatolitic biostromes associated with packstones, cross-bedded grainstones, and breccias from the storm-influenced deep inner ramp (Grotzinger et al., 2005) of the upper Omkyk Member at Zebra River. *Cloudina* is found attached to large stromatolitic heads, commonly with encrusting botryoidal cement, in recumbent straight or sinuous form attached to the upper surfaces of, or embedded vertically or subhorizontally within, stromatolite heads (Fig. 2C). The measured density of individuals on stromatolite heads has a mean of 7.86 per 100 mm^2 (range = 2–15 per 100 mm^2; n = 228). Individuals show growth modes A and B. Inter-reef muds bear *in situ*, spiny *Namacalathus* (Penny et al., 2016) and *Cloudina* debris.

(3) Thin microbial mat communities from the low-energy, flaggy wackestone units of both the outer and inner ramp highstand systems tract settings of the Spitzkop Member at Swartpunt (Wood et al., 2015). Here, *Cloudina* grew horizontally attached to undulating microbial mats (Fig. 2D), commonly with a notable preferred orientation (Penny et al., 2014). The mean density on bedding planes is 5.40 per 100 mm^2 (range = 2–19 per 100 mm^2; n = 293). Individuals show growth modes A and B.

Tube Diameter Distribution of Cloudina

Normalized tube-diameter distribution of all measured *in situ* *Cloudina* (n = 1149) follows an exponential distribution (Fig. 3A). By contrast, raw mean and range (Fig. 3C) and normalized distributions (Figs. 3B, 3D, and 3E) for each setting reveal size differences between assemblages. Shapiro-Wilk tests show that the size distributions of *in situ* assemblages are not normally distributed (Table DR2). Kolmogorov-Smirnov tests reject the null hypothesis that these size distributions are from the same population distribution. *Cloudina hartmanae* and *C. riemkeae* reefs and the inter-stromatolite mud at Zebra River (Fig. 3D) are all statistically distinct at the 95% confidence level from each other and from all other settings (Table DR3). Other
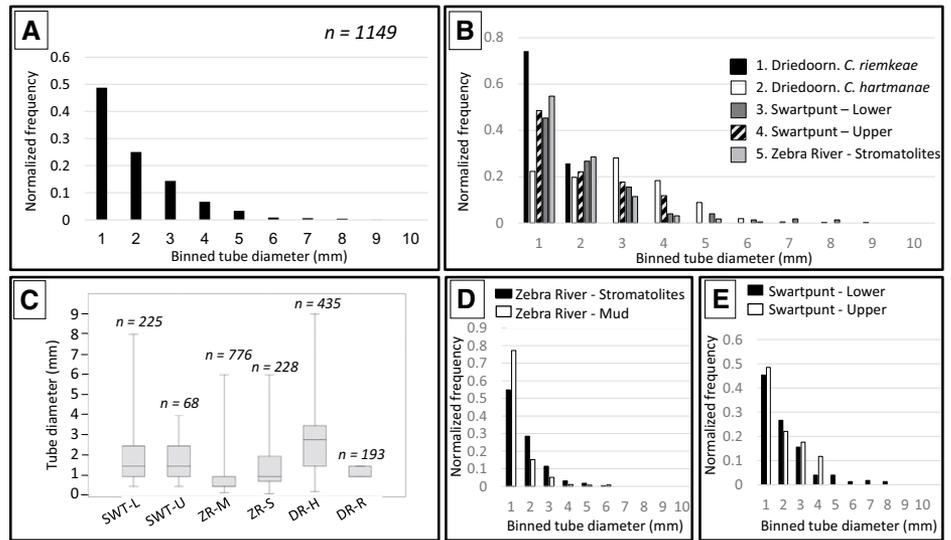

Figure 3. Normalized frequency distribution of *Cloudina* in binned tube diameter from Nama Group, Namibia. A: Combined *in situ* data from Driedoornvlagte (*C. hartmanae* and *C. riemkea* reefs), Zebra River, and lower and upper Swartpunt. B: Distributions from *in situ* Driedoornvlagte (*C. hartmanae* and *C. riemkeae*) reefs, Zebra River stromatolites, and upper and lower Swartpunt. C: Box and whisker plots for Driedoornvlagte *C. hartmanae* (DR-H) and *C. riemkeae* reefs (DR-R), Zebra River stromatolites (ZR-S) and inter-reef mud (ZR-M), and lower and upper Swartpunt (SWP-L and SWP-U). D: Distribution from Zebra River stromatolites compared to individuals in inter-reef mud. E: Distribution from lower and upper Swartpunt assemblages.

assemblages are significantly different from others at a 90% confidence level, except for upper Swartpunt which shows statistical similarities to several other assemblages.

Within a measured transect through the *C. hartmanae* reef, four successive assemblages (labeled 1–4) are distinguished by the position of final dolomitized layers with sharp tops (Fig. 4A). The transect reveals a marked periodicity in tube diameter, where mean, maximum, and minimum all vary synchronously through time within each successive assemblage (Fig. 4B). The largest minimum, mean, and maximum tube sizes occur commonly, but not always, toward or within the final dolomitized layers of each assemblage. The intervals of notable increase and decrease of tube diameter occur over 1.3–3.2 cm of restored vertical thickness. A further rise and fall of maximum measurements is also evident in assemblage 3. We estimate most *Cloudina* individuals to range from 20 to 50 mm in length, with a dominant growth mode A where inflation to maximum tube diameter occurs within the first 10 mm of growth.

DISCUSSION

Cloudina occupied diverse carbonate settings, in terms of water depth and hydrodynamic energy, and colonized varied substrates including other *Cloudina* individuals, thrombolites, stromatolites, and thin microbial mats. All of these substrates were almost certainly lithified as facilitated by the high supersaturation of carbonate settings.

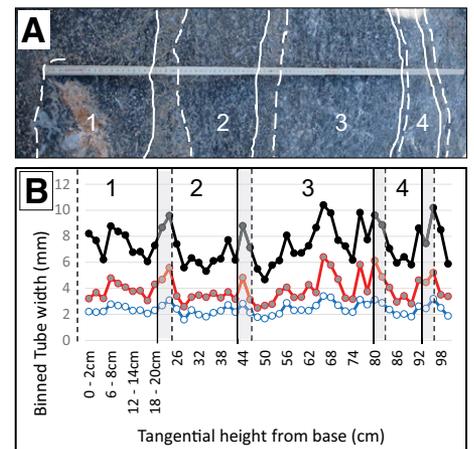Statistical tests show that the *Cloudina* tube diameter distribution within inter-stromatolite

Figure 4. Size distribution of *Cloudina hartmanae* along tangential 100 cm transect through a reef, Driedoornvlagte, Namibia. Continuous white line is base of dolomitized layer; dashed white line is top of dolomitized layer. A: Field image of transect showing successively numbered assemblages. Restored approximate vertical height for each successive assemblage is 15.4, 14.8, 22.5 and 7.1 cm for assemblages 1–4 respectively. Ruler is 100 cm long. B: Maximum (black), minimum (blue), and mean (red) *Cloudina* size at 2 cm intervals through transect. Shaded areas show dolomitized layers.

mud at Zebra River is significantly different (95% confidence level) from that of all *in situ* cohorts (Figs. 3C and 3D). This confirms that detrital *Cloudina* size distribution should not be used as representative of any *in situ* community. Contrary to previous assessments (Germs, 1972), however, the exponential rather than bimodal distribution

of tube diameter (Fig. 3A) shows that size should not be used as a species-specific trait. It is possible, however, that the restriction of growth mode C to some small (<1 mm diameter) individuals provides support for a separate species possessing a distinct growth strategy. We also note that over the 6 m.y. interval explored here, *Cloudina* appears to be morphologically unchanged.

Statistical tests show (1) that *C. hartmanae* and *C. riemkeae* reef types have distinct tube-diameter populations at a high confidence level (95%), and (2) a possible difference between most other localities (confidence level 90%) (Figs. 3B and 3C). Within reefs, we also note a marked periodicity in tube diameter mean and range through the lifetime of each successive assemblage. Given that the majority of *Cloudina* individuals inflate in tube diameter within the first 10 mm of growth reaching up to 50 mm in length, we infer this periodicity to represent changes in the size of each successive subcommunity that occupied the upper living reef surface, rather than any size increase through the lifetime of individuals (i.e., growth mode B). This in turn suggests that each apparent unit as bounded by dolomitic surfaces or truncations may in fact be composed of several successive subassemblages.

From these data we can conclude that individual size in *Cloudina* was controlled by the environment, and moreover that *Cloudina* could respond rapidly to changes in the environmental determinants of size. While it is possible that *Cloudina* was a rapidly evolving specialist responding to environmental change, the fact that documented size changes are cyclical suggests that *Cloudina* shows considerable intraspecific size variation with a highly flexible and responsive growth pattern. Environmental controls on *Cloudina* size may have included fluctuations in nutrient levels, hydrodynamic energy, space availability, or carbonate supersaturation. In addition, we note that *Cloudina* could produce varied skeletal innovations according to ecological need, such as the additional skeletal structures between closely aggregating individuals in reef settings, inferred to impart rigidity (Penny et al., 2014; Wood and Curtis, 2015).

The broad size range and highly flexible growth of *Cloudina*, as well as a capability for diverse substrate colonization, also imply a generalist strategy. A similar generalist behavior with considerable intraspecific size variation has been noted in the contemporary skeletal metazoan *Namacalathus* (Penny et al., 2016). Indeed, such generalist behaviors might be expected of suspension-feeding benthos which show colonization via repeated broadcast larval spat falls to create dense stands of individuals, thus minimizing competition and increasing feeding efficiency (Wood and Curtis, 2015).

Exploitation of matgrounds is a dominant Ediacaran ecological strategy, but unlike soft-bodied Ediacaran biota, *Cloudina* had a preference for hard substrates. In the Nama Group, skeletal metazoans occupied exclusively carbonate habitats, but soft-bodied biota were restricted to clastic, usually transgressive tract settings, commonly within the same conformable sequences (Wood et al., 2015). So while contemporary, these biotas were spatially segregated with no apparent competition for substrates or other resources. Unlike the unlithified clastic microbial mat habitat, however, which was highly susceptible to removal by increasing bioturbation during the Cambrian, the lithified microbial substrate–epibenthic metazoan association persisted through the Paleozoic and beyond.

Ediacaran skeletal metazoan communities were of very low diversity, rarely reaching a maximum of three taxa (e.g., in the Nama Group: *Cloudina*, *Namacalathus*, and *Namapoikia*). This is in notable contrast to the first skeletal benthic metazoan communities of the early Cambrian Stage 2, which show as many as seven taxa (Riding and Zhuravlev, 1995). Although similarly attached to either microbial or other skeletal substrates, these metazoan communities were biogeographically distinct and also show specialist niche occupancy (Zhuravlev et al., 2015).

CONCLUSIONS

In the terminal Ediacaran Nama Group, *Cloudina* displays a large *in situ* individual size range with an exponential distribution. We show size to be environmentally determined, responding rapidly to potentially periodically fluctuating controls, such as nutrient flux or supersaturation levels. We conclude that *Cloudina* was an aggregating generalist, able to colonize the varied lithified substrates available in Ediacaran carbonate settings. This flexibility enabled *Cloudina* to form ecologically diverse and responsive communities despite low taxonomic diversity via intraspecific cohorts adapted to different environmental conditions.

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